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TECHNICAL REPORT 15

Second NPAFC-IYS Workshop on
Salmon Ocean Ecology in a Changing Climate

Technical Editors: Jeongseok Park and Laura Tessier

Vancouver, Canada, 2019

Second NPAFC-IYS Workshop on *Salmon Ocean Ecology in a Changing Climate*

Portland, Oregon, USA, May 18–20, 2019

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Preface

The International Year of the Salmon (IYS; https://yearofthesalmon.org) is an international framework for collaborative outreach and research, and seeks to increase understanding and raise awareness of the challenges facing salmon and the measures to support their conservation and restoration against increasing environmental variability. The overarching theme of the IYS is "Salmon and People in a Changing World", and the proposed research themes are (1) status of salmon; (2) salmon in a changing salmosphere; (3) new frontiers: (4) human dimension; and (5) information systems. These five research themes are integrated into the current NPAFC Science Plan (2016–2020), whose goal is to understand variations in Pacific salmon production in a changing climate (https://npafc.org/science-plan/). The North Pacific Anadromous Fish Commission (NPAFC), in a partnership with Salmon Ocean Ecology Meeting (SOEM), hosted the Second NPAFC-IYS Workshop on "Salmon Ocean Ecology in a Changing Climate" on May 18–20, 2019 at the Embassy Suite by Hilton Portland Downtown, Portland, OR, USA.

The workshop was attended by over 150 international salmon experts and scientists. Workshop participants presented 55 oral presentations and 24 posters addressing the following topics (and sub-themes) related to the IYS research themes:

- Current status of salmon and their environments (biological traits of key salmon populations; migration and distribution; growth and survival)
- Salmon in changing ocean conditions (linkage between salmon production, climate and ocean changes; modeling the future for salmon)
- New technologies/integrated information systems for salmon research and management (new technologies; integrated information and management systems)

Oral and poster presentations given at the workshop are available at https://npafc.org/workshop-presentations-2019. As a special session at the workshop, there was also a discussion of the preliminary results from the successful winter high seas survey in the Gulf of Alaska that occurred during February to March 2019.

The Workshop Organizing Committee consisted of Richard Brodeur (Vice-Chairperson; SOEM; Northwest Fishereis Science Center, NOAA, USA), Ed Farley, Jr. (Chairperson; Auke Bay Laboratories, Ted Stevens Marine Research Institute, NMFS, USA), Jim Irvine (Pacific Biological Station, DFO, Canada), Ju Kyoung Kim (Inland Life Resources Center, FIRA, Korea), Svetlana Naydenko (Pacific Branch of VNIRO (TINRO), Russia), Mark Saunders (Vice-Chairperson; International Year of the Salmon (IYS) North Pacific Steering Committee, Canada), Michael Schmidt (SOEM; Long Live the Kings, USA), Shigehiko Urawa (Vice-Chairperson; Hokkaido National Fisheries Research Institute, FRA, Japan), Brian Wells (Vice-Chairperson; SOEM; Southwest Fisheries Science Center, NOAA, USA), and Jeongseok Park (NPAFC Secretariat, Canada).

On behalf of the Workshop Organizing Committee, we thank all presenters and participants for sharing information and addressing the topics related to the IYS research themes at the workshop and for submitting materials for this volume.

Technical Report No.15 is a compilation of extended abstracts submitted by workshop presenters. Material in this report has not been peer-reviewed and does not necessarily reflect the views of NPAFC member countries, or authors' agencies. I thank Laura Tessier (2019 NPAFC Intern; IYS Coordinator now) for the help of editing the extended abstracts. Abstracts have been edited for clarity and publication purposes.

Jeongseok Park
Deputy Director, NPAFC

Contents

Preface i

Contents ii

Extended Abstracts

Topic 1: Current Status of Salmon and Their Environments

Status of Salmon in a Changing Environment: A Perspective from Alaska
Andrew R. Munro, Richard E. Brenner, and William D. Templin.....1

Changing Productivity, Variability, and Synchrony within Stock Aggregates can Limit Management Effectiveness
Cameron Freshwater, Sean C. Anderson, Kendra R. Holt, Ann-Marie Huang, and Carrie A. Holt.....4

Unprecedented Far East Salmon Catches in 2018: What Should We Expect in Future?
Andrey S. Krovnin, Nataliya V. Klovach, and Kirill K. Kivva.....7

Topic 1-1. Biological traits and key salmon populations

Characterizing Juvenile Chinook Salmon Residency and Early Growth in the Lower Fraser River Estuary
Lia Chalifour, David C. Scott, Misty MacDuffee, John F. Dower, Terry D. Beacham, and Julia K. Baum
.....13

Linking Freshwater Environmental Factors to Up-river Migration Timing of Fraser River Chinook Salmon
Kaitlyn Dionne, Chuck Parken, and Brittany Jenewein.....16

Temporal Forms of Pink Salmon in Sakhalin-Kuril Region and their Abundance Dynamics
Alexander M. Kaev.....19

Current Status of Chum Salmon Populations in the Rivers with and without Hatchery Stock Enhancement on the Sanriku Coast, Japan
Yuki Minegishi, Tatsuya Kawakami, and Jun Aoyama.....23

Variation in Out-migration Timing and Estuary Reliance of "ocean-type" Chinook Salmon in the Fraser River Estuary, BC
David C. Scott, Lia Chalifour, Misty MacDuffee, Julia K. Baum, and Scott G. Hinch.....25

Direct and Carryover Effects of Freshwater, Marine and Fish Conditions on Juvenile, Ocean, and Adult Survival of Snake River Chinook Salmon
Jennifer L. Gosselin, Eric Buhle, Chris Van Homes, Susannah Iltis, and James J. Anderson.....28

Juvenile Salmon Migration Observations in the Discovery Islands and Johnstone Strait in 2018 Compared to 2015–2017
Brett Johnson, Julian C.L. Gan, Sean C. Godwin, Martin Krkosek, and Brian P.V. Hunt.....31

Topic 1-2. Migration and distribution

What can We Learn About the Return Migration of Fraser River Sockeye Salmon from Catches in Alaska?
Pasan Samarasin, Stephen J. Latham, Charles M. Guthrie III, and H. Andres Araujo.....40

Inter-Annual, Stock-Specific Distribution and Migration of Juvenile Sockeye Salmon (*Oncorhynchus nerka*) from 1997–2017
Erika D. Anderson, Jackie R. King, Chrys Neville, Strahan Tucker, and Terry D. Beacham.....44

Long-term Trends of Distribution and Regional Composition of Hatchery-released Juvenile Pink and Chum Salmon in the Sea of Okhotsk during the Fall of 2011–2017
Alexander V. Bugaev, Alexandra I. Chistyakova, and Shigehiko Urawa.....46

Timing of Spawning of Wild Chum Salmon in a Non-enhanced River and their Seaward Migration in Northern Honshu, Japan
Masaya Iida, Yuta Yagi, and Tomoaki Iseki.....49

Genetic Characterization of Juvenile Chum Salmon (*Oncorhynchus keta*) Migrating out of the Yukon River Delta
Genevieve M. Johnson, Christine M. Kondzela, Jacqueline A. Whittle, Katharine Miller, and Jeffrey R. Guyon.....51

Morphological and Genetic Subdivision of Sockeye Salmon Samples, *Oncorhynchus nerka*, Collected within the Period of Spawning Migration in Outfalls of Kamchatka Rivers
Anastasia M. Khrustaleva and Nataliya V. Klovach.....54

Trace Elements Content in the Pink Salmon (*Oncorhynchus gorbuscha* Walbaum, 1792) from Sakhalin-Kuril Region
Nadezhda K. Khristoforova, Anna V. Litvinenko, Vasiliy Yu. Tsygankov, Maxim V. Kovalchuk, and Natalia I. Erofeeva.....59

Migration and Homing Behavior of Chum Salmon Tagged in the Okhotsk Sea, Eastern Hokkaido
Hayato Saneyoshi, Yousuke Koshino, Ryoutarou Ishida, Itsuki Tatsuoka, Hokuto Shirakawa, Yasuyuki Miyakoshi, and Kazushi Miyashita.....63

Topic 1-3. Growth and survival

A Model of Smolt-to-adult Survival in Terms of Salmon Growth through the Size Distribution of Predators
James J. Anderson.....65

Indigenous Community Partnerships towards Foundational Understanding of Wild Salmon Survival
William I. Atlas, William G. Housty, and Jonathan W. Moore.....69

Changes in Juvenile Salmon Prey Fields Associated with a Recent Marine Heat Wave in the Northern California Current
Elizabeth A. Daly, Toby D. Auth, Richard D. Brodeur, and Kym C. Jacobson.....71

Southeast Alaska Pink Salmon Growth and Harvest Forecast Models
James M. Murphy, Emily A. Fergusson, Andrew Piston, Steven Heinl, Andrew Gray, and Edward Farley
.....75

Effect of Temperature and Amount of Food on the Growth Rate / Aerobic Scope of Juvenile Chum Salmon
Yuki Iino, Takashi Kitagawa, Takaaki K. Abe, Tsuyoshi Nagasaka, Yuichi Shimizu, Katsuhiko Ota, Takuya Kawashima, and Tomohiko Kawamura.....82

Spatial and Temporal Trends in Juvenile Sockeye Salmon Diets across Oceanographic Regimes on the Coast of British Columbia
Samantha E. James, Evgeny A. Pakhomov, and Brian P.V. Hunt.....85

The Role of Environmental Conditions in Various Types of Estuaries for the Productivity of Pacific Salmon Populations of Kamchatka
Maksim Koval and Sergey Gorin.....90

Is Juvenile Salmon Condition Driven by the Nutritional Quality at the Base of the Plankton Food-web?
David Costalago, Brian P. V. Hunt, Ian Perry, Chrys Neville, Kelly Young, and Ian Forster.....94

Trophic Relationships between Juvenile Salmon during a 22-year Time Series of Climate Variability in Southeast Alaska
Emily A. Fergusson, Andy Gray, and Jim Murphy.....97

Density-dependent Marine Survival of Hatchery-origin Chinook Salmon may be Mediated by Pink Salmon
Neala W. Kendall, Benjamin W. Nelson, and James P. Losee.....101

Bottom-up Links to Juvenile Salmon Growth and Survival in Puget Sound, WA, USA
Julie E. Keister, Amanda K. Winans, BethElLee Herrmann, Julia Bos, and Iris Kemp.....105

Quantifying Juvenile Salmon Prey Quality and Exploring Trophic Linkages in Puget Sound, WA, USA
Amanda K. Winans, BethElLee Herrmann, Minna Hiltunen, Ursula Strandberg, Michael Brett, and Julie E. Keister.....107

Topic 2: Salmon in Changing Ocean Conditions

Sustainable Conservation and Use of Chum Salmon under Warming Climate and Changing Ocean Conditions
Masahide Kaeriyama.....109

Topic 2-1. Linkage between salmon productions, climate and ocean changes

Changing Ocean Conditions and Some Consequences for Juvenile Salmon Feeding in Coastal Waters
Richard D. Brodeur and Elizabeth A. Daly.....113

Is a Warming Bering Sea Leading to Smaller Chinook Salmon?
Megan V. McPhee, Jared E. Siegel, and Milo D. Adkison.....117

Competitive Interactions between Natural Populations of Pink and Chum Salmon from Puget Sound and Coastal Washington, USA
Marisa N.C. Litz, Aaron M. Dufault, Andrew M. Claiborne, James P. Losee, and Tyler J. Garber.....120

Ecosystem Indicators Development for Coho and Chinook Salmon
Kathryn Sobocinski, Correigh Greene, Neala Kendall, Joe Anderson, Mara Zimmerman, and Michael Schmidt.....126

Mechanisms for Shifts in the Distribution and Abundance of Juvenile Sockeye Salmon in the Eastern Bering Sea during Late Summer, 2002–2018
Ellen Yasumiishi, Curry Cunningham, Ed Farley, Kristin Cieciel, Jamal Moss, Wesley Strasburger, Lisa Eisner, Alexander Andrews, Jeanette Gann, Jim Murphy, Andrew Dimond, and Elizabeth Siddon.....129

Long-term Shifts of Chum Salmon (*Oncorhynchus keta*) Distribution in the North Pacific and the Arctic Ocean in Summer 1982–2017
Tomonori Azumaya and Shigehiko Urawa.....132

A Compound Specific Stable Isotope Analysis of Chinook Salmon Stocks Caught in the Northern and Southern Strait of Georgia
Jacob E. Lerner and Brian P. V. Hunt.....134

Detecting the Effects of Management Regime Shifts in Dynamic Environments Using Multi-population State-space Models
Matthew R. Falcy and Erik Suring.....136

Topic 2-2. Modeling the future for salmon

State of the Salmon: Improving Predictions of Salmon Survival during a Period of Rapid Change
Sue C.H. Grant, Bronwyn L. MacDonald, David A. Patterson, Kendra A. Robinson, Jennifer L. Boldt, Keri Benner, Jackie A. King, Lucas Pon, Chrys M. Neville, Joe A. Tadey, Mike Hawshaw, and Dan T. Selbie.....139

Evaluating Impacts of Time-varying Productivity in Stock-recruit Relationships on Biological Benchmarks
Carrie A. Holt and Catherine G.J. Michielsens.....145

Improving Terminal Abundance Estimates of Spring- and Summer-run Age 5_2 Fraser River Chinook Salmon by Incorporating a Second CPUE Dataset from the Albion Test Fishery
Brittany T. Jenewein, and Karen Rickards.....148

Assessing the Early Marine Ecology of Juvenile Chinook Salmon in a Warming Bering Sea
Kathrine G. Howard, Sabrina Garcia, and James Murphy.....152

Patterns of Synchrony and Environmental Thresholds in the Performance of Forecast Models Used for U.S. West Coast Chinook and Coho Salmon Stocks
William H. Satterthwaite, Kelly S. Andrews, Jennifer L. Gosselin, Correigh M. Greene, Chris J. Harvey, Mary Hunsicker, Stuart H. Munsch, and Jameal F. Samhouri.....157

Quantifying Thermal Impacts on Columbia River Steelhead Marine Growth Using Bioenergetics Models
Hillary L. Thalmann, Elizabeth A. Daly, and Richard D. Brodeur.....161

Topic 3: New Technologies/Integrated Information Systems for Salmon Research and Management

Evaluation of an Environmental DNA Method as a Potential Tool for Monitoring Salmonid Fishes in the Wild
Hitoshi Araki, Hiroki Mizumoto, Takashi Kanbe, and Shunpei Sato.....164

The RAFOS Ocean Acoustic Monitoring (ROAM) Tag: A Highly Accurate Fish Tag for At-sea Movement Studies
Camrin D. Braun, Godi Fischer, H. Thomas Rossby, Heather Furey, Amy Bower, and Simon R. Thorrold 168

Interactive Mapping and Dynamic Data Visualization—Eye Candy or Useful Tool for Fisheries Research?
Dion Oxman and Sabrina Larsen.....171

Topic 3-1. New technologies

Comparison of Coded-wire Tagging with Parentage-based Tagging and Genetic Stock Identification in Large-scale Coho Salmon Fisheries Applications in British Columbia, Canada
Terry D. Beacham, Colin Wallace, Kim Jonsen, Brenda McIntosh, John R. Candy, David Willis, Cheryl Lynch, Jean-Sébastien Moore, Louis Bernatchez, and Ruth E. Withler.....173

Developing an Inter-individual Communication Biotelemetry System and Application to Chum Salmon Returned to off Japanese Waters
Takashi Kitagawa, Nobuhiko Sato, Shigenori Nobata, Hiromichi Mitamura, Yoshinori Miyamoto, Nobuaki Arai, Keiichi Uchida, Hokuto Shirakawa, and Kazushi Miyashita.....176

A PIT Tag Based Method for Investigating Survival of Juvenile Cowichan River Chinook during their First Year of Life
Kevin A. Pellett, Will Duguid, Jeramy Damborg, and Jamieson Atkinson.....178

The Current Status of Research on Geomagnetic Navigation in Pacific Salmon
Nathan F. Putman, Hiroshi Ueda, and David L.G. Noakes.....182

Integrating Multiple Intrinsic Markers to Infer Habitat Use of Sockeye Salmon Stocks (*Oncorhynchus nerka*) in the North Pacific Ocean
Wade D. Smith, Boris Espinasse, Evgeny A. Pakhomov, and Brian P.V. Hunt.....187

The Genomic Basis of Fitness and its Potential for Understanding Responses to a Changing Climate
Charles D. Waters, Jeffrey J. Hard, David E. Fast, Kenneth I. Warheit, Curtis M. Knudsen, William J. Bosch, and Kerry A. Naish.....191

A Compilation and Meta-analysis of Salmon Diet Data in the North Pacific Ocean
Caroline Graham, Evgeny A. Pakhomov, and Brian P.V. Hunt.....196

Topic 3-2. Integrated information and management systems

Supplementation of Atlantic Salmon in the Southern Extent of their Range: Evaluation of Age-1 Hatchery Smolt Stocking in a Small Coastal Watershed
James P. Hawkes, Graham S. Goullete, Alejandro M. Moctezuma, Ernie J. Atkinson, and Oliver N. Cox 197

Dynamic Ocean Management for Salmon: Integrating Spatially-explicit Environmental and Fishery Datasets to Describe and Predict Fish Distributions
Jordan T. Watson, Rob Ames, Camille Kohler, Robert Nigh, Robert Ryznar, and Jenny Suter.....200

The International Salmon Data Laboratory (ISDL)
Scott A. Akenhead.....203

Status of Salmon in a Changing Environment: A Perspective from Alaska

Andrew R. Munro[1], Richard E. Brenner[2], and **William D. Templin[1]**

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Keywords: Pacific salmon, stock status, Eastern North Pacific, abundance

Salmon are an important natural, economic, and cultural resource for many people across the northern Pacific Rim, including all five North Pacific Anadromous Fish Commission (NPAFC) member nations. Monitoring and understanding the status of salmon stocks is critical to the management and conservation of this shared resource, especially within the context of a changing and increasingly variable environment that these stocks interact in (e.g., ocean warming and ocean acidification). It is unclear what the future holds for our salmon populations, but we need to think about, and prepare for, the inevitable changes.

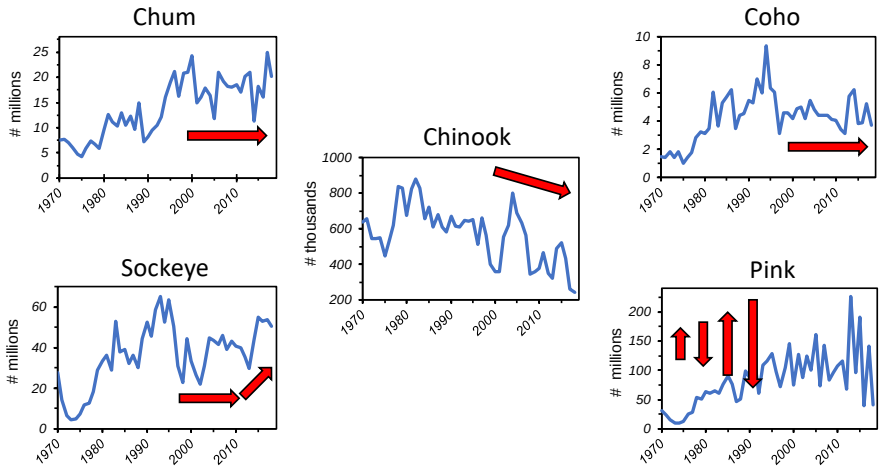

Fig. 1. Catch of chum, coho, Chinook, sockeye, and pink salmon in Alaska salmon fisheries from 1970 to 2018 (from Brenner et al. 2019). The red arrows indicate general trends in recent years.

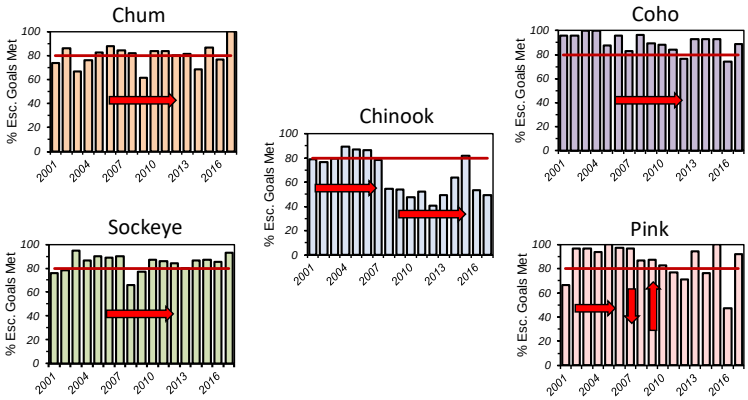

Fig. 2. Percentage of escapement goals met for chum, coho, Chinook, sockeye, and pink salmon across Alaska from 2001 to 2017 (from Munro 2018). The red horizontal line at 80% is a benchmark target used to evaluate the performance of the Alaska Department of Fish and Game in meeting escapement goals. The red arrows indicate general trends in recent years.

Across Alaska, trends in commercial harvest and the ability to meet escapement goals amongst the five native Pacific salmon species have varied over time (Figs. 1, 2). For chum and coho salmon, harvest and meeting escapement goals has been stable. Sockeye salmon harvest has been variable through time, with a recent increase being driven by large runs to Bristol Bay, yet escapement goals are consistently met. Variability in the abundance of pink salmon runs between even and odd-year broodlines is increasing as reflected in both commercial harvest and the ability to meet escapement goals. Chinook salmon runs in Alaska have declined in the last decade, leading to restrictions throughout Alaska for commercial, sport and subsistence fisheries. Similar trends have been observed

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elsewhere (Irvine et al. 2018; Klovach et al. 2018). Despite these restrictions, meeting escapement goals has been challenging and has led to listing of several Alaskan stocks as "stocks of concern" (Table 18 in Munro 2018).

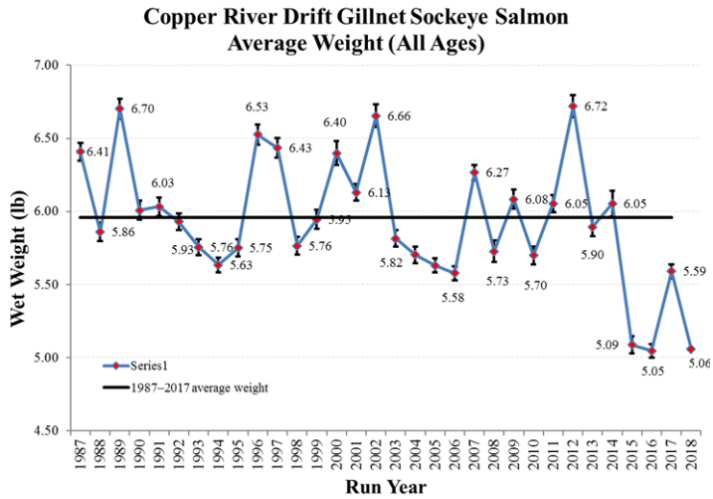

Fig. 3. Average annual weights of Copper River sockeye salmon caught in the commercial drift gillnet fishery from 1987 to 2018 (S. Haught, ADF&G, unpublished data).

In addition to these broad-scale changes, salmon returns throughout Alaska have displayed changes in several life history characteristics such as size, age at return, and timing. These changes, however, have not manifested themselves uniformly within or among species nor are they unique to Alaska. Studies have documented declining age at maturity and size at age in Chinook salmon (Lewis et al. 2015) and recent declines in the weight of sockeye salmon relative to long-term averages (Fig. 3). There are also patterns emerging at the basin scale. For example, recent Bristol Bay sockeye runs have been good, with 2018 being the largest run on record, whereas returns of sockeye salmon to rivers that enter the Gulf of Alaska were generally poor that same year (Brenner et al. 2018). Similarly, recent even-year pink salmon returns have been particularly poor for Gulf of Alaska stocks, but returns of pink salmon in western Alaska have increased (Fig. 4).

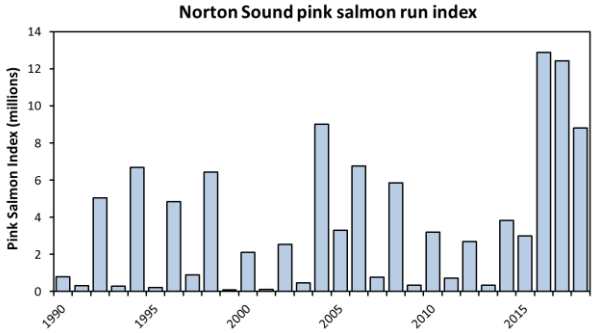

Fig. 4. Index of Norton Sound pink salmon run from 1990–2018 (S. Garcia, ADF&G, unpublished data).

The mechanisms driving these observed patterns are not well understood, and hypotheses are currently being debated, examined, and tested. For example, it is hypothesized that some of these changes, particularly in stocks from the Gulf of Alaska, may be related to the anomalous pool of warm water prevalent in the northeast Pacific Ocean from 2014 to 2017. Species interactions and large-scale environmental patterns such as El Nino events and the Pacific Decadal Oscillation may also explain some of the recent observations and trends. However, the challenge is to gain a better understanding of the underlying mechanisms as well as the ecological and environmental drivers of salmon populations, which can best be met by sound hypothesis-driven science. Admittedly, hypothesis testing in the traditional sense is difficult (or even impossible) in complex ecosystems such as the North Pacific Ocean, but sound science involves an iterative process of proposing plausible mechanisms and representing them in models, then testing the models and their assumptions with data, followed by refining our concept of the mechanism. Performing sound science with rigorous methods will not only help scientists better understand salmon populations but also provide information that is useful for fisheries management in the face of a rapidly changing environment. The monitoring of southeast Alaska Chinook salmon stocks which, like elsewhere, have declined significantly in recent years (Fig. 5a), provides a good example of this approach. It was hypothesized that these declines might be related to poor marine survival. Estimates of freshwater and marine survival based on juvenile coded-wire tagging studies indicate that marine survival for brood years since 2001 have declined to below

average despite above-average freshwater survival for some of the same brood years (Fig. 5b). This information has been instrumental in developing management strategies that resulted in heavily restricted fishing for southeast Alaska Chinook salmon for the past two years.

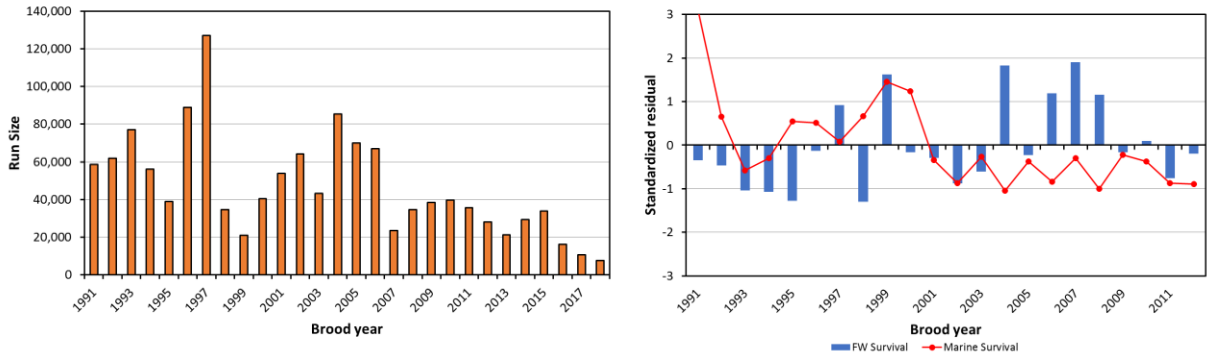

Fig. 5. Taku River Chinook salmon a) (on the left) run size from 1991 to 2017 and b) (on the right) standardized residuals of estimated freshwater and marine survival for brood years 1991 through 2012 (CTC 2019).

Although there are many indications that salmon production in the ocean is changing, the challenges that all nations with salmon resources face are to: 1) take careful and consistent measurements of the ecosystem, 2) investigate drivers of community and ecosystem changes, 3) consider what these changes may mean to the present and future status of salmon stocks, and 4) predict how various stocks may respond to the changing "pasture" they all share in the North Pacific Ocean. Ultimately, we must thoughtfully and collaboratively address these challenges if we are to adapt our efforts to effectively manage salmon stocks in a changing environment. The challenge can best be met with using scientific methods. To do so, we must pose crucial questions and match them with well-designed studies and analyses that recognize the limitations in quality and quantity of current data and identify future needs. Through the use of sound science, we will gain a better understanding of the drivers and mechanisms affecting salmon populations, which can then be developed into useful tools and resilient strategies to be used with confidence by managers and policy makers in increasingly uncertain times. With a well provisioned toolbox, managers and stakeholders will be able to make informed, educated decisions that will ensure the use of salmon as a sustainable resource.

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Changing Productivity, Variability, and Synchrony within Stock Aggregates can Limit Management Effectiveness

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Keywords: population dynamics, portfolio effects, simulation model

Asynchrony among component populations can increase the temporal stability of ecological aggregates, a process commonly referred to as the portfolio effect (Doak et al. 1998; Tilman 1999). Within salmon species, population diversity reduces aggregate variability in spawner returns and catches, as well as the probability of fishery closures (Schindler et al. 2010) and can increase long-term resilience given environmental uncertainty (Anderson et al. 2015). Aggregate variability is linked to two metrics—the weighted mean coefficient of variation among components (component variability) and an index of synchrony (Loreau and de Mazancourt 2008; Thibaut and Connolly 2013). Component variability and synchrony may increase due to anthropogenic disturbance (Griffiths et al. 2014) or large-scale environmental processes (Kilduff et al. 2015), resulting in less predictable returns, boom-and-bust fisheries, and increased risk of overharvest. Greater aggregate variability may also be exacerbated by declines in population productivity associated with reduced survival or fecundity (Peterman and Dorner 2012; Minto et al. 2014; Britten et al. 2016). Although changes in component variability, synchrony, and productivity may independently constrain fisheries management, it is not necessarily clear how these processes will interact. We paired a retrospective analysis of observed trends in the dynamics of Fraser River sockeye salmon (*O. nerka)* with a closed-loop simulation model to evaluate the impact of greater aggregate variability under various productivity regimes (Freshwater et al. in press). The closed-loop simulation is analogous to the quantitative component of a management strategy evaluation (MSE; Punt et al. 2016) and includes a biological model, as well as a model of the mixed-stock fishery that harvests these populations.

The retrospective analysis indicated that generational-means (i.e., 4-year) of Fraser River sockeye salmon productivity declined from the late 1980s through 2005, stabilized for several years, then began to decline again (Fig. 1a). Component variability in recruit abundance exhibited interdecadal cycles, increasing by approximately 50% in the 1950s, 1980s, and 2010s, then declining (Fig. 1b). Similarly, synchrony was high in the 1950s, low and stable through the 1980s, and increased rapidly beginning in 1990 (Fig. 1c).

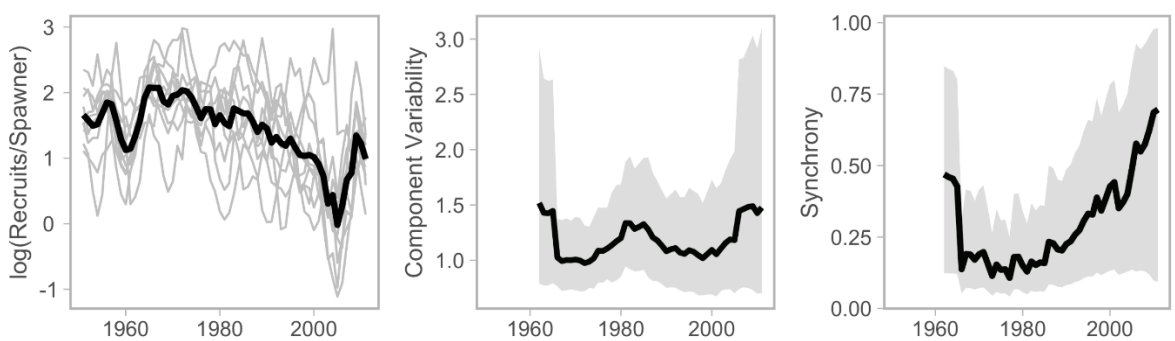

Fig. 1. Observed trends in stock-specific log (recruits per spawner) (a), mean component coefficient of variation (b), and synchrony index (c). All values are lagged by four years (one generation; productivity) or 12 years (three generations; component variability and synchrony). In panel (a) grey lines represent productivity trends for 10 individual stocks and the mean (black line). In panels (b) and (c), black lines represent estimates and grey bands represent 95% confidence intervals.

Simulations demonstrated that the effect of increasing component variability and synchrony differed among performance metrics and was moderated by the underlying productivity regime. When productivity was simulated at its reference value, greater synchrony led to declines in median aggregate return abundance (~7–16% across component variability scenarios; different colour symbols in Fig. 2a). Conversely, aggregate return abundance

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increased by ~9% when component variability was high and synchrony was low (purple symbols Fig. 2a) due to individual stocks experiencing more frequent large positive recruitment deviations. Since high component variability increases the skew of the log-normal distribution of stock-specific recruitment, the normalizing effects of asynchronous dynamics are more evident when component variability is high (Fig. 2a). Increased synchrony also reduced the proportion of management units (groups of stocks harvested in the same marine fishery; MUs) above their escapement goal (Fig. 2c). These declines are driven by reduced aggregate abundance when synchrony is high (Fig. 2a), as well as declines in performance in stock-specific abundance as component variability increases. Finally, increasing variability and synchrony simultaneously lead to severe declines in aggregate catch stability (~40%; Fig. 2e).

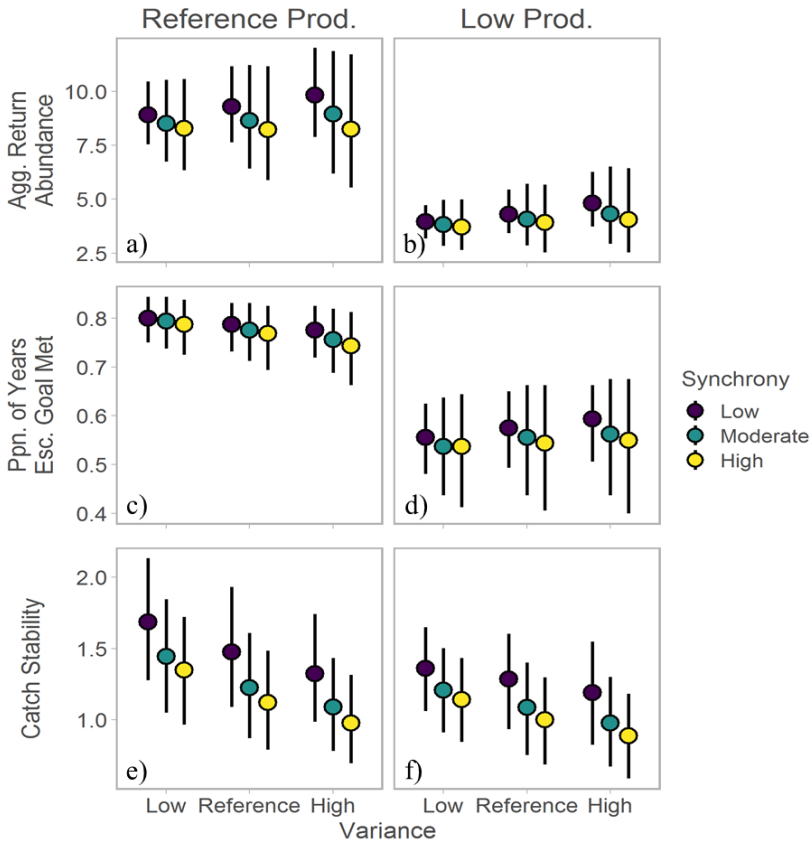

Fig. 2. Effects of component variability and synchrony for reference and low productivity scenarios on three performance metrics: aggregate return abundance (a, b), proportion of years escapement goals met (c, d), and catch stability (e, f). Points represent medians and whiskers 90% probability intervals among 1500 Monte Carlo trials.

Median performance declined under the low productivity scenario for all performance metrics (Fig. 2b, d, f). Relative to the reference productivity scenario, variation among trials in return abundance declined (Fig. 2b), while variation in the proportion of MUs above their escapement goals increased (Fig. 2d). Greater component variability also increased the probability that these escapement goals would be exceeded (i.e. the effect of component variance was reversed relative to reference scenario; Fig. 2d). Finally, the effects of greater synchrony on catch stability were reduced when productivity was low (Fig. 2f).

Pacific salmon populations often exhibit evidence of reduced productivity (Peterman and Dorner 2012; Dorner et al. 2018), increased variability (Satterthwaite and Carlson 2015), and increased synchrony (Kilduff et al. 2015; Satterthwaite and Carlson 2015; Freshwater et al. 2018); however, the cumulative impacts of each process are rarely considered simultaneously. Here we show that increases in component variability and synchrony will have severe impacts on catch stability, but relatively modest effects on aggregate return abundance. Such patterns are concerning because they suggest harvests in weakened ecological portfolios will increasingly be driven by boom-and-bust cycles even if median catches remain high over longer time horizons. Greater variability in catches may have strong negative impacts on communities that rely on stable fishing opportunities. Indeed, observed declines in aggregate stability have been associated with substantial socio-economic costs, as documented by the federal inquiry into declines in Fraser River sockeye salmon (Cohen 2012; Peterman and Dorner 2012). Additionally, we show that most performance metrics were more strongly impacted by reductions in productivity than component variability or

synchrony, but that the interactions among these processes are not uniform. In some cases, declines in productivity reduced or even reversed the negative impacts of greater component variability and synchrony.

These simulations have several implications for managers responsible for multistock fisheries or other ecological aggregates. First, we found that declines in productivity and increases in aggregate variability will have multiplicative effects that may constrain management objectives. The magnitude of these effects will be determined by whether changes in aggregate variability are driven by component variability or synchrony, how conservation- vs. catch-based objectives are prioritized, and whether the focal unit of concern are individual stocks, the aggregate as a whole, or an intermediate unit. Second, even relatively conservative, abundance-based harvest control rules (such as the one included in our simulation) appear to be sensitive to changes in component variability, synchrony, and productivity. Less responsive or data limited harvest control rules may be even more vulnerable to weakening portfolio effects.

Systems-based approaches are increasingly favored in natural resource disciplines such as fisheries because they can stabilize the availability of ecosystem services (Link 2018). Climate change and other anthropogenic impacts are likely to increase component variability and synchrony, while reducing productivity, which is likely to weaken portfolio effects and reduce the efficacy of systems-based approaches. Since stability can be increased along multiple axes of biodiversity the most precautionary approach is to main intact ecological portfolios wherever possible.

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Unprecedented Far East Salmon Catches in 2018: What Should We Expect in Future?

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Keywords: Far East salmon stocks, long-term climate change, 60-year cycle, record salmon catch of 2018, sea surface temperature anomalies, chlorophyll "a"

Introduction

The analysis of catch statistics of Far East salmons for more than 100-year period (1911–2018) has revealed some features of their long-term variations, characterized by the 55–70 year-cycle (Klyashtorin and Lyubushin 2007). It was also found that periods of high abundance and biomass of salmon stocks coincided with the warming in the Northern Hemisphere in 1916–1945 and 1982–2013. However, the climatic reasons of warming in the North Pacific for these two periods were different (Krovnin et al. 2016, 2018). The growth of the Far East salmon stocks in 1916–1945 was associated with warming of surface water in the eastern ocean which extended westward along the Aleutian Islands to the coast of Kamchatka and the eastern Sea of Okhotsk. The second period of high biomass and, respectively, catches of the Far East salmons coincided with a sharp warming of surface water in the western and central North Pacific.

Despite the relationship between high stock levels of Far East salmons and North Pacific warming, its biophysical mechanisms are still not clear. It is generally assumed that an increase in mean annual sea surface temperature is favorable for development and survival of juvenile salmon during the early marine period of their life cycle and increases survival of fish during the first wintering in the ocean. However, there is no reliable confirmation of these assumptions. Therefore, more attention to environmental conditions in the spawning rivers during the warming periods is required.

Multidecadal variability of climate and its use for predicting the tendencies of salmon abundance

The 60-year periodicity is observed in the long-term variations of many climatic indices both in the North Atlantic (Atlantic Multidecadal Oscillation (AMO), North Atlantic Oscillation (NAO), Atmospheric Circulation Index (ACI), proposed by Klyashtorin and Lyubushin (2007)) and North Pacific (Pacific Decadal Oscillation (PDO), Aleutian Low Pressure Index (ALPI)) that suggests the existence of a single climatic signal, at least within the hemisphere. Klyashtorin and Lyubushin (2007) showed that the long-term changes in salmon abundance better corresponded to dynamics of the ACI calculated for the North Atlantic sector than to dynamics of the North Pacific indices (PDO and ALPI).

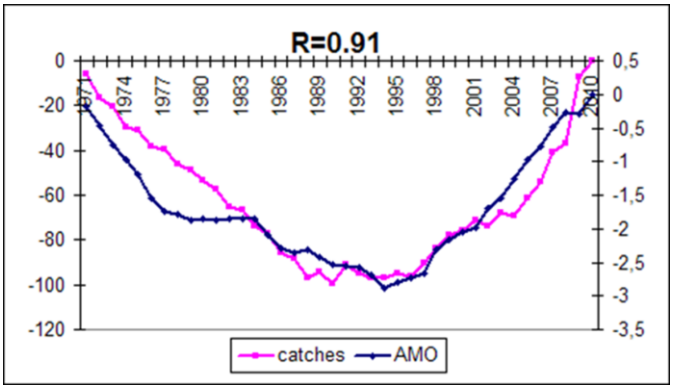

Fig. 1. Cumulative sums of anomalies of total Far East salmon catches and AMO index.

In 1971–2010, there was a high positive relationship between cumulative sums of anomalies of the AMO index and catches of Far East salmons (Fig. 1). This is confirmed also by Table 1, in which loadings of the first two principal components of the 34 climatic and Far East salmon catch time series for the 1972–2010 period is given. In this Table, rows "Regions 1A÷6A and 1P÷5P" designate area-averaged sea surface temperature anomalies (SSTA) in the North Atlantic and North Pacific regions identified on the basis of the cluster analysis (Fig. 2), and rows "PC1" and "PC2" correspond to time series of the first two principal components of the joint SSTA field in the

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northern oceans. All climatic characteristics are calculated for the winter season (January–March). As seen from the Table 1, PC1 (27.6%) of 34 physical and biological time series is determined by AMO (r = 0.91) and is characterized by high positive correlations with the main Far East salmon stocks. Moreover, this PC shows the high positive correlation coefficients with SSTA in the southwestern North Pacific and North Pacific index (NPI). PC2 (17.3%) is clearly associated with the PDO (r = -0.78), but its correlations with catches of Far East salmons are not statistically significant.

VARIABLE	PC1	PC2
	27,60%	17,30%
North Atlantic Oscillation (XII-III)	-0,04	0,53
Arctic Oscillation (XII-III)	0,00	0,72
West Atlantic TP	0,19	-0,65
East Atlantic TP	0,19	-0,05
Scandinavia pattern	-0,33	-0,38
Tropical/NH pattern	-0,27	0,53
Pacific/North American TP (XII-III)	0,43	-0,46
North Pacific Index	0,55	0,58
West Pacific TP	0,32	-0,05
Southern Oscillation Index (XII-III)	-0,14	0,51
Atlantic Multidecadal Oscillation	0,91	-0,26
Tw at Kola Section (0-200 m)	0,42	0,44
Tropical North Atlantic	0,66	-0,56
Region 1A	0,56	0,45
Region 2A	0,54	0,40
Region 3A	0,75	-0,18
Region 4A	0,59	-0,46
Region 5A	0,94	-0,04
Region 6A	-0,12	0,31
Region 1P	0,24	-0,53
Region 2P	0,13	0,70
Region 3P	-0,22	-0,16
Region 4P	0,78	0,25
Region 5P	0,74	0,45
PC1 (28.9%)	0,84	-0,28
PC2 (17.6%)	0,34	0,62
Pacific Decadal Oscillation	0,18	-0,78
North Pacific Gyre Oscillation	0,29	0,22
WK pink (even years)	0,86	-0,01
EK pink (odd years_	0,67	0,22
South Kurils pink	0,60	0,12
WK sockeye	0,85	0,10
EK sockeye	0,57	-0,06
EK chum	0,46	-0,44

Table 1. Loadings of the first 2 principal components of the 34 climatic and salmon catch time series for the 1972–2010 period.

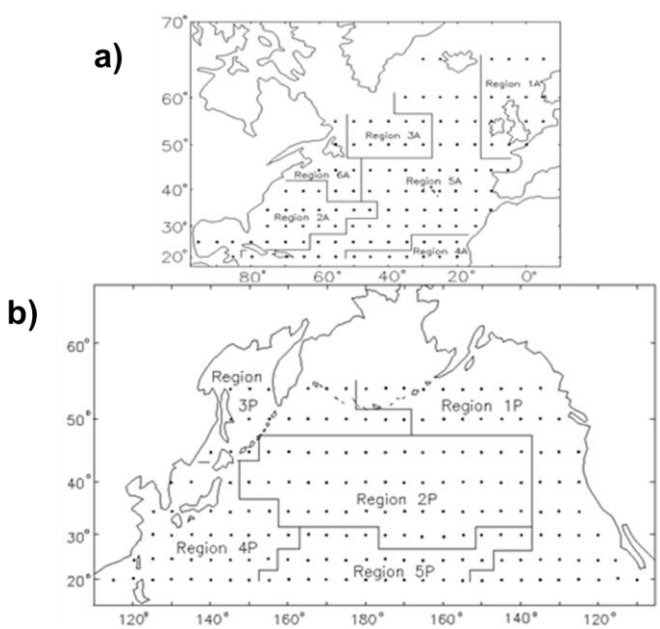

Fig. 2. Results of cluster analysis of mean winter SSTA field in the North Atlantic (a) and North Pacific (b) (Krovnin 1995).

Thus, the increase in salmon catches in 1990s–2000s were associated, to a great extent, with climatic processes in the North Atlantic sector. The effects of the North Atlantic climate variability on the winter North Pacific SST were realized via the teleconnection patterns over the Eurasian sector. There was evidence of strengthening of the North Atlantic impact on the western North Pacific since the late 1970s, associated with the eastward shift of the NAO centers. The shift to warmer SST regime in the western North Pacific in the late 1980s corresponded well to shifts in the state of the Eurasian teleconnection patterns. However, we do not know exactly which biophysical mechanism(s) lies behind the growth of Far East salmon stocks during this period of warming. Favorable conditions that promote the development and survival of juvenile salmon as they migrated from rivers into the sea have been forming since the late 1970s.At the same time, an increase in SST in the western and central North Pacific has been associated with cooling in traditional wintering areas in the Gulf of Alaska and off the eastern Aleutian Islands, which may result in wintering fish moving westward into warmer waters..

The existence of the 60-year cycle in variations of the Far East salmon stocks and climatic characteristics became a basis for predicting the trends of salmon abundance several decades in advance (Klyashtorin and Lyubushin 2007). These authors predicted decrease in catches from the early 2000s till the early 2020s. However, it is clear now that their forecast was not realized (Fig. 3), for a few reasons. Firstly, the ACI calculated for the North Atlantic region does not completely reflect the whole complexity of processes in the climatic system of the ocean. In particular, it does not consider longitudinal and latitudinal shifts of the large-scale atmospheric centers in the region (Icelandic Low and Azores High) which result in differences in mechanisms of the North Atlantic impact on the western North Pacific climate. Secondly, the 60-year signal was obtained on a basis of relatively short time series which length did not exceed 150 years. This period covers only about two and a half cycles. Thus, the cycle has low reliability compared to the PDO index. The period of its variations during the last two decades was reduced from 50–60 to 10–15 years due to intensifying the short-term variability in the North Pacific climate. During the last 10 years there were very considerable variations in catch volumes of main Far East pink salmon stocks. These wide variations in pink salmon catches, and in a broader context, in their stocks were associated with the above-mentioned changes in climatic conditions.

Nevertheless, the use of multi-decadal variability in climatic parameters is now perhaps the only way to predict tendencies in Far East salmon stocks for 20–30 years in advance.

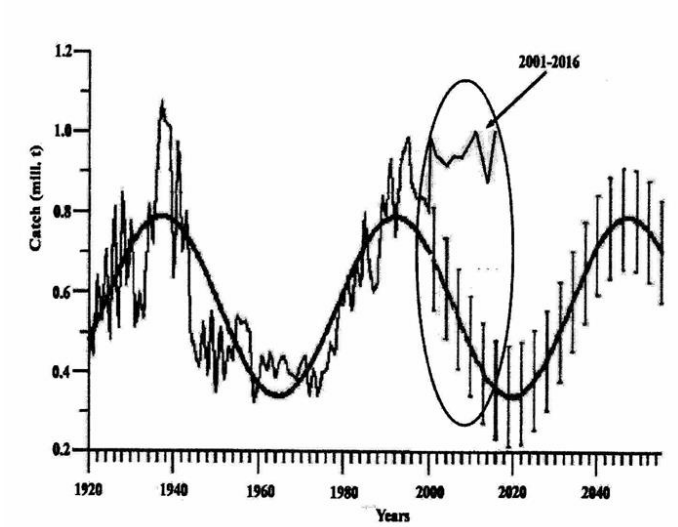

Fig. 3. Long-range forecast of total Pacific salmon catches based on cyclic character of changes in their stock (Klyastorin and Lyubushin 2007). Ellipse covers the period of discrepancy between actual and predicted catches.

Environmental conditions in the North Pacific during 2017–2018

The period from 2014 to 2018 was characterized by drastic surface warming in the northern North Pacific including the Bering and eastern Okhotsk Seas. This warming started in the Northeast Pacific in January 2014, and then spread westward to the Kamchatka coasts. Finally, this led to essential increases in catches of East and West Kamchatka salmon stocks, such as pink salmon. In some sense, the situation of the last five years repeats the situation of the 1916–1945 period.

Despite the similarity of climatic conditions during 2014–2018, which were favorable for the formation of very strong year classes of salmon stocks, in 2018 the unprecedented record catch of Far East salmons exceeded 677,000 metric tons, was fixed. This drastic growth of total catch was, to a great extent, associated with a four-time

increase in West Kamchatka pink salmon catch, compared with previous even 2016 year (301,316 metric tons and 74,823 metric tons, respectively), while the East Kamchatka pink salmon catch increased from 68,990 metric tons in 2016 to 111,250 metric tons in 2018, i.e., 1.6 times.

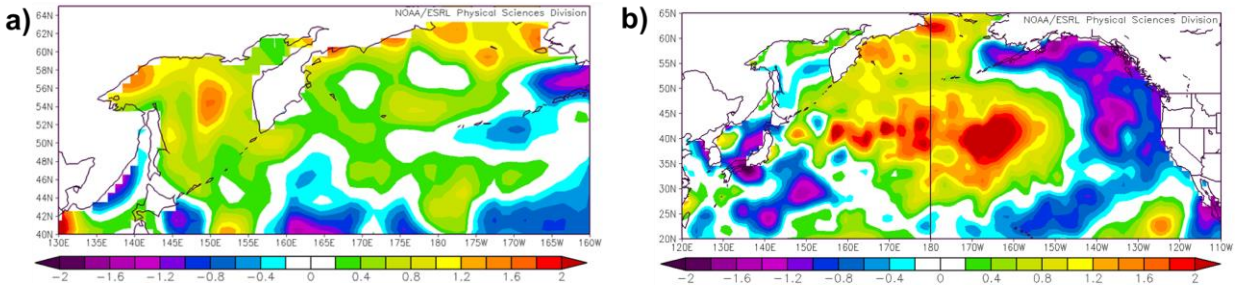

Fig. 4. Differences of SSTA in May-June between 2017 and 2015 (a) and SSTA in January–April between 2018 and 2016 (b).

It is interesting to compare thermal conditions for Kamchatka pink salmon stocks at different stages of their marine period of life cycle for generations of 2014 and 2016 years.

Figure 4a shows the difference of the North Pacific SSTA in May–June between 2015 and 2017, i.e., during the early marine period of life of the 2014 and 2016 generations. Apparently, in the coastal waters of West Kamchatka SST in 2017 was higher, on the average, by 0.7–0.9 °C than in 2015; off the northeastern coast of the peninsula this difference exceeded 1.0°C. In our opinion, such thermal differences hardly became the reason of sharp improvement of growth and survival of the 2016 generation, in comparison with the 2014 generation. Wintering conditions for two consecutive even generations of the Kamchatka pink salmon in 2016 and 2018 were somewhat different. In particular, the 2018 SST off the Pacific side of the eastern and central Aleutian Islands decreased essentially (by 1.2–1.6 °C) though it remained above the norm (Fig. 4b). At the same time, SST in the central part of the ocean increased considerably. The area of positive differences of SSTA (up to 1.0–1.2°C) stretched to the north up to the Chukotka coast. The observed changes in temperatures may result in the shift of wintering pink salmon concentrations to the west and to the southwest from the traditional areas, but how this could affect the 2018 catch remains unclear. It is quite probable that warming of the considerable water area to the west of 165–170°W could favor expansion of total wintering area and cause high survival of the 2016 Kamchatka pink salmon generations in the winter of 2017–2018. The summer season of 2018 was colder than in 2016. Along the migration routes for spawning, SST was close to norm, and off the both Kamchatka coasts SSTA reached 0.8–1.2°C (Fig. 5). Once again, it remains unclear how this could affect the approaches of pink salmon to the peninsula.

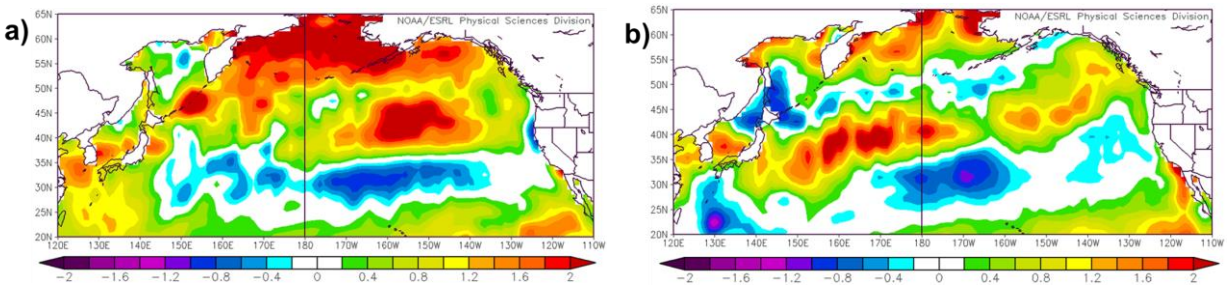

Fig. 5. SSTA patterns in the North Pacific in July–August: 2016 (a), 2018 (b)

One more reason for the record catch in 2018 may be the production of very favorable food conditions. We used the data on chlorophyll "a" concentration as an indicator of food abundance. Analyses and visualizations used in this study were produced with the Giovanni online data system, developed and maintained by the NASA GES DISC (https://giovanni.gsfc.nasa.gov/giovanni/). Chlorophyll "a" characterizes intensity of photosynthesis, and, thus, it can be considered as an indicator of phytoplankton biomass, the primary chain of food web, which eventually determines conditions of salmon feeding.

We considered the annual changes in chlorophyll "a" concentrations for Kamchatka pink salmon generations in 2011, 2014, and 2016 for four regions of the North Pacific (Fig. 6). In waters off of West Kamchatka, the spring peaks of chlorophyll "a" content in 2015 and 2017 (during the earliest marine period of West Kamchatka 2014 and 2016 pink salmon generations) almost coincided in time and continued from beginning of April to mid-June (Fig.

7a). Moreover, the maximum concentrations in 2015 were more than 1.5 times higher than in 2017. Thus, it is not likely that food conditions for West Kamchatka pink salmon juveniles in 2017 were much better than in 2015.

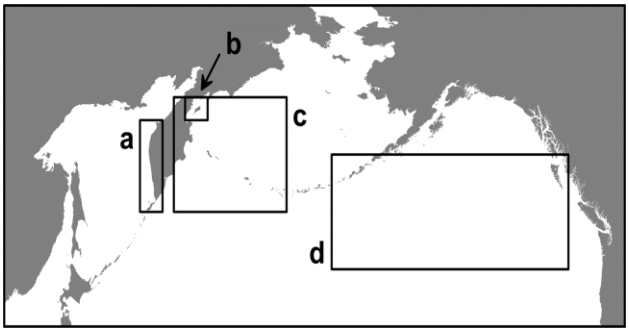

Fig. 6. North Pacific regions, for which chlorophyll "a" concentrations were calculated and averaged.

In the Karaginsky Gulf, where East Kamchatka juvenile pink salmon migrate from rivers, the peak of chlorophyll "a" concentration in 2017 was observed in mid-May, while in 2015 it was noted one month earlier, though the secondary maximum was fixed in the first decade of May (Fig. 7b). The maximal zooplankton development is commonly observed one month later than that of phytoplankton. Thus, it is very possible that maximal zooplankton development in mid-June could match the mass migration of juvenile pink salmon into the sea that created very good feeding conditions for very good feeding conditions for fish during their migration. Note the strong peak of chlorophyll "a" in early May of 2012, but possibly it occurred too early to form favorable feeding conditions for the 2011 generation, which was poor.

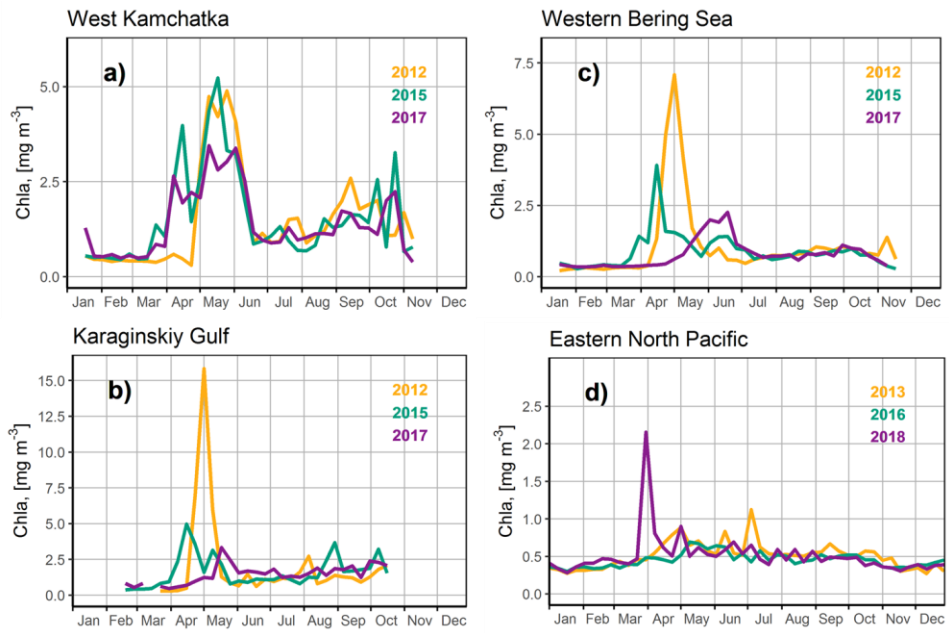

Fig. 7. Annual changes in chlorophyll "a" concentration.

An interesting situation was observed in the southwestern Bering Sea, where young East Kamchatka pink salmon migrate in summer for feeding. The peak of chlorophyll "a" concentration in 2017 was fixed there in mid-June, two months later than in 2015 (Fig. 7c). This possibly favored the formation of very good conditions for pink salmon feeding in the second half of summer and early autumn of 2017 and could contribute to the higher biomass and, as a result, higher catches of this stock in 2018, compared to 2016.

Finally, in the Northeast Pacific main wintering area of Kamchatka pink salmon stocks, there was a very prominent maximum of chlorophyll "a" in late March of 2018, which was not observed in either 2013 or 2016 (Fig. 7d). It is very likely that this resulted in a formation of favorable feeding conditions and better survival of pink salmon in the 2018 winter-spring period before their spawning migrations toward the Kamchatka.

Overall, these results did not allow us to identify one specific factor responsible for the record catch of Far East salmons in 2018. Most likely, they were the result of a combination of subtle changes in environmental and feeding conditions throughout 2017–2018.

Conclusion

Long periods of changing abundance and biomass of Pacific salmons are clearly associated with the corresponding climatic "epochs" and may be predicted with some degree of certainty. However, the reasons for very sharp increase/decrease in catch during the specific long period of high/low abundance are uncertain and require special consideration and research.

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Characterizing Juvenile Chinook Salmon Residency and Early Growth in the Lower Fraser River Estuary

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Keywords: Chinook salmon, subyearling migrant, estuary, otolith daily growth, early marine growth

The Harrison River is a tributary of the lower Fraser River system which produces the highest proportion of fall-run, subyearling migrant Chinook salmon (*Oncorhynchus tshawytscha*) in the Salish Sea (Fraser et al. 1982; Murray and Rosenau 1989). Subyearling migrant Chinook, which emigrate to estuarine and marine waters within the first year, may be more dependent on nearshore habitats than yearling migrants during their first year of ocean residency (Weitkamp et al. 2014). Some cohorts emigrate as early as first emergence from their eggs as fry in March, while others arrive in the estuary well into their first year, in June and July (Levings et al. 1986; Healey 1991). Previous studies have inferred salmon stock composition based on catch timing, fork length and known life history strategies (Levy and Northcote 1982). Current technology allows us to precisely identify stock groups using tissue samples and genetic analysis (Beacham et al. 2011). Otolith studies can give a detailed picture of the life history of individual fishes, including quantitative measures of residency in different water bodies (Miller et al. 2010; Volk et al. 2010). Using a combination of genetic and otolith analyses, we assessed the stock-specific utilization of three habitat types in the lower Fraser estuary by emigrating Chinook.

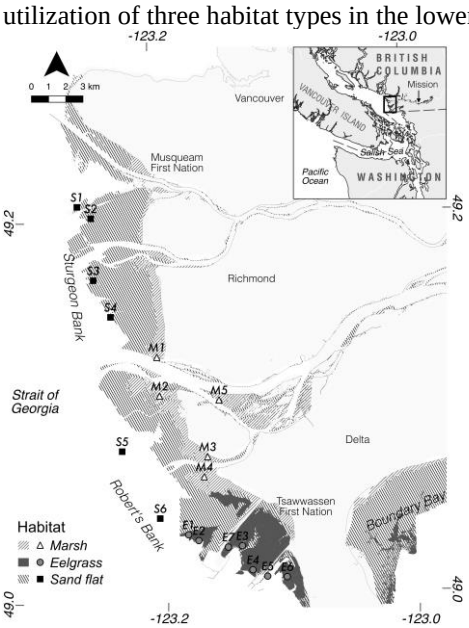

Fig. 1. Sites sampled in 2016 and 2017 in three distinct habitats within the Fraser River estuary, British Columbia, Canada: five marsh sites (white triangles; M1–M5), six sand flat sites (black squares; S1–S6), and six eelgrass sites (grey circles; E1–E6). All sites were sampled each year, with the exception of E6, which was replaced by eelgrass site 7 (E7) in 2017.

Table 1. Salmon catch by habitat in the Fraser River estuary.

	2016			2017		
Species (total N)	Marsh	Eelgrass	Sand flat	Marsh	Eelgrass	Sand flat
Chinook (1,193)	435	19	61	500	129	49
Chum (1,088)	120	4	5	394	464	101
Sockeye (147)	17	6	14	5	103	2
Pink (43)	39	1	3	0	0	0
Coho (4)	4	0	0	0	0	0
Steelhead (2)	0	0	0	0	2	0
TOTAL	**615**	**30**	**83**	**899**	**698**	**152**

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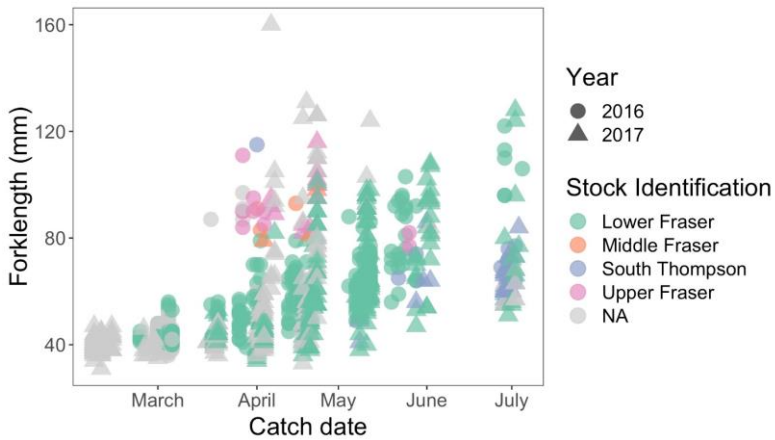

Fig. 2. Catch day and size of juvenile Chinook salmon in the Fraser River estuary for 2016 (circles) and 2017 (triangles). Each marker denotes a fish, and colours correspond to stock identification, grouped by region. Lower Fraser (green) includes fish identified as 'Harrison' and 'W_Chilliwack'; Middle Fraser (orange) includes 'Horsefly' and 'L_Cariboo'; South Thompson (blue) includes 'Deadman', 'L_Thompson', 'Little_R', and 'South_Thom'; and Upper Fraser (pink) includes 'Goat', 'Horsey', 'Indianpoint', 'Morkill', 'Nechako', 'Slim_C', 'Stuart', and 'Torpy'. Fish that were measured but not sampled for genetic stock identification are grey.

In 2016 and 2017, we surveyed 17 sites across the lower estuary (Fig. 1), sampling 2,477 juvenile Chinook salmon and collecting 836 tissue samples for genetic stock identification. We caught the majority of all salmon in brackish marsh habitat in both years (*n* = 1,514/2,477; 61%; Table 1), despite anomalous flow and temperature conditions in 2016 (Chandler et al. 2017), and annual variation in escapement. In 2016 and 2017, we caught 733 and 1749 salmon, the majority of which were Chinook Salmon (515 and 678), respectively. Overall, we captured juvenile Chinook from 18 different populations, with stream-type populations generally captured in very low numbers. Catch composition was dominated by subyearling migrants identified as Harrison/Chilliwack (*n* = 701), arriving the earliest near the end of March, and present the longest until mid-July in 2016 and mid-June in 2017 (Fig. 2). We retained a subsample of these lower Fraser River juveniles from 2016 to assess entry timing and estuarine growth prior to capture using visual and chemical analyses of the otoliths via LA-ICP-MS (*n* = 98 otoliths; preliminary results reported for *n* = 50 otoliths).

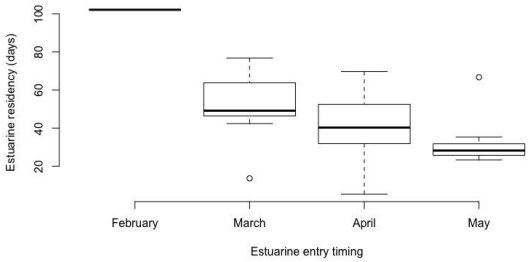

Fig. 3. Juvenile Chinook estuarine residency prior to capture by month of estuarine entry. Estuarine entry point was determined using chemical analysis of sagittal otoliths via LA-ICP-MS. Daily growth and number of days after entry were subsequently determined using visual measurements of the otoliths.

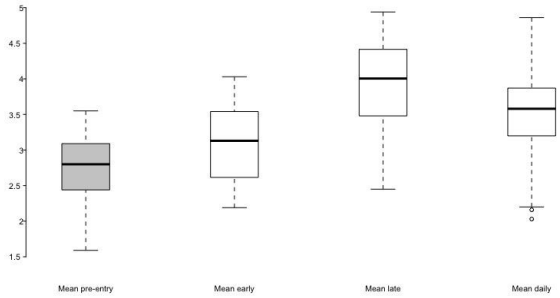

Fig. 4. Mean daily otolith growth of juvenile Chinook for the fresh water period just prior to estuarine entry ('Mean pre-entry'), the first 7–14 days after entry ('Mean early'), the last 7–14 days prior to capture ('Mean late'), and the overall mean estuarine growth ('Mean daily'). Box and whisker plots depict the median (black line), 25th and 75th quartiles (box), and range of values (whiskers) for each group, with points past the whiskers depicting extreme measurements outside of the standardized interquartile range.

Most lower Fraser Chinook entered the estuary in March and April, with fish that entered earlier spending a longer period in the estuary prior to capture (Fig. 3). The majority of fish appeared to reside in the estuary for 30–50 days (*n* = 23/50), with some captured after fewer than 20 days (*n* = 4/50), and one fish 102 days after estuarine entry. As expected, we found that daily growth rates improved over time (Fig. 4), as fish grew and presumably experienced better foraging success. In our preliminary data, we did not find a significant difference in daily growth rates among fish cohorts by estuarine entry timing (Fig. 5), indicating that the broad range of emigration timing to

the estuary may result in similar growth. There is a slight trend toward better growth in summer months (May, June), which may align with greater food production in the estuary.

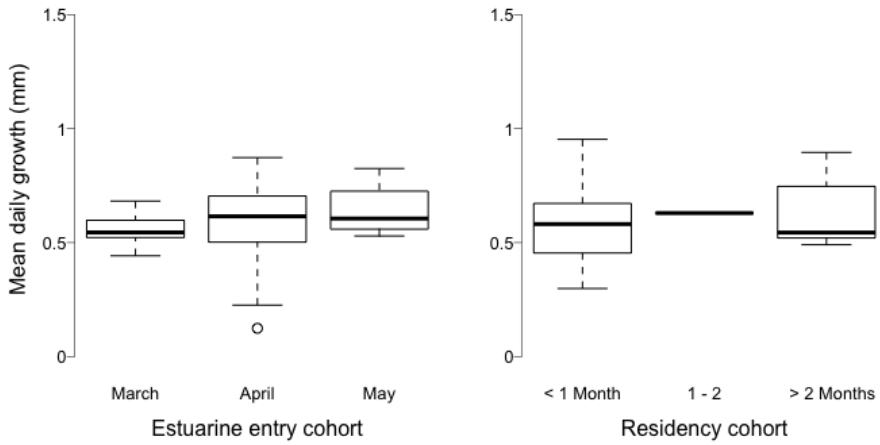

Fig. 5. Mean daily growth in fork length for cohorts of Chinook that enter the Fraser River estuary in different months (left panel) and reside in the estuary for varying time periods (right panel). Box and whisker plots depict the median (black line), 25th and 75th quartiles (box), and range of values (whiskers) for each group, with points past the whiskers depicting extreme measurements outside of the standardized interquartile range.

Lower Fraser River subyearling migrant Chinook appear to have a strong portfolio of varying life history strategies when it comes to ocean entry. A variety of life history strategies may make Chinook populations more resilient to shifts in climate, flow rates, food availability and other stressors (Phillis et al. 2018). This study clarifies the entry timing, minimum residency period, and daily growth rates for lower Fraser River Chinook salmon. We recommend that future studies focus on linking early marine growth to adult returns to elucidate the impacts of estuarine residency on survival.

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Linking Freshwater Environmental Factors to Up-river Migration Timing of Fraser River Chinook Salmon

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Keywords: Chinook salmon, Fraser River, migration timing, freshwater environment

Stocks of Fraser River Chinook salmon (*Oncorhynchus tshawytscha*) are separated into five management units (MUs) based on their run timing through the lower Fraser River and overarching life history. The Albion test fishery, located approximately 50 km upstream of the mouth of the Fraser, estimates run-timing through the collection of biological samples that allow for genetic stock identification (GSI) in addition to providing a continuous index of Chinook salmon abundance back to 1980 (Dempson et al. 1998). Fraser River Chinook demonstrate great diversity in their adult migration timing from the ocean and into freshwater, with some populations returning as early as April and others as late as September, despite similar timing for the onset of spawning (Parken et al. 2008). Run-timing is a useful tool for managing fisheries on population aggregates such as those found in the Fraser, but it is important to recognize that this trait is largely heritable and has been theorized to be an adaptation to environmental conditions up river (Healey 1991; Quinn et al. 2002; Keefer et al. 2004). Previous research successfully linked GSI with coded-wire tags in the Albion test fishery providing an opportunity to improve management at the population level for Fraser Chinook (Parken et al. 2008). However, this work also allows the opportunity to link run-timing to the lower Fraser River with environmental conditions upstream on the spawning grounds.

Environmental variables such as water temperature and discharge can have varying effects on migrating salmon depending on the period of time and duration of exposure. Arrival at spawning grounds during optimal environmental conditions is key to finding mates and successfully incubating eggs but can be negatively affected by sublethal effects due to poor environmental conditions during migration. To understand which environmental conditions are driving the onset of migration timing for each stock, we took a two-step approach. First, population level and management unit level yearly and average run-timing estimates were updated from Parken et al. (2008) using a hierarchical Bayesian model. Next, a principal components analysis was performed to examine how the average timing of the spring freshet, average timing when spawning tributaries are warmest, distance travelled, total time in freshwater prior to spawning, and the average maximum historical temperature in the spawning tributary are linked to lower river run-timing for 20 populations of Fraser River Chinook among five MU's.

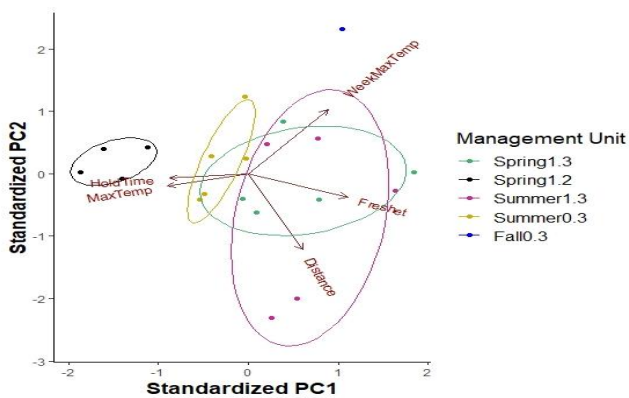

Fig. 1. Principal components plot of freshwater environmental variables linked to Fraser River Chinook salmon run-timing for 20 populations (points) within five management units (circles). Standardized PC 1 and PC 2 explain 60% of the variance in the data.

The timing of the spring freshet, distance to spawning tributary, and the length of time spent holding in freshwater prior to spawning are the environmental variables most strongly associated with the first three principal components and explained 80% of the variance. The distinct clustering of the Fraser Chinook MUs across the first two components provides insight into which freshwater environmental factors these populations have most closely adapted their freshwater migration timing (Fig. 1). Stocks, represented by the points in Fig. 1, that are closer to the ends of the factors represented in the figure as the red arrows are more positively correlated with those variables. Run-timing for the Spring 1.3 MU is most strongly associated with the timing of the spring freshet, and least with

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average maximum summer temperature and length of time spent holding in freshwater. The Summer 1.3 MU is most strongly aligned with the timing of peak summer temperatures and distance to the spawning grounds. The Summer 0.3 MU is affiliated with the timing of maximum temperatures while the Spring 1.2 MU is distinct from the rest of the groupings and strongly correlated with holding time prior to spawning and the average maximum temperature.

Overlap of the MU groupings are evident in Fig. 1, however the variables most strongly correlated with each MU differ and have underlying support in their respective biology. The Spring 1.3 and Summer 1.3 MUs encompass populations that spawn in 130 streams throughout the Fraser River watershed whereas the Fall 0.3, Summer 0.3 and Spring 1.2 management units spawn in 27 streams. Consequently, the principle component analysis groupings are more widespread for the Spring 1.3 and Summer 1.3 MUs than the others as environmental conditions are likely to be more varied over such a large number of streams. Several populations within the Spring 1.3 MU have their migrations timed to coincide with the spring freshet in spawning streams as the fish require high water levels to cross physical barriers to reach their spawning grounds (e.g., beaver dams, R. Bailey, pers. comm). The Spring 1.2 MU is unique relative to the other MUs as they arrive early to the Fraser River and hold in freshwater near the spawning grounds for an extended period of time until the onset of spawning, yet these populations do not travel a significant distance to the semi-arid Nicola and Lower Thompson watersheds. The Summer 1.3 MU experiences high summer temperatures throughout their migration but they also travel to some of the farthest tributaries within the Fraser River watershed. Migration timing for the Summer 0.3 MU is strongly linked to the timing of peak summer temperatures. A plausible explanation for this is that these spawning tributaries are large, lake-headed systems that provide a stable spawning environment. The Fall 0.3 MU is also distinct in that it represents one genetically distinguishable stock of Fraser Chinook and the migration timing is late enough to not be affected by high discharge levels, warm summer temperatures, and the MU has a short migration distance.

Fraser River Chinook exhibit great diversity in spawning locations and run timing within the watershed. Recent declines in Chinook throughout the entire Pacific have increased interest in understanding the anthropogenic and natural dynamics that impact these populations throughout their life history. While considerable focus for understanding Chinook salmon declines has been on the marine environment, the Fraser Chinook MUs that spend the most time in freshwater are declining faster than those that spend less time in freshwater (DFO 2018). In the Fraser River watershed, climate change projections suggest that precipitation will decrease in the summer but increase in other seasons (Morrison et al. 2002). This change in precipitation patterns in conjunction with a predicted increase in magnitude and duration of peak summer air temperatures will both affect the timing of the spring freshet and stream temperatures during the migratory period for adult Fraser River Chinook. For example, river temperatures within the Thompson watershed (a tributary of the Fraser) are predicted to experience prolonged periods of temperatures greater than 21 degrees Celsius (Morrison et al. 2002) which are known to be problematic for Chinook salmon (Strange 2010; Bowerman et al. 2018). Additionally, many of the snow dominated watersheds are expected to have shifts in runoff where snow accumulation is reduced, resulting in earlier peak flows and a subsequent rise in stream temperatures (Rood and Hamilton 1995). The migration timing of Chinook salmon may be an important biological trait to monitor for climate change adaptation, and for planning ocean and freshwater fisheries along their migration routes.

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Temporal Forms of Pink Salmon in Sakhalin-Kuril Region and their Abundance Dynamics

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Keywords: Sakhalin, Iturup and Kunashir Islands, pink salmon, temporal forms, abundance, extreme factors (floods, storms in seacoasts)

At the present time, we have accumulated lots of data on the occurrence of different pink salmon groupings that have different timing of runs in the same rivers. First, such groupings were noticed in rivers of the southeastern coast of Alaska and British Columbia along the American coast (Royce 1962; Vernon 1962) and in rivers of Iturup Island and southeastern coast of Sakhalin Island along the Asian coast of North Pacific (Ivankov 1967; Volovik et al. 1972). According to modern views, distribution of temporal forms of pink salmon over the reproduction area is rather wider than that suggested not long ago (Ivankov 2011). Fishes from these groupings differ in body size, fecundity, gonads maturity during spawning escapement, timing of migration, and spawning areas. Whilst earlier they were considered the same species, currently some scientists suggest giving them a rank of ecological subspecies (Ivankov and Ivankova 2017). However, there is no point in discussing such nuances until obtaining reliable genetic investigation results, because in these groupings we can observe a wide overlap with both the time of their entering the rivers and the spawning areas (Kaev 2012). At the same time, the notions about such temporal groupings continue to remain at the level of acceptance that these groupings are expedient for a fuller colonization of a habitat area by pink salmon (Ivankov 2011; Ivankov and Ivankova 2013, 2017). In this paper, we consider peculiar features of abundance dynamics for such groupings, which we name so far as the temporal forms.

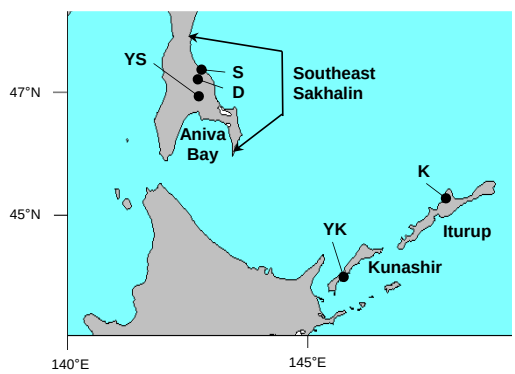

Fig. 1. Areas of study of pink salmon on Sakhalin and the southern Kuril Islands (Iturup, Kunashir) and the location of meteorological stations: *YK*—Yuzhno-Kurilsk, *K*—Kitovoye, YS—Yuzhno-Sakhalinsk, *D*—Dolinsk, *S*—Starodubskoye.

Indices		Early form		Late form		*F*
		M	*SD*	*M*	*SD*	
Aniva Bay, *N*=20 (4.1 - 7.3 - 12.9)*						
Males:	FL, cm	45.0	1.71	48.9	1.84	47.9
Females:	FL, cm	46.4	1.34	48.1	1.23	16.9
	Fecundity	1453	133	1379	89	4.3
	Fecundity/FL	31.3	2.31	28.6	1.42	19.3
Iturup Island, *N*=32 (4.0 - 7.1 - 12.0)*						
Males:	FL, cm	46.7	1.66	48.6	1.84	17.6
Females:	FL, cm	48.9	1.07	48.8	1.37	0.0
	Fecundity	1550	102	1417	133	20.4
	Fecundity/FL	31.7	1.79	29.0	2.28	28.3

* In brackets are critical values of Fisher criterion (*F*) for three standard levels of significance.

Table. 1. Mean length of fish, absolute and relative fecundity of females for early and late forms of pink salmon over the observation period in Aniva Bay and on Iturup Island.

Pink salmon from commercial catches at the eastern Sakhalin and southern Kuril Islands are represented by the two temporal forms (early and late). A migratory run of the early form begins in the first half of July, the late one in the first half of August. We studied biological characteristics of these forms both in Aniva Bay and on Iturup

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Island (Fig. 1). Specimens of the late form appeared to be larger. For the first turn, this is related with the increase in male length, whereas the length of females does not increase when temporal forms change (Table 1). As a rule, the early-form males during their migratory run are smaller than females. The migratory run of the late form is tested by the mass appearance of large males; on average, males become larger than females. Usually when the late-form fish run to the seacoast, a noticeable increase in catches takes place, and a portion of males grows. An absolute fecundity of the early-form females is somewhat greater, but this difference is not always confirmed statistically. At the same time, a relative fecundity (Fecundity/FL) of the early-form females is significantly higher. This is considered as an important feature proving a higher level of mortality of the early temporal form and can also be judged by the higher variability of its abundance (Kaev 2012).

The objective of this study is to quantify the different temporal fish forms of pink salmon during their migratory runs from Iturup and Kunashir islands based on long-term observations. We excluded the Aniva Bay pink salmon because in the last ten-year period a system of monitoring for their stock was broken. So, calculations for early- and late-form portions of fish in their runs to the seacoast were done for the southeastern Sakhalin pink salmon using the same methods (Kaev 2012; Kaev and Romasenko 2017) when pink salmon were sampled in the monitoring regime beginning in 2004. For the previous years, we used a ratio of catches before and after 3 August (mean date for the beginning of domination of the late form in coastal runs) for calculations. In some years, this date was 28 July or 8 August depending on particular features of catch dynamics. The Accuracy of such calculations was determined by comparing the similarity of data on fish abundance of the early (r = 0.88) and late (r = 0.98) forms obtained using the mentioned and routine methods in 2004–2017.

We considered some environmental factors that could affect the ratio of different temporal forms and cause significant decreases in pink salmon abundance. These factors include floods in rivers during and after salmon spawning, along with storms that occur when downstream-migrated juveniles begin feeding in the seacoast (Kaev 2018). Rain floods were considered by the value of daily precipitation, and their peak values were accepted as a sum of the largest precipitation taken over two adjacent days. The occurrence of storms was judged by the average value of the maximum windflaws recorded 4–8 times during day and night. These values were calculated based on the data of meteorological stations (http//rp5.ru, data collection since 2005) in Yuzhno-Sakhalinsk, Dolinsk and Starodubskoye for the southeastern coast of Sakhalin Island, and in Kitovoye for Iturup Island and in Yuzhno-Kurilsk for Kunashir Island (Fig. 1). There was no data on the wind strength in 2016 (impact on generation of the 2017 return) or on the amount of precipitation in 2015–2016 (impact on the corresponding generations of the 2017 and 2018 returns) at Kitovoye station. The meteorological data taken at Yuzhno-Kurilsk station appeared to be untenable to give characteristics of reproduction conditions for Iturup pink salmon (Kaev 2018).

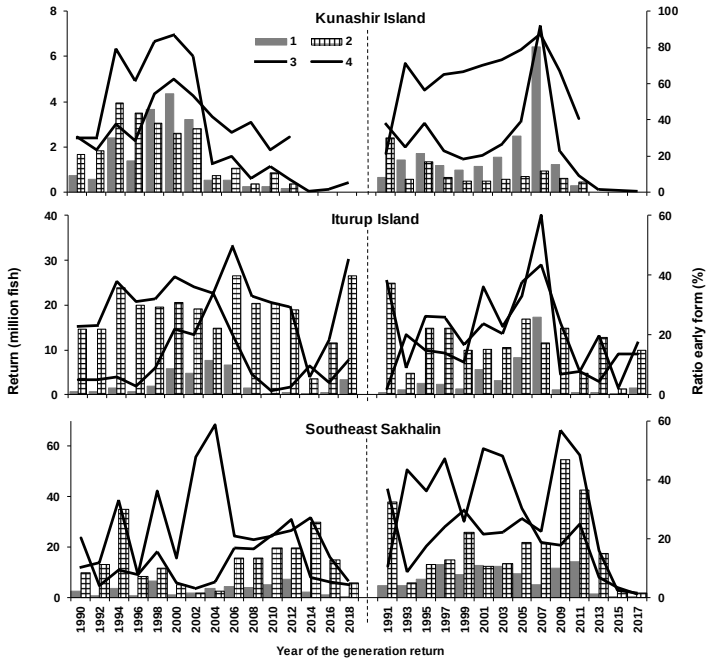

Fig. 2. Abundance dynamics of early (1) and late (2) temporal forms of pink salmon during odd-and even-numbered years in 1990–2018 from Kunashir and Iturup islands and southeastern Sakhalin coast: 3—total numbers of both forms, 4—percentage of the early form.

We have studied ratios of early and late temporal forms of pink salmon in their runs to the seacoast since 1990, covering the last period of the high level of pink salmon stock in the region that began from the late 1980s and completed by the mid-2010s (Kaev and Irvine 2016). At first glance, changes in abundance for early and late forms were similar as there was a synchronous alternation of years with high or low fish numbers of each of these forms (Fig. 2). However, the year periods with the high-abundant fish of the early form were shorter overall, with a noticeable and abrupt drop in pink salmon stocks in the last years. A decline in abundance for the early form came ahead of one to three generations or was more intensive at the synchronous (in adjacent years) development of this process that is well illustrated by the percentage reduction of the early-form fish in their runs.

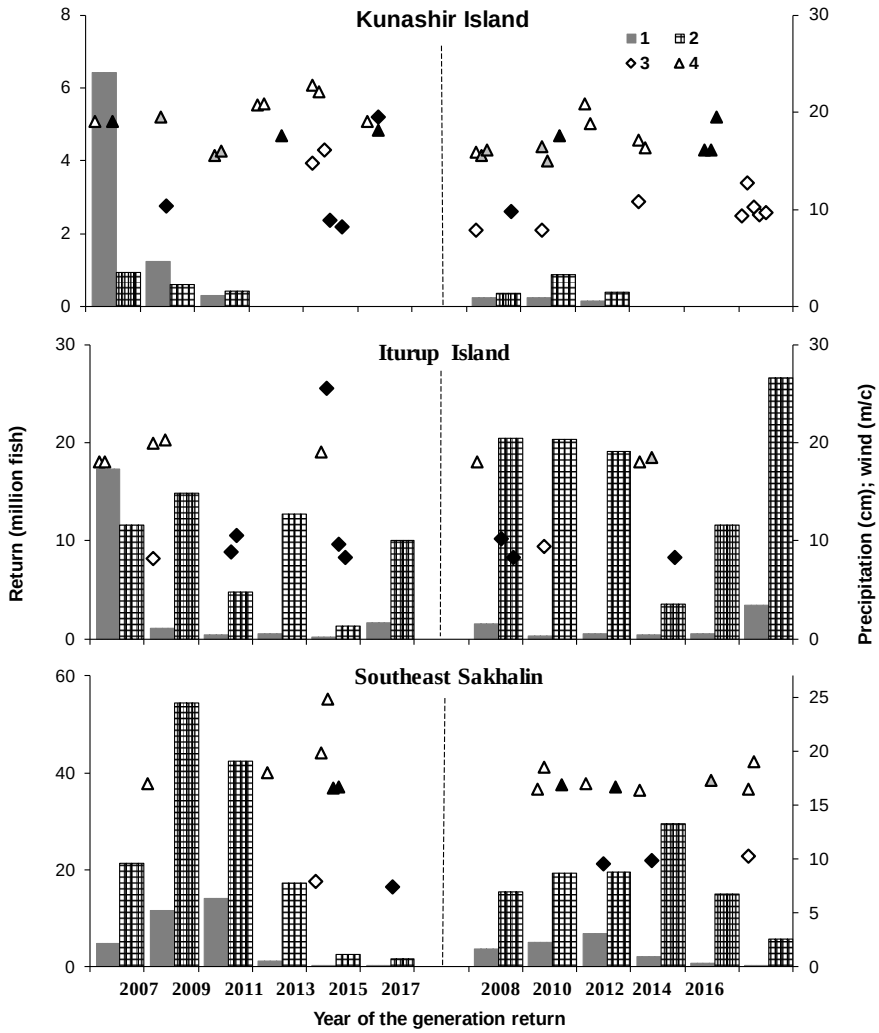

Fig. 3. Numbers of early (1) and late (2) temporal forms of pink salmon during odd-and even-numbered years from Kunashir and Iturup islands and southeastern Sakhalin coast, and occurrence of days with the extreme large precipitation during and after spawning, and strong winds during juvenile feeding in the sea coastal waters: 3—precipitation, 4—winds (as colors of symbols 3 and 4—explanation in text).

Declines in abundance for both temporal forms occurred in all cases when they were impacted by extreme floods eroding the ground with redds, or strong storms during the period of mass fry migration from rivers (Fig. 3). The large numbers of adults that returned in 2007 to Kunashir and Iturup islands were not an exception. Thus, the first storm on Kunashir (2 May) occurred before the beginning of the mass fry migration from rivers, and the second storm (1 June) affected mainly the late migrants. This is because the earlier migrated grown-up juveniles did not enter the group of risks associated with the storms. On Iturup, storm winds (11 and 13 May) occurred before the beginning of the mass fry migration from rivers too. For a better perception of which temporal forms were more

strongly affected by the factors considered, the corresponding symbols in Fig. 3 are colored differently. Symbols indicating precipitation that affects only the spawning process of the early form are colored white, and those affecting the spawning of both forms are colored black. Symbols indicating storm winds, observed during the downstream migration of the first, second and last parts of fry are colored white, grey and black, respectively. Not all the presented data completely fit the trends considered. Thus, on Iturup Island, we could expect a further decrease in abundance for both temporal forms in 2014, but not to the extent that was observed with the late form, as the storm winds affected mainly the first half of fry migrants. The reason for such disproportional decreases in fish abundance of the late form appeared to be related to the migration of part of these fish to the southern Sakhalin coast that, in its turn, caused an additional late peak in a seasonal dynamics of catches in that year at southeastern Sakhalin (Kaev and Zhivotovsky 2017). The reasons for significant decreases of pink salmon abundance at southeastern Sakhalin in 2013 remain uncertain. We can only suggest the development of some negative environmental processes that had a stronger effect on the formation of abundance of the early form, because the storm winds recorded on 13 May during feeding of the small number of fry migrants, could not cause such a high rate of decrease in the abundance of the early form. A similar situation occurred in 2018. If the increase in abundance of pink salmon (including the early form) on Iturup Island was expected, then such a significant decrease in abundance of pink salmon (especially the late form) at southeastern Sakhalin appeared to be unexpected. This is because the impact of the considered extreme environmental factors was recorded only for the early form of this generation: large precipitation events only occurred during the first half of spawning of their parents, and storm winds were observed during the first tierce of fry migration from rivers.

Thus, there are differences in abundance formation for early and late temporal forms, which are due to a combination of the differences in timing and spawning areas in the same rivers and the timing of fry downstream migration (Kaev and Romasenko 2017). With the variation of pink salmon abundance dynamics, extreme environmental factors are very significant for its decrease because of their impact on both the results of spawning and habitat conditions for juveniles after their migration from rivers. Of course, a spectrum of environmental factors influencing abundance formation is wider. Some of them are beyond the researchers' control that causes in some cases an unexpected decline of pink salmon abundance. The primary response of the early form to deterioration of reproduction conditions meets the introduced viewpoint about the reasons of higher fecundity for females of this form compared to females of the late form. Therefore, we suggest that the decrease in abundance for the early form simultaneously with the decrease in its portion in the run to the seacoast can serve as an indicator of the forthcoming general depression in pink salmon stocks.

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Current Status of Chum Salmon Populations in the Rivers with and without Hatchery Stock Enhancement on the Sanriku Coast, Japan

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Keywords: chum salmon, hatchery-based stock enhancement, wild fish, natural spawning

Chum salmon (*Oncorhynchus keta*) are one of the most important fish species in northern Japan. The hatchery-based stock enhancement program has been implemented since the 1800s and resulted in significant increases of returning adults with the increase of juvenile release. However, the adult return has been decreasing after the peak in 1996 despite the fact that almost constant number of juveniles have been annually released (Hokkaido National Fisheries Research Institute, 2018). In addition, the existence of wild fish and natural spawning was recently reported in many rivers over Japan (Miyakoshi et al. 2012; Morita et al. 2013; Aoyama 2017; Iida et al. 2018), although the chum salmon stock has long been believed to consist of the hatchery-origin fish. Therefore, there is a need to evaluate the status of chum salmon populations of both wild and hatchery-origin fish.

On the Sanriku coast (the side of the Pacific Ocean of the Japan's mainland), Japan, there are two contrasting rivers, the Otsuchi and Koduchi Rivers, in terms of implementation of stock enhancement program. These two rivers are similar-sized, and next to each other at their river mouths. For the former, a large-scaled hatchery-based stock enhancement program has long been implemented with releasing about 20 million juveniles annually whereas for the latter, it has been suspended since the 2011 off the Pacific coast of Tohoku Earthquake and the following tsunami. This situation allows us to assess and compare the population status of chum salmon with and without stock enhancement.

In the present study, in order to evaluate the current status of chum salmon populations in rivers with and without hatchery-based stock enhancement program, adult fish, their spawning redds and carcasses were assessed through the whole spawning season in 2017–2018 in the Otsuchi and Koduchi Rivers on the Sanriku coast, Japan. A quantitative survey was performed from 1 September 2017 to 21 February 2018, once every ten days in the Otsuchi River and one to three times a week in the Koduchi River to collect tissues and scales from fresh carcasses. The study area was 0.5 to 1.0 km upstream from the hatchery weir in the Otsuchi River and 1.0 to 4.0 km upstream from the river mouth in the Koduchi River. Adults, their spawning redds and carcasses were visually counted while walking gently and slowly along or in the survey reaches. In the Otsuchi River, a total of 106 spawning redds were found from 10 November 2017 to 31 January 2018, and the total number of adults and carcasses was 170 and 214, respectively, suggesting that the hatchery weir unexpectedly allowed some fish to pass upstream to spawn. In the Koduchi River, at least 363 spawning redds were counted from 10 October 2017 to 31 January 2018, and returning adults and carcasses were 2,044 and 1,764, respectively.

The present study suggested that most of the returning adults to the Otsuchi River were caught by the hatchery weir for the stock enhancement and then natural spawning was less abundant than the Koduchi River. This indicated that the population in the Otsuchi River consisted of mostly the hatchery-origin fish whereas those in the Koduchi River should be wild. As the hatchery weir catch in the Otsuchi River in this season was officially reported to be 2,787, the stock of the Otsuchi River was obviously larger than that of the Koduchi River. It is, however, noteworthy that the difference in the numbers of returning adults between these two rivers was considerably smaller compared to that in the numbers of juveniles with and without hatchery release.

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Variation in Out-migration Timing and Estuary Reliance of "ocean-type" Chinook Salmon in the Fraser River Estuary, BC

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Keywords: Pacific salmon, Chinook salmon, estuary, outmigration timing, juvenile salmon

Estuaries connect freshwater and ocean environments for Pacific salmon, providing important habitats during a crucial transition period for juveniles where feeding opportunities are abundant, and the risk of predation is relatively low. All Pacific salmon migrate through estuaries twice during their lifespan and many will reside for days to months during their downstream migrations (Healey 1982; Weitkamp et al. 2014; Moore et al. 2016). Chinook (*Oncorhynchus tshawytscha*) and chum salmon (*O. keta*) migrate downstream in their first year of life as fry are known to rear in estuaries, from a few days up to a few months for some Chinook populations (Levings et al. 1991; Volk et al. 2010; Carr-Harris et al. 2015).

The Fraser River estuary in British Columbia is home to a diverse assemblage of salmon populations, and juvenile salmon originating from throughout the watershed migrate through the estuary each year. Chinook, chum and pink (*O. gorbuscha*) salmon rely on tidal-marsh habitats in the estuary for rearing and feeding, particularly juvenile Chinook salmon with "ocean type" life history, which depend on these habitats for extended periods before ocean entry (Levy and Northcote 1982). Many Fraser populations of Chinook have experienced persistent declines in survival over the past several decades, but the South Thompson ocean-type population has increased (CTC 2018; Riddell et al. 2013; Ruff et al. 2017). Beamish et al. (2010) found that these individuals were arriving in the marine environment later than other populations and hypothesized that the late ocean entry timing was conferring a survival benefit to South Thompson Chinook.

Research in the Fraser estuary and other estuary systems across the Pacific Northwest have demonstrated the importance of estuary rearing for juvenile Chinook salmon with ocean-type life histories. In the Fraser, Levy and Northcote (1982) demonstrated high densities of Chinook rearing in tidal marsh channels and hypothesized that growth in the estuary was greater than upstream freshwater habitats. Moore et al. (2016) described estuaries as important stop-over habitats for juvenile salmon and found that in the Skeena estuary 25% of juvenile Chinook salmon spent at least 33d in the estuary. Larger Chinook salmon resided in the estuary for longer durations, growing at an estimated 0.5 $mm \cdot d^{-1}$, evidence that estuary residency provides growth opportunities (Moore et al. 2016). In the Columbia estuary McNatt et al. (2016) found many juvenile Chinook salmon remained in the marsh for 2–4 weeks and increased in fork length by 10–20 mm, with an average growth rate of 0.53 $mm \cdot d^{-1}$. The ability for juvenile Chinook to grow quickly during this estuary residence period is incredibly important as size at ocean entry is thought to be a major determining factor in early marine survival (Woodson et al. 2013). Based on these previous studies it seems likely that growth occurring in estuary habitats is important to the early marine survival of ocean-type Chinook in the Fraser River.

Our objective was to compare the outmigration timing, size, and estuary residence period among and within populations of juvenile ocean-type Chinook in the Fraser River estuary. Ocean type Chinook populations are thought to be reliant on estuaries for critical growth periods before ocean entry, therefore should be adapted to enter the estuary during peak productivity periods. Environmental conditions in the Fraser estuary vary considerably over the out-migration period, including salinity, turbidity and marsh productivity, therefore variation in out-migration timing and estuary residence will likely lead to variation in growth rates within and across populations for juvenile Chinook which contributes to variable size at ocean entry and may impact early marine survival.

We conducted an extensive juvenile salmon monitoring program throughout the Fraser River delta over three years (2016–2018), surveying at 36 sites that span the North, Main and South Arms of the river, and Roberts and Sturgeon Banks and encompass three habitat types using beach and purse seine, and fyke net methods. We sampled bi-weekly throughout the spring and summer season, starting in late March and extending until mid-July in 2016–2017, and expanded until mid-August in 2018.

We conducted fish surveys in intertidal and subtidal habitats using beach and purse seines. Beach seines are primarily deployed in intertidal marsh channels with sufficient depth and width to deploy the net. A 20 m long x 2

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m deep beach seine with a 2 m deep bag with 6.3 mm stretch mesh was deployed from a small boat using the round-haul method. A purse seine was used in sandflat and eelgrass sites. The purse seine (30 x 3 m, 6.3 mm stretch mesh bunt, 12.7 mm stretch mesh wings), was set from a boat and towed for 1 min. In 2017 we also studied three marsh sites using a fyke net method previously utilized in the Fraser estuary by Levy and Northcote (1982). Our net consisted of two wings (14 m x 2.4 m; 1/4" mesh) and a trap box (1.2 m wide x 3.0 m long x 3.0 m high; 1/4"-mesh). The net was set across a small marsh channel at high tide and passively captured fish as the tide fell before being pulled to the side of the channel when the water depth reached 0.5 m and all fish were removed.

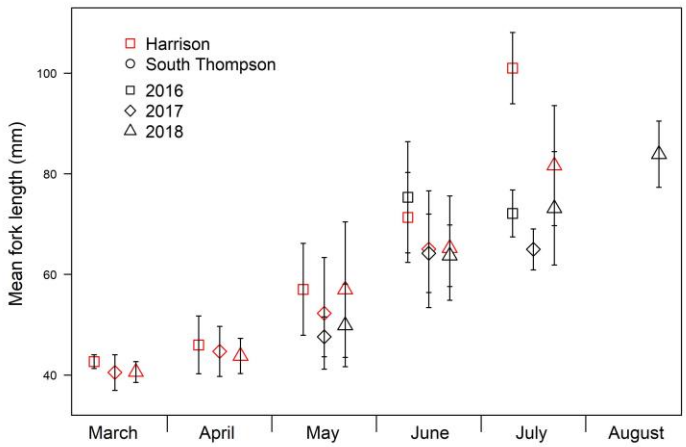

Fig. 1. Mean fork length and standard deviation for each month in each year of our study of juvenile Chinook salmon captured in the Fraser estuary, BC for which genetic stock identification was determined. Red symbols indicate Harrison River population and black symbols indicate South Thompson ocean type population. Squares represent averages from 2016, diamonds 2017 and triangles 2018.

We used genetic stock identification to determine the spawning location of origin of estuary-caught juvenile salmon. Samples were analyzed at the Pacific Biological Station by Fisheries and Oceans Canada by microsatellite DNA analysis which allows the identification of juvenile salmon to the population or Conservation Unit level.

Over three seasons (2016–2018) we captured 5,242 juvenile Chinook salmon, the majority in brackish marsh habitats, and have collected 1,696 tissue samples for genetic stock identification. Our initial results demonstrated that ocean-type Chinook originating from the Harrison River arrive in the estuary the earliest, near the end of March, and were present the longest until mid-July (Fig. 1). Harrison Chinook also arrived the smallest, with individuals increasing in mean fork length over the season, ranging from 35 mm to 77 mm (Fig. 1). Conversely, ocean-type Chinook from the South Thompson were not captured until late June in both years, ranging from 41 mm to 106 mm and last detected in August (Fig. 1). Overall, we captured juvenile Chinook from 18 different populations, and individuals from stream-type populations are generally captured in low numbers.

Our results confirm that ocean type Chinook salmon are the most estuary-reliant juvenile salmon in the Fraser estuary across the spring and summer outmigration period. Across three seasons we captured juvenile Chinook fry in the estuary from late March through until mid-August. This agrees with and extends the residence period noted by Levy and Northcote (1982) which demonstrated their presence into July. Genetic stock identification also allowed us to confirm that the early arriving Chinook fry almost entirely originated from the Harrison River population, and that individuals from this population were found in the estuary as late as July with fork length increasing over time. Our data also showed that although juvenile Chinook from the Harrison River were present in the estuary from late March until as late as July, the abundance peaks in late April and early May before quickly dropping off with relatively low abundance in late May and June. Therefore, although some juvenile ocean-type Chinook from the Harrison remained in the estuary for an extended period of time, the vast majority were likely only present for a few weeks, and this may be the first period of high mortality for this population. Regardless, these data demonstrate the continued direct importance of Fraser estuary habitats to this population of Fraser Chinook.

While our data confirm much of Levy and Northcote's (1982) work, our ability to utilize genetic stock identification revealed new insights into variation between and among ocean-type Chinook populations in the Fraser River. We demonstrated that juvenile ocean-type Chinook present in the estuary arrived in two separate waves, with Harrison River fry arriving from late March until June, and ocean-type Chinook from the South Thompson beginning to arrive in late May and early June. We found that by June and July, the majority of individuals captured

were South Thompson Chinook, and they were the only individuals captured into August. These data also supported Beamish et al. (2010) which demonstrated similar trends in the marine environment of the Strait of Georgia. We found a difference in size between populations, with the majority of Harrison fry arriving to the estuary shortly after emerging from the gravel and were captured in large number at small sizes (35–50 mm) while the majority South Thompson fry arrived in the estuary at a larger size (45–75 mm) after a brief freshwater rearing period.

Our results provide important new insights into the variation in life history of juvenile Chinook salmon with ocean type life history types. Levy and Northcote (1982) demonstrated the ocean-type Chinook are the most estuary reliant species of juvenile salmon in the Fraser River and our data supports that conclusion. However, while they assumed one wave of juvenile Chinook which arrived in the estuary in early spring reared and grew in the estuary for several months, we demonstrate a second wave of ocean-type Chinook which appear later in the season in the same estuary habitats. Overall, our data demonstrates the large variability in early life history strategy both between and within populations of ocean-type Chinook salmon in the Fraser estuary. Further research to determine which life history strategies result in the greatest prospective of marine survival will aid our understanding of juvenile Chinook life history strategies and guide restoration targets for Fraser Chinook.

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Direct and Carryover Effects of Freshwater, Marine and Fish Conditions on Juvenile, Ocean, and Adult Survival of Snake River Chinook Salmon

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Keywords: carryover effects, Columbia and Snake rivers, cross-life-stage survival, fish length, freshwater and marine environment, mark-recapture, Bayesian, smolt and adult salmon

Carryover effects are particularly relevant to mitigation strategies in river environments that aim to increase ocean survival. Since direct environmental effects in the ocean are not amenable to freshwater management intervention, understanding the relative magnitudes of carryover effects is important. Furthermore, evaluating covariates of juvenile and adult life stages in the same model facilitates comparison of their effects and their strength of evidence in a common currency. The objectives of this study are to: 1) quantify and assess the weight of evidence for direct and carryover effects on salmon survival, and 2) determine how river conditions affect the survival of both downstream juvenile and upstream adult migrants. Here we define "direct effects" on stage-specific survival as those related to conditions in the same life stage (or reach), and "carryover effects" as those related to conditions experienced in the previous life stage.

We examined how freshwater and marine environmental conditions and individual-level fish condition indices affect survival in three life stages: 1) downstream-migrating smolt, 2) ocean, and 3) upstream-migrating adult. We used fish detection data from passive integrated transponder (PIT) tagged wild spring/summer Chinook salmon originating upstream of Lower Granite Dam (LGR; Snake River, Washington, USA; ptagis.org). We analyzed individuals with passage timing and fork lengths observed at LGR in outmigration years 2002–2015. We tested the effects of the following stage-specific covariates: 1) juvenile stage: passage timing or river temperature, flow, percent spill and fish length measured at LGR, number of Snake River bypasses experienced, and snow-water-equivalent (SWE) index (Jorgensen et al. 2016); 2) ocean stage: sea surface temperature index (SSTarc) (Johnstone and Mantua 2014), North Pacific Gyre Oscillation (NPGO) index (Di Lorenzo et al. 2008), carryover effects from river environment (listed in previous stage), and number of hydrosystem bypasses experienced; and 3) adult stage: Bonneville Dam passage timing or river temperature, flow and percent spill (Fig. 1). Furthermore, for relevant reaches, we tested two passage-types in which juveniles had a run-of-river or barge-transported experience through the hydrosystem.

We applied a hierarchical Bayesian Cormack-Jolly-Seber (CJS) model to estimate probabilities of apparent survival (hereafter survival; ϕ) and detection (p) with covariates and annual random effects:

$$\text{logit}(\phi_{md}) = \mathbf{x}_{md}\boldsymbol{\beta}_d + \epsilon_{t[m]d} \quad \text{Eq. (1a)}$$

$$\epsilon_{td} \sim N(0, \sigma_d)$$

$$\text{logit}(p_{md}) = \mathbf{z}_{md}\mathbf{b}_d + e_{t[m]d} \quad \text{Eq. (1b)}$$

$$e_{td} \sim N(0, s_d)$$

where survival from site d to $d + 1$ ($d = 1, \ldots, D - 1$) for capture history m ($m = 1, \ldots, M$) in year t is a function of covariates $\mathbf{x}_{md}$ with regression coefficients $\boldsymbol{\beta}_d$, plus a random effect $\epsilon_{t[m]d}$ associated with the year of migration. The model for detection probability at site d is analogous. Detection sites, reaches, and associated covariates are depicted in Fig. 1. We fitted candidate models to the capture histories of PIT-tagged Chinook using Hamiltonian Monte Carlo algorithm implemented in Stan (mc-stan.org).

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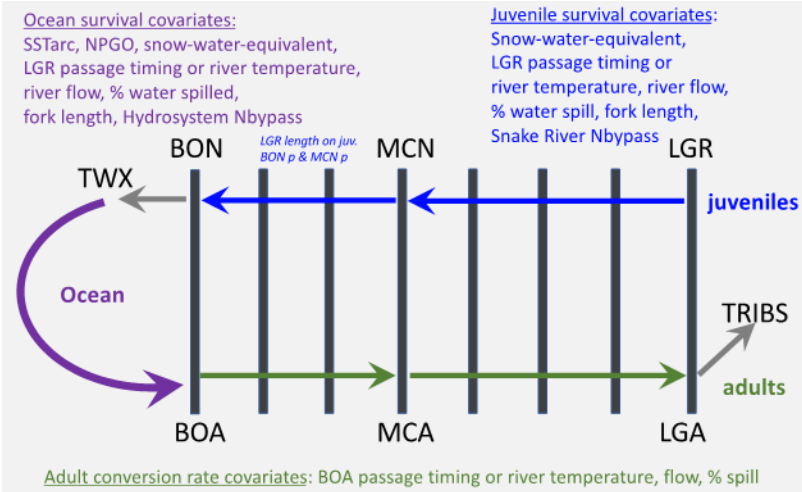

Fig. 1. Juvenile (blue), ocean (purple), and adult (green) reaches where apparent survival and detection probability were estimated. Covariates associated with survival and detection probabilities are represented with matching colors. Survivals were estimated in the juvenile reaches between Lower Granite (LGR), McNary (MCN), and Bonneville (BON) dams, and the estuary trawl (TWX), in the ocean reach, and in adult reaches between Bonneville (BOA), McNary (MCA), and Lower Granite (LGA) dams.

We calculated annual and interannual posterior medians of survival for each relevant reach that run-of-river and transported rear-type fish migrated through in the hydrosystem, estuary and ocean (Fig. 2). For the run-of-river fish, juvenile survival tended to be higher in the Snake reach (LGR-MCN) than in the mainstem Columbia reach (MCN-BON). Survival below the hydrosystem was relatively high to the estuary trawl, and low in the ocean (approx. 1%). Adult upstream survival (assumed equivalent to conversion rate) was lower in the Columbia reach than the Snake reach. For transported fish, survival from the point of release below BON to the estuary trawl was similar to that of run-of-river fish. Ocean survival and upstream adult survival both tended to be lower for transported fish than run-of-river fish.

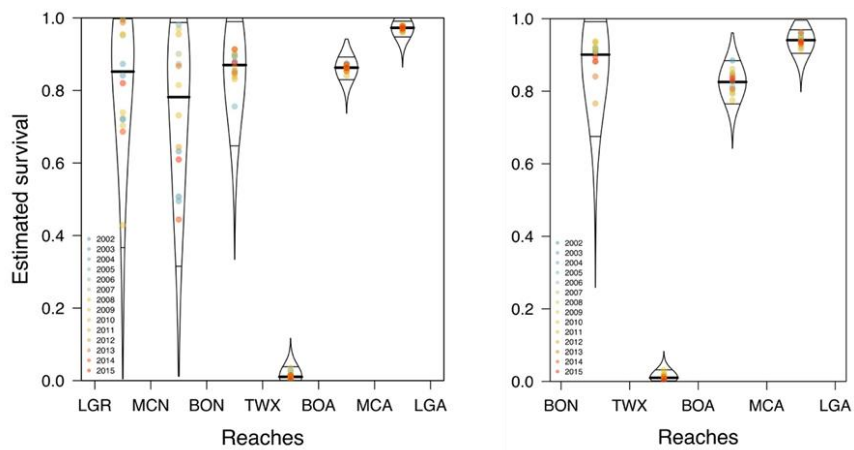

Fig. 2. Posterior distributions of apparent survival of wild Chinook salmon across reaches and life stages for run-of-river fish (left) and transported fish (right). See Fig. 1 for acronym definitions. Thick and thin horizontal lines represent posterior medians and 90% credible intervals, respectively, of the interannual hyper-means. Points represent posterior medians of the annual values.

River and sea surface temperature indices generally showed the strongest relationships with survival across juvenile, ocean and adult reaches in our preliminary results. For run-of-river fish in the juvenile reaches, river temperature had a negative relationship with survival in the Snake reach but positive in the Columbia reach, which still equated to a negative influence overall through the hydrosystem. Flow, spill and fish length showed positive relationships with juvenile survival. Snow-water-equivalent effects were highly uncertain. In the ocean reach, SSTarc showed a strong negative influence (Fig. 3). Carryover effects were negative for river temperature, and positive for fish length and snow-water equivalent. In the adult reaches, river temperature showed negative relationships with conversion rates. Percent water spilled showed a negative effect in Columbia reach (BOA-MCA) but less so if any, in Snake reach (MCA-LGA). For transported fish, the SSTarc index also showed strong negative influences on survival of these fish (Fig. 3). The effects from juvenile fish length were positive and stronger than the other covariates tested for carryover effects. In the adult reaches, river temperature had negative influences. Percent water spilled also had a negative influence but primarily in Columbia reach.

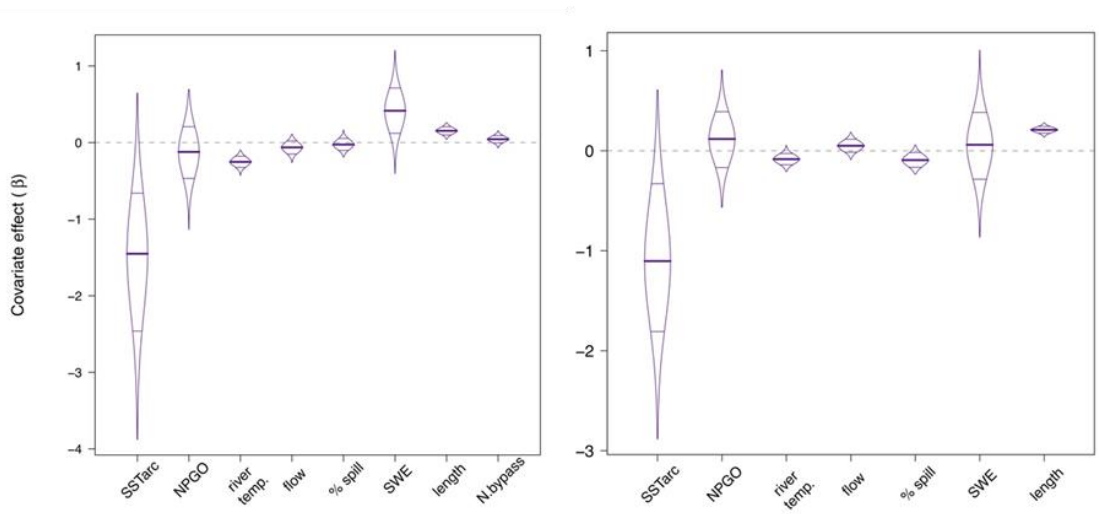

Fig. 3. Posterior distributions of covariate effects (on the logit scale) of ocean survival for wild Chinook salmon with run-of-river (left) or transported (right) downstream passage experiences.

We advise caution in interpreting these preliminary results, given multicollinearity among covariates. Still, some strong patterns were evident. The strongest and clearest effect was from SSTarc. Compared to covariates of freshwater carryover effects, the SSTarc effect was stronger (e.g., log-odds ratio ranges: -0.3 to -1.6 for river temperature, -0.4 to -1.7 for both flow and spill, -0.5 to -1.8 for fish length). Even if there are large ocean effects, identifying carryover effects from the river environment will help inform river management. Given the ranges of conditions examined in the current study, the partial influence from decreasing river temperature could increase ocean survival from about 0.5% to 2.6% for run-of-river fish. Similarly, given the ranges observed, the partial influence from increasing SWE could increase ocean survival from about 0.5% to 2.2%, and the influence from increasing fish length could increase ocean survival from about 0.4% to 2.9% for run-of-river fish.

This study identified positive effects of fish length on juvenile and ocean survival. With the current model, we did not detect an effect from the number of hydrosystem bypasses on juvenile or ocean survival. These findings are consistent with a recent study (Faulkner et al. 2019) that also found positive effects of juvenile length on ocean survival, but weak negative effects (if any) from number of bypasses experienced.

River conditions in a given year are experienced by both juveniles migrating downstream and adults migrating upstream. However, the effects may not always be the same for both these life stages. River temperature mostly had negative effects on survival. Yet, increasing percent spill was found to be beneficial to juvenile survival while detrimental to adult conversion rates. Comparison of the effects on juveniles and adults would require further examination in a currency that accounts for high ocean mortality.

Overall, we found a clear negative effect from SSTarc on ocean survival. But despite this strong effect, we also detected negative and positive carryover effects from river temperature and fish length, respectively, on ocean survival. The current study finds support for river temperature and fish length as among the most important and controllable environmental and fish conditions that could help improve ocean survival via freshwater-marine carryover effects.

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Juvenile Salmon Migration Observations in the Discovery Islands and Johnstone Strait in 2018 Compared to 2015–2017

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Summary

The Hakai Institute Juvenile Salmon Program has been monitoring juvenile salmon migrations in the Discovery Islands and Johnstone Strait since 2015 with the specific purpose to understand how ocean conditions experienced by juvenile salmon during their early marine migration impacts their growth, health and ultimately survival. We found that during the two of the warmest years of sea-surface temperature recorded in British Columbia waters, juvenile sockeye, pink, and chum left the Strait of Georgia one to two weeks earlier than previously. The temporal distribution of sockeye migration timing out of the Strait of Georgia north through the Discovery Islands was skewed right, indicating that many sockeye migrate together in late May and abundance tails off late into June and July. Pink and chum migrations are more protracted, lasting from early May to late July. Our results indicate that juvenile sockeye exit the Strait of Georgia *en masse*, likely in response to ocean temperature and foraging conditions. This report summarizes migration timing, fish length and weight, sea-louse loads, purse seine catch composition, and ocean temperatures observed from the first four years of this research and monitoring program. Combining key variables from this research program with observations from freshwater and high-seas sampling will provide, for some stocks, a complete account of the conditions salmon experience during their migration from their natal river to the high seas. These measures will further our knowledge of what drives early marine mortality, and better our understanding of how salmon are adapting to climate change.

Introduction

The first months after marine entry are a critical period for juvenile salmon growth (Beamish and Mahnken 2001), which may ultimately be responsible for inter-annual variability and long-term declines in British Columbian salmon stocks (Peterman et al. 2010; Beamish et al. 2012). Two of the leading causes of the decline are the impacts of climate change on marine food web dynamics, and the population level effects of pathogens and predators (Cohen 2012). The Discovery Islands and Johnstone Strait are a region of reduced food availability for migrating juvenile salmon and may act as a bottleneck in their early marine survival (McKinnell et al. 2014). The Hakai Institute Juvenile Salmon Program has been monitoring juvenile salmon migrations in the Discovery Islands and Johnstone Strait (Fig. 1) since 2015 to determine the factors that influence early marine survival of sockeye, pink, and chum salmon (Hunt et al. 2018). This report summarizes migration timing, fish length, parasite loads, species composition, and ocean temperatures observed in 2018 and compares these metrics to our observations between 2015 and 2017. We also compare the past four years of this research and monitoring program to historical observations where possible. These measures provide essential support information for ongoing research into the growth, survival, and the impact of ocean conditions experienced by salmon during their early marine migration through this critical region. We report on the interannual variability of juvenile sockeye, pink, chum, coho, and herring population characteristics in relation to the ocean conditions fish experienced in the Strait of Georgia, Discovery Islands and Johnstone Strait in 2015, 2016, 2017, and 2018.

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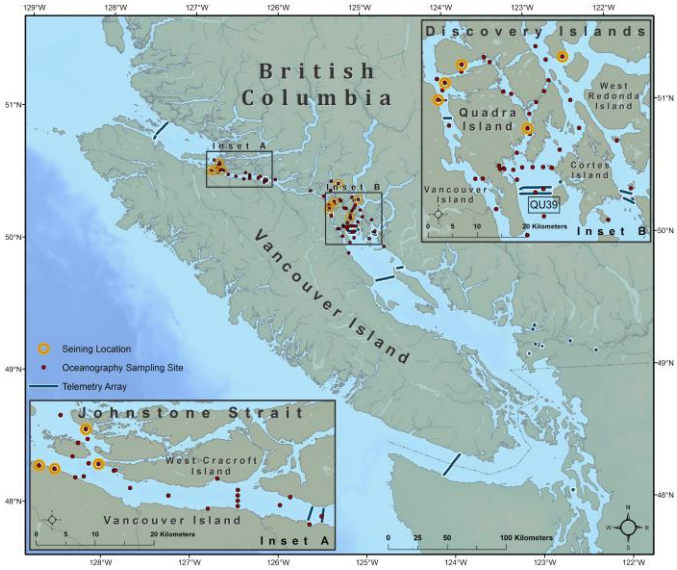

Fig. 1. Juvenile salmon sampling and oceanography stations in the Discovery Islands and Johnstone Strait in 2018.

Methods

Field methods

See Hunt et al. (2018) for a detailed description of field and lab methods. Briefly, we collected juvenile salmon weekly from the Discovery Islands and Johnstone Strait during their northward migration from the Strait of Georgia to Queen Charlotte Strait near northern Vancouver Island, British Columbia. We sampled from May to July each year, beginning in 2015, using hand-operated purse seine nets (bunt: 27 m x 9 m with 13 mm mesh; tow: 46 m x 9 m with 76 mm mesh) (Groot et al. 1985; Godwin et al. 2015). We sampled near-shore marine habitats where depth was > 10 m and distance from shore was usually less than 300 m, effectively sampling sockeye (*Oncorhynchus nerka*), pink (*O. gorbuscha*) and chum (*O. keta*) salmon, and incidentally capturing coho (*O. kisutch*), Chinook (*O. tshawytschya*) and Pacific herring (*Clupea pallasii*). All animal care complied with Animal Care Guidelines under permit A16-0101. We collected temperature data by deploying a Maestro conductivity, temperature, and depth profiler (RBR Ltd. Ottawa, Canada) to depths > 30 m at station QU39 (Fig. 1) in the northern Strait of Georgia.

Data Analysis

We report 'study-period anomalies' in relation to the averages from 2015–2018 to characterize interannual variability. Measurements from the Discovery Islands and Johnstone Strait regions of the salmon migration were combined in analyses unless otherwise indicated. We used sites that we sampled in all years for calculations. All analyses were conducted using R (R Core Team 2017).

The aim of the program was initially focused on capturing sockeye and better understanding the ecology of co-migrating sockeye, pink and chum schools. In 2015 and 2016, we focused on capturing sockeye, and only enumerated and sampled pink and chum when we also caught sockeye. In 2017, however, we transitioned to enumerating and sampling pink, chum, and other species even when sockeye were absent. To make consistent observations between years migration timing, catch intensity, and catch proportion statistics for sockeye, pink, and chum are calculated based on seines that captured at least one sockeye.

The peak migration date for each species was estimated by calculating the median date of capture in the Discovery Islands. We favored this approach over a 'catch per unit effort' approach because of the nature of our sampling design. Every year seines were conducted before sockeye arrived and after sockeye disappeared, thus we are confident we effectively capture the vast majority of out-migrating juvenile sockeye. This allowed us to constrain the period over which we calculated cumulative abundance to 1 May–9 July and provided a consistent period to make inter-annual comparisons of migration timing. The Fraser River is an even-year-dominant system for pink salmon, and very few out-migrating pinks are caught in odd years; consequently, only even years were included in the calculation of the pink migration study-period averages.

Catch intensity was calculated to provide a measure of inter-annual abundance for sockeye, pink, and chum. We defined catch intensity as the average number of a species caught when > 1 of that particular species was caught, and when sockeye were also caught. In effect, catch intensity summarizes the abundance of each species in a community of co-migrating sockeye, pink, and chum salmon.

Species proportions were calculated by dividing the total number of each species caught by the sum of all species caught that season. Only seines that caught sockeye were used in the calculation of species proportions so that we could make consistent comparisons among years. To test whether fork lengths from 2018 were significantly different than the study-period averages we conducted an independent two-group *t*-test. Fork length distributions were visualized by calculating length frequency distributions using kernel density estimates from fork length data.

The abundances of *Caligus clemensi* and *Lepeophtheirus salmonis* sea lice were determined by calculating the mean number of lice on all fish observed, according to the definition in Margolis et al. (1990). Only motile (i.e., pre-adult and adult) stages were included in analyses while nauplius, copepodid, and chalimus life stages were excluded because these juveniles were not enumerated in every year. Sea lice were picked and counted from fish in the laboratory, and a dissecting microscope aided identification. Mean abundance estimates and 95% confidence intervals were bootstrapped 10,000 times from the counts of lice obtained for each species of louse, respecting the hierarchical nature of observations on sockeye, pink and chum from the same seine, in the Discovery Islands and Johnstone Strait from the past four years.

Ocean temperatures were averaged from the top 30 m of the water column because juvenile salmon inhabit surface waters in the northern Strait of Georgia and Discovery Islands (Levings and Kotyk 1983; Beamish et al. 2012; Johnson et al. 2018). We measured temperatures at station QU39 in the northern Strait of Georgia in May and June—the period during which salmon migrate through the region. To visualize temperature anomalies a local polynomial regression function from the *R* 'stats' package called `loess` (Cleveland et al. 1992; R Core Team 2018) was applied to ocean temperatures from all years to represent the average seasonal temperature trend. Average annual temperatures (in °C) are used to calculate interannual differences and the number of standard deviations each annual observation is from the study-period average, which allows us to characterize interannual variability.

Results

Migration timing was similar in 2018 compared to 2015, and 2016 for sockeye, pink, and chum, which were among the earliest migration timings recorded in the Discovery Islands compared to previous measurements (Neville et al. 2016) or indicated by catch-abundances by purse seine or trawl surveys in the northern Strait of Georgia and Discovery Islands (Groot et al. 1985; Preikshot et al. 2012; Neville et al. 2013; Fig. 2). Catch intensity was high for pink and chum, but low for sockeye. Pink and chum fork lengths were longer than the average from 2015–2017, but sockeye fork lengths were shorter than average. There appears to be a pattern of pink and chum length anomalies varying together and sometimes opposite of sockeye. Sea-louse abundance was low in 2018 relative to the previous three years. Sea-surface temperatures in 2018 during the smolt migration period in the northern Strait of Georgia were the warmest recorded between 2015 and 2018.

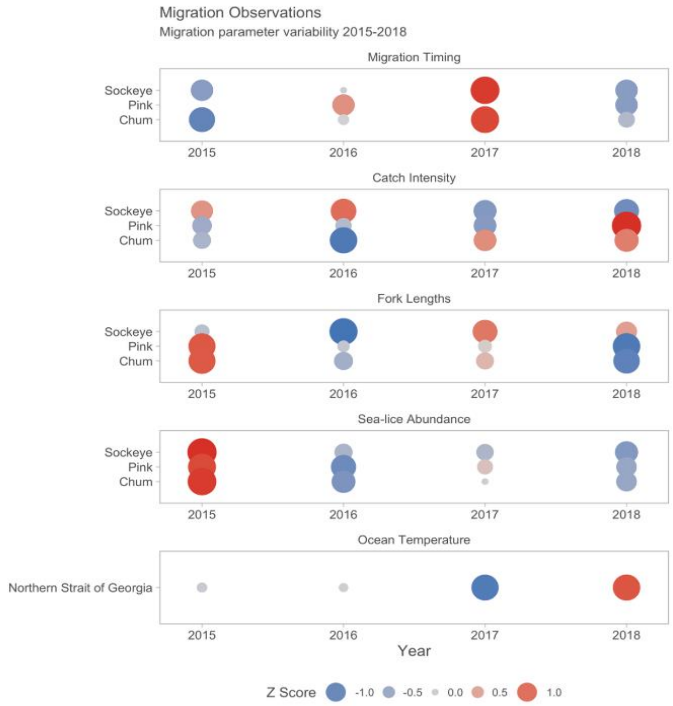

Fig. 2. The number of standard deviations (z score) from the study-period average (2015–2018) for key migration parameters. Size and colour saturation of circles indicates the magnitude of the anomaly. Blue colour indicates less than average; grey indicates average; red indicates greater than average. Peak migration date is based on the median date of fish capture in the Discovery Islands. Length is based on the average fork length from the Discovery Islands and Johnstone Strait combined. Parasite load is the average abundance of all sea-louse species in their motile life stages for both the Discovery Islands and Johnstone Strait regions. Ocean temperature describes the mean ocean temperature in the top 30 m at station QU39 in the northern Strait of Georgia in May and June.

Migration timing in the Discovery Islands in 2018 did not differ from the study-period average by more than 5–7 days—the expected accuracy of the calculations—for sockeye, pink, or chum (Fig. 3; Table 1). The peak migration date for sockeye in the Discovery Islands was on May 23, five days earlier than the study-period average of May 28. The peak migration date for pink in the Discovery Islands was on June 12, one day earlier than the average of June 13. The peak migration date for chum in the Discovery Islands was on June 12, three days earlier than the average of June 15.

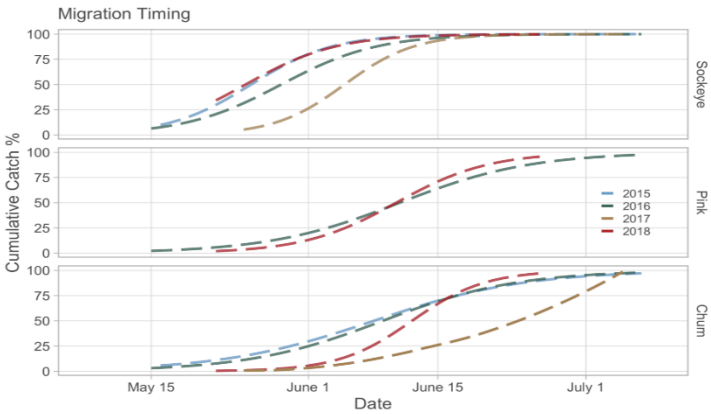

Fig. 3. Cumulative catch of sockeye, pink, and chum, in the Discovery Islands and Johnstone Strait between 2015 and 2017.

Table 1. Migration timing statistics for the cumulative catch of sockeye, pink, and chum salmon in the Discovery Islands in 2018, compared to the study-period average (2015–2018). Q1 is when 25 % of the species passed through the regions, peak date is the median when 50 % passed through, Q3 is 75%, and Spread is the difference between Peak Date and Q1. The region DI indicates the Discovery Islands and JS indicates Johnstone Strait.

Year	Region	Species	Q1	Peak Date	Q3	Spread
2015–2018	DI	Chum	June 06	June 15	June 23	8
2015–2018	DI	Pink	June 05	June 13	June 13	9
2015–2018	DI	Sockeye	May 26	May 28	June 04	2
2015–2018	JS	Chum	June 11	June 19	June 23	7
2015–2018	JS	Pink	June 16	June 23	June 23	6
2015–2018	JS	Sockeye	June 03	June 05	June 18	3
2015	DI	Chum	June 03	June 05	June 22	2
2015	DI	Sockeye	May 23	May 23	June 01	0
2015	JS	Chum	June 09	June 16	June 19	7
2015	JS	Sockeye	May 26	May 29	June 13	3
2016	DI	Chum	June 02	June 15	June 15	13
2016	DI	Pink	June 02	June 15	June 15	13
2016	DI	Sockeye	May 24	May 28	June 04	4
2016	JS	Chum	June 02	June 10	June 24	8
2016	JS	Pink	June 18	June 24	June 24	6
2016	JS	Sockeye	June 02	June 03	June 18	1
2017	DI	Chum	June 13	June 26	July 04	13
2017	DI	Sockeye	June 05	June 07	June 07	2
2017	JS	Chum	June 20	June 27	June 28	7
2017	JS	Sockeye	June 06	June 14	June 21	8
2018	DI	Chum	June 07	June 12	June 20	5
2018	DI	Pink	June 07	June 12	June 12	5
2018	DI	Sockeye	May 23	May 23	June 04	0
2018	JS	Chum	June 14	June 21	June 23	7
2018	JS	Pink	June 14	June 21	June 23	7
2018	JS	Sockeye	June 07	June 07	June 21	0

Sockeye catch intensity in 2018 was low relative to previous years and relative to pink and chum in 2018 (Fig. 4). Pink catch intensity in 2018 was the highest of the four years measured. Pink out-migrants are more abundant on even years, the result of the odd-year dominant life-cycle of Fraser River pinks (Heard 1991), but 2018 catches indicate either good production or good survival in the early marine environment for pink salmon relative to 2016—the only other odd-year dominant brood year recorded by the Juvenile Salmon Program.

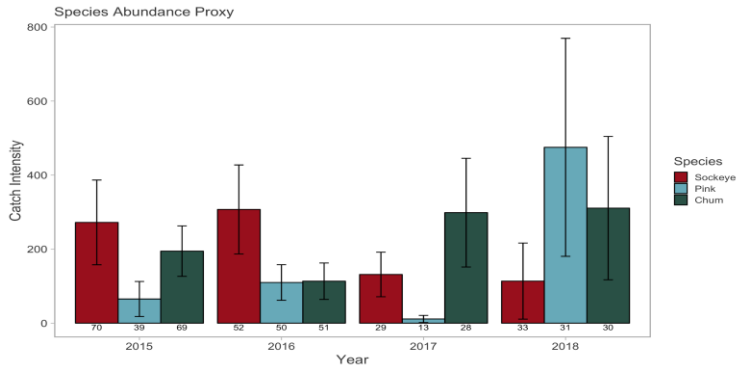

Fig. 4. The catch intensity (our proxy for total abundance) of sockeye, pink, and chum salmon in the Discovery Islands and Johnstone Strait. Numbers under each bar indicate the number of seines in which the species was caught, and error bars indicate the 95 percent confidence region.

Catch proportion was dominated by pink salmon in the Discovery Islands and Johnstone Strait in 2018 making up 51.5 % of the catch (Table 2) while chum made up 32.6 % and sockeye 13.1 % (Fig. 5). This was the first year in the study period in which pink dominated the catch proportion.

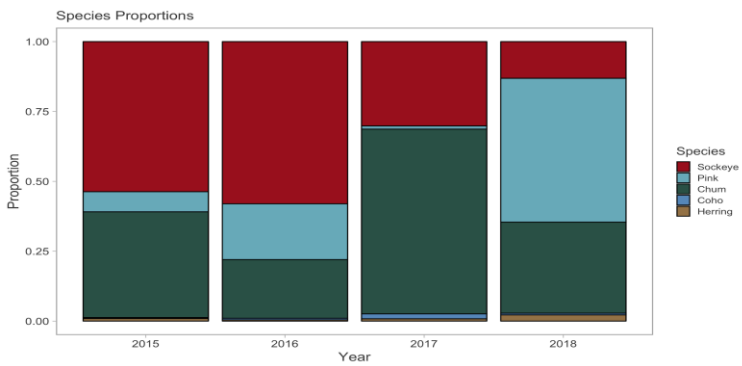

Fig. 5. The annual proportion of fish captured in the Discovery Islands and Johnstone Strait combined.

Table 2. The species proportions of total catch in each year for sockeye, pink, chum, herring, coho, and Chinook.

Year	Chum	Coho	Herring	Pink	Sockeye
2015	0.378	0.003	0.009	0.072	0.537
2016	0.210	0.006	0.005	0.200	0.580
2017	0.661	0.018	0.008	0.012	0.301
2018	0.326	0.006	0.022	0.515	0.131

In 2018, sockeye were longer, pink were shorter, and chum were shorter than their respective study-period averages in the Discovery Islands and Johnstone Strait combined (Fig. 6). Mean sockeye length was 117 mm (Table 3) which is 8 mm longer than the study-period average ($p < 0.0001$, 95% CI 5.5–11.2). Average pink lengths were 96 mm, which is 10 mm shorter than the study-period average ($p < 0.0001$, 95% CI 11.8–7.2). Chum were on average 104 mm, which is 8 mm shorter than the study-period average ($p < 0.0001$, 95% CI 9.9–5.8). Interestingly, sockeye length was, again, the opposite anomaly compared to pink and chum which tend to vary together (Fig. 2). The length frequencies observed here represent the range of fish sizes caught in the nearshore area at the specified times. There are currently no quantitative data available to weight these estimates relative to the proportion of fish that migrate in nearshore versus deep-water habitats, nor is there published data that tests whether population characteristics differ between nearshore and deep-water habitats. These data need to be produced before we can report population-level length frequency estimates.

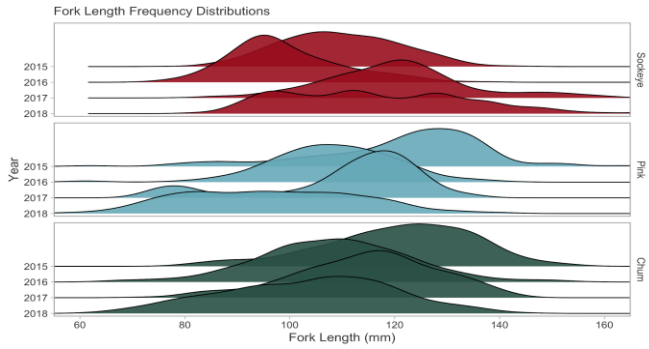

Fig. 6. Distributions of juvenile salmon fork lengths for each year in the Discovery Islands and Johnstone Strait. Note that these distributions contain multiple age classes.

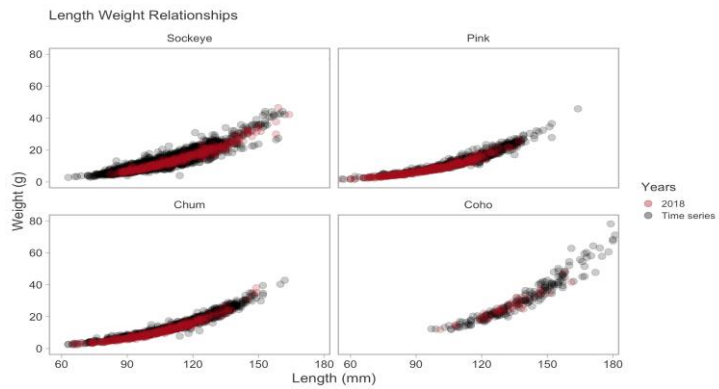

Fig. 7. Length and weight regressions for juvenile salmon caught in the Discovery Islands and Johnstone Strait in 2018 coloured red, compared to all other years in black.

Table 3. Mean fork lengths for each year, species, and region with the 95 % confidence interval (95% CI). DI stands for Discovery Islands, JS for Johnstone Strait. The column N indicates the number of fish measured.

Year	Region	Species	N	Fork Length	CI
2015	DI	Sockeye	455	108.9	1.0
2015	DI	Pink	47	109.6	5.5
2015	DI	Chum	121	115.5	2.8
2015	JS	Sockeye	334	110.7	1.2
2015	JS	Pink	98	127.1	2.2
2015	JS	Chum	112	126.4	2.0
2016	DI	Sockeye	516	97.6	0.9
2016	DI	Pink	96	103.9	2.6
2016	DI	Chum	124	103.3	2.6
2016	JS	Sockeye	316	101.5	1.1
2016	JS	Pink	94	112.6	1.9
2016	JS	Chum	104	115.0	2.1
2017	DI	Sockeye	260	121.3	2.0
2017	DI	Pink	17	90.9	8.6
2017	DI	Chum	111	106.2	2.4
2017	JS	Sockeye	220	119.4	1.4
2017	JS	Pink	51	117.1	1.9
2017	JS	Chum	151	120.7	1.6
2018	DI	Sockeye	84	116.2	3.6
2018	DI	Pink	205	87.8	1.8
2018	DI	Chum	190	97.4	2.3
2018	JS	Sockeye	85	117.6	4.4
2018	JS	Pink	110	112.4	1.8
2018	JS	Chum	110	114.2	1.8

Motile sea lice abundance in 2018 was among the lowest recorded in the Discovery study period while Johnstone Strait parasite loads were average (Fig. 8). Notably, no *Lepeophtheirus salmonis* were detected on sockeye in Johnstone Strait, despite being present in the Discovery Islands.

Ocean temperature in the top 30 m of the water column in May and June during the juvenile salmon out-migration at station QU39 in the northern Strait of Georgia was 0.28°C warmer on average than they were between 2015–2017 (Fig. 9; Table 1). In the context of the last four years, 2018 was the warmest 30 m depth-integrated temperature observed in the northern Strait of Georgia in May and June, despite 2015 SST along the B.C. coast breaking records for high temperatures (Chandler et al. 2017). In the past four years, temperatures were well above long-term averages which could make Fig. 9 misleading because if we included temperature data from before 2015 in this analysis, 2018 would appear warmer for more of the year.

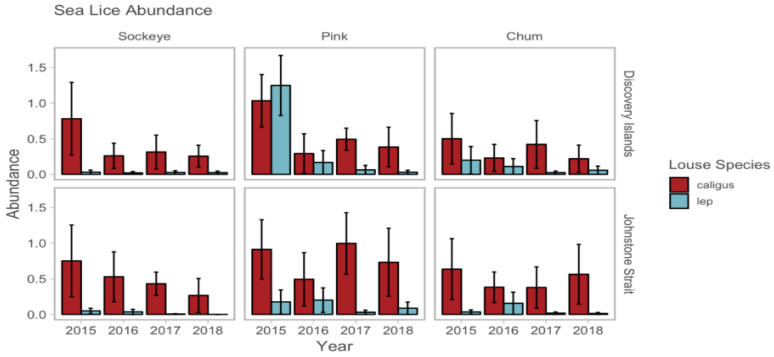

Fig. 8. *Lepeoptheirus salmonis* (lep), and *Caligus clemensi* (caligus) sea lice abundance on sockeye, pink, and chum salmon.

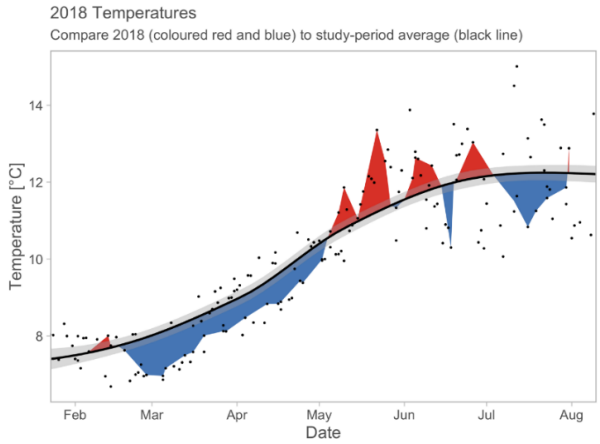

Fig. 9. Thirty-meter depth-integrated ocean temperatures at station QU39 in the northern Strait of Georgia is the solid black line which represents average temperatures from 2015–2017. Blue areas represent temperatures from 2018 that are below the 2015–2017 average and red areas represent above average temperatures. The shaded grey area is 1 SE of the loess regression. The black dots are the daily minimum and maximum temperatures observed over the study-period.

Discussion

A period of above-average sea-surface temperatures began in 2013 in British Columbia and the warmest sea-surface temperatures observed in British Columbia's time series occurred in 2015 and 2016 when temperatures were more than 1°C warmer than normal (Chandler et al. 2018). Temperatures at most stations in BC were still above average in 2017, but it was not as warm as the previous two years. In 2018, BC sea-surface temperatures were similar to those in 2017. In the northern Strait of Georgia, however, temperature anomalies at Departure Bay and Sentry Shoal were greatest in May and June during the peak salmon migration period (Chandler 2019). This is consistent with what we observed at station QU39 in the northern Strait of Georgia in 2018—the warmest sea-surface temperatures we've observed in our study period. Warmer conditions have been demonstrated to be associated with increased salmon growth rates, however, if anything fish were larger in 2017 when conditions were cooler. This points to factors in addition to temperature that drive growth.

In 2014, a DFO chartered purse seiner measured that 80% of sockeye passed through the Discovery Islands by June 19. This was considered 'normal' given previous estimates of run timing (Neville et al. 2016). We observed 80% of sockeye migrate through the Discovery Islands by June 1 in 2015 and 2018, and by June 5 in 2016, which is roughly two and a half weeks earlier than observed in 2014. Sockeye from 2014 and 2017 are from the same genetic-stock cyclic-dominance cohort, and sockeye in 2017 exhibited the latest migration timing of all four run cycles observed, suggesting that this run cycle tends to migrate later than the others. However, it may also be that some other factor, such as cooler sea surface temperature in 2014 and 2017, affected their migration timing. In 2017 Chum migrations were also later than average, and as a result, we did not completely capture the tail end of the migration. It could also be that a higher proportion of chum remained in the Strait of Georgia in 2017. Sockeye

leave the Strait of Georgia 12–20 days before pink and chum, which may be driven by water temperatures and foraging conditions (LeBrasseur and Parker 1964).

Sockeye migration timing through the Discovery Islands and Johnstone Strait is positively skewed (Johnson et al. 2018), meaning that the tail of the migration distribution is longer on the right and the peak abundance is on the left of the temporal distribution of sockeye abundance over time. The number of days between the 25th and 50th percentile of sockeye catch abundance is short, two days on average, indicating that their northern migration is punctuated (Table 1). Further effort should be directed at identifying the factors that govern this punctuated migration dynamic.

There are better foraging conditions for juvenile salmon found in Queen Charlotte Sound where upwelling nutrients contribute to higher productivity (McQueen and Ware 2006). Sea-surface temperatures in the northern Strait of Georgia in 2017 were the coldest year of those between 2015–2018, which we would expect to be favourable for juvenile salmon forage quality, however the timing of transition to upwelling in Queen Charlotte Strait was late and low in magnitude (Chandler et al. 2018). The degree to which Queen Charlotte Strait and Sound act as a refuge area for juvenile salmon to forage and recover after migrating through the prey-limited Discovery Islands and Johnstone Strait region requires further investigation. This will help us to further compartmentalize the regional conditions juvenile salmon experience in their early marine phase.

In 1983, two trawl surveys were conducted in Discovery Passage and the surrounding channels and found that pink and chum abundance peaked in late June (Levings and Kotyk 1983). We observed peak pink and chum migration timing to be June 14, up to a week earlier than observed in 1983. However, the direct comparison of these estimates and the interpretation of statistics in this report are subject to some unknown degree of bias as a result of gear selectivity, and potentially non-random distributions of fish lengths in the habitats sampled. This highlights the need for quantification of the fine-scale distribution and habitat use by juvenile salmon along a gradient of depth and distance from shore. This will better our understanding of the representativeness and comparability of common sampling methods used to describe juvenile salmon populations migrating through coastal channels.

The Hakai Institute Juvenile Salmon Program has now captured the entire four-year life cycle of Fraser River sockeye salmon, two years of odd-year dominant pink juveniles, and four years of chum migrations. However, we have only observed the early marine conditions experienced by a genetically distinct community of co-migrating salmon, four separate times. Each annual observation between 2015 and 2018 is a unique cohort of sockeye genetic stocks, and pink, chum, coho and herring proportions. Replicated observations of sockeye genetic cohorts will be possible beginning May 2019, when we observe the same sockeye genetic cohort, we observed in 2015.

Finally, it is important to acknowledge that anomalous atmospheric and ocean conditions have dominated the last four years, and our data collected since 2015 reflect that. Ongoing research will reveal the extent of the juvenile salmon response to conditions in the preceding years. Furthermore, as adult salmon return from the high seas, having experienced these anomalous conditions, we will gain a better understanding of what the overall impact to salmon productivity will be. As we continue to disentangle the web of local and global weather and climate interactions, we will be able to identify how those processes interact and drive the key factors influencing early marine survival of Pacific salmon.

Data

The data used for this analysis is available at https://doi.org/10.21966/99MG-0S52. Some of the models and methods used to produce our time-series statistics and visualizations for this program will undergo ongoing development as we seek to improve the accuracy of current estimates, incorporate historical observations from other organizations, and add new variables to our annual observations. The development of our annual observations data, code, and analyses can be observed and contributed to from our code and data repository at https://github.com/HakaiInstitute/jsp-time-series. An interactive data explorer tool for this developing time series can be accessed online at http://hecate.hakai.org/shiny/JSP/.

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What can We Learn About the Return Migration of Fraser River Sockeye Salmon from Catches in Alaska?

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Keywords: migration route, marine distribution, Fraser River sockeye

At large spatial scales, aggregating across populations, North American sockeye salmon populations have largely overlapped marine distributions in the North Pacific Ocean (e.g., Bristol Bay and British Columbia stocks, Quinn 2018), but we do not have a good understanding of the marine distribution of sockeye salmon at smaller scales. For example, we do not know how sockeye salmon from different British Columbian rivers are distributed in the North Pacific Ocean. Similarly, we do not know where genetically distinct stocks within a river are distributed in the ocean. Blackbourn (1987) hypothesized that different Fraser River sockeye stocks may reside in different areas in the North Pacific Ocean based on correlations of their run timings and sea surface temperatures in different North Pacific 'grids', but this remains conjectural and based on only circumstantial evidence. Understanding the marine distributions and migratory routes at more granular levels (e.g., stocks within rivers) is beneficial because conservation and fisheries management mostly occur at such scales. Also, it is of considerable scientific interest to understand mechanisms governing long-distance animal movement. Here, we focus on the marine distributions and migratory paths of Fraser River sockeye salmon stocks, whose fisheries management is governed by the Pacific Salmon Treaty between the United States and Canada.

In their return migration from the open ocean, adult Fraser sockeye are thought to take a northeastward route from marine feeding grounds, and then migrate southeast as they approach coastal waters toward southeast Alaska to the Fraser River (McKinnell et al. 2012). Historically, Fraser River stocks have a highly consistent sequence of arrival at the river mouth (Woodey 1987). The earliest stocks arrive at the river mouth in late June and the last stocks arrive at the river mouth in late August. This pattern is well established with historical data and any useful migration model must be consistent with the sequence of stock-specific return. Here, we evaluate how well empirical data match results predicted by two simple return migration models.

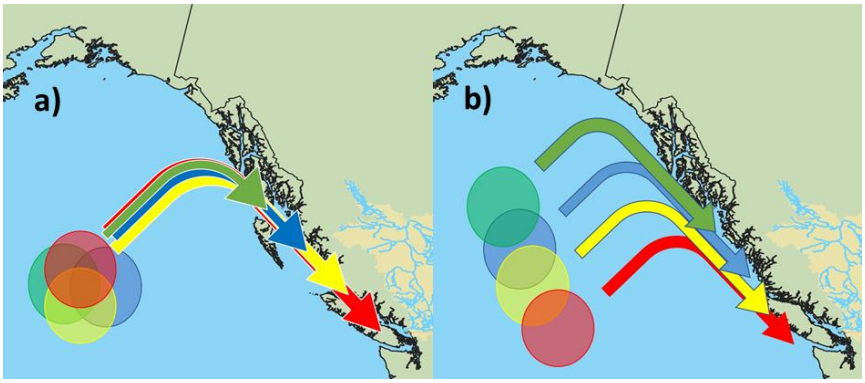

Fig. 1. Two migration models evaluated in this study: a) model 1-Fraser stocks with highly overlapped marine distributions and very similar migration routes (initiation date of the return migration differs among stocks and accounts for different arrival dates), b) model 2-Fraser stocks with more distinct marine distributions but similar migration trajectories (timing need not differ among stocks to account for different dates of arrival at the Fraser River).

The first model hypothesizes that different Fraser River stocks have similar or highly overlapping distributions in the North Pacific Ocean shortly before the start of their return migration (Fig. 1a). The returning adults swim at similar speeds along very similar migratory paths all the way to the Fraser River, but they start their migrations at different times, thereby accounting for their different arrival timing. Thus, different stocks would be sequentially available to various coastal fisheries during different weeks as they migrate toward the mouth of Fraser River. According to this model, there would be no difference in stock-specific availability to coastal fisheries at an annual scale because all stocks eventually migrate through the same areas. The second model hypothesizes that different Fraser stocks have less overlapped spatial distributions shortly before the start of their return migration but share a similar trajectory in returning to the river mouth (Fig. 1b). Because their initial distributions differ, the paths of their

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return migrations are also spatially offset. This accounts for their different return timing and results in some stocks having a higher latitude of landfall than others, resulting in differential stock-specific availability for coastal fisheries.

Fraser River sockeye salmon caught in fisheries in Southeast Alaska (henceforth "SEAK"), North of Vancouver Island (NVI) and South of Vancouver Island (SVI) were analyzed (Fig. 2). Genetic stock identification was used to identify the origin of fish caught in these fisheries and only fish identified as being from the Fraser River with a probability greater than 50% were further examined. Table 1 provides sample sizes of the Fraser River sockeye caught in the three fisheries from 2005–2017. The program CBayes (Neaves et al. 2005) was used to estimate probabilities of stock origin for each individual. At an annual scale, we compared the relative proportions of each stock detected at the three fishing locations. Although NVI and SVI catches spanned the whole migration season, SEAK catches were possibly missing very early timed stocks because of timing of the fishery. Therefore, we also compared the stock compositions of weekly catches among the three locations by employing a timing index. The purpose of this analysis was two-fold: 1) to determine if differences in the annual stock-specific results were driven by differences in fisheries timing; and 2) to evaluate if timing compositions of catches from equivalent dates differ among locations and if observed patterns are consistent with model expectations. The timing index integrated the historical run-timing data of each Fraser stock to calculate a weighted average timing value for the weekly catch, allowing comparison of the average timing of the catch for any given week among fisheries locations. The index has a relatively low value when the catch is composed of mostly early-arriving stocks and a relatively high value when the catch is composed of late-arriving stocks. We compared the rate of change of the timing index over weeks for the three locations using linear regression analyses.

Table 1. Sample sizes of Fraser River sockeye salmon (probability > 0.5) caught in Southeast Alaska (SEAK), North of Vancouver Island (NVI), and South of Vancouver Island (SVI).

Year	SEAK	NVI	SVI
2005	236	1662	1760
2006	25	3430	2947
2007	225	2321	3143
2009	52	2646	2759
2011	74	2792	2443
2012	127	1782	2814
2013	432	2210	2675
2014	352	3726	1666
2015	220	2072	1225
2016	135	1791	1572
2017	299	2792	2128
Total	2185	27224	25132

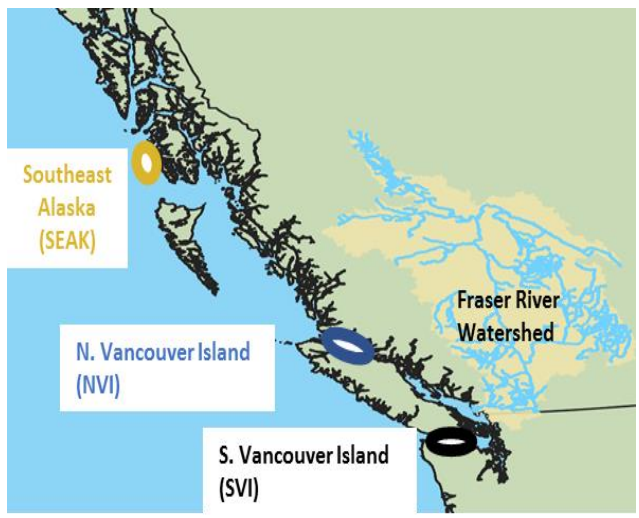

Fig. 2: Fraser sockeye sampling locations in this study (SEAK fishery locations are approximately 700 km northwest of NVI).

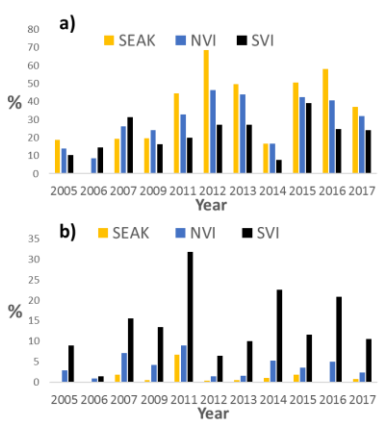

Fig. 3. Annual prevalence of Chilko and Harrison sockeye in catches from SEAK, NVI and SVI: a) Chilko sockeye, b) Harrison sockeye.

In most years, Chilko sockeye was the most abundant stock of Fraser sockeye salmon, and its annual proportions showed a north-south latitudinal trend among the three fisheries. The Chilko proportion was highest in SEAK catches, intermediate in NVI catches, and lowest in SVI catches (Fig. 3a). This trend was observed consistently since 2011. For the Harrison stock, which exhibits a sea-type life history where juveniles migrate to the oceans in their first year, the opposite latitudinal trend was observed. The proportion of Harrison was highest in SVI catches, intermediate in NVI catches, and lowest in SEAK catches (Fig. 3b). This trend was observed in all years with available data (2005–2007, 2009, 2011–2017).

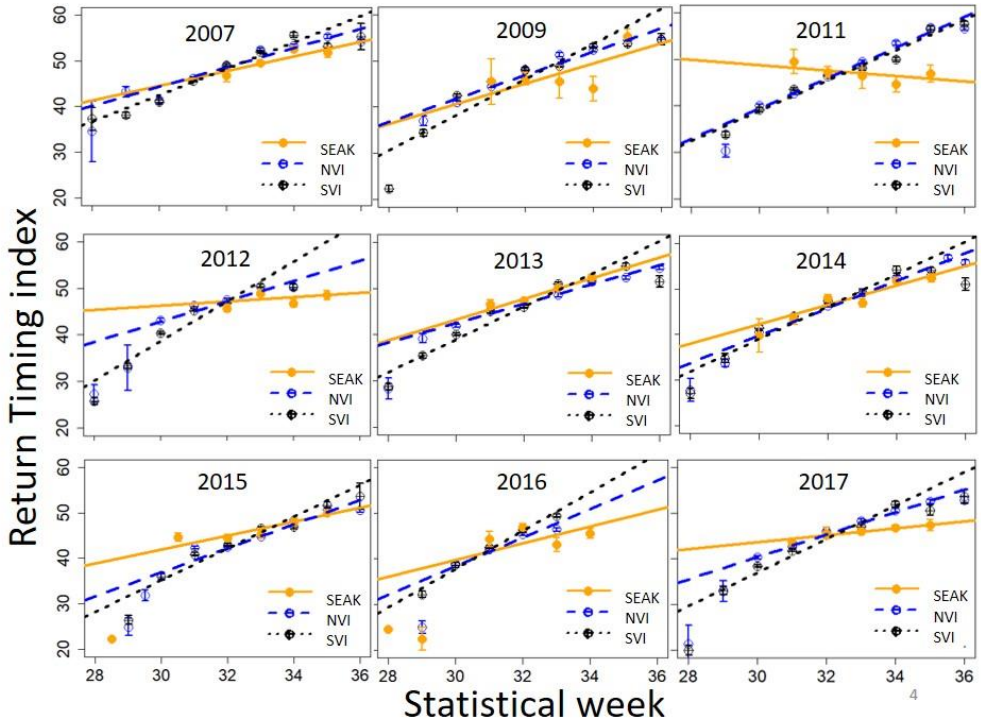

Fig. 4. Linear regression of the timing indices (weighted averages of stock-specific arrival timing) of weekly catches for SEAK, NVI, and SVI from 2007–2017.

The timing index analysis showed consistent trends among years, with the same relative positions and slopes from 2007–2017, with only 2011 being exceptional (Fig. 4). Typically, the slope of the timing index trend line was steepest for SVI, intermediate for NVI, and shallowest for SEAK. The y-intercept was lowest for SVI, intermediate for NVI, and highest for SEAK. Because of differences in slopes and intercepts, the timing index trend lines of the three locations typically intersected near or during statistical week 32, which is near the peak of the migration season with respect to timing near the mouth of the Fraser River.

Our results suggest that Fraser stocks differ in their availability to various coastal fisheries either due to differences among stocks in their marine distributions at the start of the return migration or because of the migration route itself. For example, Harrison stock proportions among the three areas indicate Harrison fish rear in a more southerly location of the North Pacific than Chilko sockeye, or that they take a more southerly route, or both. The annual stock proportion results seem more consistent with the second rather than the first migration model because the differences in stock proportions among the three fishery locations could be accounted for by initial offsets in latitude. However, observed trends at the annual level could result from differences in fisheries timing as well. Whereas annual samples from NVI and SVI span the whole sockeye migration season and are weighted toward abundance of Fraser stocks, SEAK fisheries target pink salmon and Fraser sockeye are bycatch (i.e., the distribution of catch across weeks may not reflect the abundance of Fraser sockeye). Examination of the timing index allowed us to account for this potential problem.

Both hypothesized migration models predict parallel timing index trend lines for the three locations. Furthermore, because we expected Fraser sockeye to migrate in a southeastward direction as they approach coastal

waters, we predicted the SEAK trend line to be highest (i.e., with the latest mean timing index for any given date) and SVI to be lowest. However, observed results were not consistent with these expectations. In all years (2007–2017), the three regression lines intersected, which clearly disproves the first migration model. These results are also not consistent with the second migration model because later in the sockeye salmon migration season, SEAK timing indices were lower than both NVI and SVI. Sockeye stocks migrating along similar trajectories to the Fraser River from even very different starting spatial distributions cannot produce such results while also faithfully reproducing the sequential arrival of stocks. Overall, our results suggest that the returning Fraser sockeye stocks have different starting spatial distributions and take different paths when returning to the Fraser River, requiring a more complex migration model to explain consistently observed trends.

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Inter-Annual, Stock-Specific Distribution and Migration of Juvenile Sockeye Salmon (*Oncorhynchus nerka*) from 1997–2017

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Keywords: sockeye, salmon, stocks, migration, distribution

Juvenile sockeye salmon have marine distributions and migration patterns that vary between stocks and may be influenced differently by changing ocean conditions and food supplies. Fisheries and Oceans Canada conducts juvenile salmon surveys to increase our understanding of Pacific salmon populations, migrations and distributions (Fig. 1). The focus of these surveys has expanded from abundance measures to include environmental conditions and Genetic Stock Identification (GSI, Beacham et al. 2014). Tissue was collected from juvenile sockeye salmon, *Oncorhynchus nerka*, from 6,179 surface tows from 1997–2017, primarily within coastal waters off British Columbia.

Fig. 1. Fisheries and Oceans Canada Juvenile Salmon Survey. Photo credit Jackie King.

Sampling was most intensive during the summer (2,158 tows) and fall (2,483 tows) seasons, and the majority of juvenile sockeye salmon (7,120 out of 9,266 individuals) were caught in the summer. Variation at 14 microsatellite loci was used to allocate juvenile sockeye salmon to their stock of origin. In order of abundance, allocated juvenile sockeye salmon were Chilko (12.4%), Harrison (11.8%), Great Central (8.1%), Sproat (5.5%), Lower Adams (5.0%), Okanagan (3.9%), Lower Shuswap (3.6%), Lake Washington (2.4%), Birkenhead (2.2%), Stellako (2.2%), as well as 148 less abundant stocks. Broad patterns of stock migration appear to remain stable through time. The highest catches per unit effort for juvenile Chilko sockeye salmon were measured in the summer along the East Coast of Vancouver Island from the Strait of Georgia to Queen Charlotte Strait (Fig. 2).

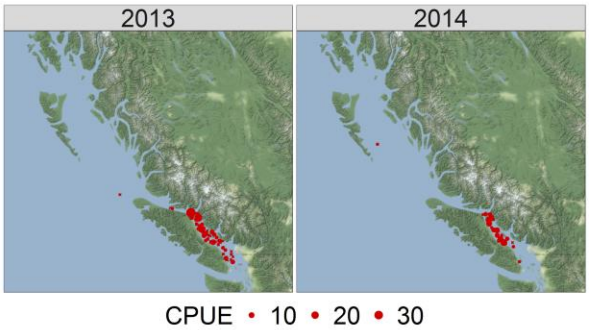

Fig. 2. Chilko Juvenile Sockeye Salmon Catch Per Unit Effort in Summer 2013 and 2014. Sampling locations varied between years, accounting for some of the variation.

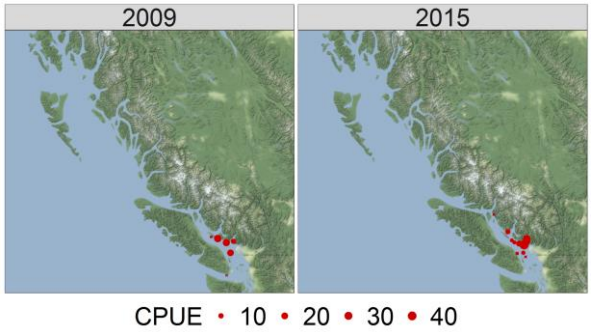

Fig. 3. Harrison River Juvenile Sockeye Salmon Catch Per Unit Effort in Fall 2009 and 2015.

Unlike many cyclic juvenile sockeye salmon stocks, Chilko stock was present in measurable catch numbers every year from 1997–2016. This makes the stock ideal for investigating the influence of changing ocean conditions. The sea-type or river-type stock, Harrison River, is found at high catch per unit effort in the Strait of

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Georgia and Juan de Fuca Strait in the summer and fall (Fig. 3). This supports research that Harrison juvenile sockeye salmon remain in coastal BC waters for longer than the larger, lake-type Fraser River stocks (Beamish et al. 2016) and this delay in migration may be related to attaining adequate body size for migration. Nevertheless, spatial analysis demonstrates northward migration of most stocks during the first marine season (Fig. 4). Relationship between catch per unit effort and sea surface temperature varies by stock within the same catch region. For example, there is both a positive correlation with sea surface temperature for Birkenhead in Queen Charlotte Sound, and a negative correlation for Lower Shuswap in Queen Charlotte Sound (Fig. 5). Similar stock-specific results were found in Fraser sockeye salmon forecasting (Xu et al. 2019). This diversity contributes to a portfolio effect that may dampen salmon population fluctuations (Schindler et al. 2010) and has implications in forecast models with climate change.

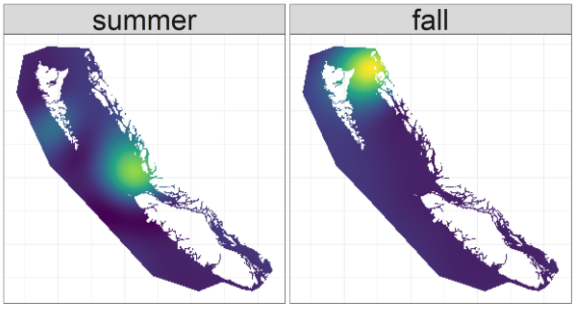

Fig. 4. Lower Shuswap juvenile Sockeye Salmon Distribution using ordinary Kriging of log CPUE in 2008.

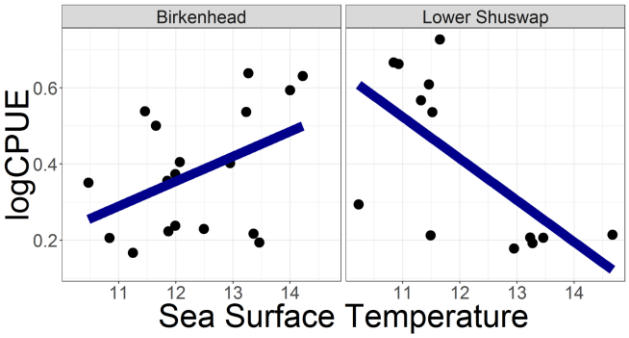

Fig. 5. Relationship between sea surface temperature (°C) and juvenile log catch per unit effort (logCPUE) of two sockeye salmon stocks in summer within Queen Charlotte Sound.

Acknowledgements—Thank you to the numerous people who have contributed to 77 surveys within this data set since 1997.

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Long-term Trends of Distribution and Regional Composition of Hatchery-released Juvenile Pink and Chum Salmon in the Sea of Okhotsk during the Fall of 2011–2017

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Keywords: juvenile pink and chum salmon, hatchery origin, distribution, the Sea of Okhotsk, trawl surveys, otolith mark

The Sea of Okhotsk is the most important feeding area for juvenile pink and chum salmon of Asian origin during the first summer and fall (Radchenko et al. 2018; Urawa et al. 2018). General long-term tendencies of distribution and migration of hatchery-released juvenile pink and chum salmon in the basin of the Sea of Okhotsk in the fall of 2011–2017 were figured out as a result of otolith mark analysis for fish samples caught by the trawl surveys of TINRO-Center (Fig. 1). Otolith samples were collected from 6,924 pink and 9,870 chum salmon (Table 1). Subsamples to examine otolith marks were made at every station of trawling, where the number of juvenile fish in the catch was appropriate to take 50 individuals or so for the subsampling. The North Pacific Anadromous Fish Commission (NPAFC) otolith mark release database (http://npafc.taglab.org/arkSummary.asp) was used for the identification of hatchery origins. The statistics of the hatchery releases of otolith-marked pink and chum salmon in Russian Far East and Japan was also cited from the official data by NPAFC.

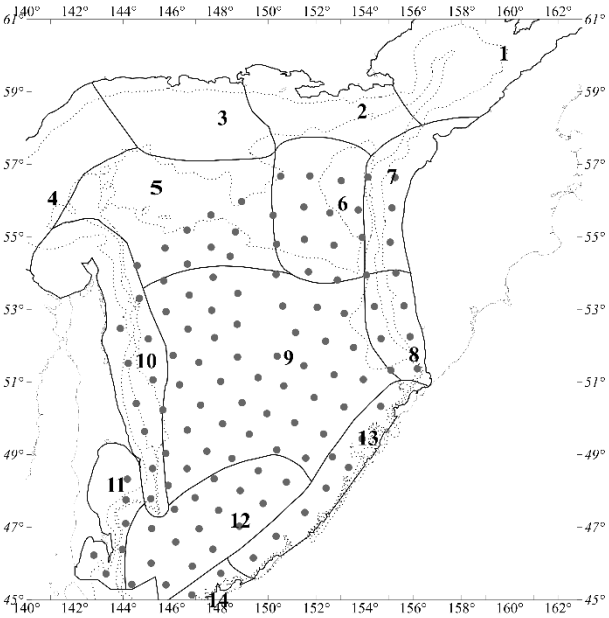

Fig. 1. The standard scheme of trawling stations in the fall complex pelagic surveys by TINRO-Center in the Sea of Okhotsk. *Legend:* the numbers and lines mark biocenotic districts of the research (Volvenko 2003).

Earlier studies suggested that stable tendencies in the dynamics of ocean currents in the Sea of Okhotsk induced the cyclic character of juvenile salmon migrations in the basin (Chistyakova and Bugaev 2013, 2016). Their suggestion mainly concerned pink and chum salmon from the southern coasts (Sakhalin, the Southern Kurile Islands, Hokkaido and Honshu). Considerable numbers of fish from this group migrated shifting in the north or northeast direction to the coast of West Kamchatka up to 55–57°N, followed by later cyclic migration in the southwest or south direction toward the South Kurile Islands. Detailed schemes of juvenile salmon migrations in the Sea of Okhotsk off West Kamchatka were also made by other fish biologists (Yerokhin 2002; Varnavskaya 2006).

Our long-term data confirmed the cyclic fall migrations of juvenile pink and chum salmon in the Sea of Okhotsk (Fig. 2 and 3). At the same time the regional intraspecific composition of hatchery fish in the trawl catches was relatively stable at the level of interannual variations (Table 1). Both hatchery and wild fish might be engaged in the same migration process, because the distribution of marked fish coincided with the spatial structure of the

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total trawl catches by species. The detailed scheme of the distribution of juvenile salmon is consistent with the interannual variations of the migration intensity at the level of even or odd years.

Table. 1. Actual occurrence of regional origins of otolith-marked juvenile pink and chum salmon caught by the trawl surveys of the TINRO-Center in the Sea of Okhotsk during the fall of 2011–2017.

Species	Years of survey	Total number of samples	Regional origins of otolith-marked fish							
			Kuril Islands	Sakhalin	Southwest continental coast	Northern continental coast	Western Kamchatka	Hokkaido	Honshu	Total
Pink	2011	730	21	9						30
	2012	894	10	4				3		17
	2013	800	9	8		1		2		20
	2014	1,000	9	4				2		15
	2015	750		8		4		3		15
	2016	600		11		1		3		15
	2017	2,150		23		9		13		45
	Total	6,924	49	67	0	15	0	26	0	157
Chum	2011	857	2	7		3		26	4	42
	2012	2,370	15	24		1	4	140	29	213
	2013	800	1	5			1	15		22
	2014	1,960	8	7		1		42	3	61
	2015	1,073	2	14	4			22	2	44
	2016	1,160		22	2	2	3	20	1	50
	2017	1,650		26	1	6	1	40	3	77
	Total	9,870	28	105	7	13	9	305	42	509

Pink and chum salmon released from hatcheries in the south part of the Sea of Okhotsk (Sakhalin, the Southern Kuril Islands, Hokkaido and Honshu) might migrate north- and northeast-ward up to 55–57°N and to the coastal waters of the southwestern Kamchatka. Later juvenile fish migrated back in the south and southwest direction, reaching the south Kuril straits connecting to the North Pacific Ocean.

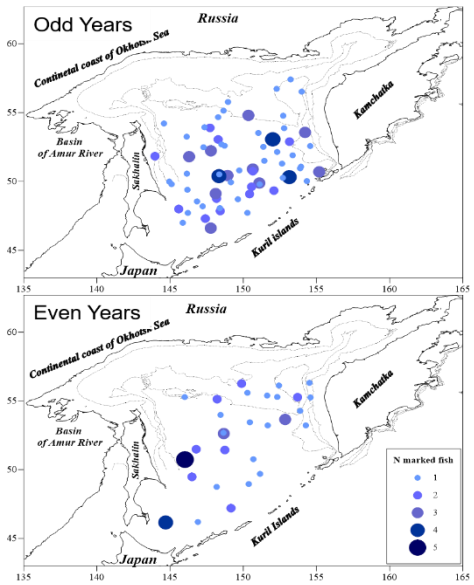

Fig. 2. Distribution of otolith-marked juvenile pink salmon in the Sea of Okhotsk during the fall of odd years (2011–2017) and even years (2012–2016).

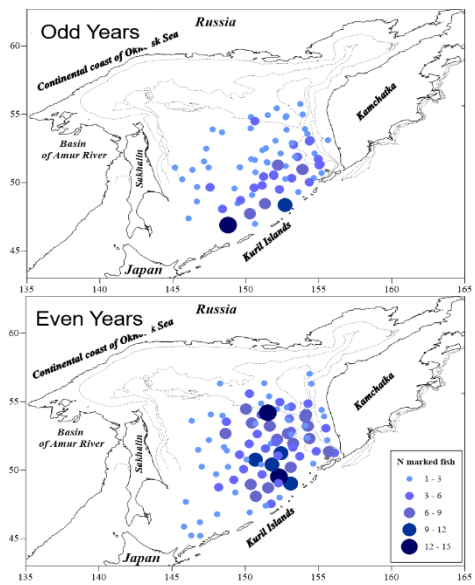

Fig. 3. Distribution of otolith-marked juvenile chum salmon in the Sea of Okhotsk during the fall of odd years (2011–2017) and even years (2012–2016).

The density of hatchery pink salmon was higher in the central and eastern parts of the Sea of Okhotsk in odd years, and in the western and southern parts in even years (Fig. 2). The distribution of hatchery pink salmon strongly depends on production indices of major regional groups of hatchery stocks in Sakhalin and southern Kuril Islands. However, more researches are required for the tendency of pink salmon distribution, because the observation period examined in current work included the period when the dominant brood line of pink salmon shifted.

Most catches of hatchery chum salmon in the Sea of Okhotsk consisted of Japan and Sakhalin origins (Table). Otolith mark survey confirmed that juvenile chum salmon from all regional populations in Japan migrate into the Sea of Okhotsk (Chistyakova and Bugaev 2013), although their migration route is different by regional populations (Urawa et al. 2018). Spatial distribution of hatchery chum salmon may be affected by the abundance of pink salmon. In even years when West Kamchatkan juvenile pink salmon was not abundant, the density of hatchery juvenile chum salmon was higher in the central and eastern part of the Sea of Okhotsk (Fig. 3).

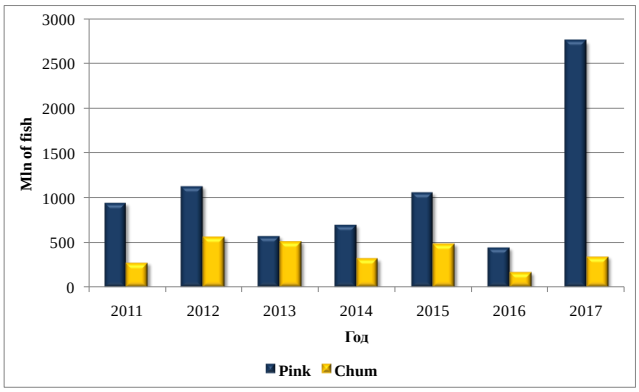

Fig. 4. Relative abundance (in million) of juvenile pink and chum salmon in the Sea of Okhotsk estimated by TINRO-Center trawl surveys in the fall of 2011–2017.

Relative abundance of hatchery and wild juvenile chum salmon in the Sea of Okhotsk was evaluated based on the data for the dynamics of the total abundance of juvenile fish (Fig. 4), the ratio of otolith-marked fish in the catches, and the ratio of marked fish in hatchery-released fish, suggesting that wild fish were dominant in most years (Urawa et al. 2018). In addition, there was an attempt to evaluate the efficiency of hatchery systems in Russian Far East and Japan (Shevlyakov and Chistyakova 2017). However, the available data were not enough to evaluate the hatchery efficiency, because of insufficient number of otolith-mark releases from hatcheries in both countries. Therefore, future research in this field requires large-scale otolith-mark releases in Russia and Japan.

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Timing of Spawning of Wild Chum Salmon in a Non-enhanced River and their Seaward Migration in Northern Honshu, Japan

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Keywords: Chum salmon fry, Wild fish, Natural spawning, Seaward migration

Chum salmon (*Oncorhynchus keta*) have a wide geographic distribution around the northern Pacific Rim, with northern Honshu Island, Japan being located at the southernmost limit of their distribution (Salo 1991). Information on the ecology of wild chum salmon is needed for their sustainable management in Japan, as it enables the development and application of effective conservation measures (Miyakoshi et al. 2012; Nagata et al. 2012). Wild fish in this paper are considered to be fish that have reproduced naturally for more than one generation, regardless of parental origin (hatchery fish or wild fish) (Morita and Ohkuma 2015). We investigated the timing of spawning of wild chum salmon in a non-enhanced river and their seaward migration in the northern Honshu, Japan.

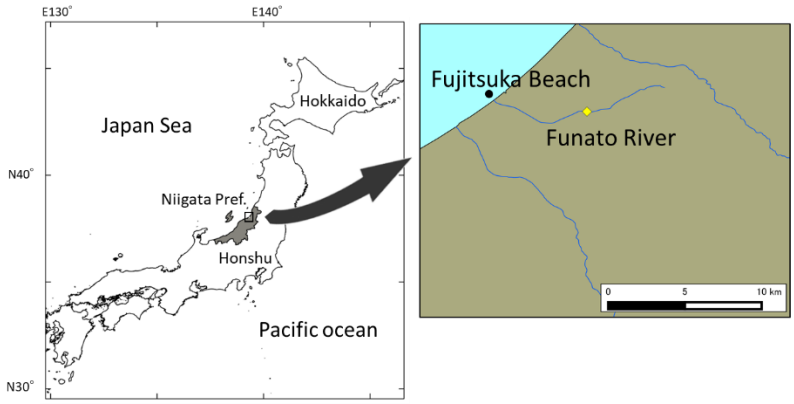

Fig. 1. Map showing the study area where chum salmon fry were collected in the surf zone of Fujitsuka Beach, and the study site where the spawning redds of chum salmon were observed in the Funato River, Japan.

The survey area was 1050 m and was established in Funato River where hatchery chum salmon fry had never been stocked (Fig. 1). Spawning redds were counted visually once every ten days from early October to early January in 2015–2018. The river temperature was recorded using a temperature logger. Chum salmon fry were collected from February to June at 0.4–0.8 m depth by using a small seine net (2 m wide, 1 m deep mouth, 4.5 m long, with wing nets 1 m long and a central bag with a 1 mm mesh), in Fujitsuka Beach close to the mouth of Funato River (Fig. 1). Sea surface water temperature (SST) and salinity (SSS) were measured on each sampling date. A generalized linear model (GLM) with a binominal distribution was performed to evaluate the influence of SST and SSS on the presence–absence of the chum salmon fry.

Spawning redds were observed mainly from the middle of October to the middle of December. Chum salmon fry were collected mainly from early March to early May when SST and SSS ranged from 7.4ºC to 17.5°C and 3.9ºC to 32.7ºC, respectively. Most samples were under 40 mm in fork length (38.0 ± 3.7 mm, n = 2038). The period that chum salmon fry were present mostly matched the timing of the emergence of the wild fry, which was estimated by the cumulative water temperature of Funato River. The GLM showed that the probability of chum salmon fry occurrence decreased with increasing SST and SSS. The model also predicted that the probability was 30.2%–62.5% even when the SSS ranged from 10 to 30, and the SST was 15°C (upper thermal limits for chum salmon juveniles in Hokkaido; Irie 1990). Stocking of hatchery chum salmon fry ends by late March every year in northern Honshu, Japan.

The results suggest that the seaward migration of wild chum salmon fry at Fujitsuka Beach (southern limits of the distribution) repeats about two months after the end of the stocking, and they are adapted to a warmer environment than fry in northern areas, such as Hokkaido.

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Genetic Characterization of Juvenile Chum Salmon (*Oncorhynchus keta*) Migrating out of the Yukon River Delta

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Keywords: juvenile chum salmon, Yukon River, genetic stock composition, seasonal runs

To identify critical life history stages for salmon survival, it may be informative to compare adult returns with abundances at various life-history stages. The transitional period from freshwater to saltwater is speculated to be a major source of mortality for salmon and information about early life stages may help reduce uncertainty around survival estimates and future run-size predictions. Past genetic studies demonstrated that relative abundances of Yukon summer-run and fall-run juvenile chum salmon (*Oncorhynchus keta*) caught on the eastern Bering Sea shelf during late summer/early fall are correlated with adult returns for their respective year classes (Kondzela et al. 2016). We are interested in testing whether earlier life history stages are also correlated with adult returns. Our study provides insights into the relative proportions of summer-run and fall-run juvenile chum salmon that out-migrate from the Yukon River during the spring/summer period.

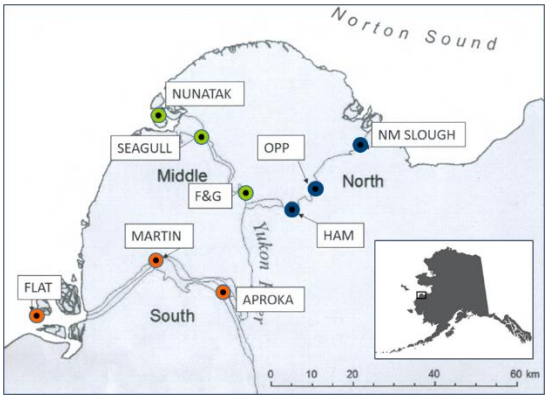

Fig. 1. Sampling sites of juvenile chum salmon in the Yukon River delta during spring/summer of 2016. Three sites were sampled from each main channel (North, Middle, South). Sampling did not occur at every site every day, but each site was sampled three times per week.

Juvenile chum salmon were caught with a surface trawl towed at nine field sites, three from each main channel in the Yukon River delta during the out-migration between 18 May 2016 and 27 July 2016 (Fig. 1). Approximately 5,000 fish were collected for genetic analysis during the majority of out-migration (18 May–1 July) and stored at the Auke Bay Laboratories at -80°C. Chum salmon collections were subsampled to maintain adequate sample sizes while minimizing laboratory costs. After sorting by sample location, trawl, and date, every third fish collected was systematically subsampled. DNA was extracted from muscle tissue into 96-well plates using a QIAcube and the Qiagen DNeasy Blood & Tissue Kit, as described by the manufacturer (Qiagen, Inc.) and stored at -20°C. A total of 1,783 samples were genotyped at 13 microsatellite loci: *Oki2* (Smith et al. 1998), *Oki100* (Beacham et al. 2009a), *Omm1070* (Rexroad et al. 2001), *Omy1011* (Spies et al. 2005), *One101*, *One102*, *One104*, *One111*, *One114* (Olsen et al. 2000), *Ots103* (Beacham et al. 1998), *Ots3* (Greig and Banks 1999), *Otsg68* (Williamson et al. 2002), and *Ssa419* (Cairney et al. 2000). After the microsatellite loci were amplified with the polymerase chain reaction and then analyzed on the Applied Biosystems 3730*xl* DNA Analyzer, genotypes were identified with GeneMapper® 5.0 software (Life Technologies, Inc.). Summer-run and fall-run composition estimates were made with the BAYES program (Pella and Masuda 2001) by comparing the genotypes to a 31-population, Yukon River subset of the coastwide chum salmon microsatellite baseline (Beacham et al. 2009b, c). We tested the following null hypotheses that the relative proportions of fall-run to summer-run juvenile chum salmon are the same for 1) each of three time periods: Early (18–31 May), Late (1–15 June), and Extra Late (16 June–1 July); 2) the three river channels at the mouth: South, Middle, and North; and 3) small (29–41 mm) and large fish (42–66 mm).

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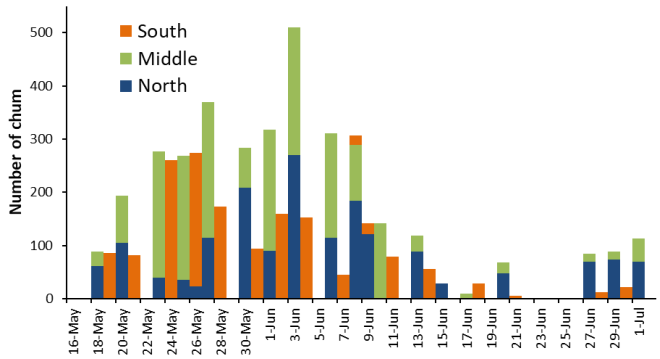

Fig. 2. Number of juvenile chum salmon collected at three main channels (North, Middle, South) in the Yukon River delta during spring/summer of 2016.

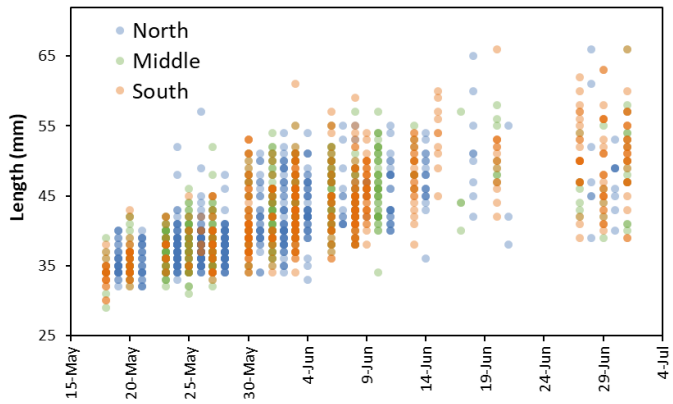

Fig. 3. Length (mm) of juvenile chum salmon collected at three main channels (North, Middle, South) in the Yukon River delta during spring/summer of 2016.

Most of the out-migration occurred between 18 May–21 June (Fig. 2) and over this time period there was a general increase in fish length (Fig. 3). A later, small pulse from 27 June–1 July was comprised of fish of more variable lengths. About three-quarters of the 2016 juvenile chum salmon were from summer-run populations and one-quarter from fall-run populations (Fig. 4). At finer spatial and temporal scales, differences were observed in the seasonal run proportions. Higher proportions of fall-run fish were present in the latter part of the out-migration and in the southern channel of the river. Seasonal proportions also differed by fish length. Although the majority of small and large fish, separated by median size, were from the summer-run, the proportion of fall-run was nearly four times higher for large fish than small fish. Future analyses will compare the seasonal run proportions of out-migrating juveniles with those of juveniles collected on the eastern Bering Sea shelf during the 2016 summer/fall surveys, as well as the returning adults to the Yukon River.

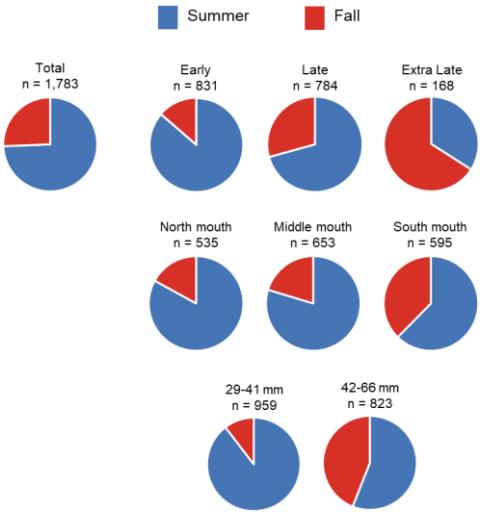

Fig. 4. Summer and fall run composition of juvenile chum salmon collected in the Yukon River delta during spring/summer of 2016. Seasonal run compositions of total samples, by three time periods (Early, Late, Extra late), by three main channels (North, Middle, South), and by fish length (29–41 mm and 42–66 mm).

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Morphological and Genetic Subdivision of Sockeye Salmon Samples, *Oncorhynchus nerka*, Collected within the Period of Spawning Migration in Outfalls of Kamchatka Rivers

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Keywords: sockeye salmon, *Oncorhynchus nerka*, mixed samples, morphological characteristics, genetic heterogeneity, SNP, clusterization and classification of samples

Sockeye salmon are characterized by extremely complex population structure: populations reproducing in different river watersheds (metapopulations) are subdivided into seasonal races, ecotypes, and subpopulations of isolated spawning grounds. Because of the genetic and morphological differentiation of the intraspecific forms, samples collected in the downstream reach of a river are normally heterogeneous. This includes both mixed samples from an estuary and samples collected during sockeye salmon spawning run in lower river flow. The objective of the paper was to analyze subdivision of sockeye salmon samples from the low course of East and West Kamchatka rivers, where (in tributaries and lakes) the most commercially important Asian stocks are reproduced.

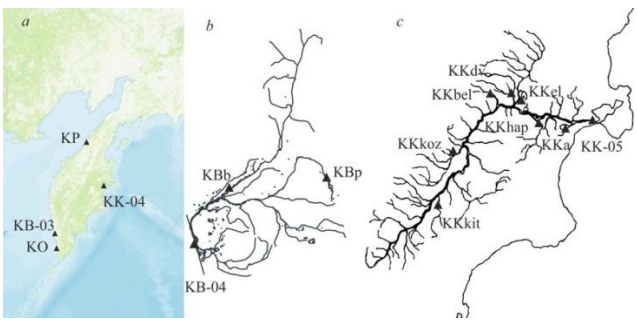

Fig. 1. Sampling location map: a—Kamchatka Peninsula, our data; b—Bol'shaya River drainage (Khrustaleva et al. 2014); c—Kamchatka River drainage (Khrustaleva et al. 2015; Habicht et al. 2010). Samples: KP—Palana River, KB-03—Bol'shaya River, 2003, KO—Ozernaya River, KK-04—Kamchatka River, 2004, KB-04—Bol'shaya River, 2004, KBp—Plotnikova River, KBb—Bystraya River, KK-05 − Kamchatka River, 2005 (early race), KKa—Azabachye Lake (early race), KKhap—Khapitsa River, KKbel—Belaya River, KKdv—Dvuyurtochnaya River, KKel—Elovka River, KKkoz—Kozyrevka River, KKkit—Kitilgina River.

Table 1. Characteristics of sockeye salmon samples from East and West Kamchatka

Place of catch (mixed sample ID)	Sample ID	*n* of biologically (genetically) analyzed samples	Dates of catch	Sample description	Proportion of females, %
Palana R., lower course (KP)	1_Early	93(30)	10 July 2003 11 July 2003 12 July 2003	Mass run	51
	2_Middle	62(44)	17 July 2003 18 July 2003		61
	3_Late	46(20)	20 July 2003 21 July 2003		54
Bolshaya R., lower course (KB)	1_Early	16(16)	23 July 2003	Beginning of the summer sockeye salmon run	47
	2_Middle	53(50)	29 July 2003	Summer sockeye salmon, main run	42
	3_Late	54(35)	30 July 2003		57
Ozernaya R., mouth (KO)	1_Early	50 (45)	04 August 2003	Main run	68
	2_Middle	49 (21)	05 August 2003		53
	3_Late	50 (24)	07 August 2003		80
Kamchatka R., lower course (KK-04)	First runners	0 (20)	29 June 2004 30 June 2004	Summer sockeye salmon, mass run	–
	1_Early	49 (28)	01 July 2004 02 July 2004		51
	2_Middle	71 (33)	05 July 2004 06 July 2004 07 July 2004		55
	3_Late	20(20)	09 July 2004		47

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Samples for the analysis were collected during mass spawning run of sockeye salmon in the lower courses of West (in 2003) and East (in 2004) Kamchatka Rivers (Table 1, Fig. 1a), as well as juveniles (underyearlings) and spawners were caught in Bol'shaya River drainage in 2004 (Khrustaleva et al. 2014) (Fig. 1b), and early race spawners were collected in the outfall of Kamchatka River in 2005 and in Azabachye Lake in 2004 (Khrustaleva et al. 2015). Moreover, Dr. Chris Habicht (Habicht et al. 2010) open data on allele frequencies of the same loci in samples from tributaries of the middle and upper reaches of the Kamchatka River were analyzed (Fig. 1c). Polymorphism of 45 previously described SNP loci (Smith et al. 2005; Elfstrom et al. 2006; Habicht et al. 2010) were investigated. The SNP genotyping was performed using TaqMan PCR at the School of Aquatic and Fishery Sciences (University of Washington) (Seeb et al. 2009). Statistical analysis included both standard approaches and clustering of the samples in the STRUCTURE 2.3.4. (Pritchard et al. 2000).

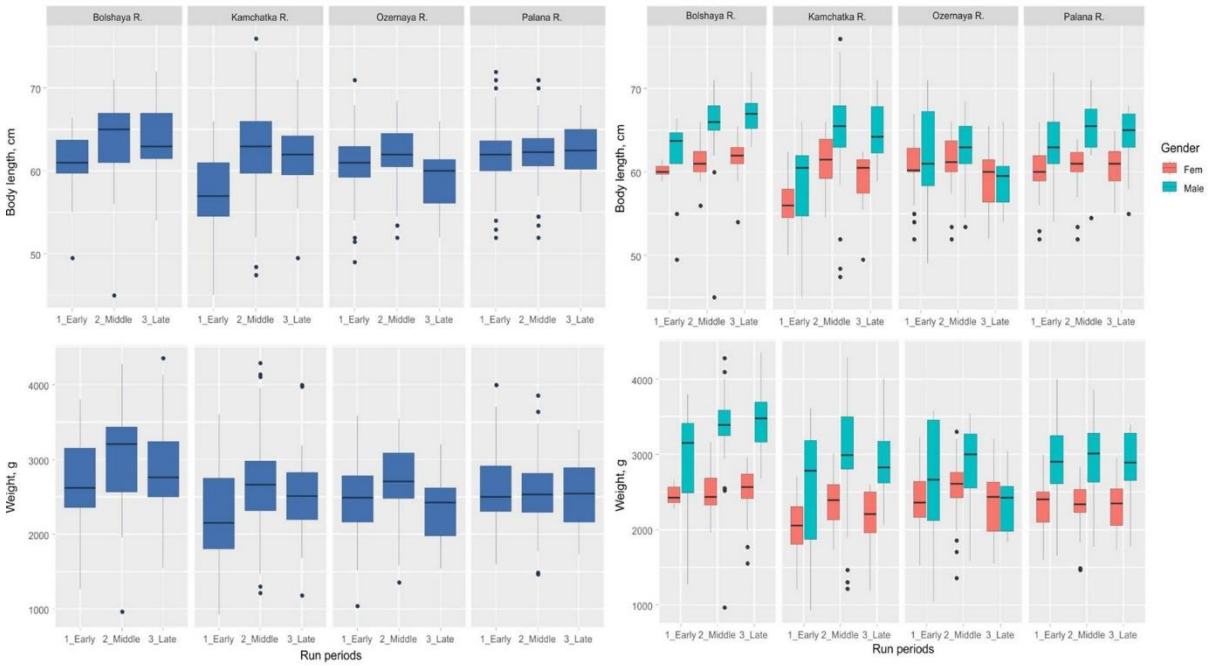

Fig 2. Boxplots of body length (*SL*) and weight (without internal organs) estimates of sockeye salmon from rivers of western and eastern Kamchtka by the periods of mass run.

Morphological and genetic heterogeneities of sockeye salmon samples collected in different periods of its spawning run as well as in mixed samples from the outfalls of West and East Kamchatka rivers were studied.

The size-mass characteristics of sockeye salmon in western Kamchatka rivers did not differ significantly (Mann-Whitney *U*-test) between the periods of the mass movement, with a number of exceptions (Fig. 2). Sockeye salmon from the 1_Early party of Bolshaya River were noticeably smaller, than caught during the mass run (29 and 30 July), but significant differences were revealed only for length estimates ($p = 0.03$). In Ozernaya River fishes from 1_Ealy and 2_Middle groups were larger, than those caught two days later (3_Late). Comparison of the first two samples revealed significant differences in gonad mass ($p = 0.022$), probably due to different ratios of males and females in the catch. The individuals from 1_Erly group were significantly larger than those caught on August 7 (3_Late), differences were found in all the biological characteristics studied ($p < 0.001$). A cause of the revealed differences is the different sex ratio in the samples, since the males of the Western Kamchatka sockeye are significantly larger than the females (Bugayev 1995): in the 2_Middle sample, the proportion of males was much higher than in 3_Late (Table 1). Fish from the first and third samples did not differ at any of the considered traits.

On the contrary for Kamchatka River the size-mass characteristics of adult fish caught on July 1−2 (1_Ealy), were significantly lower ($p < 0.05$) than in samples of later terms. The latter groups (2_Middle and 3_Late) did not differ among themselves either in length or in mass.

There wasn't any periodicity in estimates of allele frequencies of 45 SNP loci during mass spawning migration of sockeye salmon in the rivers of west coast of Kamchatka ($p > 0.05$, exact *G* test).

The heterogeneity of allelic frequencies of 34 polymorphic SNP loci was revealed by the periods of the mass run of sockeye salmon in the mouth of the Kamchatka River (exact *G* test): the samples of the first (First runners and

1_Ealy) and the second (2_Middle and 3_Late) half of the mass run differed significantly ($p < 0.01$). However, these differences were mainly due to the variability of only two loci (*One_RF-295* and *One_MHC2_251v2*). The identified genetic and morphological heterogeneity of the samples may be explained by a successive approach to the river mouth of spawning groups, reproduced in different parts of the river basin.

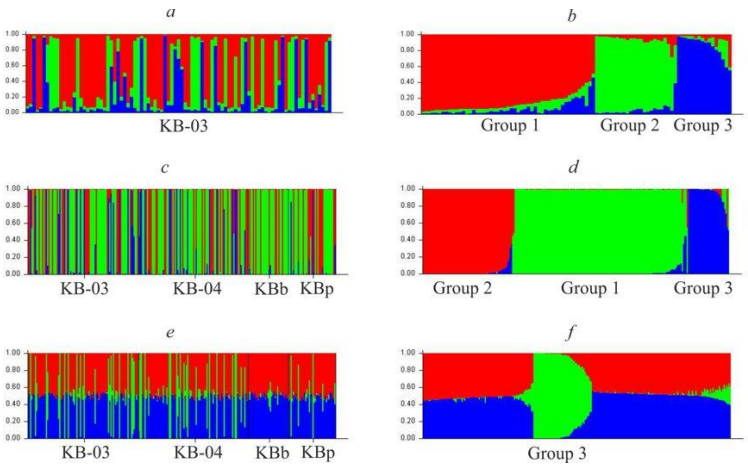

Fig. 3. Classification of mixed samples of sockeye salmon from Bol'shaya River drainage based on the algorithm of the STRUCTURE 2.3.4 (K = 3): a, b, e—individuals sorted by dates and places of catch; b, d, e—individuals are ranked according to the probability of assigning them to the groups; e, f—classification performed excluding mitochondrial loci.

Allele frequencies of polymorphic loci in pooled samples from estuaries of West Kamchatka were analyzed in STRUCTURE in order to identify relatively genetically homogeneous groups of individuals in mixed samples. For instance, Bolshaya River sample can be divided into three groups (Fig. 3a). These groups are also identified when all the samples from the Bolshaya River watershed are included (Fig. 3b). Analysis of the distribution of allelic frequencies of 36 polymorphic SNP loci in these groups showed that the first two groups differed only in the frequencies of the combined mitochondrial locus *One_CytB_CO1* haplotypes, while the third group differed from the first two at most of the loci (Fig. 3c).

In the Bolshaya River basin late sockeye salmon (summer race) is represented by two ecological forms (ecotypes): the lake type (mainly populations of Nachikinskoe Lake, located in the upstream of the Plotnikova River) and the river type, reproduced in large tributaries: Bystraya River, Plotnikova River, Karymchina River, Bannaya River and others (Bugaev et al. 2002a; Zaporozhets et al. 2013). Analyzing the results obtained, it can be assumed that group 3 is mainly represented by lake fish, apparently from the Nachikinskoe Lake. In favor of this assumption the fact argued that in the basin of Bystraya River individuals belonging to this group were absent, and among the juveniles of the upper reach of Plotnikova River met sporadically. Moreover group 3 was relatively small and mainly represented by age class 2.3.

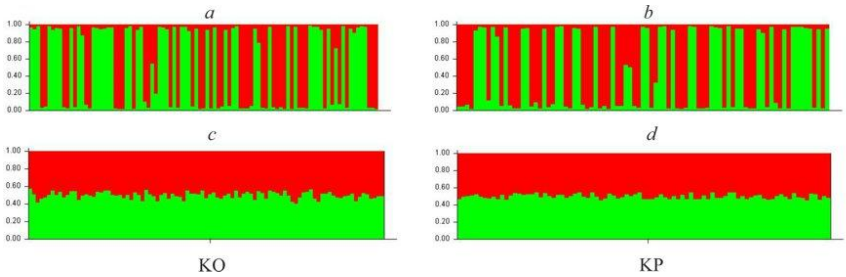

Fig. 4. Classification of mixed samples of sockeye salmon from Ozernaya River (a, c) and Palana River (b, d) drainages based on the algorithm of the STRUCTURE 2.3.4 (K = 2); c, d—classification performed excluding mitochondrial loci.

In the mixed samples from Ozernaya River and Palana River there wasn't any phenotypic or genetic heterogeneity (Fig. 4). In both rivers reproduction of sockeye salmon is concentrated in a watershed of one large lake, therefore the habitat conditions of the populations are more uniform, and the isolation between them is predominantly sympatric. In addition, the sockeye salmon of both lakes are mainly represented by one seasonal race: in Palana River—99%, and in Ozernaya River—98% of all sockeye falls on the late form (Bugaev and Dubynin 2002; Bugaev et al. 2002).

According to the results of the analysis in STRUCTURE in the mixed sample from the mouth of Kamchatka River in 2004, two groups of individuals were distinguished—group 1 and more numerous group 2 (Fig. 5). Moreover, in the beginning of the run group 2 was predominant, whereas in the second half of the run the individuals assigned to group 1 were encountered much frequently (Fig. 5a). The groups are significantly differentiated by most loci (20 of 34), with greatest contributions of *One_MHC2_251v2* and *One_GPH-414*.

Analysis of the phenotypic traits in both groups showed that group 2 was represented mainly by small and younger individuals, whereas in group 1 fish were, on average, older and larger. In addition, the proportion of individuals spent in fresh water for two years was significantly higher in group 1.

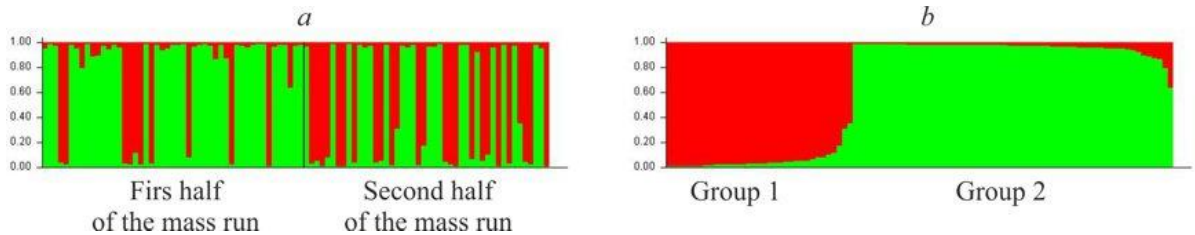

Fig. 5. Classification of a mixed sample of sockeye salmon from the Kamchatka River drainage, 2004, based on the algorithm of the STRUCTURE 2.3.4 (K = 2): a—individuals sorted by dates of catch; b—individuals are ranked according to the probability of assigning them to the groups

We assumed that these groups belong to different subpopulations of summer sockeye salmon in Kamchatka River watershed (Bugaev 2011). Group 1 can be attributed to the grouping E, reproduced in the middle and lower reaches of the river, some of them enter the Azabachye Lake and stay there for several months. Group 2 can be classified as grouping B, which occupies upstream tributaries. Juveniles of the grouping spend winter on spawning grounds and migrate downstream at the age of 1+ (Bugaev 2011). Our findings are supported by the results of multidimensional scaling (MDS) using a matrix of Euclidean distances calculated by the allelic frequencies of SNP loci in sockeye samples from different parts of Kamchatka River (Fig. 6). According to the first coordinate, three groups of populations can be distinguished in the diagram: a grouping of tributaries of the middle course, which also included group 1 and a sample of early sockeye from the outfall in 2005; salmon from upper tributaries, represented by one sample from Kitilgina River and forming a shared cluster with group 2; and a set of samples from the tributaries of the lower reach and from the Kozyrevka River. We can hypothesize that the most numerous in the watershed sockeye salmon of Azabachye Lake can also be sporadically represented in both groups. Most likely, it migrates a bit later, and our samples did not cover it.

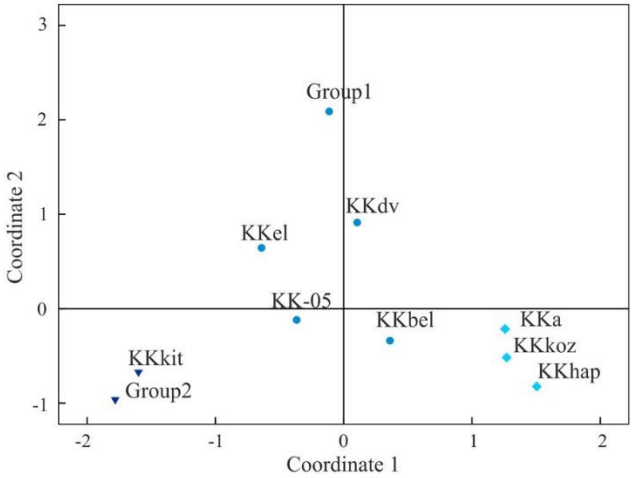

Fig. 6. Multidimensional scaling diagram (MDS), plotted on Euclidean distances, for samples of sockeye salmon from the Kamchatka River drainage.

Differences between the samples collected during mass spawning run in the main course of Kamchatka River indicate a successive character of migration of different spawning groups reproducing in distinct parts of the watershed: at the beginning of the run, individuals reproducing in the spawning grounds of the middle reach of the river predominate, then the upstream groups migrate and, probably, some days later Azabachye Lake fish comes.

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Trace Elements Content in the Pink Salmon (*Oncorhynchus gorbuscha* Walbaum, 1792) from Sakhalin-Kuril Region

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Keywords: Pacific salmon, pink salmon, Sakhalin-Kuril region, trace elements, impact zone

The Sakhalin-Kuril region (SKR) is one of the main areas of catch of Pacific salmon in the Far East of Russia. The leading fishing facilities are pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*). In 2016, the catch of these species in the SKR amounted to 105.4 thousand metric tons (74 thousand metric tons of pink salmon and 31.4 thousand metric tons of chum salmon), which was almost one quarter of the production of these salmon in the Far East of Russia. The total capacity of fish-breeding enterprises at the end of 2015 amounted to 956.5 million salmon fry (Report 2016). Most of the plants in the SKR are located in the southern part of Sakhalin and in the Central part of the Iturup Island, on the coast of the Sea of Okhotsk.

In autumn, the Okhotsk pink salmon offspring begin to migrate into the ocean to the Polar front zone. Salmon feed in the spring in the area near Kuril Islands, then head to spawn in native rivers (Shuntov 2001; Temnykh 2004).

The Kuril-Kamchatka region is characterized by the impacts of geochemical conditions that are created by upwelling, underwater and surface volcanism, which carry biogenic and other elements from the depths of the Kuril-Kamchatka trench. The Kuril Island region supplies the surrounding Pacific Ocean waters with a high content of chemicals due to volcanic and seismic activities. Pacific salmon which swim out for the winter and migrate to spawn, encounter these chemicals. This inevitably leaves its "trace" in the microelement composition of fish organs and tissues, which regulates the levels of elements, particularly toxic ones, that are caught in the fishery hydrobionts (Kovekovdova 2011; Kovekovdova et al. 2013; Khristoforova et al. 2014; Khristoforova et al. 2015a; Khristoforova et al. 2015b; Khristoforova et al. 2016; Khristoforova et al. 2018). However, there is limited information about how micronutrient content in active swimmers varies during their extensive migrations, such as Pacific salmon during feeding, wintering and spawning when they pass through geochemically impacted zones.

The purpose of this work is to determine the concentrations of trace elements in the pink salmon tissuesreturning to the river Reidovaya (Iturup Island) and the river Firsovka (the southern part of the Eastern Sakhalin).

Material and methods

Essential (Zinc and Copper) and non-essential (Nickel, Cadmium, Lead, Arsenic, Mercury) elements were quantified. All of them can be tracers of natural biogeochemical provinces. This was repeatedly noted earlier in the study of the content of heavy metals Fe, Mn, Zn, Cu, Cd, Pb, Ni, Cr in marine benthic organisms from the shallow waters of the Kuril Islands and organisms-fouling navigation buoys (Kavun and Khristoforova 1991; Malinovskaya and Khristoforova 1997; Kavun et al. 2002).

Our study focused on mature pink salmon individuals (*O. gorbuscha* Walbaum, 1792) that spawned in the Reidovaya river and Firsovka in early October 2016 from the fish farms "Reidovy" and "Firsovka" (Fig. 1). The producers were kept in cages at the hatcheries until they sexually matured, at which point three females and three males were selected. All elements except Hg were determined from an acid mineralization according to GOST 26929-94 on an atomic absorption spectrophotometer Shimadzu AA 6800. Data on the mass concentration of Hg was obtained by the method of stripping voltammetry at the analyzer "Tom'analit" (TA-4) (Khristoforova et al. 2015b). The results are presented in $\mu g \cdot g^{-1}$ of crude mass (Table. 1). For comparison, our data on the concentrations of elements in pink salmon caught in the ocean waters near the Kuril Islands in July 2013, as well as data on the

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ranges of their contents in pink salmon from the Sea of Japan are presented (Kovekovdova 2011). The mean value, standard deviation, and validity of the differences compared (using the Mann–Whitney U-test) were calculated in SPSS Statistics 21 for Mac OS X.

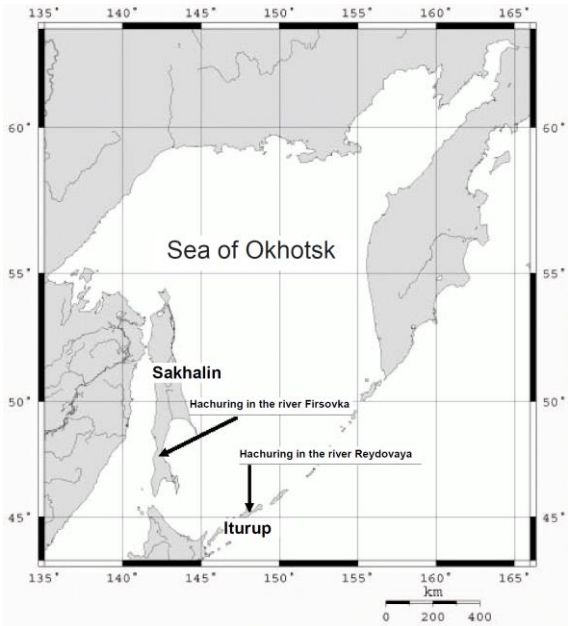

Fig. 1. Location map of the "Firsovka" and "Raidovy" hatcheries in the Sakhalin-Kuril region.

Table 1. Trace elements in organs and tissues of pink salmon of the Sakhalin-Kuril region and comparison areas, $\mu g \cdot g^{-1}$ of crude mass ($m \pm \sigma$).

Organs and tissues	Zn	Cu	Ni	Cd	Pb	As	Hg
Sakhalin island. Hatchery "Firsovka", 06.10.2016, the weight range of fish 780–2100 g							
Muscles	1.74±0.061	0.20±0.040	0.09±0.008	0.08±0.009	0.59±0.050	0.90±0.074	0.03±0.009
Liver	2.86±0.065	0.28±0.012	0.13±0.006	0.19±0.018	0.92±0.035	1.12±0.096	0.09±0.009
Gonads of males	2.76±0.021	0.26±0.014	0.11±0.006		0.87±0.014		0.07±0.003
				0.12±0.012		1.09±0.035	
eggs	2.51±0.058	0.25±0.016	0.12±0.007	0.11±0.019	0.82±0.043	0.98±0.049	0.07±0.004
Iturup Island. Hatchery "Reidovy". 09.10. 2016, the weight range of fish 1278–2362 g							
Muscles	1.96±0.075	0.24±0.076	0.12±0.007	0.14±0.012	0.67±0.050	0.94±0.064	0.04±0.005
Liver	3.14±0.069	0.32±0.034	0.18±0.009	0.21±0.018	0.96±0.035	1.25±0.098	0.12±0.009
Gonads of males	3.09±0.045	0.33±0.071	0.18±0.009	0.19±0.034	0.89±0.014	1.14±0.085	0.11±0.008
eggs	3.01±0.078	0.29±0.036	0.15±0.008	0.18±0.035	0.84±0.045	1.13±0.086	0.09±0.006
Ocean waters near the Kuril Islands, July 2013, fish mass range 1168–1458 g (by: Khristoforova et al., 2015)							
Muscles	1.29±0.079	0.108±0.012	**Not detect.**	0.037±0.005	0.503±0.059	0.930±0.093	0.030±0.009
Liver	2.97±0.089	0.165±0.008		0.152±0.015	0.902±0.108	1.118±0.089	0.120±0.021
Gonads of males	2.43±0.029	0.090±0.010		0.017±0.006	0.297±0.029	0.310±0.017	0.053±0.006
eggs	2.35±0.076	0.087±0.006		0.023±0.006	0.327±0.025	0.337±0.060	0.070±0.010
Sea of Japan, range of trace elements found in 1992, 2001, 2008 (by: Kovekovdova, 2011)							
Muscles	0.57–3.25	0.032–0.087		0.005–0.012	0.012–0.013	0.300–1.370	0.007–0.015
Liver	3.00–4.35	0.119–0.165		0.080–0.145	0.020–0.025	0.450–0.800	0.010–0.025
eggs	2.90–3.90	0.037–0.090		0.001–0.003	0.007–0.020	0.100–0.320	0.003–0.005

Note. Maximum Permissible Concentration (MPC) of toxic elements ($mcg \cdot g^{-1}$ of raw mass) in seafood in Russia: Pb—1.0, As—5.0, Cd—0.2, Hg—0.2 (SanPiN ..., 2002); in Canada: Hg—0.5; in the USA: Cd—3, Pb—1.5, As—86.

Results

Mercury (Hg) had the lowest concentrations of all the trace elements. Salmon from Firsovka had Hg concentrations of 0.03 ± 0.009 $\mu g \cdot g^{-1}$ in their muscles, and the gonads (male and female) had Hg concentrations of

0.07 ± 0.003 and 0.07 ± 0.004 μg·g^{-1} in males and females, respectively. In Reidovaya salmon, Hg concentrations in muscles were 0.04 ± 0.005 μg·g^{-1}, while the gonads of males and females had Hg concentrations of 0.11 ± 0.008 and 0.09 ± 0.006 μg·g^{-1}, respectively. Ni and Cd are characterized by minor amounts in the gonads of pink salmon but are found in larger amounts than Hg. Ni was 1.2–1.5 times higher than Cd in the muscles, however in the muscles and gonads of fish from the hatchery "Firsovka," Cd distribution was almost identical to Ni. In pink salmon from the hatchery "Reidovy," there were greater concentrations of Cd than Ni, typically 0.14 ± 0.012 in the muscle and 0.19 ± 0.034 and 0.18 ± 0.035 μg·g^{-1} in the male and female gonads, respectively. Cu was found to be twice the concentration of Ni in the muscles and gonads of salmon, with subsequent increasing concentrations of Pb, As and Zn. The levels of Pb in the fish organs and tissues were as follows: muscle varied from 0.59 ± 0.050 to 0.67 ± 0.050 μg·g^{-1}, male gonads ranged from 0.014 to 0.89 ± 0.014 μg·g^{-1}, and the calf of females was between 0.82 ± 0.043 and 0.84 ± 0.045 μg·g^{-1}. It is important to note that the concentrations of toxic elements in the studied pink salmon individuals did not exceed the maximum Russian permissible concentration in foods (PC) and were below the standards adopted in Canada and the United States. Despite the mercury concentrations in Iturup salmon being five times lower in the muscle and two times below PC in the calf, concentrations of Pb in male and female pink salmon gonads from the island are approaching Russian sanitary standards. Levels of Pb in pink salmon muscle were 1.5 and 1.7 times lower than PC in fish from Iturup and Sakhalin, respectively. Cd concentration is also close to PC and almost reaches its value in the gonads of fish from "Reidovy." In the gonads of salmon from "Firsovka" and in the fish muscle of fish from both plants, the concentrations of this toxic element were approximately half the acceptable PC. Only concentrations of As were significantly below PC where even the gonads did not exceed ¼ of the permissible concentration. Thus, the concentration of Pb and Cd in the pink salmon of the Sakhalin-Kuril region are close to the sanitary standard. The concentrations of these elements in the fish fillet are well below the amount allowed by sanitary standards and do not cause any concerns for consumers (Sanitary rules. 2002).

Discussion

According to the level of pink salmon stock in the Sakhalin-Kuril region, the three most important areas are the Iturup Island, the Southeastern coast of Sakhalin and the Aniva Bay. In catches on the East coast of Sakhalin and the Southern Kuril Islands, the late (autumn) form of pink salmon dominates (Kaev 2007).

In a previous study, the trace element composition of pink salmon caught in July 2013 in the Kuril Islands waters of the Pacific Ocean during its anadromous migration to the rivers of the Sea of Okhotsk were described (Khristoforova et al. 2015b). However, the present work studied pink salmon in October 2016 as they moved from the ocean into their native river, which would be their second time crossing the very rich waters of the Kuril-Kamchatka Region.

The difference between the trace elements found in the muscle and liver of salmon from the ocean waters near the islands did not exceed twice the amount found in fish from the Firsovka River. Sakhalin fish had much more variation in the levels detected in their tissues, which were 3–7 times higher than the fish from other areas (Table 1). Pink salmon from the Sea of Japan had the lowest concentrations of elements, which were significantly lower than in the fish of the Sakhalin-Kuril region. The greatest differences were found for Pb, whose concentration in muscles, liver and eggs of SKR fish was approximately 50 (49–56), 40 (42–44) and 60 (63–65) times higher, respectively, than in pink salmon from the Sea of Japan.

The exception to these findings was Zn, where greater concentrations were detected in the organs and tissues of pink salmon from the the Sea of Japan compared to fish in the SKR, which is a consequence of the anthropogenic influence on the Sea of Japan.

During winter, the fish that reproduce in the rivers of the Sakhalin-Kuril basin feed in the Sea of Japan and in the North-West Pacific Ocean. From the feeding area in the Sea of Japan, pink salmon migrate to spawn in the rivers of Northern Primorye, Western Sakhalin, the Amur basin, as well as Eastern Sakhalin, the southern Kuril Islands and the rivers flowing into the Aniva Bay. However, they mainly reproduce in the rivers of the first three regions. Fishing is based on the late oceanic group, which are selected based on the study of salmon.

Therefore, as the Asian pink salmon leave the nursery and return to spawn, not all of them will pass through the impact zone on the Kuril Island, or specifically pass by it on the seaside (the Sea of Japan) (Khristoforova et al. 2015b).

Pacific salmon (specifically Sakhalin-Kuril pinks) often feed in a high-altitude area (145 to 165°E and South to 40°N) where there is an abundance of zooplankton (Birman 1974). These zooplankton, which have absorbed copious amounts of phytoplankton growing on biogenic and other elements supplied by volcanism and upwelling in this area, transmit the microelements in their biomass to organisms of the next trophic level, including Pacific salmon.

The pink salmon that spawned in October migrated through the rivers of Reidovaya and Firsovka, which means that they were feeding in the North-Western Pacific Ocean and passed through the impacted geochemical zone twice. The transfer of trace elements through trophic levels explains why these salmon had significantly higher concentrations of all trace elements (except Zn) compared to the Japanese pink salmon.

Immature pink salmon that were caught in the ocean waters near Kuril Islands in July 2013 had to swim from the Sea of Okhotsk to the Southeast zone of the subarctic front from the southern and central parts of the Kuril Ridge (Shuntov and Temnykh 2011). These fish were captured on the outskirts of the geochemical impact zone and can not have accumulated the same levels of microelements compared to mature fish that came to spawn in the rivers Reidovaya and Firsovka.

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Migration and Homing Behavior of Chum Salmon Tagged in the Okhotsk Sea, Eastern Hokkaido

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Keywords: migration, archival tag, chum salmon, tagging, water temperature

Chum salmon (*Oncorhynchus keta*) are one of the most important species for commercial fisheries in Hokkaido in northern Japan. The Okhotsk coast in eastern Hokkaido is the principal area of salmon production in Japan. Commercial catches of chum salmon have been supported by intensive hatchery programs (Miyakoshi et al. 2013). In Hokkaido, returning chum salmon are fished in coastal waters mainly via set nets that are operated from September to December. Recently, coastal sea water temperatures in autumn have been higher than the historic mean. In years with high coastal sea water temperatures (> 20°C), it has been frequently observed that the peak timing of chum salmon landing was delayed and exploitation rates by coastal set net fisheries were low. In addition, high water temperatures might affect the distribution of chum salmon in coastal areas and the number of fish caught by each set net. In order to determine the effects of sea water temperature on commercial landings, the responses of migrating chum salmon to sea water temperature needs to be elucidated.

To understand migration routes, depths, and temperatures experienced by returning chum salmon in the Okhotsk Sea, we caught chum salmon in the coastal waters, applied archival tags to them, and released them in late August or early September from 2016 to 2018. We report the outcomes of the tagging experiment for chum salmon in the Okhotsk Sea.

From 5 to 7 September 2016, 28 to 30 August 2017 and 28 to 31 August 2018, tagging experiments for chum salmon were conducted in the Okhotsk Sea from the research vessel *Hokuyo maru* (237 tonnes, Wakkanai Fisheries Research Institute, Hokkaido Research Organization). At a total of 8 or 9 sites in each year, we visually counted the number of chum salmon and fished for chum salmon at night (Fig. 1). At each site, fishing lights were used, and chum salmon that appeared were fished with a lure with raw bait (a slice of squid or Pacific saury) on the hook. The captured chum salmon were anesthetized, tagged with an archival tag on the base of the dorsal fin, and measured for fork length and weight. After recovery from anesthesia, the tagged fish were released into the sea. At the fishing sites, the vertical distributions of the sea water temperature and salinity were measured using CTD (Seabird SBE9plus, Sea-Bird Electronics, Inc., Bellevue, WA, USA).

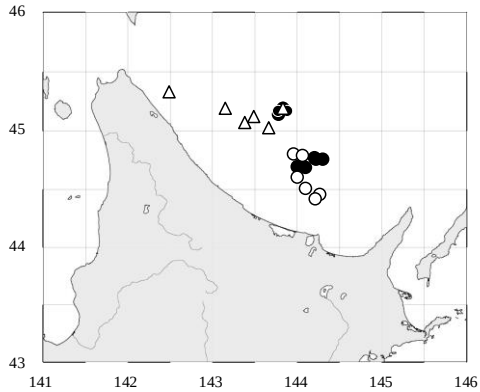

Fig. 1. Map of the sites where the fishing for chum salmon was conducted in the Okhotsk Sea in 2016 (○), 2017 (●), and 2018 (△).

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After release, recaptured tagged fish in Japan were reported by the fishermen's cooperative associations when they were caught in commercial fisheries or by the Kitami Region Salmon Enhancement Program Association. Tagged fish were also recaptured by the weirs that are installed in the rivers for broodstock collection and recaptures by anglers in Russia were reported through researchers in Russia and Japan.

In the years 2016, 2017, and 2018, there were a total of 14, 14 and 10 chum salmon tagged and released from the research vessel, respectively. Many chum salmon were counted and caught at sites west of the Kitami-Yamato Bank (approximately 80 km north of Cape Notoro) in 2016 and 2017, and at sites northwest of the Kitami-Yamato Bank (approximately 90 km northeast of Cape Hinode) in 2017 and 2018. At the sites where many chum salmon were counted or caught, the sea water temperatures were 15–18°C at the surface layer, 5–15°C at a depth of 15 m, and < 2°C at depths > 50 m.

Of the tagged chum salmon that were released, there were a total of six, two and one fish that were recaptured in 2016, 2017, and 2018, respectively. Many tagged fish were recaptured at the Okhotsk coast, Hokkaido, except the fish that was tagged in 2018, which was recaptured in the southwestern region of Sakhalin Island, Russia. In 2018, the recaptured fish was released on 29 August at site approximately 100 km southeast of Cape Soya. The tagged fish was recaptured on 18 September. In our study, the migration from the Sea of Okhotsk in Hokkaido through the Soya Strait was confirmed for the first time.

Some of the tagged fish migrated diurnally between the surface layer and a depth of 200 m. During daylight hours the tagged fish preferred sea water temperatures of 1°C at a depth of 200 m. In 2018, the tagged fish which were recaptured in the southwestern region of Sakhalin Island swam a depth of 150 m with a sea water temperature of 3°C without rising to the sea surface for four days. This may be a behaviour that allows the fish to regulate their cavity temperature (Azumaya and Ishida 2005). Our study suggests that sea water temperatures are affecting salmon behavior in the coastal areas.

In the Okhotsk Sea off the coast of the Shiretoko Peninsula and Abashiri region, biotelemetry studies were conducted on chum salmon in the 1980s (Soeda et al. 1985; 1987; Shimamura et al. 1987; Yoza et al. 1985). In their papers, many findings on migratory behavior of chum salmon were reported. We observed many migratory behaviors of chum salmon in our study that were similar to the findings of previous studies. However, our study also showed a new migration route and a migratory behavior. Because the sea water temperatures around Hokkaido in autumn have been higher in recent years, the monitoring of chum salmon behavior relative to the climate changes is important.

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A Model of Smolt-to-adult Survival in Terms of Salmon Growth through the Size Distribution of Predators

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Keywords: growth, size, size-selection, survival, prey, salmon, gape-limited predators, apex predators

As a general rule, survival of juvenile salmon to adult spawners is thought to be determined by growth during the first year in the marine environment through size-selective removal of the smaller fish by predation and overwinter starvation (Beamish and Mahnken 2001). Numerous studies support this hypothesis (e.g., Beamish et al. 2004; Moss et al. 2005). However, other populations do not fit the "bigger is better" rule (Claiborne et al. 2014; Miller et al. 2013), nor does the estimated magnitude of size selection mortality account for the observed mortality (Beacham et al. 2018). Additionally, studies indicate significant ocean mortality on adult salmon (Seitz et al. 2019). However, studies on individually tagged salmon clearly indicate that large smolts have higher adult survival (Passolt and Anderson 2013). This paper explores a possible basis for the conflicting studies through a model that describes mortality of fish growing through a range of predator gape sizes.

The model is based on the assumption that predators only eat prey smaller than their gape size, so predation decreases as prey grow (Anderson 2019). The resulting smolt-to-adult ratio (SAR), characterizing ocean survival as a function of ocean entry size class *i*, is

$$SAR_i = \exp\left(-H + \frac{s}{A\Phi(m/s)} \cdot \frac{x_i\Phi(-x_i) - \varphi(x_i)}{f(x_i, \bar{x}, m/s, C)}\right) \tag{1}$$

where x is the fish size normalized to the predator gape distribution as $x_i = (l_i - m)/s$ with l_i the ocean entrance length of fish in size class i, m is the mean predator gape size and s is its standard deviation. The model assumes the distribution of gape-limited predator sizes can be represented as a normal distribution such that the normalized prey distribution can be represented by standard normal cumulative and density functions, Φ and φ. The ratio of the growth rate to the predator encounter rate is $A = \bar{g}/\lambda$ where $\bar{g}$ is the mean cohort growth rate and λ is the predator encounter rate. The contribution of apex predators is $H = \mu_H \cdot t_H$ where μ_H is the mortality rate and t_H is the exposure duration. The growth rate of size-class i relative to the mean cohort growth rate is described by the empirical function

$$f(x_i, \bar{x}, m/s, C) = \frac{g_i}{\bar{g}} = 2\left(1 - 1\Big/\left(1 + \exp\left(C\left(1 - \frac{x_i + m/s}{\bar{x} + m/s}\right)\right)\right)\right) \tag{2}$$

Figure 1 illustrates the relative growth rate as a function of ocean entrance size l_i for different values of the growth compensation parameter C which accounts for increased growth rate of small members of a cohort after ocean entrance (Ali et al. 2003).

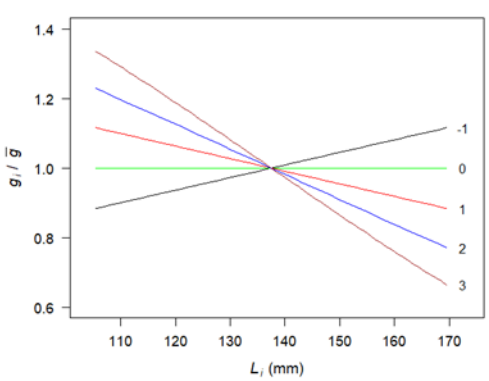

Fig. 1. Effect of ocean entrance fish length on relative growth rate from eqn (2) for values of C -1 to 3.

To estimate the effects of the parameters on SAR, the model was fit to profiles of SAR vs. initial fish length. Convergence of a nonlinear weighted least-squares algorithm (nls) (R Core Team 2016) requires initial values of the

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predator distribution parameters *m* and *s*. Thus, the data was fit using 1 mm incremented points on a $m \times s$ grid to yield best fit values of *A*, *C*, *H* and residual square error (RSE) for each point.

To explore the processes controlling ocean survival the model was fit to SAR vs. length data of hatchery reared Snake River yearling Chinook salmon (*Oncorhynchus tshawytscha*). The juveniles were collected at Lower Granite Dam, measured for length and tagged with passive integrated transponder tags. The SAR was estimated for fish binned in successive 4 mm increments of tagging length. Data is available at the DART database (http://www.cbr.washington.edu/dart). Data for 2008 consisted of smolts that, after tagging, were placed in transport barges and released below Bonneville Dam, the last dam on the Snake-Columbia River hydrosystem. Data for 2009 consisted of fish that were released back into the river after tagging.

The range of the $m \times s$ grid was determined from stomach contents of the major salmon predators: Pacific hake (*Merluccius productus*) and jack mackerel (*Trachurus symmetricus*) captured salmon ranging between 50–250 mm in length (Emmett 2006), Aucklets (*Aethia cristatella*) captured salmon approximately 120 mm in length (Tucker et al. 2016) and apex predators, such as salmon sharks, have been observed to capture adult salmon between 57–100 cm in length (Seitz et al. 2019). From these observations the grid range of mean gape size was set at m = 50–250 mm and the standard deviation of gape size was set at s = 4–204 mm. The apex predators are generally classified as gape-unlimited predators and their effects are mostly captured by *H*.

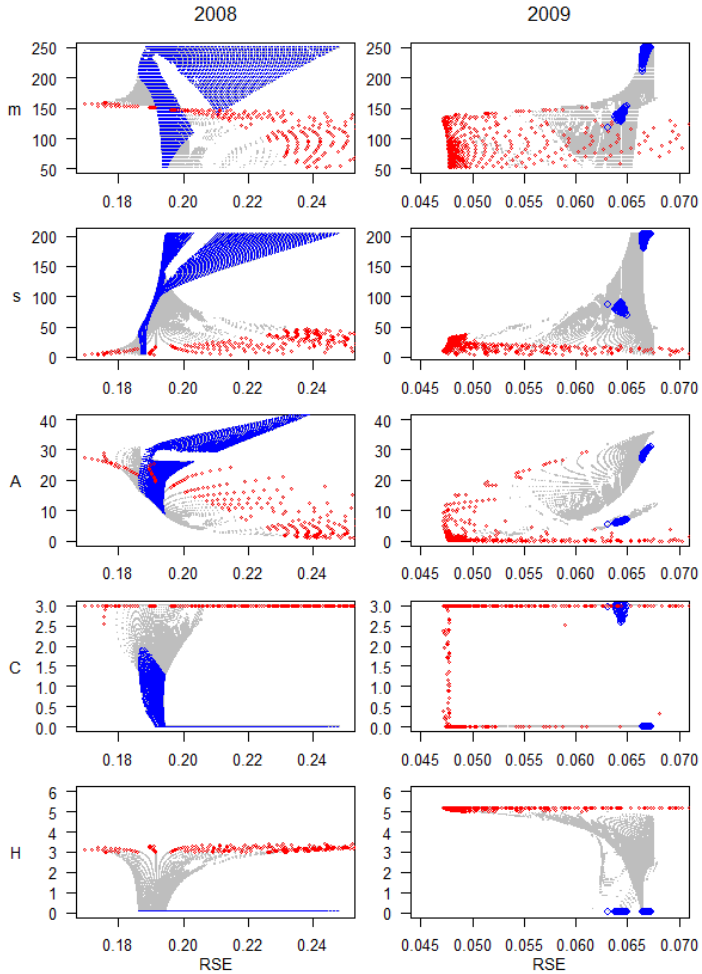

Fig. 2. Fitted model parameters for *m* x *s* grid points vs. RSE for smolt migration years 2008 and 2009. Region I parameter sets (red) encompass the upper boundary of *H* and Region II points (blue) encompass the lower boundary.

Figure 2 illustrates the parameter space depicted by individual plots of (*m*, *s*, *A*, *C*, *H*) against the corresponding RSE of each regression. Critical parameter regions correspond to the upper and lower ranges of apex predation *H* depicted by red and blue points in the figures. Region I (red points) corresponds to parameters with

high apex predator mortality and Region II (blue points) corresponds to parameters with low apex predator mortality.

Table 1. Best fit parameters for Snake River spring Chinook salmon migration year 2008 and 2009 for Region I and II of the parameter spaces. S_{apex} and S_{gape} are survivals resulting from apex and gape-limited predators respectively. The ratio of growth to predation, $g / \bar{\mu}$ is based on l_0 = 134 mm (see text).

Region	Year	m	s	A	C	H	$\bar{g} / \bar{\mu}$	S_{apex}	S_{gape}	RSE
		mm	mm	mm	~	~	mm	~	~	~
I	2008	156	4	27.3	3	3.2	27.3	0.421	0.491	0.169
I	2009	131	9	6.8	3	5.2	25.5	0.005	0.806	0.047
II	2008	149	89	11.6	1.5	0.1	20.1	0.95	0.033	0.192
II	2009	141	75	6.1	3	0.1	11.2	0.95	0.004	0.064

Table 1 gives the parameters corresponding to the minimum RSE for each region. The mean size of the gape-limited predators is similar for both years and regions. However, the size standard deviation for Region I is a factor of 10 smaller than for Region II. Correspondingly, the contributions of apex predators are different for the two regions. In Region I, apex predators control SAR while in Region II, gape-limited predators control SAR. Also note Region I parameters have lower RSE, indicating better fits with the assumption of high apex predation.

To evaluate the model, A and C can be estimated independently. A can be related to the ratio of growth to mortality rates as $\bar{g}/\bar{\mu} = A\Phi(m/s)/\Phi(-\bar{x}_o)$. For the independent estimate of the ratio, $\bar{g}$ was estimated between 0.5 to 1 mm·d^{-1} using otolith ring widths of Snake River spring Chinook captured off the Washington coast (Miller et al. 2014) and $\bar{\mu}$ was estimated as ~ 0.08 d^{-1} from a regression of survival of acoustically tagged juvenile spring Chinook salmon transiting through the Columbia River plume (Brosnan et al. 2014). Thus, $g / \bar{\mu} \approx 11$ is within a factor of two of the model estimates. The compensation parameter C was limited to values between 0 and 3, which corresponds to the observed 10–50% increase in growth after release from diet restriction observed by (Ali et al. 2003). The H parameter can be in part evaluated by computing the corresponding predation exposure from $t_H = H/\mu_H$. Using H (Table 1) and μ_H ~ 0.008 d^{-1}, from survival of Gulf of Alaska adult spring Chinook tagged with pop-up satellite archival tags (Seitz et al. 2019), t_H falls between one and two years, which is within the typical ocean residence of spring Chinook.

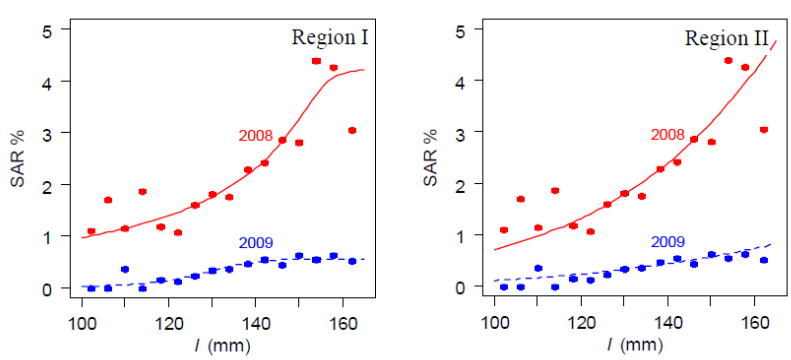

Fig. 3. Chinook salmon SAR vs. juvenile fish length binned in 4 mm intervals with lines produced by eqn (1) using parameters from Table 1 for Region I and II parameters.

Figure 3 illustrates the fit of SAR vs l for the two regions. The Region I parameters capture a distinct step-like pattern for both 2008 and 2009 while Region II parameters do not. Importantly, the step feature, produced with Region I parameters, results because the mean fish entrance length (~ 133 mm) and mean predator gape (~ 143 mm) are similar while the standard deviation is small (~ 6 mm). This allows fish with ocean entrance size greater than the predator gape mean to quickly escape predation such that their SAR changes little with size. Alternatively, with Region II predators, fish of all entrance sizes experience gape-limited predators and SAR increases with size.

The model reveals that processes controlling marine survival of the spring Chinook salmon can be explained by alternative predator-prey dynamics. For Region I parameters, the gape-limited predators that exhibit a narrow

gape-frequency distribution requires a significant level of apex predation. For Region II parameters, the wider predator size distribution allows the SAR to be explained with little apex predation. With Region I ecology, fish recruitment is largely insensitive to ocean growth while with Region II ecology recruitment depends on growth over the first year or more of ocean residence. Importantly, a distinct step in the SAR vs. length profile only occurs when apex predators dominate. As an aside, the model demonstrated that changes in growth ring spacing with age is not a sensitive indicator of the effects of size-selective predation on stock recruitment.

In summary, the model introduces the effects of the predator size distribution on the survival of growing prey and suggests that fish recruitment is not wholly controlled by processes occurring during early ocean residence; apex predators can also have significant impacts. Finally, a central take-away of the analysis is that the predator size distribution is an important dimension that needs to be considered when studying fish recruitment.

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Indigenous Community Partnerships towards Foundational Understanding of Wild Salmon Survival

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Keywords: Indigenous science, sockeye salmon, marine survival, life-cycle monitoring

Salmon are foundational to the ecological and cultural integrity of British Columbia's remote North and Central Coast (NCC). With largely intact habitats, low human population density, and provincially legislated protections under the Great Bear Rainforest Agreement, this remote region supports hundreds of unique, locally adapted populations of salmon, and is critical to the long-term conservation of wild salmon in British Columbia. However, in recent years populations of sockeye salmon and other species on the North and Central Coast have experienced decreases in abundance and productivity (Peterman and Dorner 2012), resulting in declining opportunities for sport, commercial, and First Nation's subsistence fisheries (Connors et al. in review). While declining smolt-to-adult survival has been hypothesized as a possible driver of populations declines (McKinnell et al. 2001), a lack of population monitoring data, and limited understanding of population dynamics currently hinders management and recovery efforts.

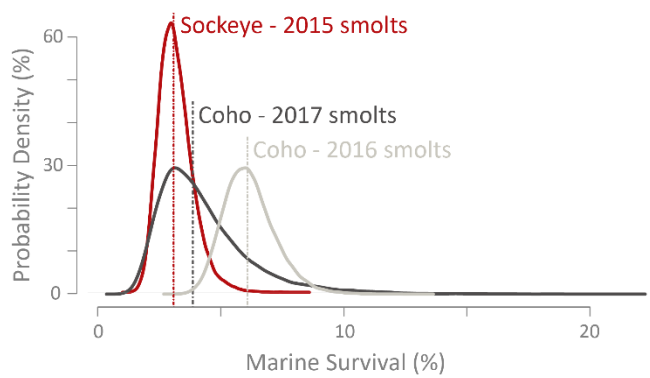

Fig. 1. Probability densities for smolt-to-adult survival estimates among Koeye River sockeye and coho salmon.

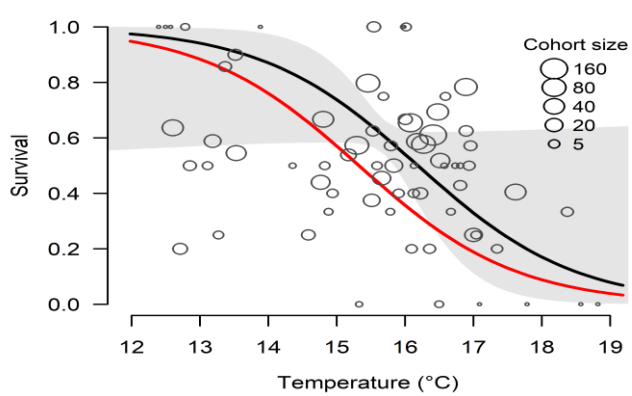

Fig. 2. Median estimate and 95% credible intervals (gray shading) for the relationship between temperature and survival from the model relating survival probability to temperature and injury (model 1). Black and red lines reflect expected survival for a fish without injury and with gillnet or predator injury respectively. Circles represent apparent survival to spawning for each cohort of tagged sockeye, with circle size scaled to the number of fish in each cohort.

In Canada, First Nations play a large and growing role in the management and conservation of wild salmon. These communities trace their ancestry and occupation of their traditional homelands back more than 10,000 years, and salmon are among the most important traditional foods for coastal Indigenous people (Marushka et al. 2019).

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The Koeye River is a major salmon bearing river in the traditional territory of the Heiltsuk Nation. Since 2013, we have run a collaborative life-cycle monitoring program in the Koeye River. Working with the Heiltsuk Nation, QQs Projects Society, the Hakai Institute, and Simon Fraser University, we aim to provide improved monitoring of salmon escapement (Atlas et al. 2017), smolt production, and the role of survival across the freshwater and marine life cycle in driving recruitment variation.

Salmon research in Koeye involves two related components: First, each spring we operate a smolt trap in the lower Koeye River, enumerating sockeye and coho smolts and tagging approximately 2,000 of each species with uniquely coded Passive Integrated Transponder (PIT) tags. These tagged smolts are redetected on a network of in-river Radio Frequency Identification (RFID) antennas when the fish return as adults, allowing us to estimate smolt-to-adult survival, and evaluate the role of individual length, condition and migration date on the probability of survival at sea. Second, every year in June we install a weir in the lower Koeye River for sockeye enumeration. Returning adult sockeye are captured and tagged fish visually identifiable FLOY tags as well as PIT tags. This tagging allows us to track the fate of individual adult salmon from river entry to spawning to evaluate the impacts of climate on migration success and make subsequent mark-recapture estimates of sockeye spawner abundance.

Since 2016 an average of about 75% of tagged adult sockeye have survived to reach the spawning grounds, however, survival among migrating adult sockeye declined dramatically when temperatures exceeded 16°C. Furthermore, fish with gillnet or predator injuries had a 30% lower probability of survival to spawning.

Over the first few years of smolt tagging, outmigrant smolts have had variable survival. Sockeye that went to sea in 2015 returned in 2017 and 2018, with an estimated smolt-to-adult survival of 3% (CI: 1.9–4.6%). Coho which went to sea in 2016 had an estimated smolt-to-adult survival rate of 6.5% (CI: 4.5–8.7%), while coho that went to sea in 2017 had an estimated survival rate of 4% (CI: 2.0–8.0%).

These results demonstrate the power of community-led research and monitoring in providing foundational understanding of salmon populations in remote regions like the NCC.

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Changes in Juvenile Salmon Prey Fields Associated with a Recent Marine Heat Wave in the Northern California Current

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Keywords: Ichthyoplankton, trophic ecology, prey, Chinook salmon, California Current

Juvenile Chinook salmon feed primarily on late larval and early juvenile fishes when they enter coastal waters (Daly and Brodeur 2015). The late larval and early juvenile life stage of most marine fishes are difficult to sample effectively (Brodeur et al. 2011), which led us to explore alternative indices of potential fish prey abundance. The majority of marine fishes in the northern California Current (NCC) spawn in late winter and early spring (Brodeur et al. 2008). Winter-spawned fish larvae that grow and survive through spring provide a food base for juvenile coho, steelhead, and Chinook salmon during their first marine summer. Therefore, we used the winter ichthyoplankton biomass as a proxy for potential salmon food during this critical growth period (Daly et al. 2013).

The five most dominant fish prey consumed by juvenile yearling and subyearling Chinook salmon, and yearling coho salmon in May–September 1998–2010 were originally chosen as the taxa to calculate the winter ichthyoplankton biomass (i.e., Pacific sand lance, sculpins, smelts, northern anchovy, and rockfishes). Biomasses of these taxa were significantly correlated with adult salmon return abundance (Daly et al. 2013).

The ichthyoplankton data used for the index come from five stations sampled bi-weekly along the Newport Hydrographic (NH) line in January–March 1998–2019. The stations in the index are fixed and are located from 9.3 km offshore to just off the shelf at 46.3 km (Peterson et al. 2014). Rarely sampled ichthyoplankton taxa (present in < 2.5% of the samples) and rarely- (or never-) eaten taxa (e.g., myctophids) were omitted from the biomass index. With inconsistent station and bi-weekly sampling, the biomass of each taxon was first averaged by station within each month/year, then by each month/year, and finally by each year for an overall annual average for each taxon. The biomass of the five taxa was summed to get one annual value and ln-transformed and entered into a Principal Coordinate analysis (PCO) and the axis-1 scores from that analysis were used as the index for each year.

Ocean regimes of 'cold' and 'warm' were established based upon NOAA's Ocean Indicator stoplight chart where the mean of the ranks were divided into two ranked groups (lower rank half = cold, higher rank half = warm; https://www.nwfsc.noaa.gov/research/divisions/fe/estuarine/oeip/g-forecast.cfm#TableSF-02).

During 'cold' regimes, the colder and more productive ocean conditions coincided with higher winter ichthyoplankton biomass and a community dominated by coastal fish larvae such as Pacific sandlance, smelts, and various sculpins, salmon showed higher marine survival (Daly et al. 2017). In contrast, during the warm ocean periods, the winter ichthyoplankton biomass was low and primarily comprised of offshore taxa such as rockfishes and winter–spawned northern anchovy. The five taxa index was a combination of both coastal and offshore taxa, which related well to salmon returns for the first 17 years the index was used.

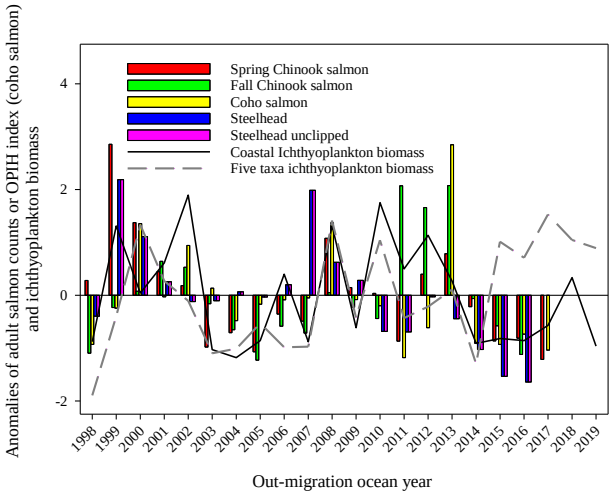

Fig. 1. Anomalies of the coastal and the five taxa ichthyoplankton biomass (no lag) and the adult salmon counts at Bonneville Dam lagged by time typically spent in ocean (two years for spring and fall Chinook salmon and steelhead and unmarked steelhead; and 1 year for coho salmon OPIH index).

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The marine heat wave and El Niño of 2014–2016 coincided with dramatic increases in sea surface temperatures through much of the Northeast Pacific (+2.5°C; Bond et al. 2015), and this warming contributed to changes in the winter ichthyoplankton biomass and community not previously observed in the 22-year time series (Auth et al. 2018). Since 2015, the biomasses of offshore ichthyoplankton taxa increased significantly along the NH line, and these taxa were increasingly consumed by juvenile salmon (Daly et al. 2017; Brodeur and Daly 2019). Moreover, the juvenile salmon that out-migrated in 2015 have returned as adults to the Columbia River one to two years later in much reduced numbers compared to previous years (Fig. 1).

Throughout the study period, one of the key taxa eaten during warmer ocean conditions was juvenile winter-spawned rockfishes, which coincided with lower survival to adults than the years when the salmon consumed coastal prey such as Pacific sandlance (Daly and Brodeur 2015). Additionally, the community of taxa eaten by juvenile salmon and that comprising the winter ichthyoplankton cluster into similar warm and cold ocean regimes (Daly et al. 2017).

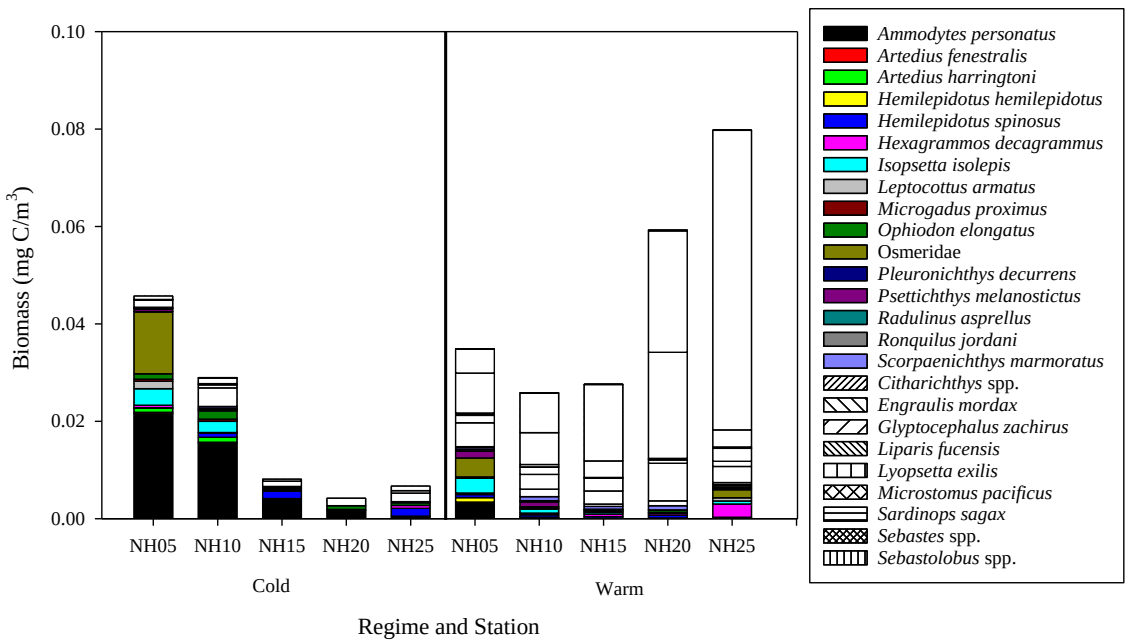

Fig. 2. Average biomass of ichthyoplankton by regime and Newport Hydrographic (NH) line stations of NH05-25. Regime was established using the rank of the mean of the ranks divided into two groups (lowest half = cold, higher half = warm) from NOAA's NWFSC Ocean Ecosystem Indicator website: https://www.nwfsc.noaa.gov/research/divisions/fe/estuarine/oeip/g-forecast.cfm#TableSF-02. Taxa listed in color are considered coastal, and taxa in white pattern are considered offshore.

When averaging all the ichthyoplankton taxa that salmon consume by ocean regime and station, there are distinct inshore to offshore changes in biomass. In the cold regime years, the highest mean larval fish biomass was inshore and was comprised of taxa known to be primarily coastal (Richardson and Pearcy 1977; Auth and Brodeur 2006; Auth 2011) with biomass declining in an onshore to offshore gradient (Fig. 2). In the warm ocean regime years, the highest mean larval fish biomass was found at the furthest offshore station (46.3 km), with biomass declining in an offshore to onshore gradient (Fig. 2).

In the last few years, the high biomass of winter ichthyoplankton has been out of phase with the salmon returns (Fig. 1). The five taxa index was a combination of cold and warm regime ichthyoplankton, which worked well until the recent marine heat wave that resulted in a substantial increase in the observed cross-shelf differences in ichthyoplankton biomass. Inclusion of offshore taxa in the original five taxa index did not qualitatively change the results, as the typical abundance of these taxa was low compared to the inshore taxa. However, the marine heat wave of 2014–2016 resulted in such high abundances of offshore taxa that their inclusion resulted in a noticeable change in the index. As such, we have modified the winter ichthyoplankton biomass index to include only the cold regime coastal ichthyoplankton taxa (see Fig. 2 for detailed list of the coastal and offshore taxa). In addition, the number of taxa included in the new Index of Coastal Prey Biomass (ICPB), and the coastal and offshore composition index, was expanded beyond the top five fish prey of juvenile salmon.

Table 1. Biomass from 1998–2019 of coastal taxa sampled in January–March along the Newport Hydrographic line, the rank of the biomass from highest (1) to lowest (22), Axis-1 principal coordinate community analysis on the composition of coastal and offshore taxa by year, and the rank of the community from coastal taxa dominated (1 = most coastal taxa) to offshore taxa dominated (22 = most offshore taxa).

Year	Coastal biomass (ln [(mg C per 1000 m^3)]	Rank biomass	Coastal and offshore taxa composition axis 1 PCO scores	Rank PCO
1998	0.48	17	-8.74	11
1999	1.64	4	-19.07	6
2000	0.97	11	-27.84	5
2001	1.27	6	-13.56	9
2002	1.95	1	-14.02	8
2003	0.40	21	-1.58	13
2004	0.32	22	20.43	16
2005	0.49	16	33.77	20
2006	1.16	8	-34.18	1
2007	0.48	18	10.37	14
2008	1.64	3	-31.33	3
2009	0.62	13	-3.26	12
2010	1.87	2	11.79	15
2011	1.21	7	-28.79	4
2012	1.55	5	-32.28	2
2013	1.09	10	-16.00	7
2014	0.46	19	-13.55	10
2015	0.51	14	31.50	18
2016	0.49	15	34.14	21
2017	0.64	12	39.67	22
2018	1.12	9	29.53	17
2019	0.43	20	33.00	19

Table 2. Linear model regression results of the adult counts at Bonneville Dam lagged two ocean years for spring and fall Chinook salmon and steelhead (outlier years 1999 and 2007 removed), and Oregon Production Index, Hatchery (OPIH) for coho salmon lagged one ocean year (outlier year 2013 removed) and the following indicators: the original five taxa winter ichthyoplankton biomass index, coastal taxa winter ichthyoplankton biomass, five taxa composition axis-1 principal coordinate analysis score, and coastal and offshore composition axis-1 principal coordinate analysis score. Significant (< 0.05) *P* values and adjusted R-square values are listed. *P* values > 0.05 but < 0.1 are listed in red, and non-significant relationships are listed as 'ns'. For adult salmon returns see: https://www.nwfsc.noaa.gov/research/divisions/fe/estuarine/oeip/ad-returns.cfm and http://www.fpc.org/web/apps/adultsalmon/Q_adultcounts_annualtotalsquery.php.

Indicator	Spring Chinook adult returns 1998–2017 lag 2 yr	Coho OPIH 1998–2017 (no yr 2013) lag 1 yr	Fall Chinook salmon adult returns 1998–2016 lag 2 yr	Steelhead adult returns 1998–2016 (no yr 1999 & 2007) lag 2 yr
Five taxa biomass	ns	ns	ns	ns
Coastal taxa biomass	0.02; 23.9%	0.07	0.02; 24.5%	ns
Five taxa composition score	0.0006; 47.6%	0.03; 21.3%	0.0008; 46.7%	0.02; 27.6%
Coastal and offshore taxa score	0.001; 46.6%	0.08	0.001; 43.9%	0.01; 29.4%

Since 2014, the new ICPB has been below average with the exception of 2018 (which was more of an average year) and the coastal biomass index in 2019 was the 20th lowest in the 22-year time series (Table 1). The community composition of ichthyoplankton in 2019 was once again dominated by offshore taxa, with the community indicator suggesting poor food conditions for piscivorous juvenile salmon that out-migrate into the

ocean in 2019 (Table 1). Adding the more recent data, our original biomass of the five taxa no longer shows a significant relationship to adult returns of Chinook and coho salmon or steelhead (Table 2). However, the ICPB is significantly correlated with yearling spring Chinook and subyearling fall Chinook salmon adult counts to Bonneville Dam. However, this relationship does not hold for coho salmon OPIH ($p = 0.07$). The community analysis (PCO axis 1 scores) of the ichthyoplankton composition with either the original five taxa or the composition of the coastal and offshore taxa were significant for all the salmon we examined, with the exception of coho salmon and the coastal and offshore taxa ($p = 0.08$; Table 2).

In conclusion, warm ocean conditions clearly affect both the biomass and the community composition of winter ichthyoplankton in the NCC. Winter ichthyoplankton, especially coastal taxa represented in the ICPB, are an important indicator of future food conditions for piscivorous juvenile salmon during a vulnerable and critical time in their life cycle. Survival of juvenile salmon that out-migrated into the ocean since the marine heat wave of 2014–2016 has uniformly been poor. Ichthyoplankton abundance and species composition in 2019 were similar to those observed during 2015–2018, suggesting a continuation of the poor salmon returns for at least the next several years.

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Southeast Alaska Pink Salmon Growth and Harvest Forecast Models

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Keywords: pink salmon, *Oncorhynchus gorbuscha*, Southeast Alaska, juvenile abundance, juvenile growth

Growth and harvest forecast models are used to provide insight into the role of temperature in the early marine ecology of Southeast Alaska (SEAK) pink salmon (*Oncorhynchus gorbuscha)*. The onset of the Gulf of Alaska marine heatwaves in 2014–2015 (Bond et al. 2015) has highlighted the importance of understanding the resilience of salmon to a warming climate as the frequency and magnitude of marine heatwaves are expected to increase with warming Arctic conditions (Di Lorenzo and Mantua 2016). Pre-season harvest forecasts using adult pink salmon data have been a persistent challenge due to the presence of a single adult age and high variation in spawner-recruit relationships. Juvenile models have been developed to assist harvest forecasts for SEAK pink salmon (Orsi et al. 2016; Wertheimer et al. 2018; Murphy et al. 2019) using data collected during Southeast Alaska Coastal Monitoring Survey (SECM) (Murphy et al. 1999; Orsi et al. 2016; Fergusson et al. 2019) and have become the primary tool used for pre-season harvest guidance in SEAK pink salmon fisheries. Temperature is an important environmental covariate in the harvest forecast model, but it is unclear how it contributes to the forecast performance (Murphy et al. 2019). Although environmental conditions are often used to account for changes in survival, they also play an important role in the distribution and migration of salmon. These two ecological processes are confounded within the harvest model as juvenile abundance is measured with catch-per-unit-effort (CPUE) data. Growth models are developed to provide ecological insight into the role of temperature in the early marine ecology of juvenile pink salmon. Otolith thermal mark recoveries of hatchery chum salmon are reviewed to provide insight into the overall migratory pattern of juvenile salmon in SEAK. Finally, run-size forecast models based on juvenile pink salmon abundance in the northern Bering Sea are included to add insight into critical periods in the marine survival of Alaskan pink salmon.

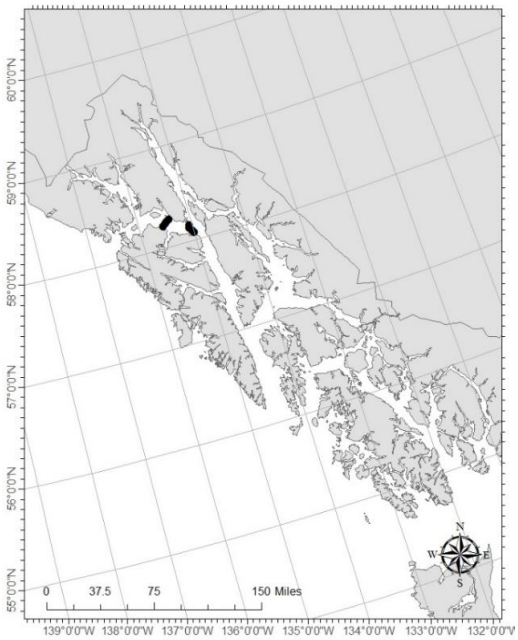

Fig. 1. A map of Southeast Alaska identifying the eight stations (black dots) within Icy Strait sampled by the Southeast Alaska Coastal Monitoring survey.

Data on juvenile salmon associated oceanographic and ecosystem indicators have been collected during SECM surveys since 1997 within the northern region of SEAK (Fergusson et al. 2019). Data from eight stations along two transects in Icy Strait (Fig. 1) are used in harvest and growth models of SEAK juvenile pink salmon.

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Oceanographic data collected at these stations consist of conductivity-temperature-depth (CTD) profiles of temperature (°C) and salinity (PSU), a water sample for chlorophyll-a (ug·L^{-1}), and a 60 cm bongo net tow for zooplankton. The overall average 20 m integrated water column temperature was used to estimate the Icy Strait Temperature Index (ISTI) (May–August and May–July). Fish were sampled at each station with a NETS Nordic 264 rope trawl fished for 20 min at each station at least once during June–August with tow speeds of approximately 1.5 m·sec^{-1} and typical fishing dimension of 18 m wide by 24 m deep.

Table 1. Average surface trawl catch-per-unit-effort (CPUE) in Icy Strait, the May–August Icy Strait Temperature Index (ISTI) and observed and predicted harvest of pink salmon in Southeast Alaska (SEAK), 1997–2017.

Juvenile Year	Ln(CPUE+1)	ISTI (°C)	SEAK Harvest (millions)	Predicted SEAK Harvest (millions)
1997	2.48	9.48	42.45	34.39
1998	5.62	9.57	77.82	86.85
1999	1.60	8.97	20.25	28.43
2000	3.73	9.04	67.02	64.00
2001	2.87	9.44	45.32	41.80
2002	2.78	8.56	52.47	56.53
2003	3.08	9.78	45.31	39.11
2004	3.90	9.66	59.12	55.64
2005	2.04	10.26	11.61	12.53
2006	2.58	8.88	44.80	46.99
2007	1.17	9.31	15.90	14.88
2008	2.49	8.29	37.95	56.26
2009	2.09	9.61	24.03	25.19
2010	3.67	9.62	58.86	52.44
2011	1.35	8.90	21.25	25.52
2012	3.15	8.73	94.70	59.67
2013	1.91	9.16	37.20	30.48
2014	3.40	9.37	35.10	52.34
2015	2.19	9.86	18.40	22.42
2016	3.89	10.56	34.30	39.00
2017	0.31	8.93	7.65	7.04

Peak monthly (June and July) juvenile catch-per-unit-effort (CPUE) and associated environmental variables were used in a multiple linear regression model to forecast harvest based on the approach described in Wertheimer et al. (2006). CPUE was standardized to 20-minute trawl set and calibrated to the NOAA Ship *John N. Cobb* with fishing power coefficients for the vessels that have conducted SECM surveys over time (Wertheimer et al. 2010). The model was defined as:

$$Harvest = \alpha + \beta(\ln(CPUE + 1)) + \gamma_1 X_1 \ldots \gamma_n X_n + \varepsilon,$$

where γ is the coefficient for environmental covariates X (e.g., water temperatures, climate indices, fish size and condition) and ε is the normally distributed error term. A backward/forward stepwise regression model selection procedure identified candidate models via Akaike Information Criterion (AIC) and small sample AIC (AICc). Mean and Median Absolute Percentage Error (MAPE, MEAPE) statistics from jackknife cross validations were used to define forecast accuracy of candidate models, and the harvest forecast was based on the 80% bootstrap confidence interval of the model with the highest forecast accuracy. A two-parameter model, including CPUE and the Icy Strait

Temperature Index (ISTI), has been the most consistently selected model over time and accounts for 78% (R^2) of the variability in harvest data (Fig. 2; Table 1). Temperature is a significant negative covariate in the model and partial residuals identify a negative linear relationship between temperature and harvest across the range of observed temperatures (Fig. 2). A linear relationship is more consistent with a simple ecological process such as temperature effects on juvenile distribution and migration; a threshold or non-linear relationship may be more likely if temperature is altering ecological rate processes.

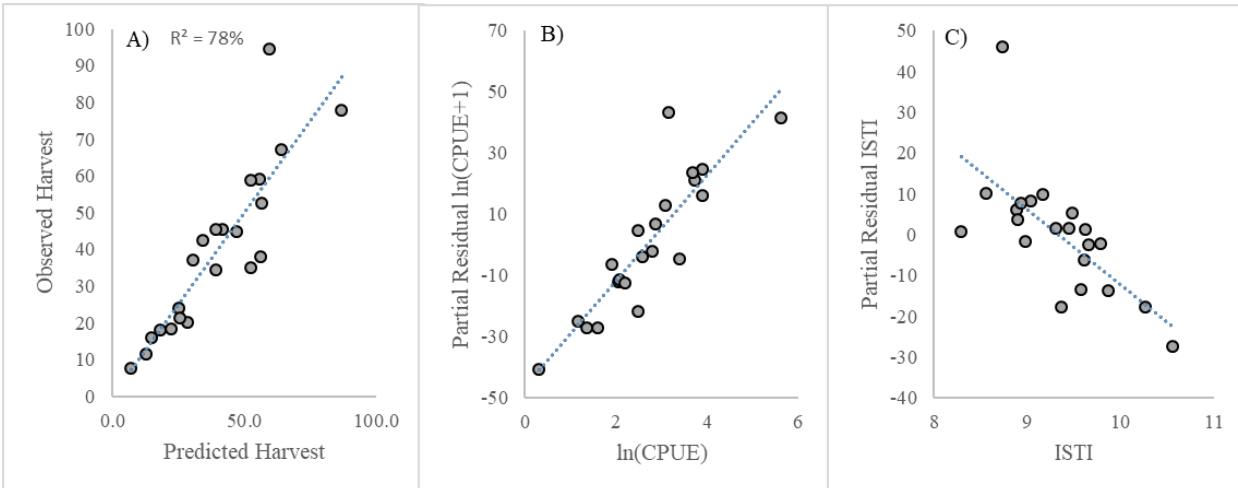

Fig. 2. The harvest forecast model for Southeast Alaska pink salmon, 1997–2018 juvenile years. Plots are: A) the relationship between predicted and observed harvest (millions of fish), B) the partial residuals for the peak monthly catch-per-unit-effort, ln(CPUE), of juvenile pink salmon in Icy Strait, and C) the partial residuals for the May–August Icy Strait Temperature Index (ISTI) (°C). The model explains 78% (R^2) of the variation in pink salmon harvest.

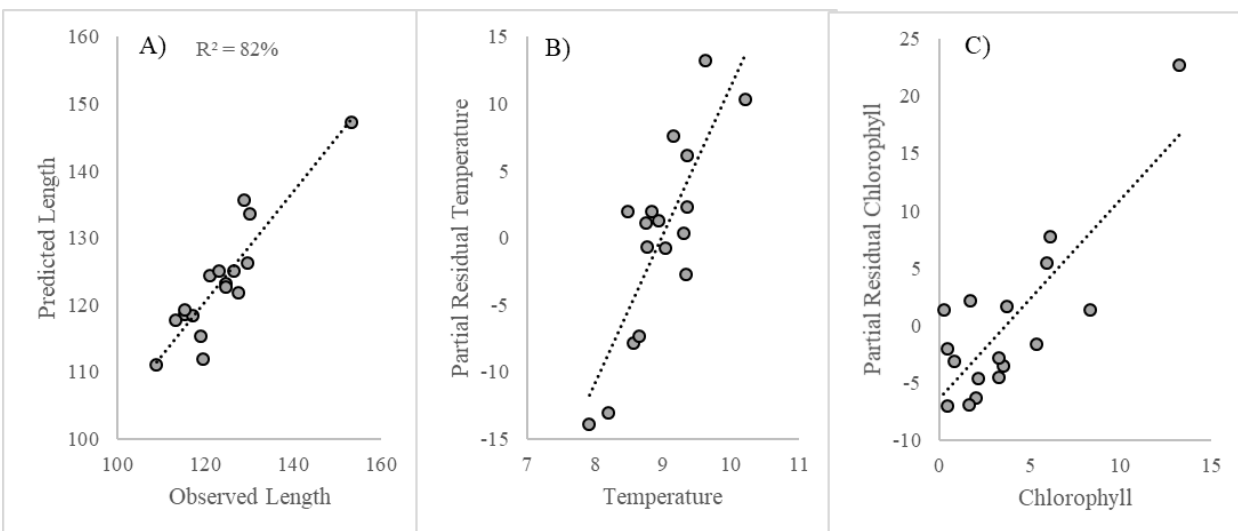

Fig. 3. The growth model for Southeast Alaska pink salmon in Icy Strait, 1999–2015 juvenile years. Figures included are: A) the relationship between observed and predicted lengths (fork length mm) of juvenile pink salmon on 24 July 24, B) partial residuals for the May–July Icy Strait Temperature Index (°C), and C) partial residuals for May chlorophyll (ug·L^{-1}). This model explains 82% (R^2) of the variation in the average length of juvenile pink salmon.

A similar stepwise model selection approach was used to identify environmental variables important to juvenile pink salmon growth. Year-to-year variation in juvenile pink salmon growth was approximated by their length (fork length) standardized to 24 July based on their apparent growth rate between the June and July SECM surveys. A two-parameter model including May chlorophyll (ug·L^{-1}) and the May–July ISTI index was identified as the best fitting model to average annual size of juvenile pink salmon. The model accounted for 71% (adjusted R^2) of the variability in the year-to-year variation in the average size of juvenile pink salmon, 1997–2018, and 82% of the

variability from 1997–2015 (Fig. 3; Table 2). May chlorophyll data were not available in 2016 and 2017. The poor fit of the model in 2018 is likely due to the late outmigration timing of juvenile pink salmon (Scott Vulstek, personal communication), which highlights complications of modeling juvenile growth with size data. The essential point of this model is that temperature is a significant positive covariate in the growth of SEAK juvenile pink salmon. Reconciling the opposite effects of temperature in the growth and harvest models leads to the inference that growth and survival of pink salmon are not linked, or that ecological processes other than survival are contributing to the significance of temperature in the harvest model. The temperature effect in the harvest model may simply reflect changes in the migratory pattern of juveniles.

Table 2. Average upper 20 m water column temperatures (May–July), May Chlorophyll-a concentrations, observed average length (estimated fork length on 24 July), and predicted average length of juvenile pink salmon in Icy Strait, 1999–2015.

Year	Temperature (°C)	Chlorophyll (ug ·L^{-1})	Length (mm)	Predicted Length (mm)
1999	8.56	3.54	115	119
2000	8.77	5.90	127	125
2001	9.03	0.45	117	118
2002	8.20	5.33	113	118
2003	9.31	2.03	121	124
2004	9.33	8.33	129	136
2005	10.21	1.66	130	134
2006	8.75	0.48	119	115
2007	8.94	3.71	125	123
2008	7.91	3.29	109	111
2009	9.36	2.16	123	125
2010	9.35	0.83	125	123
2011	8.65	3.26	115	119
2012	8.48	0.25	119	112
2013	8.83	6.13	130	126
2014	9.14	1.69	128	122
2015	9.62	13.23	153	147
2016	10.20	--	145	--
2017	8.56	--	121	--
2018	8.92	4.55	109	--

Table 3. Number of juvenile chum salmon hatchery otolith thermal marks recovered in Icy Strait by Southeast Alaska Coastal Monitoring surveys, 1997–2017.

Month	DIPAC[1]	NSEAK[2]	SSRAA[3]
June	3974	819	13
July	1611	2086	211
August	432	433	382

[1]Douglas Island Pink and Chum, Inc.
[2]Includes Northern Southeast Regional Aquaculture Association, Kake Nonprofit Fisheries Corp. and Armstrong-Keta Inc.
[3]Southern Southeast Regional Aquaculture Association.

Otolith thermal marks of juvenile chum salmon recovered during SECM surveys provide some insight into the migratory pattern expected for SEAK pink salmon (Table 3). Hatchery chum salmon origins vary by month with the

stocks closest to Icy Strait (DIPAC) accounting for the largest proportion in June. Recoveries of thermal marks from other hatchery stocks in northern SEAK are highest in July. Thermal mark recoveries from stocks farthest away from Icy Strait (SSRAA) reach their peak in August. This highlights that some proportion of juvenile salmon from all regions of SEAK migrate through Icy Strait, and therefore change in juvenile migration patterns have the potential to alter the relationship between juvenile CPUE and abundance. The combination of trawl CPUE and temperature may be a more accurate measure of juvenile abundance than trawl CPUE data alone if the proportion of SEAK juveniles that migrate through Icy Strait (the northern migration corridor) increases in warm years. If true, this increases the importance of the initial or early marine life-history stage to the overall marine survival of SEAK pink salmon.

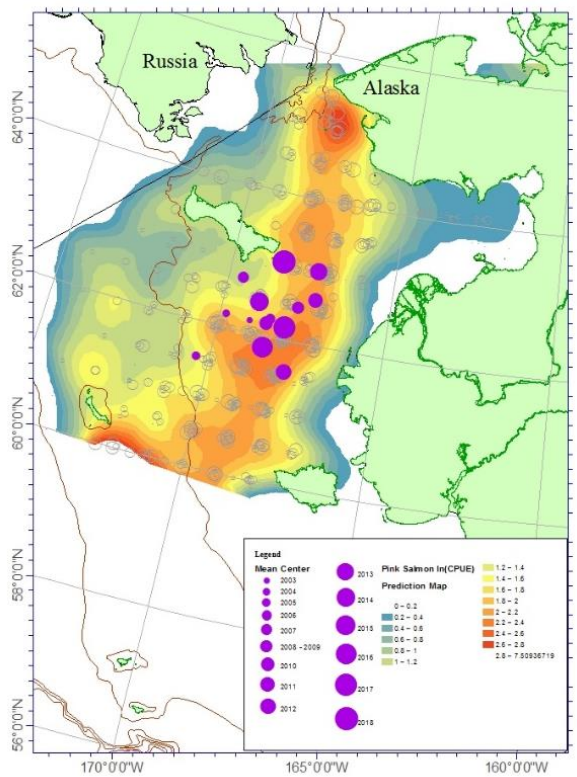

Fig. 4. Spatial distribution of juvenile pink salmon based on catch-per-unit-effort (CPUE) data from surface trawl surveys in the northern Bering Sea, 2003–2018. Color contours are from local polynomial prediction surface of ln (CPUE+1) (hollow circles) created using ArcGIS software from Esri, and filled circles identify the spatial center of juvenile pink salmon distribution and are scaled by year.

Juvenile abundance models from the northern Bering Sea provide insight into the importance of the early marine life-history stage of pink salmon to their marine survival. Surface trawl catch rates from the northern Bering Sea trawl surveys (Fig. 4) were used to construct an index of juvenile pink salmon abundance as:

$$Index = \frac{\sum_i^I \ln(CPUE_i+1)}{I}\theta,$$

where $CPUE_i$ is the catch-per-unit-effort at station i, θ is the mixed-layer-depth (MLD) adjustment, and I is the total number of stations sampled by year. Effort is the area swept by the trawl in km^2, and the MLD adjustment, θ, is:

$$\theta = \frac{\sum_i^I C_i M_i}{\sum_i^I C_i},$$

where C_i is catch of juvenile pink at station i, M_i, is the ratio of MLD to trawl depth when trawl depth is shallower than mixed layer depth, and 1.0 when trawl depth is below the mixed-layer depth, and I is the total number of stations sampled in that year (Murphy et al. 2017). This juvenile abundance index explains 73% (R^2 = 73%) of the year-to-year variability in adult returns to Norton Sound and the Yukon River (Fig. 5; Table 4), highlighting the importance of the early or initial marine life-history period to the marine survival of pink salmon in the northern Bering Sea.

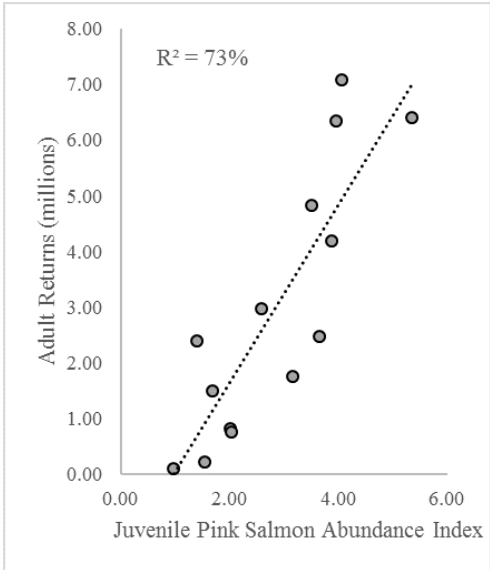

Fig. 5. The relationship between the juvenile pink salmon abundance index and adult returns to Norton Sound and the Yukon River for the 2004–2018 return years. This model explains 73% (R^2) of the variation in adult pink salmon returns to the northern Bering Sea.

Table 4. Average catch-per-unit-effort (CPUE), Mixed-Layer-Depth (MLD) adjustment, and abundance index for juvenile pink salmon in the northern Bering Sea, and adult returns to the Yukon River and Norton Sound, 2003–2017 (juvenile years).

Juvenile Year	Ln (CPUE)	MLD Adjustment	Juvenile Index	Adult Return
2003	2.65	1.49	3.95	6.35
2004	2.51	1.46	3.66	2.49
2005	1.96	1.79	3.52	4.84
2006	1.69	1.20	2.02	0.83
2007	3.22	1.20	3.87	4.19
2008	--	--		0.34
2009	1.38	1.01	1.39	2.39
2010	1.43	1.08	1.54	0.23
2011	1.47	1.15	1.69	1.50
2012	0.80	1.21	0.97	0.11
2013	3.10	1.02	3.17	1.76
2014	1.96	1.04	2.04	0.77
2015	4.25	1.26	5.35	6.39
2016	2.57	1.00	2.58	2.98
2017	3.94	1.03	4.05	7.08

Critical periods in the natural mortality schedule of salmon are important to our understanding of their underlying production dynamics and the scientific advice provided to fisheries management. The initial or early marine period of juvenile pink salmon has largely been believed to be the primary determinant of year-class strength (Parker 1968; Mortensen et al. 2000; Willette et al. 2001; Wertheimer and Thrower 2007) due to the high and variable mortality that occurs during this stage. The importance of the initial marine period to the survival of SEAK pink salmon increases and the negative influence of temperature on survival decreases if trawl CPUE and temperature are used together as an index of juvenile abundance. The inability to identify the origin of juvenile pink salmon limits attempts to test the role of temperature within the harvest forecast model; however, the data included here provide ecological support for considering temperature as a factor in abundance estimates of SEAK juvenile pink salmon.

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Effect of Temperature and Amount of Food on the Growth Rate / Aerobic Scope of Juvenile Chum Salmon

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Keywords: metabolic rate, aerobic scope, juvenile chum salmon, growth rate, growth-dependent mortality

In Japan, the return rates of chum salmon (*Oncorhynchus keta*) have declined recently (NPAFC 2018). The decline appears to be influenced by high juvenile mortality during northward migration to the Okhotsk Sea (Urawa 2000). In particular, the high juvenile mortality due to low growth rates during the long northward migration to the Okhotsk Sea can occur in the Sanriku coastal area of Honshu island, Japan (Honda et al. 2017). Their growth depends on coastal environmental conditions such as water temperature and prey abundance (Weatherley and Gill 1995), but how these factors lead to low growth is still unknown. Because of low food intake and high energy expenditures on respiration and locomotion, they probably allocate less energy to their growth. Therefore, it is necessary to evaluate the metabolic performance of juvenile chum salmon, but few studies have considered their energetics. The aim of this study was to determine how the metabolic performance of juvenile chum salmon under different food levels and temperatures affects their growth rates.

Chum salmon eggs were collected from returning adults at Katagishi Hatchery, Iwate, Japan on 10 November 2017 (Group 1) and 11–12 December 2017 (Group 2). Group 1 eggs were artificially fertilized, and the juveniles were reared in a tank at the research station of Iwate Fisheries Technology Center with natural fresh water, fed on artificial pellets until 16 February 2018. Group 2 juveniles were reared at the same place until 14 April 2018. The juveniles of both groups were transported and put into 100–200 L tanks supplied with filtered natural seawater (100 individuals per tank) in the Iwate Fisheries Technology Center. Group 1 were reared at four temperature conditions (6.0–8.1, 10, 12, and 14°C within ± 0.5°C) and fed 4% of body mass on artificial pellets for 15 days. Group 2 were reared at four temperature conditions (8.0, 10, 12, and 14°C within ± 0.5°C) and fed 1% of body mass for the same number of days as Group 1. Juveniles were randomly selected and measured their fork length (FL, mm) on the first and the fifteenth day (n = 8 per experimental condition) and calculated mean daily growth rate (mm·day^{-1}) over the two weeks.

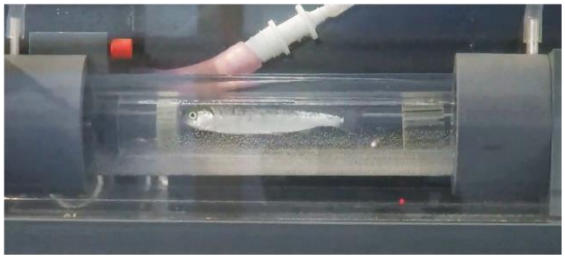

Fig. 1. Measuring metabolic rate of chum salmon juvenile in a Blazka-type swim tunnel respirometer (Loligo Systems, Denmark).

On the fifteenth day, resting metabolic rate (RMR) and maximum metabolic rate (MMR) of the individuals were measured with a Blazka-type swim tunnel respirometer (0.28 L, Loligo Systems, Denmark, Fig. 1). Randomly selected fish were placed in the respirometer one by one and their oxygen consumption rate as RMR was measured continuously for three hours at a water speed of 3–4 cm·s^{-1}. After measuring RMR, maximal exercise was achieved using a maximum swimming speed (U_{max}) test based on a protocol described previously (Hammenstig et al. 2014). Water speed was increased by an additional 1.25–1.5 cm·s^{-1} for one minute until the fish was unable to swim against the current or to remove themselves the back grids (we considered those situations as the fish showed the signs of fatigue). As soon as they showed the signs of fatigue, the water speed was reduced to 3–4 cm·s^{-1} and we measured

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their oxygen consumption rate. MMR was taken as the value for the 15-minute period during which they were exhausted. Aerobic scope (AS, mg $O_2 \cdot kg^{-1} \cdot min^{-1}$) for each fish was calculated based on a protocol described previously (Eliason and Farrell 2016) as the difference between MMR and RMR (n = 2–3 per experimental condition).

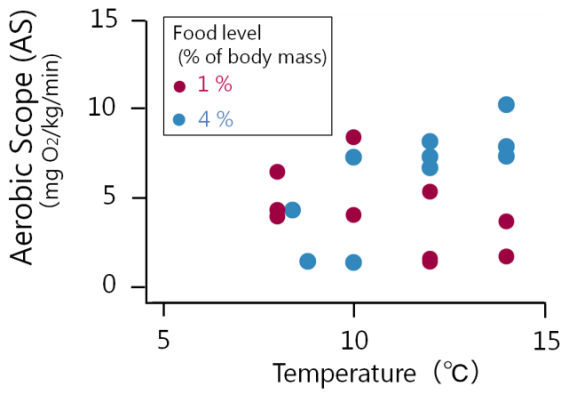

Fig. 2. Aerobic Scope (AS) of juvenile chum salmon at each temperature and food level.

Results were as follows. At the high food level (fed 4% of body mass), FLs (n = 32, mean ± SD) were 49.2 ± 3.8 and 60.9 ± 3.9 mm in the first and fifteenth day, respectively. The growth rates were 0.65, 0.86, 0.83, and 1.02 $mm \cdot day^{-1}$ at 6.0–8.1, 10, 12, and 14°C, respectively. AS were the highest at 14°C (8.5 ± 1.5 mg $O_2 \cdot kg^{-1} \cdot min^{-1}$, Fig. 2). At the low food level (fed 1% of body mass), FLs were 49.2 ± 3.8 and 60.9 ± 3.9 mm in the first and fifteenth day, respectively. The growth rates were 0.14, -0.04, -0.08, and -0.05 $mm \cdot day^{-1}$ at 8.0, 10, 12, and 14°C, respectively. AS was the highest at 10°C (6.3 mg $O_2 \cdot kg^{-1} \cdot min^{-1}$; Fig. 2).

The growth rates at the high food level were similar to, or higher than that of wild juvenile chum originating from the rivers along the Sanriku coastal area (median: 0.68 $mm \cdot day^{-1}$; Honda et al. 2017). At the condition, AS were higher at higher temperatures. On the other hand, a thermal effect on their growth was not found clearly at the low food level. Their growth rates were lower than that of wild and AS were high at low temperatures. These results suggest that higher temperatures allowed juveniles to allocate more energy to their growth when they had access to surplus food, in comparison to lower temperatures where more energy could be allocated to more energy when food was limited. Previous studies showed that juvenile chum salmon distributed in Japanese coastal areas with temperatures between 5–13°C (Seki 2005, 2013) had the highest growth rates at 10°C (Kaeriyama 1986). Juvenile chum salmon may inhabit areas with suitable temperatures for their own growth. However, in the present study, at the high hood level, they showed higher growth at temperatures above 13°C, while at the low food level, a thermal effect on their growth was unclear. This indicates that 5–13°C could be the temperatures at which they just inhabit, and that food condition affects the growth of juvenile chum more than temperature. From 2007 to 2009, the amount of warm water, brought by the Tsugaru warm Current and the Kuroshio Extension increased in waters of the Sanriku coastal area (Wagawa et al. 2016), which could cause low prey abundance, low metabolic performance, and low growth of the juveniles. This could lead to low survival of juveniles and as a result, lead to low return rates of adults.

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Spatial and Temporal Trends in Juvenile Sockeye Salmon Diets across Oceanographic Regimes on the Coast of British Columbia

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Keywords: sockeye salmon, diet, zooplankton, foraging success, juvenile

The Fraser River watershed is one of the world's largest sockeye salmon (*Oncorhynchus nerka*) producers. However, productivity in several populations has declined since the early 1990's (Peterman and Dorner 2011). It is believed that bottom-up environmental conditions and trophic interactions during the juvenile salmon early marine migration are contributing factors (Beamish and Mahnken 2001; Aydin et al. 2005; Ware and Thomson 2005; Farley and Trudel 2009). The phenology of bottom-up oceanographic processes and of the juvenile salmon outmigration are intrinsically linked (Chittenden et al. 2010; Malick et al. 2015). Indeed, the timing and size of the spring phytoplankton bloom has been demonstrated to be significantly correlated with salmon productivity (Malick et al. 2015). Furthermore, marine survival has been found to be higher when the juvenile marine outmigration overlaps with periods of high prey abundance (Chittenden et al. 2010). Long term changes to zooplankton assemblages in the Strait of Georgia have been observed (Johannessen and Macdonald 2009; Li et al. 2013), potentially impacting both the quality and quantity of prey along the juvenile salmon migratory route. Changes in the prey community may therefore explain the variability of sockeye salmon survival and returns to the Fraser River in British Columbia in recent years.

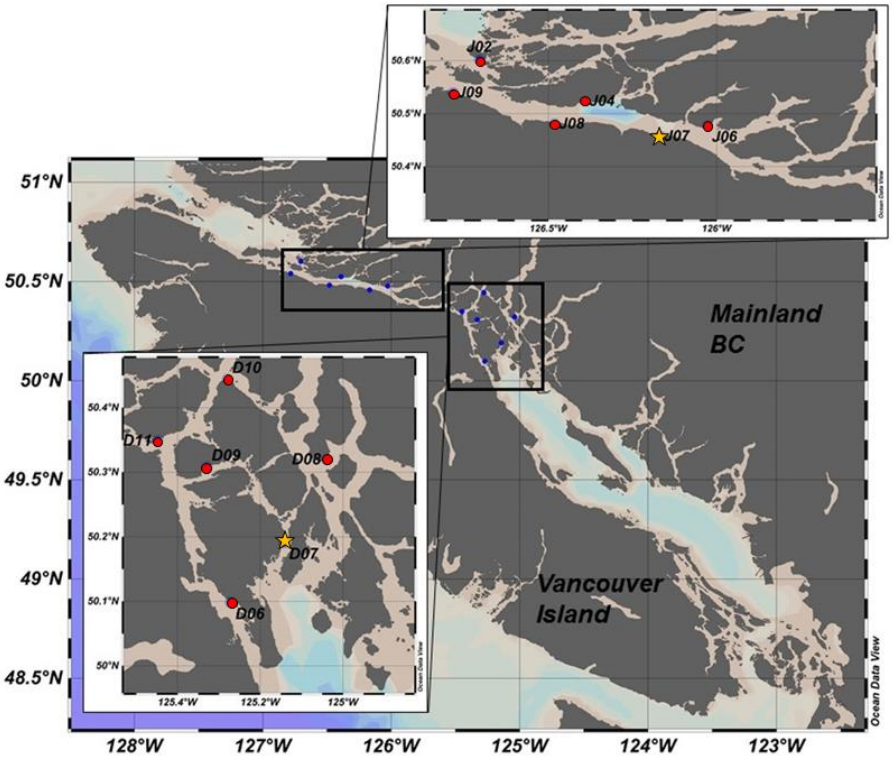

Fig. 1. Map of study area located between Vancouver Island and mainland British Columbia. Inset maps show locations of sampling sites in the Discovery Islands (bottom) and Johnstone Strait (top). All sites were used in the spatial analyses; those marked with a star were selected for temporal analyses.

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Upon leaving the Fraser River, juvenile sockeye salmon spend their first summer at sea transitioning between the different ocean regimes of the BC coastline. Juveniles first encounter the highly stratified and productive waters of the Strait of Georgia (Jackson et al. 2015) where they have been shown to reside for 43–54 days (Preikshot et al. 2012). The majority of juveniles then travel through the tidally-mixed channels of the Discovery Islands and Johnstone Strait, before continuing north through Queen Charlotte Sound and Hecate Strait *en route* to the Gulf of Alaska (Tucker et al. 2009) (Fig. 1). Johnstone Strait, an area with strong winds and intense tidal mixing, is a section of the migration where juvenile salmon are thought to experience an 'energy deficit,' a hypothesis known as the 'trophic gauntlet' (Mckinnell et al. 2014). This area is characterized by cooler, denser, and less productive water than in the Discovery Islands and Strait of Georgia immediately to the south. To date, very little is known about juvenile salmon diets in the Discovery Islands and Johnstone Strait. Recent research has shown that this region does support lower zooplankton biomass (Mahara 2018) and that growth is reduced relative to other sections of the outmigration (Journey et al. 2018). However, the connection between environmental conditions, prey phenology, and juvenile salmon diet and growth across fine spatial and temporal scales during the outmigration remains unexplored. This research looks to test the trophic gauntlet hypothesis and shed light on the fine scale differences in environmental conditions, prey fields, and juvenile sockeye diets across space and time.

Juvenile sockeye salmon were sampled from stations in the Discovery Islands and Johnstone Strait between May and July in 2015 and 2016 to capture the peak of the outmigration. Samples were collected using a modified purse seine deployed from an 8 m twin-outboard motored vessel. From each seine, 10 sockeye were taken for detailed dissections and analyses. For the purpose of the spatial analysis, samples collected between June 1 and June 9, 2015 were analyzed from six sites in each region. The sites closest to Queen Charlotte Strait and the Strait of Georgia experienced stronger influences from these regions, thus the following sub-regions were used for analyses: northwestern Johnstone Strait (J02), Johnstone Strait (J04–J09), Discovery Islands (D08–D11), and Southern Discovery Islands (D06, D07). To determine fine scale temporal changes, samples were analyzed from one site in each region (J07, D07) from late May, early June, and late June of each year. Zooplankton were sampled by conducting horizontal surface tows with a 250 µm net at each sampling location after fish were captured. Environmental data were measured by taking YSI readings at the surface and at 1 m depths, as well as secchi readings from the location of fish capture.

Prey samples and stomach contents were analysed to the lowest taxonomic level possible and a gut fullness index (GFI) was calculated by dividing the weight of the stomach contents by the weight of the fish and converting to a percentage. For visualization of diet and zooplankton composition data, the taxonomic categories were simplified into the following major groupings: Amphipods, Barnacles, Calanoid Copepods, Cladocerans, Decapods, Euphausiids, Larvaceans, and 'Other.' The latter category consisted mainly of gastropods, bivalves, polychaetes, insects, and fish and zooplankton eggs. Detailed taxonomic information was retained for multivariate analyses. Abundance and biomass data were arcsin transformed and Bray-Curtis (BC) rank dissimilarities calculated. Differences in prey and diet composition were assessed using non-metric multidimensional scaling (NMDS) ordinations of the BC matrix. A similarity of percentages analysis (SIMPER) was used to determine which taxa contributed most to groupings of fish/zooplankton. Average GFIs from each sampling event were compared to regional values reported by Brodeur et al. (2007) to determine whether the values in this section of the coast were above or below regional averages.

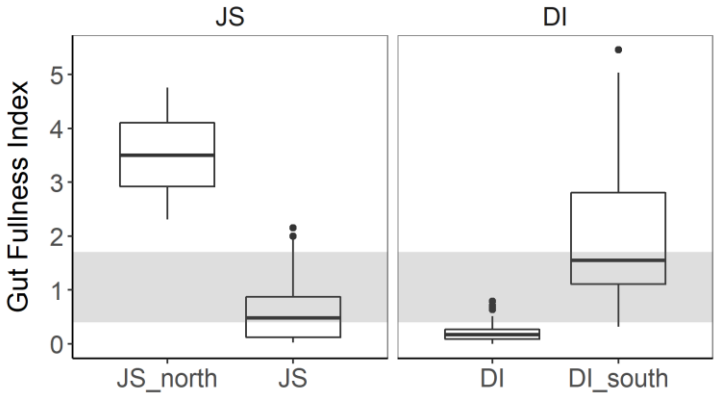

Fig. 2. Gut fullness index averaged across samples from the northwestern extent of Johnstone Strait (JS_north, *n* = 10), Johnstone Strait (JS, *n* = 52), the Discovery Islands (DI, *n* = 41) and the southern extent of the Discovery Islands (DI_south, *n* = 18) from June 2015. The grey box represents the first to third quartile of gut fullness values for juvenile sockeye collected along the northeast Pacific coast from California to Alaska in 2000–2002 (Brodeur et al. 2007).

Spatially, GFIs were low in the Discovery Islands and Johnstone Strait in June 2015, providing support for the trophic gauntlet hypothesis (Fig. 2). However, fullness indices were higher than the regional average at the sites nearest to the stratified waters to the north and south. These areas represent 'fronts,' where the convergence of stratified and mixed waters resupplies nutrients from depth to the surface waters, increasing local productivity (Boyd 1973; Simpson and Hunter 1974; Franks 1992). The higher productivity, as well as physical dynamics along fronts, causes plankton to accumulate, attracting higher trophic levels (Polovina et al. 2001; Genin et al. 2005). The high GFIs observed in these locations indicates that biological 'hot spots' may be present at the interface between mixed and stratified waters. Given the low foraging success observed in the well-mixed waters, these types of frontal areas may in fact be important foraging grounds for juveniles to facilitate their migration through otherwise challenging conditions.

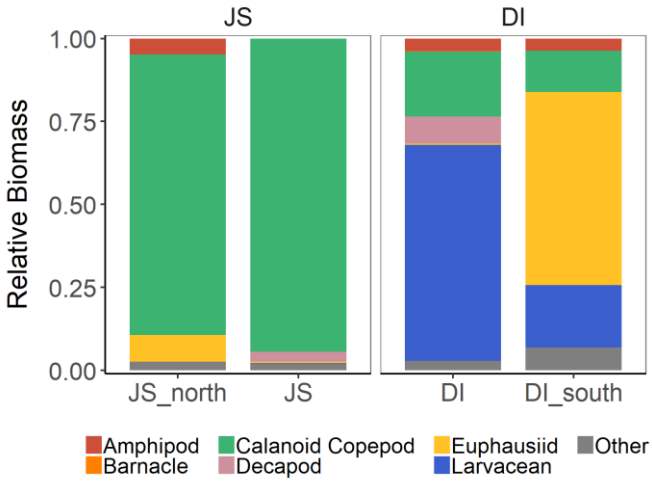

Fig. 3. Relative biomass of diet items averaged across samples from the northwestern extent of Johnstone Strait (JS_north, *n* = 10), Johnstone Strait (JS, *n* = 52), the Discovery Islands (DI, *n* = 41) and the southern extent of the Discovery Islands (DI_south, *n* = 18) from June 2015. Only items contributing > 5% to relative biomass are included.

Analysis of the stomach contents across the four sub-regions in June 2015 revealed two unique diet types: one dominated by larvaceans and euphausiids in the warmer, fresher water of the Discovery Islands and the other dominated by large calanoid copepods in the cooler, saltier water of Johnstone Strait (Fig. 3). This differentiation agrees with recent research that identifies unique zooplankton communities across the different ocean regimes in this region (Mahara 2018). These two regions represent two separate water masses with unique prey assemblages. The Discovery Islands, despite being tidally mixed, are influenced by the warmer, seasonally stratified waters of the Strait of Georgia from the south, while Johnstone Strait receives water from the continental shelf being flushed through Queen Charlotte Strait. Thus, oceanographic conditions appear to be linked to the type and quality of prey available to migratory salmon.

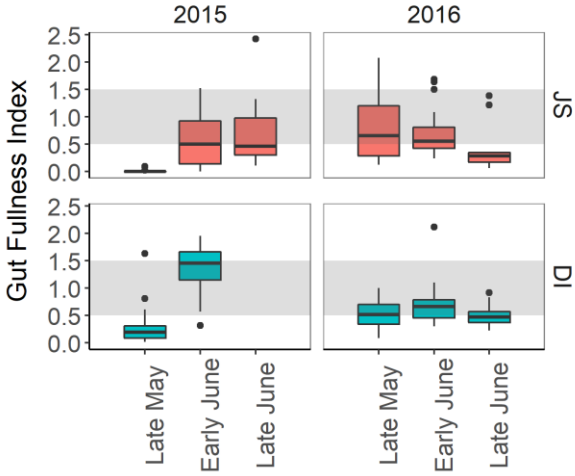

Fig. 4. Average gut fullness indices for juvenile sockeye salmon sampled in the Discovery Islands (DI) and Johnstone Strait (JS) in 2015 and 2016 across three time periods. Grey area represents the interquartile range of gut fullness values for juvenile sockeye collected along the northeast Pacific coast from California to Alaska in 2000–2002 (Brodeur et al. 2007).

Preliminary results from the temporal analyses suggest that the GFI varies across the migratory period, rather than remaining low. In 2015, gut fullness increased during the migratory period in both regions (Fig. 4). GFIs early in the 2015 migration were low, with a higher abundance of empty stomachs in Johnstone Strait in particular. In 2016, GFIs in the Discovery Islands remained low relative to the regional average throughout the entire migratory period, while values in Johnstone Strait decreased (Fig. 4). Thus, juvenile sockeye arriving early in 2015 experienced reduced foraging success, which may have been due to a mismatch in timing with the quantity and quality of their prey. In 2015, the peak abundance of zooplankton in the surface waters occurred in mid June, one week after the peak juvenile sockeye outmigration. In contrast, peak zooplankton abundance in the surface in 2016 was observed in mid-May, two weeks prior to the peak juvenile sockeye migration.

Diets in the Discovery Islands displayed greater temporal variation both within and between seasons than those in Johnstone Strait (Fig. 5). In 2015, diets in the Discovery Islands were dominated by small zooplankton (e.g., cladocerans and barnacles) early in the season and calanoid copepods near the end of the season. In 2016, the abundance of smaller zooplankton was higher throughout the migratory period, varying between 'other' zooplankton (e.g., zooplankton eggs, echinoderm brachiolaria, gastropod veligers) and larvaceans throughout the migration. In contrast, Johnstone Strait was dominated by calanoid copepods throughout the migratory season in both years, with higher abundances of larvaceans and decapods early in the 2015 migratory period. Therefore, a higher abundance of smaller zooplankton in 2016 may have contributed to the lower GFIs observed.

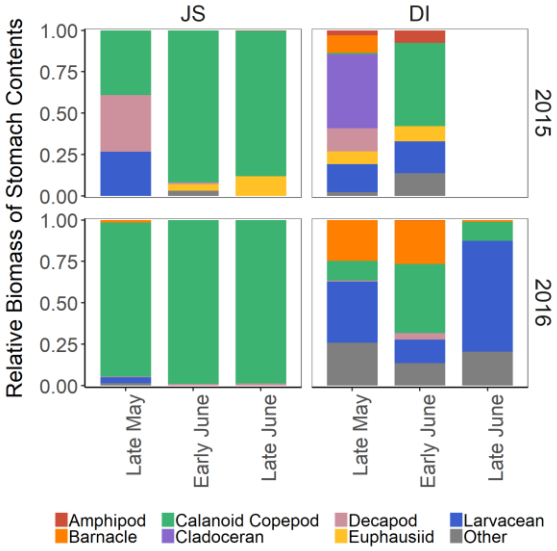

Fig. 5. Relative abundance of prey items averaged across fish sampled in each time period in the Discovery Islands (DI) and Johnstone Strait (JS) in 2015 and 2016. Only items contributing > 5% to relative abundance are included. No sampling was conducted in the Discovery Islands in Late June 2015.

In summary, juvenile sockeye can experience low foraging success in the tidally mixed Discovery Islands and Johnstone Strait, which may limit growth and affect their survival in years when they experience poor feeding conditions north or south of the mixed zone. However, we identified foraging hotspots at the southern and northern-most sites, where the mixed zones interfaced with stratified waters. These interface zones may provide essential energy to juveniles during their outmigration. While overall GFIs were lower than the regional average, they were variable over time, suggesting that conditions experienced by juvenile salmon can be favourable depending on the timing of their migration. Furthermore, prey and diets were composed of significantly different taxa between two neighbouring regions within a 150 km stretch of the salmon migratory route. Diets in the Discovery Islands were dominated by smaller meroplankton and larvaceans and exhibited seasonal succession, and those from Johnstone Strait were dominated by calanoid copepods throughout the entire migratory period in both years. This research demonstrates how bottom-up factors can influence the foraging success of juvenile salmon across fine spatial and temporal scales and provides new insight into foraging dynamics in mixed coastal waters.

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The Role of Environmental Conditions in Various Types of Estuaries for the Productivity of Pacific Salmon Populations of Kamchatka

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Keywords: estuary, hydrology-morphological conditions, aquatic communities, environmental factors, ecosystem, anadromous fish, Kamchatka

Estuaries are unique water systems that are under the influence of various natural and anthropogenic factors. They are of significant interest to specialists of various disciplines of Earth sciences, and in the last half century many countries have conducted detailed studies of them, including basic aspects of estuarine ecosystem ecology (Elliott and Hemingway 2002; McLusky and Elliott 2004; McLusky and Wolanski 2011; Day et al. 2012; Wolanski and Elliott 2015).

In the Russian Federation, such studies were carried out to a lesser extent, and focused mainly on the European part of the country (Chlebovich 1986). With regards to the Pacific coast of the Russian Federation, this large region is still poorly studied. Within its area, tidal estuaries of the Kamchatka region (including the Kamchatka Peninsula and the continental part of Koryakia) are more interesting because they are characterized by the maximum variation of types of estuaries in Russia due to differences in the physiographic conditions of this territory (Gorin 2012; Mikhailov and Gorin 2012; Gorin and Koval 2015).

Until recently, the majority of studies done on the estuaries of the Kamchatka peninsula were icthyological. These are estuaries of selected rivers located in the Karaginsky Bay of the Bering Sea, estuaries of the Avacha River (Eastern Kamchatka), Bolshaya River (Western Kamchatka) and adjacent coastal waters. In the 1970–1990's, they were chosen as assessment areas to determine the influence of environmental conditions on estuaries and coastal waters, specifically how this affects the abundance of the most important fisheries resources of the Kamchatka, such as Pacific salmon, herring, and smelts (Karpenko 1998; Vasilets 2000; Maximenkov 2007). Due to remoteness and isolation, most other Kamchatka estuaries have never been studied.

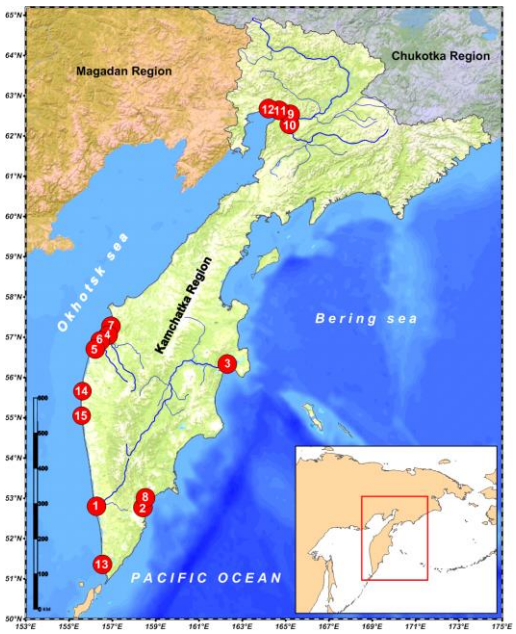

Fig. 1. The location of the rivers which estuaries were studied on the territory of Kamchatka region since 2002: 1) Bolshaya; 2) Bolshoy Vilyui; 3) Kamchatka; 4) Hairuzova; 5) Moroshechnaya; 6) Belogolovaya; 7) Kovran; 8) Avacha; 9) Penzhina; 10) Talovka; 11) Shestakova; 12) Mikina; 13) Ozernaya; 14) Icha; 15) Krutogorova.

Due to this knowledge gap, we began an integrated research program in 2002 to study Kamchatka estuaries. The main purpose of our studies is to assess the impact of abiotic, biotic and anthropogenic factors in various types of estuaries on the reproduction of anadromous fish populations of Kamchatka (primarily Pacific salmon). At the

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same time, our results enable us to compare features of functioning estuarine ecosystems under different climatic, hydrologic, and morphological conditions.

Our studies are based on a comparative method, which is indispensable for the analysis of complex phenomena (which are influenced by many interrelated factors) such as river mouth areas, estuaries, and coastal sea waters (McLusky and Elliott 2004; McLusky and Wolanski 2011; Day et al. 2012; Wolanski and Elliott 2015). For the full use of this method, we selected several Kamchatka estuaries which differed by morphological structure, the degree of interaction between river run-off and tides, and the level of reproduction of anadromous fish in that river basins (Fig. 1).

Using integrated field research, we studied environmental conditions and, wherever possible, the main biotic components of estuarine communities (e.g., plankton, benthos, fish fauna, marine mammals) in different seasons of the year. We also estimated the impact that anthropogenic activities were having on estuarine ecosystems. The field research results were analyzed using all available literary, archival and survey information.

Since 2002, integrated field studies were conducted in estuaries of the fifteen rivers: Bolshaya (2002–2005; 2010–2012; 2016); Bolshoy Viluy (2002–2004; 2006–2007); Kamchatka (2009–2010); Hairuzova (2011–2013); Moroshechnaya (2011); Belogolovaya (2011–2013); Kovran (2012–2013); Avacha (since 2013); Penzhina and Talovka (2014–2016); Shestakova and Mikina (2015); Ozernaya (2017); Icha and Krutogorova (2018) (see Fig. 1).

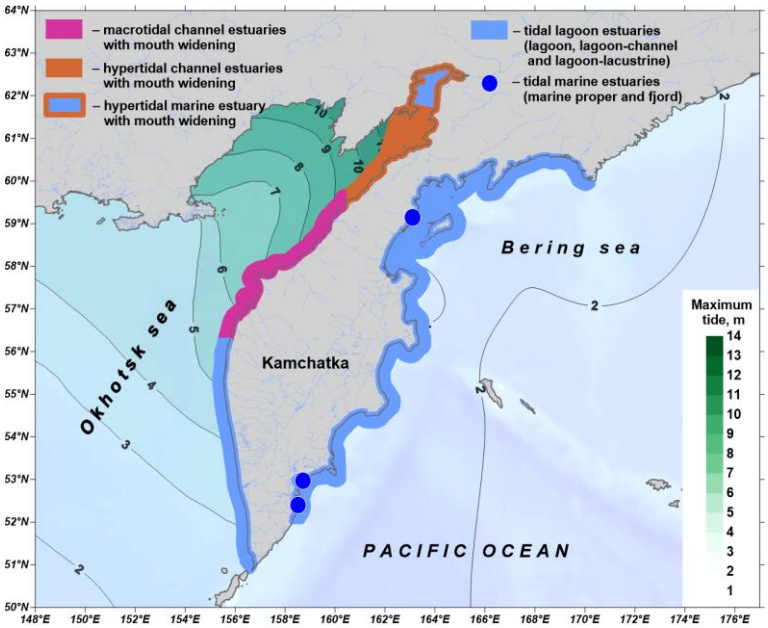

Fig. 2. Distribution of the various types of estuaries in the territory of the Kamchatka region.

As a result of hydrological and morphological studies, the typification of Kamchatka estuaries was carried out for the first time. All of Kamchatka estuaries by type and subtype were classified (Gorin 2012; Mikhailov and Gorin 2012; Gorin and Koval 2015). It has been established that "the lagoon-channel estuaries" dominate on the western coast of the Kamchatka peninsula (Fig. 2). Such estuaries were formed in the mouths of large and medium rivers, which flow into coastal areas with medium tides (up to 2–4 m) with extreme sea swell and open flat coast. "The channel estuaries with mouth widening" are widely distributed on the northwestern coast of Kamchatka. A necessary condition for the formation of these water systems are high (from 4 to 10 m) sea tides. On the eastern coast of the Kamchatka peninsula place there are "lagoon-lacustrine estuaries," which were formed when small rivers flowed into water reservoirs less than 10 km long, and were separated from the sea by sand and pebble coastal bars (wave-surf accumulative forms). The lagoon-channel estuaries can also be found on the flat areas of this region. The "marine estuaries" of Kamchatka are represented by Avacha Bay and Karaga Bay. They are located on the eastern coast of the peninsula and are semi-enclosed bays, and at the top they flow into large rivers. Also, within the territory of the Kamchatka region there are only two waterways which can be considered fjords, due to their peculiar morphological structure, and as estuaries (according to the hydrological regime). They are known as Vilyuchinskaya Bay and Russkaya Bay (Gorin 2012; Mikhailov and Gorin 2012).

In the results of biological studies, the main habitat areas with the abiotic conditions and composition of biological communities in Kamchatka estuaries were identified. According to the distribution of fauna in Kamchatka estuaries there are usually three main ecological zones. These zones (with a certain degree of

convention) were determined as the freshwater, estuarine and neritic zones. The estuarine zone classifications generally matched the boundaries of the estuary based on the hydrological criteria, such as their bathymetry and salinity. In this zone, as a rule, species that have adapted to the extreme hydrological conditions dominate the river mouth. In the areas of contact between the major ecological zones, there were transitional subzones, and the fauna present was made up of representatives of the two adjacent communities. The abundance, distribution and species composition of hydrobionts in estuaries are subject to daily variability associated with the tidal phases. Marine species migrate to the tide from the sea to the estuary, and then to the lower reaches of the rivers flowing into them. Freshwater fauna migrates at ebb tide from the rivers to the estuary and then to the sea (Koval and Gorin 2016).

Due to the hydrological and morphological characteristics in the various subtypes of estuaries in the Kamchatka region, the composition and ecology of aquatic communities are determined by the dominant environmental factors (Gorin and Koval 2015). For example, in the lagoon-channel estuaries, one main abiotic environmental factor is strong variability in water salinity. In the lagoon-lacustrine estuaries, it is the low concentration of dissolved oxygen coupled with the presence of hydrogen sulfide. In the channel estuaries with mouth widening, it is the significant tidal fluctuations of water levels, which periodically dry out parts of the estuary. The greatest variety of environmental conditions are observed in the different lagoon-channel estuaries which may include both water channels and basins with different salinities. The most extreme habitats of aquatic animals are found in the lagoon-lacustrine estuaries and the channel estuaries with mouth widening: in the first case, due to the periodic appearance of hydrogen sulfide, and in the second case, due to the stressful influence of tides (permanent variability of water level, salinity, temperature, turbidity, speed and direction of water flow, etc.).

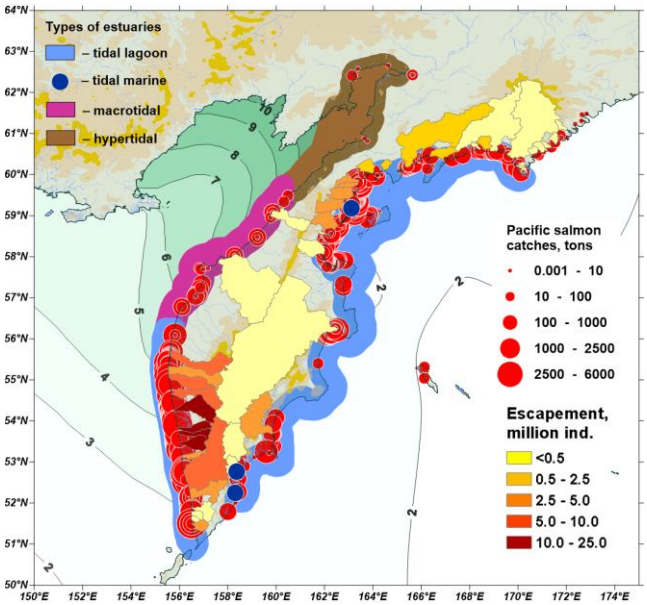

Fig. 3. Distribution of tides, types of estuaries, commercial catches and escapement of Pacific salmon on the Kamchatka region, 2018.

The analysis of information about the main area of reproduction and fishing of Pacific salmon in the Kamchatka region and our data suggests that the survival of Kamchatkan Pacific salmon during the early marine period of their life cycle is directly related to the specific hydrology-morphological conditions they are exposed to in the various types of estuaries. These conditions also could determine the distribution, biological particularities, and reproduction level of Pacific salmon populations which would specifically affect salmon fisheries in the different areas of Kamchatka peninsula (Fig. 3).

We predict that the low abundance of Pacific salmon in the rivers placed on the northwest coast of Kamchatka (where tides level variation more then 5–6 m) is a result of the hydrological and morphological specifics of the macrotidal and hypertidal estuaries, including: 1) silty substrate making the lower parts of the rivers unsuitable for salmon spawning; 2) long length of the estuary and extremely strong tidal effects that cause high mortality of juvenile salmon during downstream migration; 3) aggregation of predators (especially marine mammals) that increase mortality of adult salmon during upstream migration (Koval et al. 2012; Koval and Gorin 2013).

To test this hypothesis in the coming years, we plan to conduct a series of integrated studies on several Kamchatka estuaries to characterize the morphological structure, hydrological regime and fishery resources, which differ from the previously studied waterways. For example, studies are planned to provide information on Karaga

Bay and Ossora Bay (northeastern Kamchatka, type of estuaries: marine). This is one of the main regions of reproduction and fishing of Pacific salmon in the Russian Far East (primarily pink salmon of odd years). These estuaries differ between themselves in the degree of influence of the rivers on their hydrological regime and the size of river basins. Also, we plan to study the estuary of Vilyuchinskaya bay (southeastern Kamchatka, type of estuary: marine; subtype: fjord). Many species of marine and anadromous fish are produced in this estuary (Pacific salmon, smelts, chars, capelin, flounders, saffron cod, etc.). However, economic activity in this estuary is almost completely absent.

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Is Juvenile Salmon Condition Driven by the Nutritional Quality at the Base of the Plankton Food-web?

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Keywords: Strait of Georgia, fatty acids, juvenile salmon

A first step towards understanding the impact of long-term changes in oceanographic conditions and zooplankton communities on salmon is characterizing the food-web pathways that support them. Salmon's juvenile phase includes their transition from freshwater to the ocean, and there is evidence pointing to the importance of nutritional condition during these early life stages as being critical for the success of the adults' return (Beamish and Mahnken 2001). The study of the food quality and plankton-based energy sources for Pacific salmon during the fish's early ocean phase offers information on how salmon condition relates to the environment. The Strait of Georgia (SoG) supports the early marine phase of salmon emanating from British Columbia's biggest salmon producer, the Fraser River, and most smolts in the region out-migrate between February–June.

We thus analyzed the regional and seasonal fatty acid (FA) composition dynamics of zooplankton and particulate organic matter (POM) in the SoG. Specifically, we quantified the FAs 20:5n3 (EPA) and 22:6n3 (DHA), which are essential for the fish development, and we calculated the DHA to EPA ratio (DHA:EPA), which is commonly used as a proxy for nutritional quality of food for fish (Kainz et al. 2004) and for the nutritional condition of the fish themselves. In particular, higher DHA:EPA values have been linked to relatively higher abundance of dinoflagellates compared to diatoms and better fish condition.

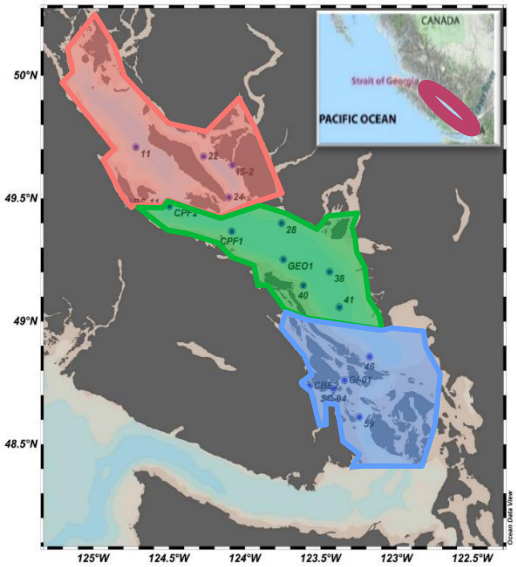

Fig. 1. Map of the Strait of Georgia with the sampling sites (blue points) and the three regions established for this study (red = north, green = central, blue = south).

Methods

Particulate organic matter (POM) and zooplankton samples were collected between 2015–2018 by filtering 10 L of surface water through 47 mm GF/F filters and with a pair of 64 µm mesh-size bongo nets, respectively. Immediately after collection, zooplankton were size-fractionated on board through a set of sieves and flash-frozen in liquid nitrogen. In the lab, we sorted the zooplankton samples according to the following size groups: small (64–

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250 µm), medium (500–1,000 µm) and large (1,700–8,000 µm). Additional samples of large zooplankton were sorted by species for taxon-specific analyses.

We grouped samples according to their location in three main regions: North—north of 49.48°N, where the influence from the Pacific Ocean and from the Fraser River are weak; Central—between 49.48°N (southern tip of Texada Island) and 49°N (southern part of the Fraser River Delta), which is the area receiving most of the influence from the Fraser River; and South—south of 49°N, which comprises the Gulf Islands region and is subjected to a greater influence from the Pacific Ocean than the rest of the SoG (Fig. 1). Samples were prepared for fatty acid (FA) analysis as in Forster et al. (2011).

Results and Discussion

Potential prey (i.e., large zooplankton) for smolts have better nutritional quality in the southern SoG than in the northern region (Fig. 2), which suggests that fish that remain in the southern region for longer might benefit from the prey quality more than smolts that migrate north immediately after leaving the river.

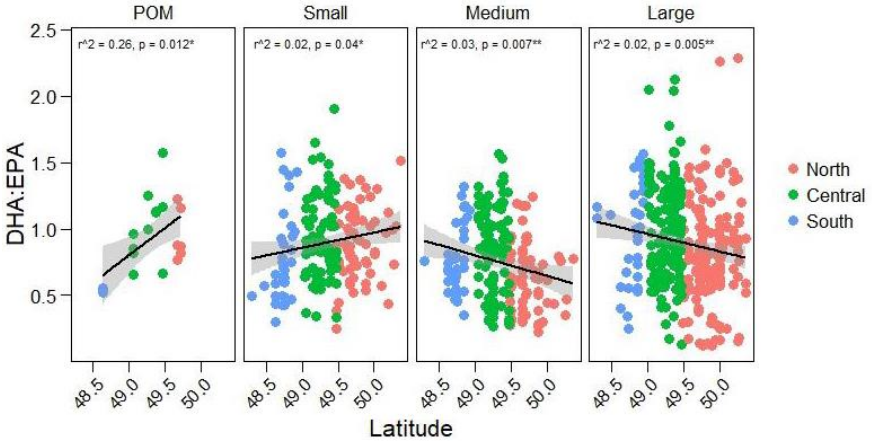

Fig. 2. DHA:EPA increases from south to north in POM and in small zooplankton, but decreases with latitude in medium and large zooplankton, which are the potential prey for juvenile salmon.

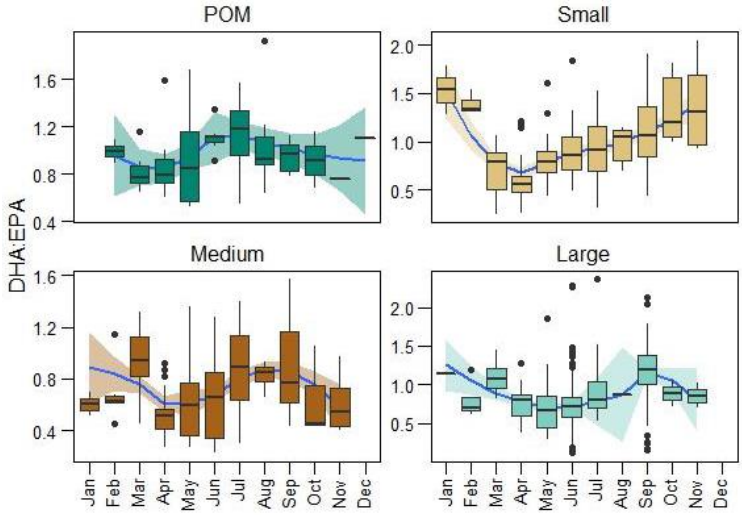

Fig. 3. DHA:EPA values were significantly lower in spring (April–June) than in summer (July–September) and winter (January–March) for POM and all zooplankton size fractions.

Regarding the seasonal patterns of plankton FAs we found that, for the period 2015–2018, DHA:EPA in POM was higher between May–August (Fig. 3). However, in all zooplankton size fractions DHA:EPA values were significantly lower in spring (April–June) than in summer (July–September) (Fig. 3). DHA:EPA > 1 indicates a dominance in the contribution of dinoflagellates, whereas a value < 1 suggests a greater contribution of diatoms (Budge and Parrish 1998). Thus, our seasonal data of DHA:EPA in POM accurately captures the diatom-rich spring bloom in the SoG (Fig. 3). Therefore, smolts out-migrating later in the season (i.e., summer) might encounter better quality food than in spring.

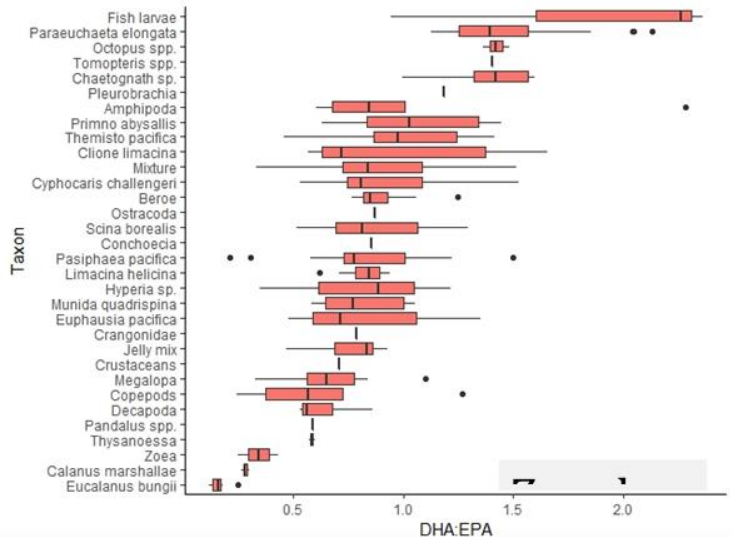

Fig. 4. Fish larvae, *P. elongata*, *Octopus* spp. and *Tomopteris* spp. are the potential salmon prey with the highest nutritional quality, whereas *C. marshallae* and *E. bungii* presented the lowest nutritional quality. All individuals were obtained from the large zooplankton size fraction (i.e., larger than 1,700 µm).

We also showed that fish larvae, chaetognaths, most amphipod species and the carnivorous copepod *Paraeuchaeta elongata*, among other groups, have higher DHA:EPA than POM, whereas other copepod species (e.g., *Calanus marshallae* and *Eucalanus bungii*), decapods and euphausiids have lower DHA:EPA (Fig. 4). This indicates that a diet based on species from the former group might translate to a better salmon juvenile nutritional condition compared to salmon that feed mostly on decapods and euphausiids. Consequently, we hypothesize that the decrease in the juvenile salmon condition might be explained by a disruption in the food-web pathways to juvenile salmon between POM and zooplankton.

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Trophic Relationships between Juvenile Salmon during a 22-year Time Series of Climate Variability in Southeast Alaska

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Keywords: diet, climate change, nutritional quality, feeding intensity

Marine growth and survival of juvenile Pacific salmon (*Oncorhynchus* spp.) has been linked to marine temperatures and feeding conditions during their first few months at sea (Beauchamp et al. 2007; Farley et al. 2007; Fergusson et al. 2013). Evidence from the Bering Sea (Siddon et al. 2013; Eisner et al. 2017), Prince William Sound (Armstrong et al. 2011; McKinstry and Campbell 2018), and Southeast Alaska (SEAK; Landingham et al. 1998; Sturdevant et al. 2012) suggest that the juvenile salmon prey community is responsive to environmental change, and that these changes are reflected in their species richness, abundance, and nutritional quality. Therefore, understanding what salmon consume under varying environmental conditions is important to understanding how their growth and survival is affected by climate change.

To identify differences in the diet composition among juvenile salmon species and in relation to shifts in seawater temperature during the summer months of 1997–2018, we examined a 22-year time series in periods of warm and cool years for juvenile pink (*O. gorbuscha*), chum (*O. keta*), sockeye (*O. nerka*), coho (*O. kisutch*) and Chinook (*O. tshawytscha*) salmon. Diet information included diet compositions from June–August in Icy Strait (58°N, 135°W), Alaska, a major fish migration corridor in northern SEAK. Up to 30 average sized fish per species and year (10 per month) were collected during annual Southeast Coastal Monitoring surveys (Fergusson et al. 2019). No coho samples were available in 1999 and no Chinook salmon samples were available in 2001–2006 and 2009–2011. Warm and cool years were defined by annual deviations from the grand average of the monthly averages of the upper 20 m water column temperatures at 8 stations in Icy Strait (Fig. 1). Eleven warm years and 11 cool years were identified over the 22-year time series. Years with anomalously warm and cool temperatures corresponded with basin scale warming and cooling events including the 2005 and 2015 El Niños, 2002 and 2008 La Niñas, and the 2014–2016 Gulf of Alaska marine heat wave.

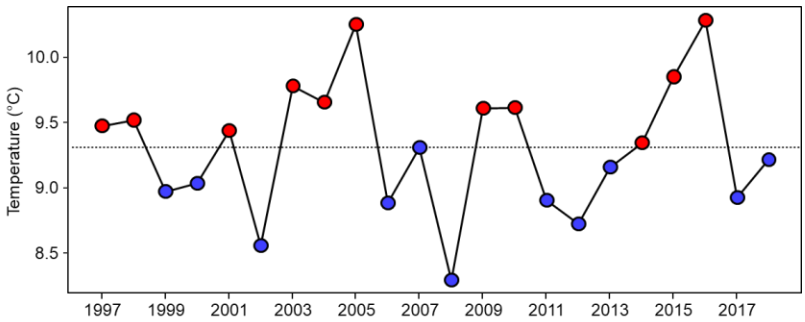

Fig. 1. Average upper 20 m water column temperatures (°C) and 22-year average temperature (dotted line) collected May-August during annual Southeast Coastal Monitoring project sampling in Icy Strait, Alaska, 1997–2018.

In the laboratory, stomach contents of each individual fish were microscopically identified to lowest taxa possible, grouped, and weighed (± 1.0 mg). Percent composition by weight was calculated as (weight of prey item/weight of all prey items)*100. There were very few empty stomachs observed over the time series (34 of 1,627 samples) and were observed for each species. We tested for differences among species and between warm and cool years using the PRIMER v. 7 (Clarke and Gorley 2015) multivariate statistical package. Diet data was square-root transformed and a Bray-Curtis similarity matrix was calculated prior to analysis. We used a two-way crossed analysis of similarity (ANOSIM) procedure, with species and year group (warm or cool) as factors, to test for differences in diet composition among species and year group. The ANOSIM Global R-statistic ranges between 0 and 1, where 0 indicates no separation between tested groups and 1 indicates complete separation. When significant differences among groups were found ($p < 0.05$), pairwise comparisons were used to identify which groups were significantly different (Table 1). Finally, we used the Bootstrap Averages procedure to visualize the trophic relationships among species and between year groups.

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Table 1. Global R values of Analysis of Similarity (ANOSIM) test results of diet differences between juvenile salmon species and year group (warm or cool). Values greater than 0.4 (> = moderate separation) are indicated in bold, significant differences ($p < 0.05$) are indicated by an asterisk.

		Cool years				
		Pink	Chum	Sockeye	Coho	Chinook
Warm years	Pink	0.080	0.101*	0.091	**0.633***	**0.628***
	Chum	0.351*	0.098	**0.523***	**0.925***	**0.930***
	Sockeye	0.084	0.182*	0.012	**0.655***	**0.720***
	Coho	**0.752***	**0.931***	**0.815***	0.008	0.268*
	Chinook	**0.624***	**0.915***	**0.858***	**0.542***	0.097
		Warm years				
		Pink	Chum	Sockeye	Coho	Chinook
Warm years	Pink					
	Chum	0.055				
	Sockeye	0.032	0.270*			
	Coho	**0.692***	**0.900***	**0.709***		
	Chinook	**0.609***	**0.917***	**0.699***	0.318	
		Cool years				
		Pink	Chum	Sockeye	Coho	Chinook
Cool years	Pink					
	Chum	0.041				
	Sockeye	0.003	0.252*			
	Coho	**0.644***	**0.893***	**0.750***		
	Chinook	**0.664***	**0.909***	**0.874***	0.376*	

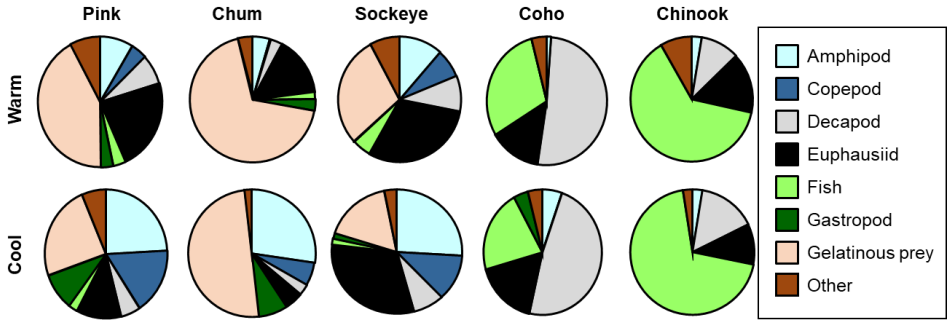

Fig. 2. Average diets (% weight composition) of juvenile pink, chum, sockeye, coho, and Chinook salmon in warm and cool years. Fish samples were collected in June–August during annual Southeast Coastal Monitoring project sampling in Icy Strait, Alaska, 1997–2018.

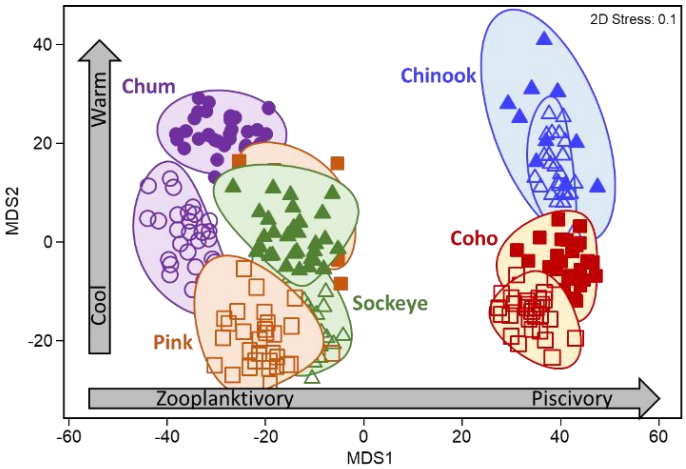

Fig. 3. Bootstrap average MDS ordination plots of diets (average % weight composition) of juvenile pink, chum, sockeye, coho, and Chinook salmon in warm and cool years. Fish samples were collected in June-August during annual Southeast Coastal Monitoring project sampling in Icy Strait, Alaska, 1997–2018.

The diet composition varied among and between the zooplanktivorous (pink, chum, and sockeye) and piscivorous (coho and Chinook) juvenile salmon species (Table 1, Figs. 2 and 3). However, for each species, diet compositions did not differ significantly between warm and cool years. For the zooplanktivores, diets of pink salmon were similar to both chum and sockeye diets in both warm and cool years. Diets of chum and sockeye salmon differed significantly in both warm and cool years. Chum salmon consumed high proportions of gelatinous prey and amphipods whereas sockeye salmon consumed a variety of prey including copeopds, amphipods, euphausiids, and gelatinous prey. Pink and sockeye salmon increased consumption of euphausiids and fish larvae in warm years and amphipods and copepods in cool years. The piscivorous coho and Chinook salmon diets contained similar prey (fish and decapod larvae and euphausiids). Coho salmon diets consisted of decapod larvae and euphausiids with small proportions of fish larvae. In contrast, Chinook salmon diets consisted of fish larvae with small proportions of euphausiids and decapods. The coho and Chinook salmon diets differed significantly in cool years when the coho salmon increased consumption of gastropods and amphipods. The fish prey was not broken out by species so differences in fish prey species consumed in warm and cool years was not possible. Juvenile coho and Chinook salmon predation on euphausiids, decapod larvae, and larval fish is common throughout much of their range along the coasts of Washington, British Columbia, and Alaska (Brodeur et al. 2007; Weitkamp and Sturdevant 2008).

Overall, the diet differences between the zooplanktivorous and piscivorous juvenile salmon was stronger than the differences within these trophic groups or between warm and cool years. These results suggest that the feeding environment in Icy Strait is relatively stable and/or the juvenile salmon are able to trophically adapt to changes in the prey field during this critical early marine growth period. Additionally, this study only addresses the quantity of food consumed and does not incorporate the quality of the prey. The % lipid content of major zooplankton in Icy Strait has shown inter-annual fluctuations from < 0.01 to > 20% lipid content (Fergusson unpublished data). This shift in available lipids could benefit or hinder the growth and survival of the juvenile salmon. Without longterm monitoring studies such as the Southeast Coastal Monitoring project, comprehensive analyses would not be possible, which also underscore the importance of incorporating trophic measures into long-term monitoring of pelagic ecosystems.

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Density-dependent Marine Survival of Hatchery-origin Chinook Salmon may be Mediated by Pink Salmon

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Keywords: Chinook salmon, pink salmon, hatcheries, density dependence, marine survival, aquaculture

Density-dependent effects between pink salmon (*Oncorhynchus gorbuscha*) and other species, including other species of Pacific salmon, have been documented by a number of studies. Density-dependent interactions between pink and Chinook salmon (*O. tshawytscha*) have also been previously hypothesized in the Salish Sea (Claiborne et al. in press; Ruggerone and Goetz 2004; Ruggerone et al. 2019), a rich and diverse but highly-impacted inland sea in Washington State and British Columbia. In the central and southern parts of the Salish Sea, almost all pink salmon spawn in odd-numbered years and juveniles emigrate in even-numbered years. Juvenile Chinook and pink salmon are both found there between April through July of even years (Duffy et al. 2005; B. Berejikian, NOAA Fisheries, unpublished data).

Increasing the abundance of adult Chinook salmon in the Salish Sea is currently an ecosystem management priority (Riddell et al. 2013). Chinook salmon have been produced by hatcheries for over 100 years (Beamish et al. 1997), and increased production has been proposed (WDFW 2019). Our objectives are to examine historical patterns of Chinook salmon survival and identify the potential need for future work examining the mechanisms behind our observations. We seek to answer the question: in the past, when more hatchery Chinook salmon have been released into the central and southern Salish Sea in years when juvenile pink salmon are and are not also emigrating (pink years vs. non-pink years, respectively), has there been an associated increase in the number of hatchery Chinook salmon that have survived during their migration in the ocean and returned as adults?

We first used data from 33 Pacific Salmon Commission's Chinook Technical Committee CWT stocks with release numbers and marine survival rates over ocean entry years (OEY) 1983–2012. These data included the total number of tagged Chinook salmon juveniles released from a given hatchery and estimates of the numbers of tagged fish recovered in the North Pacific Ocean at age 2 years (for those released as sub-yearlings) or age 3 years (for those released as yearlings) (Joint Chinook Technical Committee (CTC) 2018). These stocks were grouped into eight regions (Fig. 1).

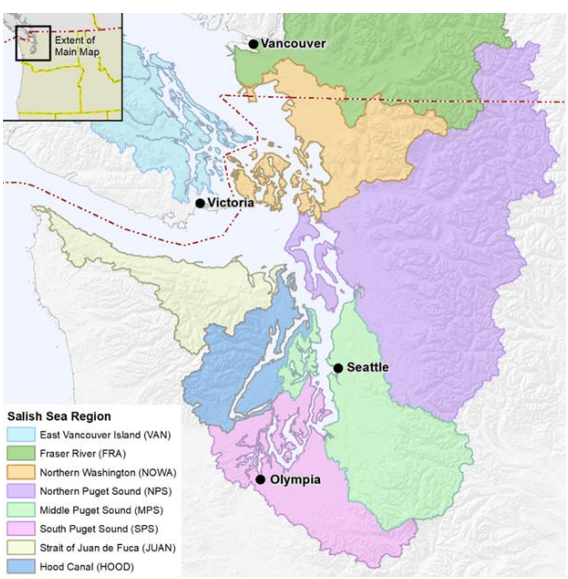

Fig. 1. Map of the eight southern Salish Sea regions from which hatchery Chinook salmon assessed.

To evaluate factors associated with marine survival of hatchery Chinook salmon, we fit multiple hierarchical regression models to survival rates from CWT data. Specifically, we modeled instantaneous mortality rate from

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release to age 2 for each stock i in region r in year t ($M_{i,r,t}$) as a function of multiple covariates. We explored model formulations that included covariates including juvenile Chinook life history (sub-yearling vs. yearling release; $LifeHist_j$), release region, the standardized number of hatchery releases per region ($Hatch_{r,t}$), presence of pink salmon in the Salish Sea ($Pink_t$), and release year. Based on model selection criteria that considered model fit and complexity, the best-performing model was:

$$M_{i,r,j,t} = \beta_{0_i} + LifeHist_j + Region_r + \beta_1 Hatch_{t,r} + Pink_t + \beta_2\left(Pink_t \times Hatch_{t,r}\right) + \varepsilon_i \,.$$

This model explained 44% of the variation in the observed mortality rates from release to age 2.

Regional effects appeared to be important in explaining marine survival to age 2 or 3 of hatchery Chinook salmon, specifically JUAN, MPS, NPS, and FRA (Fig. 1 and Table 1). The interaction between the presence of juvenile pink salmon in the Salish Sea and juvenile hatchery Chinook release numbers was also found to have "significant" explanatory power in the best-performing model (Table 1). The coefficient value suggested a significant negative interaction between juvenile pink salmon and hatchery release number. Therefore, in even-numbered years, greater hatchery Chinook salmon releases were associated with decreased marine survival. Predicted mean marine survival rates in these pink years were lower than those in non-pink years.

Table 1. Summary of posterior distributions for regression coefficients in the best-performing model. Included are the estimates for the posterior mean, standard deviation, and 95% credible intervals (CIs). Parameter estimates and credible intervals shown in bold do not overlap with zero.

Parameter	Mean	SD	2.5% CI	97.5% CI
Intercept (Region 1 [JUAN])	**5.46**	**0.36**	**4.72**	**6.18**
Region 2 (HOOD)	-0.81	0.73	-2.20	0.67
Region 3 (SPS)	-0.81	0.49	-1.76	0.17
Region 4 (MPS)	**-1.19**	**0.47**	**-2.09**	**-0.27**
Region 5 (NPS)	**-1.07**	**0.43**	**-1.91**	**-0.22**
Region 6 (NOWA)	-0.80	0.53	-1.87	0.25
Region 7 (VAN)	-0.79	0.45	-1.66	0.13
Region 8 (FRA)	**-1.99**	**0.49**	**-2.95**	**-0.99**
Life history	-0.07	0.31	-0.68	0.56
Juvenile hatchery Chinook salmon abundance	-0.12	0.10	-0.31	0.07
Juvenile pink salmon presence	0.12	0.07	-0.01	0.25
Juvenile pink salmon presence x juvenile hatchery Chinook salmon abundance	**0.54**	**0.13**	**0.28**	**0.80**

We simulated the numbers of sub-yearling Chinook salmon that had survived over the range of observed releases of juvenile hatchery fish; the predicted numbers were termed "recruits." We simulated survival rates for stocks in each geographical region in pink and non-pink years. The relationship between the numbers of recruits and the numbers of juveniles released was different for juveniles released in pink and non-pink years. Across regions, in non-pink emigration years, increases in hatchery Chinook production are associated with generally linear increases in age-2 recruits (Fig. 2). However, in pink years, increases in Chinook hatchery production were associated with a leveling off or even a diminishing number of recruits, which suggests the presence of density-dependent mortality. This suggests that the presence of emigrating juvenile pink salmon may somehow alter the relationship between the abundance of juvenile Chinook hatchery released and their marine survival. Therefore, hatchery Chinook salmon may have experienced density dependent survival in years when there are higher total numbers of salmon in the Salish Sea. Greater understanding of potential density-dependent interactions in the Salish Sea in the past may help inform Chinook salmon hatchery production and encourage future work evaluating potential mechanisms behind the findings.

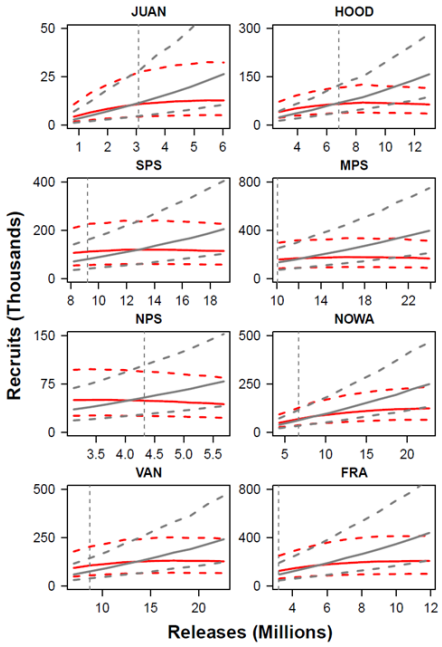

Fig. 2. Projected sub-yearling Chinook salmon recruits (age 2) in the ocean (y-axis) vs. the total number of juveniles released in each region (x-axis). Grey lines show projected values in non-pink years while red lines show values in pink years. Dashed lines depict 95% posterior predictive intervals. Vertical dashed lines show average annual number of releases for the most recent 5 years in each region.

In our second analysis we used a dataset that included all sub-yearling Chinook salmon released into the central and southern parts of the Salish Sea along with estimates of the numbers of adult hatchery Chinook salmon returning to Puget Sound (i.e., total run size; before any fish were caught in Puget Sound) between 1980 and 2015. We examined the relationship between the numbers of juvenile hatchery Chinook salmon released in pink years vs. non-pink years in the six Puget Sound regions and the associated total run-reconstructed index numbers of adult Chinook salmon that returned to Puget Sound. We plotted these cohort-specific values for each region and used simple linear regression to estimate trends between pink- and non-pink-year emigration cohorts for each region. For pink year emigrants, this relationship was negative in 5 of the 6 regions Fig. 3), statistically significantly at the 0.05 level for two regions (SPS and MPS). This relationship was significantly positive for NOWA. For non-pink-year emigrants, the slope of the regression line was positive for three regions (MPS, NPS, and NOWA [significantly so for this region]) and negative for the three others. In five regions, the linear trend in pink years was more negative than it was in non-pink years. Notably, there was only one region (NOWA) where the relationship between hatchery releases and returns was significantly positive in either pink or non-pink years (Fig. 3).

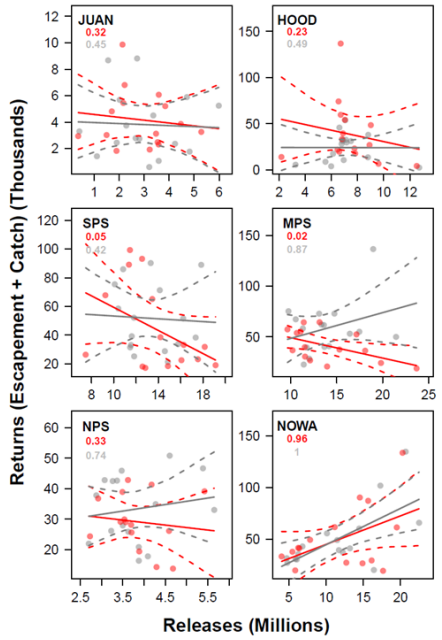

Fig. 3. Run reconstruction of the total numbers of adult hatchery Chinook salmon from each region returning to Puget Sound (y-axis) vs. the number of juveniles released that produced those adults (x-axis). Grey line is the regression trend line of data from non-pink years while red line is the best-performing regression line of pink-year data. Dashed lines depict 95% credible intervals for each series. Red and grey numbers are the probability of each slope being > zero.

Recovery of Chinook salmon in the Salish Sea will be a complicated and difficult process (Marshall et al. 2016) that will need to address the range of the 4-Hs of human impacts on salmon (Ruckelshaus et al. 2002). The story of density-dependent mortality of hatchery Chinook in the Salish Sea is by no means complete, though we have found signs of such mortality when many juvenile hatchery Chinook and pink salmon are present in the system. The findings of this paper cannot and should not simply be extrapolated to inform future hatchery releases; environmental conditions faced by hatchery Chinook in past years will not be the same as those faced in the future. However, by considering potential density-dependent interactions of hatchery Chinook salmon with pink salmon in the Salish Sea and exploring the mechanisms behind these findings, hatchery management practices and research can be further informed to benefit Chinook salmon conservation.

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Bottom-up Links to Juvenile Salmon Growth and Survival in Puget Sound, WA, USA

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Keywords: Zooplankton, juvenile salmon, Puget Sound, climate variability

Over the past several years, the Northeast Pacific has experienced a broad range of conditions ranging from "normal" to unprecedented warm temperature anomalies. Such extreme climate variability had clear impacts on the biology and provided the opportunity to explore the mechanisms through which large-scale climate change influences salmon through bottom-up processes. We used data from several monitoring programs in the Strait of Juan de Fuca and Puget Sound to explore spatial and interannual variability in ecosystem response to environmental change over 2014–2017. We focus on changes in temperature and zooplankton relationships to juvenile salmon growth and survival in four regions, from north to south: the San Juan Islands, Admiralty Inlet, Central Basin, and South Sound.

Monthly CTD casts have been conducted since 1997 by the Washington Dept. of Ecology to measure temperature, salinity, and fluorescence. The fluorometer was calibrated to chlorophyll biomass using filtered Niskin water samples at each station. Zooplankton were collected bi-weekly in spring through fall of 2014–2017 by multiple partners using 60-cm diameter, 200-µm, full water-column vertical net tows. Biomass was calculated using carbon conversions from abundances of taxa identified in the laboratory to species and life stage. Juvenile salmon growth was calculated from the change in weight over the time from hatchery release to recapture on Canada Department of Fisheries and Oceans R/V *Ricker* trawl surveys conducted in Puget Sound once per summer in most years since 1999. Smolt-to-adult coho survival data were calculated by M. Alexandersdottir under a contract from the Tulalip Tribes from coded wire tag returns (available only through 2015).

Temperatures showed strong seasonal cycles and a latitudinal gradient from cooler in the north where there is more connection to the ocean, to warmer in the more isolated regions to the south. The coolest year overall at all sites was 2014; 2015 and 2016 were record-breaking warm; 2017 was cooler, with Central and South Basin remaining slightly warmer than in 2014 while the San Juan Islands and Admiralty Inlet sites returned to approximately 2014 temperatures. Chlorophyll biomass was highest in Admiralty Inlet and Central Basin where spring and fall blooms occurred in most years. There were mixed interannual patterns among sites: in Central Basin chlorophyll was highest in 2014 and 2017, and considerably lower in 2015–2016. Chlorophyll was relatively low in the San Juan Islands and South Sound, and differences among years were not as apparent there.

Cumulative total zooplankton biomass curves showed spatial and temporal differences. In all regions, biomass was lowest in 2014 and higher in 2015. This was also true for all taxa that are important juvenile salmon prey (crab larvae, amphipods, etc.). In the San Juan Islands where biomass was relatively low overall, biomass peaked in 2015 whereas at the other stations, biomass was even higher in 2016. In 2017, biomass was lower at the northern two sites, but stayed high at the Central and South sites where water temperatures also stayed relatively warm.

Growth of juvenile Chinook salmon from hatcheries in Puget Sound showed a clear relationship with sea surface temperature anomalies measured at Race Rocks Lighthouse, which also correlates with the Pacific Decadal Oscillation. Regions showed strong spatial coherence, with highest growth observed in the very warm years of 2005 and 2015–2016, and low growth during cool periods. Coho salmon smolt-to-adult survival was higher for fish that out-migrated during the warm year of 2015 compared to 2014 in nearly every stock calculated across Puget Sound. Survival data are not yet available for Chinook salmon or for years beyond 2015, but anecdotes of poor 2017 returns indicate that future cohorts did not survive as well, despite continued high zooplankton biomass in most regions of Puget Sound.

In conclusion, the large interannual differences in temperature had strong effects on plankton phenology, biomass, and community structure with responses differing among local sub-basins of Puget Sound. In contrast to expectations, during the warm years, zooplankton biomass and juvenile salmon growth were strongly elevated, and returns of 2015 coho salmon outmigrants indicated relatively high survival. This contrasts with reports from the Washington and Oregon coast and demonstrates the need for monitoring and indicator development within Puget

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Sound to better forecast salmon returns. High temperatures and sufficient food during their critical early marine life stage may have contributed to high growth and over-winter survival of salmon. But returns of subsequent years' cohorts suggests that something other than Puget Sound conditions controlled survival—possibly Pacific Ocean conditions were too poor for adult salmon to overwinter.

Acknowledgments—This study was conducted as part of the Salish Sea Marine Survival Project (SSMSP). Zooplankton samples were collected by Kwiáht (San Juan Islands), the Port Gamble S'Klallam Tribe and WA Dept. of Fish and Wildlife (Admiralty Inlet), King County (Central Basin), and the Nisqually Indian Tribe (South Sound). Funding for the zooplankton sampling and this analysis came from the SSMSP via Long Live the Kings, NOAA via the Tulalip Tribes, the WA Dept. of Natural Resources, and the University of Washington.

Quantifying Juvenile Salmon Prey Quality and Exploring Trophic Linkages in Puget Sound, WA, USA

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Keywords: zooplankton, juvenile salmon, prey quality, essential fatty acids, Puget Sound

Prey composition and quality are critically important to the growth of juvenile salmon and to their survival to adulthood. Juvenile fish need more than just sufficient caloric intake—they also need to have a balanced composition of essential nutrients to achieve high growth rates. Eicosapentaenoic acid (EPA, 20:5ω3) and docosahexaenoic acid (DHA, 22:6ω3) are essential fatty acids (EFA) needed for fish well-being and growth that must be acquired through diet (Bell et al. 1997; Glencross 2009; Daly et al. 2010). High growth rates in the early marine period of a juvenile salmon may be critical to future survival (Beamish et al. 2004; Cross et al. 2009; Duffy and Beauchamp 2011). Puget Sound serves as an important nursery area for juveniles to feed and grow for several weeks to months before migrating to the ocean, but little is known about the fatty acid content and composition, and therefore quality as prey, of the zooplankton. The goal of this project was to gain insight into the lower trophic level food web that supports salmon growth by addressing these main objectives: 1) Assess dietary quality of juvenile salmon prey taxa in Puget Sound and adjoining waters; 2) Assess spatial variability in availability of essential fatty acids (EFAs) across Puget Sound basins; 3) Assess temporal variability across seasons in availability of EFAs.

Zooplankton samples were collected from March through October 2017 in seven different basins of Puget Sound and adjoining waters. Samples to quantify zooplankton biomass were collected biweekly from the upper 30 m of the water column, where juvenile salmon feed during the daytime, using oblique tows of 60 cm diameter, 335 µm mesh bongo nets. Samples were preserved, quantified, identified, and life-staged or measured. Individual carbon (C) biomass was estimated from lengths or life stages using calculations from the literature. Each taxon-specific C biomass was multiplied by its density in the sample to estimate biomass at each site. Samples for fatty acid analyses were collected opportunistically in deeper tows (usually > 30 m). Organisms were kept chilled and alive while they were sorted by species and size, quickly dipped in tap water to remove salt, then frozen in -80°C until further analysis. Forty-five different fatty acids were quantified. The taxon-specific EPA+DHA content (µg FA mg·C^{-1}) was multiplied by the biomass of each taxon, at each station in each month, to estimate site-specific monthly "EFA availability" to predators.

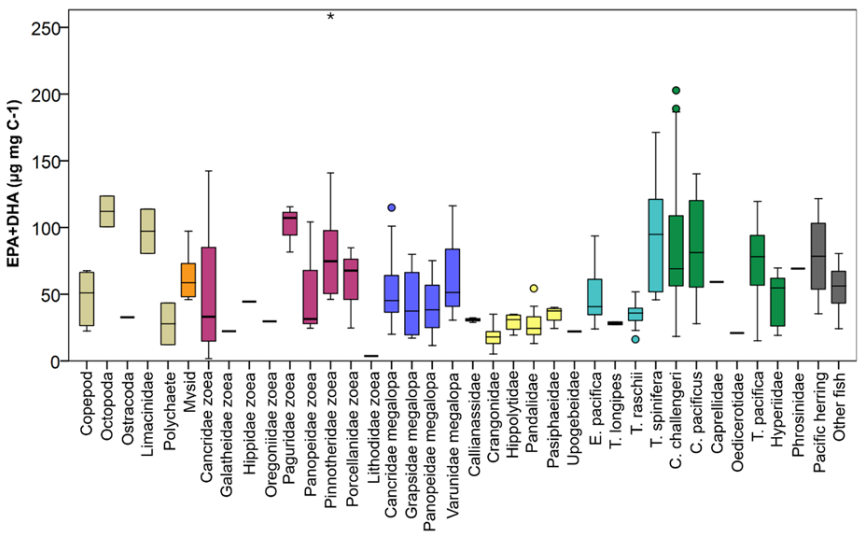

Fig. 1. EPA + DHA content of juvenile salmon prey from samples collected in Puget Sound and surrounding waters in 2017.

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Broad taxonomic groups differed in fatty acid % composition. Amphipods, mysids, crab larvae, krill (euphausiids), and larval fish were found to be a good source of EPA and DHA, while shrimp and copepods were slightly inferior sources of EFA (Fig. 1). Some biomarkers for diatoms (16:1ω7 & 16:3ω4) were dominant drivers of separation in Non-metric Multidimensional Scaling ordination. The timing and magnitude of peak availability of EPA and DHA varied among basins. Bellingham Bay had the highest availability of EPA and DHA in our data, suggesting good offshore feeding conditions for hatchery stocks of Nooksack River Chinook salmon entering Bellingham Bay. Conversely, stations in South Sound had very low EPA+DHA availability in the spring of 2017, suggesting that hatchery origin salmon juveniles from the Nisqually River that moved offshore early may have experienced poor feeding conditions. Overall, EFA availability was observed as: 1) high in Bellingham Bay in the spring and summer, 2) increasing from the spring to summer in N. Whidbey Basin, 3) decreasing from the spring to summer in N. Hood Canal, and 4) low in South Sound and San Juan Islands in the spring, and increasing in summer.

In conclusion, EFA composition in salmon prey items varies among taxa. Hyperiid and gammarid amphipods were the highest quality prey items, followed by mysids, crab larvae, krill, and fish. The quality of copepods and shrimp was markedly lower. Chinook salmon juveniles negatively select for larval stages of the bay ghost shrimp (*Neotrypaea californiensis*) and small copepods (Schabetsberger et al. 2003). Thus, it seems that salmon may select good quality diet items, but whether the selection is based on the food quality and is not coincidental remains to be explored in controlled feeding trials. Future studies will reveal the potential value of EFA availability in explaining temporal and spatial variation in juvenile salmon performance.

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Sustainable Conservation and Use of Chum Salmon under Warming Climate and Changing Ocean Conditions

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Keywords: chum salmon, global warming, carrying capacity, dSST, intra- and inter-specific interaction, North Pacific Ocean, Arctic Ocean, sustainable conservation management

Since the 2000s, there has been a decreasing trend in southern populations (e.g., Japan, Korea, and British Columbia in Canada) of chum salmon (*Oncorhynchus keta*) but northern populations (e.g., Russia and Alaska in the USA) are stable or increasing. In the 2000's, it was predicted that: 1) the population of Japanese chum salmon would be half of its maximum carrying capacity by the 2010's due to internal natural growth rate. (Kaeriyama 2004), and 2) global warming affected the distribution of chum salmon in the North Pacific in this century (Kaeriyama 2008). Objectives of this paper are to 1) evaluate the influences of a warming climate and changing ocean conditions on distribution, growth, survival, and carrying capacity for Pacific salmon, and to 2) address potential progression of global warming for establishing the sustainable conservation and management of Pacific salmon.

Sea surface temperature (SST) in the North Pacific Ocean and the Arctic Ocean in 1930–2018 was obtained using the COBE-SST database in the Japan Meteorological Agency (Ishii et al. 2005). The carrying capacity of sockeye (*O. nerka*), chum (*O. keta)*, and pink salmon (*O. gorbuscha*) were calculated from the NPAFC Salmonid Catch Statistics 1925–2017 (https://npafc.org/statistics/) based on a replacement point on the Ricker's reproduction curve. A year-class population was set as 20 brood-year populations in each species. To evaluate distribution area of chum salmon, I defined their optimum temperature range (OT: 8–12ºC) and adaptable temperature range (AT: 5–8ºC) of chum salmon based on growth rate, feeding behavior and catch per unit effort (CPUE) as population density, and the resident duration of juvenile chum salmon in coastal seas around Japan as a period from 5ºC to 12ºC in the SST (Kaeriyama 2004, 2018). This paper analyzed scales of female adult chum salmon at age 4 returning to the Ishikari and the Tsugaruishi Rivers in order to evaluate the yearling growth.

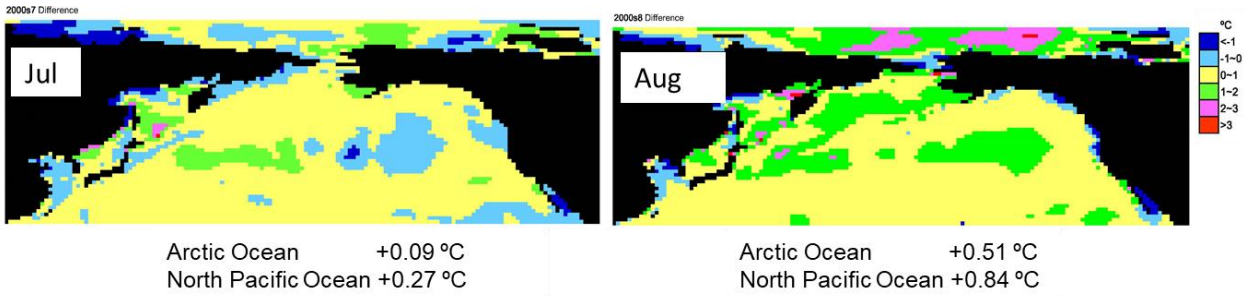

Fig. 1. Difference between predicted and actual SSTs in July and August of the 2000s in the North Pacific and Arctic Oceans. North Pacific Ocean: northward of 40ºN. The predicted SST is based on the IPCC-A1B scenario (Kaeriyama 2008).

Since the 1930s, the decadal mean of SST (dSST) basically increased 0.18ºC in the Arctic Ocean, and 0.10ºC in the North Pacific Ocean (northward of 40ºN). This represents that the SST increased 1.0ºC in the North Pacific Ocean and 1.8ºC in the Arctic Ocean in a century. The dSST showed higher in northern (0.13ºC in the Okhotsk Sea, 0.14–0.15ºC in the Bering Sea) than in southern (0.07ºC in the Gulf of Alaska) ocean ecosystems (Table 1). Actual SSTs were higher than predicted SSTs by the IPCC-A1B scenario (Kaeriyama 2008) in July and August of the 2000s in the North Pacific and the Arctic Oceans (Fig. 1). This result suggests that global warming is progressing faster than predicted (the A1B Scenario).

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Table 1. Simple regression analysis relating to the temporal changes in the decadal mean of SST (dSST) in the North Pacific Ocean (NPO), Arctic Ocean (AO), Okhotsk Sea (OS), Western- and Eastern-Bering Sea (W-BS, E-BS), and Gulf of Alaska (GA) from the 1930s to the 2010s.

Ecosystem	Slope	Intercept	R^2	F	*P*	*n*
NPO	0.100	6.013	0.865	44.687	< 0.001	9
AO	0.177	-1.774	0.928	89.770	< 0.001	9
OS	0.130	3.328	0.893	58.393	< 0.001	9
W-BS	0.150	3.583	0.865	45.000	< 0.001	9
E-BS	0.138	3.319	0.891	57.114	< 0.001	9
GA	0.072	8.197	0.452	5.767	0.047	9

The total carrying capacity of chum, pink, and sockeye salmon linked with the SST in the Okhotsk (R^2 = 0.897, $p < 0.001$) and Bering Seas ($R^2 > 0.810$, $p < 0.001$), despite no-correlation with climate-change indices such as the PDO and the ALPI (Fig. 2).

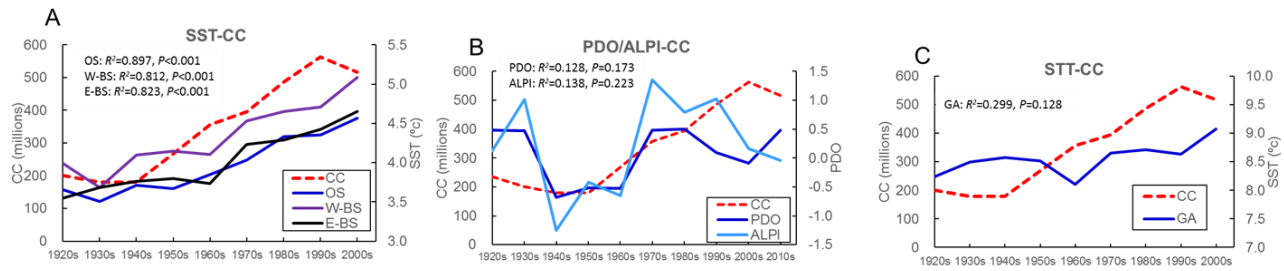

Fig. 2. Temporal changes in the decadal mean of SST (dSST), climate change indices and total carrying capacity of sockeye, chum, and pink salmon. OS: Okhotsk Sea, W- and E- BS: Western and Eastern Bering Sea, GA: Gulf of Alaska, CC: carrying capacity, PDO: Pacific Decadal Oscillation, ALPI: Aleutian Low-Pressure Index.

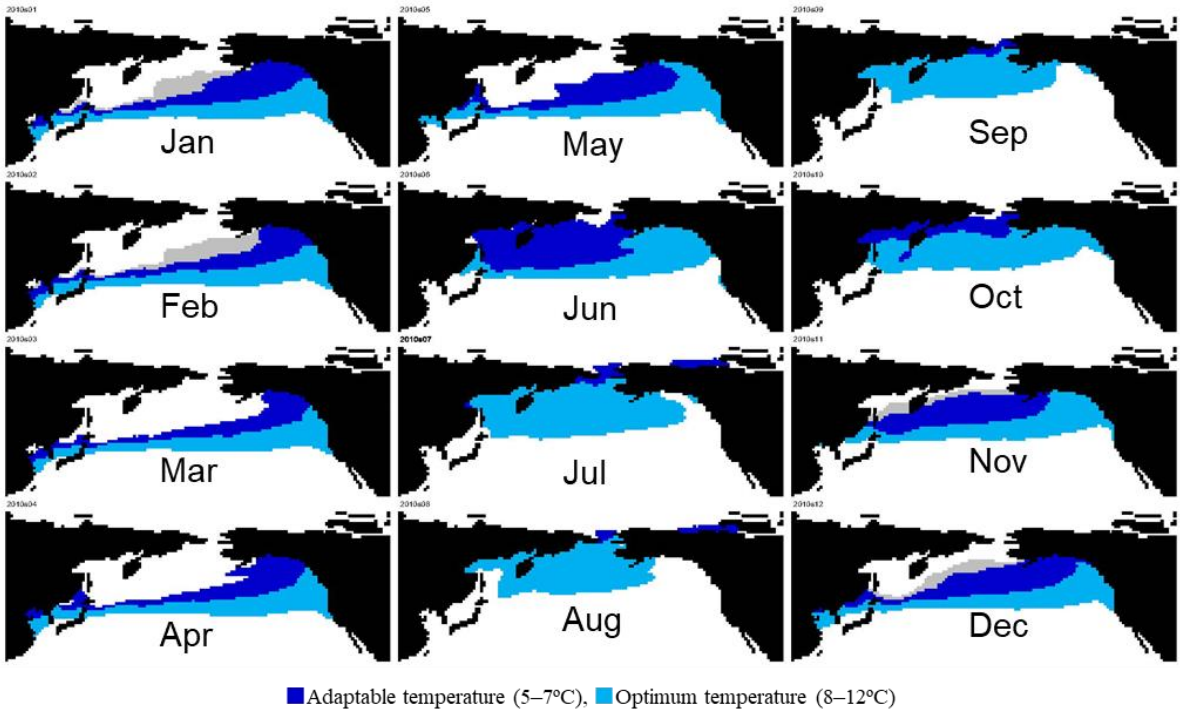

Fig. 3. Monthly change in areas of adaptable and optimum temperatures for chum salmon in the 2010s.

The monthly changes in areas AT and OT indicated that chum salmon appears like to distribute wider area in the eastern than in the western North Pacific Ocean (Fig. 3). Temporal changes in areas of AT and OT for chum salmon from the 1930s to the 2010s are as follows (Fig. 4):

- In the Okhotsk Sea, the area of AT showed an increasing trend for June, however, the area of OT showed has recently decreased in August.
- In the Bering Sea, areas of AT in June and OT in July were markedly increased.
- In the Arctic Ocean, the area of AT has gradually increased since the 1980s.
- In the Gulf of Alaska, the area of OT in the summer has decreased.

These results suggest that Okhotsk and Bering Seas are favorable ecosystems for survival and carrying capacity of Russian chum and pink salmon since the 2000s.

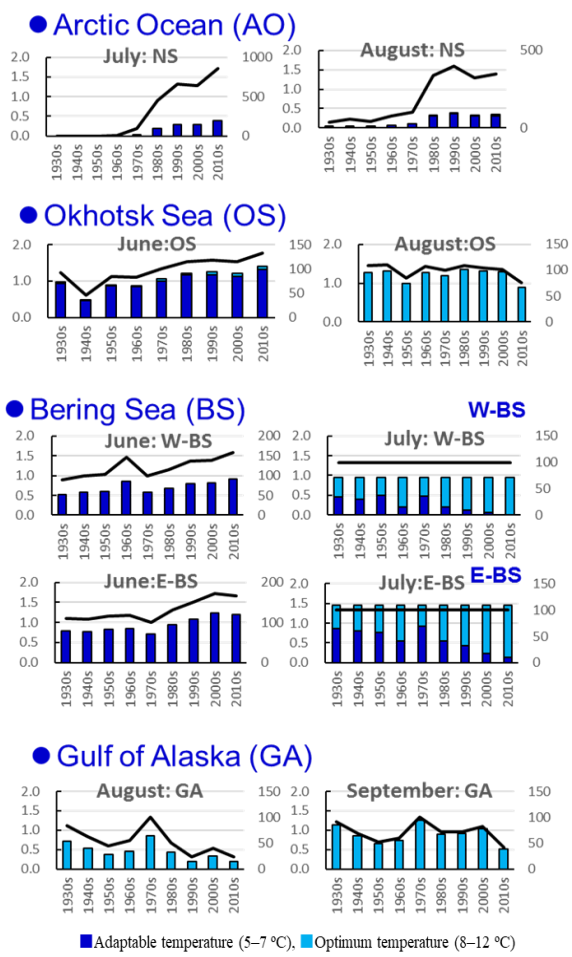

Fig. 4. Temporal changes in areas of adaptable and optimum temperatures for chum salmon from the 1930s to the 2010s.

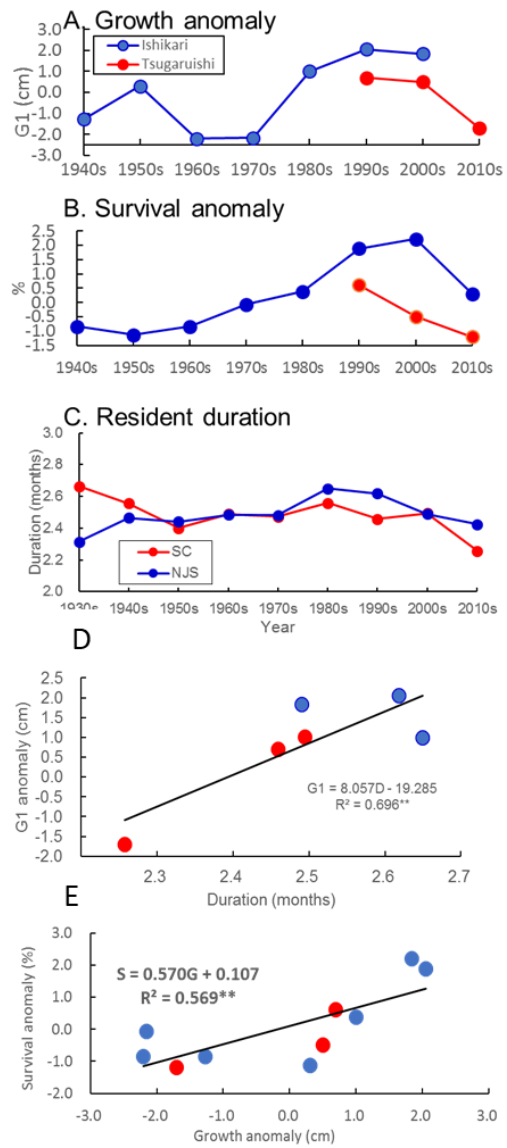

Fig. 5. Temporal changes in anomalies of growth at the age-1 (A) and survival (B), and resident duration of juvenile (C) for chum salmon returning to the coast in the Northern Japan Sea (NJS) and Sanriku (SC) from the 1930s to the 2010s. Relationships between the resident duration and the growth anomaly at age 1 (D), and between growth anomaly at age 1 and survival anomaly for chum salmon returning to the northern Japan Sea (blue circle) and the Sanriku coasts (red circle) from the 1940s to the 2010s (E).

In the 2010s, the area of OT has quietly departed from Hokkaido even though it touched Hokkaido until the 2000s. Therefore, Japanese juvenile chum salmon will have a difficult time migrating to the Okhotsk Sea (Kaeriyama and Urabe 2018). Temporal changes in the growth at age 1, the survival rate, and the resident duration of juvenile chum salmon in Hokkaido and Sanriku Coast from the 1940s to 2010s suggest that the decline in resident duration leads to decreased growth at age-1 and survival rates for Japanese chum salmon with the progression of global warming (Fig. 5).

In the near future, Japanese and Russian chum and pink salmon will have the following issues during the summer, depending on the progress of global warming and the decrease in the carrying capacity: 1) an intraspecific interaction between wild and hatchery salmon, and 2) a population density-dependent effect. Under the changing climate, therefore, Japan needs to establish sustainable conservation management for chum salmon, based on the back-casting approach. Final goals for the management are: 1) how to conserve and use the salmon, 2) how to establish the monitoring and management systems for interaction between aquatic ecosystems and Pacific salmon, and 3) how to provide restoration and resilience for wild salmon and river ecosystems.

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Changing Ocean Conditions and Some Consequences for Juvenile Salmon Feeding in Coastal Waters

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Keywords: Chinook salmon, coho salmon, trophic ecology, ocean environment, California Current

The early marine juvenile stages of Pacific salmon (*Oncorhynchus* spp.) occur in coastal waters off the west coast of USA in early summer, during what has been termed a critical life-history phase. The dominant salmon species represented in this region are juvenile coho (*O. kisutch*) and Chinook (*O. tshawytscha*) salmon, but chum (*O. keta*), pink (*O. gorbuscha*), and sockeye (*O. nerka*) salmon, steelhead (*O. mykiss*) and cutthroat trout (*O. clarkii*) are found in lower abundances. Following a period of variable freshwater residence, these anadromous salmon enter a highly dynamic but generally productive coastal ocean ecosystem in the Northern California Current (NCC), where they grow quickly and put on reserves for their first winter at sea and subsequent adult life history stage.

The general feeding habits of many of these species has been greatly resolved based on NCC sampling over the past 40 years beginning in 1979, when juvenile salmon diets were first described in detail (Peterson et al. 1982). Chinook, followed by coho, steelhead, cutthroat and sockeye salmon tend to be most piscivorous (Brodeur and Pearcy 1990; Pearcy et al. 1990; Brodeur et al. 2007; Baldwin et al. 2008; Brodeur et al. 2013), with generally increasing reliance on fish prey through ontogeny (Daly et al. 2009). The remaining species are generally smaller at ocean entry and utilize a more varied diet of euphausiids, copepods and other invertebrate taxa and rarely fishes (Brodeur et al. 2007). Here we focus mainly on yearling Chinook and coho salmon since they comprise the bulk of the catches in coastal surveys over this time period. The stomach collections for this study come from two different sampling programs: salmon were collected from 1979 to 1985 during a purse seine survey conducted by Oregon State University and since 1998 were collected in a National Marine Fisheries Survey using surface trawl nets (see Peterson et al. 2010 for detailed sampling methods). Sampling was conducted from May through September but in this analysis, we examined mainly the June cruises which were the most consistently sampled time period for which we have diet data (all years represented for Chinook and all but four for coho salmon).

The reliance on fish prey is seen in the diets of both species for most of the time period (Figs. 1 and 2), although notably in some years the prey consisted of a large proportion of invertebrate taxa, especially for coho salmon during several years. During this sampling period, the salmon have out-migrated into some very cool and productive ocean conditions (e.g., 1982, 1985, 1999, and 2008) but increasingly more warm and low production ocean conditions due to strong El Niño (1983, 1998, 2010, 2016) or low upwelling (2005, 2015, and 2017) conditions in more recent years. These environmental changes resulted in dramatic shifts in diets sometimes in sequential summers. During cool ocean conditions, the diets of both species are dominated by fish taxa associated with cool waters and euphausiids, whereas during warm conditions, the diets consist primarily of offshore taxa such as juvenile northern anchovies, rockfishes, and hyperiid amphipods, all of which may be of lower trophic value.

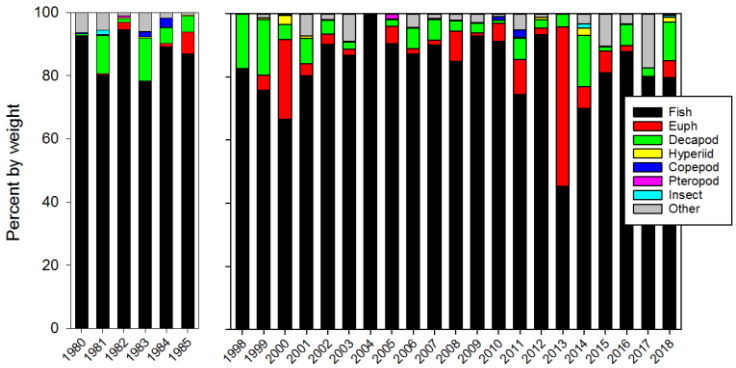

Fig. 1. Time series of June diets for yearling Chinook salmon analyzed from the 1980–1985 period (left panel) and the 1998–2018 period (right panel) by percent by weight of the major prey taxonomic categories. Sample sizes are 368 and 2033 stomachs for the earlier and later periods, respectively. All years have a minimum of 15 individuals analyzed.

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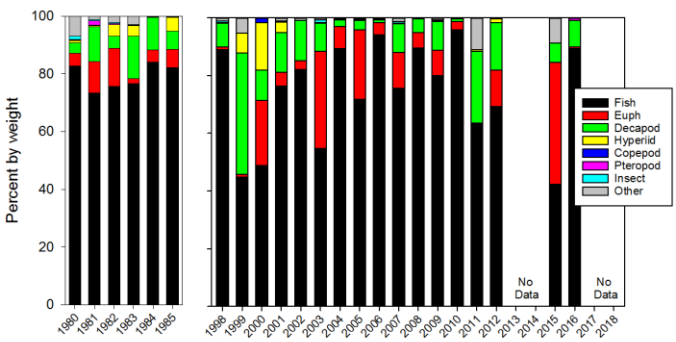

Fig. 2. Time series of June diets for yearling coho salmon analyzed from the 1980–1985 period (left panel) and the 1998–2016 period (right panel) by percent by weight of the major prey taxonomic categories. Sample sizes are 647 and 2466 stomachs for the earlier and later periods, respectively. All years shown have a minimum of 15 individuals analyzed.

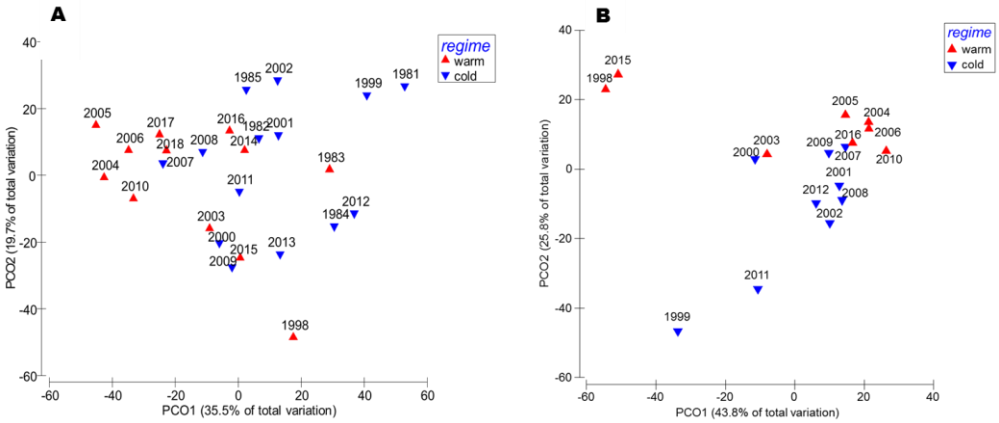

Fig. 3. Principal coordinate analysis (PCO) of juvenile yearling Chinook salmon (A) and coho salmon (B) diet composition. Years in blue were years with negative Pacific Decadal Oscillations (PDO) conditions, and years in red were years of positive PDO conditions. No 1980s data were available for coho salmon at the finer taxonomic resolution that was available for the later years.

An ordination of the diets based on the 20 top prey taxa (Daly et al. 2017) by year shows significant differences between cold and warm ocean years for Chinook salmon (ANOSIM between regime is $p = 0.002$; Global; $R = 0.254$) (Fig. 3a). Although the Chinook salmon diets in the recent (2015–2018) warm years were somewhat similar to those in other warm years (negative values on axis 1) (Fig. 3a), they were not found to be as extreme as an earlier warm period (2004–2006). Juvenile coho salmon showed less differentiation between warm and cold years ($p = 0.038$; Global $R = 0.119$) and much of the variation was driven by a few extreme warm (1998 and 2015) and cold years (1999 and 2011; Fig. 3b).

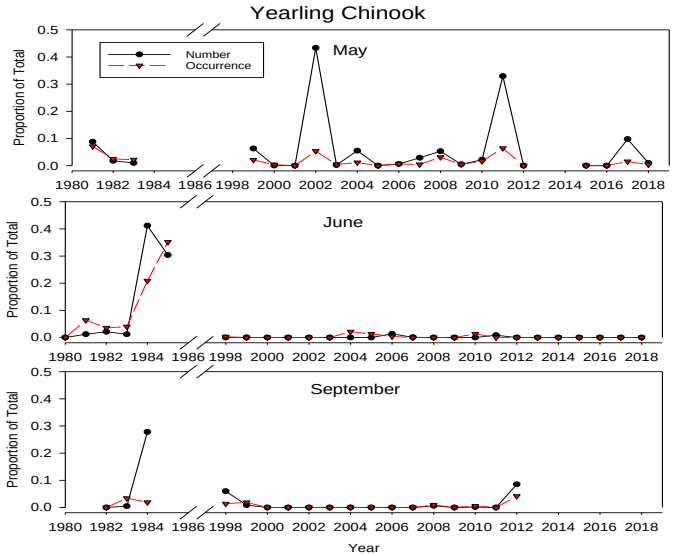

Fig. 4. Pteropods as a proportion of juvenile yearling Chinook salmon diets by number and occurrence by year and month.

In addition to changing coastal preyscapes for juvenile salmon based on ocean temperature changes, we also observed long-term trends in specific taxa (declines in sand lance, smelt and euphausiids; increases in warm-water rockfishes and flatfishes). One notable example has been the declining utilization of some shelled mollusks (pteropods) in the recent years compared to the 1980–1985 period for both Chinook (Fig. 4) and coho (Fig. 5) salmon. Although warming ocean temperatures could be driving this change, it may be potentially related to changes in ocean chemistry due to increased greenhouse gas emissions. Pteropods are extremely vulnerable to ocean acidification and it has been shown that recent increase in acidic waters in the California Current may result in pteropod shell dissolution and eventual mortality (Bednaršek et al. 2014). Although pteropods may not have historically been as important to the mostly piscivorous species we examined compared to other more planktivorous salmon species (e.g., pink salmon, Armstrong et al. 2005), the loss of potential prey diversity could have consequences in terms of long-term survival of these salmon. Declines in pH-sensitive taxa such as pteropods may be an early indicator for yet unobserved changes occurring in other salmon prey taxa such as crustaceans or fish due to increased ocean acidification.

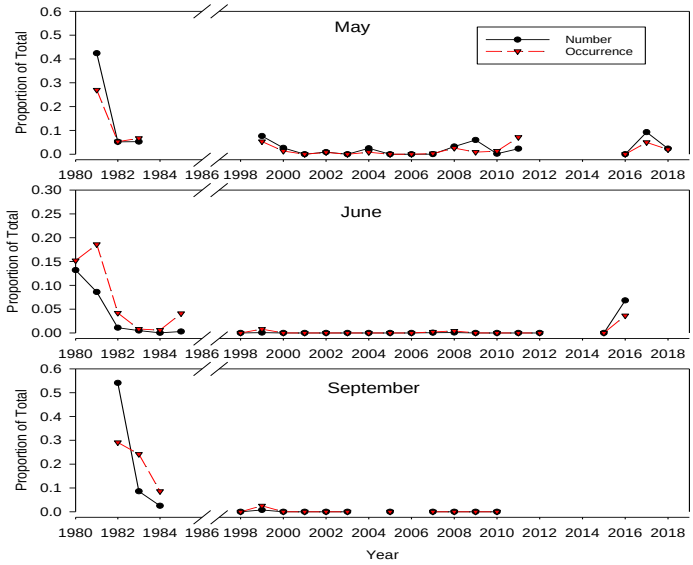

Fig. 5. Pteropods as a proportion of juvenile yearling coho salmon diets by number and occurrence by year and month.

In conclusion, juvenile Chinook and coho salmon are for the most part highly opportunistic predators and may serve as indicators and integrators of the changing ocean environment. Salmon show some changes related to the recent warm period, but they also appear to be able to switch to different prey as resource availability changes. In addition to changing abundance levels of prey, ocean warming may affect the timing or spatial distribution of key prey resources leading to a trophic mismatch (Siddon et al. 2013; Daly et al. 2017). Higher ocean temperatures also result in increased bioenergetic demands for higher consumption rates requiring more food to maintain the same metabolism (Daly and Brodeur 2015). Strong relationships exist between the diet composition of juvenile Chinook salmon in a given summer and the body condition and survival of that cohort in the ocean (Daly et al. 2017) such that diet information can provide a useful indicator of eventual salmon health and survival in coastal waters. We encourage continual monitoring of salmon feeding in coastal waters with a view towards understanding links between feeding success and survival in a rapidly changing ocean.

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Is a Warming Bering Sea Leading to Smaller Chinook Salmon?

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Keywords: age at maturity, body size, Chinook salmon, environmental variation

The past 50 years have seen declines in size and age of adult Chinook salmon (*Oncorhynchus tshawytscha*) along its entire eastern Pacific range, including Alaska. Ohlberger et al. (2018) summarized five hypotheses for the observed declines, including four previously proposed hypotheses: 1) size-selective harvest; 2) influence of hatchery production; 3) competition among Pacific salmon populations in the ocean; and 4) climate/environmental variation. The authors additionally proposed a new hypothesis: 5) increased predation upon older Chinook salmon. While none of these hypotheses are mutually exclusive, Ohlberger et al. (2018) concluded that hypotheses 1–4 were insufficient to explain the range-wide declines. Here, we suggest that hypothesis 4, climate variation, plays an important role for earlier maturation of Chinook salmon, at least towards the northern part of its range. We summarize two previously published studies (Siegel et al. 2017, 2018) demonstrating that environmental forcing, as expressed by sea surface temperature (SST), is associated with earlier maturation and thus smaller adult size of Chinook salmon.

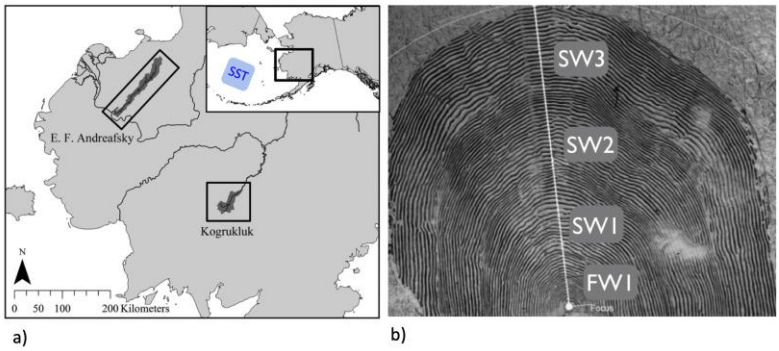

Fig. 1. Map of study area, showing location of East Fork of the Andreafsky River and the Kogrukluk River; inset shows their location in western Alaska and the region of the central Bering Sea for which average April–December SSTs were calculated (a) and image of Chinook salmon scale showing annual growth zones where FW = freshwater growth and SW = saltwater growth (b). Adapted from McPhee et al. (2016) and Siegel et al. (2018).

The studies of Siegel et al. (2017, 2018) were based on retrospective analyses of adult salmon scales collected over several decades at weirs on two rivers in western Alaska (Fig. 1a): the Kogrukluk River (Kuskokwim River drainage; brood years 1977–2006) and the East Fork of the Andreafsky River (Yukon River drainage; brood years 1990–2005). Adult scales (25 per sex and age class) were digitized and measured as described in McPhee et al. (2016), and annual growth zones (Fig. 1b) were quantified and used to infer annual growth in length. Run reconstructions that accounted for harvest were used to estimate the age composition of recruits on a per-brood-year basis and to derive age-weighted mean annual growth (as described in Siegel 2017). Environmental variability was represented by annual SST from the central Bering Sea (60.0–54.3ºN, 178.1ºE–170.6ºW) averaged over April–December (Fig. 1a; see Siegel et al. 2017 for details).

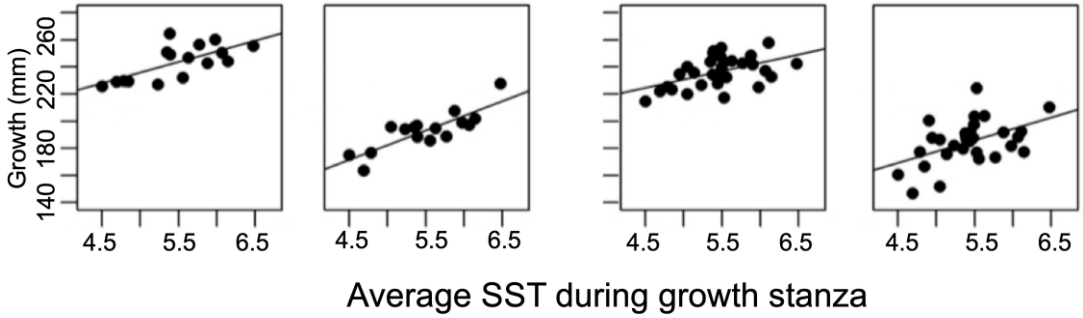

Fig. 2. Average annual growth versus annual average April–December SST for Andreafsky River SW1 (a) and SW2 (b) and Kogrukluk River SW1 (c) and SW2 (d). Adapted from Siegel et al. (2017).

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Using probabilistic maturation reaction norms that accounted for growth history (i.e., using each annual growth increment rather than total length at maturation), we found that faster early marine growth was associated with earlier age at maturity (Siegel et al. 2018; see also McPhee et al. 2016). By examining correlations between SST, annual average growth, and average recruit age, we found that early marine growth was faster in years with warmer SST (Fig. 2), and that warmer years were associated with younger average age of recruits (Fig. 3). Additionally, by fitting maturation models to average growth over the time series to calculate a 'probability of maturation for average growth' (PMAG), we found that males were more likely to mature at the youngest age (age 3) in warmer years, even after accounting for the effects of growth (Fig. 4). Taken together, these results provide support for the idea that environmental variation plays an important role in determining the size of Chinook salmon.

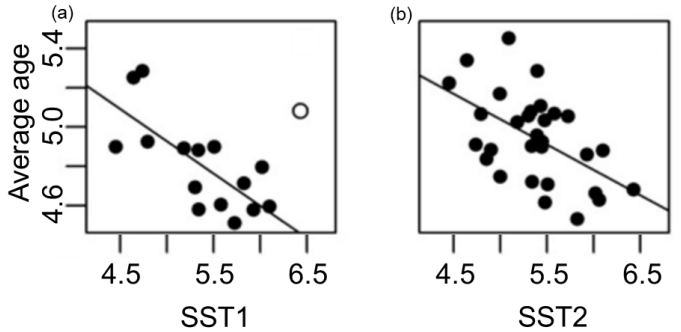

Fig. 3. Average age of Andreafsky River recruits versus SST during the first year of marine growth (a) and average age of Kogrukluk River recruits versus SST during the second year of marine growth (b).

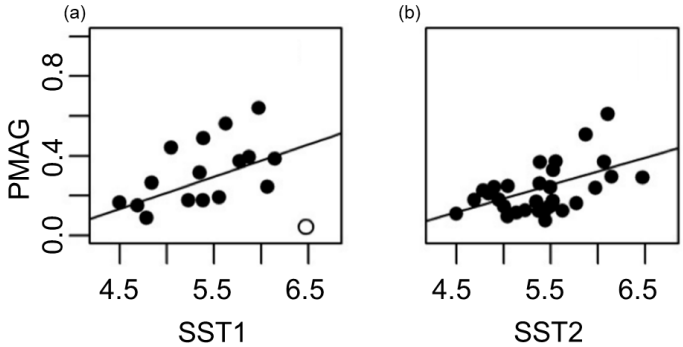

Fig. 4. Probability of maturation with average growth (PMAG) for the earliest male maturation decision (age 4) for Andreafsky River Chinook salmon versus SST during the first year of marine growth (a) and for Kogrukluk River Chinook salmon versus SST during the second year of marine growth (b). Adapted from Siegel et al. (2017).

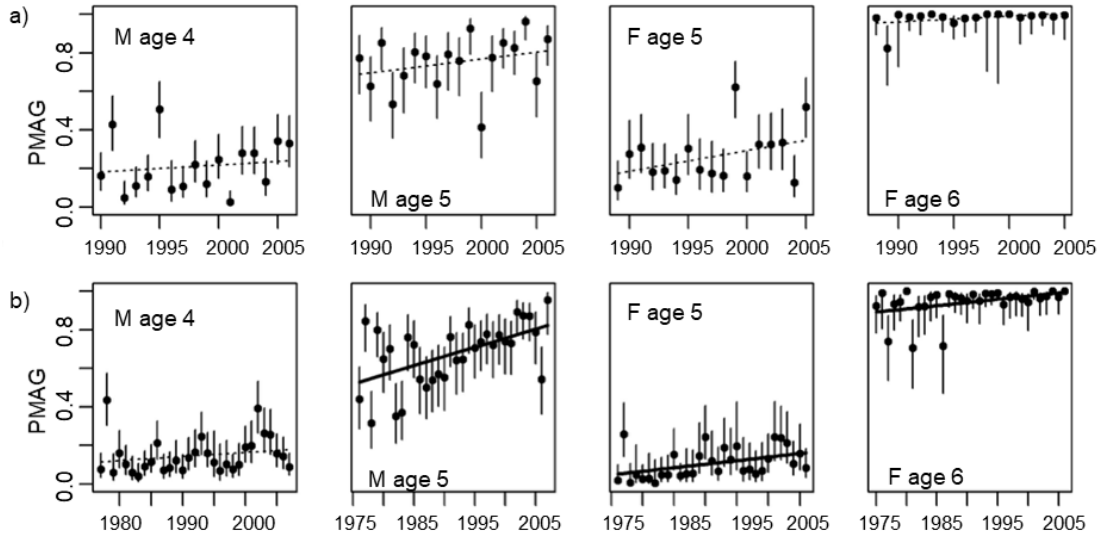

Fig. 5. Probability of maturation with average growth (PMAG) against time for the two major maturation decisions (age 4 and 5 for males, M; age 5 and 6 for females, F) for the Andreafsky River (a) and the Kogrukluk River (b). Adapted from Siegel et al. (2018).

The central and eastern Bering Sea has not warmed steadily over the three decades covered by our study, suggesting that other mechanisms are also influencing age at maturity in these populations [although we note that the western Bering Sea shows a more pronounced warming trend (McPhee unpublished data), and these stocks are thought to spend a significant amount of their life cycle rearing there (Bugaev and Myers 2009)]. However, we found that temporal trends in PMAG were uniformly positive (Fig. 5), indicating a shift in the size threshold at which these salmon mature and suggesting that additional forces are causing Chinook salmon to mature earlier. One explanation could be fisheries selection reducing the number of older fish making it to the spawning grounds. Alternatively, increased natural mortality of the oldest fish (hypothesis 5 of Ohlberger et al. 2018) might contribute to these patterns, if the slowest growing of the older fish were most susceptible to predation. At this time, insufficient data exist to test these hypotheses, but future simulation studies could help identify the range of mortality values that could give rise to the observed patterns.

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Competitive Interactions between Natural Populations of Pink and Chum Salmon from Puget Sound and Coastal Washington, USA

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Keywords: Pink Salmon, Chum Salmon, competition, age-at-maturity, productivity, ocean conditions

Natural populations of pink (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) make up the highest returns of Pacific salmon to Washington, USA and many stocks spawn in the same watersheds, leading to density dependent interactions that persist across all life stages (Fig. 1). From 1967–2017, annual returns of pink salmon used in this study averaged 2,210,481 (range: 413,269 to 7,813,504) and from 1968–2017, returns of chum salmon averaged 1,010,333 (range: 174,334 to 2,662,673; Fig. 2). In this region, pink salmon predominantly return in odd years and are associated with reduced survival of chum salmon, but also other species, including Chinook salmon (*O. tshawytscha*, Ruggerone and Goetz 2004) and southern resident killer whales (*Orcinus orca*, Ruggerone et al. 2019). For chum salmon, stocks interacting with pink salmon exhibit strong biennial patterns in abundance (Gallagher 1979) with regular even- and odd-year variations in size (Pratt 1974), age-at-maturity (Smoker 1984), and productivity (Ruggerone and Neilsen 2004). However, there has not been a comprehensive review of these biological attributes in decades. Competition between pink and chum salmon in Washington can occur during any life history stage, except in coastal populations where there are no pink salmon producing systems. Interestingly, coastal chum salmon populations also exhibit strong inter-annual variations in adult abundance and size, suggesting that competition during the overlapping marine period may be most critical for establishing the distinct even- and odd-year patterns.

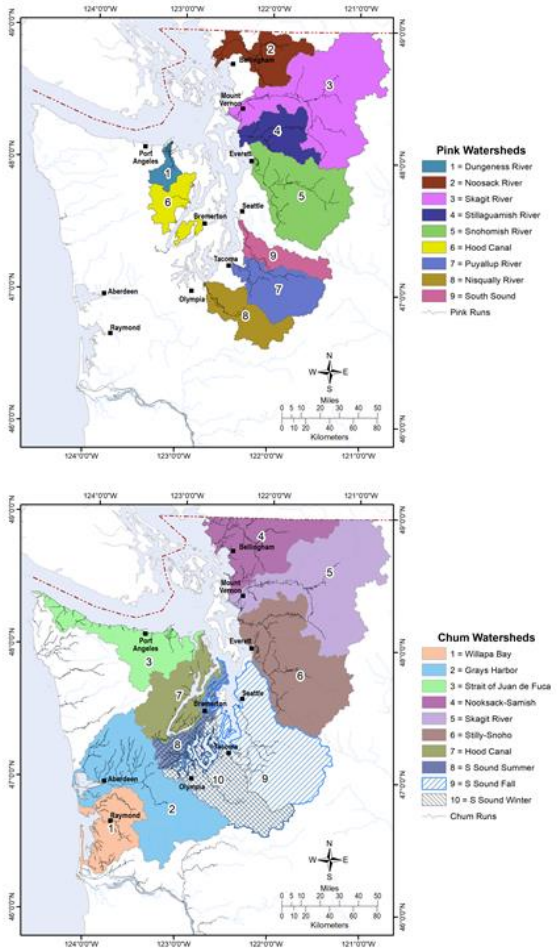

Fig. 1. Location of and pink salmon (top) and chum salmon (bottom) watersheds in Puget Sound and coastal Washington, USA (Map: D. Gombert, WDFW).

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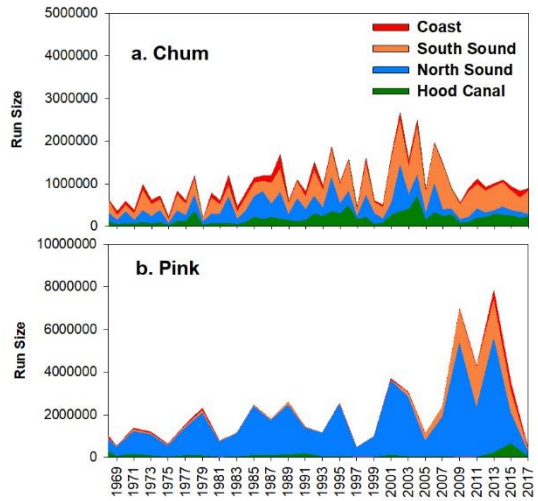

Fig. 2. Reconstructed run sizes of a) chum salmon and b) pink salmon returning to Puget Sound and coastal Washington, USA (1967–2017).

In this study, we investigated the effects of competition between natural populations of Puget Sound and coastal Washington pink and chum salmon over five decades using a weight of evidence approach to determine where and when competition occurs. Specifically, we tested for even- and odd-year differences in chum salmon abundance and adult weight by return year, and fry production, fry size, and adult age-at-maturity by brood year using Student's *t*-tests. We used natural log-transformation for fry and adult abundances, fry size (FL, mm) and adult weight (kg). For age composition proportions, we used a logit transformation. In addition, we used Ricker residuals (standardized to a mean of 0 and standard deviation of 1) from spawner and recruit relationships to evaluate temporal trends in productivity from ten populations of each species to determine whether there were regular inter-annual differences in chum salmon productivity by brood year.

We were also interested in the effect of environmental variation on pink and chum salmon productivity. To analyze this, we first quantified spatial covariation across regions by calculating Pearson correlation coefficients for each stock within a species (Malick and Cox 2016). Next, we ordinated productivity across populations using two complementary approaches: principal component analysis (PCA) and nonmetric multidimensional scaling (NMS). By using both methods, the goal was to reduce the number of variables in the time series and detect patterns in temporal variation. Lastly, we regressed PC or NMS axes scores on environmental variables to determine which parameter best explained variation in productivity across populations. We selected basin-scale environmental variables based on previous analyses (Stachura et al. 2014) and aligned them with scores of the PC and NMS axes for the period of fry outmigration (brood year +1), which is recognized as a period of high but variable mortality. The environmental variables were aggregated by winter (October–March) or summer (April–September) and included the Multivariate El Niño-Southern Oscillation Index (MEI, Kobayashi et al. 2015), the North Pacific Gyre Oscillation Index (NPGO, DiLorenzo et al. 2008), and the Pacific Decadal Oscillation Index (PDO, Mantua et al. 1997).

Our analysis focused on four regions: Washington Coast (Willapa Bay, Grays Harbor, and the Strait of Juan de Fuca; all fall run timing), South Puget Sound (aggregated populations with summer, fall, and winter run timing), North Puget Sound (Nooksack, Samish, Stillaguamish, Snohomish, and Skagit River systems; all fall run timing), and Hood Canal (fall run timing only). Overall, chum salmon run sizes were 25% lower in pink (odd) run years for coastal populations, 23% lower in South Sound, 55% lower in North Sound, and 24% lower in Hood Canal. South Sound chum salmon summer and fall runs and North Sound Stillaguamish-Snohomish and Skagit chum salmon fall runs had abundances that were significantly (Student's *t*-test $p < 0.05$) lower in odd years (Fig. 3). The Skagit system supported the largest pink salmon population, accounting for 40% of the total returns of Washington pink salmon over the study period. Therefore, it is not surprising that Skagit chum salmon populations displayed the greatest inter-annual variation in biological attributes at every life history stage.

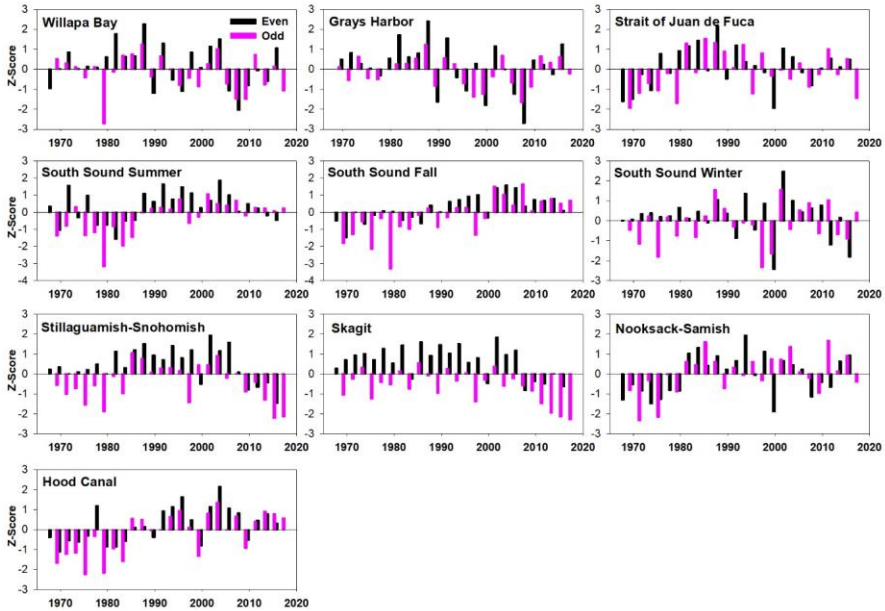

Fig. 3. Standardized run sizes of chum salmon by return year (black = even year and pink = odd year) from the Coast: Willapa Bay, Grays Harbor, and Strait of Juan de Fuca (all fall run timing); South Sound: summer, fall, and winter run timing; North Sound: Stillaguamish-Snohomish, Skagit, and Nooksack-Samish (all fall run timing); and Hood Canal (fall run timing only).

We compiled chum salmon fry abundance estimates from screw trap catches in pink-producing rivers in the Strait of Juan de Fuca (Dungeness, 2005–2017), South Sound (Nisqually, 2008–2017), North Sound (Skagit, 1996–2017), and Hood Canal (Duckabush, 2010–2017). Overall, we determined that 62% fewer chum fry emigrated from freshwater with juvenile pink salmon in even years compared to odd years when there were no juvenile pink salmon (Fig. 4). The difference was significant for the Dungeness ($p = 0.02$) and Skagit ($p < 0.01$) Rivers (fall run timing), but not for the Nisqually (winter run timing) or Duckabush (fall run timing). However, fry lengths (average ± SD) determined from Dungeness catch ($n = 14{,}738$) did not significantly vary between even (39.3 ± 4.2 mm) and odd years (39.8 ± 5.2 mm), suggesting that chum and pink salmon fry were not directly competing for resources during the outmigration period.

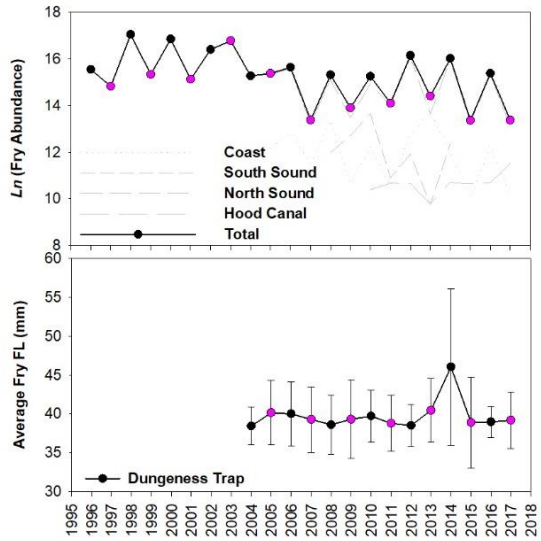

Fig. 4. Fry abundances summed across region (top) and average (± SD) fry lengths (bottom) sampled from the Dungeness River population in the Strait of Juan de Fuca, Washington USA by brood year (black = even brood year and pink = odd brood year).

Using age data processed from thousands of chum salmon scales sampled each year on spawning grounds or in commercial and recreational fisheries throughout Washington, we found biennial differences in age-at-maturity (Fig. 5). Odd brood years (outmigration with pink salmon) produced 15% more 3-year-olds than 4-year-olds, while even brood years (outmigration without pink salmon) produced 17% more 4-year-olds than 3-year-olds, and these

differences were highly significant ($p < 0.01$). The net result was higher overall adult chum salmon abundances returning to Washington in even (non-pink salmon) years than odd years. This suggests that competition pressure on the high seas during the second ocean winter may be determining age-at-maturity and that chum salmon might be interacting with pink salmon originating from areas outside of Puget Sound during this period. Moreover, commercially harvested chum salmon weighed 0.15 kg less in odd years when abundances were lower, although this difference was not significant. However, we did note that average chum salmon weight from commercial landings decreased by 0.02 kg yr^{-1}, meaning that on average, chum salmon in 2017 weighed 0.96 kg less than they did in 1970.

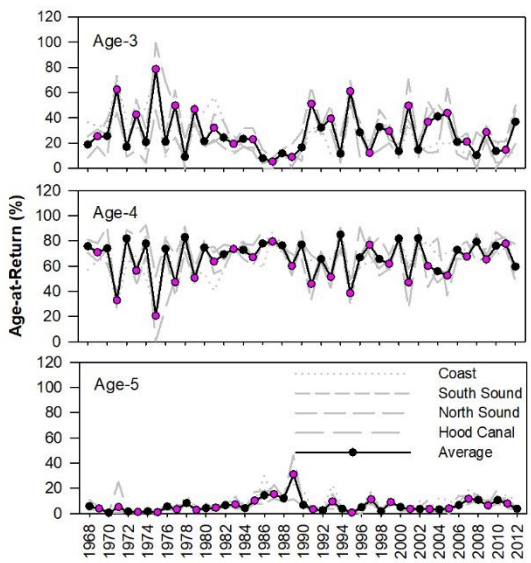

Fig. 5. Average age-at-return (%) for age-3 (top), age-4 (middle), and age-5 (bottom) chum salmon spawners by brood year (black = even brood year and pink = odd brood year) determined from scale ages across regions of Puget Sound and coastal Washington, USA.

For pink salmon, we did not find any trends in productivity, but there was evidence of regional covariance at fine spatial scales (Fig. 6), with populations fluctuating between exceptionally high (> 7 million in 2013) and low (< 500,000 in 2017) abundances in recent years, concurrent with dramatic shifts in ocean conditions. When ordinated in multivariate space, we found that the first PC and NMS axes were inversely related (r = -0.98), capturing 44.7% and 57.6% of the variation in the pink salmon dataset, respectively. When regressed against summertime NPGO values, both axes scores were significantly ($r^2 = 0.49$ for PC and $r^2 = 0.41$ for NMS, both $p < 0.01$) correlated with that index (Fig. 7). These results suggest that climate patterns captured by the phase of the NPGO, such as sea surface height (associated with variation in salinity, nutrients, and chlorophyll-*a*) may be important drivers for survival of pink salmon during the outmigration period. The second axes explained 17.7% (PC) and 22.9% (NMS) of the variation in pink salmon productivity, but neither were associated with any environmental variables.

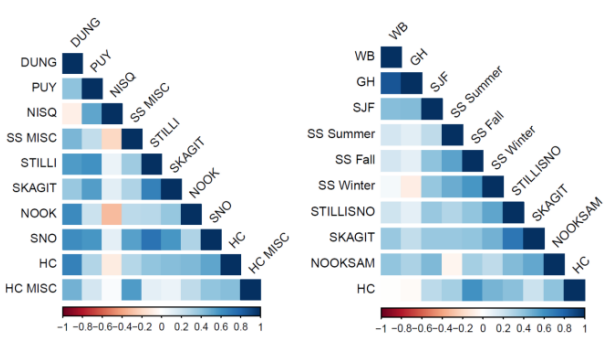

Fig. 6. Pearson correlation coefficients (*r*) for comparisons between standardized Ricker residuals in populations of pink salmon (left) from the Coast: DUNG = Dungeness; South Sound (SS): PUY = Puyallup, NISQ = Nisqually, and SS MISC; North Sound: Skagit, NOOK = Nooksack, SNO = Snohomish; and Hood Canal: HC and HC MISC. Values are also shown for chum salmon (right) from the Coast: WB = Willapa Bay, GH = Grays Harbor, and SJF = Strait of Juan de Fuca (all fall run timing); South Sound (SS): summer, fall, and winter run timing; North Sound: STILLISNO = Stillaguamish-Snohomish, Skagit, and NOOKSAM = Nooksack-Samish (all fall run timing); and Hood Canal (HC, fall run timing only).

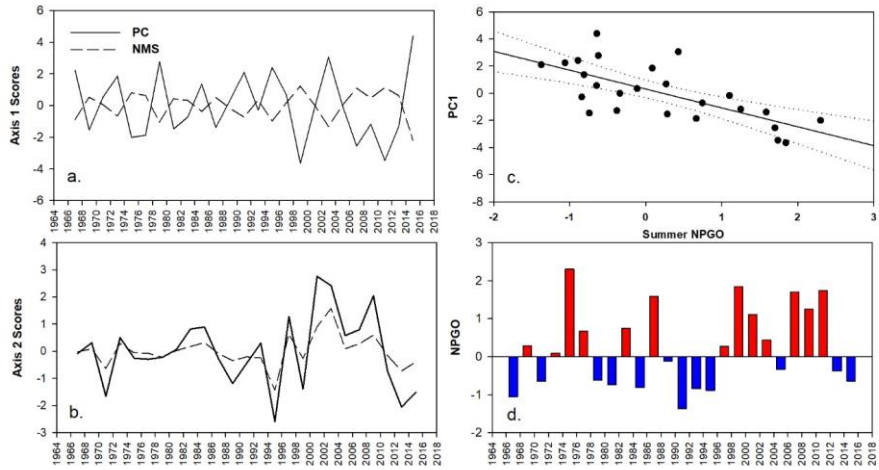

Fig. 7. Scores for a) axis 1 and b) axis 2 pink salmon productivity ordinated using Principal Component Analysis (PCA) and nonmetric multidimensional scaling (NMS); c) the association between PC1 scores and summer (April–September) North Pacific Gyre Oscillation Index (NPGO) values; and d) summer NPGO values.

Chum salmon also displayed regional covariance in productivity, but only three fall populations had significantly lower values in odd brood years (Willapa Bay and Grays Harbor on the Coast and Skagit in North Sound). Similar to previous findings (Malick and Cox 2016), we did note that productivity trended downwards in some chum salmon populations (the summer and winter runs in South Sound and fall Stillaguamish-Snohomish run in North Sound), especially after 1996 (Fig. 8). However, fall chum in Hood Canal trended upwards over the entire time series. Unlike pink salmon, when we ordinated chum salmon productivity residuals in multivariate space, neither the resulting PC nor NMS axes were correlated with any environmental variables, meaning that variation in chum salmon productivity could not explained by the basin-scale indices.

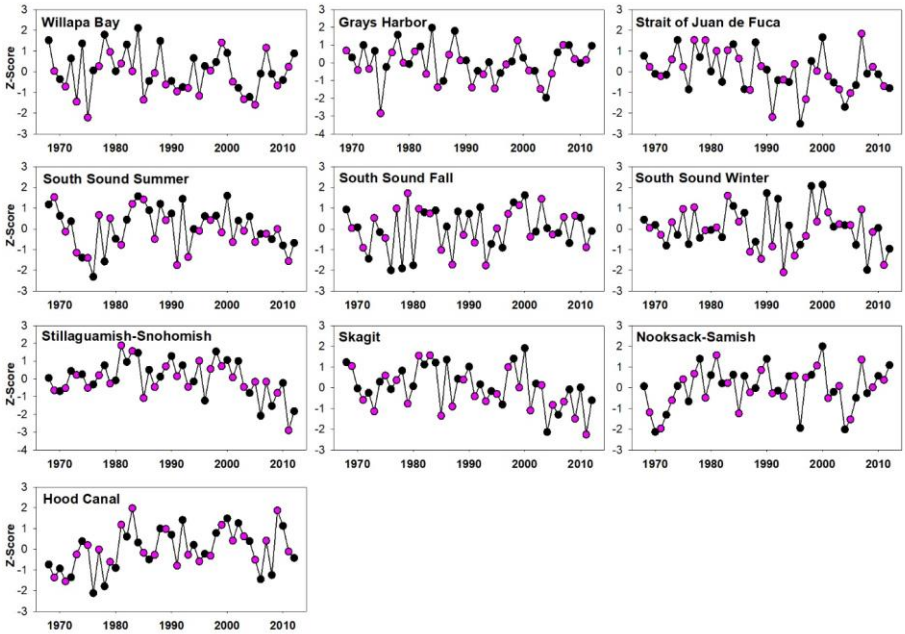

Fig. 8. Standardized Ricker residuals for chum salmon populations by brood year (black = even year and pink = odd year) from the Coast: Willapa Bay, Grays Harbor, and Strait of Juan de Fuca (fall run timing); South Sound: Summer, Fall, and Winter run timing; North Sound: Stillaguamish-Snohomish, Skagit, and Nooksack-Samish (fall run timing); and Hood Canal (fall run timing only).

Overall, we found compelling evidence of biennial differences in chum salmon attributes at all life history stages, including populations where there are no pink salmon, suggesting that both direct and indirect competition with pink salmon occurs. The magnitude of the effect seems to vary with pink salmon abundance. Across all of Washington, but especially in the Skagit River of North Puget Sound where populations of pink salmon are the most abundant, numbers of adult chum salmon spawners and outmigrating fry were lower in years overlapping with pink salmon. Chum salmon productivity was also lower in odd brood years, indicating that pink salmon affect recruitment. Inter-annual differences in abundance were related to variation in age-at-maturity, with odd brood

years producing more 3-year-olds and even brood years producing more 4-year-olds. This result implies that competitive interactions affecting growth rates during the second ocean year are critical for determining when chum salmon return to spawn. However, pink salmon productivity was also sensitive to basin-scale environmental variation, suggesting that while competition can drive productivity patterns in natural populations, other factors such as environmental variability may be equally important for survival.

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Ecosystem Indicators Development for Coho and Chinook Salmon

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Keywords: Ecosystem, indicators, Pacific salmon, generalized additive models

Recent work on Chinook and coho salmon and steelhead trout has shown a decline in the marine survival of Salish Sea populations that was not evident in populations from coastal regions (Zimmerman et al. 2015; Ruff et al. 2017; Kendall et al. 2017). The causes of this decline in marine survival are likely complex, and may include bottom-up processes that drive prey availability, top-down processes, including increasing abundances of predators that may be exacerbating mortality, as well as a multitude of anthropogenic factors such as habitat loss, contaminants, and hatchery management practices that may contribute to disease, reduced fish condition, and ultimately increased mortality. The cumulative effects of these factors are unknown. Previous work showed that for Chinook, a single oceanographic climate index (North Pacific Gyre Oscillation) did not perform well in explaining survival patterns (Ruff et al. 2017). Recent work on the development of indicators of Puget Sound steelhead survival showed that predator abundance, patterns in hatchery releases, and timing of freshwater input, as well as oceanographic conditions, were informative in predicting marine survival (Sobocinski et al. in review). While the three species with observed declines in marine survival (Fig. 1) have different life-histories, and are therefore subjected to variable pressures at multiple scales, there are some commonalities in factors explaining marine survival over the 40-year time period from the late 1970s to present.

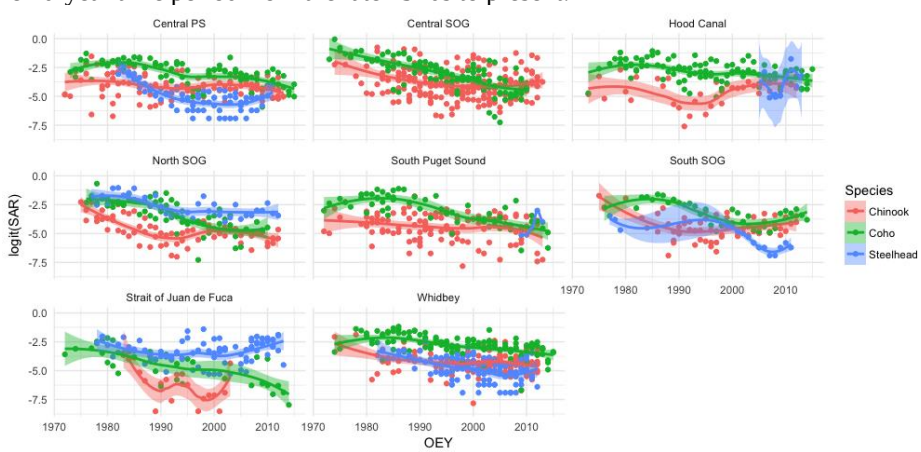

Fig. 1. Marine survival trends for three species of salmon across the subbasins of the Salish Sea, including Puget Sound (Central Puget Sound (PS), South Puget Sound, Whidbey, Hood Canal), the Strait of Juan de Fuca, and the Strait of Georgia (South Strait of Georgia (SOG), Central SOG and South SOG). Survival is shown as logit transformed smolt-to-adult return rates from the 1970s to 2015.

We developed hypotheses related to predation, competition, environmental variation, and anthropogenic impacts to frame our analysis and to identify a suite of factors that was best at explaining variation in survival time series for populations in Puget Sound, WA, USA. From these hypotheses, we generated time series of available and relevant data to use as indicators for each hypothesis (Table 1). We used generalized additive modeling to describe variation in survival with multiple covariates at ocean, regional, and local scales. We used smolt-to-adult return ratios (SAR) as the response variable; updates to the survival dataset using the methods of Ruff et al. (2017, Chinook) and Zimmerman et al. (2015, coho) allowed for analysis up through ocean entry year 2015. For each hypothesis we generated multiple generalized additive models and used best subsets model selection to identify the combination of indicators explaining the most variance in salmon marine survival.

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Table 1. Hypotheses relating to Chinook and coho marine survival and indicators associated with each.

HYPOTHESIS	INDICATORS
H1: PREDATOR BUFFERING (ABUNDANCE)	Seal Abundance Orca Abundance SOG Herring Abundance PS Herring Spawning Stock Biomass PS Pink Salmon Abundance (Outmigrating) Fraser Pink Salmon Abundance (Outmigrating) Yearling Chinook Hatchery Release Abundance Subyearling Chinook Hatchery Release Abundance Yearling Coho Hatchery Release Abundance Index of Ocean Salmon
H2: PREDATOR BUFFERING (TIMING)	Seal Abundance Orca Abundance Yearling Chinook Hatchery Release Date Subyearling Chinook Hatchery Release Date Yearling Coho Hatchery Release Date Subyearling Coho Hatchery Release Date CV of Subyearling Chinook Hatchery Release Date
H3: FOOD AVAILABILITY AND COMPETITION (DENSITY-DEPENDENT)	SST Salinity PS Herring Spawning Stock Biomass PS Pink Salmon Abundance (Out) Fraser Pink Salmon Abundance (Out) Index of Ocean Salmon Fraser River Flow (Spring) PS River Flow (Apr.-May) Chl *a* (JDF Strait) SOG Wind Index Upwelling Index Yearling Chinook Hatchery Release Abundance Subyearling Chinook Hatchery Release Abundance Yearling Coho Hatchery Release Abundance Precipitation (Spring) Stratification Index at Race Rocks Max Air Temp (Spring)
H4: FOOD AVAILABILITY TIMING (DENSITY-INDEPENDENT)	Cumulative Degree Days Date of 75% Cumulative Flow Duration between 25% and 75% Cumulative Flow Spring Transition Date Yearling Chinook Hatchery Release Date Subyearling Chinook Hatchery Release Date Yearling Coho Hatchery Release Date Subyearling Coho Hatchery Release Date CV of Subyearling Chinook Hatchery Release Date
H5: WATER QUALITY	SST Salinity River Flow (Spring) Sea Level Precipitation (Spring) Stratification Index at Race Rocks Max Air Temp (Spring) SOG Wind Index PDO PNI NPGO NPI
H6: WATER DELIVERY TIMING	Cumulative Degree Days Date of 75% Cumulative Flow Duration between 25% and 75% Cumulative Flow Date of Max. Freshwater Flow Spring Transition Date
H7: ANTHROPOGENIC IMPACTS	Population Yearling Chinook Hatchery Release Abundance Subyearling Chinook Hatchery Release Abundance Yearling Coho Hatchery Release Abundance Coho/Chinook Harvest Total Salmon Harvest

In general, hypotheses related to freshwater delivery performed poorly, while those related to predation, competition, and water quality explained more variance (30–40% for the best models). For Chinook, the factors with strongest support included sea surface temperature in Puget Sound, spring river flow in Puget Sound, seal abundance, subyearling Chinook hatchery release date, and yearling coho hatchery release date. For all except water temperature, the relationship between marine survival and the indicator was negative. For coho, the variables with

the most support included North Pacific Index in the summer (negative relationship with SAR), spring precipitation (negative relationship with SAR), stratification in the Strait of Juan de Fuca (parabolic relationship), the CV of Chinook subyearling hatchery release date (positive relationship with SAR, where the greater the variation in release date, the higher survival is), maximum spring temperature (negative relationship with SAR), seal abundance (negative relationship with SAR), summer NPGO (positive relationship with SAR), and Strait of Georgia herring abundance (positive relationship with SAR). These variables collectively hint at numerous causes of decreased survival for all three species of interest, from unfavorable ocean conditions, to increased predation and prey limitation. Lack of data for some potentially important ecological variables (for example, young of the year forage fishes in Puget Sound) may limit the explanatory power of our models related to marine survival.

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Mechanisms for Shifts in the Distribution and Abundance of Juvenile Sockeye Salmon in the Eastern Bering Sea during Late Summer, 2002–2018

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Keywords: Sockeye salmon, shifts, distribution, abundance, Eastern Bering Sea

Objectives

Climate change is altering the distribution and abundance of marine species in Arctic and sub-Arctic oceans. The eastern Bering Sea is a critical rearing habitat for juvenile sockeye salmon during summer (Farley et al. 2007). Southeast Bering Sea shelf water temperatures ranged from 4–10°C, with anomalous warm 2002–2005, cool 2006–2013, and warm 2014–2018 periods (Fig. 1). In response to warming, significant shifts north and increases in abundance were detected for juvenile sockeye salmon and age-0 pollock in the eastern Bering Sea, 2002–2018 (Fig. 2, Fig. 3) (Yasumiishi et al. in prep.). In addition, juvenile sockeye salmon consumed more age-0 pollock during warm years and more zooplankton during cool years (Fig. 4). To get a better understanding of the mechanisms for shifts, we examined spatio-temporal covariates of the distribution and abundance of juvenile sockeye salmon. Covariates included station level sea temperature, large copepod densities (prey), juvenile pink salmon (competitors), and age-0 pollock (competitors and prey).

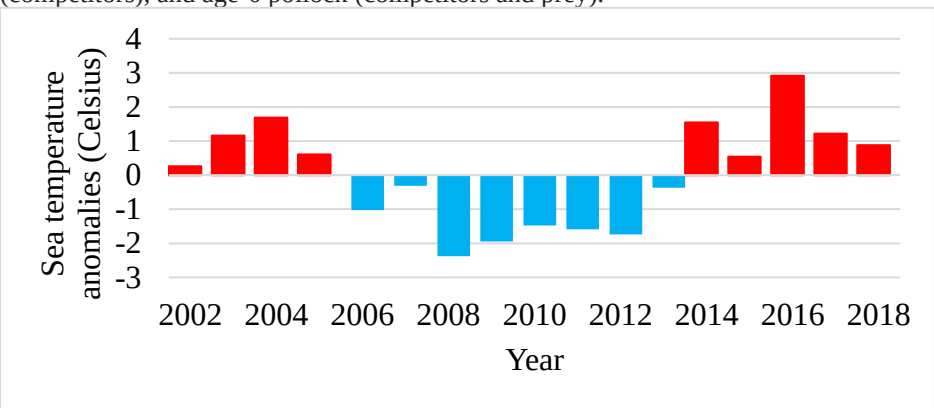

Fig. 1. Sea surface temperature anomalies sampled in the eastern Bering Sea during the summer Alaska Fisheries Science Center bottom trawl survey, 2002–2018 (courtesy Bob Lauth).

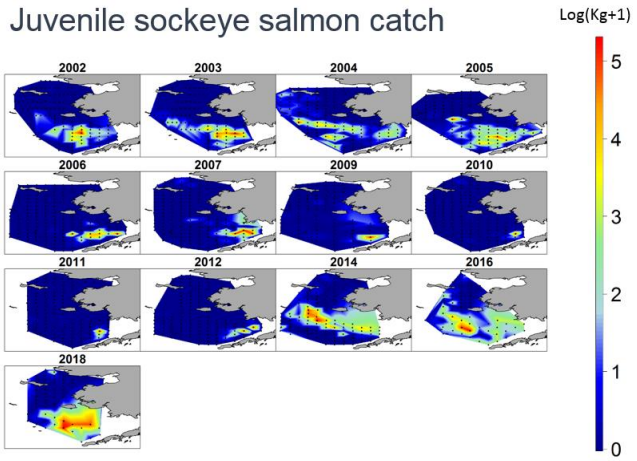

Fig. 2. Distribution and relative abundances of juvenile sockeye salmon sampled in surface waters of the eastern Bering Sea during late summer, 2002–2018.

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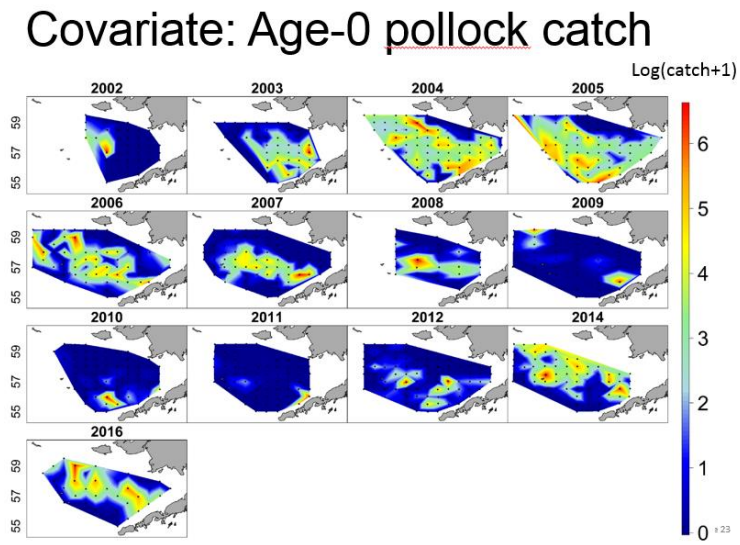

Fig. 3. Distribution and relative abundances of age-0 pollock sampled in surface waters of the eastern Bering Sea during late summer, 2002-2018.

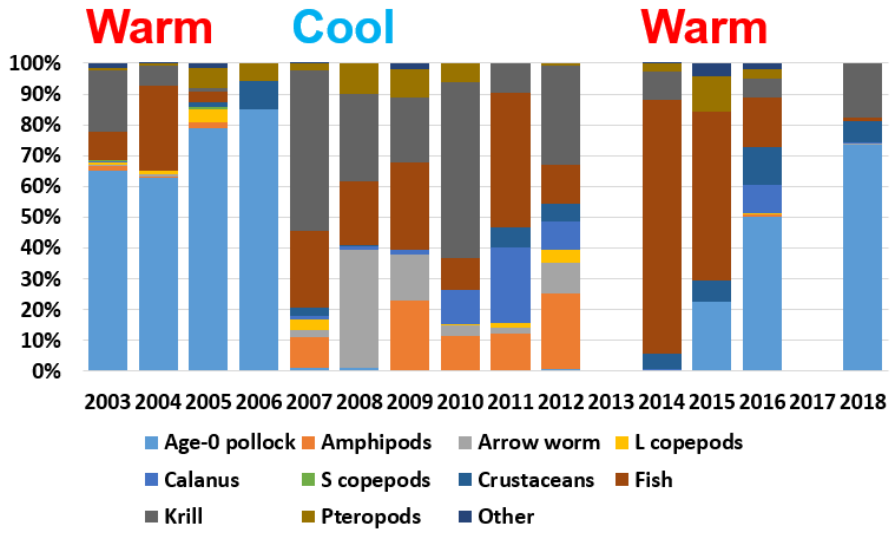

Fig. 4. Diets of juvenile sockeye salmon in the eastern Bering Sea during late summer, 2002–2018.

Methods

Juvenile sockeye were collected in surface (0–20 m depth) waters of the eastern Bering Sea during late summer as part of the Alaska Fisheries Science Centers' Bering Aleutian Salmon International Surveys (BASIS), 2002–2018 (Farley et al. 2007; Moss et al. 2009). A total of 1,521 stations were sampled. Surface trawl surveys were not conducted in the south (< 60°N) during 2013 and 2015 and north (≥ 60°N) during 2008 so these years were left out of the analysis. The survey area we used in our analysis included from nearshore (~50 m) to the shelf (< 150 m depth), latitudes 54.7°N to 65.5°N, and longitude -173°W to -159°W. Stations were approximately 30 nautical miles apart and 60 nautical miles apart in the south starting in 2016. A trawl net was towed from a vessel in the upper 20 m. The trawl was towed at 3.5–5 knots (6.5–9.3 km·h^{-1}) for approximately 30 minutes. Area swept by the net at each station was estimated as the product of horizontal net opening and distance towed. On average the horizontal spread of the net was 55 m (Farley et al. 2007). Distance towed was calculated as the haversine distance from the time of equilibrium to haulback (i.e., the initial retrieval of the net). All fish caught were sorted and weighed (kg) by species at each station. At each station, sea temperature was sampled using a CTD and bongo tows were used to sample large copepods.

We implemented a spatial delta-generalized linear mixed model for multiple categories and environmental covariates using the vector autoregressive spatio-temporal (VAST) package in R (Thorson et al. 2015; Thorson and Kristensen 2016a; Thorson et al. 2016b). We examined spatial covariates of the distribution and abundance of

juvenile sockeye salmon. Spatial covariates included station level sea temperature, large copepod densities, juvenile pink salmon catch, and age-0 pollock catch.

Results

Distribution and abundance of juvenile sockeye salmon was positively related to the annual index of summer sea temperature but not related to spatial temperatures during the survey location or time. No synchrony was found in the spatial distribution and abundance of juvenile sockeye in relation to the spatial distribution and abundance of large copepods (prey). Juvenile sockeye salmon distributed with juvenile pink salmon and age-0 pollock. The most significant finding was the overlap in the distribution of juvenile sockeye salmon and age-0 pollock, but an inverse pattern in abundance in regions of overlapping distributions. There were higher abundances of juvenile sockeye salmon in areas of lower abundances of age-0 pollock.

Conclusions

Warming in the eastern Bering Sea was associated with shifts in the distribution and abundance of juvenile sockeye salmon on a temporal scale rather than on a localized spatial scale within years in the survey area of the eastern Bering Sea during late summer. Sea temperature prior to the survey is likely be more important in determining distribution and abundance of juvenile sockeye. The finding of an inverse pattern between the localized abundances of juvenile sockeye and age-0 pollock indicate competition or predation in that one species is moving away or being preyed upon the other (juvenile sockeye on age-0 pollock). Understanding how the distribution and abundance of Pacific salmon has changed in response to past and present ecosystem change on spatial and temporal scales will help us understand how Pacific salmon will respond to future ecosystem change.

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Long-term Shifts of Chum Salmon *(Oncorhynchus keta)* Distribution in the North Pacific and the Arctic Ocean in Summer 1982–2017

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Keywords: chum salmon, distribution area, North Pacific, Arctic Ocean

Chum salmon *(Oncorhynchus keta)* is widely distributed in the North Pacific Ocean and adjacent waters. The thermal limit of chum salmon habitats is between 2.7℃ to 15.6℃ (Azumaya et al. 2007). Azumaya et al. (2007), Kaeriyama (2008) and Kaeriyama et al. (2012, 2014) predicted a northward shift and decrease of the distribution area of chum salmon as a result of global warming. There is possible shift in the distribution area of chum salmon with recent warming of SST already. However, it is not clear how the distribution area of chum has changed from the past to the present. Thus, we examined the interannual change in the distribution area of chum salmon in the North Pacific and the Arctic Ocean from 1982 to 2017.

The area that was enclosed by the upper thermal limit (15.6℃), the lower thermal limit (2.7℃) was assumed as the acceptable habitat of chum salmon. The distribution area of chum salmon in July, August and September were estimated using the gridded SST from 1982 to 2017. The SST data between 30°N and 75°N, 140°E and 120°W are based on NOAA High-resolution Blended Analysis of Daily SST Data Set (https://www.esrl.noaa.gov/psd/data/gridded/) and the resolution of SST data are 1/4˚ x 1/4˚. Composite maps of the area of chum salmon distribution were constructed from the decadal average SST from 1982 to 1991 and 2008 to 2017.

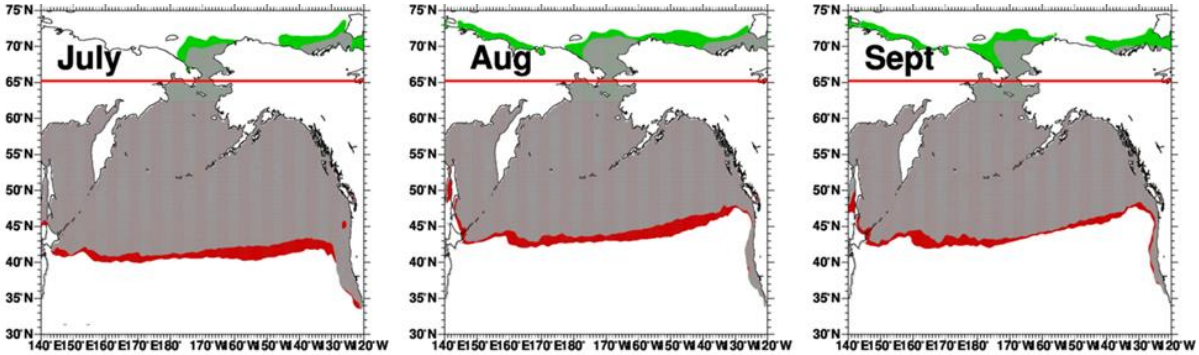

Fig. 1. Horizontal areas of chum salmon distribution. Gray shows the area of chum salmon distribution. Red and green show the difference between the area of decadal composite distribution from 1982 to 1991 and the area of decadal composite distribution from 2008 to 2017. Red (green) shows that the southern (northern) limit of chum salmon distribution has shifted northward for 36 years. The northern region of the horizontal red lines of 65°N was assumed as the Arctic Ocean.

Long-term trends of SST in the North Pacific and the Arctic Ocean in the summer of 1982–2017 were positive except for the US west coastal area in July to September and the western area of the Arctic Ocean in July. The southern and northern limit of chum salmon distribution has shifted northward. The area of chum salmon distribution in the North Pacific in summer has decreased approximately 860 x 10^3 km^2 during the last 36 years (Fig. 1, Table 1). On the other hand, the area of chum salmon distribution in the Arctic Ocean has increased approximately 328 x 10^3 km^2 (Table 1). The interannual change in area of chum salmon distribution in summer had a statistically significant negative trend ($p < 0.01$) which was about -12 x 10^3 $km^2 \cdot year^{-1}$ to -27 x $10^3 km^2 \cdot year^{-1}$ (Table 2).

The distribution of chum salmon in both the North Pacific and the Arctic Ocean in summer has shifted northward and the area of chum salmon distribution has decreased approximately 5% (744 x 10^3 km^2) during the last 36 years. These changes may influence the carrying capacity during the ocean life of chum salmon.

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Table 1. The decadal composite area of chum salmon distribution in the North Pacific, the Arctic Ocean, and in both the Arctic Ocean and the North Pacific in summer (x 10^3 km^2).

Regsion	**July** (1982–1991)	**July** (2008–2017)	**Aug** (1982–1991)	**Aug** (2008–2017)	**Sept** (1982–1991)	**Sept** (2008–2017)
North Pacific (30°N–65°N, 140°E–120°W)	13950	12966	11314	10360	11219	10476
Arctic Ocean (65°N–75°N, 140°E–120°W)	307	536	443	787	272	684
Arctic Ocean and North Pacific (30°N–75°N, 140°E–120°W)	14257	13502	11767	11147	11491	11160

Table 2. Long-term trend of the area of chum salmon distribution in the North Pacific, the Arctic Ocean and in both the Arctic Ocean and the North Pacific in summer (x 10^3 $km^2 \cdot year^{-1}$). Positive (negative) values indicate that the area of chum salmon distribution has increased (decreased) for 36 years.

Region	July	August	September
North Pacific (30°N–65°N, 140°E–120°W)	-36	-34	-28
Arctic Ocean (65°N–75°N, 140°E–120°W)	9	12	16
Arctic Ocean and North Pacific (30°N–75°N, 140°E–120°W)	-27	-23	-12

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A Compound Specific Stable Isotope Analysis of Chinook Salmon Stocks Caught in the Northern and Southern Strait of Georgia

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Keywords: Chinook salmon, compound specific stable isotopes, Strait of Georgia

Chinook Salmon are experiencing concurrent declines across their range (Irvine and Fukuwaka 2011). The situation is pronounced in British Columbia where fishery restrictions have been implemented to protect depleted local Chinook stocks. These stocks are critical to multiple stakeholders including resident killer whales, recreational and Indigenous fisheries (Riddell et al. 2013). Though the marine distribution and ecology of these stocks is poorly resolved, it is known that different stocks inhabit different regions of the NE Pacific, and that they may therefore be exposed to food webs of varying structure, prey biomass and nutritional quality (Weitkamp 2010; Miller et al. 2011; Shelton et al. 2018). Differences in regional food-web ecology and its impacts on Chinook salmon stocks are a significant unknown portion of Chinook life history (Riddell et al. 2018). This study aimed to sample Chinook salmon stocks captured from two regions of the BC Coast (Northern Vancouver Island and Southern Vancouver Island) and to use compound specific stable isotope analysis to investigate the food-web ecology of stocks in each region.

Adult Chinook were collected from recreational fishing derbies and trawl surveys during July and August of 2018. Locations in Northern Vancouver Island included Malcolm Island and Campbell River. Locations in Southern Vancouver Island included Sidney and the Strait of Juan de Fuca. All Chinook were analyzed for genetic stock ID. Fraser River and Puget Sound Chinook stocks were chosen for analysis and sub-sampled from both regions when possible. From the Northern region, three Harrison, three Chilliwack and two Snohomish Chinook were sampled. From the Southern region, one Harrison and three Snohomish fish were sampled. In addition, three adult herring from both the Northern and the Southern region were also sampled to provide a 'baseline' isotopic signature for a potential prey species. The following two CSIA analyses were conducted:

i) Essential/non-essential amino acid $\delta^{15}N$ values were used to determine the trophic level of the organism.
ii) Essential amino acid $\delta^{13}C$ values were used to investigate the primary producer source materials underpinning the food web.

Trophic level was calculated using the formula: $TL = ((\delta^{15}N_{Glu} - \delta^{15}N_{Phe} - 3.4)/7.6) + 1$. For all Chinook and herring samples, $\delta^{13}C$ values from 8 essential amino acids (His, Ile, Lue, Lys, Met, Phe, Thr, Val) were standardized and analyzed with a principal component analysis to investigate differences in food web sources in the two regions.

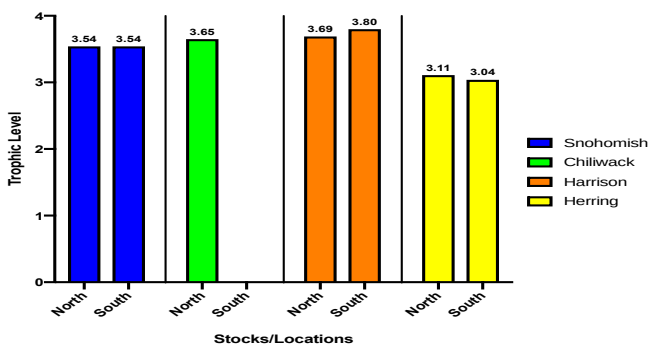

Fig. 1. Trophic Level determined for Chinook and herring from North Vancouver Island and South Vancouver Island.

The trophic level of Chinook stocks ranged between 3.54 and 3.8 (Fig. 1). There was little variation between North and South populations, though the Puget Sound Chinook trophic level was lower than the two Fraser River populations (Fig. 1). For both herring groups, trophic level was ~ 3, but was slightly higher in the north. These results indicate that adult Chinook are feeding at lower trophic levels such as on euphausiids and copepods, not exclusively on forage fish. Herring feed on zooplankton and a trophic level of ~3 was therefore expected for both groups (Schweigert et al. 2010). Principal component analysis of $\delta^{13}C$ showed that Chinook were separated from

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herring along the y-axis (Fig. 2). Because the $\delta^{13}C$ of essential amino acids is conserved through the food web, this suggests that sampled Chinook had not been feeding on these herring stocks. Furthermore, given that herring were predicted to provide baseline $\delta^{13}C$ for the regions sampled, the Chinook were most likely not feeding significantly in region were captured. Finally, Chinook stocks grouped closely together in this analysis, suggesting similar resource use in the months prior to capture, while conversely the north and south herring stocks were well separated indicating that they resided in different food webs.

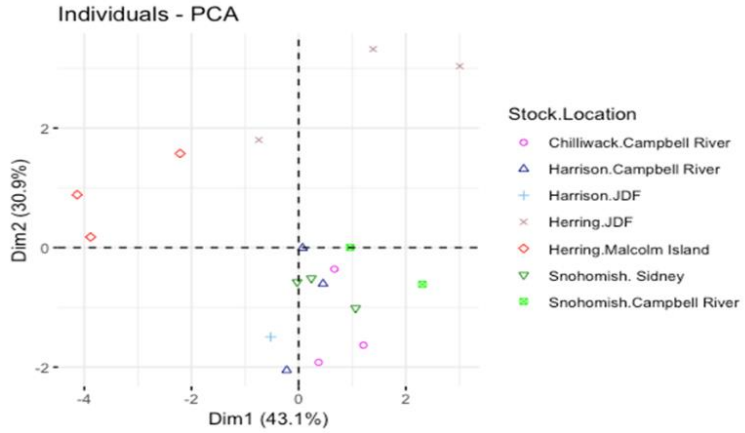

Fig. 2. Principal Component Analysis of $\delta^{13}C$ of 8 essential amino acids in Chinook/Herring stocks grouped by sampling region.

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Detecting the Effects of Management Regime Shifts in Dynamic Environments Using Multi-population State-space Models

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Keywords: Regime shift, nonstationary, population dynamics, relative reproductive success, viability, coho

Detecting the effectiveness of management actions intended to increase the abundance of threatened or exploited species can help resolve uncertainties about cost-effective management tactics. However, the complexity of ecological systems can make it difficult to identify important factors causing change in population abundance. This difficulty extends from detecting naturally-caused ecosystem regime shifts to management induced regime shifts and the attendant change in population dynamics parameters. The adult abundance of naturally-produced coho salmon (*Oncorhynchus kisutch*) on the Oregon Coast generally declined until these fish were listed as threatened under the Endangered Species Act in 1998. The subsequent rebuilding of Oregon coastal coho adult abundance is coincident with increased habitat restoration, reduced hatchery production, and reduced harvest. Importantly, ocean survival also improved, thereby complicating the assessment of management effectiveness at the adult life stage. Our objective was to assess change in the freshwater production of juveniles (smolts) through time in order to determine if recent increases in adult abundance could be related to management affecting the freshwater juvenile production.

Table 1. Six different three-variable generalized additive models were identified by Rupp et al. (2012b) to predict coho ocean abundance. These models were refitted with smolt-to-adult survival as the response variable. The annual smolt-to-adult survival prediction is an average of the logit transformed values predicted by each of the six generalized additive models. Variables used in the models are four-year moving average of Pacific decadal oscillation index (PDO), date of spring transition between down-welling and upwelling (SPR), upwelling index (UWI), sea surface height (SSH), spawner abundance (SPN), Multivariate El Niño-Southern Oscillation index (MEI), and sea surface temperature (SST). The three letters following the dot give the three consecutive months over which the variable was measured. The coefficient of determination (R^2) and ordinary cross validation (OCV) are given for individual models and the model averaged ensemble.

ID		Variables		R^2	OCV
Model 1	PDO.MJJ4	SPR	SPN	0.71	0.36
Model 2	PDO.MJJ$_4$	MEI.OND	UWI.JAS	0.57	0.07
Model 3	PDO.MJJ$_4$	SPR	MEI.OND	0.68	0.45
Model 4	PDO.MJJ$_4$	UWI.JAS	SST.AMJ	0.61	0.24
Model 5	PDO.MJJ$_4$	SSH.AMJ	UWI.JAS	0.77	0.50
Model 6	PDO.MJJ$_4$	UWI.SON	SST.J	0.74	0.46
Models 1 - 6 ensemble				0.75	0.47

Table 2. Three models of Oregon coastal coho population dynamics (columns) are distinguished from one another by whether or not (i) the relative reproductive success (RRS) of hatchery-origin fish is estimated, and (ii) a quadratic function of freshwater stream flow is used as a covariate in smolt recruitment. All three models permitted change in the mean, across-population inflection point in coastal coho smolt recruitment before ($\bar{\mu}_{\gamma 1}$) and after ($\bar{\mu}_{\gamma 2}$) 1998. The probability (Pr) that smolt recruitment declined was found by conducting random permutations of the posterior distributions. The odds ratio for improved recruitment is computed directly from the associated probabilities.

Model ID	A	B	C
Change recruitment?	Yes	Yes	Yes
Estimate RRS?	Yes	No	No
Include Flow?	Yes	Yes	No
$\bar{\mu}_{\gamma 1}$	623	657	656
$\bar{\mu}_{\gamma 2}$	407	434	434
Pr $[\bar{\mu}_{\gamma 1} > \bar{\mu}_{\gamma 2}]$	0.87	0.86	0.86
Oddsratio $\bar{\mu}_{\gamma 2} > \bar{\mu}_{\gamma 1}$	1 in 6.8	1 in 6.2	1 in 6.1

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We combined 46 years of data associated with 18 populations of Oregon coastal coho. Spawner-to-smolt relationships were modeled with Bayesian hierarchical state-space implementations of the logistic hockey stick recruitment function. We also develop a method of estimating the relative reproductive success of hatchery spawners. We found more evidence for decline than increase in productivity in the spawner-to-smolt life stage, suggesting that changes in physical oceanographic conditions are responsible for recent increases in adult abundance. The reproductive success of hatchery-origin fish relative to natural-origin fish was 0.51 with a 95% credible interval from 0.19 to 0.89. While some management effects may unfold on longer time-scales than we observed, we nonetheless contend that carefully tailored models of non-stationary population dynamics are needed to understand and the effectiveness of management actions intended to recover populations.

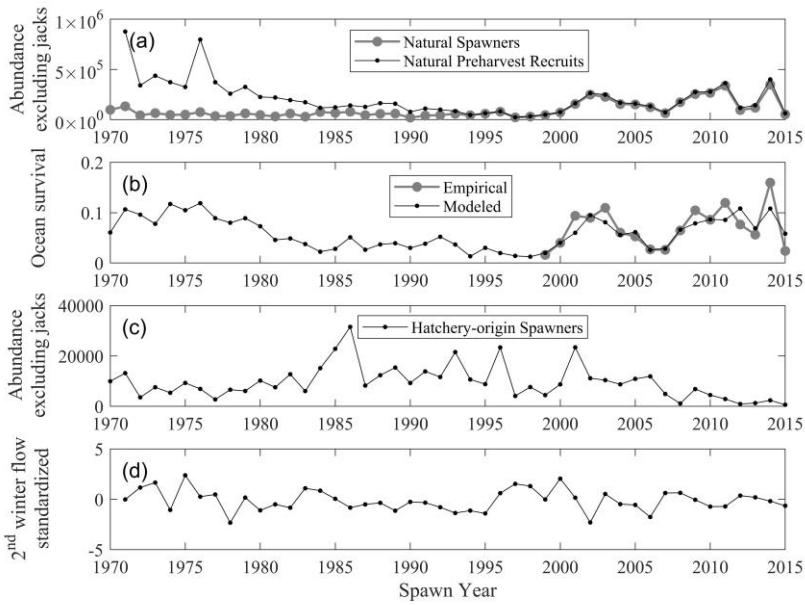

Fig. 1. The abundance of natural-origin adult coho declined until the late 1990s (a), which is coincident with the pattern in ocean survival rate (b), but multiple biologically conservative actions also began in the late 1990s, including reduction in hatchery production (c). Mean second winter stream flow from November–March in four sites were standardized (z-score) over 1961–2015 and averaged together (d).

Fig. 2. Eighteen populations of coho salmon on the west coast of Oregon, USA, are defined by drainage basins. Abundance has been estimated annually since 1970 (see text for exceptions). Smolt-to-adult survival has been recorded since 1998 at sites located within Nehalem, Siletz, Yaquina, Alsea, Lower Umpqua, and Coos.

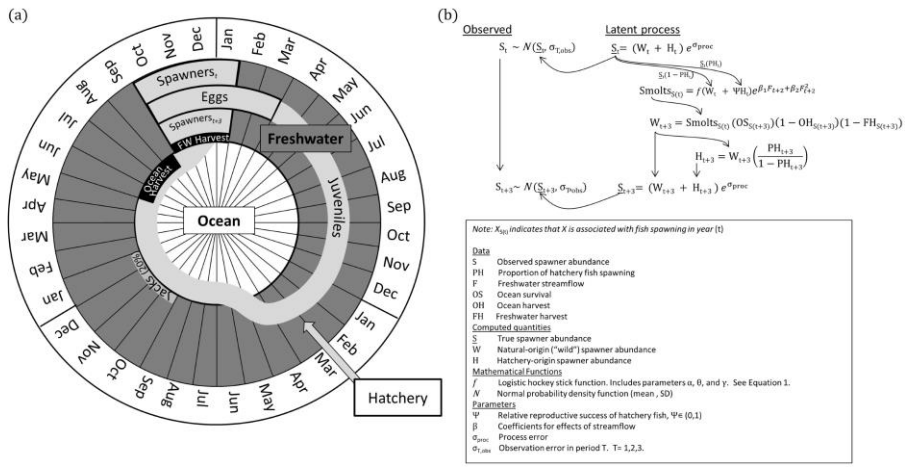

Fig. 3. Life cycle of Oregon coastal coho (a). Jacks are precocious males and not included in the data or models presented here. The state-space model (b) of coho population dynamics decomposes spawner abundance into hatchery and natural-origin components using annual estimates of the proportion of hatchery fish. Hatchery and natural-origin fish produce smolts, but reproductive success of hatchery fish is some fraction (Ψ) of natural-origin fish that can be estimated empirically.

The latent process generating spawner abundance is recursive, but hatchery-origin fish are added to match the observed fraction of hatchery-origin spawners. Process error is logarithmic, reflecting the common assumption that recruitment is a multiplicative survival process. Each year's estimate of spawner abundance is assumed to be normally distributed around the true abundances, reflecting unbiased sampling error. The magnitude of the sampling error is allowed to vary across three time periods when different sampling designs were used. The parameter of the recruitment function controlling the inflection point (γ) was allowed to vary across two periods (before and after 1998) that reflect times of pre- and post-biological conservation management.

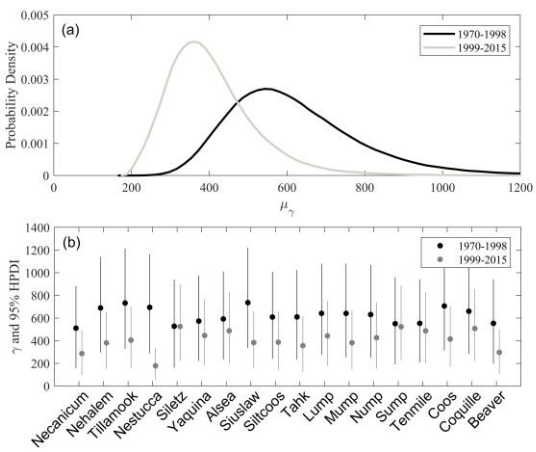

Fig. 4. Posterior probability distribution of the mean, all-population distribution of inflection points (γ) in logistic hockey stick smolt recruitment functions from 1970 to 1998 and 1999 to 2015 (a). Individual population point estimates and 95% highest probability density intervals for inflection points (γ) in logistic hockey stick smolt recruitment functions from 1970 to 1998 and 1999 to 2015 (b). Model A used in both (a) and (b).

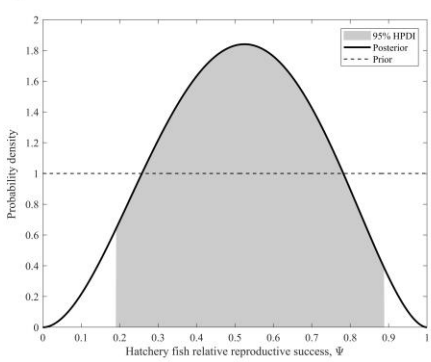

Fig. 5. Posterior probability density of hatchery fish reproductive success relative to natural-origin fish (solid line). Shaded area is the 95% highest probability density interval [0.19, 0.89]. The prior distribution used in the analysis is equi-probable over the entire range of possible values for hatchery fish relative reproductive success (dashed line).

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State of the Salmon: Improving Predictions of Salmon Survival during a Period of Rapid Change

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Keywords: salmon, productivity, abundance, trends, forecasts, Pacific, status, growth, climate change, survival, Fraser Sockeye, survival, integration, habitat change, ecosystem

The planet is warming. Earth's average land-ocean temperature has risen by close to 1°C over the last century, with the most recent five years measuring as the warmest on record (Morice et al. 2012; Hartmann et al. 2013). Global climate change is already affecting Canadian Pacific salmon and their ecosystems, and these impacts will increase with further warming (IPCC 2014; White et al. 2016; Holsman et al. 2018; Bush and Lemmen 2019). In light of environmental change, it is critical that we track and understand how salmon are responding currently, and how they will respond to future change.

Information on climate-habitat conditions and Fraser River Sockeye salmon responses across life stages has been integrated annually since 2014. This work provides additional qualitative information on survival of Fraser River Sockeye survival to refine the pre-season quantitative return forecasts. This approach is being expanded to help predict the vulnerability of salmon populations to future climate and habitat change. Such vulnerability assessments results will support salmon management, recovery, and habitat restoration activities consider future change.

Quantitative forecasts of Fraser Sockeye returns by population are produced annually to support fisheries management processes (MacDonald and Grant 2012; DFO 2018, 2019). Challenges in determining factors that influence Fraser Sockeye survival (recruits-per-spawner) have resulted in very uncertain return forecasts. These factors act alone or cumulatively, and can vary by year and population, and in recent decades, salmon ecosystems have been experiencing unprecedented changes related to climate and habitat changes (Grant et al. 2019; MacDonald et al. 2018).

An annual qualitative process was initiated by the State of the Salmon Program in 2014 to inform the quantitative forecast. This process integrates biological and environmental observations and data across research programs relevant to Fraser sockeye. This involves the collaboration of salmon and ecosystem experts working on the following life stages: upstream migration, spawners, egg stage, lake-rearing, downstream migration, and juvenile ocean-rearing. Observations during each of these stages are flagged if experts indicate they could affect survival at that particular stage. Individual observations are then integrated across life-stages to produce an overall prediction of survival.

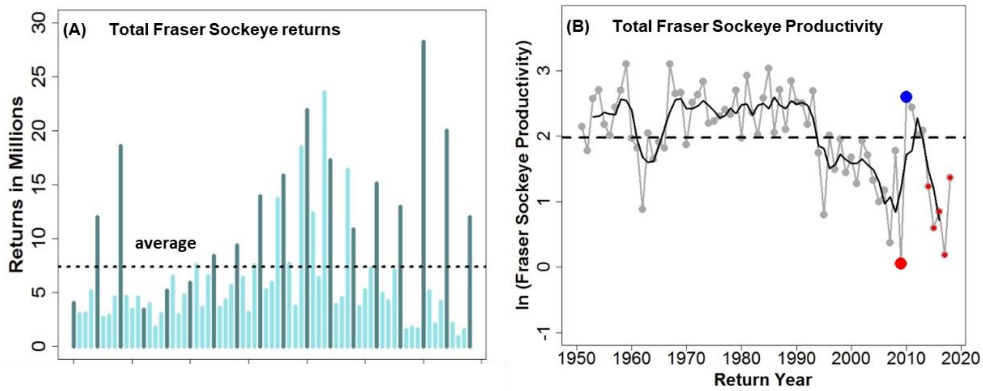

Fig. 1. (A) Total Fraser Sockeye annual returns (dark blue vertical bars for the 2018 cycle and light blue vertical bars for the three other cycles). Recent returns from 2016 to 2018 are preliminary, and 2018 (the last data point) is an in-season estimate only. (B) Total Fraser Sockeye productivity ($\log_e$ (returns/total spawner)) is presented up to the 2018 return year. The grey dots and lines represent annual productivity estimates and the black line represents the smoothed four year running average. For both figures, the dashed line is the time series average.

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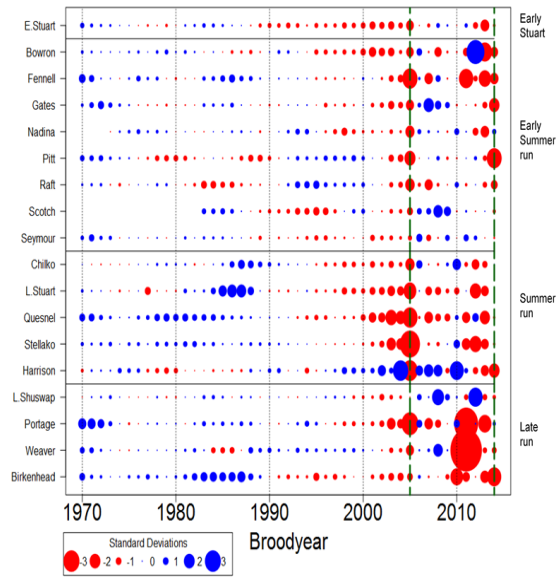

Fig. 2. Fraser Sockeye productivity (Ricker model residuals for all populations except Scotch, Seymour and Late Shuswap, which are Larkin residuals) up to the 2014 brood year (2018 return year) across 18 different populations and 4 different management groups (Early Stuart, Early Summer run, Summer run and Late run, named based on the migration timing of adults returning to their spawning grounds). Prior to the 2005 brood year, four year moving averages are plotted while annual estimates are provided for the more recent years. For the 2012 to 2014 brood years (2016 to 2018 return years), preliminary estimates of recruits by age are not yet available; preliminary in-season returns divided into population group using escapement proportions were applied to estimate recruits for each population. Both freshwater and marine factors contribute to the observed productivities. Red dots indicate below average productivity and blue dots indicate above average productivity. The smallest dots represent average annual productivity and the larger the diameter, the greater the deviation from average. The 2005 and 2014 brood years (2009 and 2018 return years) have been highlighted using a broken vertical green line.

The Fraser Sockeye aggregate has exhibited declines in total returns and survival in the last decade (Fig. 1). This trend was interrupted for a brief period from 2010 to 2013, when survival and returns improved to average. Poor returns and survival resumed from 2015 to 2018. Trends in aggregate Fraser sockeye returns and survival are largely determined by the populations that make up the greatest proportion of the total abundance in each year, namely Summer Run (e.g., Chilko), and Late Run populations (e.g., Late Shuswap on dominant cycle years).

Across individual Fraser Sockeye populations (Fig. 2), however, there can be considerable variability in survival. Examination of disaggregated data for the 19 populations shows that trends were synchronous across most populations in the early period of declining productivity and returns, suggesting that this was driven by broad-scale regional factors (Fig. 2). In more recent years, productivity has been asynchronous across Fraser Sockeye populations, indicating that local drivers, or unique population-specific factors, have contributed to the observed trends (Fig. 2). However, in the last two years, the return to poor productivity and returns has been largely synchronously poor across populations.

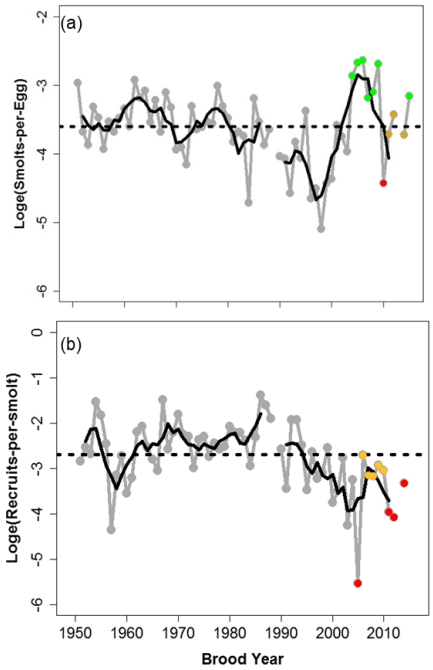

Fig. 3. (A) Chilko River Sockeye freshwater survival ($\log_e$ smolts-per-egg) and (B) 'marine' ($\log_e$ recruits-per-smolt) annual survival. The filled grey circles and grey lines are annual values and the black line is the smoothed four-year running average survival. Freshwater survival has generally increased in the past decade, with the notable exception of 2010), when poor survival was associated with density-dependent factors caused by the large escapements in this brood year. Marine survival has generally been below average for the past decade, and particularly low in the 2005 and last three brood years: 2011 2012 and 2014 (2013* is a gap in the time series).
*Note: Chilko 'marine' survival includes a freshwater period during their downstream migration as smolts from the outlet of Chilko Lake to the Strait of Georgia, and their entire marine residence period. The horizontal dashed line indicates average survival.
*Note: High water levels prevented accurate counting of smolts in 2015, therefore freshwater and marine survival estimates are unavailable for the 2013 brood year (2017 return year).

Total Fraser sockeye salmon survival is influenced by both freshwater and marine ecosystems. Fraser sockeye typically return to freshwater to spawn as four-year old fish, after spending their first two winters in freshwater, and their last two winters in the ocean. These populations use various freshwater and marine habitats throughout their life. Specifically, after their second winter in freshwater, most smolts leave their rearing lakes and migrate down the Fraser River to the Strait of Georgia. Most Fraser sockeye migrate north through the Strait of Georgia in approximately 40 days (Preikshot et al. 2012; Neville et al. 2016) and exit this system via the Johnstone Strait. Juveniles continue their northward migration along the continental shelf, and move into the Gulf of Alaska by their first winter at sea (Tucker et al. 2009). They subsequently spend one more winter in the marine environment before they return to their natal freshwater spawning grounds as adults.

Freshwater and marine survival data can help us potentially link survival with environmental conditions, by identifying the ecosystem in which trends in survival diverge across populations. This level of survival data is available for Chilko and Cultus sockeye, though the Cultus time series is confounded by low numbers of returns and high levels of hatchery enhancement. While both of these populations have exhibited declines in their marine survival (Fig. 3B for Chilko), trends in their freshwater survival diverge substantially, and drive the overall returns and statuses of these populations.

Differences in freshwater survival between Chilko and Cultus Sockeye populations is attributed, in part, to unique characteristics of their rearing lakes. Freshwater survival for Chilko sockeye has increased in the past decade (Fig. 3A for Chilko), and this population is healthy in comparison to most other Fraser sockeye in terms of overall survival and returns. Chilko sockeye rear in Chilko Lake, which is located in a remote, high alpine location, and is glacially fed with cool water. Cultus sockeye, in contrast, rear in a warm coastal lake that lies very close to a large urban centre (Vancouver, B.C.), and is subject to considerable agricultural and other sources of nutrient inputs (Putt et al. 2019), recreational use, and human development. Cultus Sockeye have exhibited a decline in freshwater survival, and this population is critically endangered, having negligible wild salmon production. Cultus survival data are not presented here, since this time series has many gaps and higher uncertainty. Chilko and Cultus emphasize differences in survival that can occur between populations, quite likely linked to differences in the suitability of the habitats they occupy.

In the last three return years, since 2016, many impacts of climate change have been observed in ecosystems that Fraser sockeye rely on (Schmitt et al. 2016; Holsman et al. 2018; Bush and Lemmen 2019; Grant et al. 2019). These impacts have been documented through the qualitative Fraser sockeye forecast process (MacDonald et al. 2018), and used to guide science recommendations on potential survival of returning cohorts of Fraser sockeye.

The warm 'Blob,' present in the Northeast Pacific Ocean from the latter half of 2013 to fall 2016, consisted of sea-surface-temperatures (SST) that were 3–5°C above seasonal averages and extended down to 100 m depths (Bond et al. 2015; Ross 2017). Climate modeling has shown that this marine heatwave can best be explained by human-caused warming (Walsh et al. 2018), suggesting that these events will become more frequent, and longer lasting in the future (Smale et al. 2019). The recent warming had profound effects on marine food webs, shifting zooplankton composition at the base of the salmon food web towards less nutritious, southern species (Galbraith and Young 2017). Detailed annual scientific information is compiled on the Northeast Pacific Ocean through DFO's State of the Pacific Ocean reporting process (Chandler et al. 2016, 2017, 2018).

British Columbia air temperatures have also been increasing across all seasons in recent decades (Pike et al. 2008; White et al. 2016). High temperatures in freshwater are particularly problematic in the Fraser River, where they now regularly exceed critical thermal limits for salmon during summer months, falling above 18–20°C (Eliason et al. 2011; Martins et al. 2012; MacDonald et al. 2018). Patterns of stream flow are changing throughout BC/Yukon as snowpacks melt earlier in spring, causing early freshets (Pike et al. 2008; Pike et al. 2010a, 2010b). There are examples where salmon smolt outmigrations have concurrently shifted earlier (MacDonald et al. 2018). Freshwater impacts of climate change will vary with local conditions across BC and the Yukon and will interact with other human induced landscape changes. For many salmon populations, these impacts will have negative effects on condition and/or survival, which will act cumulatively across their life stages (McDaniels et al. 2010; Healey 2011).

Through the State of the Salmon qualitative forecast process, experts integrated observations and data on anomalously warm conditions, ecosystem changes, and expected or reported salmon responses across the various life-stages, prior to the returns of Fraser sockeye for 2017–2019 (MacDonald et al. 2018). In each of these years, below average survival was predicted as a result of this integration process. Consistent with this advice, Fraser sockeye survival was below average in 2017 and 2018 (Figs. 1 and 2), providing early validation for this expert-judgement process. Preliminary return numbers and productivity in 2019 were the lowest on record.

Also notable in 2019, a major landslide was discovered in June 2019 on the Fraser River at Big Bar, near Lillooet, B.C. This landslide has effectively blocked passage of all Fraser sockeye populations that spawn upstream

of this location. This blockage lies upstream of the Thompson system, but downstream of tributaries for major populations like Chilko, Quesnel, Early and Late Stuart, and Nadina, Stellako, and Bowron. At the time of writing this report, mitigation of the slide is being attempted, though significant impacts on the survival of fish spawning upstream of this slide are anticipated in 2019.

DFO's State of the Salmon Program is expanding on lessons learned from the qualitative forecasting process for Fraser sockeye, due to its success in guiding predictions, and in fostering collaboration and integration of science and expert judgement. Leads from this program are coordinating an approach for a broader group of scientists to conduct vulnerability assessments for Canadian Pacific Salmon, in light of climate and habitat change. This work is essential to inform management actions and ensure the best possible outcomes for salmon in a changing climate. It is a critical time in human history, when biodiversity losses are occurring at an unprecedented rate (WWF 2017; IPBES 2018). However, mitigation is still possible as long as we are able to prepare accordingly, and capitalize on our collective knowledge.

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Evaluating Impacts of Time-varying Productivity in Stock-recruit Relationships on Biological Benchmarks

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Keywords: time-varying productivity, Ricker model, benchmarks, reference points, simulation, Kalman Filter

Time-varying models that account for changes in productivity are increasingly being applied to assess fish stocks, including Pacific salmon (Peterman et al. 2000; Dorner et al. 2008; Peterman and Dorner, 2012), but their reliability under different harvest and productivity scenarios has not been thoroughly evaluated. In particular, the Kalman filter has been used as an analytical tool to identify time-varying productivity in Pacific salmon stocks assessed with a Ricker stock-recruit relationship (Peterman et al. 2000). While variability in the underlying spawner and recruitment data, e.g., due to variability in a stock's exploitation history, may impact the relative performance of models, this has not been considered in model evaluations. In addition, the implications of time-varying productivity on the derivation of biological reference points or benchmarks have not been quantified for Pacific salmon. Here, we evaluated stock-recruitment models with and without time-varying productivity parameters in a closed-loop simulation model of sockeye salmon (*Oncorhynchus nerka*). This modelling approach allowed us to evaluate biases and precision of parameter estimates under various hypotheses about trajectories in productivity and exploitation rates, and their implications on biological benchmarks.

We addressed this overarching goal with the following objectives.

(1) Evaluate the bias and precision of parameter estimates from a standard stock-recruit model against one that includes time-varying productivity, using simulated stock-recruitment data based on different scenarios of temporal changes in productivity and exploitation rates.

(2) Evaluate the bias and precision of a biological benchmark, spawner abundances at maximum sustainable yield, S_{MSY}, derived from the estimated parameters of standard and time-varying models.

(3) Provide suggestions on best practices when considering time-varying productivity in stock assessments and when deriving benchmarks.

Methods

The standard Ricker model assumes productivity remains unchanged over time and is formulated:

$$(1) log_e\left(\frac{R_t}{S_t}\right) = \alpha - \beta S_t + v_t ,$$

where S_t is the total number of spawners in the brood year t, R_t is the number of adult recruits produced by those spawners, α is the productivity at low spawner abundance in the absence of density dependence, β is the rate at which recruitment is reduced by density-dependence and the inverse of the abundance of spawners at maximum recruitment or capacity, and v_t are random normal deviations with variance ${\sigma_v}^2$, $v_t \sim N(0, {\sigma_v}^2)$.

We incorporated time-varying productivity into the Ricker model by allowing the productivity parameter, α, to vary over time t according to a random walk:

$$(2) log_e\left(\frac{R_t}{S_t}\right) = \alpha_t - \beta S_t + v_t ,$$

$$(3) \alpha_t = \alpha_{t-1} + \omega_t,$$

where ω_t are random normal process errors with variance ${\sigma_\omega}^2$, $\omega \sim N(0, {\sigma_\omega}^2)$. Parameters of the time-varying Ricker model (Eqns. 2 and 3) were estimated using a recursive Kalman Filter algorithm with maximum likelihood estimation (Harvey 1989; Peterman et al. 2000, Britten et al. 2016).

The Monte Carlo simulation framework used to evaluate standard and time-varying Ricker models included spawner and recruitment dynamics each year followed by the impacts of harvest on spawner abundances in the following year. We evaluated performance of standard and time-varying stock-recruitment models for tracking true underlying productivity, under three productivity scenarios (constant, declining and increasing) and three exploitation rate scenarios (low and high constant exploitation and a stepwise decline in exploitation). Our

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simulation model was a simplified version of models previously developed to evaluate benchmarks for southern British Columbia chum salmon (Holt and Folkes 2015; Holt et al. 2018), which captures the general population and management dynamics for Pacific salmon stocks.

Results and Discussion

Results indicated that time-varying models tended to perform as well as or outperform standard stock-recruitment models that did not account for time-varying productivity (e.g., Fig. 1, under scenario of underlying declines in productivity). Ignoring trends in productivity within the model led to significant over-estimates of the benchmark, S_{MSY} when exploitation rates were constant and high (Fig. 1). However, S_{MSY} was slightly underestimated by the standard model when both exploitation rates and productivity declined over time, as has been observed for Fraser River sockeye salmon. In contrast, time-varying models tended to be unbiased on average. Although models that incorporate time-varying productivity will provide biological benchmarks that are less biased relative to true underlying benchmarks, some biological benchmarks trend downwards (i.e., become less precautionary) when productivity declines as few spawners are needed to sustainably maximize yield.

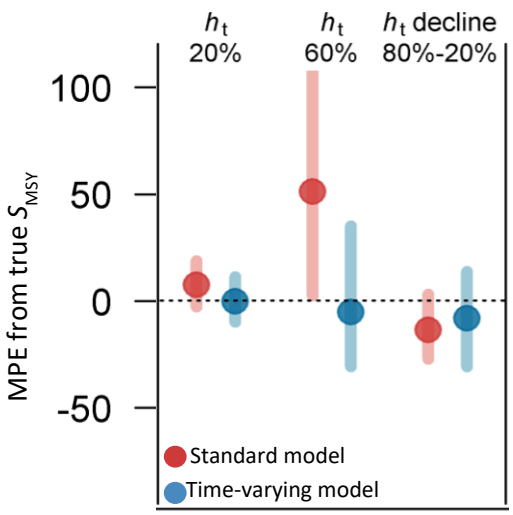

Fig. 1. Mean percent error in estimate of spawner at maximum sustainable yield, S_{MSY}, for the standard Ricker model (red) and time-varying Ricker model (blue). Bars represent 95% confidence intervals. Results from 3 exploitation rate scenarios are shown: constant low exploitation rate (h_t 20%), constant high exploitation rate (h_t 60%), and a step decline in exploitation rate halfway through the time-series (h_t decline 80%-20%). The upper 97.5% upper CL for MPE of the standard model under constant high exploitation rate is above the upper limit of the plot at 182%.

We suggest several best practices when considering revisions to benchmarks or biological reference points due to persistent shifts in productivity to ensure decision making is sound and transparent (adapted from Duplisea and Cardigan (2012)). These recommendations include documenting evidence of changes in exploitation of the stock, documenting evidence for the changes in productivity, calculating stock-recruitment parameter estimates and benchmarks with and without time-varying productivity and comparing values, and importantly, supporting decisions for benchmarks or reference points with simulation models that include management procedures with the assessment and application of those reference points (e.g., in harvest control rules) and uncertainty in future trends in productivity (as shown for Pacific salmon by Collie et al. (2012)).

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Improving Terminal Abundance Estimates of Spring- and Summer-run Age 5_2 Fraser River Chinook Salmon by Incorporating a Second CPUE Dataset from the Albion Test Fishery

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Keywords: Chinook, abundance estimation, Fraser River, Bayesian model, fisheries management

Fraser River Chinook salmon (*Oncorhynchus tshawytscha*) are currently managed as five stock aggregates that share similar ages and return timing (Fig. 1). An in-season Bayesian model has been used since 2012 to estimate the total abundance of two of these aggregates: spring- and summer-run age 5_2 Chinook. This model predicts the terminal aggregate abundance to the mouth of the Fraser River using cumulative weekly catch-per-unit-effort (CPUE) from the Albion test fishery and reconstructed annual run size. These predictions are used as an in-season tool to manage Fraser River fisheries in line with the expected abundance of the aggregated spring- and summer-run age 5_2 Chinook via a "zoned" approach (DFO 2018). The abundance of these aggregates has been declining in recent years, and it is critical to improve the precision of the in-season model for sustainable fishery management.

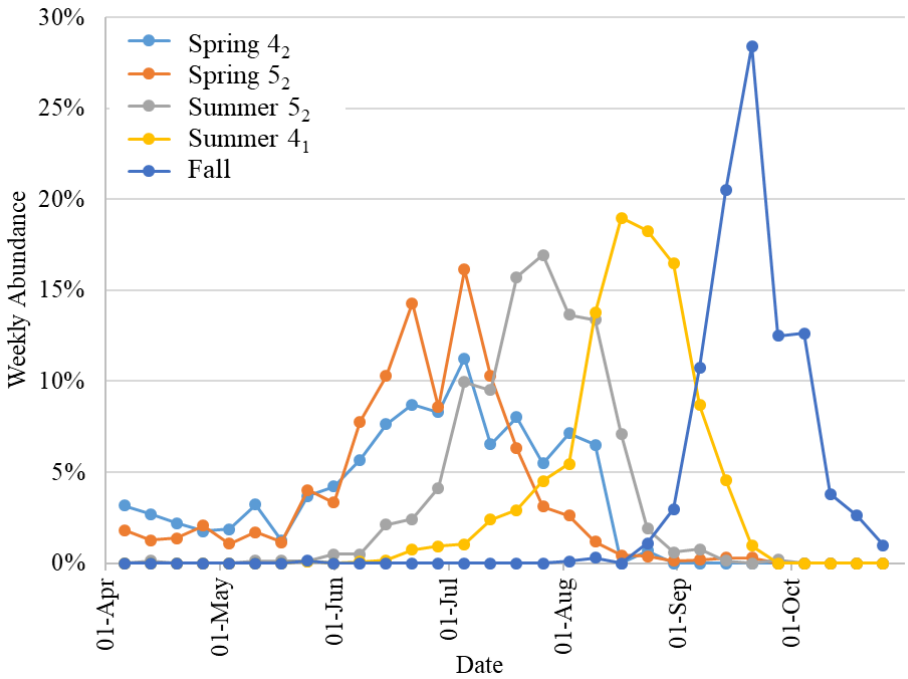

Fig. 1. Run timing of Fraser Chinook stock aggregates at the Albion Test Fishery, based on 2000–2001 data.

The current model uses cumulative catch-per-unit-effort (CPUE) data from the test fishery at Albion (near Fort Langley, B.C., Canada), which since 1981 has used a single panel (SP) net 200 fathoms long with 203 mm mesh. Catch and effort data are cumulated by week, starting the first full week in May (stat week 5_1), to provide the input to the model. Run size values used in the model are derived from a separate model that reconstructs the run size of Chinook salmon at the mouth of the Fraser River (terminal return) for individual populations and stock aggregates (English et al. 2007). The in-season abundance model fit to these data is a log-linear regression of cumulative CPUE against the terminal return, and a different regression is fit for each statistical week from 5_1 through 7_2 (first week of May until second week of July; see Chamberlain and Parken 2012). This regression is then used to predict the terminal return based on the cumulative CPUE for that stat week. The final in-season estimate typically occurs with stat week 6_2, when the cumulative CPUE is most often the best in-season predictor of the terminal return.

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In 2004, the test fishery at Albion began fishing every other day with a variable mesh net (VMN) that consists of eight panels of four different mesh sizes (152 mm, 178 mm, 203 mm, and 229 mm; two 25-fathom panels each). The CPUE data from this VMN has not yet been used as an input for the run size model, as several years of data were required before its predictive abilities could be assessed. The objective of this study was to incorporate the VMN data into the in-season run size model to determine its effect on the precision of the weekly estimates. The predictive abilities of three different abundance index (CPUE) inputs to the Bayesian model were assessed: a model with only SP CPUE inputs, a second with only VMN CPUE inputs, and a third with both SP and VMN CPUE inputs (hereafter called a 'combo model').

The predictive Bayesian model is run using the statistical software R (v. 3.6.0); it also makes use of the modeling software OpenBUGS (v. 3.2.3 rev 1012). Predicted run sizes from three versions of the model that incorporated three datasets (SP only, VMN only, and a combination of these datasets) were compared across 10 statistical weeks (May through mid-July) over six years (2012–2017). CPUE for statistical weeks 5_2 through 7_3 in each year was calculated as the sum of weekly catch divided by the sum of weekly test fishing effort (thousand fathom minutes) as follows:

$$CPUE_{week} = \frac{\sum Catch}{\sum Effort}$$

Cumulative CPUE was the cumulative sum of weekly CPUE, starting with week 5_2 as the sum of CPUE in week 5_1 and 5_2; this value and the annual terminal abundance estimate were the abundance index inputs into the model. For predictions made in statistical weeks 5_2 and 5_3, SP data from 2014 and 2016 and VMN data from 2013 and 2016 were excluded from the model inputs due to a cumulative CPUE of 0, which prevented the model from completing calculations. Retrospective performance of the model was examined by comparing median run size estimates and 95% prediction intervals to the reconstructed annual run size estimate using mean average percent error (MAPE). MAPE is a measure of prediction accuracy of a forecasting method and expresses accuracy as a percentage where a low value suggests less error.

Table 1. MAPE summary for the run size prediction model with each of three datasets. Note that there is no MAPE calculated for the combo model in statistical week 5_2 and 5_3 as the model cannot support cumulative CPUE input of zero. Grey stat weeks are the weeks when the model estimate is used to inform fishery management.

Stat Week	combo	VMN	SP	Best model prediction
5_2	NA	50.0%	35.8%	SP
5_3	NA	33.5%	31.4%	SP
5_4	31.7%	46.7%	33.2%	combo
6_1	36.0%	41.7%	45.3%	combo
6_2	25.1%	35.4%	37.9%	combo
6_3	21.2%	24.2%	33.7%	combo
6_4	26.7%	23.7%	30.5%	VMN
7_1	24.2%	25.2%	24.5%	combo
7_2	21.0%	30.9%	28.0%	combo
7_3	22.4%	34.8%	27.2%	combo

Generally, the combo model had lower MAPE and smaller prediction intervals than the model that incorporated only either SP or VMN data (Table 1). However, model performance varied depending on the statistical week and year, which may be the result of a hyperstable relationship developing between CPUE and terminal abundance. All models performed worse in years of low terminal run abundance (e.g., 2017, Fig. 2). MAPE for the model incorporating only SP data increased since the model was developed in 2012. When examining model outputs from only the statistical weeks in which in-season management decisions are made (week 5_2, 5_4, and 6_2), the combo model typically had the lowest MAPE values, but not always. In most years, the combo model performs equally as well as the SP model at predicting the correct management zone (Table 2). There is a light improvement for 2015 where the combo model was able to predict the correct management zone earlier than the SP model. None of the models were able to detect the high abundance observed in 2014.

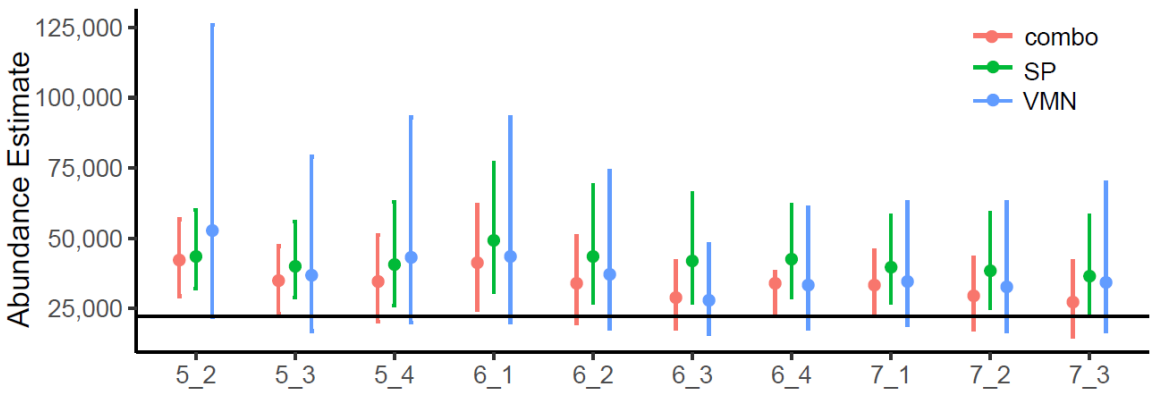

Fig. 2. Estimates of terminal run size in 2017 with 95% predictive intervals for each statistical week when incorporating each of the three datasets (SP = single panel data only; VMN = variable mesh data only; combo = both SP and VMN datasets). Solid line is the post-season terminal run size estimate.

Table 2. Comparison of the in-season model prediction with the post-season abundance estimate in terms of the zoned management approach. Green cells indicate the in-season prediction matches the post-season prediction.

Year	Stat Week	Fishery Zone (Post-season)	In-season model prediction		
			combo	SP	VMN
2012	5_2	zone 2	zone 1	zone 2	
	5_4		zone 2	zone 2	zone 2
	6_2		zone 2	zone 2	zone 2
2013	5_2	zone 1	zone 1	zone 1	zone 2
	5_4		zone 1	zone 1	zone 1
	6_2		zone 1	zone 1	zone 2
2014	5_2	zone 3		zone 1	zone 2
	5_4		zone 2	zone 1	zone 2
	6_2		zone 2	zone 2	zone 2
2015	5_2	zone 2	zone 2	zone 1	zone 2
	5_4		zone 2	zone 1	zone 2
	6_2		zone 2	zone 2	zone 2
2016	5_4	zone 1	zone 1	zone 1	zone 2
	6_2		zone 1	zone 1	zone 2
2017	5_2	zone 1	zone 1	zone 1	zone 2
	5_4		zone 1	zone 1	zone 1
	6_2		zone1	zone 1	zone 1

Future model development would benefit from exploration of whether incorporating environmental variables may allow for more accurate estimation of terminal abundance of these aggregates, particularly given the potential impact of future climate change on Chinook abundance and return timing. Another future consideration could be an assessment of separating the VMN CPUE by mesh size.

In summary, incorporating both the SP and VMN net data improves the in-season median estimate of run size and modestly reduces uncertainty in some years. Incorporating VMN data could also make the overall dataset more representative of the stock aggregates since a greater range of sizes are caught. The model still does not detect very high and very low returns well in-season. While using the combo model results in no change to in-season management actions, there may be a desire to move to a management system of allocating catch numbers instead of using the zoned approach. To do this, more precise estimates of in-season run size are required to ensure confidence

in management actions. This model was originally developed in response to a very specific management strategy; there is a need to adapt the tool to match changes in management and conservation objectives.

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Assessing the Early Marine Ecology of Juvenile Chinook Salmon in a Warming Bering Sea

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Keywords: Chinook salmon, *Oncorhynchus tshawytscha*, Yukon River, juvenile abundance, marine, adult forecasting, climate

Yukon River Chinook salmon (*Oncorhynchus tshawytscha*) returns have declined dramatically since the late 1990s, leading to severely restricted subsistence harvests and closures of commercial and sport fisheries in attempts to meet spawning escapement needs (Estensen et al. 2015). Despite extraordinary harvest reductions, pervasive failures to meet escapement objectives in the Yukon River and other Alaskan systems have occurred throughout recent years (Munro and Volk 2014). Although causes of this production decline are unclear, concurrent declines throughout Alaska (ADF&G 2013) have placed emphasis on ocean conditions and the marine life history stage of Chinook salmon.

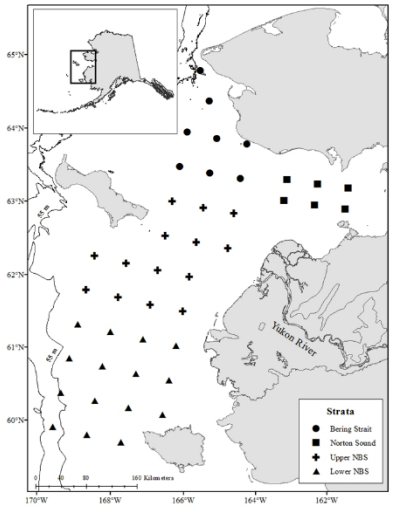

Fig. 1. Northeastern Bering Sea survey stations with symbols representing each of four spatial strata.

The northeastern Bering Sea (NBS) is the primary rearing habitat of Yukon River juvenile Chinook salmon during their first summer at sea (Murphy et al. 2009). NBS pelagic trawl surveys were initiated in 2002 and have continued through 2018. NBS surveys use a pelagic trawl net modified to fish at the surface to collect fish samples, principally juvenile salmon, using a systematic spatial sampling design (Fig. 1; Murphy et al. 2017). The NBS surveys have occurred primarily in September, assessing juvenile salmon well after they experience a critical transition from freshwater to marine environments (Farley et al. 2007).

Survey catch and oceanographic data have been used to estimate juvenile Chinook salmon abundance in the NBS. The NBS survey grid is subdivided into four strata: 1) Lower NBS (60°N–62°N), 2) Upper NBS (62°N–64°N), 3) Norton Sound, and 4) the Bering Strait (Murphy et al. 2017; Howard et al. 2019). Within each stratum, juvenile Chinook salmon catch was expanded by a mixed layer depth (MLD) correction. Juvenile salmon were assumed to be uniformly distributed throughout the mixed water layer (depth of upper portion of water column of uniform density); however, because trawl gear does not sample through the entire mixed layer at all stations, a correction was applied to the juvenile Chinook salmon catch to account for the proportion of the mixed layer not trawled. Catch per unit area (CPUA, #/km^2) was calculated for each stratum, weighted by stratum area, and summed across strata to estimate an overall CPUA for the NBS. Total juvenile abundance was estimated by multiplying the overall CPUA by the total NBS survey area (Murphy et al. 2017; Howard et al. in press).

Genetic tissues samples were collected from all juvenile Chinook salmon caught during NBS surveys to estimate stock composition and stock-specific juvenile abundance. Stock composition was estimated by comparing

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genotypes of catch samples with reference baseline allele frequencies using the Bayesian statistical approach implemented in the software package *BAYES* with a flat prior (Pella and Masuda 2001). Juvenile Chinook salmon stock composition from four reporting groups was estimated: 3 Yukon River stock groups (Lower Yukon, Middle Yukon, Canadian Yukon), and Other Western Alaska (Howard et al. 2019). Between 2003 and 2018, Yukon River-origin Chinook salmon have comprised between 72% and 96% of the total juvenile Chinook salmon catch from NBS surveys (Fig. 2). Stock-specific juvenile abundance was the product of the juvenile Chinook salmon abundance and the genetic stock proportion of that stock group (e.g., total Yukon).

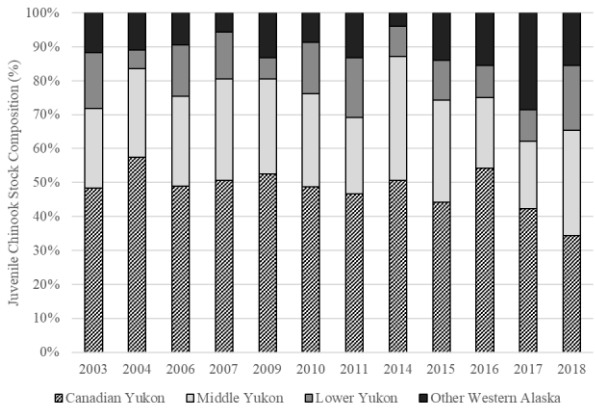

Fig. 2. Relative proportional stock composition of juvenile Chinook salmon in the northeastern Bering Sea surveys in 2003–2018, inadequate or no samples available in 2005, 2008, 2012 and 2013.

Total Yukon juvenile abundance estimates from the NBS were used to forecast adult Chinook salmon runs to the Yukon River (Murphy et al. 2017; Howard et al. in press). The projected range of adult survivors for each juvenile cohort was estimated by the 80% prediction interval of a linear regression model of total Yukon River juvenile and adult abundance (2003–2013 juvenile years, Fig. 3). Projected survivors were apportioned to run year based on recent 3-year average maturity schedules (Howard et al. in press). Juvenile abundance estimates from the NBS can be used to forecast adult run sizes up to 3 years in the future because Yukon River Chinook salmon primarily emigrate to sea at 2 years old (stream-type) and primarily return to spawn as age-5 and age-6 fish.

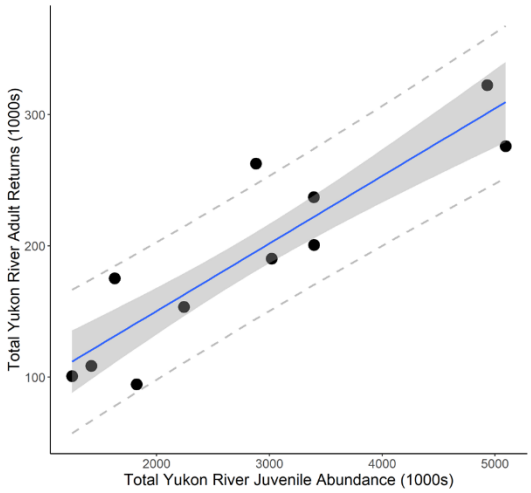

Fig. 3. Cohort relationships of northeastern Bering Sea juvenile Chinook salmon abundance and adult returns (black circles) for total Yukon River stock groups. The linear model fit is represented by the solid line (R^2 = 0.80, F (1,9) = 36.57, p < 0.001), 80% confidence interval of the linear model is represented by the shaded area, and the 80% prediction interval is represented by the dashed lines.

Adult run forecasts to the Yukon River have been provided to fishery managers and stakeholders since 2013 (Fig. 4). From 2013–2017, adult Chinook salmon runs fell within the forecasted range based on NBS juvenile Chinook salmon abundance whereas the 2018 run size fell outside the forecasted range. Discussions with managers and stakeholders indicated that the trade-off between forecast accuracy and forecast precision (width of a forecast range) was such that wider ranges than those provided by the 80% prediction interval were deemed less useful for decision-making. Juvenile Chinook salmon data from the NBS through 2018 contributes to forecasts for 2020–2022 (adults return at age-4, age-5, and age-6). Based on the most recent juvenile abundance data, fishery managers and stakeholders should expect decreasing Chinook salmon run sizes to the Yukon River over the next 3 years. These predicted Chinook salmon run sizes have the potential to meet escapement objectives and provide for some subsistence harvest opportunity but are unlikely to support significant additional harvest opportunities. It should be

noted that interannual variability in the proportions maturing at each age class can potentially introduce considerable error in forecast estimates. A more nuanced predictor of maturity beyond the recent 3-year average could enhance the development of the forecast.

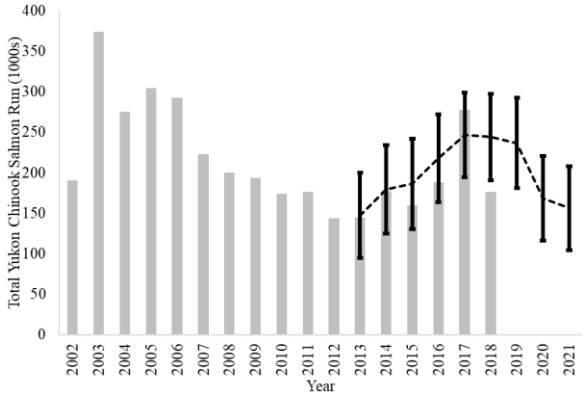

Fig. 4. Adult run size of total Yukon River Chinook salmon stock groups (grey bars) and projected run size based on northeastern Bering Sea juvenile abundance forecast (black dashed line and error bars indicating forecast range).

In addition to providing forecasts of adult run abundance, NBS surveys have played an important role in our understanding of the early marine ecology of juvenile Yukon River Chinook salmon. Results from the NBS surveys have shown that mean marine survival from September of the first year in the ocean to adulthood is low and typically remains between 5%–8% for total Yukon Chinook salmon (Howard et al. in press). While there is no evident relationship between the number of Yukon River adult spawners and total Yukon juvenile abundance resulting from those spawning events (Fig. 5), there is a strong, positive relationship between total Yukon juvenile abundance and total Yukon adult returns. Taken together, these results suggest that juvenile cohort strength is defined by September of their first year in the ocean (Fig. 3). These results are not unexpected as the early marine stage is believed to be a critical time for juvenile salmon (Hartt 1980; Pearcy 1992; Beamish and Mahnken 2001; Farley et al. 2007). However, these results indicate the first winter at sea may be less influential to cohort strength for this stock than factors occurring earlier in their marine (or possibly freshwater) life history.

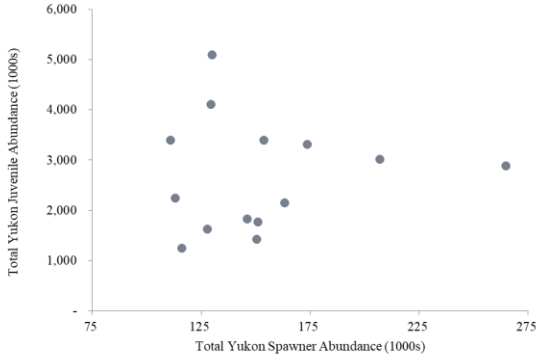

Fig. 5. Lack of relationship between the number of total Yukon River Chinook salmon spawners and the total juvenile abundance produced from those spawning events indicates the number of spawners is a poor predictor of juvenile cohort strength or future brood returns.

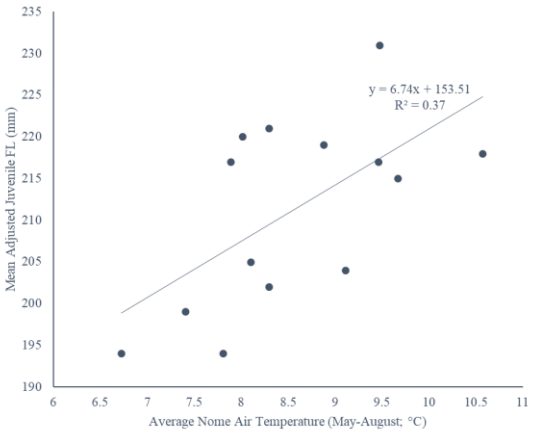

Fig. 6. Mean summer air temperature in Nome (Norton Sound) preceding juvenile capture in northeastern Bering Sea surveys and mean adjusted fork length of juvenile Chinook salmon sampled on surveys.

In river smolt and early marine juvenile data reveal important changes associated with warmer temperatures. An outmigration study in the Yukon River found that Chinook and chum salmon smolts entered the marine environment earlier as spring air temperature increased, and river ice break up occurred earlier (Howard et al. 2019). Warmer spring/summer air temperatures also correlated with larger juvenile Chinook salmon captured during NBS surveys in September (Fig. 6). A higher proportion of Chinook salmon maturing as age-3 and age-4 ("jack") fish was associated with those juvenile cohorts that were larger on average when measured during September NBS surveys (Fig. 7), supporting other research that suggests higher early marine growth may be associated with earlier age at maturation (Siegel et al. 2017). Juvenile Chinook salmon diet and condition was also influenced by warmer temperatures. In warm years juvenile Chinook salmon marine diet consisted of sand lance (*Ammodytes* spp.) and decapods whereas in colder years diet contained higher proportions of capelin (*Mallotus villosus*). Energy density of juvenile Chinook salmon muscle tissue also increased with warm sea surface temperatures in the NBS suggesting that prey quality and quantity during warm years is adequate to foster energy storage for the oncoming winter (Garcia and Sewall in press; Fig. 8).

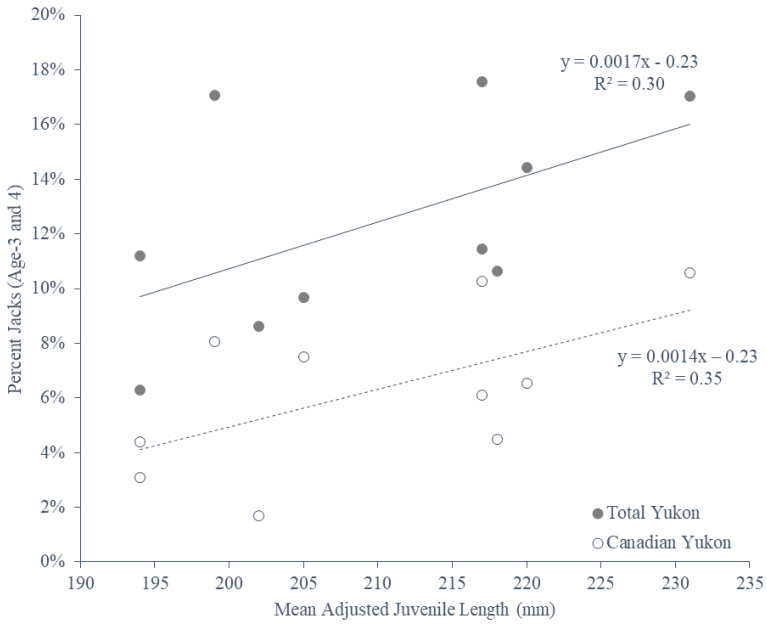

Fig. 7. Relationship between northeastern Bering Sea juvenile Chinook salmon length and proportion of adults maturing as age-3 and age-4 ("jacks") from those cohorts for total Yukon River (black circles) and Canadian-origin (grey circles) stocks.

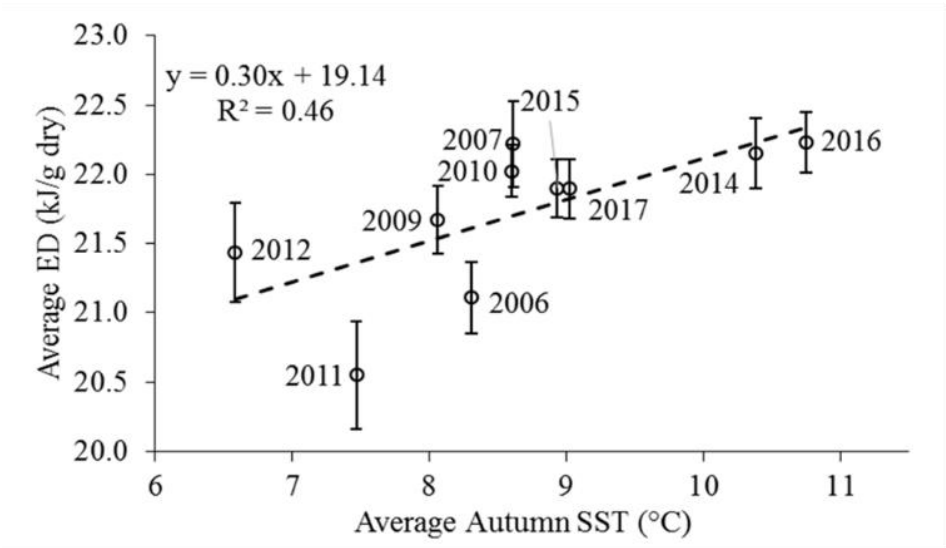

Fig. 8. Annual mean energy density (ED; kJ·g^{-1}) of dry tissue mass by average autumn sea surface temperature (SST) for juvenile Chinook salmon caught during surface trawl surveys in the northeastern Bering Sea (2006–2017). Simple linear regression model fit shown by dashed line (*n* = 10 years). Error bars represent 95% confidence intervals. Data unavailable for 2008 and 2013.

It is apparent from available data that conditions experienced prior to their first September at sea are highly influential to Yukon River Chinook salmon productivity, cohort strength, phenology, growth patterns, and size and age at maturity. While freshwater factors cannot be excluded from contributing to observed population patterns,

additional work understanding the ecology of Chinook salmon in their first few weeks to months in the ocean will be critical to identifying mechanisms responsible for structuring Yukon River Chinook salmon productivity patterns. The NBS surveys have elucidated the influence of warm sea surface temperature on size, growth, diet and condition of juvenile Chinook salmon. Increases of up to 3°C in sea surface temperature and further reductions in sea ice are predicted for the Bering Sea in the 21st century (Wang et al. 2012). How this predicted warming may affect juvenile Chinook salmon remains to be seen. Future NBS surveys will continue to inform fisheries management on the Yukon River and provide further evidence of how juvenile Chinook salmon will adapt to a warming Bering Sea.

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Patterns of Synchrony and Environmental Thresholds in the Performance of Forecast Models Used for U.S. West Coast Chinook and Coho Salmon Stocks

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Keywords: nonlinear, ecosystem-based management, environmental indicator, portfolio, threshold

Preseason abundance forecasts drive management of salmon fisheries off the U.S. West Coast, yet little is known about how environmental variability influences forecast performance. Understanding shared patterns in forecast performance can identify scenarios with heightened management risk due to shared over/under-forecasting of a large proportion of the fishery stock portfolio, and identifying drivers of this synchrony may aid in the development of improved forecasts. We examined temporal patterns, synchrony, and potential drivers in shared trends of forecast performance for 21 Chinook and 15 coho salmon stocks on the U.S. West Coast. For select Chinook salmon stocks of particularly high management importance, we tested for nonlinear and threshold relationships between forecast performance and environmental indices.

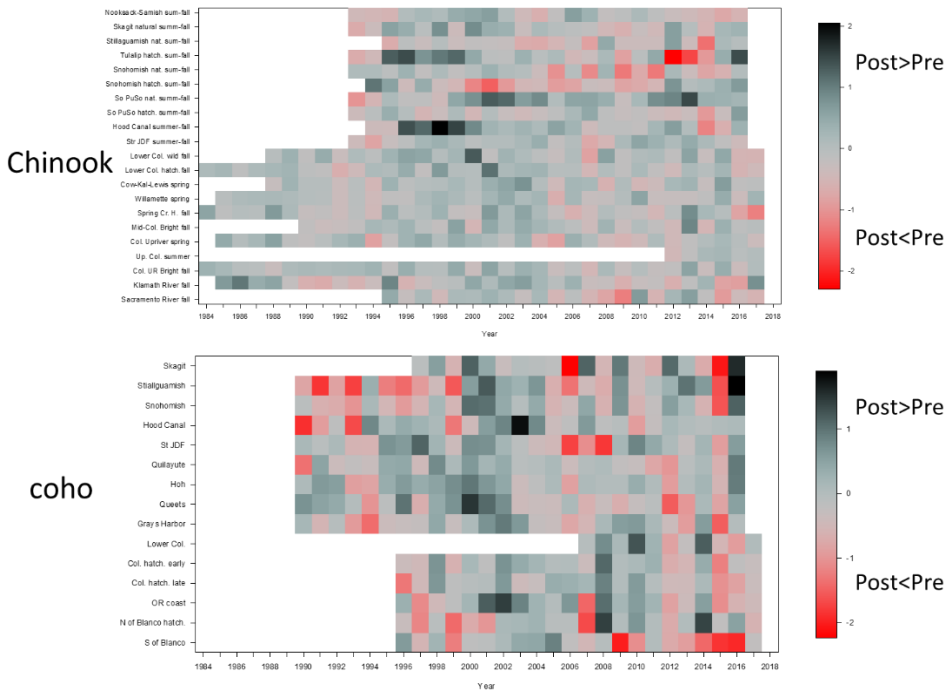

Fig. 1. Heat map of log (postseason estimate/forecast) by year (white = no data). Note that within each species, stocks are ordered as they would be encountered moving along the coastline from north to south. Occasional periods of nearly uniform under- or over-forecasting across stocks seem visually apparent within species, especially for coho. Sustained runs with multiple consecutive years of under- or over-forecasting within stocks appear more common for Chinook.

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We quantified correlation and synchrony in stock forecast performance (Fig. 1, defined as log of postseason abundance estimates divided by preseason forecasts) using data from a core set of years 1997–2016 for which we had forecast performance data for all stocks except Lower Columbia Natural Coho and Upriver Columbia Summer Chinook (which we excluded from this portion of the analysis). For straightforward interpretation, we calculated the mean pairwise correlation across stocks for all stocks combined, for all Chinook salmon stocks, and for all coho stocks. To further explore potential common trends in forecast performance, we used dynamic factor analysis (DFA), implemented via the MARSS R package (Holmes et al. 2012), to identify common trends in forecast performance and the loading of each stock onto these trends. Because MARSS can accommodate missing values, we included all available data in this analysis. We tested whether stocks tended to cluster together in their factor loading due to geography, forecast type, hatchery influence, or other factors. We also examined correlations between shared trends extracted by the DFA and environmental indices.

Fig. 2. Factor loadings for the best-supported dynamic factor analysis model applied to coho stocks. The inset shows the shared trends.

Forecast performance was asynchronous across all stocks and species (mean pairwise correlation of $r = 0.10$) but slightly more synchronous within species ($r = 0.14$ for Chinook, $r = 0.23$ for coho). Most strong positive correlations in forecast performance were between geographically proximate stocks. DFA applied to all stocks revealed a single shared trend, seen most strongly among southern coho stocks. However, the best-supported DFA model explained only 13% of the variance and loading on the single shared trend was low for most stocks. The best-supported DFA model for Chinook extracted only one trend and explained only 18% of the variance. For coho, the best-supported DFA model consisted of two shared trends, explaining 32% of the variance (Fig. 2). Loadings for coho stocks tended to cluster geographically but not with respect to hatchery versus wild nor by forecast type.

Our exploration of nonlinearities and thresholds focused on Chinook stocks of particular concern for United States West Coast fisheries management and conservation: Klamath and Sacramento River fall Chinook which are key ocean fishery stocks recently declared overfished, and Puget Sound Chinook stocks which were identified as the highest priority prey for endangered Southern Resident Killer Whales. We tested for nonlinearities and thresholds in the relationships between putative environmental drivers (freshwater conditions during spawning and rearing, localized ocean conditions at ocean entry, and intermediate to basin-scale ocean conditions throughout ocean residency) and forecast performance by comparing linear and nonlinear (generalized additive models, GAMs) models. We considered 95% confidence intervals on the second derivative of the fitted relationship excluding zero as evidence for a threshold (Large et al. 2013).

For this analysis, we calculated annual forecast performance *Py* for each stock as:

$$P_y = \frac{\frac{f_y - o_y}{o_y}}{\frac{1}{N}\sum_{i=y_{min}}^{i=y_{max}} \left|\frac{f_i - o_i}{o_i}\right|}$$

where N is the number of years with data, f_y is the preseason forecast and o_y is the postseason observation or estimate for year y. Positive values indicate that fewer Chinook returned to spawn than expected (overforecasting),

negative values indicate more Chinook returned to spawn than predicted (underforecasting), and values far from zero indicate unusually large errors.

Because our exploratory approach tested a large number of stock-index-location-lag combinations, spurious relationships were a concern. We therefore simulated 200 versions of each forecast performance timeseries by randomly resampling (with replacement) a score for each year, modeled the relationship between the resampled timeseries and the environmental indices tested for the corresponding stocks, and tracked the frequency of simulations where a nonlinear model was selected as well as the distribution of R^2 values. Given a proportion s of resampled relationships with R^2 above a critical threshold C, and k fitted relationships with $R^2 > C$ in the empirical data in n stock-index-location-lag test combinations, we calculated the probability of observing at least k relationships at least this strong by chance using a Bernoulli model.

We found 13 cases (12 nonlinear) where an environmental index could explain at least 50% of the variation in forecast performance and 55 cases (42 nonlinear) where the index could explain >33% of the variation in forecast performance. No relationships with $R^2 > 0.16$ were found for Klamath River Fall Chinook while two relationships with $R^2 > 0.40$ were found for Sacramento River Fall Chinook. All other relationships with $R^2 > 0.33$ were for Puget Sound stocks. The null model suggests it is unlikely we would see so many cases of $R^2 > 0.33$ by chance ($p = 0.16$ for all Puget Sound stocks combined, $p = 0.0012$ for South Puget Sound natural summer-fall Chinook) but the number of relationships with $R^2 > 0.50$ observed is consistent with null model expectations. However, comparing against the null model is likely conservative because tests of forecasts based on different approaches arguably reflect distinct hypotheses, and we did not consider all driver-lag-model combinations equally likely a priori (e.g., we hypothesized sibling-based models would be most sensitive to recent ocean conditions and relatively insensitive to freshwater or long lags).

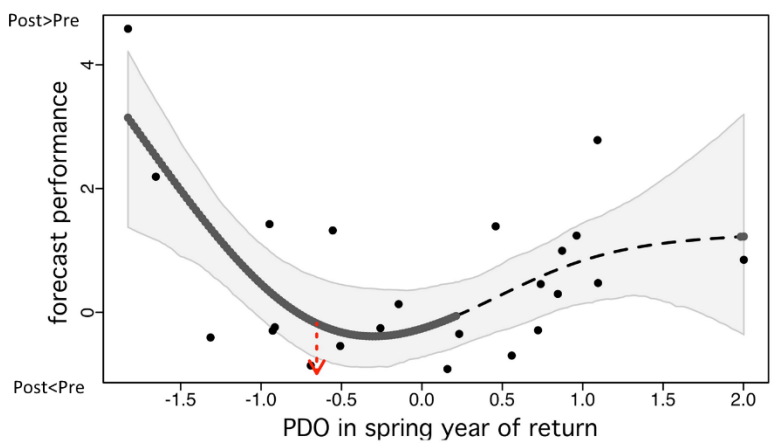

Fig. 3. Fitted relationship between PDO (Pacific Decadal Oscillation) in spring of the return year and performance for Sacramento River Fall Chinook. The dashed line shows the best fit GAM, with the thick grey line indicating potential threshold locations (i.e., where the 95% confidence interval (CI) on the second derivative excludes zero) and the red arrow indicates the most likely threshold location (the value of the environmental driver where the second derivative is furthest from 0 within the 95% CI). The shaded region shows the 95% confidence interval on the fitted relationship.

For Sacramento Fall Chinook, which uses a sibling-based forecast, the top two environmental indices explaining errors in preseason forecasts were related to ocean conditions in the year of return (Pacific Decadal Oscillation (PDO) and the North Pacific Index). This is concurrent with when managers need to make forecasts, but PDO can be predicted one year in advance with some skill (Lienert and Doblas-Reyes 2013). In addition, it is consistent with the expectation that performance of sibling-based forecasts would be most affected by conditions experienced after the return of younger members of the cohort that inform the forecasts. For Puget Sound stocks, which employ a variety of forecasting methods, a variety of indices operating over a range of lags displayed good explanatory power, although overall freshwater indices were rarely supported, possibly because freshwater effects are directly or indirectly incorporated (e.g., via smolt counts) into the forecasts.

We found evidence of thresholds in most (60/65) cases where nonlinear models were preferred. Figure 3 displays an illustrative relationship between Sacramento Fall Chinook forecast performance and PDO in spring the year of return, which took on extreme values in 2008–2009, years associated with a fishery collapse and closure. Returns of many Puget Sound stocks seemed to show a shared response in overforecasting 2014 returns, which was correlated with unusual sea level height off Alaska in 2013. Further research into conditions characterizing the 2014 return year is advised.

The individual relationships identified here should be approached with caution due to the exploratory nature of this study, but warrant further investigation and consideration by managers. Null model results suggest that individual relationships should be approached with caution, but it is unlikely that they are all spurious. The thresholds we identified here identify conditions under which precautionary management may be warranted in a

particular year, suggest that some indices merit consideration for inclusion in forecasts, and offer insights into ways forward for improving salmon forecasts given increasingly dynamic ocean conditions.

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Quantifying Thermal Impacts on Columbia River Steelhead Marine Growth Using Bioenergetics Models

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Keywords: steelhead, thermal variability, bioenergetics, trophic ecology, California Current

Columbia River steelhead *(Oncorhynchus mykiss)* is an anadromous, E.S.A.-listed salmonid with a diverse life history that is heavily mediated by the marine environment. Steelhead stocks have been in broad decline since the 1980s due to warming temperatures and loss of freshwater habitat, yet they remain understudied compared to other Pacific salmonids due to their relatively complicated life histories, including a long freshwater residence and multiple spawning events (Kendall et al. 2017). Steelhead spend 1 to 4 years in freshwater before entering the Northern California Current (NCC) ecosystem to disperse to offshore habitat (Daly et al. 2014).

In recent years, the NCC has experienced anomalously positive phases of the El Niño Southern Oscillation and the Pacific Decadal Oscillation, resulting in elevated sea surface temperatures. Unusually weak atmospheric forcing between winters 2013 and 2016 also resulted in formation of the "Blob"—a poorly-mixed warm water mass that increased sea surface temperature by nearly 2.5°C (Di Lorenzo et al. 2016). These events contributed to multi-trophic level shifts within the NCC biological community, leading to variability within the community composition and bioenergetic content of steelhead prey (Auth et al. 2018; Brodeur et al. 2019a). Such variability is thought to impact steelhead marine growth, but less is known regarding the contribution of marine-derived prey to the overall size and growth of early marine steelhead.

Bioenergetics models quantify growth based on thermodynamic principles and may provide insight into how both the freshwater and marine environments contribute to steelhead growth. In these models, energy from food consumption is partitioned into three components: energy required for metabolism, waste removal, and growth (Deslauriers et al. 2017). Bioenergetics models can also be parameterized to include environmental factors such as water temperature to explore the effects of warming water temperatures on steelhead food consumption and growth. The objective of our study is to capture bioenergetic variability in early marine steelhead weight and specific growth rate given shifts in temperature and prey caloric content characteristic of warm and cool ocean conditions.

Juvenile steelhead were collected from Columbia River-influenced coastal nearshore waters during surface trawl surveys associated with the Bonneville Power Administration (BPA) Plume Survey on the F/V *Frosti* in May 2015–2016. Fish caught in 2015–2016 were compared to a subset of steelhead collected from previous May BPA surveys (2001, 2002, 2004, 2006–2011). All captured steelhead were measured, weighed, and stomachs were removed for analysis. Ocean regimes of 'cold' and 'warm' were established based upon ecosystems indicator data compiled in NOAA's Ocean Indicator stoplight chart (https://www.nwfsc.noaa.gov/research/divisions/fe/estuarine/oeip/g-forecast.cfm#TableSF-02).

We examined five different growth scenarios where steelhead fed at different consumption rates in warm and cold ocean years in order to assess changes in growth across the first twelve days of marine residence. Fish fed at rates of 100% and 50% of maximum consumption in cold years, and 100%, 50%, and 20% of maximum consumption in warm years. Each simulation was parameterized with average daily temperatures between May 10th and 21st at the mouth of the Columbia River Estuary in warm and cool years using temperature logger data from the SATURN Observation Network (http://www.stccmop.org/datamart/observation_network). All fish were 90 g at day 0 of the simulations based on average weight of steelhead across all survey years. Bioenergetics simulations were conducted using Fish Bioenergetics 4.0 (Deslauriers et al. 2017) and parameterized using values obtained for juvenile Rainbow Trout (Tyler and Bolduc 2008). Steelhead energy density was set to 4967 $J \cdot g^{-1}$ (Myers 2018), and average marine prey energy density and average proportion of indigestible prey were determined from Davis et al. (1998) and Marin Jarrin (2012). Marine prey energy density was elevated by 30% in cold ocean years to illustrate the temperature-influenced trends in prey energy density observed by Daly and Brodeur (unpublished data). Variability in weight and specific growth between scenarios was assessed using a 2-way ANOVA.

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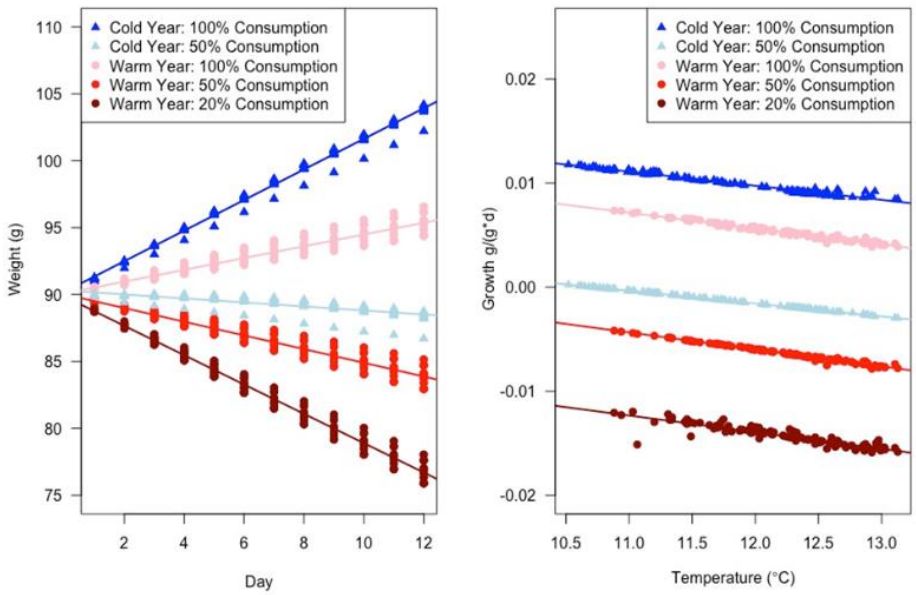

Fig. 1. (a) Simulated Columbia River steelhead weight during the first 12 days of marine residence given different prey energy densities, temperature, and consumption rates associated with warm and cold ocean years. (b) Simulated specific growth rate during the first 12 days of marine residence under temperatures experienced at the mouth of the Columbia River Estuary in warm and cold ocean years. All fish in this simulation were 90 g at day 0 and prey energy density was elevated 30% in cold ocean years.

Our bioenergetics simulations suggest that many of the size-specific differences observed between steelhead in warmer and cooler ocean years are manifested during the early marine residence as opposed to the freshwater residence (Fig. 1a). In our simulations, fish that were the same weight upon entering the marine environment experienced significant changes in their weight by only the second day in the ocean based upon the different temperatures, prey energy densities, and consumption rates characteristic of warm and cool ocean conditions (2-way ANOVA; $F_{44, 540} = 387.76$, $p < 0.001$, partial $\eta^2 = 0.96$). Specific growth rate of steelhead was also significantly different between scenarios, with highest specific growth in scenarios with cooler temperatures and higher feeding rates (Fig. 1b; 2-way ANOVA; $F_{4, 590} = 31.86$, $p < 0.001$, partial $\eta^2 = 0.99$). By day 6 in the marine environment, fish feeding at 50% of their maximum consumption rate under warm year conditions were 11.7% lighter than fish that experienced high consumption rates in cooler conditions. This is comparable to the 17.6% reduction in weight observed in spring Chinook salmon in 2015, a Blob-influenced year, compared to 2008, a relatively cool ocean year (Daly et al. 2017). Similar to previous work on early marine Chinook salmon (Litz et al. 2018), steelhead growth appears to be strongly influenced by their feeding rate at sea. However, ocean temperature and prey energy density also appear to influence steelhead growth during the early marine residence.

Based on plankton and micronekton sampling occurring during anomalous conditions in 2015 and 2016, the prey field available to juvenile steelhead in coastal waters was likely altered compared to normal conditions. Adult euphausiid abundance in the water column appeared to be exceptionally low and they seemed to be replaced by several offshore or southern gelatinous taxa (Peterson et al. 2017; Brodeur et al. 2019a). Juvenile rockfishes were also available in higher abundance on the shelf compared to cooler years, similar to what was observed during the El Niño of 2010 (Adams et al. 2017; Auth et al. 2018). Similar to juvenile Chinook salmon (Daly et al. 2017) and several forage fish species (Brodeur et al. 2019b), steelhead exhibited some plasticity in their feeding, resulting in normal stomach fullness levels during anomalous conditions in 2015–2016 (Thalmann et al. In review). However, this trade-off may not be beneficial for juvenile steelhead, and it is likely that the energetic and lipid content of these prey may be much lower than the prey normally available in cold years (Daly et al. 2010; Daly and Brodeur unpublished data).

Overall, our findings suggest that the NCC ecosystem had diminished potential to support salmon populations in the Blob (2015–2016) and subsequent El Niño (2016) conditions, and that the majority of interannual differences in size were due to feeding conditions at sea. The majority of the juvenile steelhead that out-migrated into the unprecedented warm ocean conditions in 2015 returned as adults to the Columbia River after one or two years in the ocean. The count of adult steelhead returning past Bonneville Dam in 2016 and 2017 were some of the lowest numbers in the last 30 years (Columbia River Data Access in Real Time [Dart]; www.cbr.washington.eud/dart/query/adult_daily/). Through long-term monitoring of steelhead in their early ocean existence, we are able to provide insights into environmental effects on their feeding and potential survival in the ocean.

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Evaluation of an Environmental DNA Method as a Potential Tool for Monitoring Salmonid Fishes in the Wild

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Keywords: environmental DNA, migration, monitoring

There are a variety of migratory fish species in the North Pacific, including Pacific salmonids (*Oncorhynchus* spp.). While there is no doubt that they play an important role in the ecosystem and commercial fisheries, it is difficult to obtain a comprehensive understanding of their migration routes and spatio-temporal distribution precisely, partly due to the huge efforts and costs required for collecting such data with conventional research tools.

Environmental DNA (eDNA) is a new ecological tool to identify species in the wild. eDNA was first developed for detecting the presence of invasive bullfrog in France (Ficetola et al. 2008). Since then, it is increasingly recognized as a new molecular tool for detecting organisms in the wild (Takahara et al. 2013; Sigsgaard et al. 2015). How efficiently it can be applied for monitoring migratory salmonid species, however, is still not well understood. Although previous studies tried to figure out the relationship between the eDNA concentration and a biomass nearby (e.g., Takahara et al. 2012), these results might not be directly applicable to salmonid fish species because of the wide varieties of their body size and of habitat they use, such as headwaters, mid- to downstream of a river, and the ocean.

Fig. 1. Sakhalin taimen (*Parahucho perryi*) captured in Hokkaido, Japan. The photo was taken by H. Mizumoto.

To evaluate the potential of eDNA as a tool for monitoring salmonid fish species in the wild, we conducted an aquarium experiment on Sakhalin taimen (*Parahucho perryi*) (Mizumoto et al. 2018). Sakhalin taimen is a large and rare salmonid species distributed in Sakhalin, Russia, and Hokkaido, Japan (Fig. 1). They were historically distributed in many rivers in these areas, but they experienced a sharp decline of populations in almost all these areas presumably due to human activities (Rand 2006; Fukushima et al. 2007, 2011). It takes them a long time to reach sexual maturation (Yamashiro 1965), and the persistence of their populations is susceptible to environmental changes (Fukushima et al. 2011). They also require a vast area of watersheds and estuarine habitats during their life cycle, migrating from a river mouth to spawning grounds in headwaters for reproduction and migrating back to the sea for wintering and foraging.

We first developed an eDNA detection system for Sakhalin taimen, making primers and a probe for this species based on DNA sequences in NCBI database. *In silico*, we compared available DNA sequences in NADH dehydrogenase subunit 2 (ND2) from species belonging to genera *Hucho, Oncorhynchus, Salvelinus, Salmo, Brachymystax, Coregonus, Prosopium, Stenodus* and *Thymallus*. We then tested the species specificity of designed primers and the probe by trying to amplify DNA from tissue samples of Sakhalin taimen, chum salmon (*O. keta*), pink salmon (*O. gorbuscha*), sockeye salmon (*O. nerka*), rainbow trout (*O. mykiss*), masu salmon (*O. masou*

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masou), Dolly Varden (*Salv. malma malma*), white-spotted charr (*Salv. leucomaenis leucomaenis*), and brown trout (*Salmo trutta*), using qPCR. The result clearly suggested the species specificity of the primers and the probe to DNA from Sakhalin taimen only (Fig. 2).

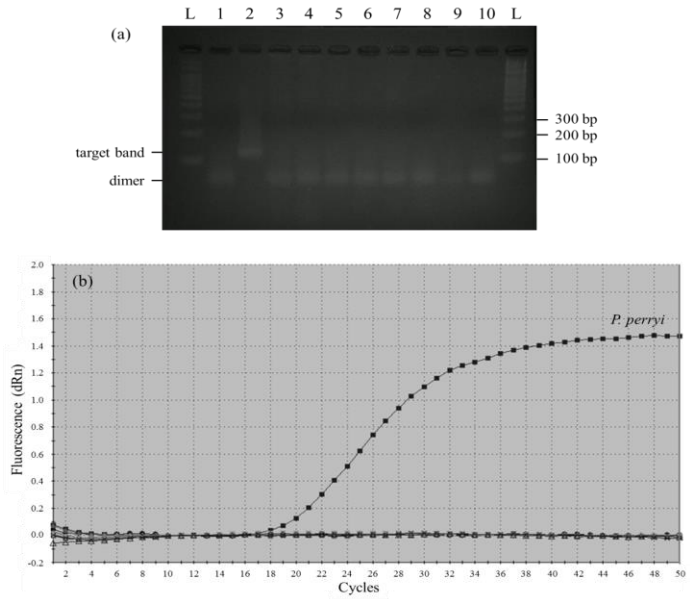

Fig. 2. Validation of species-specificity of new primers by tissue-DNA based PCR and qPCR (cited from Mizumoto et al. 2018). (a): A gel image showing results of an electrophoresis of standard PCR products. The expected size of band was 124 bp. 1: distilled water (negative control), 2*: Parahocho perryi*, 3: *Oncorhynchus keta*, 4: *Oncorhynchus nerka*, 5*: Oncorhynchus gorbuscha*, 6*: Oncorhynchus mykiss*, 7: *Oncorhynchus masou masou*, 8: *Salvelinus malma malma*, 9: *Salvelinus leucomaenis leucomaenis*, 10*: Salmo trutta*, L: a DNA ladder of 100 bp intervals. (b): Amplification plots of qPCR. X-axis represents the number of PCR cycles and Y-axis represents the strength of fluorescence. The same tissue-oriented DNA templates above were applied to the standard PCR (a) and to the qPCR (b). These species cover all coexisting salmonid species with Sakhalin taimen at least within their potential distribution in Japan.

Following the confirmation of the species specificity of our eDNA detection system for Sakhalin taimen, aquarium experiments were conducted using Sakhalin taimen with different ages and sizes (Mizumoto et al. 2018). In two types of tanks of different sizes (40L-tank and 2000L-tank, hereafter), we put Sakhalin taimen with age 0+, 1+, 2+ and > 20+. The average fork lengths were approximately 28mm for 0+, 100mm for 1+, 184mm for 2+, and 800mm for > 20+ at the beginning of the experiments. Inlet water was drawn from the nearby Kashiwagi River (42°53'25.7"N, 141°32'19.4"E) and fed into the 40L- and 2000L-tanks at the rates of 4.0 and 12.9 $L \cdot min^{-1}$, respectively. No recycling of water was used during the experiments. All equipment was sterilized by spraying bleach solution (10 or 20% sodium hypochlorite) and rinsed with DNA-free water before the experiments. To mitigate the effect of human disturbances, all the tanks were covered by plastic sheets. After 3–5 days of fish introduction, we collected two 1L water samples per sampling period from the outlet of each tank for eDNA analyses. Water samples were filtered immediately after the samplings with glass-membrane filters with a mesh size of 0.7 µm (Whatman GF/F, GE Healthcare Japan, Tokyo, Japan). Every time before filtering tank water, we filtered 500 mL pure water with the same type of filter to serve as a negative control. To prevent cross-contamination, all filtration equipment was sterilized and carefully rinsed with pure water in each filtration. No detection of eDNA from any negative control was observed throughout the experiments.

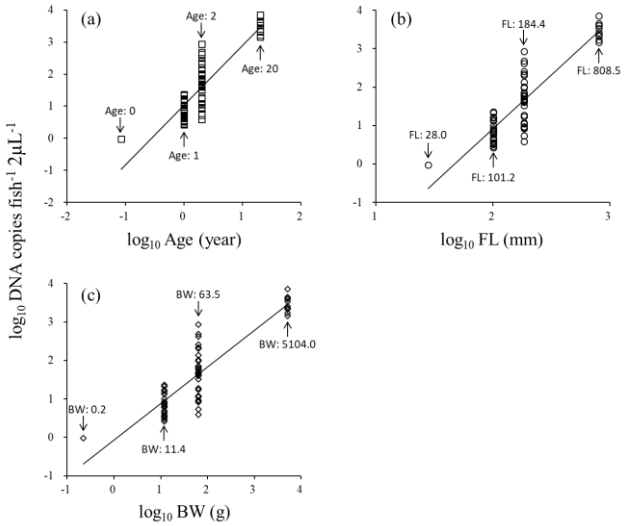

Fig. 3. Relationships between the log-transformed eDNA concentration (log10 DNA copies per 2 μL template DNA samples) per fish and their log-transformed age (a), average Fork Length (FL) (b) and Body Weight (BW) (c). n = 66 in all analyses and correlations were statistically significant in all cases (p < 0.001). (a): y = 1.85x + 1.04, r = 0.87. (b): y = 2.80x - 4.69, r = 0.89. (c): y = 0.95x - 0.07, r = 0.89. (modified from Mizumoto et al. 2018)

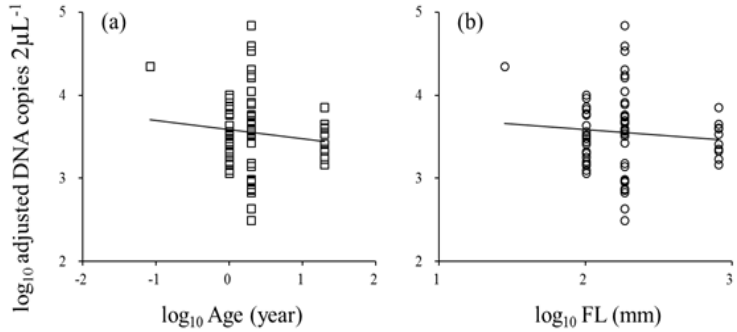

Fig. 4. Relationships between the log-transformed eDNA concentration adjusted to the total body weight of fish at each group and their log-transformed age (a) and average fork length (FL) (b). None of the correlations were statistically significant (a: y = -0.11x + 3.58, r = -0.11, p > 0.05, b: y = -0.13x + 3.85, r = -0.091, p > 0.05), indicating constant eDNA concentration among different age- and FL-groups when their total body weights were adjusted. n = 66 in both analyses. (Mizumoto et al. 2018)

We found positive relationships of eDNA concentration with fish age, fork length, and body weight (Fig. 3). They indicate a clear association between the biomass of Sakhalin taimen and eDNA concentration, at least under the controlled environment with flowing river water. In addition, the body size effect was cancelled out when the total body weight per tank was adjusted (Fig. 4). The latter strongly suggests that the eDNA concentration can be a reasonable indicator of biomass, in terms of body weight, nearby.

Currently we are applying this tool to identify the potential presence of Sakhalin taimen in > 120 river systems in Hokkaido, Japan. Although the results are still tentative, we found eDNA from this endangered species in several river systems in Hokkaido (Mizumoto et al. unpublished data). While they do not cover all the river systems with recent visual observation of Sakhalin taimen, they include a few river systems without any previous record of this species. Although further investigation is necessary to evaluate the possibilities of false positive, as well as false negative, for the precise mapping of spatial distribution of the endangered species, the above studies suggest a great potential of eDNA as a tool for monitoring salmonid fish species in general. In fact, the eDNA detection systems have also been developed for chum salmon and masu salmon in our lab. While their applicability to the monitoring survey is still ongoing, we are positive about identifying eDNA from headwaters to the open ocean, including the Bering Sea for chum salmon. However, spatio-temporal scales of eDNA detection likely varies among ecosystems, and cross-testing with conventional catch surveys would be necessary at each environment to understand the ecology of eDNA *per se* in the near future.

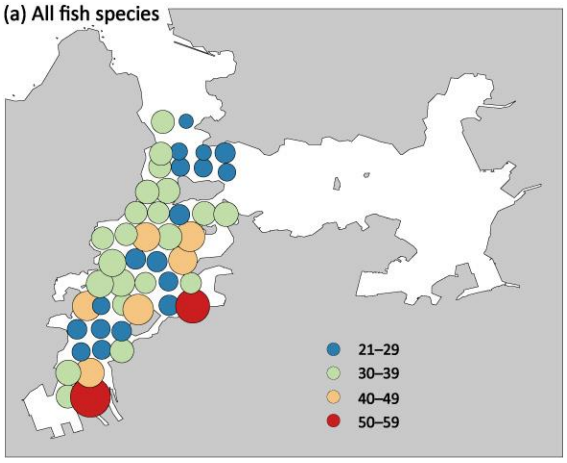

Fig. 5. Detected species diversity by MiFish metabarcoding at each station. Circles on each map indicate detected fish species number. Both size and color reflect the species number (Yamamoto et al. 2017).

An interesting option for eDNA surveys is eDNA metabarcoding. This is a method to estimate organism compositions in the wild based on the Next Generation Sequencing technology to identify the owners of DNA fragments collected as eDNA. For fish species, for example, we recently developed effective fish-universal primers for eDNA metabarcoding known as MiFish (Miya et al. 2015). Using MiFish primers, we found eDNA from more than 120 fish species in Maizuru bay, a species-rich coastal sea in Japan, based on a six-hour survey for collecting water samples (Fig. 5, Yamamoto et al. 2017). We applied it to coastal areas around Hokkaido and in a middle of Bering Sea, resulting in a wide variety of species identification including chum salmon, Chinook salmon, etc. (Araki et al. unpublished data). These results, together with a rapid development of molecular techniques, indicate that eDNA is a promising tool for monitoring salmonid fish species throughout their whole life histories in the near future.

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The RAFOS Ocean Acoustic Monitoring (ROAM) Tag: A Highly Accurate Fish Tag for At-sea Movement Studies

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Keywords: animal telemetry, ocean observing, acoustics, oceanography

Introduction

Animal migrations are some of the most fascinating and impressive biological phenomena on the planet. Nonetheless, until recently, marine ecologists have known remarkably little about the specific movements of large pelagic fishes due to the logistic challenges of tracking fish in a vast, largely opaque ocean. Light-level geolocation techniques using current generation pop-up satellite archival transmitting (PSAT) tags generally exhibit poor accuracy (±100–200 km; ~10,000 km^2) even under best-case situations when movements are confined to surface waters (< 100 m) during daytime hours (Braun et al. 2015, 2018). Poor accuracy has, in turn, led to a paucity of mechanistic studies addressing the mechanisms influencing at-sea habitat use by salmonids. Similarly, identifying the location and cause of ocean-phase mortality remains a critical question for improving salmon management and conservation efforts. This knowledge is critical as we continue to lean heavily on marine-capture fisheries to sustain human populations worldwide while experiencing drastic changes in the Earth's climate and oceans.

We are developing a new satellite archival tag technology—the RAFOS Ocean Acoustic Monitoring (ROAM) tag—to solve both accuracy and depth constraints inherent in conventional PSAT tags that will provide accurate geolocations of fish throughout the water column across ocean basins.

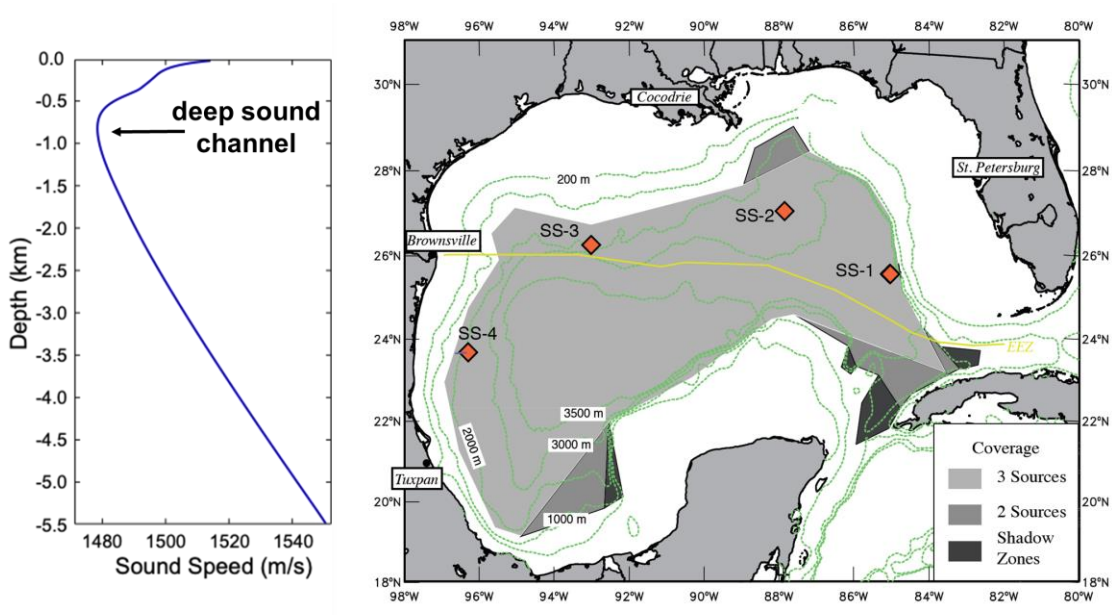

Fig. 1. Sound speed profile for the region indicating the deep sound channel used to propagate sound, and an example RAFOS array used to study deep circulation in the Gulf of Mexico using RAFOS floats (from Hamilton et al. 2018).

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Proven oceanographic instruments and infrastructure: the RAFOS system

The technical approach of RAFOS[1] builds on decades of research and development for tracking ocean currents by means of subsurface drifters capable of receiving sound (Rossby et al. 1986).

RAFOS float-tracking networks have been used to study the physical oceanography of several ocean basins from the Gulf of Mexico (Fig. 1) (Hamilton et al. 2018; Furey et al. 2018) to under-ice environments in the Southern Ocean (Chamberlain et al. 2018). These networks rely on moored acoustic transmitting units that emit a unique acoustic signal. A hydrophone onboard the RAFOS float detects the sounds from the network, and a triangulation algorithm uses the differential sound reception from multiple moorings to calculate position onboard the float (Fig. 2).

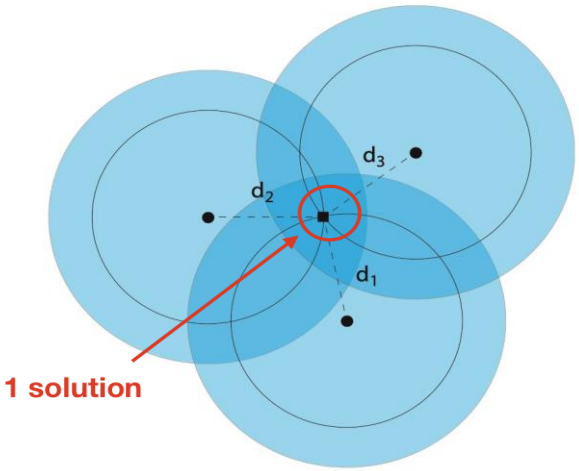

Fig. 2. Differential reception time of acoustic signals from 3 different sound sources can be used to triangulate a position with error < 1km.

Fig. 3. Example ROAM tag components and assembled prototype tag. Adapted from Rossby et al 2017.

The ROAM Tag

The ROAM tag employs the same acoustic technology and infrastructure that is widely used for tracking RAFOS oceanographic floats to geolocate fish. The ROAM tag contains a hydrophone that listens for low frequency "pongs" from the sound source network and differential reception of these sounds are used to triangulate tag position. In other words, the ROAM tag is the reverse of acoustic telemetry systems widely used in aquatic telemetry today. In order for this approach to work, we have miniaturized current RAFOS technology through the development of a new single board receiver and enclosed the tag in a cylindrical housing which functions as the hydrophone (Fig. 3) that is duty-cycled to match the sound source signals. We modeled the rest of the tag after pop-up satellite archival tags by equipping the new micro-printed circuit board ("fish-chip") with the capability to log pressure and temperature and added an electronic burn wire for predetermined pop-off and an Argos satellite transmitter for data recovery through the Argos satellite system as is conventional with animal telemetry technology. With two 1.5 V batteries the tag can, for example, listen a dozen times per day for two years while also sampling pressure and temperature every 30 minutes in order to capture vertical movements in the water column (Rossby et al. 2017). The fish tag can operate at almost any depth, depending upon the rating of the pressure sensor. By using pop-up technology and an Argos transmitter, rather than an archival tag only, the tag will transmit a summarized

[1]RAFOS is the reverse of the acronym SOFAR (SOund Fixing And Ranging)—which refers to float tracking methodology that has been reversed since the invention of SOFAR.

version of the high-resolution data it collects. Thus, we will ensure that the tag does not need to be recovered for data acquisition, making it applicable to a number of species where tag physical recovery rates are typically very low.

Testing a new fish tag

We recently performed a preliminary field test of this technology in the Mississippi River Delta (USA), which is a notoriously challenging acoustic environment due to alternating layers of warmer and cooler water as well as saline and fresh lenses. Despite the challenges inherent in this environment, we were able to hear acoustic signals as far away as 60 km (Rossby et al. 2017). The accuracy of this prediction ranged from 70 m to 560 m which depends critically on clock accuracy in the tags. Using standard RAFOS clock error recovery techniques, clock errors can be kept to a few seconds on yearlong missions. Our preliminary testing suggests this technology may be able to accurately locate tagged fish, even at depth, with error bounds (±5 km^2) that are unmatched by any current tag geolocation technique. In addition, long-range transmission testing in RAFOS float studies suggests leveraging the deep sound channel in the open ocean can render the acoustic source signals detectable by the fish tag up to 1,000 km range.

Additional testing of the prototype ROAM tag is scheduled for 2020 in which we plan to tag an oceanographic glider and program it to conduct vertical movements through the water column similar to some representative fish taxa. Such a test will confirm the range and accuracy of the ROAM tag when idealized fish behavior is added to the geolocation problem.

Summary

Current technologies are restricted to organisms that frequent the surface layer or photic zone to acquire position estimates, and accuracy using light geolocation is often ±100-200 km (~10,000 km^2). Our inability to provide position estimates below the photic zone with existing technologies further inhibits our understanding of meso- and bathypelagic organisms. The resulting data from initial deployments are enabling us to assess the feasibility of this technique for improving position estimation and resolving location at depth that are both beyond the capability of current animal telemetry technologies. Once proven, the ROAM tag should provide a transformative view of fish movements in the global ocean by increasing accuracy of movement studies by ~ 4 orders of magnitude while retaining functionality at depth. In addition, the ROAM tag will be applicable to all large and medium-sized pelagic fish species, as it does not require the fish to occupy surface waters to determine accurate positions. Using these improvements in location accuracy, ROAM tag deployments will foster in-depth understanding of biophysical drivers of fish movements (e.g., prey aggregation along fronts or vertically migrating mesopelagic biota), habitat association (e.g., seamounts), sociality among tagged individuals, and other currently cryptic behavior (e.g., spawning aggregation and location). This knowledge will greatly improve our understanding of data-deficient, commercially valuable species and will have far-reaching impacts on science and industry by revolutionizing the way we are able to study these species in the open ocean.

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Interactive Mapping and Dynamic Data Visualization—Eye Candy or Useful Tool for Fisheries Research?

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Keywords: Interactive Map, Pacific Salmon, Data Visualization

As researchers, we are constantly reminded that the scientific method begins and ends in observation. The ability to examine information to develop testable hypotheses can become problematic when dealing with large amounts of evolving data that have been collected from diverse locations and numerous organizations over extended periods of time. The addition of potential environmental and biological correlates only complicates the issue. This is especially true for salmon. For example, the North Pacific Anadromous Fish Commission (NPAFC) has over 60 years of disk and archival tag recovery data from salmon and steelhead collected on the high seas of the North Pacific. As of 2018, this dataset contains information from over 18,000 tag releases and recoveries. Similarly, temporal and spatial data associated with decades of coded-wire tag and marked otolith recoveries from salmon fisheries exist throughout the Pacific Rim. How can all this information be combined with variables such as sea surface temperature, current regimes, and chlorophyll concentrations within a temporal context over broad geographic scales in a way that helps to formulate questions, develop hypotheses, and address management concerns? By presenting large complex data sets in a dynamic format, such as an interactive map, users can easily visualize and manipulate large amounts relational data to look for patterns and correlations. Displaying data with potential correlates in a temporal context can be used to determine how patterns and relationships change over time. For salmon, decades of tag recovery information can be combined with a variety of potential environmental correlates and mapped together to create customized time-enabled dynamic displays of movement. Such mapping can provide insight into their ocean distribution and migration patterns relative to seasonal and long-term environmental change. Interactive maps help to visualize almost any kind of data while also fostering data sharing and collaborative research, providing tools to support future research and analyses, and promoting public outreach. Although these analyses are descriptive in nature, they can be used to develop hypotheses and questions to which more quantitative and statistical approaches can be applied.

In an effort to efficiently examine six decades of information contained within the NPAFC's high seas salmonid tag recovery database, the Alaska Department of Fish and Game (ADF&G), in collaboration with the NPAFC's Working Group of Salmon Marking, is developing an online Interactive Mapping System (IMS) that will allow users to visualize and study the ocean distribution and movement patterns of Pacific salmon and steelhead trout over space and time by dynamically mapping tag recoveries against a variety of environmental factors such as sea surface temperature, chlorophyll, and climate indices.

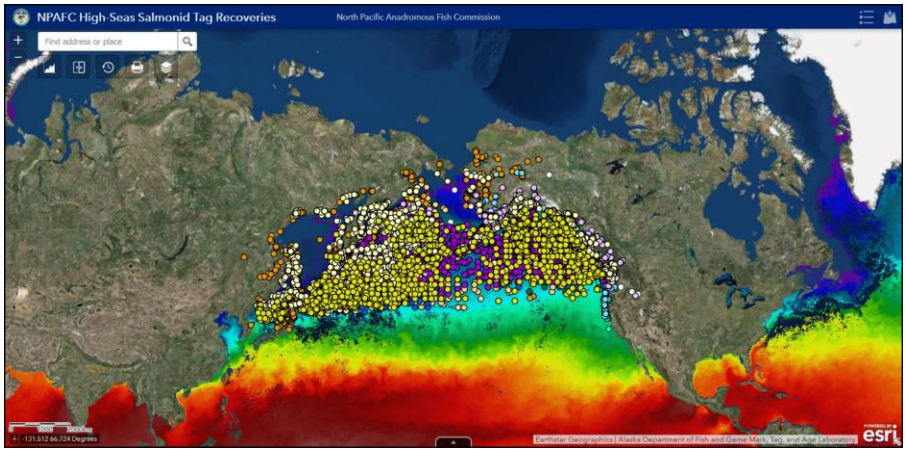

Fig. 1. Prototype Interactive Map displaying Pacific salmon high seas recoveries and releases (1956–2015), as well as average sea surface temperatures. Grey, dark orange, dark blue, dark purple, and dark yellow represent releases of tagged Chinook, chum, coho, sockeye, and pink, respectively. White, light orange, light blue, light purple, and light yellow represent recoveries of tagged Chinook, chum, coho, sockeye, and pink, respectively.

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A prototype IMS is has been completed using ArcGIS Pro v. 2.1.2, ArcGIS Online, and Web App-Builder and is currently being tested (Fig. 1). Users can search tag recoveries by tag type, species, age class, and origin to create customized maps of salmon migrations and movement patterns. They can also view recoveries in relation to environmental parameters within a temporal context to visualize how environmental change influences population dynamics over time. Applicable environmental datasets can be downloaded from the internet and incorporated into IMS functionality using the ArcGIS Online application.

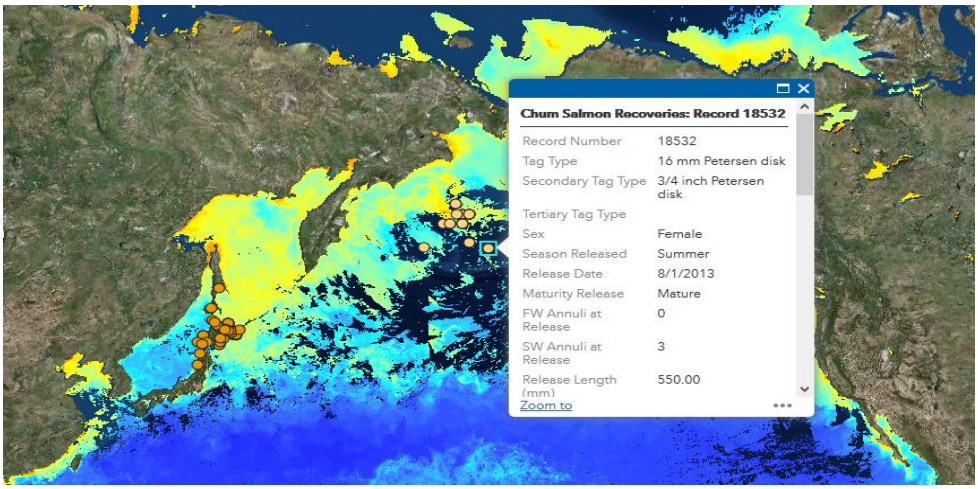

Fig. 2. Prototype Interactive Map showing chum salmon high seas recoveries and releases between 2010 and 2016, as well as average chlorophyll a concentrations. The imbedded table displays all the data associated with a specific chum salmon tag release and recovery. Orange dots are releases and yellow dots represent recoveries.

The IMS employs "Smart Mapping" techniques that allows users to symbolize data by species, age class (freshwater and ocean ages), maturity (immature or maturing), sex, geographical origin, and season. Environmental, geographical, and biological data are contained in "layers" that are time-enabled, which allows users to view the progress of releases and recoveries over time in relation to any factors they see fit to view. Release and recovery layers are also "related" at a database level, permitting users to locate and view the release data associated with a unique recovery, and vice versa (Fig. 2). Because users can select and hide layers that contain environmental data (sea surface temperature, chlorophyll, weather patterns, etc.), customized interactive maps can be created to visualize releases, recoveries, and movement pattern in relation to environmental change.

The IMS, as well as individual tag recovery data from the NPAFC High Seas Salmonid Tag Recovery Database, will be available to all users once the final version of the IMS is made public. End users will be able to view, select, and export data directly from the IMS. A test version of the prototype IMS can be found at; https://adfg.maps.arcgis.com/apps/webappviewer/index.html?id=22efe05eb7fb46349315e9815e793d9a

The next steps in IMS development include the integration of information from data storage tags to visualize detailed movements and environmental history of individuals, continued data discovery, and IMS customization to make the user interface more intuitive and user friendly.

Comparison of Coded-wire Tagging with Parentage-based Tagging and Genetic Stock Identification in Large-scale Coho Salmon Fisheries Applications in British Columbia, Canada

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Keywords: British Columbia, coho salmon, genetic stock identification, parentage-based tagging, single nucleotide polymorphisms

Since the late 1990s, all coho salmon (*Oncorhynchus kisutch*) released from many hatcheries in southern British Columbia (BC), Washington, and Oregon have received an adipose fin clip (termed mass marking) in order to facilitate mark-selective fisheries intended to harvest hatchery salmon only, with most clipped individuals carrying no coded-wire tag (CWT). This approach has resulted in reduced exploitation of naturally-spawned coho salmon, especially in sport fisheries, but the presence of many adipose-clipped salmon without a CWT has impaired the efficiency of CWT recovery. In spite of implementation of an electronic tag detection system to pre-screen a portion of the commercial catch to identify salmon with a CWT, the processing of many heads without a CWT from voluntary recreational recoveries and the increasing costs of CWT application and recovery have caused degradation of the information obtained from the current Canadian coho salmon assessment program.

A new, cost-effective approach to the assessment and management of wild coho salmon, and the associated hatchery production and fishery management is needed. Anderson and Garza (2006) noted that parentage-based tagging (PBT) provides equivalent information (hatchery of release, age of individual) for hatchery fish as do CWTs; implementation of PBT thus may overcome problems associated with CWT-based assessment and management of coho salmon fisheries in BC. Additionally, PBT provides a means of improved hatchery broodstock management, as well as assessment of hatchery-wild interactions in salmonids. Unlike CWT-based management, PBT-informed hatchery and fishery management would benefit from the complete adipose-clipping of hatchery-produced salmon. A significant advantage of the combination of mass marking and PBT implementation is the capability to identify visually, sample, and if desired, remove hatchery fish of local and stray origin in threatened wild populations. Moreover, PBT entails genotyping the entire hatchery broodstock and enables the identification of all hatchery progeny by parentage assignment (Anderson 2012; Wang 2016), thus enabling a 'mark rate' of virtually 100% of hatchery fish. Steele et al. (2013) demonstrated the equivalency of CWT and PBT in an initial evaluation of population and age assignment in steelhead trout (*Oncorhynchus mykiss*) of the Snake River basin in the Columbia River drainage. Hess et al. (2016) expanded the approach by using both PBT and genetic stock identification (GSI) to investigate run timing of steelhead trout in the upper Columbia River drainage. These applications confirmed the capability of a combined PBT-GSI technology to provide equivalent or better identification of fish as the CWT method, but were limited in geographic scale.

The study is an evaluation of the application of the PBT-GSI methodology outlined by Beacham et al. (2017) to coho salmon fisheries in BC to determine whether the genetic technologies can be used to provide more information on fishery contributions by hatchery and CU than is available from CWTs. Commercial and recreational coho salmon fisheries, and river escapements for selected populations, were sampled for both CWTs and genotypes. We evaluated the population-level resolution obtained from CWTs and the genetic methodology by CU for all 2017 and some 2016 fisheries in which coho salmon were caught, catch estimation by CU for the fisheries sampled, and stock-specific exploitation rate for selected populations of coho salmon in BC. Genotyping by sequencing methodology was used to genotype coho salmon at 304 single nucleotide polymorphisms (SNPs) in 304 amplicons. Complete broodstock genotyping for PBT analysis was conducted in 2014 for 20 hatchery-enhanced populations that included genotyping 6,061 individuals (96.4% genotyping success rate), and a stock identification baseline comprising some 267 populations ranging from southeast Alaska to Oregon was employed for GSI. A comparison of the population-specific contributions to mixed-stock fisheries, catch, and exploitation rates estimated with CWTs and PBT-GSI technologies was made. We conclude that a genetic approach can emulate

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and improve upon the results available from the current CWT program for assessment and management of coho salmon enhancement and fisheries in BC, and provide critical information to improve wild coho salmon assessment and conservation.

The detailed procedure for library preparation and genotyping was outlined by Beacham et al. (2017), and a version provided by Beacham et al. (2019). Summarized briefly, 756 individuals with up to 490 amplicons per individual were loaded on a P1 chip v3 with an Ion Chef, two chips were loaded consecutively with one run of the Ion Chef, both chips were then subsequently loaded on to an Ion Torrent Proton sequencer, and the genotype of each individual was scored and recorded with Proton software Variant Caller® at multiple SNP sites in each amplicon. Genotypes at all available SNPs for an individual at the two amplicons were assembled to provide a multi-locus individual genotype, with special emphasis on those sites in the amplicons where all individuals in a species were homozygous and alternate homozygotes were present at the same site in other species.

For seven populations where CWTs were applied and the 2014 broodstock genotyped, there were 352 CWTs recovered from individuals in these seven populations sampled in Canadian fisheries. Of these individuals, 335 were sampled for potential genotyping (individuals sampled in test fisheries were not included in the samples to be genotyped), and genotypes were obtained from 86.0% (288/335) of the initial individuals processed. PBT assignments were made for 92.0% (265/288) of the genotyped individuals, and PBT assignments were 100% accurate with respect to population of origin and age in comparison with CWTs. There were 285 additional PBT assignments made for these seven populations, which were individuals that had been adipose fin clipped but were not tagged with a CWT. For the sample provided, 335 CWTs from the seven populations were recovered, and 500 PBT assignments were made, with 49% more individual identifications through PBT than with CWTs. In addition, 680 PBT assignments were made for 13 populations where no CWTs were applied, with 367% (1,230 PBT versus 335 CWT) more individual assignments made for the same base sample. A more complete description of results available from the study was outlined by Beacham et al. (2019).

Genetic-based assessment benefits from mass marking of hatchery production, particularly with regards to escapement sampling. The proportion of hatchery-origin fish in the escapement can be determined visually as the proportion of individuals missing the adipose fin, without any further sampling required. The broodstock and non-broodstock escapement sampling in the current project generally indicated very low rates of straying among sampled populations, and thus if the escapement abundance is known or estimated, the hatchery portion of the escapement for a population can be estimated via the observed clip rate. No genotyping of non-broodstock escapement is required in order to estimate the hatchery component of the escapement. However, if survival of different release groups is required to be evaluated, escapement sampling is required to assign individuals to parents and therefore release group.

The PBT-GSI approach to fishery assessment enables catch by CU to be determined for any fishery in the province, and a means to implement the conservation/harvest balance that could be achieved by managing a combination of mixed-stock ocean fisheries and potential in-river fisheries targeting only healthy CUs (Price et al. 2017), providing substantial improvement to both CU status assessment as required by the WSP (DFO 2005) and MU fishery management. The use of PBT to identify members of hatchery or wild indicator populations and GSI to identify remaining individuals in the catch identifies the previously unknown components of the harvest when assessed with CWTs.

The strongest benefits of a PBT-GSI management system come from the additional information that it can provide, not only for improved fishery management but also for wild population conservation and management of enhancement programs. Currently, few wild populations are marked with CWTs in BC, and they are assumed to be reliable proxies for coho salmon populations over large geographic regions that may encompass multiple CUs. For the first time, analysis of northern and central coast fisheries in this study enabled comprehensive determination of fishery impacts on central/northern river systems and their constituent CUs.

This study has demonstrated the potential for implementation of a comprehensive PBT-GSI methodology for management and assessment of coho salmon in British Columbia that will remedy noted deficiencies of the current CWT-based management system. Most importantly, the genetic technology provides an immediate tool for identification of coho salmon to CU, a requirement for implementation of management of wild populations as mandated by the WSP for Pacific salmon, and a task that would be prohibitively expensive using CWTs. Moreover, the PBT-GSI technology benefits from the mass marking of hatchery-produced salmon, thereby facilitating improved hatchery broodstock management, monitoring of wild-enhanced fish interactions, and the evaluation of hatchery contributions to harvest. The ability to identify readily hatchery-produced salmon has been recognized as an imperative for managing the risks and assessing the benefits of hatchery production of salmonids at the domestic, bilateral, and international levels (Ruggerone and Irvine 2018). In Canada, extensive coho salmon conservation and enhancement efforts conducted for two decades requires comprehensive evaluation and possible modification that

cannot be achieved under the current management system. The genetic methodology developed in this study provides an opportunity for conservation-based management of Canadian coho salmon in which the economic benefit of hatchery production can be reaped without the imposition of undue and unknown risk to wild populations.

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Developing an Inter-individual Communication Biotelemetry System and Application to Chum Salmon Returned to off Japanese Waters

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Keywords: bio-logging, data-storage, biotelemetry, acoustic transmitter, data recovery rate, InterFish, inter-individual communication, *Oncorhynchus keta*

Recently, bio-logging techniques involving electronic data-storage tags and acoustic transmitters have been increasingly used to understand migratory fish movements and behaviors (e.g. Walker et al. 2000; Tanaka et al. 2000, 2001, 2005; Friedland et al. 2001; Ishida et al. 2001; Azumaya and Ishida 2005; Tsuda et al. 2006; Makiguchi et al. 2007, 2009, 2011; Kitagawa et al. 2016; Abe et al. 2019, Nobata et al. in press). The number of tags used, however, is normally limited due to the costs, and the tag recovery rate is usually low. In this study, to increase the data recovery rate, we developed an inter-individual communication biotelemetry system based on hydro-acoustic methods and ran a field test of this new bio-logging system on wild chum salmon *Oncorhynchus keta*.

Fig. 1. Inter-individual communication loggers, named "InterFish" (AquaSound Inc., Japan).

This newly developed inter-individual communication logger, named "InterFish" (AquaSound Inc., Japan, Fig. 1), is 100 mm in length and 22 mm in diameter, and uses a Gold code system, which is a kind of pseudo noise sequence known to have low interference of cross correlation which make a large number of highly distinguishable ID codes. It is capable of recording logger ID, ambient temperature and swimming depth. The loggers can share the data among themselves so that we can collect all the data by retrieving only one of the loggers. InterFish was set to repeat 20 s recording and transceiving and 40 s sleep. In December of 2017 and 2018, 22 fish attached with InterFish were released in Otsuch Bay located on the coast of Sanriku in the northern part of Honshu Island, Japan (10 fish of 59–77 cm in fork length in 2017 and 12 with 62–87 cm in 2018). Fish attached with transmitters (AQPX-1030P, AquaSound Inc.) were also released in the bay (20 fish in 2017 and 16 in 2018). Ten acoustic monitoring receivers (AQRM-1000, AquaSound Inc.) were moored in the bay.

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Fig. 2. Chum salmon attached with an InterFish.

Of the released 22 fish attached with InterFish (Fig. 2), 15 in total were recovered after one to 10 days after the release (seven fish in 2017 and eight in 2018). Depth and temperature records for the other fish (three in 2017 and four in 2018) were sporadically recorded in the recovered InterFish. Total recording time was 38.7–134.2 min in 2017 and 1.1–13.4 min in 2018. As for the transmitters, 11 and 12 were recovered in 2017 and 2018, respectively. In both years, depth and temperature records for four non-recovered fish were recorded in the recovered InterFish. As a result, it was found that this new bio-logging technique increased data recovery rate rapidly.

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A PIT Tag Based Method for Investigating Survival of Juvenile Cowichan River Chinook during their First Year of Life

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Keywords: Chinook Salmon, Cowichan, PIT, Marine Survival, Juvenile Tagging, Salish Sea

Early marine survival is a critical factor driving the productivity of many salmonid stocks including Chinook salmon. Understanding the factors which control survival and how mortality is distributed across space and time is critical to identifying management actions which improve adult abundance. Despite a growing body of research much has yet to be discovered but with the application of new technologies the answers to long standing questions are in reach. In this project, we implemented Passive Integrated Transponder (PIT) tags to track four cohorts of natural and hatchery origin Cowichan River Chinook from juveniles to return. Uniquely coded tags allowed the fate of individuals to be tracked so that successful fish within a tag group could be compared to peers. Survival to return estimates were able to be created at four different points in time to reveal spatial and temporal variability at a resolution beyond current published research.

Methods

We implanted 12 mm PIT tags into the celomic cavity of juvenile fall run ocean type Cowichan River Chinook following guidelines set out by Fisheries and Oceans Canada[1] and the Columbia River PIT tag Steering Committee[2]. Additional fish handling procedures were implemented during the tagging process including adding a water conditioner to reduce handling impacts on the mucous layer. Ice was used to maintain temperatures within two degrees and tagging activities halted when water temperatures exceeded 17.0ºC. Tag ID's were recorded electronically on hand-held scanners (HPR Lite[3]) while the last four digits were recorded manually for cross referencing with fork lengths. The scanners also associated a date time stamp with each tag to be included in the data base along with location, origin and other relevant data.

In the earliest stage, hatchery fish were held approximately three weeks after tagging to account for tag rejections and mortalities. Fish were measured, scanned and split into groups within five days of release. Wild fish were captured in-river by pole or beach seining moderate velocity runs and/or pools following methods in Pellett (2017) and Craig (2015). Origin was determined by the presence or absence of an adipose fin recognizing that 95–99% of production was clipped and some wild fish may be the progeny of hatchery Chinook reproducing in the natural environment. Fish were sorted by size and the threshold for tagging was set at 60 mm fork length. Following tagging, Chinook were held in an aerated recovery tank for a period of 5–20 minutes and released after displaying normalized behavior. Fish which failed to recover or that continued to display abnormal behavior after 20 minutes were removed from the tagging group.

Fish capture for later stages was conducted exclusively in the marine environment. In order to address the hypothesis that mortality occurs rapidly on marine entry two tag groups were created within Cowichan Bay. The first group (second stage) was captured by beach seining on the inner North side of the bay (Fig. 1). Two nets were employed for this activity ranging from 22 m to 38 m in length and 1.5 m to 2.5 m in depth. Panel size varied from 19.0 mm to 6.4 mm stretch mesh with 12.7 mm being the most common material. Nets were deployed from a 5.5 m aluminum boat (runabout style) while a team of 2–4 people pursed the net in from the shore. Approximately 5–10 sets were made per day depending on catch rates and processing time. Hatchery and wild fish were tagged in proportion to numbers encountered during the study.

For the third stage a 23 m commercial fishing vessel *Ocean Venture* was chartered to capture juvenile Chinook in Cowichan Bay. Efforts were focused in the central and inner portions of the bay but in deeper water compared to beach seining. The net was specially designed for juvenile sampling and was approximately 300 m x

[1] Canada Department of Fisheries and Oceans Animal-User Training Template section 6.0 Marking and Tagging of Finfish
[2] PIT Tag Marking Procedures Manual, Version 3.0, 2014
[3] Biomark Inc.

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20 m (Pellett and Damborg 2018). Once pursed in, crews sorted the bycatch (e.g., jellyfish, herrring, squid, stickleback) from the main net, and using a small brailer, scoop juvenile salmonids into the large live wells. Further sorting would occur until only juvenile Chinook remained. Following tagging, fish were placed in a recovery tank prior to release with compromised fish removed from the tag group.

Fig. 1. General area (red lines) in Cowichan Bay where the majority of the juvenile Chinook were captured and tagged by beach seining. Inset; aerial view of beach seine deployments.

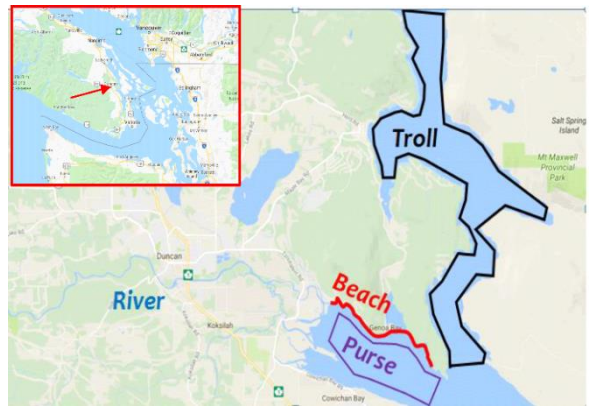

Fig. 2. Map of the Cowichan study area including approximate tagging locations for each stage. Inset: study location relative to the Salish Sea region.

The final stage was focused predominantly in the Sansum Narrows area of the Gulf Islands (Fig. 2). Fish were captured by micro trolling (Duguid and Juanes 2017) using a series of 6 lure/attractor setups deployed from a downrigger on each side of a small sport fishing boat. A total of 12 lures were deployed at depths ranging from 6–24 m and retrieved at regular intervals not exceeding 10 minutes. Isolated compartments were created within an aerated holding tank on each boat in the event multiple fish were captured so that depth could be recorded. In addition to the standard data collected, a GPS waypoint was logged for each retrieval and DNA was retained for Genetic Stock Identification. This allowed Cowichan Chinook to be isolated within the tag groups later on. Scales were not collected from the majority of fish because the difference in size between age classes was ~100 mm. Instead, fish less than 300 mm fork length were assumed to be in their first ocean year.

A series of 12 PIT tag detection antennas were installed in the Cowichan River counting fence in May of 2016 in order to interrogate returning fish for tags as they migrated upstream to spawn (Fig. 3). Prior to this time, a single antenna was installed in the counting fence located at the same site (river km 7) while detection efficiency was estimated with a second antenna located in the Skutz Falls fishway 25 km upstream. In addition, brood stock were also scanned for tags as they were often removed from locations below the fence.

Fig. 3. One of two 36 m PIT antenna transects in the lower Cowichan River (left) consisting of 6 antennas each (top right) operated by a master controller (bottom right).

Results

A total of 56,145 Cowichan River Chinook were implanted with PIT tags between 2014 and 2017 (Fig. 4). Approximately equal numbers were marked in freshwater (27,078) and marine (29,067) habitats although a higher proportion of hatchery fish were tagged in freshwater (75% vs. 30%). Overall, 32,941 wild Chinook were tagged primarily due to a higher encounter rate in marine waters. Purse seining accounted for the majority of marine captures at 20,494 followed by micro tolling (3,760) and beach seining (3,392).

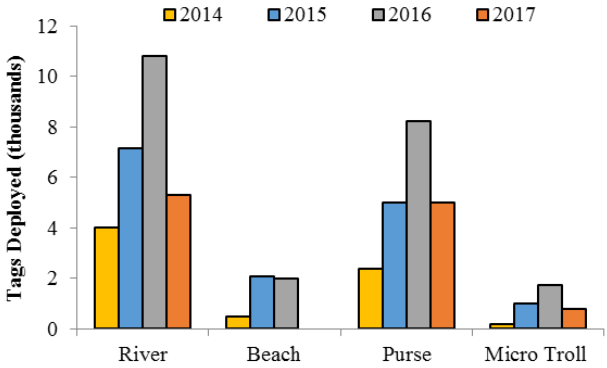

Fig. 4. Summary of PIT tag applications to Cowichan River Chinook by stage, 2014–2017.

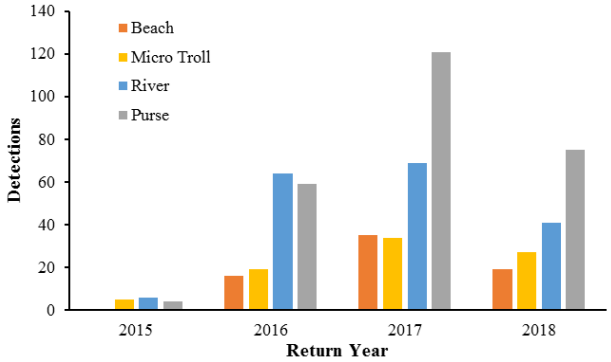

Fig. 5. Summary of PIT tag returns to the Cowichan River by stage through fall 2018.

Through the end of fall 2018, a total of 594 PIT tagged Chinook returned to the Cowichan River (Fig. 5). Returns peaked in 2017 with 259 tags while purse seining has produced the largest tag return to date at 255 fish followed by 174 from the river, 99 from micro trolling and 70 from beach seining. The age structure of Cowichan Chinook is dominated by 3 and 4-year olds with < 5% of the population reaching age 5 (Baillie et al. 2015; Lister et al. 1981). For this reason, we expect data collection from the 2016 tag cohort to be essentially complete in fall 2019 and the study to finish in 2020.

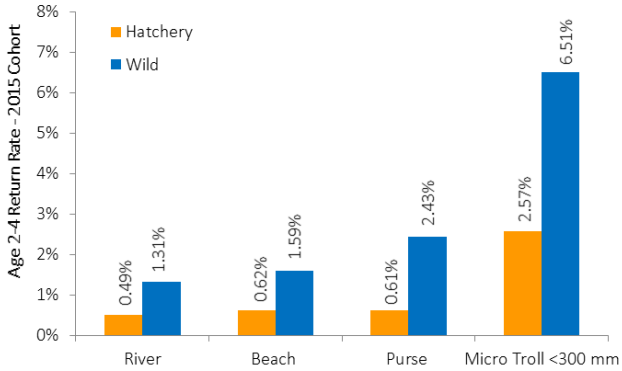

Fig. 6. Survival to return data by origin for Cowichan River Chinook PIT tagged in 2015.

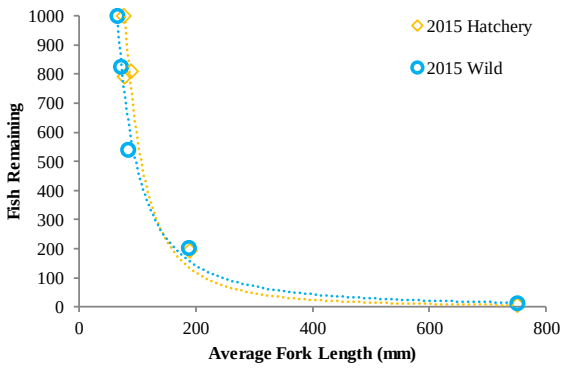

Fig. 7. Modified survivorship curves based on observed return rates for hatchery and wild Cowichan River Chinook tagged in 2015.

Current analyses were limited to the 2015 tag cohort due to constraints in tag numbers (2014) or incomplete returns (2016 and 2017). A comparison of return rates was conducted based on observed tags in the river and expanded for detection efficiency (93.4% in 2016 and 100% in 2017/2018). Survival was found to increase with time and wild fish outperformed hatchery fish at every stage (Fig. 6). Exploitation rates for hatchery coded wire tagged Cowichan Chinook are approximately 50% (Tompkins et al. 2005) and were not accounted for in these estimates.

Survival data were transformed into a variation of a survivorship curve to illustrate how mortality is distributed by size (time). Curves were generated from 2015 data only and found to be similar for both hatchery and wild Chinook (Fig. 7). Data suggest there is approximately 78% mortality in hatchery fish and 80% in wild between mid-May and the end of September of their first year. However, mortality was found to be higher between October of their first year and return with estimates of 97% and 93%, respectively.

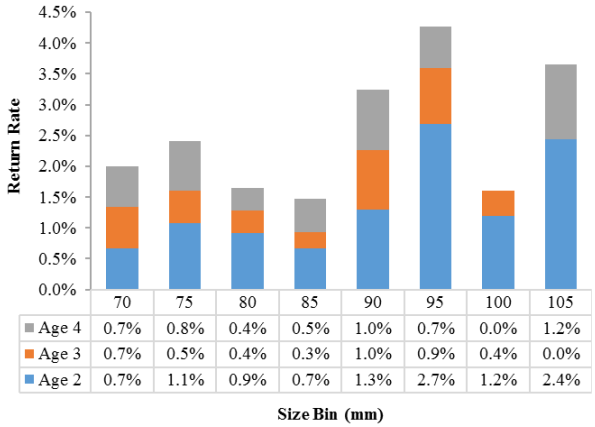

Fig. 8. Return rate by age for varying size bins of wild Chinook tagged during purse seining in 2015.

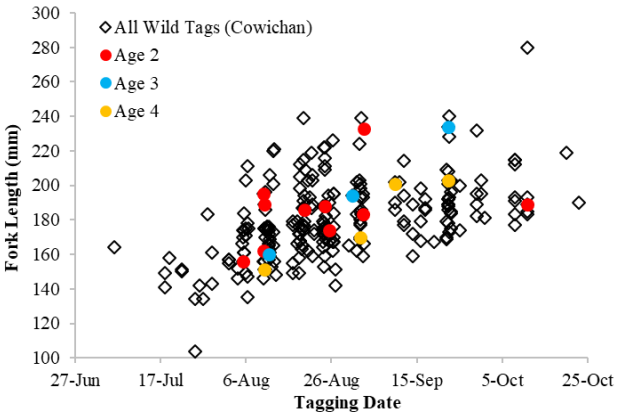

Fig. 9. Scatterplot of wild Cowichan River Chinook captured by micro trolling in 2015 with returning fish highlighted by age class.

An investigation of survival by size was conducted on wild fish tagged during purse seining in 2015 (Fig. 8). Return rates varied between 1.5% and 4.3% with the highest survival observed in the 95 mm bin. However, this was driven mainly by age 2 fish (jacks) which returned at a rate of 2.7%. In general, the proportion of age 2 returns increased with size while older age classes were more common in smaller size bins. For the 2015 wild micro troll group, a scatterplot of Cowichan Chinook identified though GSI was overlaid with individual returns by age class (Fig. 9). Survivors were found to originate from a wide range of sizes and dates at a cursory level of analysis. Both tag applications and return rates of hatchery Chinook from both stages were too low to conduct further analyses at this time.

Preliminary data from this PIT tag-based survival study are encouraging and suggest this technique holds promise for gaining new insights into the mortality of Chinook in their first year of life. The striking difference in survival observed between hatchery and wild fish through the end of September suggests the mechanism responsible for the disparity occurs after this time. Despite relatively high mortality in the first few months our results suggest significant losses continue through the first marine winter. A more thorough investigation of size related effects on survival as well as a comparison between years will be conducted once data collection is complete in fall 2020.

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The Current Status of Research on Geomagnetic Navigation in Pacific Salmon

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Keywords: magnetic map, orientation, sensory ecology, movement ecology, migration

From a human's perspective, the navigational task of ocean migrants is daunting: the open sea is vast, featureless, and in constant motion. Yet, numerous species transit ocean basins with seeming ease (Gould and Gould 2012). The migratory life-cycle is common and often includes use of spatially-restricted reproductive sites, dispersal of offspring, and eventual homing to the natal site to reproduce (Fig. 1). The life-history strategy is remarkably effective; indeed, many of the world's most important fisheries take advantage of the large numerical abundance and biomass that results (Secor 2015). The migrations of animals thus require efficient and directed movements between or among distant habitats (Fig. 1). Animal navigation can be likened to a two-step process, the "map step" whereby the animal assesses where it is relative to some goal and the "compass step" whereby the animals maintains a heading in the selected direction (Gould and Gould 2012). It has long been recognized that uncovering the mechanisms of these decisions could provide valuable insight into the movements of fish (and thus species distributions, variability in catch, etc.) (Neave 1964; Royce et al. 1968; Harden-Jones 1968). Determining the sensory basis of marine migrations is obviously challenging (Hays et al. 2016), however studies in species that spend part of their lives in terrestrial habitats have proven quite useful (Putman et al. 2017). Pacific salmon in particular have contributed substantially to what is now known about migration from the animal's perspective and point to an emerging picture that the use of cues from the Earth's magnetic field plays a central role (Quinn 2018).

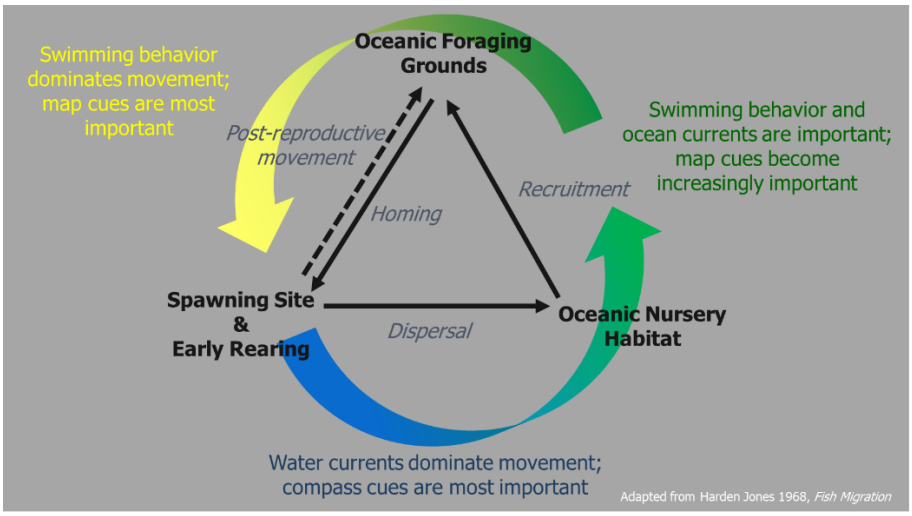

Fig. 1. The migration triangle of marine fishes (adapted from Harden Jones et al. 1968). The inner black arrows indicate ontogenetic shifts in habitat. The line for "Post-reproductive movement" is dashed to denote that not all species return to foraging grounds after spawning (notably, most Pacific salmonids do not). Outer arrows show the relative role of swimming behavior (yellower) and water currents (bluer) on the large-scale movements of fish during migration. The ability of animals to assess their position in the marine environment is an essential aspect of migratory life-histories, as it allows them to target potentially distant habitats that optimize growth and survival for a given life-stage, while still allowing them to return to previous locations that are more favorable for their offspring. For early life-stages, water currents dominate movement and because spawning typically occurs at particular sites where conditions facilitate juvenile dispersal, compass cues are sufficient to direct their journey. As fish age, swimming behavior becomes of equal importance to ocean currents and map cues are used to localize oceanic foraging grounds. For fish to return to their natal site to spawn, swimming behavior dominates movement and map cues are required for homing.

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Pacific salmon hatch in freshwater streams and juveniles swim to sea, travelling to distant foraging areas for a few months to years before returning to their natal river to spawn (Quinn 2018). Over the past three decades, experimental evidence has accumulated that salmonids use magnetic cues to guide their movements throughout the entirety of their life-cycle. Carefully controlled experiments show that juvenile salmon out-migrating from lakes use the magnetic field to maintain their swimming direction towards the sea (Quinn 1980; Quinn and Brannon 1982). Likewise, at swim-up, the vertical movement of Chinook salmon is sensitive to changes in the magnetic field, whereby upward swimming is reduced when the vertical component of the magnetic field is inverted (Putman et al. 2018). Moreover, even the alignment of rainbow trout embryos within their eggs appears to be sensitive to the direction of an applied magnetic field (Formicki et al. 2019). In each of these cases salmon are using the direction of the magnetic field for compass information.

While a compass is a useful navigational tool the map is essential for "closing the migration triangle", i.e., allowing animals to maintain population structure and return to the vicinity of their natal site to reproduce (Harden-Jones 1968; Secor 2015). The use of Earth's magnetic field as a map has long been an attractive (but contentious) hypothesis (Viguier 1882; Gould 2011). Magnetic field strength (total field intensity) and the angle at which magnetic field lines intersect the Earth's surface (inclination angle) vary from the poles to the equator, such that an animal capable of sensing these aspects of the field could extract latitudinal information (Fig. 2). Furthermore, the gradients of intensity and inclination are not entirely parallel but form a bicoordinate grid whereby longitudinal information can also be discriminated (Putman et al. 2011). Much of the work on animal navigation and migration has focused on birds, but evidence for their use of a magnetic map has been slow in coming (Thorup and Holland 2009; Mouritsen 2018). The definitive evidence that birds use a magnetic map to orient has only recently been shown in Eurasian reed warblers (Kishkinev et al. 2015; Chernetsov et al. 2017). The use of magnetic maps was first shown in taxonomic groups that have received much less attention, loggerhead sea turtles (Lohmann and Lohmann 1994, 1996; Lohmann et al. 2001) and red-spotted newts (Fischer et al. 2001; Phillips et al. 2002). In the years that followed, use of a magnetic map has been conclusively shown in a diversity of species that undertake migrations in marine habitats: spiny lobsters (Boles and Lohmann 2003), green sea turtles (Lohmann et al. 2004), Chinook salmon (Putman et al. 2014a), steelhead trout (Putman et al. 2014b), European eel (Naisbett-Jones et al. 2017), and Atlantic salmon (Scanlan et al. 2018).

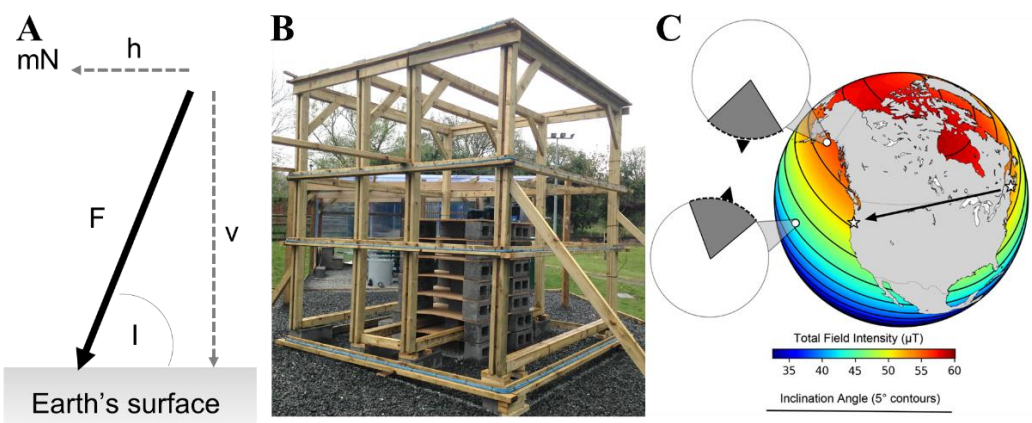

Fig. 2. (A) Earth's magnetic field can be described as a vector in which horizontal ("h") and vertical ("v") components of the field sum to the total field intensity ("F") and inclination angle ("I"). The direction of the horizontal component corresponds to magnetic north ("mN"). Total field intensity and inclination angle vary predictably over the surface of the Earth; increasing in strength and steepness towards the poles. However, these gradients are not entirely parallel and can thus provide animals information on both latitudinal and longitudinal position. **(B)** The orientation of animals to specific aspects of Earth's magnetic field can be investigated using a system of carefully spaced and wrapped coils of wire that are suspended from a non-magnetic frame and connected to a DC power supply. Changing the direction and amperage of electric current running through the wires allows animals at the center of the coil to be exposed to values of total field intensity and inclination angles that exist at sites distant to the testing location, i.e., "magnetic displacements." **(C)** A recent example of a magnetic displacement experiment shows that Atlantic salmon from a population in Maine, USA that were reared in Oregon, USA respond to a northern magnetic displacement by orienting to the south and respond to a southern magnetic displacement by orienting to the north (data from Scanlan et al. 2018). This differential response indicates an ability to detect map cues from the magnetic field, use it for orientation, and, apparently, correctly identify the direction of displacement.

These studies make use of a technique known as "magnetic displacements", which provide a powerful way to (i) show that specific aspects of the magnetic field are perceptible to animals, (ii) demonstrate that the information is used for orientation, and (iii) provide ecological context for the sensory ability (Lohmann et al. 2007; Gould 2014; Putman 2018). Understandably, perhaps, an experimental approach that yields so much information at once is at times misunderstood by those with unfamiliarity with lab-based experimental design (e.g., Courtillot et al. 1997; Durif et al. 2017). To head-off such confusion in the salmon community, a brief explanation is warranted. In these experiments, individual animals are placed within orientation arenas within a system of orthogonally-aligned coiled wires; one set of coils is aligned along the north-south axis of the arena the other is aligned in the vertical plane. Electric current run through the wires from a DC power supply generates a magnetic field which adds to or subtracts from the vertical and horizontal component of the local magnetic field (depending upon the direction of electric current) (Figs. 2A, 2B). The strength of the generated field depends upon the amperage of the electric current. Larger coils allow a larger area of field uniformity and finer-scale control of the magnetic field but require higher electric current. This allows the experimenter to precisely manipulate the magnetic field intensity and inclination experienced by the animal, such as to recreate a magnetic field that exists at a distant location along the oceanic migratory route (Fig. 2C). In these experiments, the direction of magnetic north and other sources of information or noise are either held constant or randomized across trials. Thus, if orientation responses of a group of animals differs to two or more different magnetic displacements it can be unequivocally concluded that the animals perceive the magnetic change, use it for orientation, and thus possess a magnetic map (Lohmann et al. 2007; Gould 2014).

Use of a magnetic map has been most frequently discussed as a mechanism for homing. An enduring hypothesis is that of "geomagnetic imprinting": animals remember the magnetic field values at their natal site and use the predictable gradients of Earth's magnetic field as a kind of "map" to return upon reaching maturity. However, the best evidence for magnetic maps in marine animals (excluding, perhaps, lobsters (Boles and Lohmann 2003)) shows a rather different function, to guide the movements of juveniles to oceanic foraging grounds. Studies show that before the outset of smoltification salmon possess a magnetic map based on both intensity and inclination (Putman et al. 2014a). This map is independent of prior migratory experience, given that salmon that never left their hatchery respond to large-scale magnetic displacements (Putman et al. 2014a, b; Scanlan et al. 2018). The magnetic map is also independent of a recent evolutionary history of migration, in that it is conserved across anadromous and nonanadromous populations (Scanlan et al. 2018). Likewise, it appears to be a general solution for navigation, in the offspring of Atlantic salmon that were transported from Maine to Oregon, USA respond appropriately to magnetic displacements in the North Pacific (Fig. 2C) (Scanlan et al. 2018). Such an ability appears possible because the orientation responses of juvenile salmon can be modified depending upon the magnetic conditions they experience during early rearing. Steelhead trout raised in a spatially inhomogeneous magnetic field (owing to the iron infrastructure associated with the hatchery) did not differentiate a north/south magnetic displacement, whereas those raised under more natural magnetic conditions could (Putman et al. 2014b). Finally, the orientation responses to magnetic displacements observed in the lab appear to be highly adaptive to juvenile fish during their oceanic migration to foraging grounds. Simulating this behavior in an ocean circulation model showed that it facilitates (i) movement into and retention within favorable thermal habitat, (ii) group cohesion and schooling, and (iii) following a more predictable migration route over successive generations (Putman 2015).

Magnetic displacements combined with computer simulations provide a glimpse into the largely unknown migration of juveniles to marine foraging grounds. Major questions in salmon ecology and management are related to this period of the salmon life-cycle and the information afforded by this work allows specific, process-based and testable predictions on spatiotemporal variation in individual movements, population distributions (stock structure), migratory routes, return strength, homing/straying, hatchery (and escaped farmed)/wild interactions, and responses to changing climate. Indeed, the value of understanding how salmon use magnetic cues is beginning to emerge. For instance, the routes of two adult chum salmon tracked from the North Pacific to coastal Japan using light-level geolocators and tri-axial magnetometers appear consistent with the use of magnetic map cues (Azumaya et al. 2016). At the population level, the migratory routes (and relative proportion of fisheries catch) of sockeye and pink salmon homing to the Fraser River appears related to their use of a magnetic map for navigation (Putman et al. 2013; 2014c). Annual variation in the proportion of sockeye and pink salmon that return to the Fraser River via the Queen Charlotte Strait (northern route) vs. the Strait of Juan de Fuca (southern route) from the 1950s to present is better explained by gradual drift of the geomagnetic field than changes in ocean temperatures, currents, or river outflow (Putman et al. 2014c). These studies suggest that explicitly considering the interaction between salmon and their environment, as mediated by their use of magnetic cues to navigate, could improve predictions of shifting distribution and abundance in response to changing conditions (Putman 2018).

The work to-date could be interpreted as lines of evidence for the overriding importance of magnetic cues for salmon to complete their life-cycle. The findings that salmon possess a magnetic map and are sensitive to magnetic

cues very early in life are consistent with the hypothesis that salmon imprint on magnetic field values as juveniles and recall them later as adults to complete their long-distance migration (Lohmann et al. 2008a; Bracis and Anderson 2012; Lohmann and Lohmann 2019). However, as with any laboratory experiment or correlational analysis (which includes tracking experiments), room for skepticism remains (Lohmann et al. 2008b; Putman et al. 2014c). Fortunately, the geomagnetic imprinting hypothesis could be rigorously tested by a large-scale field experiment in which fish of the same population are reared in magnetic fields that correspond to different locations along the coast and subsequently released. If salmon use magnetic cues for homing, the fish would be putatively "programmed" to return to those sites, rather than the geographic site of rearing. Differential marking of groups (external marking in addition to genetic parentage analyses) and coordination with fishers would allow for a clear test of predictions. Acoustic tagging a subset of smolts and tracking their initial movements along the acoustic arrays of Oregon, Washington, and British Columbia (Payne et al. 2010) would allow further assessments of at what point groups begin to diverge. Stable isotope analyses of returning fish (Volk et al. 2010) could also provide insight into other ecological implications of differential imprinting. The definitive evidence for geomagnetic imprinting in salmon would move us towards a process-based understanding of salmon ecology that could greatly benefit hatchery production practices, forecasting salmon returns, and predicting salmonid responses to environmental change (Putman 2018).

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Integrating Multiple Intrinsic Markers to Infer Habitat Use of Sockeye Salmon Stocks (*Oncorhynchus nerka*) in the North Pacific Ocean

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Keywords: otolith microchemistry, growth, migration, distribution, stable isotopes, environmental history

Pacific salmon (*Oncorhynchus* spp.) are renowned for their high mobility, complex population structure, and homing to natal spawning grounds. Following a year or more in freshwater and estuarine habitats, sockeye salmon (*O. nerka*) in British Columbia, for example, are thought to move north and north-west along the coast during their first summer and winter at sea before migrating offshore into the North Pacific Ocean. During their marine phase, they have the potential to occupy a vast range between the Aleutian Islands and the Washington/Oregon coasts before returning to their home rivers and spawning grounds 2–6 years later (Tucker et al. 2009; Farley et al. 2018). Recent studies on salmonids have greatly advanced our understanding of the timing of ocean entry, natal origins, and habitat use during the first year of life (e.g., Barnett-Johnson et al. 2008; Miller et al. 2010; Volk et al. 2010; Stocks et al. 2014; Campbell et al. 2015). However, much less is known about their habitat use, distribution, and migration patterns after their first autumn at sea—a period that comprises the majority of their lives. The great obstacle to resolving ocean habitat use is the logistical challenge of capturing/tracking salmon on the high seas. Yet, tracing movement pathways through the North Pacific is essential to understanding how salmon populations are and will be impacted by regionally dynamic changes in ocean conditions. To advance techniques for tracing complex oceanic movements of salmon, we evaluate the utility of integrated intrinsic genetic, chemical, and microstructural markers to infer habitat use, movement patterns, and their relationship with relative growth rates of *O. nerka* during their marine phase.

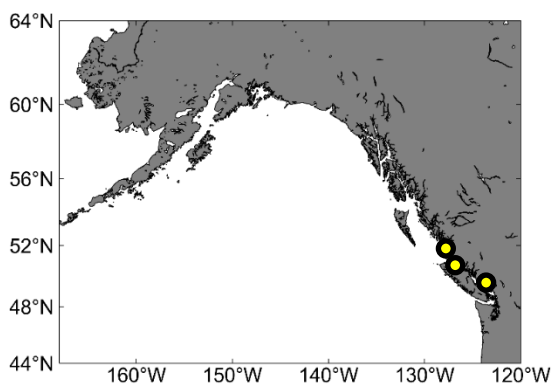

Fig. 1. Sampling locations for returning sockeye salmon (*Onchorynchus nerka*) along central and southern British Columbia, Canada, July–September 2015.

Archived otoliths collected from returning *O. nerka* captured in fisheries and research surveys between July–September 2015 (Fig. 1) were used in our analyses. These samples were opportunistically selected because genetic stock identifications and stable isotopic analyses of muscle tissue had been completed previously for specimens represented in the otolith archive. Stock identifications were determined from analyses of fourteen microsatellites following Beacham et al. (2014) using an ABI 3730 capillary DNA sequencer. Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope analyses of dorsal muscle tissue were performed using a PDZ Europa Hydra 20-20 continuous-flow isotope ratio mass spectrometer to assess dietary variation that may reflect foraging and occupancy in different food webs. A lipid correction factor was applied to $\delta^{13}C$ values (Hoffman and Sutton 2010). Otoliths were thin-sectioned, imaged, and aged prior to elemental analyses and seasonal increment widths were measured to evaluate variation in summer growth rates. Otolith microchemistry was assayed using laser ablation inductively coupled plasma mass spectrometry. Otoliths were ablated from edge to core (spot size: 47 µm; scan speed: 5 µm s^{-1}) to capture elemental variation across the entire life of each fish. Element-to-calcium ratios for lithium (^{7}Li), magnesium (^{24}Mg), strontium (^{88}Sr), barium (^{138}Ba), and lead (^{208}Pb) were collected to characterize potential

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spatial/environmental differences among fish during their summers and final winter at sea. Elemental data were averaged from each mid-point of summer (50 µm) and final winter (15 µm) growth bands to align and standardize comparisons across individuals and cohorts. We applied hierarchical cluster analyses with Ward's linkage method and Euclidean distance to objectively identify groups and patterns within temporally-aligned otolith elemental data. The optimum number of groups was determined from cubic clustering criteria. Differences in otolith chemistry among group classifications and the influence of age, sex, and genetic stock were subsequently tested with non-parametric multi-response permutation procedures (MRPP). Relative differences in growth among groups were examined with analysis of variance (ANOVA) and Tukey's Honestly Significant Difference tests were conducted to determine which groups accounted for any observed variation in growth.

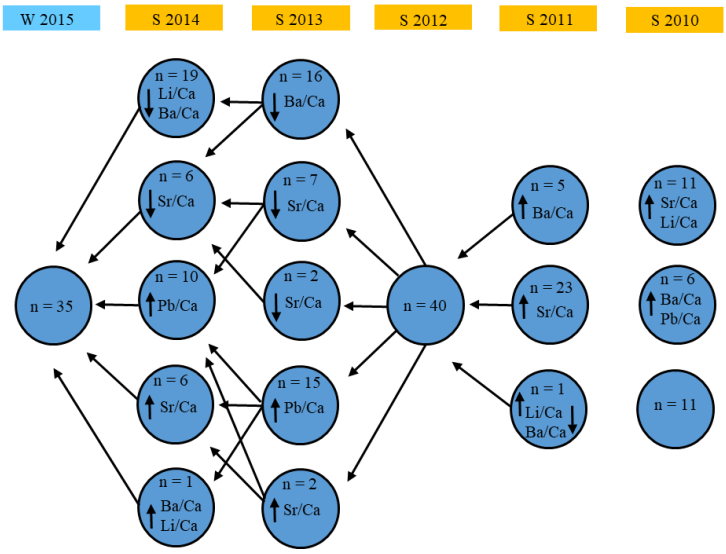

Fig. 2. Diagrammatic representation of the results of hierarchical cluster analyses based on otolith chemical composition across the lifetime of sockeye salmon examined in this study by season and year, 2010–2015. Circles represent individual group designations resulting from cluster analysis. S = summer, W = winter, Ba = barium, Ca = calcium, Li = lithium, Mg = magnesium, Sr = strontium, and Pb = lead. Sample size (n) and the relative contribution of select element-to-calcium ratios are reported. Arrows between groups indicate the direction of change, if any, in group membership across years/seasons. With the exception of summer 2010, all group classifications reflect mixed cohort analyses.

Otoliths were processed and assayed from a total of 50 *O. nerka* that were comprised of Rivers Inlet (n = 16) and Fraser River (Chilko (n = 17), Chilko South (n = 11), Harrison (n = 2), Great Central (n = 1), Middle (n = 1), and Raft (n = 3) stocks. Samples were comprised of four age classes that included sockeye from 2009–2012 cohorts. Profiles of otolith chemistry across the lifetime of individual *O. nerka* distinguished early versus late marine migrants. Distinctive groups were revealed by variation in otolith chemistry. Mean mid-summer elemental composition indicated that sockeye experienced both shared and disparate environmental conditions or locations during their time at sea. Cluster analyses of the 2010 cohort found significant differences in otolith chemistry during their first summer prior to marine residence that aligned with genetic stock identifications and spatial differences at large and fine spatial scales (Fig. 2; MRPP: T = -12.3, A = 0.48, $p < 0.01$). Three separate groups were identified from intrinsic chemical markers during the summer of 2011. Location or conditions were found to be highly similar among individuals in 2012 (Fig. 2). In the summers of 2013 and 2014, variation in otolith chemistry separated five distinct groups. Variation in otolith Sr/Ca composition was a consistently important determinant of differences among groups. Otolith Sr/Ca ratios increase significantly with salinity in sockeye salmon and can serve as powerful markers of habitat use (Zimmerman et al. 2005). Two age 1 Chilko sockeye, for example, exhibited characteristics of freshwater residence in the summer of 2013 based on low otolith Sr/Ca and Mg/Ca ratios and higher Li/Ca and Ba/Ca ratios in comparison to other individuals in the study (Fig. 2). In the winter of 2015, otolith chemistry was homogenous among our samples, implying that a shared location or set of environmental conditions were again encountered during migration. Similarly, stable C and N isotopic analyses indicated extensive dietary overlap and that the fish were feeding within the same food web and likely occurred in the same region during the spring and summer prior to spawning. Groups designated through cluster analyses were comprised of multiple stocks,

suggesting a high degree of mixing during migration. Otolith chemical composition did not differ by sex or stock (MRPP), supporting the premise that the elements considered in this study reflected underlying spatial/environmental differences among fish that could be used to reconstruct migratory pathways. Variation in otolith chemistry corresponded with differences in growth rates among some groups (Fig. 3; ANOVA (2014): F = 2.75; p = 0.04; ANOVA (2013): F = 4.22; p = 0.02).

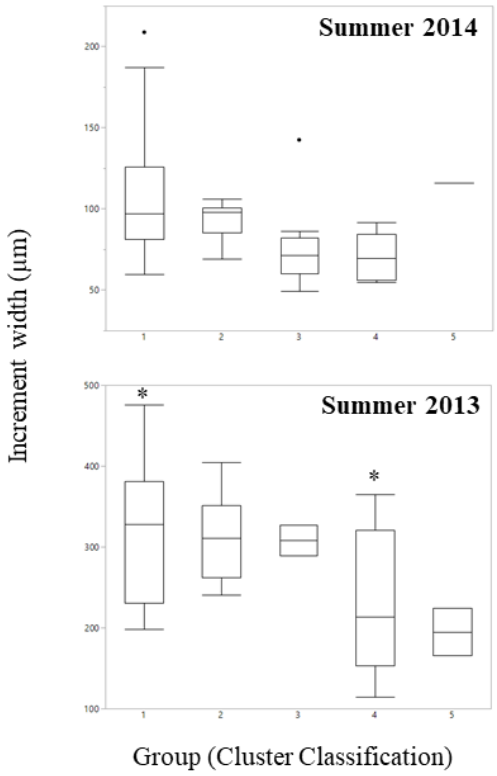

Fig. 3. Box plots depicting relative growth (otolith increment width) among designated groups based on differences in otolith chemistry using hierarchical cluster analyses for summers 2014 and 2013. Asterisks (*) denote those groups found to differ significantly by analysis of variance (ANOVA) and Tukey's Honestly Significant Difference (THSD) tests.

Our results demonstrate that otolith chemistry provides valuable information on the habitat use and environmental history of salmon during the marine as well as early life stages. Integrating microstructural growth increment information with chemical chronologies and genetic stock identifications has the potential to generate new insight into the consequences of variation in migratory pathways and identify patterns of movement, distribution, and habitat use at multi-regional scales. Distinct inshore and offshore oceanographic gradients encountered during salmon migrations in the North Pacific are likely to be recorded within salmon otoliths. Likelihood probability distributions estimated from combined oceanographic and chemical data across potential migration routes or a chemical atlas based on otolith edge chemistry of the same species collected in different locations could offer a foundation for reconstructing migratory pathways from otolith chemistry. We recommend the inclusion of otolith stable oxygen isotope analyses in future investigations to provide a seasonal water temperature proxy that may complement and strengthen inferences on movement patterns and habitat use.

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The Genomic Basis of Fitness and its Potential for Understanding Responses to a Changing Climate

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Keywords: genomewide association analysis, captive rearing, conservation, domestication selection, managed gene flow, random forest

Predicting fluctuations in the abundance and distribution of salmon populations, particularly in a changing climate, requires a comprehensive understanding of how both genomic and environmental variation affects fitness. Recent improvements in DNA sequencing technology and the increased availability of genomic resources now permit such research. Specifically, genetic markers associated with phenotypic and environmental variation can now be identified, and their integration has significant potential to provide insights into how populations may respond under different environmental scenarios.

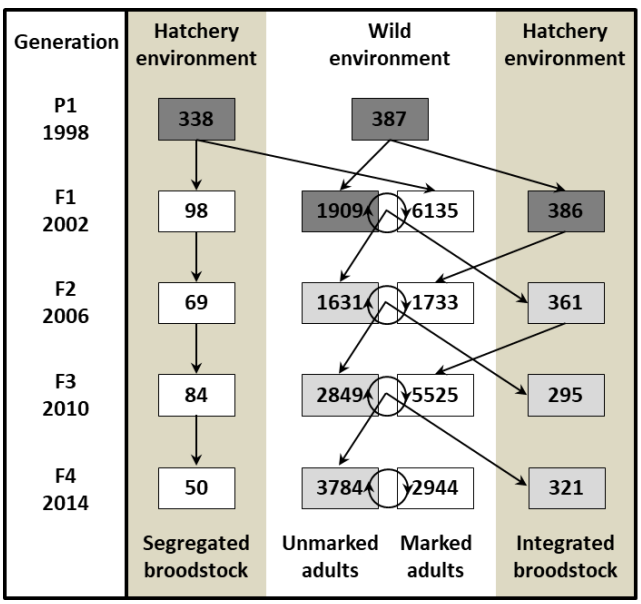

Fig. 1. Schematic illustrating the initiation (the founding P_1 generation) and subsequent propagation (F_1–F_4 generations) of the integrated and segregated hatchery lines of anadromous Chinook salmon at the Cle Elum Supplementation and Research Facility (modified from Waters et al. 2015). Each box denotes the number of spawners (wild environment) and the number of broodstock (hatchery environment) for each year surveyed. Linear arrows indicate the contribution of wild spawners or hatchery broodstock to the subsequent generation. Circular arrows represent unobserved mating between wild-born (unmarked) and hatchery-born (marked) spawners in the wild environment. Fish from the two lines are differentially marked, so only hatchery-born fish from the integrated line are permitted to spawn in the wild. Dark gray boxes represent wild adults, light gray boxes represent natural origin adults with hatchery, wild, or hybrid ancestry, and white boxes represent adults born in the hatchery.

To illustrate this potential, we highlight results from our recently published study (Waters et al. 2018). We examined how differential exposure to the hatchery environment affected variation at genetic markers associated with six fitness-related traits in adult spring Chinook salmon (*Oncorhynchus tshawytscha*) from the Cle Elum Supplementation and Research Facility (CESRF) in Cle Elum, Washington, USA. The hatchery was initiated from 1997-2002 using returning adults from a wild population in the upper Yakima River, WA, USA, a tributary of the Columbia River (Fig. 1). In 2002, both wild and first-generation hatchery adults were spawned to create the integrated (INT) and segregated (SEG) hatchery lines, respectively (Fig. 1). The integrated line uses only fish born in the wild as broodstock, and all returning adults from this line are allowed to spawn in the river. In contrast, only

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returning hatchery-origin fish are used as broodstock in the segregated line, and SEG adults are not allowed to reproduce naturally; fish from the two lines are differentially marked for external identification, so all SEG adults are removed from the system at a monitoring facility downstream from the spawning grounds. Therefore, the integrated line receives one generation of exposure to hatchery conditions and has two-way gene flow with the wild population, while the segregated line is exposed to the hatchery every generation and has no gene flow with the wild stock (Fig. 1). Importantly, tissue samples for DNA and phenotypic data have been collected from every adult fish used as broodstock since the inception of the program in 1997. Additional information regarding the ecological background and the initiation of the integrated and segregated hatchery lines at CESRF have been described elsewhere (Knudsen et al. 2006; Fast et al. 2015; Waters et al. 2015).

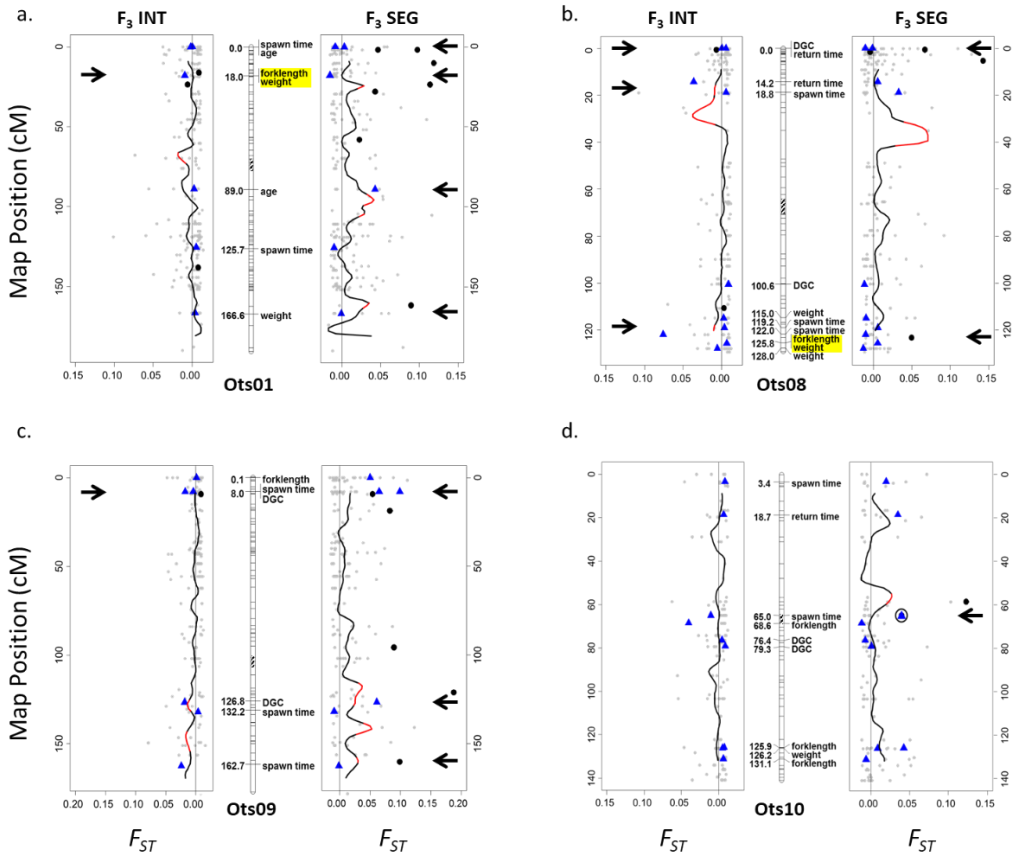

Fig. 2. Graphical representation of four Chinook salmon chromosomes (center panels, a-d) showing the map positions (cM) of loci associated with six fitness-related traits, as identified by Random Forest analyses. Loci associated with different traits mapped to the same regions, including loci on Ots01 and Ots08 that were associated with both fork length and weight (highlighted in yellow). Divergence (F_{ST}) of the F_3 INT and F_3 SEG hatchery lines when compared to the P_1 founders is displayed in the left and right panels of each figure, respectively. The F_3 generation is shown because it is the most recent hatchery generation for which there are relatively large sample sizes (> 50), and thus has greater statistical support for all outlier tests. The black line denotes the moving average of F_{ST} across the chromosome, with regions exhibiting significant levels of divergence (i.e., outlier regions) from the P_1 Founders in red (Waters et al. 2015; Waters et al. 2017). The centromere of each chromosome is shaded with diagonal black lines. Black circles represent outlier loci previously identified by F_{TEMP} and *Bayescan*, blue triangles correspond to trait-associated loci, and gray points are all other study loci. Locations where trait-associated loci are in close proximity to outlier loci or regions are marked with black arrows, including one outlier locus on Ots10 that was also associated with spawn timing (circled).

Tissue samples for DNA were sub-sampled from 465 adult fish spanning five generations: the 1998 wild founders (second founding year; P_1 Founders) and hatchery brood years 2002 (F_1 Wild and F_1 Hatchery), 2006 (F_2 INT and F_2 SEG), 2010 (F_3 INT and F_3 SEG), and 2014 (F_4 INT and F_4 SEG). DNA was sequenced using restriction site-associated DNA (RAD) sequencing (Baird et al. 2008), which yielded 9108 polymorphic genetic markers after bioinformatic processing and filtering (Waters et al. 2018). Phenotypic data were collected for the following traits: date of return to freshwater spawning grounds (return timing), length and weight at return, age at maturity, spawn timing, and daily growth coefficient. Loci associated with each trait were identified by Random

Forest, an approach suitable for simple and polygenic traits (Breiman 2001). Genetic variation at loci associated with each trait was then compared between each generation of the integrated and segregated hatchery lines to determine if integrated management limited divergence in these potentially adaptive regions. We also compared the genomic positions of trait-associated loci and highly diverged loci—interpreted as signatures of adaptive divergence (i.e., outliers)—that had been previously identified in the two lines (Waters et al. 2015; Waters et al. 2017). Overlap between outliers and trait-associated loci was interpreted as evidence that specific traits had responded to domestication selection. A complete description of methods can be found in Waters et al. (2018).

We identified 226 trait-associated loci over all traits. Notably, some loci were associated with multiple traits, and some genomic regions contained multiple loci. For example, 12 loci were associated with both fork length and weight at return (e.g., Fig. 2a, 2b). Further, two loci associated with weight, two for spawn timing, and one for both fork length and weight all mapped to a 13cM region on chromosome Ots08 (Fig. 2b). Similarly, two loci associated with fork length and one locus associated with weight mapped to a 5cM region on chromosome Ots10 (Fig. 2d). We interpreted such sites as candidates for genomic regions underlying fitness, and they were further supported by the integration of results across multiple studies (Waters et al. 2018). These regions should be specifically targeted by future investigations that aim to identify the specific genes underlying fitness-related traits.

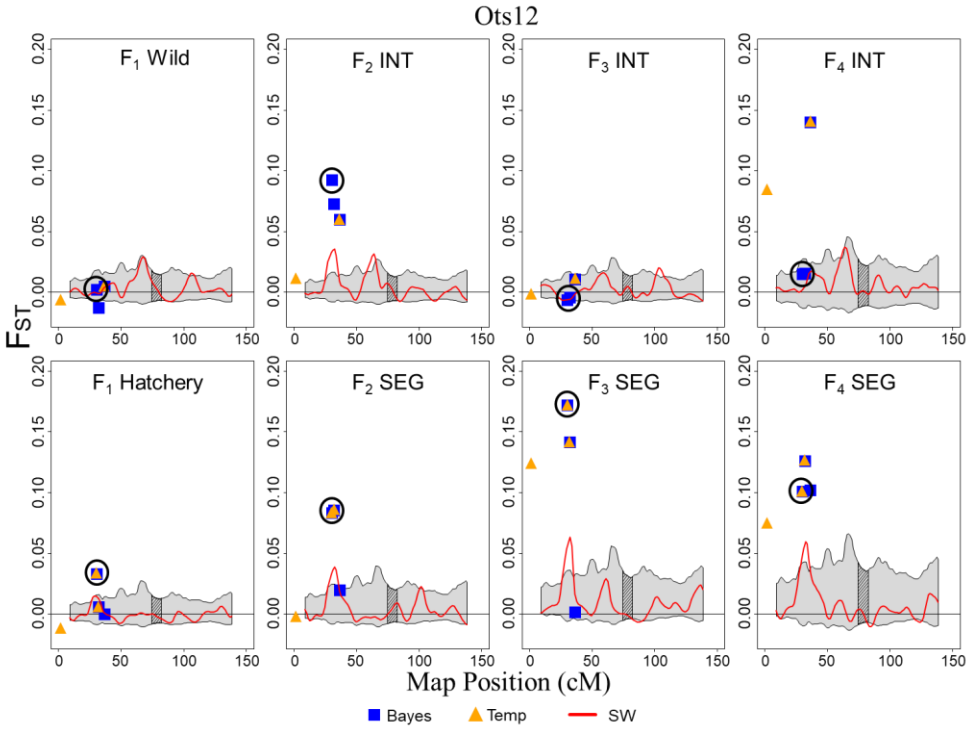

Fig. 3. Loci and regions of chromosome Ots12 showing signatures of adaptive divergence based on measures of pairwise F_{ST} between each generation of each line and the P_1 founders. The results are given for the integrated (top panel) and segregated (bottom panel) hatchery lines through the F_1, F_2, F_3, and F_4 generations. Blue squares are loci that were identified as outliers by *Bayescan* and orange triangles are outliers identified by F_{TEMP}, a method designed to detect selection in a single population over time. The red line represents the kernel smoothed moving average of F_{ST} and the gray shaded area is the 95% confidence interval. Genomic regions exhibiting significant levels of divergence (i.e. outlier regions) from the P_1 founders occur where the moving average of F_{ST} exceeds the 95% confidence intervals. The centromere of the chromosome is shaded with diagonal black lines. The black circle designates a locus predictive of return timing, Ot005185_Ots12p, which was also identified as an outlier by *Bayescan* and, in the segregated line, by F_{TEMP}. Negative F_{ST} values occur due to finite sample sizes and slight variance in sample sizes between populations.

Evaluations of genetic variation at trait-associated loci showed little evidence of divergence between the integrated and segregated hatchery lines across all traits, as each generation of the two lines overlapped extensively in multivariate space. However, numerous regions were identified where trait-associated loci overlapped with outliers. Many of these overlapping regions, primarily with loci linked to spawn timing and return timing (e.g., Fig. 2d; Fig. 3), were either unique to, or more divergent in, the segregated hatchery line. For example, four loci associated with spawn timing had also been identified as outliers unique to the segregated hatchery line. In addition, one locus linked to return timing on Ots12 was identified as an outlier by two independent methods in the segregated

line (Fig. 3). This locus was near two other outliers and was located within a region that exhibited significant divergence from the P_1 founders across all four generations in the segregated line (Fig. 3). The region was also significantly divergent in the F_2 generation of the integrated line. Together, multiple lines of evidence–phenotypic divergence, greater overlap with outliers in the segregated line than in the integrated line, and temporal consistency–suggest that these regions may be responding to domestication selection on return and spawn timing in the segregated line.

The identification of loci associated with six key traits by Random Forest is a first step towards characterizing the functional genetic basis of fitness in Chinook salmon (Macqueen et al. 2017). This study is also the first to utilize genomic approaches to demonstrate the effectiveness of a conservation strategy, integrated hatchery management, to reduce divergence at trait-associated—and potentially adaptive—loci. While we focused on genetic and phenotypic change in two hatchery lines of salmon with different levels of exposure to captivity, these genomic-based approaches may be applied to numerous organisms (captive or wild) to better understand other mechanisms of population change and predict how they might respond to future environmental conditions.

Bay et al. (2018) provide an excellent example of how genomic information can be integrated into population distribution models to predict future abundance. They employed methods similar to those used in our study to identify genomic variation associated with environmental differences between 21 populations of yellow warblers across North America. Then, using the genotype-environment (GxE) relationships and the future environmental conditions predicted under various climate change scenarios, the authors were able to identify the populations that may be most vulnerable to climate change (i.e., the populations that would require the greatest future genetic change based on the GxE relationships). Remarkably, the populations that were predicted to be most vulnerable had already experienced the largest population declines, according to contemporary population trends from bird surveys.

The utility of trait-linked markers in conservation genetics is being actively discussed and explored (Shafer et al. 2015; Garner et al. 2016; Pearse 2016; Bernatchez et al. 2017). As the availability of genomic resources improves, it is important to explore how markers associated with phenotypic and environmental variation can be applied in different contexts. We hope that the findings described here illustrate the potential of these associations to better understand factors that affect individual fitness and population abundance, both now and in the future.

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A Compilation and Meta-analysis of Salmon Diet Data in the North Pacific Ocean

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Keywords: salmon, diet, meta-analysis, trophic niche

Although the freshwater phase of the salmon life cycle has been studied in depth, there is much less information available on the marine phase, even though Pacific salmon can spend anywhere from one to seven years of their life in the ocean. With rapidly changing ocean conditions, it is important to understand this phase of the salmon life cycle. One of the most significant factors affecting the survival of salmon is the presence and abundance of nutritious prey. Although it is difficult to measure prey occurrence across the scale of the Pacific Ocean basin, information on prey presence and abundance can be obtained by studying salmon diets. Diet data can give insight into food webs, niche overlap between species/stocks, potential competition, health, and changing ocean conditions. Over the past century, there has been sporadic research on salmon diets in the ocean, and inconsistent methods have been used to quantify this information. There is an urgent need to consolidate available data in a useful way to understand salmon habitat, identify knowledge gaps, and project future changes.

In order to address this issue, we conducted a systematic review of the literature, including a keyword search using several online databases (Proquest Aquatic Sciences and Fisheries Abstracts, Web of Science Core Collection and Web of Science Zoological Record) and supplemented this with literature from the North Pacific Anadromous Fish Commission's and International North Pacific Fisheries Commission's documents and bulletins. We identified over 250 relevant sources, containing marine salmon diet data—specifically in the form of stomach content information. Diet data was found for Chinook, coho, sockeye, chum, and pink salmon, as well as steelhead, across the North Pacific basin. These data will be extracted and collated into an open-access diet database to help address questions related to salmon marine survival and will also represent a valuable resource for modeling efforts aimed at Ecosystem Based Management and understanding North Pacific ecosystem response to climate change.

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Supplementation of Atlantic Salmon in the Southern Extent of their Range: Evaluation of Age-1 Hatchery Smolt Stocking in a Small Coastal Watershed

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Keywords: Atlantic salmon, smolts, telemetry, restoration stocking, migration performance

Atlantic salmon (*Salmo salar*) populations at the southern extent of their range have experienced precipitous declines over several decades and abundance is critically low. This species requires conservation hatchery supplementation in order prevent extirpation while other interventions (e.g., habitat improvements) proceed with the goal of population recovery when conditions improve. The Narraguagus River, a small coastal Maine Atlantic salmon river, has experienced low (10–40) but persistent spawners originating from natural production of approximately 1,200 smolts annually (USASAC 2019). In an effort to enhance adult returns, an annual stocking of 40,000 age-1 hatchery reared smolts took place from 2008–2012. This effort had limited success, with 154 two sea-winter adult returns (5.6 two sea-winter adults/10,000 smolts). These rates are much lower than extrapolated numbers of 63.2 two sea-winter adults per 10,000 smolts for their wild counterpart. Hatchery inputs have been described as inferior (McCormick et al. 1998), but it is unclear why a ten-fold difference exists between these groups. In 2016, smolt stocking was reinitiated, with plans for nearly 100,000 smolts stocked annually over a four-year period. In collaboration with hatchery managers and regional biologists, we initiated a two-year telemetry study with hopes of pinpointing constraints in stocking effectiveness as well as describing the migration dynamics of these tagged fish.

We telemetry tagged smolts over a two-year period to understand migration success and behavior of hatchery smolts stocked at different densities and release times. In this study, we report migration performance of fish from freshwater through the marine transition before entering the Gulf of Maine.

The Narraguagus River located in eastern Maine, USA (44°N, 68°W) flows southeasterly from Eagle Lake a distance of 70 km to head of tide in Cherryfield, Maine (Baum and Jordan 1982; Fig. 1). The estuary is narrow (< 125 m) and short at approximately 6 km in length. Depth within the estuary is 3 m at mean low water with 3.4 m tidal fluctuation (Baum and Jordan 1982). The Bay encompasses 16,600 ha with tidal fluctuations of 4.8 m (Strategic Assessments Branch 1985).

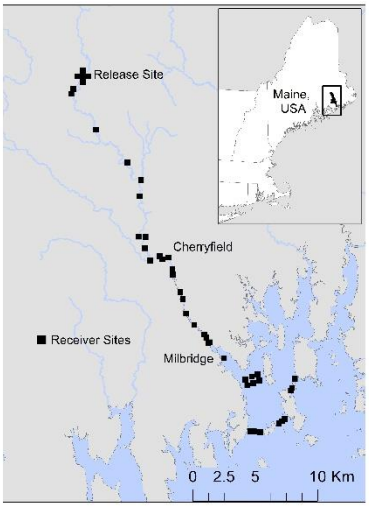

Fig. 1. Narraguagus River telemetry network with stocking location.

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We deployed 40 VEMCO receivers throughout the Narraguagus River, Estuary, and Bay (Fig. 1). We deployed VR2W receivers within the river (*n* = 13), estuary (*n* = 11) and inner bay (*n* = 6), and VR2AR (acoustic release receivers; *n* = 10) in the middle bay environment, which is the furthest seaward array within the network.

Between 26 April and 10 May 2017 (*n* = 202) and 27 April and 08 May 2018 (*n* = 150), we collected and tagged age-1 smolts from U.S. Fish and Wildlife Green Lake National Fish Hatchery in Ellsworth, Maine. Smolts were anesthetized, biometrics were collected, fish telemetry tagged (procedure described in Kocik et al. 2009) and placed into an indoor recovery pool then released the following day. There were three release dates (early, middle and late) each year which bracketed historical wild run-timing of smolts within the river. Smolts each year were stocked under different density scenarios of "low" and "high." In 2017, the "low density" tagged smolts were released at the same time and 30 km upstream of hatchery restoration smolts (33,000 per group). In 2018, the "high density" tagged smolts were released at the same time and location of restoration smolts (33,000 per group).

Duration (days; d) of smolts through the network were faster for low density smolts versus high density smolts, with duration of each group decreasing between the early and late group for both years (2017—Early = 9.5 d, Middle = 6.2 d, Late = 3.8 d; 2018—Early = 11.5 d, Middle = 9.6 d, Late = 6.2 d).

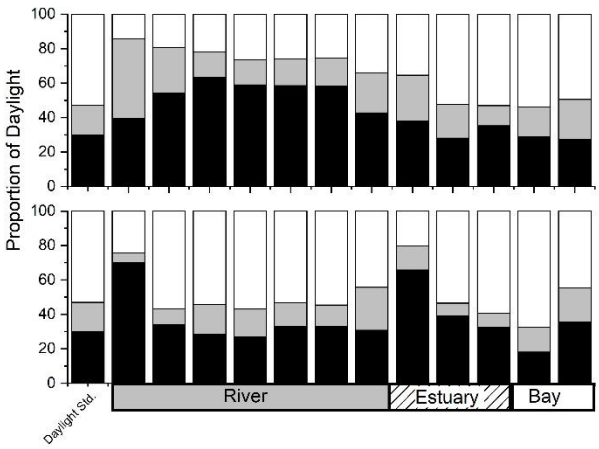

Fig. 2. Diurnal use of smolts under low (2017; top panel) and high (2018; bottom panel) density stocking. Daylight = white, Twilight (dawn/dusk) = grey, and Nighttime = black. Daylight Std. = average proportion of daylight, twilight and nighttime during the study period.

Diel movement of smolts through the telemetry network were markedly different between years. Low density smolts traveled mostly at nighttime though the river, meanwhile, high density smolts traveled during all hours of the day (Fig. 2).

Apparent survival through the river was near 100% for both years, with significant losses experienced during the transition from the river to the estuary. Cumulative apparent survival was greatest for smolts with high densities (2018: range 66–77%) versus low densities (2017: range 46–62%). Consistent patterns emerged between groups and years, with the middle group experiencing lowest and the late group highest survivals during both years (Fig. 3).

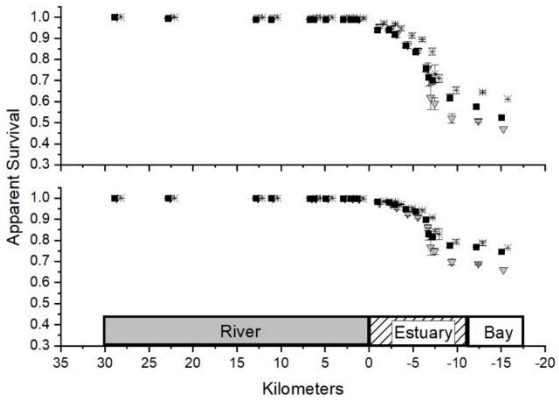

Fig. 3. Apparent survival 2017 (top panel) and 2018 (bottom panel) within river, estuary and bay environments. Black box = Early release group, grey triangle = Middle release group, and asterisk = Late release group.

Migration behavior and survival of smolts was different between years and densities. In 2017, under low densities, smolt behavior appeared similar to Kocik et al. (2009) observations of tagged wild smolts within this system, with rapid egress and movement during lowlight/nighttime conditions. Meanwhile, in 2018 under high densities, smolts were slower, but traveled during all hours of the day. Although 2018 behaviors were counter to

wild smolt movements, smolt and postsmolt survival was higher than in 2017. Both years exhibited greater apparent cumulative survival than wild tagged smolts of Kocik et al. (2009) within the Narraguagus River, and as well as, or better than other regional smolt telemetry studies (Lacroix 2008; Renkawitz et al. 2012; Hawkes et al. 2017).

Telemetry aided in evaluation of this management action and provided insight to migration success within our network. There appears to be benefit to stocking fish later in the season and in higher densities to limit losses. The use of hatchery smolts boosted the number of postsmolts making it to the Gulf of Maine, but threats beyond our network are more impactful to return rates. To this point, adult return rates from this restoration stocking are lower than the previous effort (2008–2012). To date (2018), only 26 multi-sea-winter adults have returned (USASAC 2019), which is a rate at 2.6 per 10,000 smolts stocked. Although the return rates are not final for this effort, they appear to once again be much lower than wild return rates. Understanding mechanisms influencing survival (e.g., predation) with this origin group will optimize the use of this restoration tool in order to boost returns.

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Dynamic Ocean Management for Salmon: Integrating Spatially-explicit Environmental and Fishery Datasets to Describe and Predict Fish Distributions

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Keywords: dynamic ocean management, near real-time, remote sensing, ocean distribution

Dynamic ocean management seeks to use near real-time information to allow for spatially and/or temporally flexible management measures (Maxwell et al. 2015; Hazen et al. 2018; Welch et al. 2019). Recent advances in satellite technology have facilitated such pursuits by making fully automated and quality-controlled datasets both available and readily implemented into a suite of programming environments. Thus, models that are dependent upon environmental information can be updated with as little as several hours of lag-time, allowing managers or enforcement officials to respond in near real-time.

Dynamic models in general can address a suite of different management goals but several unifying principles - data acquisition, prediction, dissemination, and automation—guide their development whether they are designed to inform hurricane evacuations, bycatch avoidance, or fish species targeting (Welch et al. 2019). For the purposes of understanding salmon distributions in the high seas, the data acquisition step would be required from two sources. First, acquisition of historical fishing data with locations and dates of non-zero catches and zero catches are necessary to train models. Second, environmental data must be matched to the fishing data; these data can originate either from data collected at the time of fishing or data extracted from satellite data based on dates and locations. Predictions can be trained using the historic catch information and developed via a variety of statistical approaches like gradient boosting, random forests, or other (often machine learning) techniques (e.g., Scales et al. 2017; Hazen et al. 2018; Cimino et al. 2019). Dissemination dictates that in order for dynamic management to be useful, there must be a developed platform such that data predictions can be communicated effectively to the managers, enforcement officials, or other users for whom the approaches were developed. Finally, each of these steps must be updated regularly so that users can respond in near real-time. In the case of high seas salmon fishing, for example, environmental data would need to be updated daily so that enforcement officials could evaluate a need for enforcement action based on updated predictions on movement of fish populations.

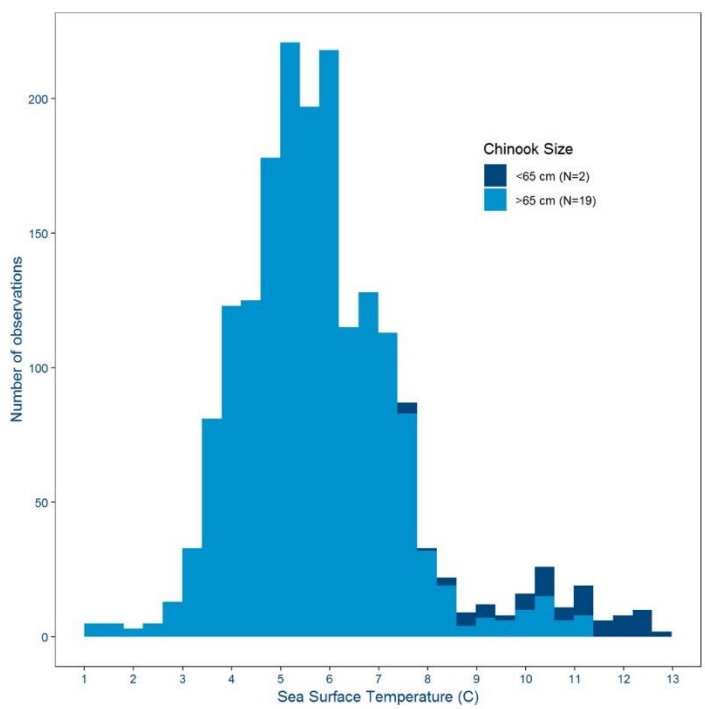

Fig. 1. Distribution of satellite-derived sea surface temperatures for Chinook tag locations. Distributions of data from Chinook with fork length < 65 cm (N = 2) and Chinook with fork length > 65 cm (N = 19) are shaded in darker and lighter colors, respectively.

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Our efforts at dynamic ocean management are still in their nascent stages but we have developed two pilot projects that provide proof of concept for each of the four steps described above (acquisition, prediction, dissemination, and automation). The first has explored the acquisition of satellite information on sea surface temperature (SST) for a time series, aggregated into statistical management areas (Watson 2019). These data have been subsequently integrated into a management database at the Alaska Fisheries Science Center that is accessible to a suite of researchers and managers. Furthermore, an additional acquisition algorithm runs each day, updating the data in the database, and thus providing a data acquisition that is automated and disseminated to users daily.

The second pilot project involves acquisition of data on fish distributions and the development of environmentally-explicit predictions. For the initial study, data on the locations of Chinook salmon were provided from satellite tag data (Seitz et al. 2019). Environmental data (SST) for each of the tag records were obtained from a NOAA ERDDAP server (Watson 2019), which yielded distributions for each environmental covariate (Fig. 1). In this case, models were demonstrated with only a single environmental covariate, but future work will include a suite of potential other covariates (e.g., Hazen et al. 2018; Cimino et al. 2019; Watson et al. 2018). This example only utilized a single environmental covariate, SST, so the model for the predictive step was a simple univariate generalized additive model. However, in future efforts, we will explore more adaptive recursive portioning and machine learning approaches. Once the predictive model was trained with Chinook data, we acquired SST data from across the North Pacific Ocean (using the ERDDAP server as described above) (Fig. 2), and we applied these data to the model to predict where expected Chinook abundance was highest (Fig. 3). In the figure, the black lines represent the exclusive economic zone boundaries for each country, facilitating a simple illustration of which high seas areas may be mostly likely to contain salmon for the date of prediction.

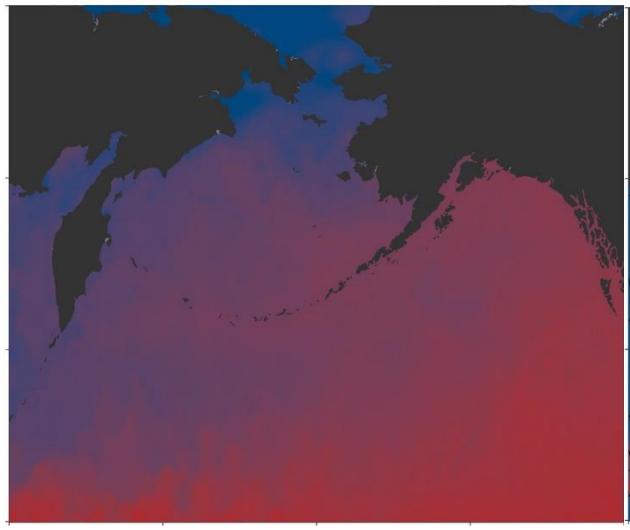

Fig. 2. Example of sea surface temperatures across the North Pacific Ocean acquired from satellite data for 5 May 2019. Redder colors represent warmer temperatures.

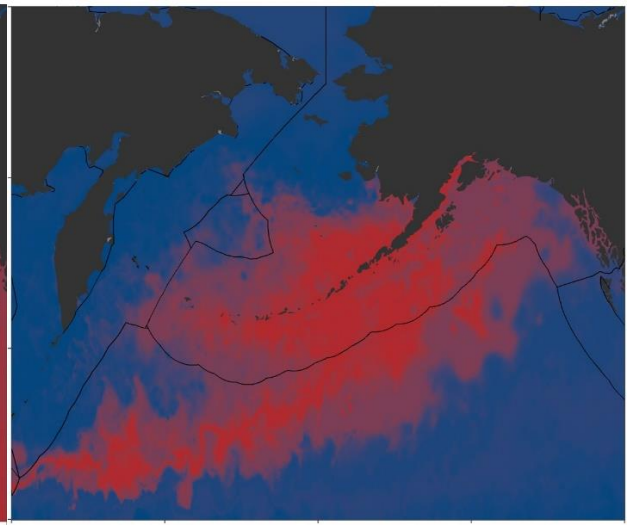

Fig. 3. Example of predicted Chinook salmon distribution using sea surface temperatures from 5 May 2019. Redder colors represent a greater likelihood of salmon occurrence. Black lines overlain are the exclusive economic zone boundaries.

While the work presented here represents only nascent steps towards predicting salmon distributions in the ocean, we illustrate a framework and proof of concept for future operationalization and development of a dynamic ocean management tool. Next steps for this work include compilation of historic salmon catches and fishing efforts that are necessary to train models on the distribution of multiple species of interest. Furthermore, in order for these models to be maximally effective for combating illegal, unreported, and unregulated fishing in the high seas, the dissemination and automation steps will need to integrate fishing vessel location data and must be portable to enforcement infrastructure.

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The International Salmon Data Laboratory (ISDL)

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Keywords: Pacific salmon, salmon, data processing, International Year of the Salmon, analysis, database

Given that salmon ecologists wish to improve the resilience of salmon to unmitigated anthropic climate change, a paradigm shift is required: *from* monitoring, passive conservation, optimal harvesting, and enhancement (spawning channels and hatcheries) *to* predicting how salmon will respond to habitat and ecosystem changes that exceed the range of historical observations. To be useful, that new prediction ability must be translated into effective actions. The mobilization of this knowledge will lead to salmon fisheries and habitat managers being better informed and able to react quickly to unexpected events. The International Year of the Salmon (IYS) has presented this as a challenge to the world. The International Salmon Data Laboratory (ISDL) is a response to that challenge.

The first ISDL workshop was held in Vancouver, Canada, on 25 January 2019 (NPAFC 2019b) with the following general objective: After salmon ecologists say *what* they need in terms of data processing, ISDL describes *how* that can be delivered with modern technology (Fig. 1). The following summarizes the ISDL workshop's progress toward this objective.

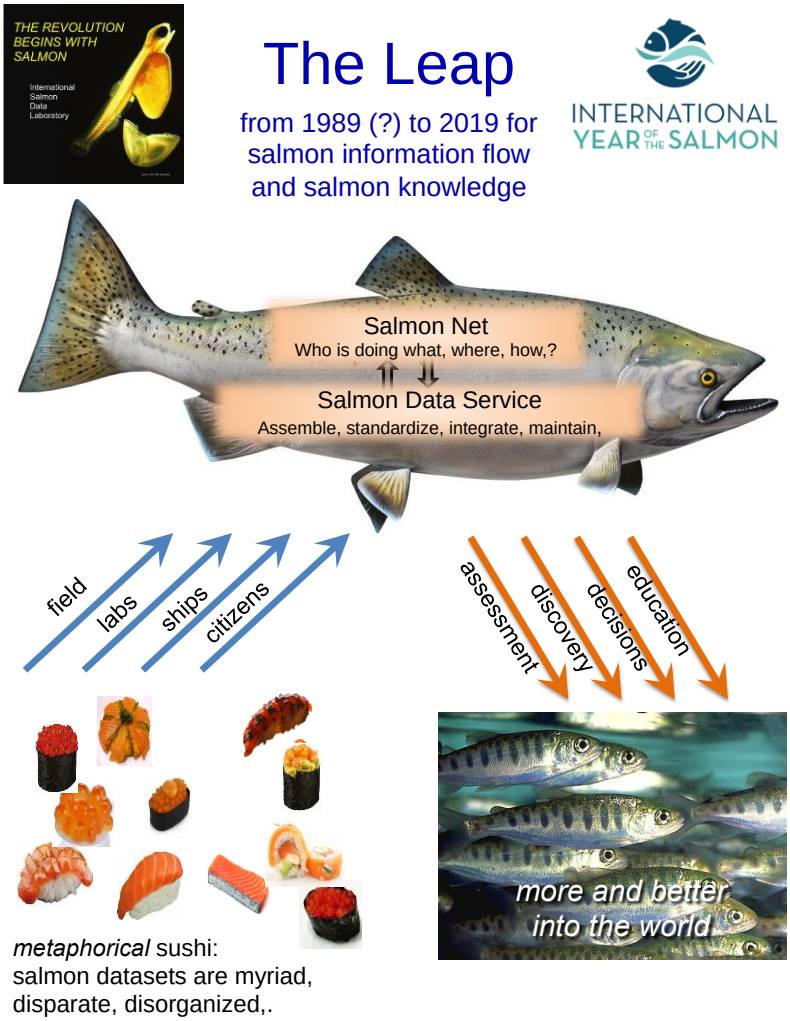

Fig. 1. A poster presented the assembly, standardization, and integration of many salmon datasets—a prerequisite to efficient, broader, and deeper analyses—as the metaphorical re-assembly of a salmon from many kinds of salmon sushi (diverse datasets) and the subsequent production of a new generation of salmon (analyses, data products).

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Prediction ability requires mechanistic models as opposed to correlations. Developing and applying those models requires that we:

(a) ***Shift to a new perspective*** on what drives salmon population dynamics. This involves comparing the success and failure of many salmon populations across multiple species each with several life-history strategies, across the northern hemisphere, in many situations. This was a goal of the immediately preceding IYS Salmon Status and Trends Workshop (NPAFC 2019a).

(b) ***Assemble and integrate*** an unprecedented breadth and depth of information about salmon and the habitats they encounter. The ISDL workshop examined a specific recent technology, the neo4j graph database, with associated software libraries and developers' tools, as the basis for a breakthrough in data mobilization. This capacity was explained by Jeff Morris (San Mateo, CA) noting that Neo4j Inc is supporting ISDL via their Graphs for Good program. A practical elucidation of the flexibility of schema for a graph database compared to a relational database, and a cogent demo wherein large salmon datasets were uploaded and visualized via neo4j was delivered by John Song (Los Angeles, CA).

(c) ***Modernize salmon data processing*** from field collections, to integration and analysis. Immediate mobilization of all types and formats of field data with the GeoOptix platform was described by Matt Denniston and Keith Steele (Portland, Oregon). Scott Akenhead pointed to the development of technologies that are capable of modernizing estimates of spawner abundance (resistivity counters) and estimates of age-1 smolt survival (tiny acoustic tags), just two examples of many possible. Bruce Patten (Nanaimo, BC) reviewed how Fisheries and Oceans (DFO) Pacific Region manages hundreds of data sources, many databases, and many data customers, highlighted by a SWOT analysis (strengths, weaknesses, opportunities, threats) of the migration from 1990's technology and practices to new tools, systems, and practices.

(d) ***Mobilize data*** for improved decision support. Sue Grant (Vancouver, BC) reviewed this requirement with reference to DFO's State Of Salmon (SOS) program and to DFO's support for the Pacific Salmon Explorer that provides interactive data visualization (sponsored by Pacific Salmon Foundation and DFO).

(e) ***Transfer knowledge*** from scientists to policy makers and to salmon fisheries and habitat managers. In an illuminating moment, Kelly Chapman (Powell River, BC) changed the thinking of everyone at the workshop by describing how this requires extensive personal engagement, in sharp contrast to the implicit assumption that "products" were sufficient in all preceding presentations.

Several ecologists offered to carry the ISDL ideas to international workshops in May and September of this year—an encouraging result that emphasized the potential value of the ISDL initiative. The suggestions for projects from this workshop and from preceding IYS workshops were combined as a strategic plan for ISDL: goals, quantifiable objectives, projects, experiments. A suite of ideas for "experiments" for this "data laboratory" were discussed while noting that ISDL plans require resourcing:

- The ecologists asked for immediate action to standardize (via glossary of parts and methods) and integrate the datasets that will be tabled via IYS Salmon Status and Trends.
- Experiments with GeoOptix (GeoOptix.com) for data capture directly to cloud servers, circumventing many existing problems (completeness, quality control, timeliness, and multiple formats).
- Demonstrations that the neo4j technologies will deliver the required breakthrough in data integration.
- Automation of data updates, for the maintenance of a database assembled from many (changing) sources, via StreamSets (streamsets.com); a necessary efficiency.
- Experiments with analysis workflows via WorkSpace (https://research.csiro.au/workspace/) to deliver results from the integrated database. Reducing the repetitive data assembly, standardization, and integration that precedes every analysis would be a welcomed benefit.

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