North Pacific Anadromous Fish Commission



TECHNICAL REPORT 18

Virtual Conference on *Winter Ecology of Pacific Salmon and Results from the Two Gulf of Alaska Expeditions*

Technical Editor: Lana Fitzpatrick

Vancouver, Canada, 2022

Virtual Conference—*Winter Ecology of Pacific Salmon and Results from the Two Gulf of Alaska Expeditions*

April 20–22, 2021 (Canada and USA) April 21–23, 2021 (Japan, Korea, and Russia)



NPAFC Secretariat

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Preface

Participants from the two Gulf of Alaska expeditions in the winters of 2019 and 2020 and scientists from Canada, Japan, Korea, Russia, the United States held a 3-day virtual conference from April 20–22, 2021 (PST), sponsored by BC's Northern Development Initiative Trust and the Pacific Salmon Foundation (PSF), to finalize the interpretations of the results from the two expeditions. The results from the conference have significantly contributed to the planning of the 2022 Pan-Pacific Winter high Seas Expedition, in particular, by all the panel members (Mark Saunders, IYS Director; Brian Riddell, PSF; Dick Beamish, DFO; Evgeny Pakhomov, UBC; Laurie Weitkamp, NOAA; Jackie King, DFO; Vladimir Radchenko, NPAFC; and Aleksey Somov, TINRO).

We also thank all presenters and participants for their time and valuable contributions to the conference and for submitting materials for this volume. The virtual conference was facilitated by Oh Boy Productions (Vancouver, BC) and coordinated by Derek Hader and Stu McNish. The recorded conference can be watched here (https://www.ohboy.ca/salmonconf2021).

Technical Report No. 18 is a compilation of 21 extended abstracts submitted by the conference presenters and the closing comments by Brian Riddell, Dick Beamish, and Vladimir Radchenko. Material in this report has not been peer-reviewed and does not necessarily reflect the view of NPAFC member countries, or authors agencies. We thank Lana Fitzpatrick (DFO) for editing the extended abstracts, which have been edited for clarity and publication purposes.

Jeongseok Park Deputy Director, NPAFC

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Introduction

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Keywords: Winter ecology, Pacific salmon, international research teams

Papers in this Technical Report summarize the results of the 2019 and 2020 expeditions to study the winter ecology of Pacific salmon in the Gulf of Alaska. Virtual presentations were made in an international conference from April 20 – 22, 2021 and are available at sites listed in Table 1. The preliminary results of the expeditions are summarized in cruise reports by Pakhomov et al. (2019) and Somov et al. (2020). The two expeditions were privately funded and organized by Drs. Richard Beamish and Brian Riddell with the help of the North Pacific Anadromous Fish Commission and the Pacific Salmon Foundation. Donors to these expeditions are too numerous to list, but range from individual contributions, to the fishing industry, to large companies and governments. Researchers in both expeditions volunteered to participate and agreed that all data collected would be generally available to the public. Participants and affiliations are listed in Table 2. The Russian Government agreed to charter their famous research ship, R/V *Professor Kaganovskiy*, in 2019 and the Canadian commercial fishing vessel, R/V *Pacific Legacy* was charted in 2020 from March 11 – April 7.

Site	Details	Web link
Site 1	Day 1	https://www.youtube.com/watch?v=66QahevVf5o
	Day 2	https://www.youtube.com/watch?v=ht3UXtXz3m0
	Day 3	https://www.youtube.com/watch?v=T68T2PPI8bM
Site 2	Oh boy productions	http://www.ohboy.ca/salmonconf2021

 Table 1. List of links to video presentations of virtual conference, April 20-22, 2021.

Both expeditions were part of the International Year of the Salmon. The concept was first proposed in a report by the North Pacific Anadromous Fish Commission in 2009 that summarized existing monitoring and research programs in all Pacific salmon producing countries (Beamish et al. 2009). The original intent of an International Year of the Salmon was to encourage greater international integration of research and monitoring efforts. A formal proposal was made to the Commission in 2016 (IYS 2016). The proposal was adopted by the North Pacific Anadromous Fish Commission in 2016 and an integrated research effort implemented in the winter of 2022 with a four-vessel, three-country (Russia, United States, and Canada) Pan-Pacific survey.

The studies of the winter ecology of Pacific salmon in 2019 and 2020 focused on understanding the mechanisms that regulate the abundance of Pacific salmon during the ocean phase of their life history. The study was in the Gulf of Alaska as most Pacific salmon from British Columbia rear in or near the Gulf of Alaska along with salmon from Japan, Russia and United States. There are estimates that up to about one third of all Pacific salmon may be in the Gulf of Alaska in the winter. The effort was in the winter to study the possibility that brood year strength of Pacific salmon was mostly determined by the end of the first ocean winter, based on evidence that adult abundance was related to growth and survival in the first months in the ocean (Karpenko 1998; Wertheimer and Thrower 2007; Pyper et al. 2005; Graham et al. 2020; Duffy and Beauchamp 2011; Beamish and Mahnken 2001; Beamish and Neville 2021). Because most salmon left the coastal areas by late fall and moved into the Gulf of Alaska, winter surveys would sample an aggregate of populations to provide indices of growth, condition, abundance and fish health that could be used to assess factors affecting survival in the early marine period. In addition to the information related to ocean survival, it was possible that estimates of abundance would be useful as an index of future adult returns. Trawl catches and a standardized survey design can be an effective method of sampling a population and estimating abundance. Estimates of abundance using trawl surveys are a standard and mostly reliable method of forecasting salmon returns in Russia (Shuntov and Bocharov 2003; Volvenko 1999, 2000).

Name	Country	Affiliation			
Tristan Blaine	Canada	Central Coast Indigenous Resource Alliance, Campbell River,			
Tristan Diame	Canada	British Columbia			
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Gerard Foley Jr.	United States	NOAA Alaska Fisheries Science Center, Auke Bay Laboratories, Juneau, Alaska			
Tessa J. Frost	United States	Southern Southeast Regional Aquaculture Association, Ketchikan, Alaska			
Sabrina Garcia	United States	Alaska Department of Fish & Game, Anchorage, Alaska			
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Laurie Weitkamp	United States	NOAA Northwest Fisheries Science Center, Newport, Oregon			
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Table 2. List of participants in the 2019 and 2020 Gulf of Alaska Expeditions.

An important objective of both expeditions was to work together as international teams. The international community that studies Pacific salmon generally know each other and cooperate effectively. However, there are very few internationally integrated Pacific salmon research studies. Even integrated projects between Canada and the United States are rare. We hoped that our example of researchers from all Pacific salmon producing countries on both expeditions would be a message to governments that better integration of research would provide needed understanding of the future of Pacific salmon faster and cheaper.

The abundance estimates of all Pacific salmon in the survey area in 2019 and 2020 were made using the methods of Russian scientists (Volvenko 1999, 2000). The estimates of 54.95 million fish in 2019 and 51.3 million in 2020 were similar but much lower than expected. However, commercial salmon catches in British Columbia in 2019 and 2020 were at historic lows and catches in Southeast Alaska were at low levels in 2019 and 2020. Chum salmon returns to Japan also continued their decline in 2019 and 2020. In addition, there was a basin-scale collapse of all Pacific salmon commercial catches in 2020 with the total catch by all countries declining to levels of the early 1980s. Thus it was possible the unexpected low abundance in our survey catches was a consequence of extremely low abundances in the Gulf of Alaska in the winters of 2019 and 2020. At the same time, there was an unprecedented marine heat wave in the Gulf of Alaska from 2014 to the end of 2019 (Bond et al. 2015; DiLorenzo and Mantua 2016; Cornwall 2019; Suryan et al. 2021). It is unclear if the unique appearance of the marine heat wave was responsible for the low abundances of salmon, but it should be clear that there needs to be a much better understanding of the factors affecting the ocean survival of Pacific salmon if we are to be responsible stewards of Pacific salmon in a future of rapidly changing ocean ecosystems as occurred from 2014 to 2019.

The papers included in this report are the interpretations of the authors and are not peer reviewed. In most cases the authors expect to expand their interpretations for peer-reviewed publications after the results of the 2022 Pan-Pacific survey are available. There were 697,000 km² surveyed in 2019 and 648,000 km² in 2020 with catches of 423 and 566 salmon in 2019 and 2020, respectively. Pacific salmon were caught in 48 of 58 sets in 2019 and 29 of 52 sets in 2020. In general, the abundances were patchy with concentrations of sockeye salmon in the northwest area of the survey and pink salmon in the southeast area. There was very little overlap in the distributions of these two species with pink salmon preferring the warmer water to the southeast, and sockeye salmon preferred the cooler water to the northwest. Pink salmon were expected to be the most abundant as they are the most abundant in commercial catches. However, at the time of our surveys, it appeared that pink salmon abundances extended south of the southern limit of our survey area. The longline surveys that tagged Pacific salmon in the 1960s also found pink salmon to be farther south in the winter and then spreading north in the spring. Chum salmon were the most abundant, followed by coho salmon in both years. The abundance of coho salmon was unexpected as was the evidence that some were in large schools containing populations from Oregon to Alaska. Chum salmon were found throughout the survey area with DNA results that showed they were from Japan, Russia, United States and Canada as has been previously shown. Chum salmon age 3 and 4 from British Columbia were in low abundance relative to these ages of chum salmon from other areas. The low abundance of these ages may be related to the poor adult returns of chum salmon to British Columbia rivers in 2019, 2020 and 2021. Chum salmon also varied in body condition which may be related to growth and condition needed to survive the first ocean winter. There was little evidence of predator attacks on salmon and a general absence of potential salmon predators which appeared to be confirmed by the eDNA results. The collective results in this report provide a few small pieces of a bigger picture of Pacific salmon ocean survival that will be clearer as we continue these integrated international studies of the ocean ecology of Pacific salmon.

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Winter Ecology of British Columbia Chum Salmon in the Gulf of Alaska

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Keywords: Chum salmon, winter ecology, Gulf of Alaska

Abstract

There were relatively low abundances of ocean age 2, 3 and 4 chum salmon from British Columbia in the catches in the 2019 and 2020 Gulf of Alaska expeditions that possibly were an index of the poor adult returns in 2019 and 2020. Catches of all chum salmon in the 2020 survey were made in 25% of the sets compared to 64% of the sets in 2019 which was another possible indication of low abundance of older chum salmon in the basin-scale fishery collapse in 2020. There was one large catch of 165 chum salmon in 2020 which appeared to be evidence that chum salmon from British Columbia can form a large aggregation or school that also contained chum salmon from Japan, Russia and the United States. If winter expeditions are continued, it may be found that the age composition and abundance of British Columbia chum salmon in the Gulf of Alaska is an index of returning adult abundance well in advance of potential fisheries

Introduction

Chum salmon (*Oncorhynchus keta*) catches in British Columbia commercial fisheries in the past 20 years (1999-2018) were 32% of the total weight of the catches of all Pacific salmon and slightly larger than catches of other comparable pink and sockeye salmon catches. However, as shown in Riddell et al. (2022), abundances have declined in recent years, resulting in historic low catches in 2019 and 2020. Very little is known about the ocean ecology of British Columbia chum salmon after they leave the coast despite spending most of their life in the ocean. Chum salmon are the first of the Pacific salmon to enter the ocean after emerging from the gravel and can spend up to 6 years in the ocean, with most in British Columbia spending 2 to 4 years in the Gulf of Alaska (Urawa et al. 2018). There is little doubt that the recent declining abundance of adult chum salmon was caused by conditions during their ocean residence because of the geographic breadth of the decline.

The 2019 and 2020 expeditions to study the ocean ecology of Pacific salmon in the winter in the Gulf of Alaska provided new information about the winter ecology of British Columbia chum salmon. We report this information and discuss the possibility that future surveys that identify the age composition and abundance of British Columbia chum salmon in the Gulf of Alaska in the winter could provide an index of adult abundance up to three years in advance of the return to natal rivers.

Expedition methods, set locations and results are summarized in the reports by Pakhomov et al. (2019) and Somov et al. (2020). A summary is also included in this technical report by Radchenko (2022). Urawa et al. (2021, 2022) summarized the results for stock-specific winter distribution and body condition of chum salmon from the 2019 expedition and compared these with previous winter surveys in the Gulf of Alaska (Urawa et al. 1997, 2009, 2016, 2018; Beacham et al. 2009).

2019 Expedition

The 2019 expedition onboard the Russian research vessel *Professor Kaganovskiy* caught 223 chum salmon that was the largest catch of all Pacific salmon in the survey. Most were caught in the southwest of the survey area, with smaller catches in the northwest and catches in 37 of the 58 sets (Figs. 1, 2). Country of origin was determined from 218 fish using DNA with the following results (Table 1): Japan 22.0%, Russia 20.2%, Alaska including the Yukon River 37.6%, British Columbia 16.1% and southern United States (mostly Washington State) 4.1%. Lengths ranged from 240 mm to 600 mm (Fig. 3). The length distribution for ocean age 1 fish was distinct for all chum salmon, including those from British Columbia. If all fish up to 330 mm were ocean age 1, there were 17% ocean age 1 fish and 83% were older. Chum salmon caught in the trawl lost most of their scales, requiring that scales used for age determination were collected opportunistically and were not optimal for accurate age determination. Consequently, ages estimated for fish < 330 mm in 2019 may be approximate. In 2019, there were 218 fish that were assigned ocean ages using scales with the following percentages: age 1- 15.6%, age 2 – 25.7%, age 3 - 44.5%,

age 4 - 13.8 % and age 5 - 0.5%. The percentage of the fish that were ocean age 1 identified from scales of 15.6% was similar to the 17% determined from the length distribution. There were 36 of the 218 fish or 16.5% from British Columbia with the following estimated ages: age 1 - 44%, age 2 - 25%, age 3 - 6% and age 4 - 3%. The percentages of ages determined only from scales for the British Columbia fish were: age 1 - 41.7%, age 2 - 38.9%, age 3 - 16.7% and age 4 - 2.8%. There was 7.8 times more chum salmon of ocean ages 2 - 5 from the combined catches from Japan, Russia and United States than from British Columbia, possibly indicating a relatively low abundance of chum salmon from British Columbia. Also, within this low abundance there were relatively few ocean age 3 fish that commonly represent much of the commercial catch in British Columbia after a period of substantial growth before returning as mature adults in the fall. Ocean age 3 fish were also identified as age 4 chum salmon, which represents their total age. More surveys are needed to interpret these results, but the low abundance relative to chum salmon from other countries and the very low return of chum salmon to British Columbia in fall 2019 could indicate that winter abundance surveys could provide an index of return abundance well in advance of potential fisheries.



Fig. 1. Survey area and set locations for 2019 (left panel) and 2020 (right panel) Gulf of Alaska expeditions. Northwest (NW), northeast (NE), southwest (SW) and southeast (SE) quadrants of survey area are indicated with the number of sets conducted in each sector.



Fig. 2. Set locations for 2019 (left panel) and 2020 (right panel) Gulf of Alaska expeditions, showing chum catches.

Year	Country of origin	Number of fish	Percent of total	Set 3 Total catch	Set 3 Ocean age 1 catch
2019	Japan	48	22.0		
	Russia	44	20.2		
	Alaska	82	37.6		
	British Columbia	35	16.1		
	Southern United States	9	4.1		
2020	Japan	22	9.9	4	0
	Russia	9	4.0	4	0
	Alaska	38	17.0	27	18
	Southern United States	22	9.9	21	12
	British Columbia	132	59.2	102	93

 Table 1. DNA results for chum salmon from the 2019 and 2020 Gulf of Alaska expeditions. Also listed are DNA results for chum salmon from set 3 in 2020 including the total catch in this set and the catch of ocean age 1 fish...



Fig. 3. Length frequency distribution for chum salmon caught in the 2019 and 2020 Gulf of Alaska expeditions, showing ocean age 1 fish. Solid bars in the 2020 panel represent fish caught in Set 3.

2020 Expedition

In 2020, the Canadian commercial trawler *Pacific Legacy* was chartered for the period March 11 to April 7 which was about one month later than the survey in 2019. The area surveyed was similar in the south but the northern areas were not fished (Fig. 1). The range in lengths for the total catch was similar to 2019, ranging from 250 mm to 700 mm. There were 234 chum salmon caught (similar to 2019) and chum salmon catches were again the largest of all Pacific salmon catches. However, the distribution and pattern of catches differed from 2019. Chum salmon were caught in only 13 of the 52 sets and 217 (92.7%) were caught in three areas with two sets in one of the three areas (Fig. 2). There were 165 fish in Set 3 dominating the total catch (70.5% of total catch) and 10 more caught in Set 4 in the same area. There were 223 fish that were identified to their country of origin using DNA as follows (Table 1): Japan – 9.9%, Russia – 4.0%, Alaska – 17.0%, British Columbia 59.2% and southern United

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States 9.9%. The length distribution for ocean age 1 chum was distinct with lengths ranging up to 370 mm (Fig. 4). For ocean age 1 fish, there were 150 fish in this length range of 370 mm or less that would be ocean age 1 (Fig. 4). DNA analysis was usable for 142 of these fish. There was 1 fish from Japan, 0 fish from Russia, 35 fish from United States and 106 fish from British Columbia. Because we used lengths to estimate ocean age 1, it is possible that the one ocean age 1 fish from Japan was actually age 2. If this is correct, then there were no ocean age 1 chum salmon from Japan or Russia, as reported by Urawa et al. (2021, 2022). Estimates of age using scales were made by several individuals for 154 fish. However, there was considerable variability among the estimates. Thus, age-specific size distributions for these older age groups were not considered to be reliable. The total catch of fish older than age 1 that were identified by DNA was 81 which compares to approximately 185 ocean age 2 and older chum salmon in 2019 (Table 1).



Fig. 4. Length frequency distribution for chum salmon caught in the 2019 and 2020 Gulf of Alaska expeditions, showing fish of British Columbia (BC) origin.

The relevance of the catches in Set 3 in 2020

In Set 3, there were 123 ocean age 1 fish (370 mm or smaller) and 93 were from British Columbia (Table 1). The remaining 30 ocean age 1 fish in Set 3 were from Alaska and the southern United States (Table 1). Chum salmon older than ocean age 1 were also found in Set 3 as follows: Japan = 4, Russia = 4, United States = 16 and British Columbia = 11. Thus, there were chum salmon from all countries and a range of ocean ages as indicated by lengths. The large catch of 165 chum salmon in Set 3 indicated an abundance of chum salmon in the general area around the set location. There was a smaller catch of 10 chum salmon in Set 4 which was close to Set 3. The same area and surrounding areas were fished extensively two to three weeks later with only one catch of 3 chum salmon. Clearly the abundance of chum salmon. There were only two other sets with larger catches of 20 (Set 19; $\approx 50^{\circ}$ N, 147° W) and 22 (Set 25; near Dixon Entrance). The generally low catches or no catches in most other areas is additional evidence that some chum salmon in 2020 were aggregated in school-like abundances and not more evenly dispersed throughout the survey area as occurred in 2019. Catches in Set 3 and possibly Sets 19 and 25 were the first evidence that some chum salmon may aggregate in large schools in the Gulf of Alaska in the winter.

Relevance of the survey results to the chum salmon fisheries of British Columbia

The catch numbers were small and these are only our first interpretations, but there was a collapse of the commercial chum fishery in all countries in 2020 and the small catch of older chum salmon in 2020 relative to 2019 may have been indicative of the poor return of mature chum salmon to British Columbia later in 2020. The abundance of ocean age 1 British Columbia chum salmon in 2019 and 2020 may be a clue to mechanisms that are regulating adult chum salmon abundance.

There is accumulating evidence that the adult abundance is related to growth in the first months in the coastal ocean (Beamish and Neville 2021; Farley et al. 2020; Graham et al. 2019; Duffy and Beauchamp 2011). Accordingly, the larger abundances of ocean age 1 chum salmon from British Columbia in 2019 and especially in 2020 might indicate improved survival resulting from improved growth in the early marine period. However the abundance of ocean age 1 fish in 2019 was not detected as ocean age 2 fish in the catches in 2020. In fact there may have been relatively few ocean age 2 fish in 2020 as indicated by the length frequencies, but catch comparisons with 2019 were not directly comparable as previously reported.

Urawa et al. (2021) reported the frequent occurrence of skinny chum salmon during the 2019 expedition. Chum salmon showed skinny condition (Condition Factor < 0.9) in 15% of the sample, most of which were ocean age 2 or 3 fish. Especially ocean age 2 fish had apparently lower condition factor than other age groups. In ocean age 2 chum salmon, the occurrence of skinny fish was 70-75% in British Columbia populations, and 30-50% in other populations. In ocean age 3 chum salmon, the occurrence of skinny fish was 60% in northern and central British Columbia populations, and around 20% in Russian and Japanese populations. High occurrence of skinny chum salmon in winter might be a cause of poor adult returns in British Columbia populations.

Thus, in addition to a critical period for survival in the early marine period, there may also be ocean conditions after the first ocean winter that continue to affect ocean survival. There is ample documentation of the occurrence and consequences of the 2014-2016 marine heat wave that affected the Gulf of Alaska (Bond et al. 2015; DiLorenzo and Mantua 2018). The warming of 2014-2016 returned in late 2018 and continued through to 2019 (Cornwall 2019). It is certainly possible that associated ecological effects impacted the survival of British Columbia chum salmon in the Gulf of Alaska after their first ocean winter. Until more is known, our comments in this report are speculative. Resolving this speculation is important as a better understanding of the mechanisms affecting ocean survival helps focus stewardship on the aspects of the life history of British Columbia chum salmon that must be accounted for and managed to conserve chum salmon and sustain fishing in a changing ocean ecosystem. It is also possible that with continued winter expeditions, it may be found that the abundance and age composition of catches of British Columbia chum salmon are an index of return abundance well in advance of potential fisheries.

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Winter Ecology of Pacific Salmon

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Winter is a highly important time in Pacific salmon (*Oncorhynchus* spp.) marine life, first, due to its duration. If we consider winter to be the four months from December to March in the latitude range of Pacific salmon ocean migration, it makes up from one-third to one half of the ocean residence time for pink *O. gorbuscha* and coho *O. kisutch* salmon originated from the marginal seas' basins. Some researchers consider winter as a critical period for Pacific salmon, likely due to a general feeling of inconvenience and danger associated with the stormy ocean environment, low water temperatures, significant decreases in forage fish and zooplankton biomasses in the upper pelagic layer that imply limited food availability. Physiological studies revealed salmon growth slowing and lowering of muscle lipid content (Naydenko et al. 2016).

The ocean distribution of salmon is complex and variable, depending on spatio-temporal scale and synergies among heredity, environment, population dynamics, and phenotypic plasticity (Myers et al. 2016). Recently, new information was collected in scarcely studied regions and seasons, and summary reviews were published on the marine life phase of Pacific salmon (Shuntov and Temnykh 2008, 2011; Beamish 2018; Pakhomov et al. 2019; Somov et al. 2020). Nevertheless, considering salmon wintering in high seas, scientists remain puzzled and often say contradictory things (as shown by Shuntov et al. 2017). In this review, species-specific distinctions in salmon ecology are highlighted that determine differences in species distributions, migrations, feeding habits, and trophic relationships and should be taken into account during planning of further salmon studies in the winter ocean.

Oceanward salmon migrations differ from return salmon migrations to spawning regions. Returning salmon use the Earth's magnetic field (Putman 2015) and the hydrochemical properties of river runoff water (Quinn 1985) for navigation to arrive exactly at the mouth of native spawning river. In the case of oceanward migrations, there is no "exact arrival point". Wintering salmon arrive in a relatively large area, characterized by favorable environmental and food conditions. If such conditions are encountered along the way, salmon might stay there until conditions deteriorate.

Pink salmon stocks are mostly originated from Russian and U.S. rivers, and most of them migrate to the ocean from the Sea of Okhotsk, the Bering Sea, and central and southeastern Alaska waters. We can delineate three large domains of pink salmon wintering likely associated with the Sakhalin Island stocks, Kamchatka Peninsula stocks, and North American stocks. In general, the pink salmon area in winter stretches from southwest to northeast. There are also pink salmon stocks overwintering in the Sea of Japan (Shuntov and Temnykh 2011).

Radchenko et al. (2018) reporting on pink salmon overwintering in the Sea of Okhotsk in 1990 serves as a good illustration of a salmon temporary residence in area, characterized by favorable environmental and food conditions. The southeastern Sea of Okhotsk under the impact of inflowing Pacific waters is distinguished by a water structure with well-expressed thermocline. In January–early February, the density of pink salmon aggregations there allowed observing their location by hydroacoustic devices. In most cases, they were found at the 80–120-meter depth. Likely, pink salmon increase a vertical range of its distribution and decrease a rate of horizontal movement in winter. It looks to be a general rule for salmon – a deeper layer of residence means fewer horizontal movements.

Pink salmon wintering in the Sea of Okhotsk likely use food resources brought there and accumulated near the so-called "liquid bottom" by inflowing waters. It is mostly represented by vertically non-migratory zooplankton consuming small food particles concentrated in upper epipelagic layer (Giering et al. 2020). Hyperiids, pteropods, appendicularians, and fish larvae were found there in pink salmon diet that became enormously diverse, while the daily food ration was twice less than in autumn. Feeding conditions allowed pink salmon to stay there until mid-March (Radchenko et al. 1997).

In the western North Pacific, pink salmon aggregate along the Subarctic Current fronts. The southern boundary position of pink salmon range in winter depends on oceanological conditions of the year. Pink salmon are more abundant there under "compressed" status of the Western Subarctic Gyre than "stretched" one since the first provides with a wider area between southern and northern Subarctic fronts (Figurkin and Naydenko 2013). There is a hypothesis that the position of the southern boundary of distribution also depends on pink salmon abundance (Ishida et al. 1999), but this is not supported by data collected in winter. In 1989 and 1991, the pink salmon run to the Asian coasts was much more powerful than in 1987 while pink salmon catches in the Subarctic Current domain

were observed southward to 38°N in 1987, compared to 40°30' - 41°N in 1989 and 1991 (Startsev and Rassadnikov 1997; Radchenko et al. 2018).

The winter survey of 2009 displayed well a relative separation of wintering areas for the southern Sea of Okhotsk stocks and Kamchatka stocks. At the same time, no finer structure of wintering aggregations that can be related to regional or seasonal subdivision of pink salmon stocks was revealed (Shuntov and Temnykh 2011). The Sea of Okhotsk stocks intermix in the deep-water area inside the sea, then migrate together through the relatively narrow southern Kurile straits, and spend the most part of winter in the same feeding areas.

Along the Subarctic Current, denser pink salmon aggregations are associated with the southern as with the northern fronts at the boundaries of the mixed water domain since zooplankton aggregations are densest at the fronts. This explains the bimodal shape of the latitudinal distribution curve (Radchenko and Rassadnikov 1997; Radchenko et al. 2018). Such a shape was also observed on the graph for pink salmon distribution in April - May 2006 (Morita et al. 2010). In the northeastern Pacific Ocean, pink salmon of numerous Alaska stocks also overwinter along the Subarctic Current fronts (Fig. 1). Since the Subarctic Current divides there into two branches, originating the Alaska Current and California Current, pink salmon likely found more favorable conditions along the southern stream with more expressed temperature gradients (Pakhomov et al. 2019). The main pink salmon aggregations are expected throughout the area where pink salmon were found in April - May 1990 (Morris et al. 1992). If this assumption is correct, a one-month trawl survey can give an estimate of pink salmon run magnitude in the main regions of the salmon fishery in North America.



Fig. 1. Distribution of pink salmon catches against the background of a map of currents in the Gulf of Alaska in the first half of March 2019, according to satellite altimetry data (courtesy of A.L. Figurkin, TINRO). AC - Alaska Current, SAC - Subarctic Current, Zn1-3 - cyclonic eddies and current meanders, Az1 - anticyclonic eddy. The approximate border of the survey area is plotted.

Chum salmon *O. keta* are the most abundant salmon in the North Pacific Ocean. Some experts placed chum salmon second (e.g., Fukuwaka et al. 2007), thereby missing the point of existence of several year classes spending mainly three-four winters at sea. Chum salmon are also the most "domesticized" salmon, considering the proportion of hatchery-originated stocks in the total species abundance. Japan led in chum salmon hatchery propagation and fishery harvest before the mid of the last decade. Then, unexpected, a decline of the chum salmon run happened, which is more frequently explained by the climate warming and deterioration of environmental conditions for salmon at the southern edge of their areas. Total chum salmon harvest in the North Pacific gradually declined since 2015.

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There are also several large domains of chum salmon winter residence in the western and central North Pacific, and the Gulf of Alaska. In the central North Pacific, chum salmon distribution looks to be more dispersed. Likely, this feeding area is of secondary importance. Chum salmon also can be found in near-bottom layers at the shelf edge in winter. Such catches were recorded as from the Bering Sea (Radchenko and Glebov 1998) and the Sea of Okhotsk, as from the eastern North Pacific. It is assumed that chum salmon can overwinter in the Sea of Japan, but its catches there in December - March are not known (Shuntov and Temnykh 2011).

The significance of the Sea of Okhotsk for juvenile chum salmon of all Asian stocks was recently shown by Shuntov and Temnykh (2008). In autumn, juvenile chum and pink salmon behave in the Sea of Okhotsk as complementary species with similar patterns of distribution and body weights. They explore food resources together and, likely, remain under impact of the same factors. At least, they demonstrate similar trends of abundance dynamics during the last twenty more years (Fig. 2). Contrary to pink salmon, almost all chum salmon left the Sea of Okhotsk area before winter with some rare occurrences in the south-eastern part of the sea only. Chum salmon juveniles start leaving Sea of Okhotsk in abundance by October. That month, their migration pathway lays through the northern Kurile straits. One month later, many juvenile chum salmon enter Pacific waters via middle Kurile straits. The remaining salmon aggregate in the southern part of the sea. They enter the oceanic realm through the southern straits in December - January.



Fig. 2. Abundance dynamics of juvenile pink and chum salmon in the Sea of Okhotsk in autumn, 1998–2020. Trends approximated by polynomial of third order are shown. After Radchenko et al. (2013) with additions for the last years.

All chum salmon age groups intermix in the North Pacific Ocean. Catches of older age groups usually occurred in the same regions as of the first marine year chum. Likely, regardless of age, chum salmon pursue the same food resources. It was revealed that the diet spectra of chum salmon of different age groups were very similar, with exception of the oldest and largest chum that likely start feeding upon micronekton more actively (Chuchukalo 2006).

Anticyclonic eddies along the major currents create the main habitat for chum salmon residence in the ocean. In the Northern Hemisphere, anticyclonic eddies accumulating weak planktonic swimmers are formed on the left side of major currents. Chains of anticyclonic eddies persist along the northern front of the Kuroshio Current, in the Gulf of Alaska, where the main currents of the Alaska Gyre form a very dynamic field of anticyclonic eddies and meanders. Chum salmon are well adapted physiologically to feeding on gelatinous zooplankton. This salmon has a bulky stomach with thin walls and an esophagus ending in a powerful sphincter that prevents food regurgitation, when a large volume is consumed. Correspondingly, chum salmon aggregations are often observed in a peripheral zone of anticyclonic eddies, where planktonic food is mechanically accumulated (Radchenko 2001).

Sockeye salmon *O. nerka* are considered as the most cold-water Pacific salmon species. However, its winter residence in areas slightly northwards of other salmon species is mostly related to a preferable water structure than to preferable temperatures, to which sockeye salmon are rather tolerant. Sockeye salmon spend the warm season mostly in the Bering Sea or adjacent Pacific waters (Radchenko and Mathisen 2004) and its migration to wintering grounds lasts not very long. In winter, most sockeye salmon aggregate in the central Pacific, where they migrate from the Bering Sea through the western Aleutian passes. Sockeye salmon dwell in areas with a typical subarctic

water structure. While the seasonal thermocline is diluted by intensive water mixing in the transitional season, a two-layer water structure is observed along the Alaska Current and the Alaskan Stream, where relatively warm Pacific waters overflow the well-mixed subsurface waters. In the western North Pacific, sockeye salmon mostly occur in the winter between 160° and 170° E, where they migrate from the western Bering Sea. According to Shuntov and Temnykh (2011), even juvenile sockeye salmon of the first marine year from the western Kamchatka coast first migrate to the Bering Sea.

Sockeye salmon catch distributions from surveys indicate that the main aggregations of Asian stocks remain mostly in eastern longitudes while American stocks are found in the western longitudes. Meanwhile, genetic analysis recently revealed examples of a longer migration of individuals from some signature sockeye salmon stocks, for example: Chilko Lake from the Fraser River watershed. The pattern of American sockeye salmon migration is well developed (Myers et al. 2007) while for Asian sockeye a widely cited circuit by KamchatNIRO authors (Lepskaya 2010; Koval et al. 2014) cannot be accepted. First, it is rare for sockeye individuals to migrate so far south in the first year of marine residence and, definitely, not southwards of 40°N (Shuntov and Temnykh 2008). Second, the sockeye salmon annual cycle of migration does not look like whirling beetle circles. Summarizing the seasonal re-distribution of juvenile sockeye salmon, an amended pattern of Asian sockeye migration is proposed to emphasize the significance of the Bering Sea for this salmon species (Fig. 3).



Fig. 3. Hypothetical pattern of Asian sockeye salmon migrations to wintering grounds. Bold arrows shaded by red show migrations of the most abundant stocks, dotted lines show secondary stocks. Red arrows show migrations in summer and autumn, brown arrows show in winter. The area of juvenile sockeye concentrations in the southwestern Bering Sea and wintering grounds are shaded by light brown.

The 2019 Gulf of Alaska survey clearly showed sockeye salmon adherence to subarctic waters with two-layer structure. Nine of ten sockeye salmon catches larger than 1 fish/hour occurred northwards of latitude 52°N, where the surface mixed layer was notably thinner - about 50 m, than the area southwards with the mixed layer depth below to 100 m (Pakhomov et al. 2019). This circumstance can impact the increase of sockeye trawl catches both due to a salmon distribution density increase throughout the area of better food conditions and due to the shrinking of the vertical distribution range. It is known that sockeye salmon are good divers, and this salmon prefers to feed near the thermocline, where vertically migrating zooplankton are accumulated due to a concentrating effect of any physical border. Such feeding behaviour can partially explain the notable prevalence of sockeye salmon night-time catches before daytime catches in our winter surveys. Biologically, sockeye salmon are more adapted to feed visually at dusk. They possess bigger eyes, adapted for visual detection of food at dusk and have many midwater zooplankton and nekton prey in their diet. In addition, sockeye salmon display a similar pattern of daily redistribution in the freshwater period in big lakes (Clark and Levy 1988).

When the food ration of chum and sockeye salmon in the Gulf of Alaska in winter are compared, diets differ significantly besides euphausids, which are preferred by most salmon species. As expected, chum salmon using plankton accumulation by water flows, mostly had a remainder of its ration based on gelatinous animals and appendicularians. Sockeye salmon fed upon fish, squid, and pteropods that were more plentiful resources in the near-boundary layer. Comparing nekton components of salmon diet from Pearcy (1992) and Pearcy et al. (1988), flatfish, and sea perch larvae and fry were mostly found in chum salmon stomachs while sockeye salmon consumed midwater micronekton species and juvenile gonatid squids. In respect to deeper dwelling fish, sockeye salmon are

exposed to attacks of interzonal pelagic predators - lancetfish *Alepisaurus ferox* and North Pacific daggertooth *Anotopterus nikparini* - much more frequently than chum salmon. In the summer of 1992, 4.3% of sockeye salmon and less than 1% of chum salmon had the typical slash-mark wounds in the Pacific waters of North Kuriles (Radchenko 1994). About 5% and in some years up to 12% of sockeye salmon migrating into the British Columbia streams carried tracks of daggertooth's attacks. A daggertooth jaw fragment was found in a sockeye salmon body (Welch et al. 1991).

Coho salmon spend up to 18 months in the ocean before returning to natal streams. Therefore, unlike other salmon species, coho do not stop growing at sea in winter. Coho from the Sea of Okhotsk stocks continue growing in the Subarctic Current zone from October to April with a daily rate from 0.43 to about 1 mm (Shuntov and Temnykh 2011). The southern border of the coho salmon range runs somewhat south of its freshwater part in Asia. While the coho salmon distribution boundary passes approximately along the 40°N, several authors indicated even more southerly limits. Likely, the border can pulsate in connection with latitudinal movements of the Subarctic front in different years. If compared with the western North Pacific, the coho salmon distribution density is a degree of magnitude higher in the Gulf of Alaska. The coho salmon migration pattern remains the most poorly studied among Pacific salmon species. Varnavskaya (2006) guessed that all coho salmon of Asian and American stocks overwinter in the southern Gulf of Alaska. However, coho salmon occurrence in the western and central North Pacific contradicts this guess. Coho salmon are common in the catch in the central North Pacific, but aggregations there in winter and early spring are rather unstable. In February - March 2009, coho salmon catches were larger than in the trawl survey in the Gulf of Alaska in 2019. In the spring of 1991, coho salmon were captured at the southern limits of that survey area only. In early February 2019, during the R/V's Professor Kaganovskiy passage to Vancouver, coho salmon were found in catches of only three out of nine trawl hauls in a small amount. It looks like quickly migrating coho salmon can be found here and there in offshore central and eastern North Pacific during winter.

At the same time, coho salmon can be found year-round throughout the North American shelf. Despite the proportion of coho abundance in the Strait of Georgia and the oceanward side of Vancouver Island changes between autumn and winter, notable numbers of coho salmon dwell in the near-coastal zone even in the most severe season. Along the western coast of Vancouver Island, coho salmon can be found in significant abundance in all winter months (Beacham et al. 2016). This is why coho salmon are always considered as the salmon species with a mostly near-coastal distribution in winter.

Spending more time near the coasts make coho salmon more susceptible to near-coastal predators. Orlov (2012) showed that, from all Pacific salmon species, Chinook *O. tshawytscha* and coho salmon were more frequently attacked by Pacific lamprey *Lampetra tridentata*. Another story is marine mammals' predation on coho salmon. Seals consumed more than half of the juvenile coho salmon abundance in the Strait of Georgia, and this consumption continued in winter months (Nelson 2020). One coho salmon individual that had a mark of seal's bite was captured offshore in the Gulf of Alaska in February 2019.

Coho salmon diet in the Gulf of Alaska in 2019 differed by a strong prevalence of pteropod *Clio pyramidata*, likely due to a deficit of micronekton in the upper pelagic layer in February - March. Coho salmon behaviour in the water column in winter can be considered from the archival tags' data. Active searching for prey and diving to 60–70 m depths are characteristic for coho salmon mainly in July and August (Fig. 4). Earlier in the season and after coho salmon start migrating inshore in autumn, they mainly swim closer to the sea surface. This shallow residence explains why coho salmon catches in winter cruises were so significant compared to other salmon species. Likely, coho salmon horizontal movements are highly intensive and require dwelling in the upper water layer that is well saturated by oxygen.

Chinook salmon are a relatively rare salmon in the trawl catches in upper pelagic layer. Juvenile and immature Chinook salmon keep themselves dispersed and were mostly captured by trawl in single numbers later in winter and spring. Few Chinook salmon were captured in the Gulf of Alaska in February - March 2019, in April - May of 1990, and in February of 2006 until R/V *Pacific Legacy* captured almost 30 fish at the southwestern coast of the Vancouver Island in April 2020. In the western North Pacific, juveniles of the first ocean winter predominate in catches in autumn and early winter. In October, they start migrating from the shelf water domain to deep-water areas with a general south-eastern direction. Near the eastern Kamchatka Peninsula coast, the peak of Chinook salmon outmigrant abundance is reached in November while most of them migrate further to the Subarctic Current area in December and January.

In the eastern North Pacific, Chinook salmon occurred in catches along the outer shelf from Alaska to the Washington State. Beyond the pelagic realm, Chinook salmon can overwinter in the near-bottom water layer. In the Bering Sea, many Chinook salmon were captured during the bottom trawl surveys as well as being bycatch during commercial fisheries for walleye pollock *Theragra chalcogramma* and other groundfish. Based on TINRO data

from 1974–1991, Chinook salmon were found throughout the whole outer shelf and upper continental slope from the Olyutorsky Bay to the Bristol Canyon (Radchenko and Glebov 1998). Chinook bycatch in the walleye pollock fishery is an important fisheries management problem. Despite all measures undertaken, including fishery restriction in areas of the most frequent salmon occurrence, Chinook salmon bycatch still exceeds 15,000 fish per year including salmon from every major North American stocks (NPMFC data, https://www.npfmc.org/bsai-salmon-bycatch/).



Fig. 4. Coho salmon behaviour in water column described by the data storage tags (NPAFC DST data files transferred from the High Seas Salmon Research Program of the University of Washington, U.S.A.).

Based on diet studies, the Chinook salmon near-bottom distribution can be related with its major prey distribution. In summer, Chinook salmon of the first and second marine years mostly consume juvenile squid dwelling in the upper pelagic layer while older salmon hunt for larger squid, keeping themselves in the near-bottom realm. Chinook salmon measurements in the Bering Sea showed that pelagic trawl catches mostly consisted of younger salmon while the bottom trawl catches were for older and larger fish (Radchenko and Glebov 1998). This is also evident in an example of Chinook salmon behaviour with the Data Storage Tag. In its second winter, this fish started diving deeper and spending more time in at depth (Myers et al. 2016). In the Strait of Georgia, overwintering Chinook salmon mostly prey for forage fish and present an important prey for residential orca whale populations (Riddell et al. 2018).

Cherry salmon *O. masou* is distinguished from all other *Oncorhynchus* species since it never became a true oceanic form in the strict sense of the term. Its distribution is almost never associated with the high seas. Only a small number of cherry salmon stocks spends part of the marine life in the waters of the western outskirts of the North Pacific. Cherry salmon are the salmon of the Sea of Japan and the Sea of Okhotsk. Only Japan reports commercial catches of cherry salmon that usually do not exceed 1,500 metric tons. In Russia, cherry salmon are the most popular species for the recreational fishery since it migrates into streams earlier than other salmon species in southern latitudes.

In winter, cherry salmon aggregate in the eastern part of the Sea of Japan. However, some individuals can be found northwards up to the Tartar Strait and also near southern Kurile Islands. Cherry salmon were found in the walleye pollock fishery as bycatch in the Kunashir Strait, which makes it similar to Chinook salmon from the Bering

Sea. The cherry salmon migration pathway from the western Kamchatka coast lays across the southern Sea of Okhotsk where it can occur in relatively high abundance up to 15–21 fish per hour (Shuntov and Temnykh 2011).

In winter, as well as during spring - summer migrations, cherry salmon feed intensively. The basis of their diet are small fish including Japanese anchovy, capelin, sand lance, juveniles of arabesque greenling, walleye pollock, as well as squid and amphipods (Shuntov and Temnykh 2011). Despite cherry salmon staying mostly in the marginal seas, it also can be preyed upon by pelagic predatory fish of the ocean realm. In August 1994, we had a rare observation of cherry salmon preyed upon by daggertooth. A daggertooth specimen with two cherry salmon in its stomach was caught in the upper layer in the Sea of Okhotsk off the Northern Kurile Islands (Radchenko and Semenchenko 1996).

Summarizing the information presented to date, the distribution, migration patterns, and feeding habits in winter differ significantly for different Pacific salmon species (Fig. 5). Since different species of salmon reside in the same areas from year to year, they seem to be guided by large-scale elements of the water structure, like the main currents, gyres, and quasi-stationary eddies. Specific wintering habitats were formed during the entire series of previous salmon generations. They were formed by the most successful - survived individuals, who then returned to the spawning grounds and left offspring. Therefore, in winter, the specialization of certain species and even geographic groups of salmon of the same species is most clearly manifested.

It can also be assumed that contemporary salmon species and forms use each and every possible tactic of survival in winter. In general, Pacific salmon species are different and behave differently in the winter ocean. That decreases the interspecific competition in the most possible degree and gives all salmon species a chance to thrive.



Fig. 5. Winter trawl survey catches of six Pacific salmon species in 1979-2020 on background of the species distribution maps from Shuntov and Temnykh (2008).

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Oceanographic Conditions During the Gulf of Alaska 2019 and 2020 Expeditions

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Keywords: Gulf of Alaska, oceanographic conditions, surface currents, chlorophyll-a, zooplankton

Pacific salmon *Oncorhynchus* spp., depending on species, spend 1 to 4 years foraging in the Gulf of Alaska (GoA) before returning to their native rivers for spawning. It has been documented that the GoA harbors salmon stocks from both western and eastern parts of the Pacific Rim. However, there is limited information available of general oceanographic conditions in this area, its spatial and temporal variability. The GoA region had been recently influenced by large-scale warming events (the "Blob") that may have altered salmon foraging habitats and underlined a possibility of short- and long-term changes in the pelagic realm. To investigate oceanographic conditions as well as their inter-annual variability, two winter expeditions were conducted in 2019 and 2020 as major contributions to the International Year of the Salmon. During February 19 - March 17 of 2019 and March 12 - April 7 of 2020, ~1 x 1-degree survey grids covering ~ 650,000 - 700,000 km², which mainly overlapped in their southern parts, were conducted onboard the R/V *Professor Kaganovskiy* and FV *Pacific Legacy* (Fig. 1). At over 100 stations, oceanographic profiles using CTD, zooplankton using Bongo and Juday nets, and micronekton using midwater trawls were collected. Preliminary findings of both expeditions were summarized in Pakhomov et al. (2019) and Somov et al. (2020). Here the major emphasis is given to the inter-comparison of the winter oceanographic conditions in 2019 and 2020 in the Gulf of Alaska.



Fig. 1. Station grid surveys during Feb-March 2019 (filled circles) and Mar-Apr 2020 (open triangles) in the Gulf of Alaska.

The warm anomaly observed during winter 2019 was only observed in the southern part of the survey during 2020 (Fig. 2). As a consequence, the mean sea surface temperature of the GoA (considering 45–60°N, 125–155°W) was 0.33°C cooler in 2020 compared to 2019. During 2020, the northern part of the GoA (north of 52°N) was on average 0.82°C cooler than in 2019, while surface waters of the southern part (south of 52°N) were 0.06°C warmer

than in 2019 (Fig. 2). The temperature and salinity fields of the 2019 and 2020 surveys at the surface appeared to be very similar and mainly latitudinally oriented (Fig. 3 A, B). Deeper than 100 m, isotherms were oriented more zonally in 2020 than in 2019, indicating that the southern boundary of the North Pacific Drift (or even entire system of currents) in the meridional section of 145–130°W may have shifted northward compared to 2019. The thickness of the mixed layer in 2020 at the majority of stations was more than 100 m and, on average, it was 10–15 m deeper than in 2019.



Longitude

Fig. 2. Sea surface temperature anomaly (1993-2015 mean) during 2019 and 2020 in the Gulf of Alaska (data from marine.copernicus.eu).



Fig. 3. Sea surface temperature (T $^{\circ}$ C) (A, B) and depth-integrated (0–150 m) chlorophyll-a standing stock (mg.m⁻²) (C, D) during 2019 (A, C) and 2020 (B, D) in the Gulf of Alaska.

During both 2019 and 2020, over most of the surveyed water area, the predominant movement of waters was in the east and north-east direction driven by the North Pacific drift (Fig. 4). According to the circulation patterns

produced using the Ocean Surface Current Analyses Real-time (OSCAR) Surface Currents model, the geostrophic field formed a southerly moving cyclonic component of the Alaskan Gyre (https://www.esr.org/research/oscar/oscar-surface-currents/; Fig. 4). We used the outputs of the OSCAR model to identify areas (domains) with similar or dissimilar dominant circulation patterns (Fig. 5). In 2019, a group of mesoscale anticyclonic eddies (Sitka and Yakutat eddies) was noted from 135 to 140–142°W between 50–56°N. In addition, between 50 and 51°N, at least two anticyclonic Haida eddies were also observed (Fig. 4). Unlike 2020, in 2019 the majority of the eddies generally closely adhered to the North-Pacific Drift. In 2020, a larger number of anticyclonic eddies were evident and can be traced further west and north (Fig. 4). In contrast to 2019, these eddies from the southern and eastern periphery were located between two domains: e.g., between the waters of the northeast moving North Pacific Drift, and the waters of the divergence zone of the North Pacific and California currents moving to the southwest. It appears that during 2019, almost all grid stations were carried out within the cyclonic circulation of the North Pacific Drift, anticyclonic waters of the Alaska Current, and cyclonic water circulation in the divergence zone between the North Pacific and California currents (Fig. 5).



Fig. 4. Geostrophic currents (left panels) during February-March 2019 (0-600 m) and March-April 2020 (0-300 m), as well as surface currents (right panels) during March 2019 and 2020 obtained from OSCAR model in the Gulf of Alaska.

Surface chlorophyll concentrations were patchy and the highest near the shelf and in the south-central to western part of the survey reaching ~0.9 and 1.9 μ g L⁻¹ in surface waters during 2019 and 2020, respectively (Fig. 3). Chlorophyll-a biomass integrated over the top 150 m of the water column showed a clearer north to south difference in 2020, with values being ~ 2-fold higher south of 50°N and generally high throughout the southern survey areas (Fig. 3 C, D). The spatial distribution of mesozooplankton during 2019 and 2020 was similar with the highest densities observed in the southern parts (below 50°N) of the surveys (Fig. 6). The zooplankton were negatively correlated to the densities of surface micronekton (Fig. 6). Taxonomically, zooplankton assemblages were different between years due to the invasion of southern origin species during 2020. During 2020, both zooplankton and micronekton standing stocks were nearly two-fold higher compared to 2019.



Fig. 5. Delineation of domains with different types of circulation in 2019 and 2020 according to "OSCAR" circulation maps for March 3–7, 2019 and March 22-27, 2020. 1 (blue): the cyclonic circulation of the North Pacific Drift waters and the Alaskan Gyre; 2 (yellow-brown): the anticyclonic circulation of shelf and coastal waters of the Alaska Current; 3 (green): the cyclonic circulation of waters of the divergence zone between the North Pacific and California currents.



Fig. 6. Spatial distribution of mesozooplankton (ind.m⁻³) and micronekton (mgWW.m⁻²) during winter 2019 and 2020 survey in the Gulf of Alaska.

Summary

- 2019 and 2020 surveys were conducted in the transitional zone and encountered both the Sub-Arctic and Alaskan Currents;
- Mean surface temperature of the region during 2020 was 0.33°C cooler than in 2019, largely due to cooling in the northern GoA;
- There was a strong north-south gradient in all oceanographic parameters and surface 7°C isotherm demarcated colder and warmer parts of surveys;
- Surface and integrated chlorophyll-a concentrations were patchy and indicative of phytoplankton bloom development in the southern part of the surveys;
- Zooplankton assemblage composition indicated a higher presence of southern species during 2020;
- Zooplankton density was highest in the southern parts of 2019 and 2020 surveys; 2020 had the nearly double amount of both zooplankton and non-gelatinous micronekton.

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Dynamics of Phytoplankton Biomass in the Gulf of Alaska Derived from Sentinel 3 OLCI Imagery

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Keywords: phytoplankton biomass, Gulf of Alaska, Sentinel 3 OLCI, above-water radiometry

Introduction

Oceanic phytoplankton are responsible for half of the world's primary production (Field et al. 1998; Chassot et al. 2010), constitute 90% of the ocean's primary productivity, and are highly diverse in size, shape, and biogeochemical function (Chassot et al. 2010). However, in the iron-poor open ocean waters of the Gulf of Alaska (GoA), phytoplankton biomass is generally very low ($< 0.5 \text{ mg/m}^3$) throughout the year, with weak seasonal or interannual variability (Evans and Parslow 1985; Vinogradov et al. 1997; Brickley and Thomas 2004; Childers et al. 2005; Peña and Varela 2007). For example, Vinogradov et al. (1997) evaluated the phytoplankton standing stock from 1978 to 1986 for the Pacific Ocean using the Coastal Zone Color Scanner (CZCS) and reported no significant interannual variability. Banse and English (1999) observed that annual mean Chlorophyll-a (Chl-a) concentration derived from the CZCS sensor showed no significant seasonal variation for the Subarctic Pacific. More recently, Westberry et al. (2016) has shown that Chl-a in the Northeast Subarctic Pacific remains invariant throughout the year. Thus this region is considered a high-nutrient low-chlorophyll region (HNLC) where iron is the primary limiting factor for the phytoplankton production (Miller et al. 1991; Brickley and Thomas 2004; Childers et al. 2005; Aguilar-Islas et al. 2016). Despite that, the Subarctic North Pacific primarily supports Pacific salmon (Oncorhynchus spp.) originating from Canada, the United States, Russia, Japan, and Korea (Beamish 2017). Pacific salmon spend a minimum of 50% of their life in coastal and open ocean waters as foragers; however, very little is known about their distribution patterns in the open ocean (Groot and Margolis 1991; Beamish 2017). Furthermore, studies have shown that Pacific salmon in the Subarctic North Pacific face unprecedented effects from changing climate (Abdul-Aziz et al. 2011; Healey 2011; Irvine and Fukuwaka 2011; Ruggerone and Irvine 2018). Thus, it is essential to understand how climate variability in the North Pacific Ocean and the associated changes in the physical and biological environment influence the abundance, distribution, migration, growth, and survival of Pacific salmon.

The objective of this study was first (Phase 1) to assess the seasonal and interannual variability in the phytoplankton biomass using Sentinel 3 OLCI derived Chl-a concentration during the Gulf of Alaska expeditions in 2019 and 2020. Phase 2 of this research focused on retrieving Phytoplankton Functional Types (PFTs) from Sentinel 3 OLCI Imagery.





Methods

The study area map and the region of the CTD/rosette are shown in Fig. 1. Surface water samples for the insitu HPLC pigment analysis and above-water reflectance measurements (HyperSAS) were collected as part of the International Year of Salmon (IYS) Expedition in the Gulf of Alaska (GoA) onboard R/V *Professor Kaganovskiy* from February to March 2019 and the 2020 Expedition onboard R/V *Pacific Legacy* from March to April 2020. Water samples for the duplicate HPLC pigment analysis were collected (~1-5 m depth) using the CTD/rosette system, and samples for the filtration were collected using 10 L plastic bottles from each station, kept in a dark environment under dim light, and immediately filtered onboard to avoid any potential degradation to the pigments (Mueller et al. 2003). Above-water radiometry measurements were only conducted during the 2019 expedition, and the measurements were acquired during good weather conditions using a manually operated radiometer (HyperSAS) installed on the bow of the vessel to collect the spectral reflectance from the seawater following Carswell et al. (2017) and Phillips and Costa (2017). The methodology for the HPLC pigment analysis, the HyperSAS data processing, and Sentinel 3A OLCI imageries are discussed below.

Phytoplankton pigment analysis

Surface water samples for the duplicate measurement of HPLC pigment analysis from each station were filtered through 25 mm Whatman GF/F 0.7 μ m glass microfiber filter paper under low vacuum (\leq 5mm Hg). Filtration was kept under a dark environment, and the filtered volumes of seawater (0.5 – 2 L) varied according to the amount of particulate matter. After the filtration, the filtrate was flash-frozen using liquid nitrogen, immediately kept in dry ice and then kept under -80°C until the laboratory analysis. Pigments were extracted with methanol and analyzed with a High-Performance Liquid Chromatography (HPLC) to identify and quantify Chl-a and other accessory pigments by the method described in Hooker et al. (2010). HPLC analysis was performed at the University of South Carolina Baruch Institute for Marine and Coastal Science (https://phytoninja.com/lab-protocols/).

Remote Sensing Reflectance

Above-water reflectance measurements (HyperSAS) were used to validate satellite-derived reflectance measurements and ultimately use these reflectance measurements to derive bio-geochemical quantities (such as Chla, coloured dissolved organic matter, and total suspended matter) and PFTs. Here, we present the validation of Sentinel 3 derived R_{rs} in relation to HyperSAS R_{rs}. HyperSAS consists of three hyperspectral radiometers such as sea surface radiance (L_t (λ)), sky radiance (L_i (λ)), and a third sensor to measure total irradiance (E_s (λ)); from these measurements, remote sensing reflectance, R_{rs} (λ), is derived. HyperSAS was installed on the bow of the R/V *Professor Kaganovsky* at a 13-meter height from the sea surface to avoid the infrastructure shadows, spray, and sun glint. Specifically, L_t (λ) and L_i (λ) sensors are at a fixed viewing zenith angle, $\theta v = 50^{\circ}$, and viewing-sun azimuth, $\varphi v = 90^{\circ}$ to avoid the effects of glint (Hooker and Morel 2003). The ideal φv is maintained by looking at the position of the sun in the sky. Measurements were acquired between 11 a.m. and 2 p.m. to mimic the time of Sentinel 3A acquisition and optimized sun illumination conditions. Radiometric measurements were limited to a solar zenith angle less than 60^o (Mobley 1999) to limit variability in the water-leaving radiance. The data from the HyperSAS were processed with ProSoft version 7.7.19 to calculate R_{rs}(λ).

The above water remote sensing reflectance $R_{rs}(\lambda)$ was calculated according to Ruddick et al. (2006).

$$R_{rs}(\lambda) = \frac{L_{t}(\lambda) - \rho s L_{i}(\lambda)}{E_{s}(\lambda)}, (sr^{-1})$$
(1)

Where $L_t(\lambda)$ is the total measured radiance by the sea-viewing sensor and ρ_s sea surface reflectance value or fraction of sky radiance measured by the sea viewing sensor (Mobley 1999). So ρ_s is estimated according to the following equations in Ruddick et al. (2006).

$$\rho_{s} = 0.0256 + 0.00039W + 0.0000W^{2} for \frac{L_{i} (750nm)}{E_{s} (750nm)} \le 0.05$$
(2)
$$\rho_{s} = 0.0256 for \frac{L_{i} (750nm)}{E_{s} (750nm)} \ge 0.05$$
(3)

Then, a NIR (Near Infrared) similarity correction was applied to the reflectance spectra following Ruddick et al. (2005) and Ruddick et al. (2006). Finally, the simulated in-situ $R_{rs}(\lambda)$ was derived from the quality-controlled hyperspectral $R_{rs}(\lambda)$ subjected to the spectral response function (SRF) of the Sentinel 3 OLCI.

Satellite data processing

OLCI Sentinel 3A Level-1 data were downloaded from Sentinel-3 Marine CODA (Copernicus Online Data Access) web service. Level-1 OLCI Sentinel 3A data were processed with POLYMER (POLYnomial based algorithm applied to MERIS) atmospheric correction algorithm (Steinmetz et al. 2011). The Level-1 OLCI data were processed using the POLYMER (v.4.10), and the processed daily imageries were binned to 8-day composites using GPT (Graphic Processing Tool) from SNAP (6.0). Quality flags such as Negative BB, Out-of-bounds, Exception, Thick Aerosol, High Air Mass, Case-2 flags, and Inconsistency (Steinmetz et al. 2016) were applied during the binning process following Giannini et al. (2021). Satellite-derived Chl-a and R_{rs} were obtained from each weekly binned composites from a 5 × 5 pixel window (900 × 900 m) centred around the in-situ sampling

region. The median values are used to avoid outliers from total valid pixels, and the average and standard deviation from the valid pixels are used to compute the coefficient of variation (CV). For the $R_{rs}(\lambda)$ match up analysis following criteria were followed (valid pixels are $\geq 17/25$ and CV at 560 nm $\leq 20\%$). On the other hand, for the Chla match up the following criteria were followed (valid pixels are $\geq 20/25$ and CV $\leq 30\%$) (Bailey and Werdell 2006). The daily acquired satellite imagery was binned into eight-day composites because of clouds, and the previous studies have demonstrated weak seasonal or inter-annual variability in Chl-a (Evans and Parslow 1985; Vinogradov et al. 1997; Peña and Varela 2007).

Results

The dynamics of phytoplankton biomass during the two GoA expeditions have been studied using the in-situ HPLC pigment data and a weekly composite of Chl-a concentration derived from the Sentinel 3 OLCI. At the same time, we have also performed a matchup analysis of in-situ measured remote sensing reflectance and satellitemeasure remote sensing reflectance. The following section shows the significant results of Phase 1 of this study.

Remote Sensing Reflectance

The in-situ $R_{rs}(\lambda)$ showed a typical open ocean water spectra with a high scattering in the blue wavelength and decreasing towards the red spectrum accompanied by the Chl-a fluorescence peak near 680 nm. Fig. 2 shows the comparison of simulated Sentinel 3 OLCI $R_{rs}(\lambda)$ from the in-situ hyperspectral measurements ($R_{rs in-situ}(\lambda)$) vs the Sentinel 3 OLCI retrievals ($R_{rs Sentinel}(\lambda)$). $R_{rs in-situ}(\lambda)$ shows a similar spectral shape and dynamic range as $R_{rs Sentinel}(\lambda)$, indicating the excellent performance of the Polymer-based atmospheric correction model. For example, $R_{rs in-si}(\lambda)$ at 443 nm shown avg. 0.0048 ± 0.0006, and the corresponding $R_{rs Sentinel}(\lambda)$ at 443 nm was avg. 0.0047 ± 0.0005, respectively. Besides, the $R_{rs in-si}(\lambda)$ at 560 nm shows avg. 0.0019 ± 0.0003, and the equivalent $R_{rs Sentinel}(\lambda)$ at 560 nm was avg. 0.0015 ± 0.0002. Finally, the $R_{rs in-situ}(\lambda)$ at 681 nm was avg. 0.0002 ± 0.0001, and the $R_{rs Sentinel}(\lambda)$ at 681 nm was avg. 0.0003 ± 0.0001. Overall, the retrieved $R_{rs Sentinel}(\lambda)$ at the blue (443 nm), green (560 nm), and red (681 nm) shows an excellent agreement with $R_{rs in-situ}(\lambda)$, demonstrating a good atmospheric correction of Sentinel 3 OLCI imagery, and therefore reliable R_{rs} Sentinel.



Fig. 2. Remote sensing reflectance acquired by OLCI Sentinel 3 (left side) and simulated OLCI Sentinel 3 remote sensing reflectance (right side) from the in-situ hyperspectral remote sensing reflectance from the 2019 Expedition.

Satellite-derived Chlorophyll-a concentration

Fig. 3 indicates the validation of in-situ vs POLYMER derived Sentinel 3 OLCI Chl-a concentration for the two Alaska expeditions. Overall, the in-situ vs POLYMER derived Sentinel 3 OLCI Chl-a showed a good agreement (r = 0.65, p < 0.001; see Fig. 3); however, POLYMER overestimated the lower range (HPLC Chl-a between 0.09 to 0.27 mg/m³) of in-situ Chl-a concentration. At the same time, POLYMER also slightly overestimated the in-situ Chl-a concentration in the higher range values (HPLC Chl-a between 0.18 to 0.50 mg/m³). The HPLC-derived Chl-a concentration from the two expeditions ranged from 0.04 to 0.52 (0.31 ± 0.12 mg/m³). At the same time, Sentinel 3 derived Chl-a concentration varied from 0.25 to 0.63 (0.37 ± 0.08 mg/m³).

Chlorophyll-a dynamics during the two expedition

The open ocean waters of the GoA are one of the high-nitrate low-chlorophyll (HNLC) regions in the world ocean where the availability of iron regulates phytoplankton growth and productivity (Miller et al. 1991). The weekly binned Sentinel 3 derived Chl-a shows low variability with values ranging from 0.4 to 0.5 mg/m³, especially in the iron-poor open ocean waters during the period of analysis for both 2019 and 2020 (see Fig. 4). Chl-a concentration in this region is known to show low values with weak variability, 0.2 to 0.6 mg/m³ (Peña and Varela 2007).

Temporally, the weekly binned Chl-a concentration for the two expeditions indicated a similar dynamic range in Chl a concentration (0.2 to 0.7 mg/m^3 ; see Fig. 5).



Fig. 3. A match up between in-situ vs. Satellite derived Chlorophyll-a for the 2019 and 2020 expeditions.

Spatially, Chl-a concentration showed an increased trend towards the shelf (see Fig. 4). For example, the latitudinal Chl-a transect for all the weekly composite combining 2019 and 2020 showed an increased Chl-a ($> 0.5 \text{ mg/m}^3$) trend towards the north 57⁰N. A very similar longitudinal increase in the Chl-a concentration was evident towards the -135⁰W. The low Chl-a concentrations ($< 0.5 \text{ mg/m}^3$) were generally observed in the open ocean, and Chl-a gradually increased ($> 0.5 \text{ mg/m}^3$) towards the northeast Alaska shelf and British Columbia (BC) coast. Unlike the iron-poor open ocean waters, the continental shelf region is highly productive and rich in marine life with often a seasonal, sporadic diatom bloom with Chl-a concentration > 3 mg/m³ (Stabeno et al. 2004; Stabeno et al. 2016). A previous study from Stabeno et al. (2004) has revealed that the Chl-a composite images derived from Seaviewing Wide Filed-of-view Sensor (SeaWiFS) for May 1977, 1988, and 1999 shows high Chl-a concentrations and sporadic phytoplankton blooms along the shelf regions of GoA. The shelf regions of GoA experience pronounced seasonal, spatial, and interannual variability in Chl-a concentration (Waite and Mueter 2013).

Conclusion

This study investigated the validation of above water radiometry measurements and the phytoplankton dynamics during the 2019 and 2020 Gulf of Alaska expedition. The $R_{rs\ in-si}$ (λ) indicates clear open ocean water spectra with a low concentration of dissolved organic matter and total inorganic particles. The matchup analysis between $R_{rs\ in-si}$ (λ) vs $R_{rs\ Sentinel}$ (λ) showed excellent agreement, same dynamic ranges R_{rs} (λ), thus indicating a reliable $R_{rs\ Sentinel}$ (λ) reflectance. The latitudinal and longitudinal Chl-a trend derived from the weekly binned Chl-a map showed very low (< 0.5 mg/m³) Chl-a concentration in the open ocean waters of the Gulf of Alaska, and Chl-a concentration showed a gradual increase (> 0.5 mg/m³) towards the northeast Alaska shelf and BC coast. In agreement with the satellite-derived Chl-a range, HPLC-derived Chl-a concentration also showed a similar range in the open ocean waters (< 0.5 mg/m³) and higher values close to the BC shelf (0.51 mg/m³). Furthermore, the HPLC-derived Chl-a concentration vs Satellite-derived Chl-a concentration also showed a good agreement.



Fig. 4. The latitudinal and longitudinal trend of Chlorophyll-a concentration extracted from the weekly Chlorophyll-a composite map for the 2019 and 2020 expedition. The standard deviation is represented as the shaded grey region.



Fig. 5. Weekly binned Chlorophyll-a concentration for the 2019 and 2020 expedition. The white regions in the map show no data due to clouds.
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At-Sea Genetic Stock Identification in the Gulf of Alaska

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Pacific salmon (Oncorhynchus spp.) are usually found in mixed-stock schools in the ocean, meaning that fish from home streams as distant as North America and Asia might be found in the same school, making stock-specific management for conservation or harvest challenging (Wood et al. 1989). To overcome the challenges of mixedstock management, stock identification methods such as genetic stock identification (GSI) using single nucleotide polymorphisms (SNPs) as markers are delivering high-throughput insights into the stock composition of salmon (Beacham et al. 2017, 2018; Miller et al. 1996). However, current GSI approaches based on second generation sequencing platforms (e.g., Illumina and Ion Torrent) mean that only sequencing large batches of individuals, known as "genotyping by the thousands" (GT-seq), is economically and practically feasible (Campbell et al. 2015; Beacham et al. 2017, 2018). These approaches require a specialized laboratory and several days turnover even under highly automated settings. For time and spatially sensitive stock identification, an in-field real-time SNPbased GSI approach with greater flexibility in sample batch size is desirable. Recent advances in third-generation single-molecule sequencing platforms like the Oxford Nanopore minION allow real-time sequencing on a pocketsized portable sequencer (Mikheyev and Tin 2014; Quick et al. 2016). Here we develop and evaluate a novel Nanopore-based in-field SNP GSI method (termed nano-to-geno or "n2g") by adapting existing technologies to the Nanopore platform. We used a concatenation approach to overcome low read numbers and high error rates inherent in the Nanopore platform (Cornelis et al. 2017; Schlecht et al. 2017).

The n2g pipeline was first tested at sea during the 2019 International Year of the Salmon (IYS) Gulf of Alaska (GoA) expedition in February and March 2019 onboard the R/V *Professor Kaganovskiy* trawler. The mobile laboratory consisted of a polymerase chain reaction (PCR) thermocycler, a mini-plate centrifuge, a microcentrifuge, a Qubit fluorimeter, a vortexer, a minION sequencer, a laptop with an Ubuntu operating system, as well as pipettes (Fig. 1). We collected fin clips of coho salmon (*O. kisutch*) and extracted DNA using QuickExtract solution (Lucigen, USA). Multiplex PCR with a custom panel of primers targeting 299 loci of known SNPs was performed according to Beacham et al. (2017).





Next, we ligated ONT barcode adapters (PCR Barcoding Expansion 1-96, EXP-PBC096, Oxford Nanopore Technologies, UK) to the amplicons by blunt-end ligation with the Barcoding Enzyme/Buffer of the AgriSeq HTS Library Kit according to manufacturer's instruction. Next, we added the ligation products, barcodes, and barcoding adapters (PCR Barcoding Expansion 1-96, EXP-PBC096, Oxford Nanopore Technologies, UK) by PCR using Q5 polymerase mastermix (NEB, USA) for individual fish identification according. Barcoded libraries of amplicons

Wetlab

were then concatenated using inverse complementary adapters adapted from Schlecht et al (2017). Amplicons with adapters added to them were subsequently amplified again with a single primer. We pooled both subsets in equimolar ratios and then concatenated them in a PCR-like reaction, using the complementary adapter sequence ligated onto the amplicons as primers (Fig. 2). The concatenated amplicons were prepared for Nanopore sequencing using the ONT Ligation Sequencing Kit (LSK109). Libraries were then sequenced on a R9.4 flow cell and basecalling was performed simultaneously using minKNOW (version 3.1.8) on an Ubuntu 14.06 platform.

Computational analysis

Deconcatenation (Porechop) DNA extraction SNP :::: PCR amplification Binning by Barcode (Porechop) Other fish Barcoding (Fish ID) P and pooling Align to reference Inverse adapter ligation (bwa) SNP Hetero-dimer priming Score SNPs 🕴 (n2g) Concatenation 0/1;1/1/;0/0 Assign to reference populations (rubias) Sequencing adapter ligation 0/1;1/1/;0/0 1/1;1/1/;0/1 Calculate stock Sequencing composition (rubias)

Fig. 2. Simplified wet-lab workflow for DNA extraction, amplification, barcoding, and concatenation before sequencing and pipeline of the following computational analysis. DNA is shown in black, amplification primers in green, fish ID barcodes in olive, concatenation adapters in red/blue, and sequencing adapters in purple.

Bioinformatic analysis started by deconcatenating reads using porechop (https://github.com/rrwick/Porechop) with a custom adapter file that only contained the concatenation adapter. We binned the deconcatenated reads by barcode corresponding to fish individuals by using porechop with the provided default adapters file. We then aligned the binned reads (corresponding to individuals using the reference amplicon sequences using BWA-MEM and indexed using samtools (Li et al. 2009; Li and Durbin 2009). Alignment statistics for all loci were generated using pysamstats (https://github.com/alimanfoo/pysamstats) and variable nucleotides observed at the relevant SNP hotspot loci from the resulting file were identified using a custom R script.

Finally, we compared the observed nucleotide distributions at SNP hotspots with to the hotspot reference and variant nucleotides and scored as homozygous reference, heterozygous, or as homozygous variant using a custom R script with 33% and 66% as cut-offs. Mixture compositions and individual assignments were performed using the R package rubias (Moran and Anderson 2019) with default parameters against the coho coast-wide baseline of known allele frequencies for these markers established by Beacham et al. (2017, 2018).

In-field SNP GSI during the IYS GoA 2019 expedition was performed on 75 coho salmon in two sequencing runs at different points during the expedition. Upon return from the expedition, 80 individuals, including all those previously genotyped aboard the vessel, were reassessed in a single n2g run using the expedition setup starting from the frozen tissues from the expedition.

Despite the absence of normalization between samples prior to multiplex PCR, barcoding, and loading, the binning distribution across samples was relatively even with only a few apparent outliers observed. The minimum

number of reads per individual sample necessary to cover sufficient loci (at a minimum depth of 10 sequences per locus) for downstream stock assignments was around 2,000 reads. Fifty of the 80 (63%) individuals passed this threshold. After alignment to the reference sequences for SNP calling, Nanopore sequence data showed, as expected, a comparatively higher error rate than Ion Torrent reference reads, with abundant indels that frequently led to lower alignment scores than those obtained by the Ion Torrent data. Specifically, regions containing homopolymer tracts were poorly resolved, as had previously been reported (Cornelis et al. 2017) and six such loci were excluded from downstream analysis.

When comparing n2g generated SNP calls with Ion Torrent data reference data, 83.9% of SNP calls generated during the IYS expedition and 83.7% of SNP calls generated during the repeat run in the laboratory matched. The agreement on SNP calls between both n2g runs was 84.4%, highlighting the inter run variability associated with current Nanopore sequencing. Stock assignment by rubias showed some discrepancies between the Nanopore and Ion Torrent based datasets. In only 61.5% of cases did Nanopore sequences lead to the same top reporting unit (repunit; large scale geographic areas such as West Vancouver Island or Lower Fraser River) assignment for individual stock ID as the Ion Torrent based sequences (Table 1).

Table 1. Relative proportion of top reporting units (contribution >3%) to the overall mixture of coho salmon. Only individuals that had successful stock ID on all three GSI runs are included. Reporting Units: SEAK: Southeast Alaska; LSTK: Lower Stikine River; NCS: North Coast Streams (BC); HecLow+HStr: Hecate Lowlands and Hecate Strait; SC + SFj: Southern Coastal Streams, Queen Charlotte Strait, Johnstone Strait and Southern Fjords; CR: Columbia River; COWA: Coastal Washington; LNASS: Lower Nass River; WVI: West Vancouver Island; OR: Oregon.

		Ion Torrent (ion_	Nanopore (nano_PBS)			
Rank	Repunit	Proportion	SD	Repunit	Repprop	SD
1	SEAK	0.437678	0.109758	SEAK	0.662083	0.218561
2	HecLow+HStr	0.178637	0.057264	LSTK	0.205116	NA
3	LSTK	0.068878	NA CR		0.050276	0.012993
4	SC+SFj	0.067989	0.025318	COWA	0.042244	0.011583
5	CR	0.067939	0.01403			
6	NCS	0.036009	0.004052			
7	OR	0.034352	0.010704			
8	WVI	0.033487	0.009144			
9	LNASS	0.032288	0.022742			

Nevertheless, mixture proportions in both datasets were dominated by Southeastern Alaska stocks (SEAK). Nanopore assignments tended to overestimate the contribution to this stock as well as Lower Stikine River stocks (LSTK). Many of the individuals assigned to these stocks using the Nanopore were assigned to the adjacent stocks of Lower Hecate Strait and Haro Strait (HecLow+HStr) as well as Southern Coastal Streams, Queen Charlotte Strait, Johnstone Strait and Southern Fjords (SC + SFj) on the Ion Torrent platform (Table 1).

Individuals from stocks well represented in the database like the Columbia River were confidently assigned to the appropriate stock on both platforms. However, indirect measure of how well the SNP call match individuals in the baseline dataset of both datasets indicated that the n2g and the Ion Torrent data showed large deviations from the normal distribution of Z-scores, suggesting that about half of the individuals were not from populations that are well represented in the database (Moran and Anderson 2019). Nanopore-based assignments showed even more aberrant distribution, presumably due to the additive effects of the sequencing platform introducing bias on top of poor baseline representation. The poor database representation could cause small differences in SNP calls to cause alternative assignments.

While we were successful in providing a proof-of-principle study demonstrating that the Nanopore platform is capable of in-field genotyping, the throughput, fidelity, and turnaround remained below the level needed to put this platform into standard operation for GSI by SNP genotyping. Several modifications in the workflow are currently being evaluated to improve the throughput, accuracy, and cost.

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Environmental DNA Survey of the Winter Salmonosphere in the Gulf of Alaska

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Environmental DNA (eDNA) is an emerging field to study the diversity and distribution of aquatic communities without the need to capture individuals. It utilizes sequencing of traces of DNA left behind in the environment by organisms to provide an unbiased account of species composition and distribution in an environment without the need for invasive sampling methods (Rees et al. 2014). The International Year of the Salmon (IYS) Gulf of Alaska (GoA) expeditions were launched in 2019 and 2020 to illuminate the factors influencing the survival of Pacific salmon in the open ocean. The winter months, when open-ocean conditions might critically impact ocean survival of first ocean-winter juvenile and subadult salmon, are the least understood but could largely determine stock performance (Beamish and Mahnken 2001; Naydenko et al. 2016; Shuntov et al. 2017; Nagasawa 2000; Ishida et al. 2000). Despite progress on salmon marine ecology during the winter, questions regarding the health and survival of salmon during this period remain unanswered, particularly in the open ocean. Specifically, the impact of predators and competitors has been notoriously difficult to assess due to the scarcity of data, in part due to the difficulty of catching large highly mobile predators of salmon in trawl surveys. Accordingly, we collected water samples during the GoA expeditions and performed an eDNA survey on the samples with the goal of describing the salmonosphere (i.e., the relative abundance and distribution of Pacific salmon, as well as their prey, competitors, and predators).

Water samples of 5 L were collected at 2–4 m below surface using a Niskin bottle at all oceanographic stations during the 2019 and 2020 GoA expeditions. Duplicate 2 L subsamples were filtered into 0.22 μ m Sterivex cartridge filters and preserved at -80°C for transport back to the laboratory. All sampling equipment was cleaned with 1.6% sodium hypochlorite solution followed by rinsing with distilled water. In 2020, an additional step of 10% sodium thiosulfate rinse was added to neutralize any residual bleach from the system. Upon return from the field, DNA was extracted from the filter cartridges using the DNeasy extraction kit (Qiagen). To assess chordate and cephalopod species diversity we amplified conserved regions of mitochondrial 16S gene using primers designed by Deagle et al. (2009). To speciate salmonids we similarly targeted the cytochrome oxidase I (COI) gene of Pacific salmon (Thomas et al. 2017). The 16S and COI amplifications were normalized prior to library preparation using a normalization plate to standardize the input material and retrieve similar sequence levels across the different samples. Library preparation was performed using the KAPA Low Throughput Library Preparation kit for Illumina platforms, as per manufacturer's instructions. The 16S and COI samples were pooled into nine libraries sequenced in single-end 300 bp on an Illumina MiSeq platform, with 7–18 barcoded libraries per run. Sequencing data were quality filtered, demultiplexed, and rarefied using the OBItools suite

(https://git.metabarcoding.org/obitools/obitools/wikis/home). Next, unique reads were queried against the nr BLAST database using a standalone local BLAST algorithm (https://blast.ncbi.nlm.nih.gov/Blast.cgi) and results were assigned to the lowest taxonomic level using MEGAN (https://bio.tools/megan). A detailed description of the workflow can be found at https://github.com/bensutherland/eDNA_metabarcoding/. R was used for filtering and assigning species detections to samples and for statistical analysis and visualization of the data. Reads belonging to common contaminants (such as humans, pigs, chickens, and cows) were excluded from the analysis.



Fig. 1. Capture and eDNA detection location of pink salmon (*Oncorhynchus gorbuscha*) in the GoA in 2019 and the distribution density calculation based on the respective data.

eDNA was able to detect all salmon species caught in 2019 except for Chinook, which had only three individuals captured. Salmon distributions detected by eDNA were in general similar to trawl catches, with the exception of pink salmon that showed a distinct distribution center in the northwest of the survey region where no pink salmon were caught in trawls, suggesting that trawl sampling might have missed a secondary distribution center (Fig. 1).



Fig. 2. Capture and eDNA detection location of steelhead (Oncorhynchus mykiss) in the GoA in 2019.



Fig. 3. Capture and eDNA detection location of chum salmon (*Oncorhynchus keta*) in the GoA in 2020 and the distribution density calculation based on the respective data.

In 2020, all salmon species captured by trawl were detected by eDNA and eDNA detections outnumbered trawl catches, presumably due to the increased detection sensitivity due to the addition of sodium thiosulfate to the sampling procedure. For instance, only one steelhead (Oncorhynchus mykiss) was captured in 2020, but steelhead DNA was detected at four stations during the survey (Fig. 2). The center of distribution for coho, sockeye, and pink salmon in the GoA in 2020 based on eDNA data was shifted to the west compared to trawl catches (Fig. 3). Given the half life of DNA in sea water, specifically in the winter environment, this could suggest eastward movement of these species towards the continental shelf in the study area during early spring of 2020. One main area of interest in eDNA data was the distribution and abundance of predators of salmon, as predators are notoriously difficult to assess in trawl surveys due to their low abundance and high motility. Only two potential predator species of salmon, North Pacific daggertooth (Anotopterus nikparini) and Pacific spiny dogfish (Squalus suckleyi), had been caught during the GoA expeditions. Indeed, these two species were also detected in the eDNA data. Additionally, salmon sharks (*Lamna ditropis*), presumed to be major predators of salmon in the open ocean, were detected during both years of the survey (Fig. 4) (Nagasawa 1998; Seitz et al. 2019). Other detections of potential predators of juvenile salmon were Dall's porpoise (Phocoenoides dalli) as well as a number of predators of presumed lesser importance such as Orca (Orcinus orca), lancetfish (Alepisaurus ferox), and Steller sea lion (Eumetopias jubatus). Dall's porpoise and salmon shark showed distribution patterns that aligned with the overall distribution of Pacific salmon in both years, suggesting that they might seek out high abundances of their prey species (Fig. 4). Specifically in 2020, where the majority of salmon appeared to be just west of the survey area, predator detections were most common on the westernmost stations (Fig. 4). Surprisingly, harbour seal (Phoca vitulina) DNA was also detected in the GoA, specifically in 2019, and seemed to show strong patterns of co-occurrence with salmon in their distribution. While this species is commonly thought to be restrained to the continental shelf, a visual observation

from a crew member of the 2019 expeditions seems to confirm these unexpected detections (Brown and Mate 1983). Many prey and competitor species of salmon in the open ocean, such as myctophids and cephalopods, perform diurnal vertical migrations which make an adequate assessment of their abundance and distribution by conventional surface trawl surveys challenging as they spend the daytime in deep waters. As DNA remains in the environment even after a species leaves, eDNA detections of vertically migrating species were only slightly affected by time of day in contrast to trawl catches that occurred almost exclusively at night (Table 1). For instance, the distribution of abundant species like Boreopacific armhook squid (*Gonatopsis borealis*) and California headlightfish (*Diaphus theta*) showed a much more even distribution in the eDNA data compared to trawl catch data (Fig. 5). The current dataset did also allow some insights into some species of salmon prey, specifically copepods. *Mesocallanus tenuicornis* and *Metridia pacifica* were the most abundant copepod species detected in 2019 and 2020, with *Mesocallanus tenuicornis* dominating in the south and *Metridia pacifica* being dominant in the north of the GoA.



Fig. 4. eDNA detection location of salmon shark (*Lamna ditropis*) and Dall's porpoise (*Phocoenoides dalli*) in the GoA in 2019 and 2020 overlayed the distribution density all salmon species (*Oncorhynchus* spp.) combined.

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Species	Time	eDNA	Trawl	
Sanid	Day	52.7%	20%	
Squia	Night	43.7%	91%	
Maaatambida	Day	79.3%	8.6%	
wryctopnias	Night	80%	86%	



Fig. 5. Capture and eDNA detection location of California headlightfish (*Diaphus theta*) in the GoA in 2019 and 2020 with the time sampling time indicated by color.

Together, eDNA surveys in combination with conventional trawl surveys allow for a more holistic impression of the open ocean environment in the GoA that salmon face during the ocean winter. Specifically, interactions with predators and competitors are becoming increasingly resolved—an unprecedented resolution due to the non-invasive and unbiased nature of eDNA sampling.

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Predation on Pacific Salmon on the High Seas

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Predation on Pacific salmon (*Oncorhynchus* spp.) at sea remains one of the big "unknowns" for salmon marine ecology (Pearcy 1992; Beamish 2018). The answers to basic questions such as who are the major predators (fish, birds, marine mammals), whether predation is random or selective (e.g., based on size or health), or how it varies in space and time are all poorly understood. Perhaps the biggest challenge to understanding predation is discovering predators "in the act" of preying on salmon by finding salmon remains in predator stomachs.

We had three objectives to examine predation on salmon on the high seas. The first objective was to summarize salmon caught during Gulf of Alaska (GoA) expeditions in 2019 and 2020 that showed signs of predator attacks as indicated by wounds (suggestive of fresh injuries) or scars (healed wounds) and attempt to identify the predator that caused the injury. Second, we report the catches of likely predators during the two expeditions. Third, we summarized what is known about salmon shark (*Lamna ditropis*) diet and predation on Pacific salmon across the North Pacific Ocean (NPO).

For our first objective, 993 salmon were examined during the two expeditions, of which 23 (2.3%) had wounds and 27 (2.7%) had scars (Table 1). The percent of salmon with injuries was higher in 2019 (7.3%) than in 2020 (3.3%); however this difference may reflect inconsistencies in noticing or recording injuries among years. Within each year, we observed differences in injuries by salmon species (Table 1; Fig. 1), but no species or year had particularly exceptional injury rates. The overall wound and scar rates estimated from the two GoA expeditions (2.3% and 2.7%, respectively) were higher than previously reported for salmon caught in the winter in the western NPO (0.1–0.5%; Naydenko and Temnykh 2016) but lower than reported wound rates in summer (often >10%; Bugaev and Shevlyakov 2007; Naydenko and Temnykh 2016). While salmon with new or old injuries were the survivors - not casualties - of predator attacks, they provided important baseline data for future studies and for comparisons to estimates from other areas.

Species	Year	Total caught	No. with wounds (%)	No. with scars (%)
Chinook	2019	3	0 (0%)	0 (0%)
	2020	26	1 (3.9%)	0 (0%)
Chum	2019	225	8 (3.6%)	14 (6.2%)
	2020	234	1 (0.4%)	3 (1.3%)
Coho	2019	95	7 (7.4%)	1 (1.1%)
	2020	118	1 (0.9%)	7 (5.9%)
Pink	2019	30	1 (3.2%)	0 (0%)
	2020	136	0 (0%)	1 (0.7%)
Sockeye	2019	73	0 (0%)	0 (0%)
	2020	51	3 (5.9%)	1 (2.0%)
Steelhead	2019	0	0 (0%)	0 (0%)
	2020	1	1 (100%)	0 (0%)
Totals	2019	427	16 (3.8%)	15 (3.5%)
	2020	566	7 (1.2%)	12 (2.1%)
	Both years combined	993	23 (2.3%)	27 (2.7%)

 Table 1. Pacific salmon observed with wounds (fresh injuries) or scars (healed wounds) caught during expeditions to the Gulf of Alaska, by species and year.

Likely predators of Pacific salmon on the high seas consist of teleost fishes (long snouted lancetfish [*Alepisaurus ferox*], daggertooth [*Anotopherus pharao*], and Pacific lamprey [*Entosphenus tridentatus*]); sharks (salmon shark, spiny dogfish [*Squalus acanthias*]); and marine mammals including pinnipeds and cetaceans (Bugaev and Shevlyakov 2007; Naydenko and Temnykh 2016). Bugaev and Shevlyakov (2007) provide descriptions and photos of the distinct wounds made by fish and pinniped predators. Based on these descriptions and field notes made when fish were collected, we assigned likely predators to injured salmon caught during 2019 and 2020 expeditions, when possible (Table 2). We were unable to determine the likely predator for nearly half (46%) the injuries. Identifiable injuries were from lancetfish and daggertooth (28%), lamprey (15%), and marine mammals (10%). These assigned predator values are similar to those reported by Naydenko and Temnykh (2016) in the western NPO (Table 2). The lack of salmon shark-inflicted wounds suggests these events often result in mortality.





Table 2. Potential predators responsible for large wounds and scars observed on Pacific salmon caught in 2019 and 2020.

 Origins were determined from field notes and descriptions in Bugaev and Shevlyakov (2007).

		Potential predator					
Species	Fish*	Lamprey	Marine mammal	Unknown			
Coho	4		1	8			
Chum	7	6	3	8			
Pink				1			
Sockeye				1			
Chinook				0			
Total	11 (28%)	6 (15%)	4 (10%)	18 (46%)			
W Pacific**	41%	15%	3%	41%			

*Daggertooth or long snouted lancetfish.

**Data from Naydenko and Temnykh 2016.

For our second objective, the 2019 and 2020 expeditions caught a total of seven potential predators in trawls: five daggertooth and two spiny dogfish. As Deeg et al. (2021) report, daggertooth environmental DNA (eDNA) was detected at one station, spiny dogfish eDNA was detected at five stations, and salmon shark eDNA at 10 stations. This low catch of predators is consistent with previous research, which also report low catches of predators in winter (Myers et al.2016; Naydenko and Temnykh 2016). However, the trawl gear used during both GoA expeditions may not be designed to effectively catch predators.

Salmon sharks are a widely distributed apex predator in the NPO (Ebert et al. 2013), where they occupy the highest trophic level along with marine mammals and sea birds (Brodeur 1988). Salmon sharks are primarily piscivorous but are opportunistic and appear to eat whatever prey is available. Salmon shark prey items include

spiny dogfish, Pacific salmon, sablefish (*Anoplopoma fimbria*), squid, walleye pollock (*Gadus chalcogrammus*), Pacific herring (*Clupea pallasii*), and lancetfish (*Alepisaurus* spp) (Nagasawa 1998). Salmon sharks are even known to consume benthic prey items like shrimp and crab (Okada and Kobayashi 1968; Nagasawa 1998). Salmon shark diets are believed to vary by season and area but research on spatio-temporal changes to diet is limited.

Much of what is known about salmon shark diet is based on stomach content analyses from sharks caught in spring and summer. For example, over 1,000 stomachs were analyzed from sharks caught in the western NPO (n=859) and Bering Sea (n=176) from May through August in 1959 and 1960. Of these stomachs, about 63% contained salmon, and the primary species identified was sockeye salmon (*O. nerka*; Sano 1960, 1962). However, stomachs from salmon sharks captured in the western NPO in April and May (1999 and 2000) contained 96% squid by mass (Kubodera 2007). It is unknown if the diet differences reported in these studies are due to preferential selection of prey or other factors such as size of the salmon shark, prey availability, or spatio-temporal differences in sampling. In the eastern NPO, stomachs from sharks captured in Prince William Sound, Alaska, from July through August contained 76% salmon, 20% fish, and 4% squid by mass (Hulbert et al. 2005). These results are unsurprising as runs of pink (*O. gorbuscha*), chum (*O. keta*), and coho salmon (*O. kisutch*) concentrate in Prince William Sound throughout the summer and into September, but even when Pacific salmon abundance is high, approximately a quarter of stomach contents were non-salmonids (Hulbert et al. 2005).

It has long been known that salmon sharks are predators of Pacific salmon (Sano 1960; Blagoderov 1994; Hulbert et al. 2005). Salmon sharks are known to aggregate in areas where salmon occur in high numbers, for example in Prince William Sound, Alaska (Hulbert et al. 2005) and southeast of the Kamchatka Peninsula (Nagasawa 1998). The primary salmon species consumed by salmon sharks likely reflects availability, with mainly pink, sockeye, and chum salmon consumed in the western NPO (Sano 1962; Nagasawa 1998) and pink, chum, and coho salmon in the eastern NPO (Hulbert et al. 2005).

Historically, Chinook salmon (*O. tshawytscha*) were rarely identified in salmon shark stomachs (Sano 1960, 1962). Recently, however, immature Chinook salmon carrying satellite transmitters were depredated by salmon sharks along the Aleutian Islands and southern Bering Sea shelf (Seitz et al. 2019). These predation events may provide novel information about the winter diet of salmon sharks as some Chinook salmon were consumed from November through January and in March (Seitz et al. 2019). However, we cannot disregard the possibility that these fish were particularly vulnerable to salmon sharks due to the presence of satellite transmitters. These predation events have been suggested to contribute to Chinook salmon's declining age at maturity (Manishin et al. 2021).

To assess the impact of salmon shark predation on Pacific salmon, more information is needed for both salmon sharks and salmon. Without information on salmon shark diet throughout the year, it is hard to assess the overall importance of Pacific salmon to their diets. Salmon shark diet studies often occur when sharks are near Pacific salmon aggregations, potentially resulting in overestimates of salmon in shark diets. Diet studies conducted outside summer months, from sharks across their geographic range and of varying sizes, are needed to resolve this issue. Salmon sharks segregate by sex; female sharks are found in higher proportions in the eastern NPO and males in the western NPO (Nagasawa 1998). While female salmon sharks in Prince William Sound, Alaska (within the eastern NPO), have been satellite tagged and tracked (Weng et al. 2008; Block et al. 2011; Carlisle et al. 2011), information on the horizontal and vertical migration of sharks outside this region, and from male sharks in general, is limited. Likewise, identifying the region- and species-specific migration patterns of Pacific salmon during their marine residence will help determine the degree to which salmon sharks and salmon species overlap. Additionally, information on salmon shark abundance would help determine if predation of Pacific salmon by salmon sharks has increased; such abundance estimates are currently not available for the NPO (Rigby et al. 2019).

To continue learning about salmon predation and predators during high seas surveys, we suggest:

- Note and take pictures of all wounds and scars on salmon. When photographing the scar or wound, ensure that a specimen identifier is visible, and try to identify the potential predator using Bugaev and Shevlyajov (2007) as a guide.
- Collect stomach contents of potential predators to identify prey. Preserve stomach contents for visual prey identification or genotyping to confirm prey identification when visual identification is not possible.
- Collect tissues from likely predators for trophic biomarkers (e.g., stable isotopes, fatty acid) analysis to determine diets over time. Different tissues have different incorporation rates which provide diet information over a longer time frame than stomach content analysis.
- Tag and release all salmon sharks with satellite tags during the Pan-Pacific survey in 2022 to further our understanding of salmon shark migration throughout the NPO.

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Pathogens and Stressors of Overwintering Salmon in the Gulf of Alaska

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Pacific salmon (*Oncorhynchus* spp.) are a keystone species across the North Pacific, supporting ecosystems, commercial opportunities, and cultural identity (Cederholm et al. 1999; Lichatowich and Lichatowich 2001; Radchenko 2006). Nevertheless, many wild salmon stocks have experienced significant declines associated with declines in marine survival (Holtby et al. 1990; Nagasawa 2000; Radchenko 2012; Naydenko et al. 2016; Shuntov et al. 2019). Salmon restoration efforts focus mainly on fresh and coastal waters, but little is known about the open ocean environment. Specifically, the health and condition of salmon during the winter months in the Northeast Pacific are poorly characterized. To address these knowledge gaps, an end-of-winter survey in the Gulf of Alaska (GoA) in February and March of 2019 was initiated under the banner of the International Year of the Salmon (IYS) initiative onboard the Russian research trawler *Prof. Kaganovskiy*. Oceanographic sampling and trawl surveys were performed to provide the baseline data for future pan basin studies. We applied high throughput RT-qPCR tools to provide the first report on the health, condition, and infection profile of coho *O. kisutch*, chum *O. keta*, pink *O. gorbuscha*, and sockeye *O. nerka* salmon in the Gulf of Alaska (GoA) during the winter.

Samples of 252 Pacific salmon were collected during trawls accompanied by oceanographic sampling. Salmon were dissected and tissue samples were preserved in RNAlater (Thermo Fisher Scientific, MA, USA). Tissue samples from gill, heart, kidney, and spleen were homogenized using TRI-reagent (Ambion Inc., Austin, Texas) and 1-bromo-3-chloropropane. Total RNA was extracted using Total RNA Isolation kits (Ambion Inc., Austin, Texas) and normalized and cDNA synthesized (SuperScript VILO MasterMix, Life Technologies). DNA was extracted using a high salt TNES-urea buffer (Asahida et al. 1996) followed by the BioSprint 96 DNA extraction kit (Qiagen, MD). For infectious agent monitoring, the cDNA was mixed with equal amounts of DNA. Amplicons of all duplicate 48 infectious agent assays were then pre-amplified using TagMan PreAmp Master Mix (Life Technologies). For host gene expression monitoring, an equivalent procedure was performed on cDNA from gill tissues only, targeting 89 host genes individually. The qPCR assays and individual samples were loaded onto 96.96 dynamic arrays (Fluidigm Corporation, San Francisco, CA, USA) and run on the BioMark platform. Cycle threshold (CT) for each assay was determined using the BioMark Real-Time PCR analysis software (Fluidigm, www.fluidigm.com). Infectious agents found in each host were summarized as a single variable representing the 'Relative Infection Burden' according to Bass et al. (2019). Salmon Fit-Chips, which contain curated biomarker panels of host genes to detect specific stressor responses in gill tissue utilized the same nanofluidics qPCR platform. Biomarker panels for hypoxia, thermal stress, osmotic stress, general stress, and viral disease development, imminent mortality, mortality related, as well as immune stimulation and inflammation were deployed in this study (Miller et al. 2011, 2017; Akbarzadeh et al. 2018; Houde et al. 2019a, 2019b). Host genes were as singletons and included three reference genes for normalization (Miller et al. 2016; Teffer et al. 2017). Salmon biomarker CTs were normalized between runs and the relative fold gene expression was calculated using the ddCT method (Livak and Schmittgen 2001; Jensen and Ørntoft 2004). Expression profiles were analyzed in R using ComplexHeatmap (Gu et al. 2016), goeveg (https://cran.r-project.org/web/packages/goeveg/), and vegan (https://cran.rproject.org/web/packages/vegan/index.html).

All 252 salmon were screened by qPCR for 48 infectious agents commonly observed in British Columbia coastal waters using high throughput qPCR. Twenty-one agents were detected, with coho containing the highest average number of infectious agents detected, followed by sockeye, chum, and pink salmon (Table 1). Infectious agent diversity was highest in sockeye, followed by coho, chum, and pink salmon (Fig.1b). To determine shifts between the coastal margin and the GoA, we compared the prevalence of infectious agents (Fig.1-2.). *Ichthyophonus*

hoferi was present at significantly higher prevalence in the GoA in all species, with pathogen loads in pink, coho, and chum higher than any observed on coastal waters (Fig. 2). This common parasite causes systemic disease in marine fish and is thought to transmit trophically, suggesting that the GoA is a reservoir for this parasite (Hershberger et al. 2002; Bass et al. 2017).

Species	Pathogen	Туре	Prevalence
	Candidatus Branchiomonas cysticola	Bacterium	56%
	Ceratanova shasta	Parasite	10%
Churren	Ichthyobodo sp.	Parasite	21%
Cnum	Ichthyophonus hoferi	Parasite	29%
	Loma sp.	Parasite	50%
	Parvicapsula pseudobranchicola	Parasite	26%
	Candidatus Branchiomonas cysticola	Bacterium	89%
	Candidatus Syngnamydia salmonis (Sch)	Bacterium	10%
	Ichthyobodo sp.	Parasite	14%
Coho	Ichthyophonus hoferi	Parasite	59%
	Loma sp.	Parasite	53%
	Parvicapsula pseudobranchicola	Parasite	18%
	Viral encephalopathy and retinopathy virus	Virus	36%
	Candidatus Branchiomonas cysticola	Bacterium	89%
	Ichthyobodo sp.	Parasite	30%
Pink	Ichthyophonus hoferi	Parasite	37%
	Loma sp.	Parasite	19%
	Parvicapsula pseudobranchicola	Parasite	26%
	Candidatus Branchiomonas cysticola	Bacterium	59%
	Candidatus Syngnamydia salmonis (Sch)	Bacterium	11%
	Ichthyophonus hoferi	Parasite	33%
Sockeye	Loma sp.	Parasite	67%
	Pacific salmon parvovirus	Virus	39%
	Parvicapsula pseudobranchicola	Parasite	16%
	Sphaerothecum destruens	Parasite	25%

Table 1.	Primary infectious agents	(prevalence $> 10\%$) in the second s	he Gulf of Alaska in 2019.
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Fig. 1. (a): Relative infection burden of salmon in the GoA compared to coastal BC (mean value, SD, and n). (b): Shannon diversity of infectious agents and pathogens of salmon in the GoA compared to coastal BC (mean value, SD). Asterix indicates significant differences with a *t*-test p < 0.05. Coho and sockeye showed significant correlation of gene expression profiles with *I. hoferi* prevalence, indicating potential for impact. Similarly, the horizontally transmitted parasite *Loma* sp. was present at higher loads and prevalence in chum, sockeye, and pink in the GoA (Fig. 2; Shaw et al. 1998, 2000). Other pathogens with significantly higher GoA prevalence in individual species were *S. destruens* in sockeye, *Ca.* B. cysticola in pink, *C. shasta* in chum, and VER in coho (Fig. 2; Table 1). The latter horizontally, vertically, and trophically transmitted virus was also observed at unusually high loads in the GoA and is a viral disease agent of marine fish (Costa and Thompson 2016), but is capable of causing disease in salmon (Korsnes et al. 2005).



Infectious Agent Prevalence GoA 2019 vs Coastal BC

Fig. 2. Comparison of selected infectious agents and pathogens with high prevalence in the Gulf of Alaska and Coastal BC. Asterix indicates significant differences in prevalence in the GoA with Fisher's exact test p < 0.05. Ratio under species indicates the number of salmon in the analysis for the respective species (coastal: GoA). See Table 1 for infectious agent and pathogen abbreviations and Supp. Table 1 for all prevalences.

Together, chum, pink, and sockeye showed lower Relative Infection Burden (RIB) in the GoA compared to coastal British Columbia (BC) (Fig. 1a). In contrast, RIB in coho was higher in the GoA than in coastal waters (Fig. 1a), although the number of infectious agents as well as their diversity was lower in the GoA for all species (Fig. 1a, b). This suggests that the higher RIB in coho in the GoA is due to the higher loads of VER, *Loma* sp., and *I. hoferi*.

Stock of origin was significantly associated with pathogen profile variation in coho salmon. Principal Component Analysis (PCA) was performed to ordinate gene expression profiles of individual salmon to identify dominant biomarker panels driving differential gene expression. We tested the correlation between observational and oceanographic data as potential drivers or co-variates with indices of variation in salmon health and condition depicted by the top PCs; those that were significant were subsequently plotted onto gene expression PCAs (Fig. 3). Since global depression of immune response genes (immune stimulation, inflammation, and viral disease development) effectively equals immunosuppression, we created the inverse vector of gene expression of said biomarker panels to depict this suppressed immune status. Immunosuppression showed an inverse relationship with the biomass of the primary prey species as well as a direct correlation with RIB in all species (Fig. 3).



Fig. 3. Association of primary prey species biomass, Relative Infection Burden, and temperature with gene expression in the Gulf of Alaska during the winter 2019. Primary prey species such as euphausiids, hydromedusae, and pteropods are highlighted in relation to immunosuppression (Imm_Sup: inverse vector of summarized biomarker panels immune stimulation, inflammation and viral disease development). K indicates condition factor.

Low prey availability could drive salmon into energetic deficit, to which they respond by suppressing the immune system, a common response to malnutrition in many vertebrates, that in salmonids has been previously described for steelhead trout *O. mykiss* and Atlantic salmon *Salmo salar* (Latshaw 1991; Lord et al. 1998; Sutherland et al. 2014; Krasnov et al. 2020). Immunosuppression would make salmon more susceptible to pathogens, which would explain the elevated infectious agent loads, and also explain the absence of immune response to opportunistic pathogens such as *Ca.* B. cysticola and *S. destruens*. Since condition factor was inversely correlated with immunosuppression and RIB, "good performance" could act protectively, as such individuals are less likely to suffer from energy deficit, thus are immunocompetent and able to fend off infections.

Coho and pink salmon that were primarily caught along the southern border of the distribution area experienced the highest ocean temperatures and showed a strong correlation of immunosuppression and RIB with increased temperature (Fig. 3). This suggests that higher metabolic demands at higher temperatures, or associated environmental changes, caused stress to malnourished individuals. Individuals of chum and sockeye salmon caught at higher latitudes (i.e., colder waters) experienced extremely high abundance of the northern sea nettle *Chrysaora melanaster*, a large jellyfish (Pakhomov et al. 2019). Thus, temperature might act as a proxy for the impact these large jellyfish had on zooplankton communities in turn affecting lower trophic level salmon in the north of the GoA in 2019. Indeed, chum followed by sockeye salmon had the lowest stomach fullness indices in the GoA (Somov et al. 2019).

All species described here exhibited signs of cumulative effects of stressors, with species-specific responses to specific stressors, such as pathogens. Across the board, ocean conditions and prey availability were the dominating factors correlating with condition of fish depicted by biomarker expression, highlighting the likely impacts of a warming ocean on winter survival at sea in the face of climate change, specifically in the northern part of the GoA that experienced a larger sea surface temperature abnormality in 2019 (Hinch et al. 1995; Miller et al. 2014). Warming, with its downstream effects on salmon energetics, could be especially disruptive in the Gulf of Alaska, where overwintering salmon from both sides of the Pacific basin congregate due to its homogeneous environment (Rand, 2002; Beacham et al. 2009; Litzow et al. 2018).

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Squid Abundances and Relevance, Gulf of Alaska Expeditions 2019 and 2020

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Squid is a major diet item of Pacific salmon (*Oncorhynchus* spp.) in offshore waters, especially for coho (*O. kisutch*), Chinook (*O. tshawytscha*), and steelhead (*O. mykiss*) (Davis et al. 1998; Aydin 2000; Davis 2003; Kaeriyama et al. 2004). Despite their importance, relatively little is known about squid populations on the high seas, including their distribution, life cycle, population structure, spawning areas, and movement at different life stages relative to ocean currents. After a proposal to include winter surveys in salmon studies (Beamish 2012), winter expeditions took place in 2019 and 2020 in the Gulf of Alaska (GoA); the ultimate goal was to discover the fundamental mechanisms that regulate salmon in the North Pacific Ocean. One of the objectives was to study squid abundance, composition and condition in the upper epipelagic layer. Methodology and some preliminary results are described in Pakhomov et al. (2019) and Somov et al. (2020). During both winter expeditions squid was an important component in coho, Chinook, and steelhead diet (Fig. 1); this finding reinforced the need of squid studies in relation to salmon. Here we present a summary on squid abundance, distribution, and relevance based on 64 epipelagic (0-30 m) trawl catches, 60 Juday plankton nets (0-250 m) in 2019 and 52 epi-pelagic (0-20 m) trawl catches, 49 Juday plankton nets (0-200 m) in 2020. We also present preliminary results of squid detected in environmental DNA (eDNA) analysis.



Fig. 1. Squid contribution to salmon diets caught during the Gulf of Alaska winter expedition in 2019 and 2020. Notes: The data adapted from Pakhomov et al. (2019) and Somov et al. (2020); SoX - sockeye, CM - chum, PK - pink, CO - coho, CK - chinook, ST - steelhead salmon; numbers on X axis indicate number of stomachs.

During both expeditions the majority (>90%) of squids were caught at night. Squids are active diel vertical migrators and usually come up to the upper layers at night to feed on zooplankton, crustaceans, and fish. In total, eleven squid taxa (Teuthida) and one octopus (Octopoda) were caught in trawl nets. All encountered species were characteristic for the Pacific subarctic zone (Jorgensen 2009; Volvenko et al. 2018). The distribution of cephalopod trawl catches are shown in Fig. 2 and total catches, abundance, weight, size ranges are presented in Table 1. Six of the squid taxa were encountered in both years; some species were caught in trawls in 2019 but not 2020 (e.g., *Taonius borealis, Gonatus madokai, Gonatus onyx, Onykia robusta*) and some were caught in 2020 but not 2019 (e.g., *Doryteuthis opalescens, Dosidicus gigas* cf., *Okutania anonycha*). Additional details for each species is provided below in alphabetical order.

Abraliopsis felis (McGowan and Okutani, 1968): This is a very abundant squid of the North Pacific. In 2019 it was occasionally encountered in southern areas and constituted only ~1% of the total squid catches. In 2020, *A. felis* was the most abundant squid (~47%) and occurred mostly in south-western part. The only steelhead caught during surveys (17 March 2020) had *A. felis* in its stomach contents (~70%). This was the only species commonly encountered in trawls that did not return eDNA results (Fig. 3) as there is no mitochondrial 16S ribosomal RNA sequence of *A. felis* available in Gene Bank, highlighting the need of voucher species.



Fig. 2. Cephalopod trawl catches, Gulf of Alaska winter expeditions 2019 and 2020. Size of circles corresponds to number of squid caught; "X" denotes locations of no catch. Blue indicates nighttime catches, yellow daytime catches.

Table 1. Squid trawl catches, abundance, weight, size ranges, and number of larvae caught in Juday net from the Gulf of Alaska winter expeditions 2019 and 2020.

Catch (h (n) Abundance (%)		Weight	Weight (%)		Size range (mm)		Larvae (n)	
Species	2019	2020	2019	2020	2019	2020	2019	2020	2019	2020
Abraliopsis felis	17	758	0.8	47.1	0.1	7.3	34-43	19-56	0	0
Belonella borealis	1	0	0.0	0.0	1.9	0.0	600	n/a	1	1
Boreoteuthis borealis	1820	199	80.5	12.4	56.3	4.9	21-130	19-140	2	2
Chiroteuthis calyx	12	1	0.5	0.1	0.1	0.0	38-60	n/a	0	0
Doryteuthis opalescens	0	343	0.0	21.3	0.0	26.5	n/a	50-116	0	0
Dosidicus gigas cf.	0	6	0.0	0.4	0.0	0.6	n/a	15-54	0	0
Gonatidae sp.	2	32	0.1	2.0	0.0	0.2	n/a	n/a	0	0
Gonatus madokai	7	0	0.3	0.0	0.5	0.0	45-55	n/a	0	2
Gonatus onyx	110	0	4.9	0.0	1.4	0.0	33-95	n/a	2	0
Japetella diaphana	1	1	0.0	0.1	0.0	0.0	34	35	1*	1
Moroteuthis robusta	1	0	0.0	0.0	2.3	0.0	346	n/a	0	0
Okutania anonycha	0	124	0.0	7.7	0.0	3.1	0	30-81	0	0
Onychoteuthis borealijaponica	289	144	12.8	8.9	37.2	57.3	64-235	24-250	0	0

* caught in the net of micro plastics study

Boreoteuthis borealis (Sasaki, 1923) syn. *Gonatopsis borealis* - boreopacific gonate squid: It was the most abundant (~81%) squid in 2019 and only third most abundant (~12%) in 2020, its catches by both numbers and weight were about ten times higher in 2019 than in 2020. Low catches of *B. borealis* in 2020 likely occurred due to shallower vertical net opening that rarely exceeded 20 m. This species occur in the upper 20 m sporadically (Watanabe et al. 2006; Bower and Tagaki 2004). In both years there were not clear spatial distribution, both juvenile and sub-adult stages were caught, and two larvae (each year) were caught in Juday nets.

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Chiroteuthis calyx (Young, 1972): This is a common species of the boreal Pacific. It was encountered very sporadically; it was not ever found in salmon stomachs. It appears to have good agreement between catch-eDNA results for cephalopods.

Doryteuthis opalescens (Berry, 1911) syn. *Loligo opalescens* - opalescent inshore squid: This species is common in coastal waters. It was caught only in one trawl set close to Vancouver Island (~25 nmi from the Juan de Fuca). It was seen in several salmon stomachs.

Dosidicus gigas cf: This species was caught in once trawl in 2020 near Dixon Entrance. Identification was done at sea and as of now is not confirmed.

Gonatus onyx (Young, 1971) - one-hooked gonatus: This is a mesopelagic squid. It was encountered in trawls and Juday net in 2019 but not 2020. The largest specimen was female, II stage of development. In Juday net, two larvae (each 4 mm) were caught at one station.

Gonatus madokai (Kubodera et Okutani, 1977) - long-armed gonatus: This is an abundant, mesopelagic species in North Pacific. It was encountered in 7,8% trawls, in total 7 specimens were caught ranging from 45 to 55 mm and one specimen 155 mm. This species was caught only in waters north of 53° N.

Okutania anonycha (Pearcy and Voss, 1963) syn. *Berryteuthis anonychus* - smallfin gonate squid: This was the most important species in salmon diets analyzed during expeditions; it comprised ~45% of the total squids found in stomachs in both years and ~90% in 2020 (Somov et al. 2019, 2020.). No *O. anonycha* were caught in trawls in 2019, however it was present in the stomachs of sockeye (n=4), coho (n=2), and Chinook salmon (n=3). All specimens in stomachs in 2019 were encountered east of 144° W longitude. Several specimens were caught in trawls after winter GoA expedition had commenced and R/V *Professor Kaganovskiy* was on route back to Russia: March 26 (n=13), March 28 (n=103), and March 30 (n=89). All catches were south of 46° N latitude. In 2020, *O. anonycha* was caught at five southernmost stations (Fig. 2). Notably, these were also the stations with the highest salmon catches and ~85% of coho were caught at sets where *O. anonycha* was present. This species was seen in the warmest waters (mean surface temperatures ~8.4 °C) compared to other common squids (mean 7.0–7.9 °C). This is consistent with previous studies indicating that *O. anonycha* abundance is the highest in summer, drops in fall and winter, rises in spring and that it appears to be associated with Western Subarctic Gyre (Katugin et al. 2002; 2005).



Fig. 3. Cephalopod eDNA preliminary results, Gulf of Alaska winter expeditions 2019 and 2020. Size of circles corresponds to number of reads detected at the corresponding sampling site; "X" denotes locations of no detection. Blue indicates nighttime detections, yellow daytime detections.

Onychoteuthis borealijaponica (Okada, 1927) - boreal clubhook squid: This is a common species in North Pacific. It was the second most abundant species in 2019 and forth in 2020; it dominated squid catches by weight in 2020 and was second dominant in 2019. In both years, the size range was bimodal and included specimens born in

fall (<110 mm) and spring/summer (>110 mm). Most *O. borelaijaponica* were caught in the eastern and, particularly, south-eastern parts of the study area.

Onykia robusta (Verrill, 1876) syn. *Moroteuthis robusta* - robust clubhook squid: This is one of the largest squids. Only one specimen was caught, in 2019, in the southern area. It was a male (developmental stage III) with a mantle length of 346 mm.

Taonius borealis (Nesis, 1972), syn. *Belonella borealis*: This is a cranch squid (Cranchiidae) inhabiting deep waters (400–3400 m) of the North Pacific, and is almost never caught in the surface trawls. One specimen was caught in 2019, a female (developmental stage VII), with a mantle length of 600 mm; remains of this species were found in two dogfish shark (*Squalis acanthias*) stomachs. In 2020 it was not caught in trawls but fragments (arms) of *T. borealis* were found in the stomach of a black rockfish (*Sebastes melanops*). One larvae was caught in Juday net in 2019 and one in 2020. These results confirm that this species can reproduce in the GoA in winter, but not in the trawl catches.

Japetella diaphana (Hoyle, 1885): This is a pelagic, subtropical octopus usually brought to the GoA with currents. One specimen was encountered each year, in the southern GoA area. One larvae was caught in the net collecting samples for a micro plastics study in 2019 and one in Juday net in 2020.

Results of this study demonstrated substantial annual differences in cephalopod abundance and composition in winter period in the Gulf of Alaska. For example, in 2019, *B. borealis* was the most frequently caught squid (~81%) which also dominated by weight (~60%). In 2020, *A. felis* was the most abundant (~47%), however *O. borealijaponica* dominated by weight (~58%). Squid distribution and abundance differences most likely were related to oceanographic conditions (0.33 °C cooler in 2019; developing spring bloom in 2020; change in water movements) and methodology (shallower vertical net opening in 2020). Cephalopod larvae occurrence in Juday nets (*B. borealis, G. onyx, J. diaphana, T. borealis*) confirm that these species use the winter in the GoA as a spawning and nursing ground. Applying molecular techniques showed better catch-eDNA reads agreement in 2020, when an addition of bleach deactivator (sodium thiosulfate) was introduced into the sampling protocol. Although, results of eDNA analysis faced a few challenges (e.g., the need for an improved references database - sequence data and taxonomy), it did provide very promising results and indications that it can greatly improve verification of species identification and monitoring in the future. Overall, squid winter studies proved to be a valuable addition to salmon studies.

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Myctophid Abundances and Ecology

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Abundant mesopelagic fishes play an important role in the trophic structure of the ocean pelagic fish community, both as zooplankton consumers and as a prey for predatory species. Since they mainly consume smaller planktonic prey than the most of commercially significant fish species and can be eaten by them, lanternfish (myctophids) provide an energy and matter transport from the small-sized part of planktonic community to the upper trophic layers. Myctophids and other small-sized mesopelagic fish are a common food of salmon, cods, sea perches, squid, and many cetaceans and seals (Kozlov 1995; Ohizumi et al. 2003; Shuntov 2016; Nielsen et al. 2019).

Migrating from the sea surface to deep layers of day-time residence, mesopelagic fish bear significant amounts of organic matter that, then, will be decomposed by bacteria and enrich the nutrients pool not far from the sea surface. From these depths, organic and mineral matters are quickly returned back to the sea surface in upwelling zones that maintain the ecosystem productivity. Such organic/mineral matter flow was named the biological pump (Radchenko 2007). Its annual capacity is comparable with the amount of "marine snow" (carcasses of dead plankton animals, semi-mineralized plankton algae cells, and other organic particles) while "marine snow" usually sinks beyond the upper ocean recycling circuit. Recently, the role of mesopelagic fish fauna was re-assessed to show its significance in the global carbon cycle and vertical organic matter transport (Davison et al. 2013). Correspondingly, these fishes received special attention during the winter Gulf of Alaska cruises in 2019 and 2020 (Pakhomov et al. 2019; Somov et al. 2020).

Myctophids are the main component of vertically migrating mesopelagic fauna and so-called sound-scuttering layers (i.e., layers of higher concentrations of small living organisms in the water column that are registered by the echo sounder) in most parts of the world's oceans. Myctophids can be found from the Central Arctic Basin to the Antarctic waters. Experts considered that there are more than 36 genera and 200-245 species of these small fish with a body size, as adults, from 2.5 to 25 cm (Paxton 1979, Bekker 1983). Currently, the most comprehensive and regularly updated fish data repository, FishBase (https://www.fishbase.org/), contains information on 33 genera and 247 valid species of myctophids (Catul et al. 2011; Froese and Pauly 2020).

Only about 14% of all Myctophidae species have been recorded in the North Pacific Ocean northward of 45°N - 16 genera and 35 species. Twelve species of 9 genera can be considered as common fish for the mesopelagic domain in this area, while four of them are non-migratory to the sea surface and rarely occur shallower than 200 m depth. The other 23 species of 11 genera were met rarely during the integrated ecosystem surveys (Shuntov and Bocharov 2012) or were reported in literature (Nelson 1994). Considering the list of midwater fishes reported to inhabit the 100-500 m depth layer of the Subarctic North Pacific Ocean and adjacent seas by Beamish et al. (1999) with 16 genera and 47 myctophid species, we excluded all tropical and subtropical *Diaphus*, *Hygophum*, and *Lampanyctus* (Nannobrachium) species dwelling southward of 37°N (Froese and Pauly 2020).

In 2019, a trawl survey for overwintering Pacific salmon was conducted in the Gulf of Alaska from February 21 to March 15 onboard the Russian R/V *Professor Kaganovskiy*, covering ~697,500 km² (Fig. 1A). In total, 58 stations were completed in the main research area. Typical survey stations conducted during both daylight and night times included a deployment of a surface (0-30 m) midwater trawl (design opening ~1200 m², 30 m depth x 40 m width, minimal 10 mm codend mesh size) for the duration of one hour at a speed of 4.5 knots. The average technical trawl parameters were the following: horizontal opening - 38.4 m, vertical opening - 32.2 m, towing speed - 4.4 knots, trawl mouth opening - 969 m², and swept area for one hour - 0.31 km².

In 2020, a similar trawl survey was conducted from March 11 to April 7 onboard the 37 m long chartered trawler *Pacific Legacy*. The survey area covered ~648,500 km² (Fig. 1B). Trawl sets were conducted using the NPAFC 1142 research trawl net with minimal 4 mm liner mesh size in the codend. The design opening of this net was 45.7 m in horizontal and 30 m in vertical directions. The actual vertical opening, measured using 2 RBR sensors attached to both head- and footrope, was typically 18–22 m during surface sets. The horizontal opening was not measured directly and calculated using the formula designed for the similar RT 80/396 trawl (Shuntov and Bocharov 2005). Throughout the survey, the average calculated horizontal opening ranged from 42–45 m, the trawl



mouth opening averaged 650 m², and the swept area for one hour was 0.31 km^2 , while the average trawl towing speed was 4.9-5.2 knots. Fifty-two trawl hauls were completed including three deeper sets at 30 m headrope depth.

Fig 1. Winter trawl survey grid in the Gulf of Alaska, A) 21 Feb to15 Mar 2019; B) 11 Mar to 07 Apr 2020. Night sets started between 8 PM and 6 AM in 2019 and 8 PM and 7 AM in 2020 (Pacific time) and are shown as solid circles. Daytime sets are shown as crosses.

In 2019, the survey grid was more regular with one-degree latitude between stations and one-and-a-halfdegree longitude between south-north transects. In 2020, stations were mostly distributed along two latitudinal and two skew sections. Twenty stations (38.5 %) were located eastward from the 2019 survey area. In 2019, twentyfour stations (41.4 %) were completed northward from 57°N between 140° and 147°30'W not surveyed in 2020. This circumstance along with about a 1-month difference in survey dates, a 1.6-times narrower vertical opening of the trawl net, and a notably smaller mesh size in the codend in 2020 created a substantially different sampling design. Bearing this in mind, we analyzed 2019 and 2020 datasets as supplementing each other rather than providing an inter-annual comparison.

Despite "vessel time" being different during the two surveys, all time indicated in this report is Pacific Standard Time (PST, GMT - 8) in 2019 and Pacific Daylight Time (PDT, GMT - 7) in 2020. Switching to Pacific Daylight Time (PDT) on Sunday, March 10, 2019, is not reflected to avoid confusion.

Fish abundance and biomass were calculated using the so-called areal method (Volvenko 2000). The catchability coefficient for myctophids was restricted to 0.1 (Shuntov and Bocharov 2012) in both years despite the difference in the mesh size of the net insert in the trawl codend. Since myctophids continuously re-distributed in the water column during the daily vertical migration, calculations made were a rough approximation to give an impression on total abundance of this group in the near-surface ocean layer at night-time in winter.

Mesopelagic fish fauna in the Gulf of Alaska in winter was mainly presented by myctophids, followed by bathylagids (Bathylagidae) and barracudinas (Paralepididae; in 2019 only). One specimen of medusafish *Icichthys lockingtoni* (Perciformes: Centrolophidae) was captured in 2019. In addition to mesopelagic fishes, a variety of fish larvae were encountered in the night trawls, belonging to the benthic families of Sebastidae, Xenocongridae, Pleuronectidae, and Paralichthyidae. Myctophids were represented by four species with a strong predomination of the blue lanternfish *Tarletonbeania crenularis* (Fig. 2). This species is common for the dilution domain between the northern and southern arms of the Subarctic Current (Bekker 1983; Froese and Pauly 2020). This species is also known as a strong migrator to the sea surface in the northeastern North Pacific (Moser and Ahlstrom 1996).

In 2019, blue lanternfish occurred in 100% of the night-time trawl hauls from 7:40 PM to 5:53 AM (Pacific time) including several hauls that finished or started at the dusk, from 4:55 PM to 7:48 AM (Fig. 3A). In 70 % of catches containing myctophids, blue lanternfish was the only myctophid species. Blue lanternfish catches at dusk were low, ranging from 1 to 9 fish per hour, while night-time catches varied between 6 and 1,173 fish per hour. The average catch was 104 fish (0.25 kg) and 277 fish (0.67 kg), north and south of the 57°N parallel, respectively. The maximum catch (1,173 fish and 3.05 kg) was recorded at night in the vicinity of 49°40'N-141°30'W. The standard length (SL) of *T. crenularis* in catches ranged from 39 to 87 mm (average SL=60.8 mm, and body weight=2.42 g). Smaller (<30 mm SL) blue lanternfish (SL=16–20 mm) occurred in the neuston samples in the upper 20 cm layer in 2019. Trawl catches were devoid of such small blue lanternfish although smaller animals (euphausiids, sergestiid shrimp, comb-jellies) were recorded. Despite blue lanternfish catches looking negligible (< 1 kg / hr on average), its

total calculated numbers and biomass in the upper epipelagic layer at night reached 5.57 billion fish and 13,480 metric tons (mt), and distribution density was about 0.02 mt under km².

In 2020, *T. crenularis* was also the most abundant mesopelagic fish in the catches. The average night-time catch was 372 individuals (0.49 kg) / hour. This was 34% more in numbers but 43% less in weight than in the southern portion of the survey area in 2019. Presumably, this was a consequence of smaller mesh size in the trawl net codend in 2020, when a high proportion of smaller *T. crenularis* (<40 mm SL) were captured, while single fish with SL of 39 mm were caught in 2019. Overall, the size of lanternfish ranged from 18 to 82 mm SL (average = 48.2 mm; Fig. 3). During 2020, the average blue lanternfish body weight was almost half of the 2019 value - 1.32 g. Similar to 2019, *T. crenularis* occurred in every night-time catch conducted between 9:19 PM and 6:52 AM. The size of the blue lanternfish catch depended more on the time of the day than on geographical location. Thus, the three biggest catches of *T. crenularis* occurred at the southernmost, easternmost, and one of the westernmost stations (Fig. 2). The majority of catches were greater than 100 fish / hour. From six smaller catches (<100 fish / hr), two were recorded in the coastal zone, one in a deeper trawl haul (below 30 m), and three others in early night, before 10:30 PM. In 2020, blue lanternfish biomass and abundance were estimated as 7,900 mt or ~6 billion individuals (Table 1; average density of 0.009 mt under km²). This biomass estimate was almost half of that in 2019.

Northern lampfish *Stenobrachius leucopsarus* was notably less abundant than the blue lanternfish in 2019 (Fig. 2). It occurred in seven trawls across the northeastern part of the survey area and mainly north of 57° N. Catches varied between 9 and 153 fish / hour (average of 49 fish, 0.038 kg). The species was mostly represented by small-sized juveniles. The SL of northern lampfish ranged from 25 to 97 mm, and body weight averaged 0.8 g. At two nearby stations with the maximum northern lampfish catches (96 and 153 fish / hr at $52^{\circ}40^{\circ}$ N 144°30'-146°W), numerous small-sized juveniles appeared to be meshed in the middle of the trawl net. Despite these juveniles being notably destroyed, their body length were estimated at < 20 mm. It is considered that *S. leucopsarus* larvae metamorphose at about 18 mm length, and 20–25 mm fish are the youngest members of the juvenile population (Smoker and Pearcy 1970). Besides these two larger catches, the average northern lampfish catch in 2019 was only 17 fish or 0.039 kg / hour.



Fig. 2. Myctophids catch distribution throughout the survey area in 2019 (upper panel) and 2020 (lower panel). Isolines represent relative abundance in individuals / km^2 .

In 2020, *S. leucopsarus* was also the second most abundant. mesopelagic species in the trawl catches. It occurred in 95 % of night-time sets and its catch ranged from 1 to 3270 fish / hour (average catch of 336 fish (0.06 kg) / hr). Standard length ranged from 14 to 90 mm (Fig. 4). A large proportion of fish (~50 %) were small individuals (< 30 mm SL) due to the smaller mesh size in the trawl codend. Catches in the northern part of the survey at sea surface temperature (SST) < 7 °C were notably larger than in the southern part (Fig. 2). The estimated biomass and abundance of *S. leucopsarus* were estimated at 980 mt and 5.5 billion fish, respectively (Table 1). In

comparison, fish less than 30 mm SL comprised only 4% of the total catch, and the smallest measured size was 25 mm in 2019, when a 10 mm mesh was used in the trawl codend.



Fig. 3. Blue lanternfish length frequency distribution in trawl catches in 2019 and 2020.

Table 1.	Myctophid s	tandard body	length (SL) i	n the catches	during the	2019 and	2020 surveys,	frequency	of occurrence,
distributio	n density, es	stimated abund	dance, and bi	omass.					

Species	SL (mm) min-max	Number of stations	Average catch (ind.)	Average catch (g)	Density x1,000 (ind./ km ²)	Density (kg/ km ²)	Total biomass (mt)	Total numbers (million fish)
Tarletonbeania crenularis	39-87	26	188	449	7.2	17.256	13,480	5,561
Stenobrachius leucopsarus	25-97	7	49	38	0.46	0.387	270	318
Diaphus theta	49-89	6	53	178	0.43	1.462	1,020	303
Symbolophorus californiensis	91-106	2	1.5	7	>0.05	0.029	20	3
Total 2019		58	291.5	672	8.09	19.134	14,790	6,185
Tarletonbeania crenularis	18-82	21	372	490	9.26	12.136	7,870	6,006
Stenobrachius leucopsarus	14-90	20	336	60	8.48	1.511	980	5,499
Diaphus theta	22-86	15	36	70	0.90	1.758	1,140	583
Symbolophorus californiensis	90-150	8	0.7	10	0.02	0.139	90	10
Total 2020		52	744.7	630	18.66	15.544	10,080	12,098

The California headlightfish *Diaphus theta* occurred in six trawl catches in 2019; in five of them together with the northern lampfish. Catches varied from 2 to 105 fish / hour (average of 53 fish, 0.178 kg); SL varied from 49 to 89 mm; and body weight averaged 3.4 g. In 2020, *D. theta* occurred in 15 out of 22 night-time sets with an average catch of 36 individuals (0.07 kg) / hour. The total biomass and abundance were estimated as 1.14 thousand tonnes and 583 million fish, respectively. The spatial distribution was similar to *S. leucopsarus* with the highest catches

observed at the same stations (Fig. 2). Size (SL) ranged from 22 to 86 mm, with the SL of most fish in the 52–56 mm size class.



Fig. 4. Northern lampfish length frequency distribution in trawl catches in February-March 2019 and March-April 2020.

Three specimens of bigfin lanternfish *Symbolophorus californiensis* occurred in two trawl catches near the southern and northern boundaries of the survey area in 2019. Its SL ranged from 91 to 106 mm. In 2020, *S. californiensis* was also the least abundant myctophid, with an average catch of 0.7 individuals / night trawl set (0.01 kg), and was present in 8 of 22 night-time sets in the southern part of survey (Fig. 2). Total biomass and abundance were estimated at 90 tonnes and 10.3 million fish, respectively. Standard lengths ranged from 90 to 150 mm.

Balanov (1995) stated that common myctophid species in the North Pacific seem to use the entire area including the Bering Sea, as a foraging ground, with reproductive areas occurring in the more southerly areas. For some species, like the blue lanternfish and northern lampfish, we hypothesize the validity of southeasterly areas as spawning grounds. Due to their exceptionally wide distribution, high abundance, and vertical migrations with a daily amplitude of several hundred meters, myctophids play a significant role in the pelagic food web, particularly in the high seas. Nevertheless, to date, studies on myctophids of the North Pacific are fragmentary and insufficient, especially in the northeastern Pacific Ocean. Significant knowledge gaps still exist regarding their standing stocks, life cycles, spawning time and distribution of eggs, larvae, and adults. Current understanding on myctophid horizontal movements is rather approximate even for the common species.

The Pan-Pacific high seas expedition in 2022 has a great potential to reveal a large picture of the role of this unique group of forage fish in the functioning of the North Pacific ecosystems. We urge that detailed ichthyological research of mesopelagic fish should be included into the cruise plans of this expedition.

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To the Question of the Use of Climatic-Oceanological Predictors to Forecast Pacific Salmon Stock Abundance in Kamchatka

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During almost 100 years (1925–2020) of fishing, an average annual catch of salmon in the Russian Far East (RFE) was about 170,000 tons, of which, approximately 110,000 tons (data for 1971-2020) were contributed by the Kamchatka stocks (Fig. 1). On average, annual RFE salmon catches consisted of 60–70% pink (*Oncorhynchusgorbuscha*), 25% chum (*O. keta*), and 10% sockeye (*O. nerka*) salmon. The other Pacific salmon species together contributed < 5% of the total. The share of chum catches in Kamchatka were slightly lower (up to 15%), while sockeye salmon catches were higher (more than 15%). In the recent decade (2011-2020), annual salmon catches in Kamchatka were generally higher than 252,000 tons. The lowest catch (~ 138,000 tons) was recorded in 2013 and the highest (~ 498,000 tons) in 2018. This appears to be a historic peak of Pacific salmon abundance in Kamchatka in the 20th and beginning of 21st centuries (Bugaev et al. 2020).





Sustainable use of salmon resources is based on accurate forecasting of stock abundance. In Kamchatka, forecasting of the Pacific salmon stock abundance is largely based on the Ricker model, i.e., stock-recruitment (Ricker 1954; Shepherd 1982), or standard sibling model that forecasts abundance of a given age-class for a given year based on the abundance of the previous age-class in the previous year (Peterman 1982). Autumn surveys in the southwestern Bering Sea and Sea of Okhotsk study juvenile salmon seaward migration. Trawl catches from these surveys are used as empirical data for pink and chum salmon in the model "juvenile fish at sea-offspring returns". Forecasts also utilize data on juvenile salmon abundance in rivers. These data were obtained by enumerating salmon juveniles in traps at selected streams in Eastern and Western Kamchatka.

Ecological indicators can play an important role in making decisions about the catch forecast. Math modeling is always limited by a number of predictors and by the method's errors. Fish abundance is the main and often the only predictor used in forecasting. In such a case for Pacific salmon, multi-factor characteristics of the environment is hardly considered that reduces the forecast informativity (Urawa et al. 2016). The purpose of this research is to find out new climate predictors that can be used in the simulation of Pacific salmon abundance forecast in

Kamchatka.Here we suggest utilization of one of the most promising oceanological factors - the index of the sea surface temperature zonal abnormalities (aSST).

Areas of fall and winter feeding of Pacific salmon of Kamchatka during the first marine year are well known (Beamish 2018). Squares (cartographic trapezoids) for assessment of average aSST indices for 1971–2020 proposed by Bugaev and Tepnin (2015) and Bugaev et al. (2016, 2018) are shown in Fig. 2.Data on aSST (grid 5 x 5° in the latitude and longitude) are taken from https://psl.noaa.gov/data/gridded/data.kaplan_sst.html. The monthly anomaly data were combined: in data set for 1856–1981, they were calculated based on vessel observations from the British Meteorological Bureau (https://www.metoffice.gov.uk; Parker et al. 1994; Kaplan et al. 1998); data after 1981 were taken from the US National Center for Environmental Prediction (https://www.ncep.noaa.gov), with the use of the optimum interpolation algorithm combining shipborne observations and remote sensing of the ocean surface on the grid 1x1° (Reynolds and Smith 1994). In our study, the base period for anomalies calculation is 1951–1980.



Fig. 2.Main areas of fall (A) and winter (B) feeding migrations of Pacific salmon of the Eastern and Western Kamchatka in the Northern Pacific Ocean: numbers - ordinal numbering of cartographic trapezoids ($5 \times 5^{\circ}$), which are the areas for calculating the average values of aSST; blue lines - East Kamchatka stocks; red lines - West Kamchatka stocks.

Data on Pacific salmon commercial catches for 1971–2020 were taken from KamchatNIRO and NPAFC (www.npafc.org). Pearson correlation coefficients (r) were calculated based on the chronological consistency of the observational series of both datasets (aSST and catch).For example, September aSST in 2019 were analyzed together with the pink salmon catches in 2020. A similar approach was used for chum salmon. However, because about 90% of chum return at age-0.3 and -0.4, the time lag was 4 and 5 years. The abundance (catch) was evaluated

as a moving average, taking into account the importance of both age classes. For example, September aSST in 2016 was analyzed together with the average catch in 2019 and 2020. A similar approach was used for sockeye salmon. The lag was 3 and 4 years, because marine life period of this species lasts mostly (about 95%) 2-3 years.

Starting from 2016, Kamchatkan specialists used multivariate regression model (*MRM*) that incorporated salmon survival levels depending on conditions of reproduction and early marine period (Neter et al. 1990; Feldman and Shevlyakov 2015).Since 2018, the model was enhanced with *Random Forest* approach with the random forest of decision trees (Breiman 2001; Feldman 2020).In both methods, monthly values of the climate indices were used: Pacific Decadal Oscillation (PDO) (https://www.ncdc.noaa.gov/teleconnections/pdo/), index of cyclone intensity in the West Pacific (WP) (https://www.cpc.ncep.noaa.gov/data/teledoc/wp.shtml), and index of Arctic Oscillation (AO) (https://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/ao.shtml). Currently, *MRM* and *Random Forest* were used only for pink salmon in Kamchatka (Fig. 3-5).This was due to the short life cycle of pink salmon that depends on environmental conditions in exact years in more degree.Studies continue to select the most relevant climate indices to forecast returns of long-cycle species (chum, sockeye, coho*O. kisutch*, and Chinook *O. tshawytscha* salmon).



Fig. 3.Observed and multiple regression model series ($R^2 = 0.89$; p < 0.001) of the logarithm of the survival index ln (R/S) on the example of the regional complex of pink salmon from the northeastern Kamchatka in 1990–2017.

Fig. 4.Stratified model spawners (stock)-recruitment the example of the regional complex of pink salmon from the northeastern Kamchatka in 1990–2017.

Fig. 5. Decision tree in the *Random Forest* model with the features WP17_21 (May-September – smolt migration and early sea period) and PDO12_13 (December-January – eggs incubation period) on the example of the regional complex of pink salmon from the northeastern Kamchatka in 1990–2017.

It was found in previous studies of the effects of climate factors on the Pacific salmon stock abundance in
RFE that parameters often co-correlate (Bugaev and Tepnin2012; Bugaev et al. 2018a, b). In overwhelmingly most cases, the key factor of the correlation was the planetary global temperature anomaly of the Earth's surface air layer averaged over all measurement points (GTa). This index was calculated using data from all available meteorological stations on Earth (including Antarctic ones) with reconstruction of sea surface temperature (ERSST v4). Two GTa indices were used in the publications mentioned: N. HEMI+dSST (for the northern Hemisphere of Earth) and GLBTs+dSST (for the planet Earth) (http://data.giss.nasa.gov/gistemp/tabledata/). Correlation between GTa and salmon abundance for 1925–2020 was strong for the whole planet (r = 0.78; p < 0.001) and for the Northern Hemisphere (r = 0.82; p < 0.001; Fig. 6). Similar results were demonstrated by Klyashtorin and Lubushin (2005). The authors identified that cycles of GTa are around 60 years long, which was similar to the Pacific salmon long-term dynamics. However, it must be noted that the data of the Pacific salmon catches is not long enough to confirm this theory.





Strong correlation between GTa and salmon abundance lead to the examination of regional links between aSST in the North Pacific and salmon stocks. A number of publications (Kotenev et al. 2010, 2015; Bugaev and Tepnin 2015; Bugaev et al. 2016, 2018a, b) revealed correlation between the aSST dynamics and salmon production (commercial catches) in the RFE. In this work, we present results continuing these studies with an addition of the most recent years. Most of statistically significant correlations were moderate r = 0.30-0.60 (Fig. 7; Table 1, 2) and that was expected since hydrological factors have only an indirect effect on the fish production. Results clearly showed better correlation for most salmon species in fall (September–October) and less correlations in winter. The systemic regularity of significant correlations between aSST and catches of all species implies that the temperature regime truly affects formation of salmon stock abundance in Kamchatka.

As an example, consider the dynamics of aSST and aSST-catches (Fig. 8) in the squares with the highest correlation (Fig. 9). There is a clear trend towards an increase of interannual variability of the September aSST in 1971–2020 for all areas. This is consistent with the overall dynamics of Pacific salmon catches in Kamchatka (Fig. 1). During this time, the temperature anomaly varied from -1.5 to 2.0 °C. Maximum catches of Pacific salmon occurred at the aSST from 0.5 to 2.0°C. Note that, based on calculated coefficient of determination for a given level of correlation ($R^2 \sim 0.25$ -0.45), correlations were not strong ~ r = 0.5-0.7 with explanatory power ~25-45%. Therefore, aSST data can only be considered as an indicator for salmon stock abundance estimation. The correlations of aSST-catches are promising for future multivariate modeling of the Pacific salmon abundance dynamics in Kamchatka.Further statistical exploration will enable the determination of the most active periods and areas in multidimensional space. That will allow aSST series to be included in *MRM* and *Random Forest* analyses along with other climatic indices. Note that despite weaker aSST-catches correlations in the winter period, it could still produce a good response in a multidimensional field.

It is also important to consider using aSST series in predicting the abundance of pink salmon in the Eastern and Western Kamchatka. Abundance of this species broadly depends on endogenous drivers and stock abundance fluctuations in odd- and even-year classes. In theory, aquatic habitat should have the same effect on fish of both broodlines, but high or low abundance of a particular year class has an additional effect. Natural mortality depends on fish density, food availability, and predators. That is why the pink salmon forecast is often made separately for odd- and even-year classes. Correlations of aSST-catches for odd- and even-year pink salmon are demonstrated in Fig. 10-11. There were moderate correlations for even-year fish (r = 0.41 catch; r = 0.54 logarithmic catch). No correlation was observed for the odd-year pink. Most likely, odd-year pink salmon are more influenced by other factors (probably taking place in the coastal ecosystem of the Western Kamchatka).Pink salmon stocks of the Eastern Kamchatka demonstrate similar correlation for both generations (odd years r = 0.56, and even r = 0.55 catch; r = 0.62, and r = 0.75 logarithmic catch). That also reinforces the potential of including aSST in forecast models.

In conclusion, our results demonstrated stable correlations between the catches of Pacific salmon and indices of the sea/ocean surface temperature anomalies (aSST) in areas of early marine/oceanic migrations of juveniles in autumn and winter in the Bering and Okhotsk Seas, as well as in the waters of the Subarctic Front in the western Pacific Ocean. That confirms the possibility of the use of aSST series for math modeling to forecast salmon returns to the Eastern and Western Kamchatka coasts using the multiple regression model (*MRM*) and *Random Forest*.



Fig. 7. Dynamics of aSST in areas (squares) of mass feeding migrations of Kamchatka Pacific salmon in September of the 1st year of the marine life in 1971–2020: A - areas for stocks of the Eastern Kamchatka, B - areas for stocks of the Western Kamchatka.

Table 1. Values of Pearson correlation coefficients and confidence probability (r/p), reflecting the dependence of the variability of the number of catches of Pacific salmon in Eastern Kamchatka on the indicators of aSST in the areas of their mass feeding migrations in autumn-winter period of the 1st year of the marine life in 1971-2020.

	Autumn				Winter								
Species	Month			Area			Month			A	rea		
		12	13	23	32	33		13	14	15	23	24	25
Pink	Sep	<u>0.34</u>	<u>0.33</u>	<u>0.42</u>	<u>0.46</u>	<u>0.47</u>	Dec	<u>0.15</u>	0.05	0.12	<u>0.34</u>	<u>0.16</u>	0.20
		0.016	0.021	0.003	0.001	0.001		0.309	0.711	0.429	0.017	0.278	0.176
	Oct	<u>0.34</u>	<u>0.30</u>	<u>0.36</u>	<u>0.36</u>	<u>0.42</u>	Jan	0.22	0.17	<u>0.18</u>	0.32	<u>0.25</u>	0.26
		0.016	0.035	0.010	0.011	0.003		0.137	0.257	0.222	0.024	0.085	0.068
	Nov	0.24	0.17	0.31	0.39	0.29	Feb	0.29	0.24	0.27	0.36	0.31	0.40
		0.101	0.240	0.033	0.006	0.045		0.045	0.091	0.061	0.011	0.028	0.005
Chum	Sep	<u>0.50</u>	<u>0.43</u>	<u>0.57</u>	<u>0.60</u>	<u>0.54</u>	Dec	0.12	0.04	0.12	0.36	0.17	0.15
		0.000	0.003	0.000	0.000	0.000		0.444	0.794	0.444	0.015	0.263	0.317
	Oct	<u>0.31</u>	<u>0.34</u>	<u>0.40</u>	<u>0.37</u>	<u>0.40</u>	Jan	<u>-0.04</u>	<u>-0.10</u>	<u>-0.08</u>	<u>0.19</u>	<u>0.02</u>	0.07
		0.033	0.023	0.006	0.011	0.005		0.817	0.514	0.591	0.197	0.878	0.627
	Nov	<u>0.21</u>	<u>0.20</u>	<u>0.34</u>	<u>0.37</u>	<u>0.22</u>	Feb	<u>0.00</u>	<u>-0.10</u>	<u>-0.08</u>	<u>0.27</u>	<u>0.11</u>	0.15
		0.161	0.189	0.020	0.011	0.150		0.987	0.518	0.594	0.068	0.450	0.325
Sockeye	Sep	<u>0.58</u>	<u>0.51</u>	<u>0.65</u>	<u>0.66</u>	<u>0.57</u>	Dec	<u>0.29</u>	<u>0.18</u>	<u>0.17</u>	<u>0.46</u>	<u>0.22</u>	0.10
		0.000	0.000	0.000	0.000	0.000		0.046	0.224	0.247	0.001	0.131	0.506
	Oct	<u>0.38</u>	<u>0.41</u>	<u>0.44</u>	<u>0.39</u>	<u>0.42</u>	Jan	<u>0.24</u>	<u>0.12</u>	<u>0.05</u>	<u>0.44</u>	<u>0.22</u>	0.11
		0.008	0.005	0.002	0.007	0.003		0.101	0.435	0.722	0.002	0.137	0.467
	Nov	<u>0.41</u>	<u>0.36</u>	<u>0.46</u>	<u>0.44</u>	0.27	Feb	0.27	<u>0.13</u>	<u>0.09</u>	<u>0.50</u>	<u>0.34</u>	0.26
		0.004	0.013	0.001	0.002	0.070		0.071	0.395	0.548	0.000	0.020	0.075

Note: Bold digits — indicate reliable correlation coefficients.

	Autumn					Winter								
Species	Month		Aı	rea		Month			Area					
		11	12	21	22	-	2	3	4	5	12	13	14	15
Pink	Sep	<u>0.06</u>	<u>0.08</u>	<u>0.11</u>	<u>0.11</u>	Dec	<u>0.15</u>	<u>0.15</u>	<u>0.20</u>	0.28	<u>0.10</u>	<u>0.03</u>	0.05	<u>0.09</u>
		0.696	0.584	0.449	0.443		0.317	0.317	0.167	0.051	0.514	0.853	0.731	0.519
	Oct	0.04	<u>0.16</u>	0.15	0.08	Jan	0.26	<u>0.18</u>	<u>0.14</u>	<u>0.14</u>	<u>0.27</u>	<u>0.12</u>	<u>0.03</u>	<u>-0.02</u>
		0.767	0.265	0.291	0.565		0.071	0.229	0.350	0.345	0.061	0.409	0.820	0.888
	Nov	0.17	0.25	0.21	0.08	Feb	0.21	0.12	<u>0.10</u>	<u>0.15</u>	0.24	0.09	0.02	0.03
		0.235	0.082	0.148	0.570		0.139	0.409	0.482	0.296	0.100	0.518	0.902	0.849
Chum	Sep	<u>0.40</u>	<u>0.57</u>	<u>0.34</u>	0.36	Dec	<u>0.31</u>	0.25	0.24	0.27	<u>0.34</u>	0.21	0.08	0.04
		0.006	0.000	0.021	0.014		0.036	0.096	0.113	0.074	0.023	0.169	0.584	0.809
	Oct	<u>0.32</u>	<u>0.39</u>	0.23	<u>0.15</u>	Jan	<u>0.30</u>	<u>0.17</u>	<u>0.14</u>	<u>0.13</u>	<u>0.33</u>	<u>0.15</u>	<u>0.03</u>	<u>-0.07</u>
		0.028	0.008	0.127	0.309		0.046	0.263	0.344	0.386	0.023	0.320	0.868	0.651
	Nov	<u>0.30</u>	<u>0.39</u>	<u>0.33</u>	0.26	Feb	0.28	0.08	0.05	0.05	<u>0.35</u>	0.17	0.02	-0.06
		0.041	0.007	0.023	0.082		0.062	0.618	0.727	0.749	0.016	0.259	0.875	0.693
Sockeye	Sep	<u>0.45</u>	<u>0.59</u>	<u>0.42</u>	<u>0.43</u>	Dec	<u>0.34</u>	<u>0.30</u>	0.27	<u>0.32</u>	<u>0.36</u>	0.24	0.12	0.08
		0.001	0.000	0.003	0.002		0.018	0.041	0.064	0.030	0.012	0.103	0.440	0.595
	Oct	<u>0.41</u>	<u>0.45</u>	<u>0.33</u>	0.23	Jan	<u>0.31</u>	0.15	0.11	0.12	<u>0.42</u>	0.16	0.00	-0.08
		0.004	0.001	0.022	0.127		0.037	0.301	0.469	0.405	0.003	0.281	0.999	0.594
	Nov	<u>0.35</u>	<u>0.41</u>	<u>0.41</u>	<u>0.28</u>	Feb	<u>0.34</u>	<u>0.08</u>	<u>0.03</u>	<u>0.07</u>	<u>0.47</u>	<u>0.19</u>	<u>-0.01</u>	<u>-0.05</u>
		0.016	0.004	0.004	0.054		0.018	0.577	0.818	0.660	0.001	0.209	0.962	0.745

Table 2. Values of Pearson correlation coefficients and confidence probability (r/p), reflecting the dependence of the variability of the number of catches of Pacific salmon in Western Kamchatka on the indicators of aSST in the areas of their mass feeding migrations in autumn-winter period of the 1st year of the marine life in 1971-2020.

Note: Bold digits - indicate reliable correlation coefficients



Fig. 8. The relationship between salmon catches in the Eastern Kamchatka (A) and the Western Kamchatka (B) and aSST in the areas (squares) of mass feeding migrations in September of the first year of the marine life in 1971–2020.



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New Information about the Ocean Ecology of Sockeye Salmon and Relevance to Populations in the Fraser River, British Columbia

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Keywords: sockeye salmon, ocean ecology, Fraser River

Abstract

Sockeye salmon (Oncorhynchus nerka) were the third most abundant of the Pacific salmon species caught in both the 2019 and 2020 Gulf of Alaska winter surveys. In 2019, 84% of the sockeye salmon catch was in the northwestern area of the survey area, an area not fished in 2020. In both years some sockeye salmon were caught in the southwestern region of the study. In 2019, additional sampling was conducted west of the study area in the central Pacific prior to the expedition and included catches of sockeye salmon originating from Canada, United States and Russia. The broad distribution of Fraser River Chilko Lake sockeye salmon from coastal regions of British Columbia, through the Gulf of Alaska into the central Pacific Ocean suggests that migration patterns may be more of a dispersion than loops and that this dispersion may be influenced by ocean climate conditions. The complexity that this possibility introduces into management for future stewardship and fishing shows that we need to include an understanding of ocean ecology into the stewardship of all future production. This is additionally highlighted by the similarity of sockeye salmon and pink salmon (O. gorbuscha) diet, although there is very little overlap in their distribution, indicating minimal competitive interactions during these winters. Although there remains much to learn about sockeye salmon during their residence in the high seas, the mixed stock catch throughout the region and comparisons with sockeye salmon returns to British Columbia suggest that catch in the winter, specifically of first winter sockeye salmon, may provide an early estimate of relative returns of sockeye salmon two years later.

Introduction

A major objective of the two expeditions was to improve the understanding of the winter ecology of sockeye salmon in the open ocean with a specific focus on fish originating from British Columbia (BC). Methods and preliminary results are summarized in two reports by Pakhomov et al. (2019) and Somov et al. (2020). In this report, we repeat some of the catch results from these two reports, but focus on the highlights as they relate to new analyses and interpretations with a focus on sockeye salmon originating from the Fraser River in BC.

Most sockeye salmon spend 1 to 3 years in fresh water before migrating into coastal areas in the spring. They move offshore in the summer and winter where they remain for 1 to 3 years before returning to natal rivers to spawn in the late summer and fall (Burgner 1991; Farley et al. 2018). Average annual commercial catches of sockeye salmon by all countries in recent years from 2000 to 2020 averaged 16.5% of the total weight of all commercially caught Pacific salmon. Since 2000, the commercial catch of sockeye salmon by all countries has an increasing trend with an average from 2000 to 2020 of 148,904 MT. Over the period from 2000 to 2020, Alaska catches averaged 109,537 MT, Russian catches averaged 32,933 MT and Canada (BC) averaged 6,427 MT. However, in BC, the recent catches in 2019 and 2020 were 2.4% and 2.7% of the average catch from 2000 to 2020. Thus, as commercial catches were increasing in Alaska and Russia, they were declining in Canada with a major collapse in 2019 and 2020. There is no clear understanding of the cause of this collapse; however, the first two expeditions are providing new information on the ocean residency of sockeye salmon that will help direct future research.

General results

The Gulf of Alaska expeditions were conducted from February 19 to March 17, 2019 and March 12 to April 6, 2020. In 2019 fishing was conducted by the Russian research vessel *Professor Kaganovskiy* (Pakhomov et al. 2019) and in 2020 the fishing was conducted by the Canadian commercial trawler *Pacific Legacy* (Somov et al. 2020). There were 64 sets completed in 2019 and 52 sets completed in 2020, however sampling locations varied (Fig. 1) due to a combination of weather and a requirement to refuel mid-trip during the 2020 expedition. In both years most sets were conducted south of 52°N and west of 137.5°W (2019 - 50%; 2020 - 65%; southwest quadrant; Table 1). In 2019 the northwest region of the survey area (north of 52°N and west of 137.5°W; northwest quadrant; Table 1). In comparison, in 2020 there were only 2% of the sets in the northwest quadrant but 31% of the sets in the northeast quadrant. Additionally, in 2020, 25% of the sets were conducted in the southeast region of the study area (south of 52°N and east of 137.5°W; southeast quadrant) whereas in 2019 13% of the sets were in this region (Fig. 1; Table 1).



Fig 1. Survey area and set locations for 2019 (left panel) and 2020 (right panel) Gulf of Alaska surveys. Northwest (NW), northeast (NE), southwest (SW) and southeast (SE) quadrants of survey area are indicated with the number of sets conducted in each sector.

Area descriptions				2019		2020		
			Sets	Sockeye	Pink	Sets	Sockeye	Pink
NW	North of 52°, west of 137.5 °	#	24	61	0	2	1	0
		%	37.5%	83.6%	-	3.8%	2.0%	
NE	North of 52 °, east of 137.5 $^{\circ}$	#	0	0	0	8	16	2
		%	-	-	-	15.4%	31.4%	1.5%
SW	South of 52 °, west of 137.5 °	#	32	12	30	29	33	126
		%	50.0%	16.4%	96.8%	55.8%	64.7%	92.6%
SE	South of 52°, east of 137.5°	#	8	0	1	13	1	8
		%	12.5%	-	3.2%	25.0%	2.0%	5.9%
Total			64	73	31	52	51	136

Table 1. Number of sets and sockeye and pink salmon catch by study area.

There were 73 sockeye salmon and 31 pink salmon caught in 2019 and 51 sockeye salmon and 136 pink salmon caught in 2020 (Fig. 2). Sockeye salmon were the third most abundant species of salmon in both years, following chum (*O. nerka*) and coho (*O. kisutch*) salmon. The northwest was not fished in 2020 (Fig. 1) but was the region most sockeye salmon were caught in 2019. In 2020 most sockeye salmon were caught in the southwest quadrant (65%) and was the region where, in 2019, 16% of the catch occurred. In both years over 92% of the pink salmon were caught in the southeast quadrant of the study area.

In 2019, five of the sockeye salmon (7.8%) were identified as being in their first ocean winter compared to 37 (71%) of the catch in 2020. In 2019 the average size of the first ocean winter sockeye salmon was 36.5 ± 5.1 cm and 519 ± 209 g. In 2020 the average size of the first ocean winter sockeye salmon was 27.9 ± 3.4 cm and 232 ± 99 g. The origin of the sockeye salmon was determined using DNA analysis conducted at the Genetics Laboratory at the Pacific Biological Station in Nanaimo, BC, using a basin-wide baseline (Beacham et al. 2005, 2006). There were similarities in the stock composition of sockeye salmon in the two years, with representation from throughout SE Alaska and BC. However, in 2019 no Columbia River sockeye salmon were caught and in 2020 no Bristol Bay sockeye were caught (Fig.3). Additionally, sockeye from Russia were identified in 2020.

In 2019, additional fishing was conducted east of the study area in the central Pacific during February 1 - 6 while the *Professor Kaganovskiy* was on route to Vancouver. The fishing used the same gear as was used during the 2019 expedition. The 9 sets were conducted at approximately 47°N and extended over a distance of approximately



970 nm (Fig. 4A). Sixty-eight sockeye were captured in this region and tissue for DNA analysis was collected from 66 of the fish. The fish collected were identified as originating from Russia, Alaska and British Columbia (Fig. 4B).

Fig.2. Catch of sockeye (red circles) in 2019 and 2020 surveys of the Gulf of Alaska.



Fig. 3. DNA results for sockeye salmon caught in 2019 and 2020 Gulf of Alaska surveys.



Fig. 4. (A) Sets conducted in February 2019 in the central Pacific. Red dots indicate the relative catch of sockeye by set. (B) DNA results for the 66 fish analyzed for stock origin.

Highlights

Minimal overlap in the winter distribution of sockeye and pink salmon:

In 2019, the sockeye salmon were caught in 18 sets with 83% of these sets and 92% of the sockeye salmon caught at night. The pink salmon were caught in 10 sets with 70% of these sets and 87% of the pink salmon caught during the day. Only one set had both species and was conducted during the day. In 2020, 12 sets caught sockeye salmon and 4 sets caught pink salmon. The sockeye were caught in similar numbers between day and night sets but 98% of the pink salmon were caught during the day. In 2020, most pink salmon were caught in set 3 (N = 126) in the southwest region of the study area. The only sets with both pink and sockeye salmon in the 2020 survey were in the coastal areas northwest of Haida Gwaii (Queen Charlotte Islands; NE quadrant).

Overall, in both years in the open ocean areas, there was very little overlap in the distribution of sockeye and pink salmon (Fig. 5). If we identify the regions of pink and sockeye salmon catch in the open ocean (ovals; Fig. 5), only 6% of the sockeye catch occurred in the area of intersection of the regions. This comparison excludes the sets northwest of Haida Gwaii in the NE quadrant, as they occur on the continental shelf and not in the open ocean region of study area.



Fig. 5. Combined 2019 and 2020 catch of sockeye (red dots) and pink salmon (green dots) in the study area. The red and green ovals represent the general distribution area for the two species. The overlap in the ovals represents an area of shared habitat or about 6% of the total sockeye catch. In the open ocean region, the two species were only caught together in one set in 2019.

There were similarities in the diet of sockeye and pink salmon in both years of the study. In 2019, the most common diet item of sockeye salmon was euphausiids (58%), followed by pteropods (16%) and amphipods (11%). The diet of pink salmon in 2019 was similar with euphausiids (50%), pteropods (12%) and amphipods (11%). In 2020, the diet of sockeye salmon was euphausiids (57.7%), pteropods (16.3%) and amphipods (10.6%). The diet of pink salmon in 2020 was again similar with euphausiids (50.0%), pteropods (11.8%) and amphipods (9.9%).

One of the interpretations for the fluctuations in abundance of sockeye salmon has been interspecific competition for prey between pink and sockeye salmon in the winter when it was proposed that their distributions overlap (Ruggerone et al. 2003; Nielsen and Ruggerone 2008). The focus for their hypothesis has been the Bering Sea, but the interspecific competition would be expected to also occur in the Gulf of Alaska. Our catches clearly showed that pink salmon were concentrated in the warmer southern areas of the survey with distributions that appeared to extend south of the survey area. Sockeye salmon, however, were caught in the cooler waters to the north. The similar diets might indicate a competitive interaction, but the distributions clearly showed that competitive interactions were minimal in the winter in 2019 and 2020.

Ocean migration pattern of sockeye salmon from the Fraser River and other areas around the Gulf of Alaska:

Juvenile sockeye salmon from the Fraser River and other rivers from Washington State to SE Alaska mostly spend two winters in the ocean (Burgner 1991; Farley et al. 2018). Ocean entry times vary, but in general, the coastal residence time is short, with juveniles moving offshore in summer and migrating quickly in a counter-clockwise direction north. The counter-clockwise movement was proposed by French et al. (1976) and by Hartt and Dell (1986). The reasons for this interpretation were summarized by Burgner (1991) and Farley et al. (2018). More recent stock identification methods using DNA generally support this proposed interpretation of a rapid movement northward with residence in the Gulf of Alaska for two winters before returning to spawn in natal rivers (Tucker et al. 2009; Beacham et al. 2014); however, sampling for the work supporting this migration model was focussed within the coastal areas.

There is another migration model for Fraser River sockeye salmon that is based on ocean currents and could be described as a one and one half loop model. Walter et al. (1997) used a model of ocean currents and sockeye salmon swimming speeds to propose that these salmon migrated northward in a counter-clockwise direction making one large loop in the Gulf of Alaska followed by a variable half loop over two winters. These authors concluded that the primary force driving the migration pattern of sockeye salmon was surface ocean currents.

In the winter surveys, sockeye salmon originating from BC were identified in both years (Table 2). In total, there were 39 sockeye salmon from BC caught in the two expeditions and 21 were from the Fraser River (Fig. 3) with 7 from the Chilko Lake. Twenty-eight of the sockeye salmon identified as originating from BC were in their first ocean winter (Table 2). In the sets conducted in the central Pacific by the Russian scientists in February 2019, 8 (12%) of the 66 sockeye salmon originated from BC (Fig. 4B) and five of these fish were in their first ocean winter. Therefore, over both years and all surveys in the Gulf of Alaska and central Pacific there were 33 fish from BC that were in their first ocean winter and 17 of these were from the Fraser River with 6 being identified as originating from Chilko Lake. These fish, including the Chilko Lake sockeye salmon were distributed from the coastal area of BC (132°W) to the central Pacific (176.2°E; Fig. 6) and identify a distribution that is broadly dispersed throughout the east and central Pacific during the first ocean winter. This dispersion of ocean age 1 juveniles could be from a number of loops from the north to the south or a dispersion into areas to the south, as the migrating fish begin a route west along the shelf and encounter the Aleutian Islands. This is a very different pattern than either of the previous two loop or loop and one half models. The much dispersed pattern of ocean age 1 Chilko Lake sockeye salmon that spans about 4,000 km shows that the ultimate survival of adults after the first ocean winter is influenced by a spectrum of ocean and climate conditions. Furthermore, previous surveys conducted in the Strait of Georgia in February 2004 captured sockeye salmon from the Fraser River. These 33 sockeye were all ocean age 1 fish and represented major stock groups from the Fraser River (Table 3). This further extends the range of Fraser River sockeye salmon. The complexity that this broad range of ocean age 1 sockeye salmon possibility introduces into management for future stewardship and fishing shows that we need to include an understanding of ocean ecology into the stewardship of all future production.

		2019		2020
	All ages	First ocean winter	All ages	First ocean winter
British Columbia	12 (16.4%)	3	27 (52.9)	25
Fraser River ¹	6	1	15	15
Transboundary	7 (9.6%)	0	3 (5.9%)	2
Southern US	-	-	1 (2.0%)	1
Alaska	18 (24.7%)	1	12 (23.5%)	3
Bristol Bay	34 (46.6%)	1	-	
Russia	-	-	4 (7.8%)	3
Unidentified	2 (2.7%)	0	4 (7.8%)	3
Total	73	5	51	37

 Table 2. Stock origin of sockeye salmon for total catch and for first ocean winter fish.

¹ Fraser River sockeye included in total British Columbia count



Fig. 6. Catch of first winter sockeye salmon originating from Canada. Catch includes 2019 and 2020 Gulf of Alaska expeditions and the sets conducted in the central Pacific in February 2019. There was an additional discovery that is important to highlight. In 2020, there were 4 sockeye caught in the Gulf of Alaska that originated in Kamchatka, Russia (Fig. 7). Three of these were ocean age 1 fish found over 4,000 km east of Kamchatka. Additionally, there was an ocean age 1 Columbia River sockeye salmon caught on the most westerly line of the study area that was over 2,000 km from its natal river if it had travelled direct in a direct line. These 3 Russian and 1 Columbia River ocean age 1 sockeye and the extreme distribution of ocean age 1 fish from the Fraser River show that juvenile sockeye salmon undergo extensive migrations in their first ocean year. Energy needed for these migrations is related to prey availability and metabolic challenges that relate to water temperature. These results show how little we understand about the factors affecting the survival of sockeye salmon once they enter the ocean. The importance of DNA stock identification is obvious, which requires that we are confident about the genetic baseline used to make these determinations.

There should be little doubt that it is time to understand where sockeye salmon are in the two years of their ocean residence and what might affect their distributions. As ocean warming events (Bond et al. 2015; Cavole et al. 2016; DiLorenzo and Mantua 2016) increase in frequency and other climate related changes in ocean conditions occur that affect sockeye salmon, this understanding becomes an essential contribution to forecasting returns and to understanding the future of sockeye salmon production in the Fraser River and other rivers.

	Stock group	Number	Percent
Lower Adams	Late Run	22	67%
Harrison	Ocean type (no winter in freshwater)	6	18%
Horsefly	Summer	2	6%
Quesnel/Raft/Mitchell	Summer	3	9%
Total		33	

Table 3. Stock composition of sockeye salmon caught by trawl in Strait of Georgia, February 2004.



Fig 7. Catch of sockeye salmon identified as originating from Russia (purple triangles), Columbia River in southern US (blue triangle) and most westerly catch of sockeye of Canadian origin (red triangle). The polygons represent the estimated distribution of North American origin sockeye salmon (blue) and Asian origin sockeye salmon (red) adapted from Myers et al. 2007.

The potential to develop an index of return for Fraser River sockeye salmon:

The stock composition of BC sockeye salmon in the two expeditions appears to be representative of the expected returns for the major populations in the Gulf of Alaska (Table 2). There was representation from Canadian, US and Russian sockeye salmon areas in the catch but also from multiple rivers and streams in both Canada and the US. This includes the major sockeye salmon producing rivers including the Fraser River in southern BC, the Babine and Stikine Rivers in northern BC, and from all regions including Bristol Bay, Cook Inlet, and SE Alaska in the US. Possibly more importantly, there was representation from smaller populations including Sproat Lake and Heydon River in southern BC, indicating that a mixture of stocks were being encountered in the catch rather than only a few.

We hypothesize that major deviations from the expected composition may be an indication of poor survival in coastal areas prior to the first ocean winter, as has been reported for other Pacific salmon (Duffy and Beauchamp 2011; Graham et al. 2019; Farley et al. 2020) and as indicated by the 72% decline in catch of chum salmon in Japan

(Beamish and Neville 2021). Catches of ocean age 1 sockeye salmon from the Fraser River were small but we proposed that the poor catch of only 3 fish in 2019 might be an indication of poor ocean survival for the brood year return in 2020. The total return of about 400,000 sockeye salmon in 2020 was an historic low return. The larger catches of ocean age 1 Fraser River fish in 2020 was interpreted to be a possible indication of a better return in 2021 and the preliminary estimate of just over 2 million fish seems to support this possibility. This is not a forecast of abundance, but an index of relative ocean survival using the relative abundance of ocean age 1 fish. Variability in the offshore survey catches of immature Pacific salmon over a number of years was proposed by Nagasawa and Azumaya (2009) to possibly result from differences in production prior to moving offshore. Russia continues to use open ocean surveys to provide reliable forecasts of Pacific salmon returns showing that abundances in open ocean surveys can be used to improve management. We know that most juvenile sockeye salmon from BC move northward and away from coastal areas off BC (Tucker et al. 2009). Thus, it may be possible to develop an index that would provide relative production estimates at least one year before sockeye salmon return to the coastal areas now used to estimate returns and fishing opportunities. In addition to an index of return abundance, the associated information related to ocean conditions could improve the understanding of future production in the expected climate related changes in ocean ecosystems.

Conclusion

We suggest that the surprising poor returns of sockeye salmon returns to British Columbia in 2019 and 2020 identify the necessity to expand research to provide a bigger picture and more complete understanding of the factors that regulate sockeye salmon abundance in the ocean. We suggest that the data collected in 2019 and 2020 should not be dismissed as being too small to be of use, but to be the first indication that more effort will provide new methods of forecasting and stewardship.

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Trends in the Observations at Ocean Station P and Relevance to the Two Expeditions

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Keywords: Line P program; long-term oceanographic monitoring; hydrography; nutrients; phytoplankton composition

Relevance of Line P to Expeditions

- Line P extends from the coast to Station P (=P26), about 1,400 kms. Stations P20-P26 have a high degree of overlap with IYS Expeditions stations (Fig. 1).
- Sampling started in 1956 and continues to this day, providing context for the Expeditions; initiated using weatherships deployed at Station P (aka Ocean Station Papa), spatial and temporal coverage changed over time with new variables added as they became standardized.
- At present, sampling occurs 3 times a year at 27 stations and it includes many biogeochemical variables.



Fig. 1. Location of Line P stations (red) with respect to IYS-1 (yellow; Feb 16 - Mar 18, 2019) and IYS-2 (cyan; Mar 11 - Apr 7, 2020) stations.

Highlights for 2019

- For most of 2019, the NE Pacific was in marine heatwave conditions for both surface and subsurface waters (up to 150 m).
- The mixing in the winter of 2018/19 was very low; less mixing implies lower than normal surface nutrient levels in the spring of 2019.
- Surface nutrient concentrations along Line P in 2019 were among the lowest on record. In particular, summer mixed layer nitrate was depleted at Station P (P26) for the first time in 60 years of observations.
- Phytoplankton community composition along Line P in spring of 2019 was similar to that of 2018 but different from previous years, with diatoms dominating phytoplankton biomass at several open-ocean stations.
- 2019 Expedition sampling grid intersected 4 eddies, mostly in the eddy-rich northern part of the Gulf of Alaska.

Highlights for 2020

- For most of 2020, the NE Pacific was in marine heatwave conditions for both surface and subsurface waters (up to 150 m).
- The mixing in the winter of 2019/20 was weak, suggesting lower surface nutrient levels in the spring of 2020, but not as low as 2019.
- Winter surface nutrient concentrations along Line P in 2020 were among the lowest on record due to increased stratification that restricted nutrient renewal from vertical transport, similar to that observed in previous years.
- A Haida eddy with lower than normal surface nutrients was present at the offshore stations of Line P in winter of 2020. By summer, surface nutrients were similar to or higher than those observed in winter.
- Phytoplankton biomass was relatively low along Line P in 2020 but community composition was similar to that of previous years, except for a decrease in diatom abundance.
- The 2020 Expedition sampling grid only intersected two eddies, but they were both large Haida eddies, which are expected to influence local zooplankton.

2019 Description

1. Temperature and stratification (Ross and Robert 2020)

In the NE Pacific, the sea surface temperatures (SSTs) were warm throughout 2019 (Fig. 2). In fact, the SSTs were so warm that the NE Pacific was in marine heatwave conditions through most of the year. This marine heatwave received a fair amount of press (see Hannah et al. 2020 for details; also Amaya et al. 2020) and was so strong in the western NE Pacific to have record breaking yearly SST anomalies (NOAA; www.ncdc.noaa.gov/sotc/service/global/map-percentile-mntp/201901-201912.png). Unlike previous years, El Niño Southern Oscillation (ENSO) had little effect on the SSTs in the NE Pacific in 2019. The above average SSTs might have been aided by the weak El Niño conditions in the first half of the year, but the warm anomalies increased in the latter half of the year during ENSO-neutral conditions.



Fig. 2. Seasonal maps of temperature anomalies in the Pacific Ocean for 2019. The colour bar on the right, showing the temperature anomaly in °C, applies to all panels. Anomalies are relative to 1981-2010 base period. Source: NOAA Extended SST v4 http://www.esrl.noaa.gov/psd/cgi-bin/data/composites/printpage.pl.

Above average temperatures [relative to both the 1981-2010 (Fig. 2, 4) and 1956-2012 (Fig. 3) means] were observed in subsurface waters as well. Temperature anomalies at Station P (based on the interpolation of Argo float data onto the location of Station P; Fig. 3), showed above average subsurface temperatures at Station P throughout

2019. This is in contrast to 2018, where subsurface temperatures were near-normal. The strongest anomalies (reaching 3 standard deviations above the mean) were at about 100 m depth, just above the permanent pycnocline. The marine heatwave was also observed across the entire line in the 2019 Line P data (Fig. 4); most strongly in the August 2019 data, which resembles Aug 2016.



2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015 2016 2017 2018 2019 2020

Fig. 3. False colour plot of temperature anomalies relative to the 1956-2012 seasonally-corrected mean and standard deviation (from the Line P time series), as observed by Argo floats near Station P (P26: 50° N, 145 ° W). The cool colours indicate cooler than average temperatures and warm colours indicate warmer that average temperatures. Dark colours indicate anomalies that are large compared with the 1956-2012 standard deviations. The black lines highlight regions with anomalies that are 3 and 4 standard deviations above the mean.



Fig. 4. Temperature anomalies (°C) along Line P from 2015 to 2019 with respect to the 1981-2010 average.

The winter stratification was stronger in 2018/19 than in either of 2017/18 and 2016/17, more similar to the winters during the 'Blob' years (2013/14, 2014/15; Freeland 2015). In 2017 and 2018, it appeared that winter mixing had returned to normal. The history of the $\sigma_{\Theta}=25.7$ kg/m³ isopycnal (highlighted with a thick black line in Fig. 2-5) illustrates this nicely. It remained very deep throughout the 2013-2015 marine heat wave, deeper even than much of the 2003-2005 warm period, and shoaled in the winter of 2015/16 to levels last experienced during 2003-2005, while in 2016/17 stratification had returned to a level similar to the winters of 2010/11 and 2011/12. This return to weak mixing suggests that nutrient supply from deep waters should have been weaker and therefore early spring nutrient levels lower in the spring of 2019. With the current marine heatwave condition, it is likely that 2019/20 will also have weaker than normal winter mixing.





Fig. 4. Coloured contour plot of density as observed by Argo floats near Station P (P26: 50° N, 145 ° W). The colours indicate potential density (yellow is denser and blue lighter). The black lines highlight the σ_{θ} =25.2 kg/m³ (thin) and 25.7 kg/m³ (thick) isopycnals.

2. Nutrients and Phytoplankton (Peña and Nemcek 2020)

Sampling for phytoplankton composition has been carried out at most of the stations along Line P since June 2010. The abundance and composition of phytoplankton are determined from phytoplankton pigments (chlorophylls and carotenoids) analyzed by high performance liquid chromatography (HPLC) as described in Nemcek and Peña (2014). The HPLC pigment data are processed using a factorization matrix program (CHEMTAX) to estimate the contribution of the main taxonomic groups of phytoplankton to total chlorophyll a (chl-a) (Mackey et al. 1996).

Line P extends from the southwest corner of Vancouver Island to Station P (Fig. 1) in the high-nutrient lowchlorophyll (HNLC) region where surface nutrient concentrations are usually high (>5 mmol m⁻³) and chl-a concentrations are low (<0.5 mg m⁻³) year-round due to iron (Fe) limitation of phytoplankton growth. In these Fepoor offshore waters, small flagellates (mainly haptophytes) dominate phytoplankton biomass whereas on the shelf there is high seasonal variability in nutrient concentrations, phytoplankton biomass and composition. In the winter of 2018/19, nutrient renewal from vertical transport was restricted in the NEP due to increased stratification, similar to that observed in winter 2014/15 during "the blob". As a result, surface nitrate and silicate values in 2019 were among the lowest on record at most stations along Line P (Fig. 6). In particular, summer mixed layer nitrate was depleted in the HNLC region for the first time since sampling started 60 years ago in 1969. Higher chl-a concentrations were observed at these offshore stations than in the transition region of Line P in spring and summer of 2019 (Fig. 6).

Phytoplankton assemblage composition along Line P shows an increase in the relative abundance of diatoms at several stations (~P15 to P22) in June 2019, similar to that observed in 2018, and consistent with the decrease in surface silicate concentration in this region. By August 2019, diatoms were more abundant farther offshore whereas phytoplankton composition was in general similar to that observed in previous years at other stations, with haptophytes dominating phytoplankton biomass (Fig. 7).



Fig. 6. Nitrate (left panels, mmol m^{-3}), silicate (center panels, mmol m^{-3}), and chlorophyll-a (right panels, mg m^{-3}) in surface waters along Line P from P4 to P26 in winter (top panels), spring (middle panels) and summer (bottom panels). The left and center panels show the average (grey line) and range (shaded area) of nutrient concentrations in 2000-2014. The right panel shows all values in 2009-2019. In all panels, data for 2019 are shown in blue and for 2015 in red.



Fig. 7. Relative phytoplankton composition in the upper layer at stations along Line P (see Fig. 1) in June (left panels) and Aug./Sept. (right panels) of 2015 to 2019.

3. Eddy activity

Four eddies intersected the sampling stations of the 2019 Expedition (Fig. 8). Three were in the northern part of the Gulf of Alaska, which tends to have more eddy activity. The southernmost eddy was a Haida eddy. Haida eddies carry coastal/shelf water with associated nutrients and micro-communities offshore into the high-nutrient low-chlorophyll region of the Gulf of Alaska (Whitney and Robert 2002; Mackas and Galbraith 2002; Mackas et al. 2005).



Fig. 8. False color mapping of satellite sea level anomaly from March 3, 2019. Also indicated are the paths of eddies tracked over their lifetimes, with symbols highlighting their positions during the 2019 Expedition. For reference, Line P stations are shown in red.

2020 Description

1. Temperature and stratification (Ross and Robert 2021)

In the NE Pacific, the SSTs were warm throughout 2020 (Fig. 9). In fact, the SSTs were so warm that the NE Pacific was in marine heatwave conditions through much of the year. This is a continuation of the marine heatwave that started in 2019 (Amaya et al. 2020; Hannah et al. 2020; Ross and Robert 2020). In contrast to the 2013-16 marine heatwave, when positive SST anomalies were amplified by a large El Niño in 2015, Fig. 9 shows that La Niña conditions grew throughout 2020. La Niña conditions in the NE Pacific typically decrease SST; thus the marine heatwave would likely have been stronger without the La Niña.

Above average temperatures [relative to both the 1981-2010 (Fig. 9, 11) and 1956-2012 (Fig. 10) means] were observed in subsurface waters as well. Temperature anomalies at Station P (based on the interpolation of Argo float data onto the location of Station P; Fig. 10), showed above average subsurface temperatures at Station P throughout 2020. This is very similar to 2019. The strongest anomalies (reaching 3 standard deviations above the mean) were at about 100 m depth, just above the permanent pycnocline. Unlike for the 2013-16 marine heatwave, there is no indication that the depth the peak temperature anomaly increased over time. The marine heatwave was observed across the entirety of Line P (Fig. 11). Note that an eddy was present near the offshore end of the line in February; thus, the deep temperature anomalies were related to that transient feature and not the marine heatwave). The anomalies were largest in the August 2020 data, which shows only slightly weaker anomalies than in 2019, despite La Niña conditions.

The winter stratification was strong in 2019/20, but not as strong as the previous winter, which showed extremely low winter mixing, similar to the winters during the 'Blob' years (2013/14, 2014/15; Freeland 2015). During 2017-2018, it appeared that winter mixing had returned to normal, but the recent marine heatwave has again reduced winter mixing. The history of the σ_{Θ} =25.7 kg/m³ isopycnal (highlighted with a thick black line in Fig. 12) illustrates this nicely. It remained very deep throughout the 2013-16 marine heatwave, deeper even than much of

the 2003-2005 warm period, and shoaled in the winter of 2015/16 to levels last experienced during 2003-2005, while in 2016/17 stratification had returned to a level similar to the winters of 2010/11 and 2011/12. This return to weak mixing suggests that nutrient supply from deep waters should have been weaker and therefore early spring nutrient levels lower in the spring of 2020, but not quite as low as in 2019. With the marine heatwave conditions appearing to be tailing off (Fig. 10) and a La Niña winter, it is likely that 2020/21 will experience stronger winter mixing.



Fig. 9. Seasonal maps of temperature anomalies in the Pacific Ocean for 2020. The colour bar on the right, showing the temperature anomaly in °C, applies to all panels. Anomalies are relative to 1981-2010 base period. Source: NOAA Extended SST v4 http://www.esrl.noaa.gov/psd/cgi-bin/data/composites/printpage.pl.



Fig. 10. Plot of temperature anomalies relative to the 1956-2012 seasonally-corrected mean and standard deviation (from the Line P time series), as observed by Argo floats near Station P (P26: 50° N, 145° W). The cool colours indicate cooler than average temperatures and warm colours indicate warmer that average temperatures. Dark colours indicate anomalies that are large compared with the 1956-2012 standard deviations. The black lines highlight regions with anomalies that are 3 and 4 standard deviations above the mean.



Fig. 11. Temperature anomalies (°C) along Line P from 2016 to 2020 with respect to the 1981-2010 mean.



Fig. 12. Coloured contour plot of density as observed by Argo floats near Station P (P26: 50° N, 145° W). The colours indicate potential density (yellow is denser and blue lighter). The black lines highlight the σ_{θ} =25.2 kg/m³ (thin) and 25.7 kg/m³ (thick) isopycnals.

2. Nutrients and Phytoplankton (Peña and Nemcek 2021)

In the winter of 2019/2020, nutrient renewal from vertical transport was restricted due to increased stratification, similar to that observed in previous years. In addition, a Haida eddy with lower nutrient concentrations than surrounding water was observed at the most offshore stations. As a result, surface nitrate and silicate values in winter 2020 were at the lower range of previous years, in particular at the most offshore stations where the eddy was present (Fig. 13). However, summer nutrient concentrations were similar or higher than winter

values at these offshore stations. At other stations, summer mixed layer nutrients in 2020 were below average values but not as low as in 2019 when nitrate depletion extended for the first time to P26. Similarly, winter and summer Chl-a concentrations were at the lower range of values from previous years (Fig. 13).



Fig. 13. Nitrate (left panels, mmol m⁻³), silicate (center panels, mmol m⁻³), and chlorophyll-a (right panels, mg m⁻³) in surface waters along Line P from P4 to P26 in winter (top panels), spring (middle panels) and summer (bottom panels). The left and center panels show the average (grey line) and standard deviation (shaded area) of nutrient concentrations in 2000-2020. The right panel shows all values in 2009-2020. In all panels, data for 2019 are shown in blue and for 2020 in red.

Phytoplankton assemblage composition in 2020 was in general similar to that observed in previous years with haptophytes dominating phytoplankton biomass at most stations (Fig. 14), except for a decrease in the relative abundance of diatoms during the summer.

Several environmental factors including temperature, irradiance and nutrient availability, as well as grazing pressure, determine phytoplankton abundance and community composition. During the Blob in 2015, changes in phytoplankton abundance and composition were observed along Line P likely in response to the increase in surface temperature and changes in nutrient availability (Peña et al. 2019). Since then, nutrient availability, phytoplankton biomass and diatom abundance have shown significant fluctuations in the NE subarctic Pacific. These include the unprecedented depletion of mixed layer nitrate, and to a lesser degree of silicate, in the HNLC region of Line P in the summer of 2019, as well as sporadic increases in diatom abundance at the most offshore stations of Line P in September of 2017 and 2019 and their decrease at most stations in summer of 2020. These changes could be due to an increase in Fe availability or to anomalous transport of nutrient-depleted waters into the region.

Phytoplankton abundance and community composition are key factors influencing trophic processes and biogeochemical cycles in the ocean. Organic matter produced by phytoplankton is continuously transferred from lower to higher trophic levels, so the abundance, composition and distribution patterns of phytoplankton ultimately affect the sustainability of all marine life. The observed changes at the base of the food web during and after the Blob could have ecosystem-wide implications.

3. Eddy activity

Because of its more southern extent, only two eddies intersected the sampling stations of the 2020 Expedition (Fig. 15). However, both of these were large long-lived Haida eddies. Haida eddies carry coastal/shelf water with associated nutrients and micro-communities offshore into the high-nutrient low-chlorophyll region of the Gulf of Alaska (Mackas and Galbraith 2002; Whitney and Robert 2002; Mackas et al. 2005).



Fig. 14. Relative phytoplankton composition in the upper layer at stations along Line P (see Fig. 14-1) in February (left panels) and Aug./Sept. (right panels) of 2016 to 2020. Blank spaces indicate no data were collected.



Fig. 15. False color mapping of satellite sea level anomaly from March 26, 2020. Also indicated are the paths of eddies tracked over their lifetimes, with symbols highlighting their positions during the 2020 Expedition. For reference, Line P stations are shown in red.

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Inter-comparison of Bongo and Juday Nets Size-fractionated Zooplankton Biomass Collected in the Gulf of Alaska During 2019

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In the North Pacific, the zooplankton data sets in the western and eastern parts were collected using different sampling gears, most often by Bongo and Juday nets. While preliminary taxonomic zooplankton inter-comparison between nets was performed, the biomass comparison is still unavailable. During winter (February-March) 2019, in the Gulf of Alaska (GoA) 34 paired zooplankton samples were collected using Bongo and Juday nets (Fig. 1). On board of R/V *Professor Kaganovskiy*, Bongo (0.5 m⁻² mouth area mesh 0.250 mm) and Juday (0.1 m⁻² mouth area, mesh 0.160 mm) nets were towed vertically from 250–0 m and 200-0 m, respectively. On board, the Bongo fresh zooplankton sample was size fractionated using 0.25, 0.5, 1, 2, and 4 mm sieves (Fig. 2). Juday nets samples were fixed in a 4% formaldehyde-seawater solution and size fractionated later using the same set of sieves. Size-fractions were then oven-dried at 50°C to the constant weight and weighed to the nearest 0.1 mg. Biomass was calculated by dividing size-fraction mass by the volume filtered estimated either using flowmeter (Bongo) or by the distance travelled multiplied by the mouth area (Juday).





A Juday - Bongo (similar mesh size) comparison was previously completed by Dave Kimmel (NMFS-AKFSC, unpublished) using samples collected in the Bering Sea. The author found "overall good taxonomic agreement between the gears. This is most evident in the station comparisons where both nets typically followed the same pattern, with some notable exceptions. It was concluded that two gears are broadly comparable and degree of agreement is linked to overall zooplankton abundances."

In the Gulf of Alaska, both nets produced patchy total zooplankton distribution and while Bongo/Juday biomass ratios ranged widely (up to 10-fold, Fig. 3), the mean daytime and nighttime ratios were 2.25 ± 1.16 (\pm SD) and 1.83 ± 0.67 , respectively. The overall Bongo/Juday ratio was 1.96 ± 0.87 (Fig. 4). In general, daytime Bongo/Juday ratios were slightly higher compared to nighttime ratios. In addition, the highest ratios were observed in the size-fraction of 2 to 4 mm (Fig. 4).

In summary, (a) the Juday net consistently caught less biomass than the Bongo net; (b) there were differences (albeit non-significant) between daytime and nighttime Bongo/Juday ratios; (c) there were differences between Bongo/Juday ratios in individual size fractions of zooplankton; and (d) Bongo/Juday ratios appeared to decline in relation to the increasing sample biomass.



Fig. 2. Example of the size fractionated zooplankton sample.





Fig. 4. Bongo to Juday net biomass ratio for zooplankton size fractions during February-March 2019 in the Gulf of Alaska. D - daytime samples; N - nighttime samples; bars - 1 standard deviation.

Winter Distribution of Chum Salmon in the Gulf of Alaska: A Review

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Keywords: chum salmon, winter distribution, North Pacific Ocean

The Gulf of Alaska is an important habitat for Pacific salmon (*Oncorhynchus* spp.). In this productive ecosystem, Asian and North American chum salmon (*O. keta*) populations intermingle in winter (Urawa et al. 1997, 2016; Beacham et al. 2009), while North American populations are dominant in summer (Urawa et al. 2000, 2009).

An international salmon research expedition was conducted in the Gulf of Alaska (47-56°N, 137-147°W) between February 16 and March 18, 2019 onboard the Russian R/V *Professor Kaganovskiy* (Pakhomov et al. 2019). A total of 223 chum salmon were caught by a surface trawl, which was the most abundant catch among Pacific salmon. Most chum salmon were distributed in south of 52°N, while some ocean age (OA)- 3 and 4 fish extended their distribution in the northern waters (Fig. 1). The regional origin of individual chum salmon was estimated by using an extended Pacific-Rim SNP baseline (Urawa et al. 2021). The SNP analysis confirmed that chum salmon in the winter Gulf of Alaska were a mixture of various populations: 22.0% Japan, 20.2% Russia, 14.8% West Alaska, 5.1% Yukon River, 6.5% Central Alaska, 11.2% Southeast Alaska (SEAK), 16.5% British Columbia (BC), and 3.7% Washington. In OA-1 fish, SEAK and BC populations were dominant, and West Alaska, Yukon and Asian populations were predominant. In OA-3 fish, West Alaska, Russian and Japanese populations were dominant, each occupying 25%. The proportion of Asian (Russian and Japanese) populations increased with ocean age: 0% in OA-1, 40% in OA-2, 50% in OA-3, and over 70% in OA-4 fish.



Fig. 1. CPUE distribution of chum salmon by ocean age (OA) in the Gulf of Alaska in February and March 2019. CPUE = number of catches per 1-h trawl.

Winter high-seas salmon surveys were conducted in the North Pacific Ocean and Bering Sea by the Japanese R/V *Kaiyo-maru* in 1996 (Ueno et al. 1996), 1998 (Ishida et al. 1998) and 2006 (Fukuwaka et al. 2006; Fig. 2). The trawl surveys clarified that OA-1 chum salmon were high density in the western North Pacific Ocean (Fig. 3), and the fish were mostly of Japanese and Russian origins (Urawa and Ueno 1997, 1999; Urawa et al. 1997; Sato et al. 2007). In contrast to young fish, older chum salmon (OA 2–4) were relatively abundant in the central North Pacific

Ocean and the Gulf of Alaska (Fig. 4). The origins of these fish were mostly Russian population in the western and central North Pacific Ocean (Urawa and Ueno 1997, 1999), but a mixture of Asian and North American populations in the Gulf of Alaska (Urawa et al. 1997, 2009, 2016; Beacham et al. 2009). West Alaskan and Asian populations were not included in OA-1 chum salmon in the Gulf of Alaska like in the 2019 estimates. It is unknown where West Alaskan chum salmon stay over their first winter. On the other hand, Japanese and Russian chum salmon migrate into the Gulf of Alaska, and Russian chum salmon are widely distributed in the North Pacific Ocean including the Gulf of Alaska (Urawa et al. 2018). There are few chum salmon in the Bering Sea during winter (Ishida et al. 1998; Figs. 3 and 4).



Fig. 2. Sampling locations for winter salmon by Japanese R/V *Kaiyo-maru* between January and March in 1996, 1998 and 2006.

Fig. 3. Winter CPUE distribution of ocean age-1 chum salmon between January and March in 1996, 1998 and 2006. CPUE = number of catches per 1-h trawl. (From Urawa et al. 2018).



Skinny chum salmon were frequently found in the Gulf of Alaska during the 2019 winter expedition (Urawa et al. 2021). Comparing the body size and condition factor (CF) of OA-2 chum salmon caught in the central Gulf of Alaska in the winter of 1996, 2006 and 2019, there was no difference in the fork length, whose average was around

400 mm (Fig. 5). However, the mean body weight was variable among the three years, and the CF was significantly lower in 2019 chum salmon. The frequency of occurrence of skinny chum salmon (CF<0.9) was 5% in 1996, 10% in 2006, and 39% in 2019. Kaga et al. (2006) reported the total lipid contents of chum salmon were significantly lower in the Gulf of Alaska than in the western North Pacific Ocean during winter (Fig. 6). The feeding intensity (stomach fullness) of chum salmon was highest during summer, lowest in February, and increased in April (Naydenko et al. 2016). The growth and energy reserves of chum salmon prior to overwintering may affect their nutrient condition during winter. The mean sea surface temperature (SST) of winter chum salmon habitats was geographically different between the western North Pacific Ocean and the Gulf of Alaska: almost 2°C higher in the Gulf of Alaska (Fig. 7). The higher habitat temperature may hasten the metabolism of overwintering chum salmon, causing their skinny condition and low lipid content in the Gulf of Alaska.



Fig. 5. A comparison of body size and condition factor (CF) in ocean age-2 chum salmon caught in the central Gulf of Alaska in the winter of 1996, 2006 and 2019. Bars indicate SD.



Fig. 6. Total lipid content in the muscle of chum salmon caught in the western North Pacific Ocean and Gulf of Alaska during the winter of 2006. Bars indicate SD. (From Kaga et al. 2006).



Fig. 7. Mean SST of pink and chum salmon habitats in the western North Pacific Ocean (NPO) and Gulf of Alaska in the winter of 1996, 1998, 2006 and 2019. OA means ocean age. Bars indicate range of SST. (Revised from Urawa et al. 2018).

The mean SST of winter chum salmon habitat in each of the western North Pacific Ocean and the Gulf of Alaska was almost stable across the three years (1996, 2006 and 2019), and the range of SST was relatively narrow (Fig. 7). These observations suggest that chum salmon select similar temperature regimes each winter. Consequently, their winter habitat may shift when the seawater temperature increases with future climate warming. Simple climate warming scenarios (homogeneous SST increase of 1.5°C or 3°C) have suggested possible shifts of summer and winter habitat space for chum salmon (Fig. 8). In summer, the habitat space in the North Pacific Ocean and Bering Sea is decreasing with increasing SST (Azumaya and Urawa 2019). In winter, current chum salmon habitat space is narrow in the western North Pacific Ocean, but extensive in the Gulf of Alaska (Azumaya et al. 2007; Fig. 8), which may be a reason for the intensive distribution of Asian and North American chum salmon populations in the Gulf of Alaska. Two climate warming scenarios have suggested the winter habitat space for chum salmon will reduce in the Gulf of Alaska, increase in the western North Pacific Ocean, and expand to the Bering Sea (Urawa et al. 2014). Extensive changes of habitat space with increasing SST may cause a strong impact on the stock-specific life history traits of chum salmon such as their migration route, growth and maturing pattern, and timing of migration and spawning.



Fig. 8. Possible habitat shifts of chum salmon in summer and winter after homogeneous SST increase of 1.5°C or 3°C in the ocean. The highest thermal limit is 15.6°C for summer and 7.5°C for winter chum salmon according to actual observations. (Modified from Azumaya et al. 2007 and Urawa et al. 2014).

In summary, OA-1 chum salmon are high density in the western North Pacific Ocean, while older chum salmon are mainly distributed in the Gulf of Alaska, where Asian and North American populations intermingle during winter. Mean SST of winter chum salmon habitats is almost stable among years, but different by regions: approximately 2°C higher in the Gulf of Alaska than in the western North Pacific Ocean. OA-1 chum salmon have lower lipid contents than older fish, suggesting the depletion of their energy serves during the first winter. Chum salmon have lower trophic condition in the Gulf of Alaska than in the western North Pacific Ocean, maybe due to higher habitat temperature. Future climate warming may affect the ocean distribution, trophic condition, and survival of overwintering salmon, and the impact may be more intensive against salmon populations inhabiting the Gulf of Alaska. Further monitoring research is required to assess the status of overwintering Pacific salmon and their habitat environments in the ocean.

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Ocean Ecology of Coho Salmon in the Gulf of Alaska in the Winter

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Abstract

Winter surveys to the Gulf of Alaska in 2019 and 2020 examined the winter ecology of Pacific salmon, a season and location about which little is known. Coho salmon *Oncorhynchus kisutch* were mostly found in the southern areas of the Gulf of Alaska south of 52°N where they appear to be in deeper water during the day. They were the second most abundant species of Pacific salmon indicating that most populations move off the shelf to spend the winter in the offshore areas covered by the surveys. Coho salmon from the Strait of Georgia and Puget Sound remained closer to shore off the west coast of British Columbia. These results indicate that large aggregations of mixed populations that are not associated with other species of Pacific salmon may form in the winter. The large schools may be associated with finding prey to maintain metabolic requirements as growth during the winter was minimal. The period of rapid growth started about late March to early April and may be associated with the appearance of large abundances of squid.

Introduction

Expeditions to study the winter ecology of Pacific salmon in the Gulf of Alaska were privately organized in 2019 and 2020 (Pakhomov et al. 2019; Somov et al. 2020). These expeditions used large pelagic rope trawls towed in the upper 32 m (2019) or 25 m (2020) of the water column as the primary sampling method. This report is an interpretation of some of the information collected for coho salmon that we consider provides new insights into the population dynamics of coho salmon. The methods and complete results are included in the two cruise reports (Pakhomov et al. 2019; Somov et al. 2020) as well as in other papers in this conference summary. Our report is preliminary as samples are still being processed because of delays related to COVID-19 controls.

Abundance and distribution

The southern survey areas in 2019 and 2020 were similar but in 2020 we were unable to survey in the northern area of 2019 survey (Fig. 1) because of weather. However, we were able to repeat sets in 2020 in one area of large catches (sets 4 and 5) and found that coho salmon were no longer in the area two weeks later. This discovery turned out to be a major contribution to the understanding of the winter ecology of coho salmon. In 2019 there were 118 coho salmon caught compared to 127 in 2020. The abundance estimates using the method of Volvenko (1999, 2000) were 13.6 million fish for 2019 and 12.0 million for 2020. In both years' coho salmon were the second most abundant Pacific salmon species in the catches, with chum salmon the most abundant. In both years, 95% of the coho salmon catches were south of 52°N and extended to the western boundary of the surveys areas. Catches at the western limit of the survey were interpreted to indicate that coho salmon distributions continued farther west outside the study area. Coho salmon in the catch are in their first ocean winter and the apparent large abundances in the winter so far offshore was unexpected, as it was generally believed that coho salmon remained in or close to coastal areas during the winter.



Fig. 1. Map of set locations and relative catch of coho salmon in the Gulf of Alaska in 2019 (left figure) and 2020 (right figure). Set 4 in 2020 is in the area of the largest and most southerly catch.

We assessed the relevance of the abundance estimate of 13.6 million coho salmon in the 2019 survey to the total production of coho salmon returning to coastal rivers from SE Alaska to California in 2019. According to catch records in the data bases of the International North Pacific Anadromous Fish Commission, the total catch of coho salmon in all fisheries from SE Alaska to California was 2.5 million. The fishing rate/exploitation rate for all fisheries can only be guessed at about 33%. This would indicate that 67% or 5.1 million fish escaped the fisheries to spawn for a total production of 7.6 million (catch and escapement). There would be a natural mortality between the abundance in the winter and the final return that produced the catch and escapement. We have no estimate of the natural mortality after the first ocean winter, but Beamish et al. (2008) reported that the percentage could be large for coho salmon. If we estimate that ocean mortality after the surveys was 50%, the abundance of all coho salmon that would return to rivers from SE Alaska to California at the time of the 2019 survey would be 15.1 million. This estimate would be for all areas and not just the survey area. This 15.1 million estimate and the estimate from the survey area of 13.6 million are very approximate, but there is enough similarity that there is a possibility that future surveys may be designed to produce useable forecasts of total returns.

Diel distributions

We observed large variations in catches of coho salmon by the time of day. There were more coho salmon caught at night (1800-0630 hrs) compared to the day and more sets caught at least 1 coho salmon at night compared to during the day. The 181 fish caught at night compared to 34 caught during the day for both expeditions (Table 1) represented a significantly larger catch at night (t test, P < 0.05). In 2020, there was a large nighttime catch of 96 coho salmon in set 4 (Fig. 1). If this catch is excluded in the total for both expeditions, the catches during the day and night remain significantly different (t test, p < 0.05), with more coho salmon caught at night. There were 21 nighttime sets that caught coho salmon compared to 11 daytime sets that caught coho salmon (Table 1), and this difference is also significant (t test, p < 0.05). A comparison of the daytime-nighttime catches of pink, chum and sockeye salmon showed that pink and chum were mostly caught during the daytime (t test, p < 0.05). Sockeye salmon catches varied between years with greater catches at night in 2019 and during the day in 2020 (Table 1). Thus, there appears to be a spatial (vertical) difference in the daytime-nighttime distributions of coho salmon and an aggregate group of pink and chum salmon.

Secolog		2019			20
Species		Day	Night	Day	Night
Coho salmon	Number of sets	8	15	3	6
	Total catch	25	72	9	109
Pink salmon	Number of sets	7	3	3	1
	Total catch	27	4	134	2
Chum salmon	Number of sets	18	18	6	5
	Total catch	160	58	51	7
Sockeye salmon	Number of sets	4	14	4	6
	Total catch	8	65	26	7

Table 1. Catch of coho salmon by day and night in 2019 and 2020 Gulf of Alaska expeditions.

Predation

Major predators of Pacific salmon that have been reported in the open ocean (Sviridov et al. 2004, Bugaev and Shevlyakov 2007) are salmon sharks (*Lamna ditropis*), North Pacific daggertooth (*Anotopterus nikparini*) and longnose lancetfish (*Alepisaurus ferox*). Pacific lamprey (*Entosphenus tridentatus*) will feed on salmon, but they rarely kill their prey. Sea lice and particularly *Lepeophtheirus salmonis*, commonly feed on salmon, but they cause abrasions and not mortalities. There are other potential predators, but there is no evidence of their feeding on salmon in the open ocean in the winter. The average size of coho salmon in the two expeditions was 40 cm (SD=43.1; N=162). Thus the known predators that would be in the survey area at this time of year and could attack fish of this size and would be salmon sharks, daggertooths and lancetfish.

Scarring and wounding data are reported in this volume by Weitkamp and Garcia (2022) and eDNA by Deeg et al. (2021). Wounds were fresh marks on the fish (including abrasions caused by sea lice), in contrast to scars which were healed wounds. In 2019 and 2020 coho salmon with wounds were about 7% and 1% of the total coho salmon catch respectively. Scars on coho salmon represented about 1% in 2019 and 6% in 2020. There were four immature North Pacific daggertooths caught in 2020 and one in 2019. There were no catches of lancetfish. There also were no catches or sightings of salmon sharks in the two expeditions. The eDNA results identified daggertooths in only one area in 2020 indicating that this potential predator was rare in the survey areas. There was evidence of salmon sharks was at the far south west of the survey area and not in an area of coho salmon abundance. In general, there was minimal evidence of predation on coho salmon in the survey area in the two expeditions.

Scale annulus formation and winter growth

Most coho salmon lose a majority of their scales when caught in a trawl net. However, some scales remain in areas such as around fins and can be used to identify winter circuli growth and when new circuli growth begins beyond the winter annulus. Once this growth outside of the winter annulus begins, there is a continuous pattern of widely spaced, prominent circuli as coho salmon have the most rapid growth of all Pacific salmon in their second ocean year (Pearcy 1992; Fisher and Pearcy 2005).

There were useable scale samples from 61 fish from both expeditions. There are still 46 coho salmon from set 4 in 2020 that remain to have scales collected and analyzed. The winter annulus was easily identified by the transition from evenly spaced, unbroken circuli to closely spaced circuli that were not continuous around the scale (Fig. 2). The beginning of the period of rapid growth outside of the winter annulus was characterized by a circuli that was thicker than a circulus that formed during the winter. These "new", thicker circuli were continuous around the scale and uniformly widely spaced. In general, there was little difficulty identifying the new growth beyond the winter annulus despite the location of the scale on the fish.



Fig. 2. Scale image of a 413mm (fork length), 790g coho salmon captured on April 5, 2020 (set 47). DNA identified the fish as originating from Nimpkish River on the east coast of Vancouver Island, BC. The red bracket identifies the area of new rapid growth (4-6 circuli) that had occurred following the winter period of reduced growth.

There was no evidence of new growth before mid-March (Table 2). It is probable that the period of rapid growth started over a few weeks and may differ among areas, but the sample of 61 fish we examined did not begin the period of rapid growth until about the end of March. We do not know the period over which the winter annulus formed, but it appears that the winter is generally a period of minimal growth. In 2019 the diet of coho salmon was approximately 90% pteropods and in 2020 approximately 70% cephalopods. This highly specialized feeding occurred despite an apparent abundance of other potential prey in the nekton samples. One interpretation is that coho salmon have a metabolic maintenance period during the winter in which they are feeding only to maintain metabolic requirements and are not actively searching for large abundances of food. This could be analogous to hibernation in some animals except that some feeding is required for coho salmon.

First evidence of large schools of coho salmon and relevance

There were 215 coho salmon caught in both expeditions with 96 caught in set 4 in 2020. This large catch in one area would represent a large concentration of coho salmon. There were 52 of the 96 fish analyzed for DNA population identification. The remaining 44 will be analyzed for DNA as sampling becomes possible according to COVID-19 related restrictions. The population composition showed that populations from southern US to SE

Alaska were in the survey area (Table 3). There also was one fish in set 4 and two fish in other catches that were identified as originating from Russia, but the baseline is restrictive making the identification uncertain. The area was resurveyed about two weeks later on April 3 and no coho salmon were caught. There were three sets made in the general area of set 4 in April 1-5 and no coho salmon were caught. Thus it appeared that there was an abundance of coho salmon from a large number of populations only in the area of set 4 in the first week of the survey and this abundance was not in the area two weeks later. Our interpretation is that the fish caught in sets 4 were part of a large school that left the area within the two weeks between sampling events. The absence of other species of salmon in the catches also is an indication that there was a large school of coho salmon from a wide range of populations. The number of different populations in the school may indicate that the school developed in size over a number of weeks-months and once fish entered the school, they tended to remain, although we recognize that this is speculation.

Table 2. Number of coho salmon with scales that could be used to identify growth outside of the winter annulus. All growth outside of the winter annulus was represented by widely spaced circuli.

Survey year	Sets	Dates	Number of fish	Number with no growth	Number with growth
2019	5-15	Feb 22-26, 2019	11	11	0
	31-49	March 3-10, 2019	5	5	0
2020	4	March 15, 2020	30	24	6
	5-13	March 16-18, 2020	7	3	4
	20-47	March 21 – April 5, 2020	8	1	7

Table 3. DNA identifications of coho salmon sampled in 2019 and 2020. Set 4 (Fig. 1) was the single largest catch of coho salmon in both years.

		2019	2020	Total	Set 4	Total excluding
United States (south)	Columbia River	5	6	11	6	5
	Oregon	2	Ő	2	Ő	2
	Coastal Washington	2	11	13	8	5
	Juan de Fuca	0	2	2	2	0
British Columbia	South	5	4	9	3	6
	Central	5	7	12	6	6
	North	12	21	33	12	21
	British Columbia general	14	2	16	1	15
United States -Alaska	SE Alaska	36	10	46	6	40
Russia	Apuka River	0	2	2	1	1
Unclassified	$\bar{@70\%}$ probability	16	7	23	5	17

There was another example of coho salmon in a large school in the winter (Beamish et al. 2018). In February 2010, one standard 30-min trawl set in the Strait of Georgia caught a large number of coho salmon that were not counted, but estimated to be about 6,000 fish. DNA was collected from 110 for population identification. These were fish that previously entered into the Strait of Georgia or Puget Sound (Table 4). Recreational fishing records showed that very few (< 20) coho salmon were caught in the Strait of Georgia in March, April and May 2010 (after the large catch in February) indicating that the rest of the fish in this large school likely had left the Strait of Georgia. Our interpretation is that the large school probably entered the Strait of Georgia in the early winter and then left, possibly because there was not an abundance of preferred prey.

There was one other observation in 2019 that indicated coho salmon can occur in schools in the winter. In set 47 on March 9, 2019 there was a camera positioned to record salmon in the net. The camera recorded 10 coho salmon in the trawl for a period of 7 minutes or 12% of the fishing time (Fig. 3). Only three of the 10 were captured, but the evidence was that coho salmon were concentrated as a group in one area in the survey track line rather than randomly dispersed in front of the net opening.

There was clear evidence of coho salmon forming schools in the winter in the preceding three examples. The fact that individuals within these schools originated from a variety of populations shows that they likely aggregated after reaching offshore areas. Potentially, these aggregations may accumulate over the winter, but their existence in early February and mid-March may indicate that an aggregation/school may exist for most of the winter.

It is possible that the fish schooled to minimize predation as is commonly interpreted. However, we observed very few predators which would indicate the schooling occurred for other reasons. Because the scales show that growth is minimal, we also speculate that the collective effort of a school is to compensate for metabolic requirements during the winter and not a focus on achieving faster growth. It is possible the school is a way of collectively finding prey and minimizing individual efforts to search for prey and avoid predation. When the school encounters an abundance of prey such as squid, the school would remain in an area and focus feeding on the particular prey.

Table 4. DNA identifications of coho salmon caught from a school in the Strait of Georgia, February 2010.

Stock Origin	Number
British Columbia southern mainland	7
East Coast Vancouver Island	10
Lower Fraser River	47
Mid Fraser River	7
Thompson River	6
Other Strait of Georgia/Fraser River	7
Puget Sound	23
Not Classified	3





Population distributions using DNA

There were 117 coho salmon sampled for DNA in the 2019 and 2020 expeditions (Table 4, Fig. 1) in addition to the 96 sampled from set 4 in 2020. The sample size is small, requiring that interpretations of population specific distributions be considered preliminary. With this understanding, the following is a summary of the geographic distributions of the samples in Table 4. Southern US populations remained in the southern survey areas; Strait of Georgia and Puget Sound populations remained close to shore on the west coast of Vancouver Island. Central British Columbia populations moved off the shelf and were distributed throughout the survey area, with concentrations in the south. Northern British Columbia populations were only in the southern areas. Alaska populations were distributed throughout the survey area with a concentration in the south.

Data from winter high seas and coastal surveys suggest that coho salmon from the Strait of Georgia and Puget Sound are less common in the more offshore areas of the Gulf of Alaska in the winter. There were a series of coastal winter surveys of Pacific salmon off the coasts of Washington State, British Columbia and SE Alaska from 1995 to 2011 (Morris et al. 2007a, Beacham et al. 2016). From 1995 to 2004, there were 456 sets in February to March with a catch of 98 coho salmon from hatcheries that had identifying coded-wire-tags. All these hatcherytagged coho salmon were caught off the west coast of Vancouver Island and 96% (N=94) were from the Strait of Georgia or Puget Sound. No hatchery-tagged fish were found in any other coastal area of the survey in the winter over this 10-year period.

There were a series of cruise reports from the same study (Morris et al. 2007b, 2007c, 2007d, 2008; Welch et al. 2004a, 2004b, 2004c) that were partially summarized in Beacham et al. (2016). There were approximately 900 sets made from 2001 to 2011 in February to March from 2001 to 2011. Approximately 990 coho salmon were caught in the winter in this 11-year period. Catches were almost all from inlets off the west coast of Vancouver Island and around the entrance of Juan de Fuca Strait. Approximately 12 coho salmon were caught from the north tip of Vancouver Island to SE Alaska. It was clear from the report of Morris et al. (2007a) and the catches reported
from cruise reports that some coho salmon are in the inlets on the west coast of Vancouver in the winter and coho salmon from the Strait of Georgia and Puget Sound are commonly found in the area at the entrance of Juan de Fuca Strait. DNA analysis of approximately 400 coho salmon from these studies indicated that about 60% of the fish originated from the Strait of Georgia, Puget Sound and Washington State. An additional 27% originated from the west and north coasts of Vancouver Island and 10% were from the central coast of British Columbia. The remaining 3% of coho salmon were from the north coast of British Columbia or Oregon, US. It is of interest that in the 169 coho salmon DNA we have examined from both Gulf of Alaska expeditions we found only two fish from the Strait of Georgia or Puget Sound. This could result from a smaller relative abundance of the combined Strait of Georgia and Puget Sound fish or from a preference to remain in coastal areas in the ocean winter. Coho salmon in the Strait of Georgia had a pattern of a percentage remaining in the strait and a percentage migrating to the west coast of Vancouver Island (Beamish et al. 1999, Chittenden et al. 2009). This pattern changed in 1995 when almost all juveniles left the strait and stayed off the west coast of Vancouver Island until they were ready to return to their natal rivers (Beamish et al. 1999, Neville and Beamish 2018). The pattern of some remaining in the Strait of Georgia changed back again about 2013 with a large abundance remaining within the strait in the 2017-2018 winter (Beamish and Neville 2021). Beamish and Neville (2021) proposed that winter residence in the Strait of Georgia was related to growth and energy levels at a critical period in the summer.

Summary of the winter distributions of coho salmon in the Gulf of Alaska

Coho salmon were mostly in the southern areas of the survey where the numbers estimated in 2019 and 2020 indicated that they were abundant. Thus, it appears that most juvenile coho salmon leave the coastal areas in the late fall and spend the winter in the offshore areas of the north eastern Pacific. There is reduced growth during the winter that may relate more to behaviour than a shortage of prey. There is evidence from other studies that some of the populations remain inshore or nearshore, but it appears from the abundance estimates that many coho salmon are well offshore in the winter, at least in the two expedition years. There also is evidence that some populations may make limited use of the offshore areas of the Gulf of Alaska. For example, some coho salmon that enter the Strait of Georgia move offshore to the west coast of Vancouver Island while others remain within the strait. Coho salmon from Puget Sound and the migrants from the Strait of Georgia spend the winter in the area close to the entrance of Juan de Fuca Strait.

Once off shore, in the area of the 2019 and 2020 surveys, coho salmon from many different populations may form large schools. There was little evidence that predators were common in the surveys in 2019 and 2020, thus the schooling behaviour may be more related to efficiency in finding food sufficient to maintain metabolic requirements and locating areas where prey/squid becomes abundant in the early spring.

What we learned

1. Most populations of coho salmon move offshore in the fall and are distributed throughout the Gulf of Alaska survey area with concentrations in the south. Coho salmon may be deeper during the day in the winter.

2. Some populations remain in coastal areas off Vancouver Island with Strait of Georgia and Puget Sound populations mostly overwintering off the entrance to Juan de Fuca Strait and west coast of Vancouver Island.

3. Large and small aggregations of coho salmon from populations from southern US to Alaska may form in January to March that are not associated with other species of salmon. The schooling behaviour may be a feeding response to maintain metabolic requirements with minimal growth occurring during the winter.

4. Predation mortality during the winter may be minimal as indicated by an absence of known predators in the winter expeditions.

5. The period of rapid growth started about late March to early April and may be associated with the appearance of large abundances of squid and other prey.

6. There were three fish identified in 2020 as originating from Russia. The DNA baseline is restricted and the identification may be incorrect. However, we have the fish and can check the identification as the baseline improves.

Conclusion

We summarized the new information from the expeditions in 2019 and 2020 about the winter ecology of coho salmon in the Gulf of Alaska. Our interpretations are preliminary as the sample sizes are small but sufficient to show that expeditions need to continue to develop a full life cycle understanding of the factors that regulate the production of coho salmon.

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Winter Condition and Trophic Status of Pacific Salmon in the Gulf of Alaska

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The marine ecology of Pacific salmon (*Oncorhynchus* spp.) during winter has been rarely studied compared to other seasons, largely because harsh environmental conditions in the North Pacific Ocean make conducting winter research surveys difficult. As a result, we do not fully understand the winter fitness (e.g., energy density, lipid content, protein content) of different age classes for each species of salmon or how winter fitness may be affected by environmental conditions, such as the recent marine heatwaves (Cavole et al. 2016; Chen et al. 2021). We also do not know the extent to which intra- and inter-specific competition may exist, although winter is considered a period when competition among salmon may be highest due to low prey biomass (Nagasawa 2000). Competition may be further intensified by large-scale hatchery releases of pink and chum salmon (e.g., Ohlberger et al. 2022). To address these and other knowledge gaps, a comprehensive ecosystem survey – the International Gulf of Alaska Expedition – was conducted on the Russian research vessel *Professor Kaganovskiy* with 21 scientists from Canada, Korea, Japan, Russia, and the United States. The survey spanned 30 days in February – March 2019 and covered nearly 700,000 km² in the Gulf of Alaska (details and protocols described in NPAFC Secretariat 2018).

A total of 423 Pacific salmon – 223 chum (*O. keta*), 93 coho (*O. kisutch*), 73 sockeye (*O. nerka*), 31 pink (*O. gorbuscha*), and 3 Chinook (*O. tshawytscha*) salmon – were caught during the expedition (Pakhomov et al. 2019), and we obtained samples from 412 of these fish representing all species except Chinook. We first assessed the winter condition and trophic status of all samples by estimating their energy density, lipid content, protein content, and stable isotopic signatures from samples of muscle tissue. We then estimated the hatchery component of chum and pink salmon by examining otoliths to determine the presence of a thermal mark (hatchery origin), which allows us to better understand the potential for competition between hatchery and wild salmon that may occur in the marine environment. However, Alaska is the only location where thermal marks are applied to 100% of hatchery origin chum and pink salmon. Therefore, hatchery-wild comparisons were restricted to fish identified as Alaskan by using thermal mark (hatchery) or genetic stock identification (wild). Comparisons of fish from other locations would be unreliable due to lower hatchery marking rates (i.e., some hatchery origin fish do not have thermal marks).

Energy densities (calories/gram) were compared between fish of different sizes within each species to assess relative nutritional condition. Chum and sockeye salmon exhibited significant, positive relationships between length and energy density ($p = 5.98 \times 10^{-9}$ and p = 0.004 for chum and sockeye salmon, respectively), while no relationship was observed for coho (p = 0.27) and pink (p = 0.23) salmon (Fig. 1).



Fig. 1. Scatterplots displaying relationship between energy density (cal/g) and fork length (mm) for four species of Pacific salmon sampled during winter 2019. Black points are empirical data, solid lines are the predicted relationships based on the linear regression models, and shaded gray regions represent the 95% model confidence intervals. Juvenile salmonids sampled in the summer and fall typically exhibit stronger, positive correlations between length and energy density (Andrews et al. 2009; Farley et al. 2011; Sturdevant et al. 2012; Moss et al. 2016), as food is more abundant and individuals allocate energy towards storage and somatic growth. The weaker relationships between length and energy density in winter compared to those from summer and fall may indicate that salmon, particularly larger individuals, rely on their energy stores during winter rather than actively feeding (Hurst 2007). The results of Farley et al. (2011) support this conclusion; ocean age 1 sockeye salmon sampled in the Bering Sea in winter 2009 had lower lipid (energy) stores than juveniles sampled in the preceding fall. However, data from additional years are needed before we can make more definitive conclusions and frame the results in a broader context.

Lipid and protein content were also analyzed to examine winter nutritional condition of salmon. An animal experiences three physiological phases as it goes from extended natural fasting to the point of starvation (Fig. 2; Castellini and Rea 1992). During the first phase, animals burn glucose and begin to mobilize stored lipids as the body switches to fat oxidation and reduces protein catabolism (Fig. 2a). The second phase involves increased oxidation of lipids and the partial sparing of protein (Fig. 2b). Animals in this phase are still considered fit enough to survive once prey items are again available. Phase 3, or terminal starvation, occurs when 30-50% of the body protein has been used (Fig. 2c). This phase is often associated with death because of extreme reductions in nutritional condition and performance.



Fig. 2. Hypothetical trends in lipid and protein budgets for fish that are: a) "fit"; b) "not starving," as they are utilizing lipids and sparing protein; c) "starving," as they break down protein for energy.

No relationships between lipid content and mass were observed for any age class of chum salmon (p > 0.05 for all age classes; Fig. 3). However, positive relationships between protein and total mass were evident in all age classes ($p = 0.02, 0.007, 1.11 \times 10^{-8}$, and 0.001 for ocean ages 1, 2, 3, and 4 respectively; Fig. 3), suggesting that chum salmon were not in the starvation phase. Coho salmon exhibited a negative correlation between lipid content and mass (p = 0.02; Fig. 4) and no correlation between protein content and mass (p = 0.15). Similarly, there was no correlation between lipid content and mass for pink salmon (p = 0.33; Fig. 4) and a negative relationship between protein content and mass (p = 0.007). Therefore, fish of these two species appeared to be starving. No relationships were observed for any age class of sockeye salmon (p > 0.05 for all age classes; Fig. 5), suggesting that these fish were also starving. However, these results must be paired with other data from the survey, such as stomach fullness and diets, as well as samples from additional years before more informed interpretations can be made.



Fig. 3. Percent lipid (upper row) and percent protein (bottom row) versus total mass (g) of chum salmon for four age classes. Black points are empirical data, solid lines are the predicted relationships based on the linear regression models, and shaded gray regions represent the 95% model confidence intervals. Chum salmon of all age classes appear to be "not starving" when compared to the three phases depicted in Fig. 2.



Fig. 4. Percent lipid (upper row) and percent protein (bottom row) versus total mass (g) of coho (left column) and pink (right column) salmon. All samples within each species are the same ocean age. Black points are empirical data, solid lines are the predicted relationships based on the linear regression models, and shaded gray regions represent the 95% model confidence intervals. Both coho and pink salmon appear to be starving.

Stable isotope measurements of carbon and nitrogen provide measures of source primary production and habitat (δ^{13} C) and relative trophic level (δ^{15} N) that are commonly used together to define ecological niche space (Newsome et al. 2007). Results indicated that coho salmon were at the highest trophic level (δ^{15} N =13.3‰), followed by pink (12.0‰), sockeye (11.7‰) and chum salmon (11.0‰; Fig. 6). The total trophic range between chum (lowest) and coho (highest) was approximately 0.7 trophic levels (based on δ^{15} N 3.4‰ per trophic level; Minagawa and Wada 1984; Vander Zanden and Rasmussen 2001). The highest trophic overlap occurred between chum and sockeye salmon (0.72), followed by pink and chum (~0.70), and then pink and sockeye (~0.62; Fig. 6). As a mid-trophic level species, pink salmon expressed the greatest degree of isotopic overlap with all other salmon. These results indicated a significant level of trophic overlap and suggested that intra- and inter-specific resource competition may be high during winter.



Fig. 5. Percent lipid (upper row) and percent protein (bottom row) versus total mass (g) of sockeye salmon for three age classes. Black points are empirical data, solid lines are the predicted relationships based on the linear regression models, and shaded gray regions represent the 95% model confidence intervals. Sockeye salmon of all age classes appear to be starving.



Fig. 6. Bayesian bivariate ellipses representing the 95% isotopic niche space of four salmon species based on δ^{13} C and δ^{15} N values.

Three of the 31 pink salmon had thermal marks (i.e., hatchery origin). All three hatchery fish were released in Prince William Sound, Alaska, U.S.A. Low sample sizes of hatchery pink salmon precluded any statistical analyses. For chum salmon, 31 of 224 fish had thermal marks (i.e., hatchery origin, 3 Canada; 3 Japan; 2 Russia; 23 U.S.A).

Energy density was compared between the hatchery (n = 23) and wild (n = 62) chum from Alaska, U.S.A., as Alaska is the only location with 100% marking of hatchery chum salmon. No differences in energy density were observed after accounting for the effect of fork length (p = 0.78; Fig. 7), suggesting that fish of both origins may be responding similarly to winter conditions. Likewise, Sturdevant et al. (2012) observed that juvenile hatchery and wild chum salmon in southeast Alaska had similar energy density in early summer, although hatchery fish had higher energy density in spring shortly after release, presumably because they had been feeding on energy-rich hatchery pellets.



Fig. 7. Scatterplot of energy density (cal/g) and fork length (mm) for hatchery (blue) and wild (red) chum salmon from Alaska, U.S.A. Points are empirical data, solid lines are the predicted relationships based on the linear regression models, and shaded gray regions represent the 95% model confidence intervals.

While preliminary, these results provide important insight regarding the fitness of Pacific salmon during the critical winter period. The weak relationships between energy density, lipid content, and protein content with size suggest that fish of all species may have reduced nutritional condition during winter. Some fish, particularly coho, pink, and sockeye, may be starving beyond the point of recovery based on their lipid and protein profiles. Additionally, stable isotope analyses demonstrated a high degree of tropic overlap within and between species and thus provide preliminary evidence that competition for resources may be substantial during winter. Pink salmon had the most trophic overlap with other species, suggesting that they may have more opportunity for competitive interactions with other salmon. However, addressing the effect of these interactions and other important gaps regarding the winter marine ecology and fitness of Pacific salmon will require data from additional years and seasons.

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North Pacific Salmon Food Webs

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This abstract introduces and presents preliminary results from the Canadian led International Year of the Salmon (IYS) food webs project that is researching the high seas feeding ecology of Pacific salmon and the structure of the food webs that support them. Feeding ecology is a critical factor in salmon growth and survival on the high seas, and the winter is expected to be a particularly stressful period since this is when ocean productivity is at its lowest (Beamish and Mahnken 2001). Although the high seas feeding ecology of Pacific salmon (*Oncorhynchus* spp.) has been sporadically researched since the 1950's, little if any data have been collected on whole food web dynamics. Since 2013 we have entered into unchartered waters in the North Pacific, with intense heat wave activity potentially leading to wholesale shifts in the structure of the food webs that support salmon (Peterson et al. 2017; von Biela et al. 2019; Litzow et al. 2020). The IYS sample sets from the 2019, 2020, and 2022 expeditions provide the opportunity to advance understanding of food web structure and salmon feeding ecology in the North Pacific, and to relate these to salmon health.

This food webs project is applying three complementary approaches to resolve salmon food web ecology: 1) stable isotope analysis, 2) fatty acid analysis and 3) stomach content analysis (Majdi et al. 2018; Nielsen et al. 2018). Stable isotopes of carbon and nitrogen occur naturally in the environment, and are taken up by phytoplankton during growth and subsequently transferred through the food web by consumers. Heavy isotopes accumulate through the food chain, and predictable enrichment factors from one trophic level to the next can be used to estimate several key food web properties, including organism trophic level, organic matter sources, trophic pathways, trophic niche and overlap, and food chain length.

Fatty acids are complementary to isotopes, providing an additional measure of organic matter sources and food web pathways, but also providing information on food quality and organism health, e.g., occurrence of essential fatty acids. Essential fatty acids (EFAs) are produced by phytoplankton and support several critical functions in salmon, including membrane health, neurological development, and physiological performance (Sargent et al. 1999; Tocher 2010). Fatty acids also provide essential energy resources for surviving periods of low food availability. Different EFAs are produced at different ratios by primary producers, and they are therefore also diagnostic of the key phytoplankton groups contributing to food webs, providing a complementary measure to isotopes in resolving food web pathways.

Stable isotopes and fatty acids have relatively slow turnover rates, and are therefore indicative of an organism's foraging experience over the previous 1–4 months. These biochemical measures thus provide insights into longer term salmon foraging experience and integrated food web properties over the winter period. Stomach content data on the other hand integrate over < 8 hours and therefore provide a short-term snapshot of foraging conditions. In addition, stomach content analysis provides species level resolution of dietary items, not typically possible with stable isotopes and fatty acids. The combined analyses therefore enable examination of both the short-and long-term foraging history of Pacific salmon, and interannual differences in food web structure.

During the 2019 and 2020 expeditions, comprehensive surveys of particulate organic matter (including phytoplankton, micro-heterotrophs, and detritus), zooplankton, micronekton and nekton (including salmon) were conducted in the Gulf of Alaska. Samples were collected for measurement of stable isotopes and fatty acids from all food web components, while salmon and micronekton samples were also collected for stomach content analysis. Stomach content analysis is reported on elsewhere, fatty acid samples remain to be processed, and here we focus on preliminary results from the stable isotope analysis.

In both 2019 and 2020, chum salmon (*O. keta*) had the lowest trophic level of the five salmon species measured, followed by sockeye (*O. nerka*), pink (*O. gorbuscha*) and coho (*O. kisutch*) salmon (Fig. 1). Given that nitrogen (δ^{15} N) and carbon (δ^{13} C) isotope ratios increase on average by 3.4 ‰ and 1.1 ‰ per trophic level, respectively, coho were approximately one trophic level above chum while sockeye and pink were intermediate between chum and coho. In 2019, there was greater isotopic overlap between chum and sockeye than in 2020. A small number of chinook (*O. tshawytscha*) were collected and one large specimen in 2019 had the highest trophic level of all salmon collected, contributing to the large error bars for chinook in that year.

Comparison of the δ^{15} N and δ^{13} C values of common species of zooplankton, micronekton, and all salmon collected in 2019, provided initial insights into trophic relationships (Fig. 2). The lowest isotope values were measured in *Euphausia pacifica* (krill), while *Neocalanus cristatus* (Copepod) was almost one trophic level above krill, indicating a high degree of carnivory for that species. The isotope values of the abundant myctophid species *Tarletonbeania crenularis* and *Diaphus theta*, and the squid *Onychoteuthis borealjaponicus*, all showed considerable overlap with sockeye, pink and chum salmon. This indicates that these micronekton and salmon species had similar diets, and were thus competing for food resources in the Gulf of Alaska in winter.



Fig. 1. Nitrogen (δ^{15} N) vs Carbon (δ^{13} C) isotope biplots for salmon species collected in the Gulf of Alaska in 2019 and 2020. No specimens from the shelf are included. Error bars are standard deviations.



presented here will be augmented by fatty acid and diet data to further resolve trophic relationships among species in the Gulf of Alaska in 2019 and 2020. Our objective is to apply the same sampling approach during the 2022 pan-Pacific expeditions, to provide an additional year of data for the Gulf of Alaska, and enable comparison of regional food web structure and salmon feeding ecology that will contribute to understanding regional differences in salmon production.

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Salmon Returns in the Northeast Pacific in Relation to Expedition Observations (and Next Steps)

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Keywords: Pacific salmon, North Pacific Ocean, Bering Sea, abundance, trends

As the previous reports to this workshop have demonstrated, there have been numerous significant new findings and new questions. The expeditions were an extension of a salmon research program in the Salish Sea (www.marinesurvivalproject.com) and intended to test the hypotheses that survival through the first winter-at-sea was a major determinant of year-class strength in Pacific salmon *Oncorhynchus* spp. However, to test this hypothesis there was limited knowledge of where specific populations of salmon rear, and very little experience in sampling juvenile salmon on the high-seas particularly in relation to their winter ecology. Based on the success of juvenile salmon surveys in Russia, it was proposed to test surface trawls as sampling gear. Both 2019 and 2020 trawl surveys were successfully completed, covered similar geographic areas (Fig. 1), and captured all species of Pacific salmon (Table 1), but they caught many fewer salmon than expected. In hindsight, however, there is very limited ability to compare our expectations with observations from these new projects. This paper considers what we can learn from these surveys, including the ability of the surface trawl to representatively sample the fish population vulnerable to the trawl net. The latter is compared against a sample of relative abundance indices for Pacific salmon from Alaska southward to the Columbia River.

Overview of salmon catches in the 2019 and 2020 Gulf of Alaska expeditions

Results of both surveys have been summarized in NPAFC Documents; the 2019 survey by Pakhomov et al. (2019) and the 2020 survey by Somov et al. (2020). After adjusting for differences in survey area between years (2020 was 0.93 of the area covered in 2019), the estimated abundances of salmon in each year were identical. Pakhomov et al. (2019; Table 1) reported an estimated abundance of 54.95 million Pacific salmon¹ and in Somov et al. (2020; Table 1), the adjusted estimated abundance in 2020 was 55.16 million Pacific salmon. However, these estimates result from different species composition and a greater number of trawl sets with zero salmon catches during the 2020 survey. In 2020, 70% of the salmon were caught in just two sets (Table 4 in Somov et al. 2020).

Plots of catch by species and set are provided in Pakhomov et al. (2019) and Somov et al. (2020). Overall, the numbers of salmon caught in these surveys were substantially less than anticipated particularly for pink salmon, catches were more heterogeneous in 2020, and salmon species seemed to have different distributions in the area sampled. However, examination of the biological samples (size and age) of salmon caught (Fig. 15, Pakhomov et al. 2019; and Fig. 3-7, Somov et al. 2020) suggest that the full spectrum of age/size were captured in the trawl nets. While the trawl nets seem to catch salmon over a full size range, it is unknown if these catches are representative of the salmon abundance and composition in the survey area. This is a continuing concern, particularly given the low catch rates of salmon and absence of predators or competitors in the trawl catches².

In future studies, there are means to provide greater confidence in results, but they require additional gears and/or survey designs; for example:

- Inclusion of alternative sampling gears;
- Replicate sampling between vessels and gears, and extending sample areas to provide contrast in salmon abundance;
- Use of alternative sampling designs, e.g., overlap of vessels and gears by sampling areas, and depth stratified sampling;
- Use of prediction to test outcomes between vessels and areas;
- And, application of new archival tags on salmon to supplement surveys by independently 'sampling' characteristics of the habitat utilized by salmon.

But within the survey years, we are limited to comparing our results with other independent observations about salmon abundance. It is notable that during 2019 and 2020, the returns of salmon to coastal fisheries were very poor for most of the northeastern Pacific Ocean; and more generally across the Pacific Ocean in 2020. The

¹ Catchability coefficients, the pro's and con's of trawl analyses are considered in Volvenko (2000).

² Records of all species caught are provided in Table 2, Pakhomov et al. (2019) and Table 3 in Somov et al. (2020).

total North Pacific 2020 commercial catch of Pacific salmon was the lowest since 1982³ and 44% less than 2018 (the last year with comparable even-year pink salmon).



Fig. 1. Sampling locations and salmon catches for the 2019 survey (Pakhomov et al. 2019, left) and the 2020 survey (Somov et al. 2020, right). The 2020 survey design was to replicate the 2019 survey but a large weather front required adjusting sites to the east and southward $135 - 140^{\circ}$ W.

Table 1. Total catch of Pacific salmon by species in the 2019 and 2020 Gulf of Alaska expeditions. During 2019, salmon werecaught in 48 of 58 (83%) stations fished. During 2020, salmon were caught in 29 of 52 (56%) stations.

Species	2019 Expedition	2020 Expedition
Pink salmon O. gorbuscha	30	136
Chum salmon O. keta	222	234
Sockeye salmon O. nerka	68	51
Coho salmon O. kisutch	94	118
Chinook salmon O. tshawytscha	3	26*
Steelhead trout O. mykiss	0	1
Total	417	566

* all 26 Chinook caught during 2020 resulted from two trawl sets as the vessel returned to the coastal shelf off the west coast of Vancouver Island (sets 51 & 52).

Species-specific trends in salmon abundance

To investigate the relative abundance of Pacific salmon in North America during 2019 and 2020, a data set of abundance trends by species from Alaska southward to the Columbia River was compiled. Management agencies were consulted to identify indices of salmon returns that have been consistently monitored over the past 22 years. A baseline for each index was defined as the average return for the period 1999 to 2018 and deviations from average were calculated for each year in the time series through 2020. An extreme event in a short time series can unduly influence an average but for each index, the median value was also calculated. For all indices, the use of median or average did not change the pattern of deviations in the time series or results for 2019 or 2020. The average values have been used.

In selecting datasets, emphasis was placed on systems with consistent survey methods through the full period but indices vary from fully developed peer reviewed run reconstructions to standardized minimum indices. 'Standardized minimum index' (developed for this review) include catch attributed to an area and spawning escapement indices representing an unknown portion of the populations within that area. These represent a

³ https://npafc.org/wp-content/uploads/Public-Documents/2021/4-NewsReleaseStatistics.pdf

minimum estimated production from a region based on surveys conducted consistently over this period (1999-2020). Indices address sockeye, pink, chum, coho, and Chinook salmon and cover the geographic range from Norton Sound south to the Columbia River. In British Columbia (BC) some data for 2019 and 2020 had not been incorporated into analytical databases yet. In these cases, past abundance was compared with post-season management reports provided by the Department of Fisheries and Oceans (DFO) staff. The Alaska Department of Fish and Game (ADF&G) provided a rich data set of 81 indices, but the number of indices and spatial scale of an index differs between species. Tables describing the ADF&G indices are provided for each species and maps of the Management Areas are available on ADF&G websites⁴.

Attribution of the cause for change in a salmon population is difficult due to their complex life history in freshwater, estuary and near-shore marine habitats, and off-shore deep-water habitats. This evaluation across many salmon populations is not meant to describe causes within any single index population, rather to provide a broad geographic assessment of patterns in change that would likely be attributed to equally broad environmental changes from climate variation, impacts on ocean ecosystems, with resulting changes to salmon survival and abundance.

Sockeye salmon (Oncorhynchus nerka)

While we were particularly interested in the distribution and condition of sockeye salmon in the Gulf of Alaska, our catches of sockeye were limited and much less than anticipated.

Alaska sockeye salmon indices

The 33 indices analyzed involve various enumeration methods and many have citable documentation as total run reconstructions (Table 2; Appendix 1). Over the time series and within regions, trends are assessed against a background of substantial variability amongst indices. For example, within the Southeast Alaska region (SEAK; Fig. 2), positive and negative deviations can be substantial and are typical within a year, and when indices are averaged within years, little trend is apparent. The years 2019 and 2020 are within the range of past deviations. But only twice (2008 and 2020) has the sign of all deviations within a year been consistent across indices.

Across the 33 indices (Fig. 3), the most striking observation is the difference between the Bristol Bay and Norton Sound indices (BB+NS, n =10) in the Bering Sea compared to the remainder of the indices entering North Pacific Ocean (NPO) waters⁵ (Table 3). Sockeye indices that enter NPO differ from BB+NS sockeye across the time series, and since 2017 show below average returns with the largest negative deviation in 2020 (-38%). Indices for the NPO populations have mixed deviations in 2019 but were strongly negative in 2020 with only 1 in 22 indices showing a positive deviation (one SEAK index was not monitored in 2020). Contrary to NPO indices, sockeye indices for Bristol Bay and Norton Sound showed positive deviations from 2015 through 2020, with only one Bristol Bay sockeye run (Togiak River) and Norton Sound being below average in 2020.

Southeast Alaska (8)	Prince William Sound (1)	Cook Inlet (3)	Kodiak Island (7)	South Alaskan Peninsula (2)	North Alaskan Peninsula (2)	Bristol Bay (9)	Norton Sound (1)
Mainstem	Copper R	Kasilof R	Afognak R	Early-run	Nelson R	Kvichak R	One
Stikine R		Kenai R	Early-run	Chignik R	Bear R	Alagnak R	combined
Tahltan L		Early-run	Karluk R	Late-run		Naknek R	Salmon L
Speel L		Russian R	Late-run	Chignik R		Egegik R	Central
Taku R			Karluk R			Ugashik R	Grand R,
Redoubt L			Ayakulik R			Wood D	and Pilgrim
Alsek R			Upper			WOOD K	К
			Station R			Igushik R	
			Frazer L			Nushagak R	
Chilkoot L			Saltery L			Togiak R	

Table 2. Summary of Alaska sockeye salmon indices (n = 33) included in this review. Appendix 1 provides details on methods applied and citations for documentation.

⁴ http://www.adfg.alaska.gov/index.cfm?adfg=commercialbyfisherysalmon.main

⁵ The two indices in the North Alaska Peninsula region (Bear and Nelson rivers) showed closer correspondence to the South Alaska Peninsula indices than to Bristol Bay sockeye and were grouped with NPO indices.



Fig. 2. Annual deviations for sockeye salmon indices in Southeast Alaska (1999–2020). Indices include 3 large rivers (Alsek, Taku, Stikine) and 5 lakes (Speel, Tahltan, Redoubt, Chilkat, and Chilkoot). Deviations are presented for each year/index value to demonstrate inter-annual variability. The overall average deviation within each year is the black solid line (SEAK, 8 indices).



Fig.3. Average deviations for sockeye salmon for 8 Alaska Management Areas (Southeast Alaska, Prince William Sound, Cook Inlet, Kodiak Island, South Alaskan Peninsula, North Peninsula, Bristol Bay, and Norton Sound) for 1999–2020. Each Management Area is presented as the average deviation within management areas and year (column bars). For comparison of indices entering the North Pacific Ocean region (NPO, 23 indices) compared to the Bering Sea (Bristol Bay and Norton Sound, 10 indices), lines present the average value across indices within these large geographic areas. Sockeye returns to Norton Sound show larger inter-annual variation compared to Bristol Bay returns but the BB+NS dashed line presents the combined trend for the 10 indices within the Bering Sea region.

			•
alue of +5% or	-5% to +5% (average)	Indices value of -5% or	
reater		greater	
8	3	12 (52%)	2019 NPO (n=23)
(70%)	2	1	2019 BB+NS (n=10)
1	2	19 (86%)	2020 NPO (n=22)
(80%)	0	2	2020 BB+NS (n=10)
reater 8 (70%) 1 (80%)	-5% to +5% (average)	12 (52%) 1 19 (86%) 2	2019 NPO (n=23) 2019 BB+NS (n=10) 2020 NPO (n=22) 2020 BB+NS (n=10)

Table 3. Number and value of abundance indices for sockeye salmon in the North Pacific Ocean (NPO) region, and Bering Sea (Bristol Bay and Norton Sound (BB+NS)) in 2019 and 2020. The range of -5% to +5% was simply used as a measure of near average returns. NPO indices in 2020 are reduced by one as Speel Lake (SEAK) was not monitored

British Columbia and Washington State sockeye salmon indices

Indices of BC sockeye salmon systems are run reconstructions for major river systems to account for differences in fishery removals over time; these indices include the Nass River, the Skeena River, Barkley Sound sockeye (southwest coast of Vancouver Island), and the Fraser River (Fig. 4). These reconstructions involve multiple sockeye populations within each watershed. To account for the cyclic dominance in Fraser River sockeye salmon and wide differences in the abundance between lines (Roos 1991), baseline averages and deviations were calculated within cycle lines. Each reconstruction is based on quantitative estimation of spawning abundance, total catches in fisheries along their adult migration routes, and were consistently conducted during this period.

For these BC indices, sockeye returns have been less than baseline averages in recent years: Nass River, -33 to -51% since 2016; Skeena River, -15% to -59% with the greatest reduction in 2019; in Barkley Sound, -46% to -72% with the largest deviation in 2019; and for Fraser River, a progressive decline from -42% in 2015 to -90% in 2020.

In Washington State, sockeye indices were examined for Baker Lake (Skagit River, Puget Sound), Lake Washington (Puget Sound), and Columbia River. Trends in these sockeye populations each differ. Returns to Baker Lake have been rebuilding from hundreds of sockeye in the 1980s to ~20,000 during the past decade. Pattern of sockeye returns to Washington Lake (Fig. 5) in 2019 and 2020 were 89% and 86% less than their baseline average, and have similar trend to Fraser River sockeye. In the Columbia River, sockeye returns have been improving over the past decade but reductions were observed between 2017 and 2019, followed by an above average return in 2020 (Fig. 5). Other smaller sockeye populations in Washington State (Gustafson et al. 1997) were not assessed.



Fig. 4. Time series deviations from average returns (1999-2020) for Canadian sockeye salmon systems: Nass River, Skeena River, Barkley Sound, Fraser River. Each of these abundance indices represents estimated total returns to rivers. Data provided by the Canadian Department of Fisheries and Oceans, Nisga'a Lisims Government, and Pacific Salmon Commission.



Fig. 5. Time series deviations for sockeye indices in the southern United States including returns to Lake Washington (Puget Sound) and the Columbia River (Bonneville Dam counts). Fraser River sockeye included for comparison with Lake Washington as these stocks likely share early-rearing environments.

Overall, sources of sockeye salmon entering the North Pacific Ocean, have been less than average during the recent period of marine heat waves (Hobday et al. 2018) and particularly so in 2020. The notable exception to this trend is sockeye salmon returning to Bristol Bay. This review suggests that sockeye abundances in the NPO could have been significantly reduced during 2019 and 2020 winter trawl surveys, but the variability between regions of production also suggests that the abundance of sockeye at sea could be highly dependent upon where different populations rear and sampling occurred. While past tagging studies have demonstrated that sockeye range widely in the NPO, we know very little about ocean rearing areas utilized by these populations.

Pink salmon (Oncorhynchus gorbuscha)

Pink salmon were expected to be the most abundant salmon sampled given their recent historic abundance across the North Pacific Ocean, but the frequency of their catch and abundance were less than for chum and similar to coho salmon. This limited catch of pink salmon is a key uncertainty from the Gulf of Alaska expeditions.

Alaska pink salmon indices

Indices for pink salmon are regional summaries (n =10, Table 4) accounting for areas of significant pink salmon production and with consistent monitoring programs through 2020. In reviewing the Alaska pink salmon data there were two issues to acknowledge: (1) the three Bering Sea indices in total account for less than 2% of the abundance represented by the Alaska pink salmon indices but would account for 30% of the Alaska indices (i.e., Bering Sea pink salmon would be over-represented in the statewide samples); and (2) returns in even and odd calendar years differ substantially in abundance and patterns of deviations. In the base period, odd-year returns averaged 1.8 times the even-year returns. To account for these issues; the Bering Sea indices are addressed on their own, and deviations in pink salmon are considered within odd and even years (averages are calculated within each line) for the remaining 7 indices.

While pink salmon in the Bering Sea region constitute a small portion of Alaska pink salmon, their abundance trend during 1999-2020 period is notable (Fig. 6). This figure presents the abundance indices (numbers of pink salmon) of returns for Kuskokwim, Yukon River, and Norton Sound on a Log₁₀ scale as the returns differ by orders of magnitude. Each index shows an increasing abundance during this period and the most northerly index (Norton Sound) shows the strongest increase, with even years showing larger returns within each index.

The remaining 7 pink salmon indices (in Southeast Alaska, Prince William Sound, Cook Inlet, Kodiak Archipelago, Kodiak Mainland, South Alaskan Peninsula including Chignik) account for average returns of 169 million pink salmon during odd years and 93 million pinks during even years in the base period (1999-2018), and

demonstrate differences in deviation patterns by year and region (Fig. 7). There are also substantial differences in the magnitude of pink salmon production between regions.



Fig. 6. Trend in pink salmon returns for three indices in the Bering Sea. Abundance presented in Log_{10} estimated numbers of pink salmon within indices to account for large differences between indices and to demonstrate growth in recent years.



Fig. 7. Deviations for pink salmon indices for: (A) odd-year pink salmon and (B) even-year pink salmon.

Region	Index/Methods	Reference	Average run/index size in base period (1999- 2018)
Southeast Alaska (SEAK)	Standardize Minimum Index ⁶ , uses total harvest and expanded aerial escapement surveys	Developed for this review	Odd years, 74.6 million Even years, 36.5 million
Prince William Sound and Copper River	Standardized Minimum Index, uses total harvest and multiple escapement surveys	Developed for this review	Odd years, 55.7 million Even years, 33.2 million
Cook Inlet	Standardized Minimum Index, uses total harvest and multiple escapement surveys	Developed for this review	Odd years, 2.7 million Even years, 2.1 million
Kodiak Mainland	Run Reconstruction with peak aerial surveys	Nemeth et al. 2010	Odd years, 1.1 million Even years, 0.7 million
Kodiak Archipelago	Run Reconstruction with peak aerial surveys	Nemeth et al. 2010	Odd years, 19.8 million Even years, 14.7 million
Chignik River	Standardized Minimum Index, uses peak aerial escapement surveys	Developed for this review	Odd years, 2.2 million Even years, 0.6 million
South Alaska Peninsula	Run Reconstruction with peak aerial surveys	Schaberg et al. 2015	Odd years, 12.8 million Even years, 5.3 million
Kuskokwim River (Bering Sea)	Standardized Minimum Index, uses total harvest and weir counts	Developed for this review	Odd years, 4,500 Even years, 17,700
Yukon River (Bering Sea)	Standardized Minimum Index, uses total harvest plus sonar (Pilot Station) & weirs	Developed for this review	Odd years, 57,900 Even years, 753,800
Norton Sound (Bering Sea)	Standardized Minimum Index, uses total harvest plus weir/tower counts	Developed for this review	Odd years, 0.776 million Even years, 3.0 million

Table 4. Summary of Alaska pink salmon indices (n = 10) included in this review.

Three observations are notable: patterns of deviations are notably different between odd and even years, the two Management Areas with the largest pink salmon returns (SEAK and Prince William Sound (PWS)) show consistent negative deviations since 2016, and in recent years, the deviations for western Gulf of Alaska indices are opposed to deviations for SEAK and PWS. The recent negative deviations for SEAK and PWS (in both even and odd calendar years) are particularly notable as these two regions alone average 75% of the total Alaska pink salmon abundance indices. In summary, given the magnitude of pink salmon production in SEAK and PWS management areas, the recent negative deviations in these areas strongly suggests a significant reduction in their abundance wherever they rear in the North Pacific Ocean, in both even- and odd-year lines since 2016.

British Columbia and Washington State pink salmon indices

Monitoring of pink salmon in north and central BC is conducted according to conservation units (Holtby and Ciruna 2007) that differ by even and odd calendar years. These conservation units would be analogous to the regional area summaries provided by ADF&G. The indices used are estimated total returns to specific areas based on catch, spawning escapements, and migration patterns (stock reconstructions of annual abundance; English et al. 2018). These indices are used to account for changes in fishing patterns and intensity between years, and differences in vulnerability (harvest rates) between conservation units.

Unfortunately, these indices have not been updated since 2017 and our information for 2019 and 2020 is limited to post-season management reports, with the notable exception of data from the Nisga'a Lisims Government (http://www.nisgaanation.ca/stock-assessments) for the Nass River watershed (Fig. 8). Pink salmon returns to the Nass River are larger in the odd-calendar years (almost 3x larger), and returns in 2019 were equal to the worst previously recorded return in 2011. However, the 2020 return was the largest return in even years since the beginning of the modern assessment period commenced in 1992. Returns to most north and central BC pink salmon

⁶ The indices were calculated for this review, a standardized minimum index includes catch attributed to an area and spawning escapement indices representing an unknown portion of the populations. The index represents a minimum estimated production from a region based on surveys conducted consistently over the full period (1999-2020).

in 2019 and 2020 were summarized from a post-season report prepared by DFO staff⁷. Returns in 2019 and 2020 to Portland Canal and south to Douglas Channel, and outer coastal lowlands were very weak. But from Douglas Channel southward, pink salmon returns were similar to recent averages within coastal fjord rivers.



Fig. 8. Deviations in pink salmon returns to the Nass River watershed. Returns are estimated as the total return to Canada to account for variation in ocean fisheries in Canada, plus spawning escapement. Deviations presented for even and odd years and baseline averages were calculated within Even and Odd-year lines.

Assessment of pink salmon in southern BC is similarly conducted by reconstruction of returns to conservation units, including the mainland fjords in Queen Charlotte Sound, Johnstone Strait, and within the Strait of Georgia; and coastal streams along the east coasts of Vancouver Island and mainland, but excludes the Fraser River. Figure 9 presents the deviations for southern BC pink salmon by even- and odd-calendar year returns. Recent returns have been substantially less than average in both even and odd-years since 2016, but returns in 2020 have not been incorporated in the reconstruction analysis as yet. Summaries of 2020 returns were provided by local fishery managers⁸. Returns in northern Vancouver Island and the fjords in Queen Charlotte Sound continue to be "well below average" but returns along the east coast of Vancouver Island and southern fjords (Johnstone Strait) were improved and "above average" in 2020.



Fig. 9. Southern British Columbia (non-Fraser) pink salmon deviations presented by even-calendar years and odd-calendar years aggregated across conservation units from southern Queen Charlotte Sound southward through the Strait of Georgia including the mainland fjords. The value for 2020 was not available yet (comments in text).

Returns to the Strait of Georgia streams improved to average in 2019, while in aggregate across the 6 odd-year conservation units the deviations were still negative (-28%). Average abundance for these Strait of Georgia populations, however, was only about 1.6 million pink salmon; and is much less than in the odd-year returns to the Fraser River. Pink salmon only return to the Fraser River in odd-calendar years (Roos 1991). Their total abundance (Fig. 10A) exceeds the sum of all other southern BC pink salmon systems, but has been declining for several years (Fig. 10B). Pink salmon also return to Puget Sound during odd-calendar years and show the same pattern of

⁷ Post-season report prepared by K. Beach, DFO, North Coast Stock Assessment, Prince Rupert, BC.

⁸ 2020 data was summarized by DFO managers at South Coast Division, Nanaimo, BC.

deviations as for the Fraser River pink salmon (Fig. 10B). Both demonstrate very poor returns in 2017 and more modest decreases in 2019.

When considered in aggregate across British Columbia for 2019 and 2020, pink salmon returns were greatly reduced in 2019 but mixed in 2020. Patterns of deviations indicate that both even- and odd-calendar year returns have been less that average for 2 to 3 cycles of pink salmon returns, not just in the most recent couple of years.



Fig. 10 (A). Total return of Fraser River pink salmon (millions of fish). Total return includes catches in Canada and the United States and total spawning escapement. 'Linear' is a simply linear regression to demonstrate the longer term trend. Data provided by the Pacific Salmon Commission, Vancouver, BC.

Fig. 10 (B). Deviations of Fraser River and Puget Sound pink salmon. Data for Puget Sound pink salmon from the Pacific Fishery Management Council (2021; Table IV-1).

Chum salmon (Oncorhynchus keta)

Chum salmon were widespread in the Gulf of Alaska during winter surveys and were the most consistently captured salmon; including all age classes, and originating from a wide diversity of rivers as assessed by DNA stock identification⁹. Because chum salmon may mature at three ages, changes in abundances may result from poor survivals of one or more brood years; but have not been investigated in this report.

Alaska chum salmon indices

Indices for chum salmon are regional summaries (n = 11) accounting for areas of significant chum salmon production and with consistent monitoring programs through 2020 (Table 5). The time series of deviations for these chum salmon indices are summarized in Fig. 11 for two groupings of indices; those entering the North Pacific Ocean (SEAK, PWS/CR, Cook Inlet, Kodiak Archipelago, Chignik, South Alaska Peninsula) and those entering the Bering Sea (North Alaska Peninsula, Kuskokwim, Yukon River summer chum, Yukon River fall chum, Norton Sound). In the Bering Sea indices, abundance shifted to positive deviations after 2004 and remained mostly positive until the

⁹ Preliminary analysis by the Molecular Genetics Laboratory, Pacific Biological Station, indicate that chum salmon from all regions of the North Pacific were collected during the 2019 and 2020 expeditions; including Japan, Russia, Alaska, Canadian Yukon, British Columbia, and Puget Sound.

sudden negative deviation in 2020 (-58%). Deviations in the North Pacific Ocean group were more modest except for the large negative deviations in 2014 (-46%) and 2020 (-51%). But for both groups an important positive deviation occurred in 2017 (the largest deviation for any year in both groups).

These summaries for two large geographic areas mask much greater variation between indices within these groups. In the North Pacific group (Fig. 12A), deviations between the 6 indices were largely random and within a \pm 50% range until 2014 when each of the six indices were negative. Following 2014, deviations between indices and years were more coherent (for both positive and negative deviations) and mostly negative deviations; including all indices in 2016, 2018, and culminating in the very poor return in 2020 (average deviation -51% over the 6 indices). The greatest reduction in chum abundance would be attributed to the SEAK region with a -56% deviation for the largest chum returns (11.4 million chum on average, 1999–2018).

In the Bering Sea region (Fig. 12B), deviations were largely negative until the 2005 return, after which deviations were mostly positive and larger, indicating growth of the index populations, until 2018 and 2019 when returns were average or slightly negative with the exception of continued growth in the Norton Sound index. But in 2020, these five indices were strongly negative (range -42% to -72%) and, on average, exceed the reductions in the NPO indices.

Region	Index/Methods	Reference	Average run / index size in base period (1999- 2018)
Southeast Alaska (SEAK)	Standardize Minimum Index ¹⁰ , uses total harvest and peak aerial escapement surveys	Developed for this review	11.3 million fish
Prince William Sound and Copper River	Standardized Minimum Index, uses total harvest and multiple escapement surveys	Developed for this review	3.7 million fish
Cook Inlet	Standardized Minimum Index, uses total harvest and multiple escapement surveys	Developed for this review	0.40 million fish
Kodiak Archipelago	Standardized Minimum Index, Total harvest and peak aerial escapement survey	Developed for this review	1.0 million fish
Chignik River	Standardized Minimum Index, total harvest and peak aerial escapement survey	Developed for this review	0.25 million fish
South Alaska Peninsula	Standardized Minimum Index, total harvest and escapement indices	Developed for this review	1.6 million fish
North Alaska Peninsula	Standardized Minimum Index, Peak aerial escapement survey	Honnold et al. 2007; Nelson et al. 2006	0.55 million fish
Kuskokwim River (Bering Sea)	Standardized Minimum Index, uses total harvest and weir/tower counts	Developed for this review	0.29 million fish
Yukon River Summer Chum (Bering Sea)	Run reconstruction using multiple surveys	Hamazaki and Conitz, 2015	2.1 million fish
Yukon River Fall Chum (Bering Sea)	Run reconstruction using multiple surveys	Fleischman and Borba 2009; Volk et al. 2009	0.71 million fish
Norton Sound (Snake, Nome, Eldorado, Kwiniuk, North rivers) (Bering Sea)	Standardized Minimum Index, uses total harvest plus aggregate of weir/tower counts	Developed for this review	0.14 million fish

Table 5. Summary of Alaska chum salmon indices (n = 11) included in this review.

¹⁰ The indices were provided for this review, a standardized minimum index includes catch attributed to an area and spawning escapement indices representing an unknown portion of the populations. The index represents a minimum estimated production from a region based on surveys conducted consistently over the full period (1999-2020).



Fig. 11. Deviations for Alaska chum salmon indices for systems flowing into North Pacific waters (6 regional indices) and into the Bering Sea (5 indices). Deviations presented are the average deviation within each year.



Fig. 12. Deviations for Alaska chum salmon by indices entering the North Pacific Ocean (A) and the Bering Sea (B).

British Columbia and Washington State chum salmon indices

Monitoring of chum salmon in north and central BC is conducted according to conservation units (Holtby and Ciruna 2007) and would be analogous to the management area summaries provided by ADF&G. The BC indices are estimated total returns to specific geographic areas based on catch, spawning escapements, and migration patterns (stock reconstructions of annual abundance; English et al. 2018). These indices are used to account for changes in fishing patterns and intensity between years, and differences in vulnerability (harvest rates) between conservation units. Unfortunately, these indices have not been updated since 2017 and our information for 2019 and

2020 is limited to post-season management reports provided by DFO staff, with the notable exception of data from the Nisga'a Lisims Government (https://www.nisgaanation.ca/stock-assessments) for the Nass River watershed (Fig. 13). Chum salmon returns in 2020 to the Nass River were well above average and continuing a rebuilding of Nass chum salmon. Figure 13 is presented as the time series of annual returns to demonstrate recent rebuilding.

However, south of the Nass River, returns of chum salmon have been declining recently with historically poor spawning abundance in 2019 and 2020. Presentations by DFO staff report that chum spawning escapements were less than the 20th percentile of the distribution of spawning abundance from the Skeena River south to Cape Caution, even in the near absence of fishing in these years.

Chum salmon in southern BC are assessed in three aggregates: Fraser River, Southern Inside (non-Fraser, mainland inlets and Strait of Georgia), and west coast Vancouver Island (WCVI). The trend for Fraser River chum salmon has been updated and included in this report but recent data for Southern Inside chum production and WCVI have not been. As with pink salmon, the returns for 2019 and 2020 were summarized from post-season reviews (WCVI ¹¹ and Southern Inside/Strait of Georgia¹²) provided by DFO staff.

In summary, chum salmon returns to the mainland inlets and northeast Vancouver Island were very poor in 2019 and 2020, particularly summer chum in the mainland fjords. Returns in 2020 were better than 2019 in a number of rivers along the east coast of Vancouver Island in south Johnstone Strait and the Strait of Georgia. Fall chum returns in 2020 were quite variable with above average returns in a few rivers of southern Strait of Georgia. The latter was not true for the Fraser River chum. Chum salmon along the west coast of Vancouver Island continued poor returns seen over the past few years, including areas with significant hatchery production. Chum salmon assessments for Fraser River Chum are based on run reconstructions including fisheries in southern BC and Washington State, in-river harvest, and spawning escapements¹³. These reconstructions demonstrate a similar pattern of chum returns as described above for Southern Inside chum salmon (Fig. 14). Fraser chum production was very poor, only -18% of the base period average in 2019 and -42% of average in 2020.

Chum salmon are distributed into Washington and Oregon¹⁴ states but their numbers have been depressed for many years, and have resulted in two Evolutionary Significant Units of chum being listed under the US Endangered Species Act (Columbia River chum: Threatened, and Hood Canal Summer-run chum: Threatened). However, Puget Sound chum salmon returns, which average 1.6 million (1999–2018) are much larger than other stocks with available indices: Willapa Bay, Greys Harbor, and the Columbia River. Deviations for Puget Sound chum are similar to Fraser River (Fig. 14); deviations were -74% in 2019 and -69% in 2020. Returns to the other three groups were average or greater in recent years but their current abundance would indicate very limited contribution of these chum salmon to the overall chum abundance in the Gulf during 2019 and 2020. It is notable, however, that Puget Sound chum were identified by DNA sampling in the 2019 and 2020 Gulf of Alaska expeditions.



Fig. 13. Chum salmon return to the Nass River system, northern BC. Annual returns provided since inception of the current monitoring systems under the Nisga'a Lisims Government. (Web link provided in text)

¹¹ https://acsbc.ca/wp-content/uploads/2020/12/2020-Salmon-WCVI-Post-season-Review-Dec-16.pdf

¹² https://acsbc.ca/wp-content/uploads/2020/12/2020-Salmon-ECVI-Post-Season-Review-Final.pdf

¹³ Data and reconstruction analysis provided by DFO biologist Brittany Jenewein.

¹⁴ Chum salmon data provided by M. Agha, Wash. Dept. Fish & Wildlife, Olympia, WA



Fig. 14. Deviations from total return of chum salmon to the Fraser River and Puget Sound.

Coho salmon (Oncorhynchus kisutch)

While the abundance of coho salmon was expected to be very limited compared to sockeye, pink, and chum salmon in the deep-water environments of the Gulf of Alaska, coho salmon were widely distributed and commonly caught in both 2019 and 2020 winter expeditions (Beamish et al. 2022 *this volume*). The distribution of coho salmon throughout the Gulf of Alaska was one of the most interesting observations.

Alaska coho salmon indices

Monitoring of coho salmon in Alaska involves a mix of individual streams (indicator streams) and regional indices (Table 6). All four indicator streams were within Southeast Alaska while the regional indices provided information for seven other regions in Alaska. Given the life history of coho salmon in freshwater systems and their opportunistic use of many habitats, a coherence between indices was not expected, but it is notable that there were similarities for the four indicators in SEAK and the regional indices. Fig. 15 presents the four indicator streams in SEAK and demonstrates strong coherence since 2015 with below average abundances building to the poorest abundance for 3 of 4 indicators in 2020. When the SEAK average deviation is plotted with the remaining seven regional indices (Fig. 16), a period of coherence and poor production from 2009 to 2014 is evident, followed by generally improved abundance through 2018, and then a definite change to lower abundances in 2019 and 2020. In 2020, indices in the North Pacific Ocean region improved compared to 2019, but in the Bering Sea large negative deviations persisted in 2019 and 2020. Indices of coho salmon abundance in 2019 and 2020 returns suggest that coho abundance was well below average across Alaska in recent years.





Region	Index/Methods	Reference	Average run / index size in base period (1999- 2018)
SEAK – Hugh Smith Lake	Run reconstruction, weir counts	Shaul et al. 2009	3,700 adults
SEAK – Taku River	Run reconstruction, mark-recapture estimation	Pestal & Johnson 2015	131,000 adults
SEAK – Auke Creek	Run reconstruction, weir counts	Clark et al. 1994	920 adults
SEAK – Berners River	Run reconstruction, peak aerial surveys and foot surveys	Shaul et al. 2017	22,600 adults
PWS/CR (Copper River delta and Bering River)	Standardized Minimum Index, total harvest and peak aerial escapement survey	Developed for this review	398,000 adults
Cook Inlet (Deshka R and Little Susitna R)	Standardized Minimum Index, total harvest and weirs	Developed for this review	406,000 adults
Kodiak (Buskin, Olds, American, Pasagshak rivers)	Standardized Minimum Index, four weir counts	Developed for this review	403,000 adults
N. Alaska Peninsula (Bering Sea)	Standardized Minimum Index, peak aerial surveys (Nelson & Ilnik R)	Developed for this review	115,000 adults
Kuskokwim River (Bering Sea)	Standardized Minimum Index, four weir counts	Developed for this review	326,000 adults
Yukon River (Bering Sea)	Standardized Minimum Index, total harvests and foot surveys	Developed for this review	248,000 adults
Norton Sound (Snake, Nome, Eldorado, Kwiniuk, North rivers) (Bering Sea)	Standardized Minimum Index, total harvest plus weir counts	Developed for this review	106,000 adults

Table 6. Summary of Alaska coho salmon indices (n = 11) included in this review.



Fig. 16. Deviations of coho salmon abundance for seven regional indices in Alaska and the trend line for the average annual value of the four indicator streams (indices) within Southeast Alaska.

North and Central BC coho

Coho assessments in north and central BC have relied on a few indicator streams that are monitored for adult returns, smolt production, and estimates of marine survival and harvest rates based on coded-wire tags. Recently,

however, indicator streams have been limited to Toboggan Creek (Bulkley River, Skeena basin) and the Nisga'a Lisims Government stock assessment program for Nass River salmon (2 indices, Zolzap Creek and main-stem mark-recapture program). There are no data for the Zolzap indicator project during 2005 through 2010. The Tyee test fishery in the lower Skeena River provides an index of coho salmon returns since 1955 and is added to the above indices. Each of these indices shows coherence in recent years with below average returns in 2018 through 2020, with poorest returns in 2018 (Fig. 17). Unfortunately, no indicators for coho salmon were identified for central BC or Haida Gwaii.



Fig. 17. Deviations for northern BC coho salmon at the Toboggan Creek indicator stock (Skeena River), and interior coho salmon via Nass River mark-recapture program & Zolzap Creek indicator stock (Nass River), and the Tyee Test Fishery index for coho salmon, standardized to September 24th end-date. Note that there are NO DATA from 2005 through 2010 for Zolzap Creek.

Coho salmon in Southern BC

As in northern BC, coho salmon assessments in southern BC rely on indicator streams. Within the Fraser River system, however, annual escapement surveys have been consistently conducted to monitor returns in 11 conservation units following the designation of the Interior Fraser River (IFR) coho salmon as Threatened by COSEWIC (2016)¹⁵. Assessments for inside marine areas of southern BC include resistivity counts (and video) in the Keogh River (northeastern Vancouver Island), Black Creek indicator stock (weir counts and tagging), and Lang Creek (mainland Strait of Georgia, weir counts and tagging). These three indices have been below average in returns since 2015 (Fig. 18), and if there were any recent change, it may be a small improvement in 2020.

Fraser River coho salmon is assessed based on the estimated spawning escapements in eleven conservation units. The data presented has not been adjusted for fishing mortality as exploitation rates have been very small (~10%) since the mid-1990s. Returns to the Fraser Basin, since the late 1990s, have fluctuated (Fig. 19) and recently show an upward trend, but within the range of observed returns between 1999 and 2018. Escapements of IFR coho salmon indicate substantial variation around the average aggregate escapement (42,000) but without trend (Fig. 19). Deviations in 2019 and 2020 would indicate improved production and are not consistent with the other BC coho indicators. An increasing abundance during the past 4 years may have resulted from improved marine survival within the Strait of Georgia (Beamish and Neville 2021).

¹⁵ https://www.canada.ca/en/environment-climate-change/services/species-risk-public-registry/cosewic-assessments-status-reports/coho-salmon-interior-fraser-2016.html



Fig. 18. Deviations for coho salmon in southern BC (excluding the Fraser River). Indices include northern Vancouver Island (Keogh River Coho), Black Creek Coho indicator stream (annual weir counts, east coast Vancouver Island), and Lang Creek Coho (weir counts, mainland Strait of Georgia).



Fig. 19. Interior Fraser River coho salmon escapements by return year (aggregate total number of spawners estimated from 11 conservation units, 1999-2020). Spawning escapement monitoring is conducted in 11 conservation units comprising the Interior Fraser River unit.

Washington, Oregon, and California coho salmon indices:

Coho production in the southern United States (US) is reported in detail annually by the Pacific Fisheries Management Council¹⁶. Coho are grouped into 3 geographic regions: Puget Sound, West Coast, and the Oregon Production Index (OPI) area inclusive of the Columbia River, Oregon, and California. At this time, 2020 returns for Puget Sound and West Coast were not included in this report but data for the OPI were complete (Fig. 20). Like many coastal coho production areas to the north, OPI coho production has been ~50% below average since the 2015 return year. Trends through 2019 for Puget Sound and West Coast Coho systems were also indicative of reduced abundance.

¹⁶ https://www.pcouncil.org/documents/2021/03/2021-preseason-report-i.pdf/ (PMFC 2021)



Fig. 20. Coho salmon abundance (catch and escapement; thousands of fish; top panel) for Oregon Production Index (OPI) and annual deviations (bottom panel) from the base period average for 1999-2018). Source: Table III-2 (p. 67) PMFC (2021).

Chinook salmon (Oncorhynchus tshawytscha)

Chinook salmon were rarely encountered during the Gulf of Alaska winter expeditions with only one exception during 2020 as the vessel returned to the coastal shelf of Vancouver Island. Past literature would suggest that spring Chinook (yearling smolts) are more likely to utilize the high seas environments than summer and fall Chinook salmon (Healey 1983). Chinook salmon are unlikely to influence the overall abundance of Pacific salmon in the Gulf of Alaska as they are the least abundant salmon species. But in North America, Chinook salmon assessment and management accounts for a disproportionate investment of agency resources. In Alaska, the declining status of Chinook salmon and their productivity led to establishing a research initiative in 2012¹⁷. Within the Pacific Salmon Commission, the Chinook Technical Committee monitors 47 indicator populations annually. Recently these data were made publicly available on the PSC website ¹⁸ and in CTC Rep. TCCHINOOK (21)-03¹⁹.

Alaska Chinook salmon indices:

Data were provided by ADF&G for 16 indices of Chinook salmon returns (Table 7) that incorporate systems included in Alaska's Chinook Salmon Research Initiative. The change from above average productivity to below in 2007 is a striking and unique pattern that points to a large-scale environmental change (Fig. 21). However, in terms of effect on overall salmon abundance in Gulf of Alaska during 2019 and 2020, it is unlikely to be a major factor.

¹⁸ https://www.psc.org/publications/technical-reports/technical-committee-reports/chinook/#35-638-wpfd-data-sets

¹⁹ https://www.psc.org/publications/technical-reports/technical-committee-reports/chinook/

¹⁷ https://www.adfg.alaska.gov/index.cfm?adfg=chinookinitiative.main

Region	River	Stock	Enumeration Method	Average Run Size	Reference
Southeast Alaska	Unuk R	large fish >660 mm	Peak Foot / Aerial survey	5,400	Hendrich et al. 2008; Lum and Fair 2018 (Table 1 update)
Southeast Alaska	Stikine R	large fish >660 mm	Mark-Recapture	38,400	Bernard et al. 2000
Southeast Alaska	Taku R	large fish >660 mm	Mark-Recapture	38,100	McPherson et al. 2010
Southeast Alaska	Situk R	large fish >660 mm	Mark-Recapture	1,400	McPherson et al. 2005
Southeast Alaska	Alsek R	large fish >660 mm	Mark-Recapture	6,100	Bernard and Jones 2010
PWS/Copper R	Copper R	not specified	Mark-Recapture	60,400	Savereide et al. 2018
Upper Cook Inlet	Kenai R	early run (large fish >750 mm	Sonar	7,900	Erickson et al. 2017; Fleischman and Reimer 2017
Upper Cook Inlet	Kenai R	late run (large fish >750 mm)	Sonar	40,100	Erickson et al. 2017; Fleischman and Reimer 2017
Upper Cook Inlet	Susitna R	Deshka R	State-space model	27,500	Reimer and DeCovich 2020
Upper Cook Inlet	Susitna R	East Susitna R sub- basin	State-space model	25,900	Reimer and DeCovich 2020
Upper Cook Inlet	Susitna R	Talkeetna R sub- basin	State-space model	17,700	Reimer and DeCovich 2020
Upper Cook Inlet	Susitna R	Yentna R sub-basin	State-space model	34,600	Reimer and DeCovich 2020
Kodiak Island	Karluk R	not specified	Weir	5,200	Nemeth et al. 2010
S. Alaska Peninsula	Chignik R	not specified	Weir	4,100	Schaberg et al. 2019 (App. A2)
Bering Sea	Kuskokwin R	not specified	Maximum likelihood model	182,250	Hamazaki et al. 2012; Larson 2021
Bering Sea	Yukon R	Canadian Yukon R	Sonar	85,000	Yukon Technical Comm. (JTC 2021, App. B11)

 Table 7. Alaska Chinook salmon indices (fish sizes referenced are mid-eye to fork of tail).



Fig. 21. Average deviations for 14 Chinook indices for rivers entering the North Pacific region, 2 indices in the Bering Sea (Kuskokwim and Yukon (Canadian production)). The large negative deviation in 2000 was observed in both Bering Sea indices.

BC and southern US Chinook salmon indices

Interpreting changes in Chinook salmon abundance indices becomes increasingly uncertain for more southerly river systems. Chinook salmon from Southeast Alaska to California have diverse life-histories (under-yearling and yearling smolts; Winter, Spring, Summer, and Fall migration timing; etc.) and are harvested in multiple ocean fisheries over 2 or 3 age-classes. Therefore, a change in an index of abundance may have multiple causes. In north and central BC, Chinook salmon are typically yearling, spring or early-summer run-timing; very similar to Alaska Chinook. Fig. 22 provides trends in deviations for the Nass River, Skeena River, and to the Atnarko River (Bella

Coola, central BC). Nass and Skeena River Chinook deviations follow a pattern similar to the Alaska indices and change to a consistent below average pattern from 2011. Atnarko River Chinook salmon have a more variable pattern with significant negative deviations in 2017-2019, but the 2020 return was above average. Atnarko Chinook salmon are a summer-run population in the southern portion of Queen Charlotte Sound (near Bella Bella, BC).



Fig. 22. Deviations for north and central BC Chinook salmon returning to the Nass River (total return to Canada), Skeena River (based on genetic stock identification), and Atnarko River (Bella Coola area). Data as provided at: https://www.psc.org/publications/technical-reports/technical-committee-reports/chinook/#35-638-wpfd-data-sets

South of Cape Caution, BC, Chinook salmon abundance is largely determined by sub-yearling fall-run Chinook stocks (wild and hatchery origin). Years of coded-wire tagging of hatchery fall-run Chinook salmon indicate these Chinook are northerly migrating and rear in the coastal zones westward to the Bering Sea. Indicator stocks for fall-run Chinook salmon from southern BC, late-summer Chinook salmon in the Fraser River, and the largest Chinook population in the Columbia R. show sustained or increasing abundances in recent years (Fig. 23).



Fig. 23. Abundance trends for summer and fall Chinook salmon indicator stocks. Cowichan River fall-run Chinook in the Strait of Georgia, Fraser River summer Chinook (5 South Thompson River populations plus one lower river), Robertson Creek fall Chinook (Canada's largest Chinook hatchery, west coast of Vancouver Island), and the largest producer of fall Chinook in the Columbia River. Data as provided at: https://www.psc.org/publications/technical-reports/technical-committee-reports/chinook/#35-638-wpfd-data-set.

Spring and early-summer Chinook that are believed to rear in the open Pacific Ocean, certainly indicate that production from these sources have been well below average for a number of years. However, returns to late-summer and Fall Chinook, from more southerly rivers, are returning at average to above average values for a variety of reasons, but are more likely distributed through coastal waters than off-shore ocean waters.

Summary

While the various indices reported in this paper are not equivalent across species and geographic areas, the consistency of reduced abundances (negative deviations) in recent years across the North Pacific Ocean strongly suggests that the 2019 and 2020 Gulf of Alaska expeditions were conducted in a period of reduced salmon abundance, particularly for sockeye, pink, and chum salmon (and likely substantially reduced). Indices for Chinook and coho salmon are more complicated due to changes in abundance from below average returns in the north to improving abundance in the southern half of the coast studied. Furthermore, trends in many indices indicate that the reduced abundance was not limited to 2019 and 2020 return years but has been declining for a few years and coincident with the marine heat waves since 2014 (Cheng et al. 2021; Hobday et al. 2018; Oliver et al. 2021).

Of equal interest were trends for sockeye, pink, and chum salmon in the Bering Sea region (Fig. 3, 6, 11). Since 2014, sockeye and pink salmon in this region have had above average returns and chum salmon have become more synchronous in both strongly positive and negative years. The separation of indices in the Bering Sea from those in the NPO, was simply based on the patterns of deviations in adult returns (abundance) but is not meant to imply that these Bering Sea populations are isolated from the salmon returning to NPO river systems. Past research clearly demonstrates the use of the Bering Sea region by juvenile salmon (Farley et al. 2005, 2007; Moss et al. 2009) but maturing salmon distribute into the North Pacific; indeed, salmon sampled in the Gulf of Alaska during 2019 and 2020 included sockeye salmon from Bering Sea populations and Yukon River chum salmon.

This review must acknowledge the limitations of different types of monitoring systems applied and certainly the more limited analyses in BC and southern US. However, we focused on data that has been collected consistently during the review period (1999-2018) and must have 2019 and 2020 data. Where 2019 or 2020 information was available but not incorporated in analytical models, post-season reports from responsible management agencies were referenced. All indices included accounting for fishing effects, but with reduced abundances in recent years, management agencies appropriately reduced fishing rates with the consequent affect that most returns would be accounted for by spawning escapement. Where spawning numbers are estimated with visual methods, their imprecision is likely to be greater but the effect on accuracy is less certain. This potential effect has not been addressed in this review.

These results provide some assurance that the lower than expected catches during the 2019 and 2020 expeditions in the Gulf of Alaska were informative of the relative abundance of Pacific salmon in the survey areas. But, these results are not informative of whether the trawl nets provided a consistent sample of the fish population vulnerable to the trawl (i.e., the catchability; Arreguin-Sanchez 1996) that would be necessary for future quantitative stock assessments or research studies. The catchability factors applied in these initial studies were developed for Russian salmon surveys and in their environments (Volvenko 2000); therefore, their applicability to these surveys in the central Gulf of Alaska is unknown. The applicability of these catchability factors will be difficult to evaluate in the absence of other fishery or stock statistics for comparison over time. As an alternative, using different fishing gear to compare catches by species and biological characteristics of the catch is suggested. We recommend direct comparison of fishing performance with Japanese research gillnets (with multiple panels of variable mesh sizes) that have been used extensively for monitoring and research of Pacific salmon in the North Pacific Ocean and Bering Sea (e.g., Ishida et al. 2001). A gillnet survey will be conducted in parallel to the trawl surveys during the winter 2022 trans-Pacific survey (https://yearofthesalmon.org/2022expedition/).

Addendum: In addition to monitoring salmon abundance, changes in body size and run timing were noted in several of these index systems. Size and age at maturity provide additional information on conditions of the marine environment to complement changes in survival and abundance.

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Appendix 1. Sockeye salmon abundance indices provided by ADF&G (n = 33). Each index is based on a run reconstruction of escapements and catches, with the exception of the Norton Sound index that is a standardized minimum index developed for this review and described in the text.

Area	River/District	Average Run size	Enumeration method	Years	Reference
Southeast Alaska	Mainstem Stikine River	47,800	Mark-Recapture	1979 to present	TRTC 21-03, Table 3
Southeast Alaska	Tahltan Lake	85,700	Weir Count	1979 to present	TRTC 21-03, Table 3
Southeast Alaska	Speel Lake	12,100	Weir Count	1983 to present	Heinl et al. 2014
Southeast Alaska	Taku River	170,000	Mark-Recapture	1984 to present	Miller and Pestal 2020, TRTC 21-03, Table 6
Southeast Alaska	Redoubt Lake	49,100	Weir Count	1982 to present	Geiger 2003
Southeast Alaska	Alsek River	75,900	Weir Count	1979 to present	Eggers and Bernard 2011, TRTC-21-03 Table 10
Southeast Alaska	Chilkat Lake	121,000	Sonar	1976 to present	Eggers et al. 2010
Southeast Alaska	Chilkoot Lake	138,300	Weir Count	1976 to present	Eggers et al. 2009
PWS/Copper R	Copper River	1,940,100	Sonar & aerial survey	1965-2020	ADF&G, developed for this analysis
Upper Cook Inlet	Kasilof River	975,700	Sonar	1969 to present	McKinley et al. 2020
Upper Cook Inlet	Kenai River	3,543,900	Sonar	1969 to present	Hasbrouck et al. Unpubl., McKinley et al. 2020
Upper Cook Inlet	Russian River (early run)	78,100	Weir Count	1965 to present	McKinley et al. 2020
Kodiak Island	Afognak (Litnik) River	42,000	Weir Count	1982 to present	McKinley et al. 2019, Nelson et al. 2005
Kodiak Island	Karluk River (early run)	414,900	Weir Count	1985 to present	Schaberg et al. 2016, McKinley et al. 2019
Kodiak Island	Karluk River (Late run)	771,900	Weir Count	1985 to present	Schaberg et al. 2016, McKinley et al. 2019
Kodiak Island	Ayakulik River	448,900	Weir Count	1970 to present	Nemeth et al. 2010, McKinley et al. 2019
Kodiak Island	Upper Station R (Late run)	278,700	Weir Count	1982 to present	Nemeth et al. 2010, McKinley et al. 2019
Kodiak Island	Frazer Lake	351,000	Weir Count	1974 to present	Honnold et al. 2007a, McKinley et al. 2019
Kodiak Island	Saltery Lake	64,600	Weir Count	1976 to present	Nemeth et al. 2010
S. Alaska Peninsula	Chignik R (early run/Black L)	1,289,000	Weir Count	1922 to present	Schaberg et al. 2019
S. Alaska Peninsula	Chignik R (Late run/Chignik R)	1,025,900	Weir Count	1922 to present	Schaberg et al. 2019
N. Alaska Peninsula	Nelson River	482,800	Weir Count	1985 to present	Nelson et al. 2006, south of Port Moller
N. Alaska Peninsula	Bear River (Late run)	482,000	Weir Count	1987 to present	Nelson et al. 2006, south of Kvichak River
Bristol Bay	Kvichak River	8,170,500	Tower Count	1959 to present	Cunningham et al. 2012
Bristol Bay	Alagnak River	3,538,500	Tower Count	1959 to present	Cunningham et al. 2012
Bristol Bay	Naknek River	5,484,500	Tower Count	1959 to present	Cunningham et al. 2012
Bristol Bay	Egegik River	7,347,400	Tower Count	1959 to present	Cunningham et al. 2012
Bristol Bay	Ugashik River	3,903,500	Tower Count	1959 to present	Cunningham et al. 2012
Bristol Bay	Wood River	7,361,300	Tower Count	1959 to present	Cunningham et al. 2012
Bristol Bay	lgushik River	1,067,500	Tower Count	1959 to present	Cunningham et al. 2012
Bristol Bay	Nushagak River	782,500	Sonar	1959 to present	Cunningham et al. 2012
Bristol Bay	Togiak River	25,845,000	Tower Count	1959 to present	Cunningham et al. 2012
Port Clarence	Salmon lake, Central Grand	50,350	Total harvest + aerial,	1997 to present	ADF&G, developed for this analysis
	River, Pilgrim River		tower/weir		

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Coastal Surveys in Alaska and Their Application to Salmon Run-Size and Harvest Forecasts

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Understanding the factors that influence the survival of salmon is important as salmon play a key role in the ecological and socio-economic framework of many communities throughout Alaska. The marine survival of salmon is believed to be determined during key critical periods (Beamish and Mahnken 2001). The first critical period occurs during the estuarine or initial marine period of salmon. Predation-based mortality can often be the key factor during this critical period of salmon. The second critical period is believed to be primarily dependent on the ability of salmon to reach a critical size or nutritional state required to survive marine winters (Beamish and Mahnken 2001). Nutritional-based sources of mortality will begin to increase in importance as salmon outgrow the predation size window of most marine predators. Coastal surveys that provide information on the abundance and ecology of juvenile salmon can add insight into the relative importance of these critical survival periods as well as the resilience of salmon to changes in marine ecosystems, such as the emergence of marine heatwaves (Barbeaux et al. 2020) and warming of Arctic habitats (Jones et al. 2020). Coastal marine surveys in Southeast Alaska (SEAK) and the northern Bering Sea (NBS) currently use juvenile salmon abundance to provide harvest forecasts for pink salmon fisheries in SEAK and adult run-size forecasts for Chinook salmon fisheries in the Yukon River. Significant relationships between juvenile (first summer at sea) and adult abundance are present in both surveys, which emphasizes the importance of the early life-history stages (freshwater and initial marine life-history stages) of salmon to structuring future adult returns.

The NBS survey was initiated in 2002 as part of the Bering Aleutian Salmon International Survey (BASIS) research program (NPAFC 2001). This survey uses surface trawl gear to sample juvenile salmon inhabiting the coastal waters of the NBS from latitudes 60°N to 65.5°N aboard chartered fishing vessels (currently the F/V *Northwest Explorer*) (Fig. 1). The NBS survey has provided insight into juvenile abundance and critical marine survival periods of salmon (Murphy et al. 2017; Howard et al. 2019; Farley et al. 2020; Howard et al. 2020; Murphy et al. 2013; Hertz et al. 2015; Honeyfield et al. 2016; Howard et al. 2016; Moss et al. 2016; Vega et al. 2017; Garcia and Sewall 2021; Murphy et al. 2021), and the ecology of other pelagic species (Andrews et al. 2016; Shink et al. 2019; Garcia et al. 2021).

A primary objective of the NBS survey is to provide juvenile-based forecast models for returning adult Yukon River Chinook Salmon. The abundance of Yukon River Chinook salmon has declined significantly over the last 20 years, resulting in various levels of commercial fisheries closures, restrictions to subsistence fishing opportunity, and the inability to meet harvests necessary for subsistence in many years (Fall et al. 2020). Although causes of their decline are unclear, Chinook salmon stock groups throughout the Yukon River (JTC 2021) and Alaska (Munro 2019) have been experiencing poor survival. Stock-specific juvenile abundance estimates of Chinook salmon in the NBS have supported adult run-size forecasts for Canadian-origin Yukon River Chinook salmon since 2013. Although the Canadian-origin stock group was the initial focus of the juvenile Chinook salmon abundance estimates (Murphy et al. 2017), advances to the western Alaska Chinook salmon genetic baseline (Howard et al. 2019) allowed comparable forecast models to be developed for the total run of Chinook salmon in the Yukon River.





The abundance of juvenile Chinook salmon in the NBS is based on the expansion of trawl catch-per-uniteffort (CPUE, catch/km²) data to the survey area within four spatial strata: 60° to 62°N, 62° to 64°N, Norton Sound, and Bering Strait. Trawl CPUE is adjusted by the proportion of the mixed-layer-depth sampled at each station. Genetic stock composition estimates are used to generate stock-specific juvenile abundance for the Canadian-origin and Total Yukon (Lower Yukon, Middle Yukon, Canadian-origin combined) stocks of Chinook Salmon (Murphy et al. 2013; Murphy et al. 2017; Howard et al. 2019; Howard et al 2020; Murphy et al. 2021). This approach to estimating juvenile Chinook salmon abundance was originally described in Howard et al. (2020), and Murphy et al. (2021). Juvenile abundance has declined for both the Total Yukon River stock group and the Canadian-origin stock group of Chinook salmon (Fig. 2a and 2b). Much of the variability in adult returns is explained by juvenile abundance (Fig. 2c and 2d), which emphasizes the importance of early life-history stages (freshwater and initial marine) to their overall survival.

The NBS juvenile-based adult run-size forecasts models for Canadian-origin and Total Yukon stocks (Fig. 3) have become important components of the annual preseason management and harvest planning for the Yukon River. The Canadian-origin forecast has been used by Alaskan fishery managers to inform planning discussions for one to three years in advance of harvest management. The Canadian-origin forecast has been used on an annual basis by U.S./Canada Yukon River Panel's Joint Technical Committee (JTC) as part of a multi-model approach to forecast adult run size since 2018 (JTC 2021). The JTC has announced their plans to integrate the juvenile forecast model, the Ricker production model, and the sibling forecast model within a Bayesian framework to provide the pre-season outlook for Yukon River Chinook salmon (JTC 2021). The conventional approach to run-size forecasts for Yukon River Chinook salmon in the Yukon River (JTC 2021). However, with the advent of the new juvenile-based forecast for the Total Yukon River stock group, fishery managers have an alternative forecast to consider that is based on near real-time information and has the benefit of informing run size up to three years in the future.

The Southeast Alaska Coastal Monitoring (SECM) survey currently includes the collection of oceanographic and surface trawl data in inshore, strait, and coastal habitats during May, June and July aboard the National Oceanic and Atmospheric Administration (NOAA) research vessel R/V *Sashin* and the Alaska Department of Fish and Game (ADF&G) vessel R/V *Medeia* (Piston et al. 2021a; Fig. 1). The SECM survey began in 1997 (Murphy et al. 1999; Orsi et al. 2000) and has provided insight into the early marine ecology of salmon (LaCroix et al. 2009; Weitkamp et al. 2011; Orsi et al. 2013; Orsi et al. 2016; Murphy et al. 2019), and other pelagic species (Orsi et al. 2007). The SECM survey has supported research on the foraging ecology of salmon (Sturdevant et al. 2012; Fergusson et al. 2013) and the zooplankton community within SEAK (Fergusson and Orsi 2017; Fergusson et al. 2021).



Fig. 2. Stock-specific juvenile abundance and the

relationship between juvenile and adult abundance for Yukon River juvenile Chinook salmon in the northern Bering Sea (Murphy et al. 2021). Juvenile abundance estimates (2003–2019 juvenile years) are shown for the Canadian-origin stock group (a), and the Total Yukon River stock group (b). Relationships between juvenile and adult abundance are shown for the Canadian-origin stock group (c), and the Total Yukon River stock group (d). No survey occurred in 2008, and the 2005 survey year was not included in the forecast models (c and d) due to multiple complications associated with that survey year.



Fig. 3. Observed stock-specific run size estimates (gray bars) and projected run size (dashed line) of Yukon River Chinook salmon from the Canadian-origin stock group (a), and the Total Yukon River stock group (b), 2003–2022 (Murphy et al. 2021). Black error bars are the 80% prediction interval of the forecasted run size.

Data collected during the SECM survey have supported harvest forecast models for SEAK pink salmon fisheries since 2004. The approach used to forecast harvest has evolved over time and is described in Orsi et al. (2016), Wertheimer et al. (2018), Murphy et al. (2019), and Piston et al. (2021b). An abundance index for juvenile pink salmon is constructed from the peak monthly (June or July) average surface trawl CPUE in Icy Strait. The

standard unit of effort is a 20 min trawl set and CPUE is log-transformed and adjusted for fishing power differences between vessels used during SECM surveys over time. Temperature is an important environmental covariate in the forecast model (Fig. 4). The temperature effect has been interpreted as an ecosystem effect on survival (Orsi et al. 2016); however, it is also possible that it reflects an ecosystem effect on survey catchability (Murphy et al. 2019). The Icy Strait Temperature Index, (ISTI, Murphy et al. 2019) has been used to describe sea surface temperature anomalies in inside waters of SEAK since the start of the survey in 1997; however, we are currently evaluating the use of satellite sea surface temperature data rather than in-situ CTD data, as it allows the spatial and temporal scale of temperature to be optimized to the harvest forecast model. Although very low pink salmon harvests have occurred in SEAK over the last three years, the harvest of pink salmon is expected to increase in 2021 (Fig. 5).



Fig. 4. The Southeast Alaska pink salmon harvest forecast model (1997–2018 juvenile years) from Murphy et al. (2019). 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, 1997–2018.



Fig. 5. Forecast model fit (hindcasts) for total Southeast Alaska (SEAK) pink salmon harvest (1998–2020 harvest years) (Piston et al. 2021b). The observed SEAK pink salmon harvest is represented by the grey bars and the model fit is shown by the black line. The 2021 harvest forecast is shown as a grey circle and the 80% prediction interval as a black vertical line.

Significant correlations between juvenile and adult abundance in these coastal surveys highlight the importance of early life-history stages (freshwater and initial marine) on the variation in marine survival of salmon. Forecast models based on juvenile abundance or indices of juvenile abundance can provide guidance on future runsize and harvests as long as mortality during later marine stages remains relatively stable or can be accounted for within a dynamic model framework or with ecosystem indicators.

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Closing Comments

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The extended abstracts provide an initial interpretation of the results from the 2019 and 2020 expeditions. A more detailed understanding is expected from the analyses of results from the trans-Pacific studies under the North Pacific Anadromous Fish Commission and International Year of the Salmon expeditions (https://yearofthesalmon.org/2022expedition).

As a high-level summary:

- 1. The 2019 and 2020 winter expeditions to the Gulf of Alaska were the first Canadian studies of this kind since the late 1960s and the first to include an international team of researchers. All researchers volunteered their participation and agreed that all data would be publicly available (see at https://iys.hakai.org/dataset). The two expeditions were the first high seas Pacific salmon research to be privately funded and organized.
- 2. The research applied a variety of methodologies to study the salmon and their ecosystem:
 - a. DNA stock identification (including first trials of on-board analyses, Deeg et al. 2021);
 - b. Environmental-DNA sampling (Deeg et al. 2021);
 - c. Pathogens and health (Deeg et al. 2022);
 - d. Body composition studies to examine fish condition (Waters et al. 2022);
 - e. Use of stable isotopes to examine dietary overlap between species (see Espinasse et al. 2020); and,
 - f. A comprehensive array of oceanographic measurements.

There was evidence that coho salmon can form large schools in the winter with fish from populations ranging from Oregon to Alaska.

- 3. The first estimates of the total population of Pacific salmon within the survey areas were made using the method developed by Russia and applied to our data by A. Somov (TNIRO, pers. comm.). When estimates were adjusted for equal sampling areas, the total population estimate was essentially identical at 54.95 million salmon in 2019 and 55.2 million salmon in 2020, over an area of 697,500 km². It was fortuitous that the studies occurred during an unpreceded marine heat wave in the Gulf of Alaska. These abundance estimates were made at a time in 2019 when there were historic poor salmon returns to British Columbia in the fall of 2019, and in 2020 when there was a collapse of the salmon catches in all countries resulting in a total commercial catch equal to low catches in the early 1980s.
- 4. Extensive oceanographic survey (Pakhomov et al. 2022) plus our biological sampling enabled us to begin to associate winter environments with salmon abundance, distribution and diet. A major objective of the expeditions was to understand how climate and ocean conditions that affected growth in the coastal ocean was related to salmon survival in the first ocean winter. Pacific salmon species are different and behave differently in the winter ocean, therefore decreasing the interspecific competition between them (Radchenko 2022). Ross and Pena (2022) provided an historical perspective of the ocean environment in 2019 and 2020 based on Canada's longest time series of Pacific Ocean observations along Line P and at Canada's Weather Station Papa (50°N, 145°W). In total, sampling along Line P now provides 75 years of detailed oceanographic data (Pena and Bograd 2007).
- 5. Our collaborations between countries demonstrated the value of international cooperation, particularly in studying Pacific salmon in an open environment the breadth of the North Pacific Ocean.

These surveys were highly informative and demonstrated the utility of trawl nets to sample Pacific salmon in the deep-water marine environments, but there are certainly further questions to address. Principle in them is the effectiveness of the trawls to representatively sample the fish community in the surface layers, including the species composition of salmon and in the broader fish community. It was notable that trawl catches did not include many salmon predators or competitors in both the 2019 and 2020 expeditions. In 2022, a charter vessel will utilize Japanese research gillnets to compare catches with trawlers fishing at similar times and places. Catches of salmon during these expeditions were not uniform across the sampled region and differed by species. The presence of zero

catch observations was twice as common in the 2020 survey as in 2019, and catches in 2020 also showed greater heterogeneity (patchiness) between sets. These observations may result from behavioural differences of salmon in winter periods (schooling) and/or result from distributions of their prey. It is notable that during both expeditions, large catches of squid, euphausiids, and myctophids (Lanternfish) occurred each night. The abundance of inhabitants of the upper epipelagic layer increased at night by more than 700 times and reached at least one animal per 16 square metres in 2019. Participants of the workshop did not know if this abundance of marine life competed with Pacific salmon.

The analyses of salmon collected in 2019 and 2020 are still incomplete, partly because of restrictions related to the COVID-pandemic that limited sample exchange and processing. However, results to date support that winter conditions can be difficult for Pacific salmon (Waters et al. 2022), that salmon from across the North Pacific Ocean were highly inter-mixed in the Gulf of Alaska, and size and age classes of salmon were also inter-mixed with the exception of a few samples (trawl sets) of greater abundances with an abundance predominately of one age-class (suggesting a role for salmon schooling in these deep-water environments).

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