North Pacific Anadromous Fish Commission
Bulletin No. 7: 1–18, 2024

Highlights of the 2022 International Year of the Salmon Pan–Pacific Winter Expedition

Laurie Weitkamp[1], Andrew Barclay[2], Richard J. Beamish[3], Maycira Costa[4], Ed Farley[5], Cameron Freshwater[6], Sara Gilk-Baumer[2], Caroline Graham[7,8], Kathrine Howard[2], Jackie King[6], Marta Konik[4], Jim Murphy[5], Chrys Neville[6], Evgeny A. Pakhomov[9,10], Vladimir Radchenko[7,11], Brian Riddell[12], Eric Rondeau[6], Mark Saunders[7,13], Aidan Schubert[7,14], Don Van Doornik[15], Bernard Yang[16,17], and Aleksey Somov[11]

Weitkamp, L., A. Barclay, R.J. Beamish, M. Costa, E. Farley, C. Freshwater, S. Gilk-Baumer, C. Graham, K. Howard, J. King, M. Konik, J. Murphy, C. Neville, E.A. Pakhomov, V. Radchenko, B. Riddell, E. Rondeau, M. Saunders, A. Schubert, D. Van Doornik, B. Yang, and A. Somov. 2024. Highlights of the 2022 International Year of the Salmon Pan-Pacific Winter Expedition. N. Pac. Anadr. Fish Comm. Bull. 7: 1–18. https://doi.org/10.23849/npafcb7/2ksd-00ig

Abstract: During February–April, 2022, an international fleet of five ships from the U.S., Canada, and Russia conducted a coordinated survey of Pacific salmon high seas habitats across 2.5 million km^2 of the North Pacific Ocean. The goal was to document use of pelagic habitats by salmon during winter to understand factors regulating salmon survival. Across all ships, 2,364 Pacific salmon (*Oncorhynchus* spp.) and steelhead trout (*O. mykiss*) were caught using surface trawls, gill nets, and longlines. Sockeye salmon (*O. nerka*), were the most abundant salmonid, followed by chum (*O. keta*), pink (*O. gorbuscha*), coho (*O. kisutch*), and Chinook (*O. tshawytscha*) salmon; steelhead trout were extremely surface-oriented and only caught with gill nets. Other commonly caught taxa included myctophids, gonatid squids, and jellyfish. Salmon showed species-specific patterns in many metrics, such as distributions and diets. Genetic data indicated that salmon originated from around the Pacific Rim and multiple stocks were typically caught together. Preliminary results from the 2022 expedition, combined with results from winter expeditions in 2019 and 2020 and historic data, begin to fill key knowledge gaps about salmon winter distributions and the pelagic ecosystems that support salmon on the high seas.

Keywords: Pacific salmon, high seas, winter ecology, sockeye salmon, chum salmon, coho salmon, pink salmon, Chinook salmon, steelhead trout

INTRODUCTION

It is highly uncertain how Pacific salmon (*Oncorhynchus* spp.) and steelhead trout (*O. mykiss*; hereafter collectively referred to as “salmon”) respond to climate-driven changes in their oceanic environment, in part due to limited information on their winter distribution and ecology in the North Pacific Ocean. Winter has been hypothesized to be a “critical period” for Pacific salmon, when mortality can be high, especially for small salmon with potentially limited energy reserves (Beamish and Mahnken 2001; Trudel et al. 2011). Winter has also been proposed as a time when abundant pink salmon (*O. gorbuscha*) may compete for prey with other salmon species on the high seas (Ruggerone and Nielsen 2004). Recent extreme environmental conditions in marine habitats, such as the North Pacific warm blob (Bond et al. 2015) suggest that this life history stage may be particularly impacted by ongoing climate change. However, limited knowledge of salmon winter marine ecology hampers the ability to provide science-based management advice both now and in the future as the oceans undergo rapid change that may be unfavorable for some salmon species and stocks.

The North Pacific Anadromous Fish Commission (NPAFC) and its precursor, the International North Pacific Fisheries Commission (INPFC), have promoted international winter research on salmon on the high seas since the 1950s (Myers et al. 2016). This historic research initially used purse seines, gillnets and longlines to catch salmon, which allowed tagging and release of salmon and collection of scales for both aging and to determine continent of origin. Sampling gear switched to surface trawls (which typically descale fish) in the 1990s as genetic stock identification methods developed. Early (1950s–1970s) winter high seas research provided information on important winter locations and dominant oceanographic features of winter salmon habitat (Myers et al. 2016). It established that the distribution of most Pacific salmon in winter was extensive and Pacific salmon moved seasonally, but there was considerable variation in patterns by species, size, and age. This early research determined that major stocks of Asian and North

---

*Full author affiliation list given at the end of the article.
All correspondence should be addressed to L. Weitkamp.
e-mail: laurie.weitkamp@noaa.gov

American salmon had characteristic seasonal distributions and movements, which included vast and broadly overlapping overwintering grounds. Winter high seas research in the 1980s–2010s was less extensive but benefitted from new methods, such as genetic stock-identification, satellite data, data-recording tags, acoustics, and computer modeling. This resulted in increased understanding of salmon distributions (horizontal, vertical), bioenergetics, and ecology, which showed species- and stock-specific variations in many of these traits during winter. Species-specific temperature preferences (e.g., sockeye, *O. nerka,* inhabit colder water than pink, or coho, *O. kisutch*) paired with projected high seas temperature scenarios were used to predict species-specific declines in high seas habitat availability in the future (Welch et al. 1995, 1998a,b; Abdul-Aziz et al. 2011). Myers et al. (2016) identified five key knowledge gaps in the distribution of salmon on the high seas in winter, specifically the role of: (1) prey distributions, (2) ecological interactions, (3) the effects of temperature on metabolism, (4) population-specific distributional differences, and (5) the effects of meso-scale oceanographic features (eddies, fronts, and jets) on these characteristics.

The 2016–2020 NPAFC Science Plan called for cooperative research on winter survival of salmon in the North Pacific Ocean (SSC 2016). This call gained urgency with recognition that ocean ecosystems were rapidly changing and recent winter high seas surveys were lacking. In response, in 2019 the first international expedition to the Gulf of Alaska was completed. This large-scale, integrated winter pelagic ecosystem research survey covered an area of 700,000 km^2 between February 16 and March 18, 2019 (Pakhomov et al. 2019). A follow-up expedition occurred March 11–April 7, 2020 (Somov et al. 2020), covering an area of 648,000 km^2. The 2020 survey overlapped the southern part of the 2019 survey but not the northern portion due to logistical reasons. Both privately-funded surveys had science teams representing the five NPAFC member countries (Canada, Japan, Korea, Russia, and the United States), were supported by the NPAFC and Pacific Salmon Foundation (PSF), and became signature events of the International Year of the Salmon's (IYS) five-year initiative (Beamish et al. 2022b).

Major objectives of the 2019 and 2020 expeditions were to: (1) test the hypothesis that the abundance of salmon is largely determined by the end of their first winter at sea; (2) determine if the high-seas catches could be used as an early indication of future returns to North American rivers, and (3) showcase effective, multi-country cooperation through an international research team working together to make discoveries (Pakhomov et al. 2019; Somov et al. 2020). Overall, the 2019 and 2020 expeditions built on historic research, made important contributions to our understanding of winter and early spring conditions in Gulf of Alaska high seas ecosystems, and advanced our knowledge of the open ocean phase of Pacific salmon (Table 1). The surveys also highlighted the value of a research program that builds upon the joint international expertise from across the North Pacific Rim countries, and laid the foundation for the expedition in 2022.

In 2020, planning began for a multi-ship survey of high seas habitats across the entire North Pacific Ocean as part of the IYS initiative (Pakhomov et al. 2021). The overall goal of the expedition was to demonstrate the utility of an international pan-Pacific winter ecosystem survey to understand how increasingly extreme climate variability in the North Pacific Ocean and associated changes in the physical environment influence the abundance, distribution, migration, and growth of Pacific salmon and associated nekton. The specific objectives were to: (1) determine species and stock-specific ocean distributions, relative abundances, and condition of salmon within the study area, and mechanisms modulating them; (2) document the spatial and temporal variation in physical and biological oceanographic conditions; (3) document the distribution and standing stocks of zooplankton and nekton that serve as the prey base for Pacific salmon and other fishes; and (4) demonstrate the ability to effectively collaborate across the five NPAFC parties and partners to conduct integrated ecosystem research that will support the sustainable management of salmon in the North Pacific Ocean. With these objectives, the 2022 survey addressed many of the key knowledge gaps for salmon high seas winter distributions and ecology identified by Myers et al. (2016).

Between February and April, 2022, ships from the U.S. (NOAA *Bell M. Shimada*, F/V *Northwest Explorer*), Canada (CCGS *Sir John Franklin*, F/V *Raw Spirit*), and Russia (R/V *TINRO*) sampled high seas salmon ecosystems across 2.5 million km^2 of the Central and Eastern North Pacific Ocean (Fig. 1), the largest such winter undertaking in the history of salmon research. The enormous geographic area covered by the coordinated survey (covering 42° longitude and 13° latitude) also provided an unprecedented opportunity to simultaneously examine the zonal (east-west) distribution of taxa, something that was previously limited due to smaller winter study areas. While thousands of samples collected during the expedition are still being processed, findings from the expedition have already increased what is known about salmon on the high seas. Here, we present initial highlights of the 2022 expedition, with preliminary comparisons to historic data and winter expeditions in 2019 and 2020. Many in-depth analyses are currently underway and should provide a wealth of detailed information in the near future.

MATERIALS AND METHODS

The 2022 IYS Pan–Pacific High Seas Expedition consisted of five ships sampling salmon high seas ecosystems across the central and northeast Pacific Ocean, across a grid of stations covering 174°W to 132°W and 45°N to 58°N; each ship sampled as many stations within its assigned area as time and weather permitted (Fig. 1). Sampling began February 5 and ended April 17, 2022, but

Table 1. Major findings from the 2019 and 2020 winter Gulf of Alaska (GoA) expeditions.

Topic	Findings
Currents and eddies	During both 2019 and 2020, the survey area was characterized by east- and northeast-moving waters driven by the North Pacific Drift. The geostrophic current field was governed by a southerly moving cyclonic component of the Alaskan Gyre. During 2019, a group of mesoscale anticyclonic eddies were observed between 50–56°N in association with the North Pacific Drift. In 2020, a larger number of anticyclonic eddies were conspicuously farther west and north. In contrast to 2019, these eddies from the southern and eastern periphery were located between two domains: 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 (Pakhomov et al. 2022a).
Water column properties	In both 2019 and 2020 there were strong north-south gradients in all oceanographic parameters and surface 7°C isotherm demarcated colder and warmer parts of survey areas. Surface temperature and salinity fields were mainly latitudinally oriented. Subsurface (> 100 m) isotherms were aligned more zonally in 2020, indicating that the southern boundary of the North Pacific Drift in the meridional section of 145–130°W had shifted northward. A warm anomaly observed during the winter of 2019 was only detected in the southern part of the 2020 survey. The mean sea surface temperature of the GoA was 0.33°C cooler in 2020 compared to 2019. However, during 2020 the northern 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 (Pakhomov et al. 2022a).
Primary productivity	Surface chlorophyll *a* concentrations were patchy and highest near the shelf and in the south-central to western part of the survey area, reaching ~0.9 and 1.9 μg L^{-1} during 2019 and 2020, respectively. Chorophyll *a* biomass integrated over the top 150 m of the water column showed a clearer north-south difference in 2020, with values being roughly two-fold higher south of 50°N and generally high throughout the southern survey areas (Pakhomov et al. 2022).
Zooplankton and micronekton	The spatial distribution of mesozooplankton densities during 2019 and 2020 was similar, with the highest densities observed in the southern parts of the survey areas (south of 50°N). Zooplankton were negatively correlated with densities of surface micronekton. Taxonomically, zooplankton assemblages were different between years due to the invasion of southern-origin species in 2020. During 2020, both zooplankton and micronekton standing stocks were nearly two-fold higher than in 2019 (Pakhomov et al. 2022a).
Salmon catches	In total, 425 and 566 salmon were captured during the 2019 and 2020 expeditions, respectively. This was despite sampling a smaller area during the 2020 survey. Overall, more heterogeneous distributions of many salmon species were observed in 2020, reflected by high patchiness of salmon catches. Two-thirds of salmon were captured in two sets in the south-central survey area, an area characterized by the highest phytoplankton biomass and warmest sea surface temperatures. This high productivity area was very dynamic, however, because when sampled two weeks later no salmon were caught.
Salmon abundance and distributions	The first-ever estimate of salmon standing stock in the Gulf of Alaska (~55 million individuals) was made from the 2019 abundances. Species-specific distribution patterns were documented and linked to environmental conditions and plankton distributions. Sockeye salmon (the most numerous species) were largely in the northern part of the GoA associated with cool waters, while pink salmon (the least abundant species) were captured in the southern-most stations in warmer waters. Low numbers of pink salmon were unexpected because 2019 was an odd year, when pink salmon were expected to be abundant. Chum salmon were the most abundant salmon and broadly distributed across the entire survey area. Coho salmon were the second most abundant salmon species caught during the expedition. This was a novel finding because coho salmon are considered to be coastal in distribution. In contrast to 2019, the 2020 expedition surveyed several stations on the continental shelf and slope but was unable to fully sample northern areas. Shelf and slope stations were characterized by a predominance of first-year winter fish, including sockeye, chum, and Chinook salmon. The larger proportion of smaller and younger sockeye salmon caught in 2020 than 2019 may reflect limited sampling in the northern GoA, where maturing sockeye salmon were caught in 2019. Pink salmon catches were significantly higher in 2020 than 2019, even though the 2020 catches represent the even year brood line, which is generally smaller than the odd year brood line.
Heterogeneity in salmon and nekton	There were north-south differences in some non-salmonid taxa, including some abundant species of jellyfish and salps. A surprising difference in salmon condition across the study area was evident. The largest difference was observed for chum salmon when fish of both good (robust) and poor (skinny) conditions would be encountered in a single trawl set.
Real-time genetic analysis	A pilot study of at-sea genetic sequencing was successful, providing real time stock estimates for individual salmon within 1–2 days of capture. This analysis showed that coho originated from Southeast Alaska to the Columbia River, with the majority from British Columbia.
Video of salmon in the net	For the first time, video footage was able to capture salmon behavior in the trawl net on the high seas. It provided preliminary evidence that salmon exhibit schooling rather than solitary feeding behavior.
Micro- and macro-plastics	According to observation and surface sampling, the Gulf of Alaska was relatively free from floating macroplastic and microplastic particles. Estimated macroplastic occurrence ranged from 0 to 2.3 pieces per km^2 based on twenty hours of daytime observation (Egger et al. 2020). There were no macroplastics spotted during 15 of the 20 hours of observation.

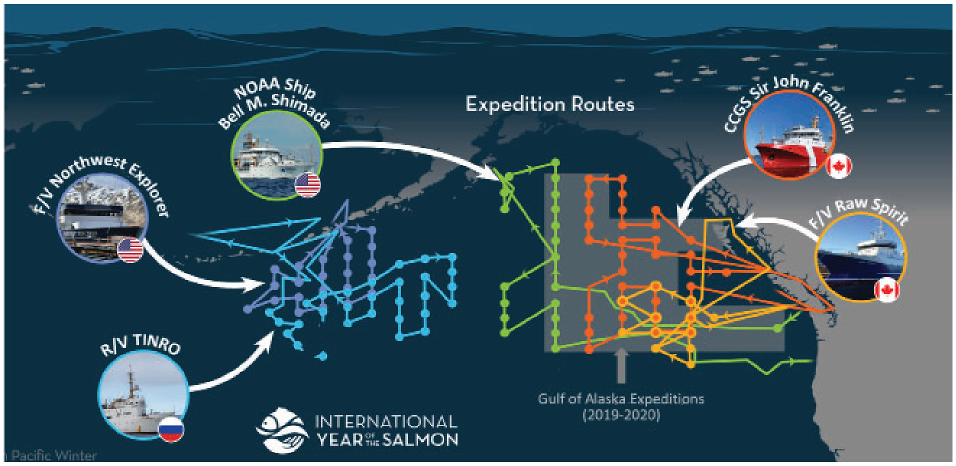

Fig. 1. Map showing the ship tracks for the five ships involved in the 2022 Expedition across the central and eastern North Pacific Ocean. The light gray polygon shows the area sampled during the 2019 and 2020 Gulf of Alaska expeditions.

was concentrated between mid-February and mid-March (Table 2).

Detailed descriptions of the common methods across all ships are provided by Pakhomov et al. (2021) and Riddell et al. (2022) and summarized here. Each of the five vessels conducted an ecosystem survey, examining the physical, chemical, and biological oceanography, and sampling all levels of the food web. Vertical casts using CTD rosettes to measure physical and chemical water column properties were made by each vessel to depths between 300 m and 2,000 m; water samples were taken at multiple depths for physical and biological property analysis, including environmental DNA (eDNA). To supplement these samples, surface chlorophyll *a* values were extracted from the GlobColour 4 km L3 8-day CHL1 AVW product (https://globcolour.info) (M. Konik et al. 2024). Zooplankton samples were collected using Bongo nets deployed vertically on all vessels; additional zooplankton net types included a Juday net (R/V *TINRO*) and Tucker trawls (CCGS *Sir John Franklin* and NOAA *Bell M. Shimada*). Additional monitoring for macro-plastics, marine mammals, seabirds, and other activities as time permitted were conducted by most ships.

Four vessels used surface trawl nets to capture salmon and associated species—CCGS *Sir John Franklin* (King et al. 2022), R/V *TINRO* (Somov et al. 2022), R/V *Bell M. Shimada* (Weitkamp et al. 2022), and F/V *Northwest Explorer* (Murphy et al. 2022). The target tow duration was one hour, although tow duration on the R/V *Bell M. Shimada* varied from 0.5–2 hours; collectively these ships fished with trawls for 113.5 hours (Table 2). The fifth vessel (F/V *Raw Spirit*) used 1 km longlines and 2.4 km gillnets made up of multiple mesh sizes to catch salmon and associated species (Neville et al. 2023). These longlines and Japanese-style gillnets were used to compare the size and abundance of salmon and associated nekton caught with surface trawls by the CCGS *Sir John Franklin*, and with historic high seas data using long lines and gillnets. Due to challenging weather conditions, long lines and gillnets were deployed only between 45–50°N and 133–141°W.

All captured salmon and other nekton were identified to species or lowest practical taxa, enumerated, and measured for weight (g) and length (fork length, FL, total length, TL, bell diameter, BD (jellyfish), or mantle length, ML (squid)). Due to breakage of jellyfish in trawls, they were not consistently enumerated but were always

Table 2. Dates of operation and number of completed in-water sampling deployments of CTDs, zooplankton nets (vertical Bongo and Tucker trawls, T, or Juday, J, nets) and fishing events using gill nets (G) or long lines (LL; F/V *Raw Spirit*) or surface trawls (all other ships) during the 2022 Pan-Pacific Expedition. Also listed are the number of Pacific salmon (all species combined) and the total number and weight of fish and invertebrates caught in trawls, gillnets, or long line gear.

Ship	Cruise dates (2022)	No. CTDs	No. Bongo tows	No. Tucker / Juday sets	No. fishing events	Total catch		Total salmon (number)
						Number[a]	Weight (kg)	
CCGS *Franklin*	19 Feb–21 Mar	35	35	32 T	34	11,511	410	221
F/V *NW Explorer*	3–17 Apr	22	18	-	22	9,844	833	633
R/V *Shimada*	1 Feb–7 Mar	51	19	10 T	21	2,298	533	162
R/V *TINRO*	2–20 Mar	32	31	32 J	32	3,985	1,009	1,146
F/V *Raw Spirit*	25 Feb–25 Mar	16	12	-	19G 17LL	279	306[a]	202

[a] Excludes jellyfishes

weighed. Identification and enumeration of "other invertebrates" (which includes small pelagic tunicates, comb jellies, and krill), was not consistent across ships and are not included here. To document variation in the shape (i.e., weight to length ratio) of individual salmon, we calculated Fulton's Condition Factor (CF) as CF = 100,000 × weight / (length^3), where weight is in g and length in mm FL. Many tissue samples were collected from salmon and other nekton for analyses, including age and growth, stock (genetics and tags), bioenergetics, physiological health, and trophic biomarkers (stable isotopes and fatty acids).

Salmon diets were analyzed at sea on the CCGS *Sir John Franklin* and R/V *TINRO*, whereas whole stomachs were preserved at sea on the other ships for analysis in the lab. Initial analysis of salmon diets from the 2019, 2020, and 2022 expeditions focused on the three most common prey items for each species/year/location group. These were pooled across the five salmon length categories used on Russian ships (< 30, 30–40, 40–50, > 50 cm), and averaged across trawl sets. Because of this compilation method, proportions could exceed 100.

Genetic analysis of individual salmon using single nucleotide polymorphisms (SNPs) with lab- and species-specific baselines was conducted by the Alaska Department of Fish and Game (ADF&G), Fisheries and Oceans Canada (DFO), and NOAA Fisheries' Northwest (NWFSC) and Alaska Fisheries Science Centers (AFSC) using *rubias* (Moran and Anderson 2018). Reporting groups were chosen based on the leave-one-out cross validation methods from Anderson et al. (2008) to obtain high assignment probabilities across baselines. These methods often resulted in broad-scale reporting groups (e.g., pink salmon) and were much finer for others (e.g., coho salmon). Genetic data for chum, *O. keta,* presented here represent consensus of assignments by ADF&G and DFO, sockeye and pink assignments were generated by ADF&G, coho assignments were generated by DFO, and Chinook, *O. tshawytscha,* assignments represent consensus by NWFSC and AFSC labs. Fish labeled as "unresolved" resulted from assignment probabilities < 80% or a lack of consensus in assignments between labs.

To explore spatial variation in catches of salmon and other commonly caught nekton across the study area, we conducted preliminary multivariate analyses of the catch data from surface trawls. Square-root transformed catch data (number or weight of individual taxa in each haul) was used to construct similarity matrices using Bray-Curtis similarity coefficients. The matrices included either the five Pacific salmon species or 15 "main taxa"—all salmon species plus blue lanternfish (*Tarletonbeania crenularis*), northern lampfish (*Stenobrachius leucopsarus*), three spine stickleback (*Gasterosteus aculeatus*), Boreopacific armhook squid (*Gonatopsis borealis*), Boreal clubhook squid (*Onychoteuthis borealijaponica*), Minimal armhook squid (*Berryteuthis anonychus*), northern sea nettle (*Chrysaora melanaster*), and water (*Aequorea* sp.), moon (*Aurelia* sp.), and fried egg (*Phacellophora camtschatica*) jellies; analyses using all identified taxa or different transformations produced similar results. These matrices were used to produce two-dimensional multidimensional scaling (MDS) plots to visually observe patterns; points closer together in MDS space have higher similarity than those further apart. Analysis of similarities (ANOSIM), a multivariate analog to analysis of variance (ANOVA) was used to test for the influence of the factor "ship" (a proxy for location, Fig. 1) to produce well-defined groups (indicating regional spatial variation in catches). This analysis produces global R values which range from 0 (no differences among groups) to 1 (strongly separated groups), and uses permutation to determine statistical significance. We also used the BIOENV algorithm to calculate the Spearman correlation coefficient between surface temperatures and the catch similarity matrices. These multivariate analyses used PRIMER-E software (Clarke and Gorley 2006).

All collected and generated data are being standardized and made available to study participants as they become available using Findable, Accessible, Interoperable, and Reusable (FAIR) data standards (Wilkinson et al. 2016).

RESULTS

Across all ships, a total of 156 CTD casts, 167 zooplankton tows (115 vertical bongo, 42 Tucker trawl, and 32 Juday net tows), 109 surface trawls, 19 gillnet, and 17 long line sets were completed at 131 stations between February 1 and April 17, 2022 (Pakhomov et al. 2023; Table 2). Mixed-layer depth as well as temperature and salinity in the mixed layer (February and March 2022 CTD casts only) varied across the study area, showing latitudinal and fine-scale variation, consistent with ocean currents, meanders, and eddy-like features (Fig. 2). Mixed-layer depth was roughly 90–100 m, but ranged from < 60 m in some northern areas to > 110 m in the southwest (Fig. 2). Water temperatures in surface waters displayed a strong north-south gradient, with the coldest temperatures (3.5°C) at the northern-most stations and the warmest water (9°C) at several southern stations, although there was high spatial heterogeneity in temperatures (Fig. 2). By comparison, salinity was relatively constant across much of the Gulf of Alaska (32 PSU), but higher (> 32 PSU) in the western portion of the study area. Surface concentrations of chlorophyll *a* were generally low across the study area, averaging 0.263 mg/m^3 with a maximum value of 0.488 mg/m^3. Initial results from zooplankton samples collected by select ships indicate many of the same species were present across the entire study area, although the contribution of different species varied spatially. A full analysis of zooplankton across the entire study area is ongoing (A. Pinchuk, E. Pakhomov, unpubl. data).

Fishing with surface trawls yielded 2,785 kg of fish, squid, and jellyfish, representing 47 taxonomic groups and 27,638 individuals (excluding jellyfish; Table 2). These

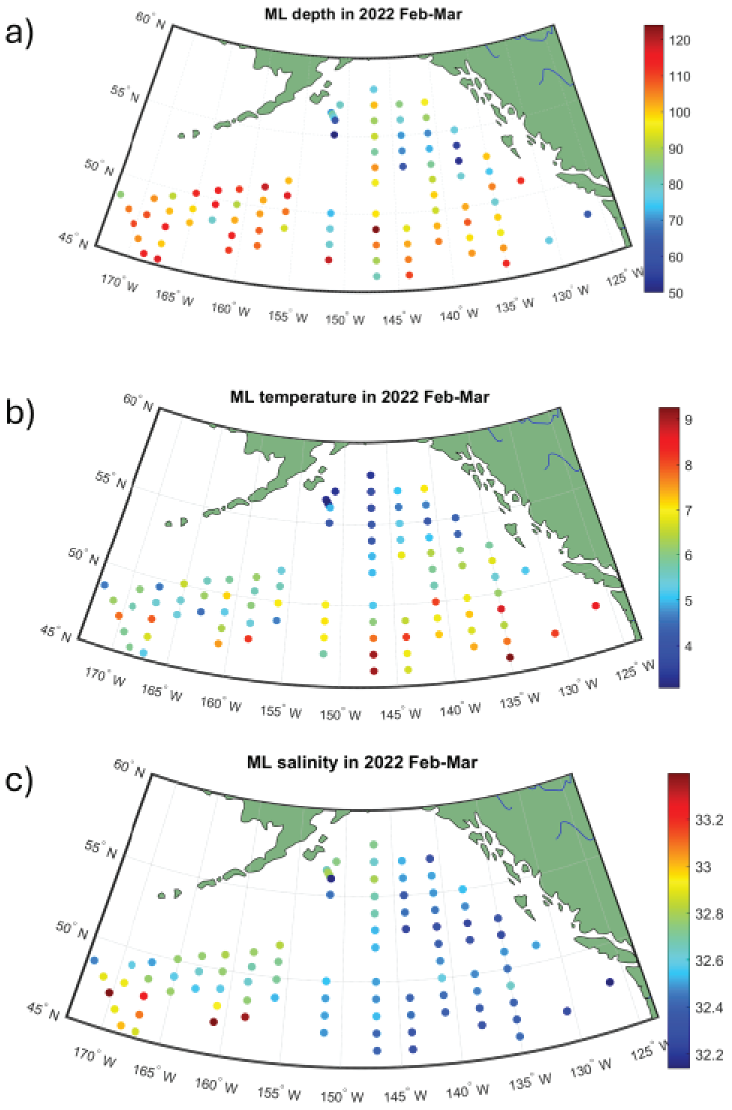

Fig. 2. Mixed layer (ML) depth (a), temperatures (b), and salinity (c) at each sampling site during February–March, 2022.

catches included five species of Pacific salmon (sockeye, chum, coho, pink, and Chinook salmon), 17 species of non-salmonid fishes, 13 taxa of squid, and 8 jellyfish taxa (Table 3). A total of 2,364 Pacific salmon and steelhead trout were caught across all sampling gears (trawls, gillnets, and longlines). For surface trawls, sockeye and chum salmon were caught most frequently (in 50–70% of tows) and had the highest abundances (1,312 sockeye, 650 chum; Table 3). However, a single haul by R/V *TINRO* (50.06°N, 165.19°W) accounted for almost half the sockeye (n = 649, by their size, mostly ocean age 1). Catches of pink (n = 92), coho (n = 63), and especially Chinook salmon (n = 15) by trawls were infrequent, smaller, and largely at southern stations.

All salmon species caught in trawls were widely dispersed throughout the study area, but there were apparent north-south differences in catch (Fig. 3). Sockeye salmon typically had the highest catches at the more northern stations (mean latitude = 49.93°N), chum were caught across the entire study area (49.27°N), and Chinook (48.61°N), pink (48.39°N), and coho (47.89°N) had the highest catches in the southern portion of the surveyed area. Correlations in catch abundances (number per haul) among salmon species were highest between pink and chum salmon (r = 0.49), followed by sockeye and pink salmon or sockeye and chum salmon (both r = 0.35), and low between Chinook or coho and other species (r ≤ 0.03), with the exception of coho and pink salmon (r = 0.15). Coho salmon were more frequently caught at night, while other salmon were either more common during the day or equally between day and night (Table 3). Consistent with these spatial patterns, on average, sockeye salmon in trawls were caught in the coldest waters (mean temperature = 5.87°C), coho (6.92°C) and pink salmon (6.99°C) were caught in the warmest waters, and chum (6.88°C) and Chinook salmon (6.59°C) were intermediate (Table 4). While average temperatures varied by species overall, the range of temperatures over which each species was caught varied from a low of 3.3°C for coho to a high of 5.6°C for chum salmon (Table 4).

No steelhead trout were caught in trawls, but it was the most abundant salmonid species caught by gillnets (n = 57) by F/V *Raw Spirit*. Longlines and gillnets also caught sockeye (n = 53), coho (n = 51), chum (n = 30), pink (n = 10), and Chinook salmon (n = 1). The location of individuals captured in the gillnet indicated that most salmon were caught within 4 m of the surface (i.e., the upper half of the gillnet). When more than one salmon was caught in a gillnet set, the spacing of fish across the net varied with some species (e.g., steelhead trout) caught in a broad range of mesh sizes whereas others (e.g., pink salmon) were captured in relatively few mesh sizes.

Table 3. Total catch of fish and invertebrates by species or taxonomic group across all ships using surface trawls in the study area in 2022. Listed are the percent frequency of occurrence in daylight and night time tows, and the total catch by number and total weight, standardized by 113.5 hours of trawling.

		Frequ. Occurr. (%)		Catch	
Common name	**Scientific name**	**Daylight**	**Night**	**Number**	**Weight (kg)**
Pacific salmon (*Oncorhynchus*)					
Sockeye salmon	*O. nerka*	72.0	67.6	1312	613.5
Chum salmon	*O. keta*	60.0	50.0	650	583.2
Coho salmon	*O. kisutch*	20.0	44.1	63	31.6
Pink salmon	*O. gorbuscha*	26.7	14.7	92	25.7
Chinook salmon	*O. tshawytscha*	10.7	5.9	15	18.5
Other fishes					
Threespine stickleback	*Gasterosteus aculeatus*	26.7	5.9	9,388	33.0
Northern lampfish	*Stenobrachius leucopsarus*	1.3	26.5	4,116	9.5
Blue lanternfish	*Tarletonbeania crenularis*	0.0	64.7	3,932	6.5
CA headlightfish	*Diaphus theta*	0.0	8.8	36	0.1
Popeye blacksmelt	*Lipolagus ochotensis*	0.0	0.9	26	0.2
Daggertooth	*Anotopterus* sp.	7.3	2.9	10	0.9
Capelin	*Mallotus villosus*	0.9	0.0	9	0.1
Unid myctophid	*Myctophidae*	0.0	5.9	20	0.1
Smooth lumpfish	*Aptocyclus ventricosus*	0.0	5.9	5	0.3
Black rockfish	*Sebastes melanops*	1.8	0.0	3	5.9
Salmon Shark	*Lamna ditropis*	0.0	5.9	2	181.9
Prowfish	*Zaprora silenus*	0.0	5.9	2	0.5
Crested bigscale	*Poromitra curilensis*	1.3	0.0	1	< 0.1
Rex sole	*Glyptocephalus zachirus*	0.9	0.0	1	< 0.1
Ragfish	*Icosteus aenigmaticus*	0.0	2.9	1	0.3
Medusa fish	*Icichthys lockingtoni*	0.9	0.0	1	< 0.1
Pacific sardine	*Sardinops sagax*	0.9	0.0	1	< 0.1
Jellyfish					
Fried egg jelly	*Phacellophora camtschatica*	53.3	73.5	-	403.3
Water jelly	*Aequorea* sp.	73.3	79.4	-	378.2
Northern sea nettle	*Chrysaora melanaster*	53.3	38.2	-	310.9
Moon jelly	*Aurelia* sp.	50.7	35.3	-	36.7
Unid true jellyfish	*Scyphozoa*	12.0	2.9	-	34.7
Lion's mane jellyfish	*Cyanea* sp.	1.3	0.0	-	0.9
Cross jelly	*Staurophora mertensii*	1.3	0.0	-	0.1
Calycopsis jelly	*Calycopsis* sp.	2.6	2.9	-	< 0.1

Table 3. Continued.

Common name	Scientific name	Frequ. Occurr.(%) Daylight	Frequ. Occurr.(%) Night	Catch Number	Catch Weight (kg)
Squids					
Minimal armhook squid	*Okutania anonycha*[a]	9.3	20.6	6,318	81.3
Boreal clubhook squid	*Onychoteuthis borealijaponica*	8.0	41.2	75	8.4
Boreopacific armhook squid	*Gonatopsis borealis*[b]	4.0	58.8	351	6.7
Unid. *Gonatoposis* squid	*Gonatopsis* sp.	1.3	8.8	672	6.7
Unid. *Gonatus* squid	*Gonatus* sp.	5.3	17.6	287	1.5
Berry armhook squid	*Gonatus berryi*	1.3	11.8	187	1.5
Opalescent inshore squid	*Doryteuthis opalescens*	0.0	2.9	20	0.1
Shortarm gonate squid	*Gonatus kamtschaticus*	5.3	11.8	12	0.9
Unid. Armhook squid	*Gonatidae*	0.0	5.9	10	< 0.1
Abraliopsis squid	*Abraliopsis felis*	0.0	5.9	8	< 0.1
Unid. Squid	*Oegopsida*	1.3	2.9	6	< 0.1
Chiroteuthis squid	*Chiroteuthis calyx*	0.0	2.9	2	0.1
Madoka armhook squid	*Gonatus madokai*	1.3	0.0	1	0.1

[a] *Okutania anonycha* is the same species as *Berryteuthis anonychus* (World Register of Marine Species, marinespecies.org)

[b] *Gonatopsis borealis* is the same species as *Boreoteuthis borealis* (World Register of Marine Species, marinespecies.org)

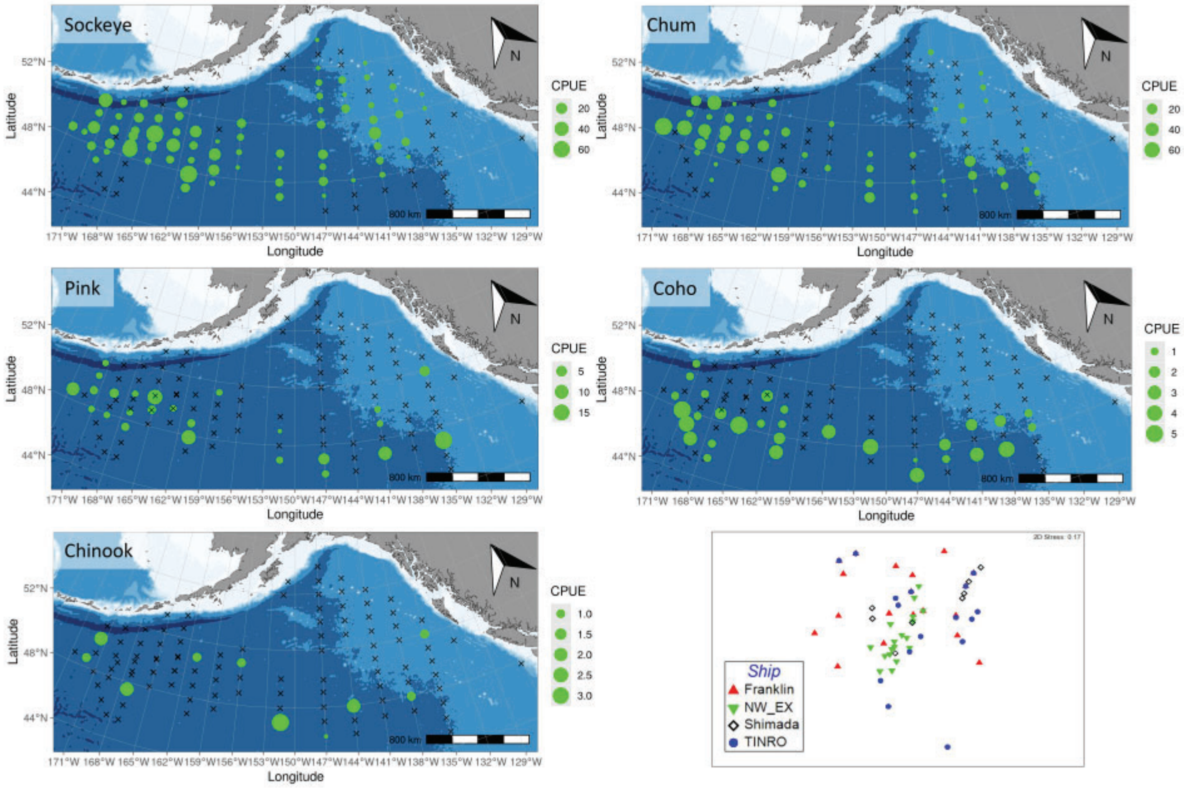

Fig. 3. Maps showing the distribution and abundance of sockeye, chum, pink, coho, and Chinook salmon caught by trawls across the study area in 2022. Note the different scales on each map; x indicates zero catch. The graph in the lower right corner is a multidimensional scaling (MDS) plot based on catches (counts) of five species of Pacific salmon in surface trawls. Each point represents a haul; points closer together indicate higher similarity in catches than those farther apart.

Table 4. Pacific salmon catches (total number and percent of total for each year) by surface trawls and mean surface temperature (and range, °C) for Pacific salmon caught in winter surveys in 2019, 2020, and 2022. Temperature data from 2019 and 2020 was provided by A. Somov.

		Year		
Species	**Variable**	**2019**	**2020**	**2022**
Chinook	Catch (%)	3 (0.7)	26 (4.6)	15 (0.7)
	Temperature	5.74 (4.7–6.6)	8.99 (8.9–9.0)	6.59 (4.7–8.6)
Chum	Catch (%)	223 (52.5)	224 (41.4)	660 (31.2)
	Temperature	6.18 (4.8–7.6)	8.09 (5.4–8.5)	6.88 (3.6–9.2)
Coho	Catch (%)	95 (22.4)	118 (20.9)	63 (3.0)
	Temperature	7.05 (4.8–8.3)	8.14 (6.4–8.4)	6.92 (5.3–8.6)
Pink	Catch (%)	31 (7.3)	136 (24.1)	92 (4.3)
	Temperature	7.29 (4.8–8.3)	8.40 (6.1–8.5)	6.99 (4.5–8.6)
Sockeye	Catch (%)	73 (17.2)	51 (9.0)	1,288 (60.8)
	Temperature	5.98 (5.0–7.5)	6.20 (5.4–8.4)	5.87 (3.4–8.6)

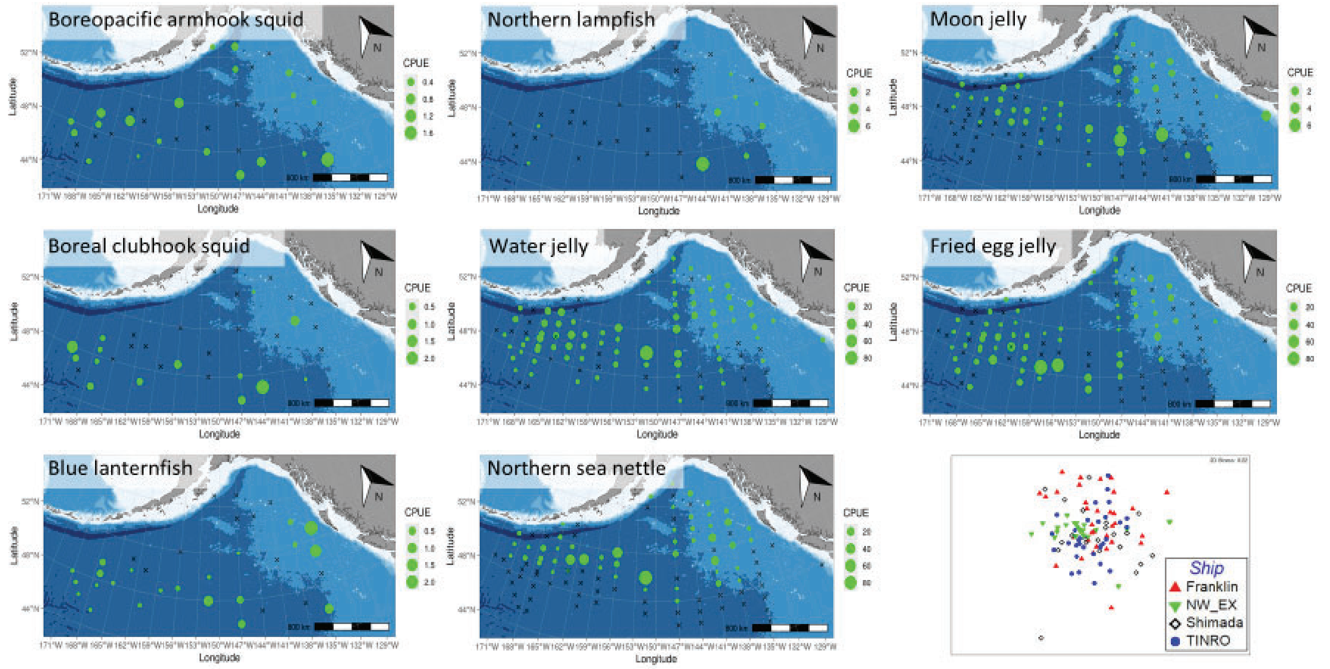
Boreopacific armhook squid
Northern lampfish
Moon jelly
Boreal clubhook squid
Water jelly
Fried egg jelly
Blue lanternfish
Northern sea nettle

Fig. 4. Maps showing the distribution and abundance of the most frequently caught invertebrates and non-salmonid fishes by trawls across the study area in 2022. Note the different scales on each map; x indicates zero catch. The graph in the lower right corner is a multidimensional scaling (MDS) plot based on catches (weight) of fifteen main taxa in surface trawls including salmon (see methods). Each point represents a haul; points closer together indicate higher similarity in catches than those farther apart.

Other commonly caught nekton in the trawls included myctophids, gonatid squid, and jellyfish. As for salmon, they were widely but patchily distributed across the study area (Table 3, Fig. 4). Four species of jellyfish (water, moon, fried egg jellies, and northern sea nettle) were caught at over half of the trawl stations and contributed roughly half of the total biomass caught in trawls. Of the 17 non-salmonid fishes caught in trawls, only three species (threespine stickleback, northern lampfish, and blue lanternfish) were caught in at least 25% of trawls, and five species were represented by a single individual (Table 3). Three squid species (Boreopacific armhook squid, Boreal clubhook squid, and Minimal armhook squid) were caught in at least 20% of trawls. Most myctophids and squid were caught at night (Table 3). Gillnets and longlines also caught Boreal clubhook squid and several other fishes—spiny dogfish (*Squalus suckleyi*), black rockfish (*Sebastes melanops*), Pacific sardine (*Sardinops sagax*); fried egg, water, and moon jellyfish were observed but not always caught.

Multivariate analyses of the surface trawl salmon and "main taxa" (see methods) catch data support the observation that these frequently caught taxa were widespread

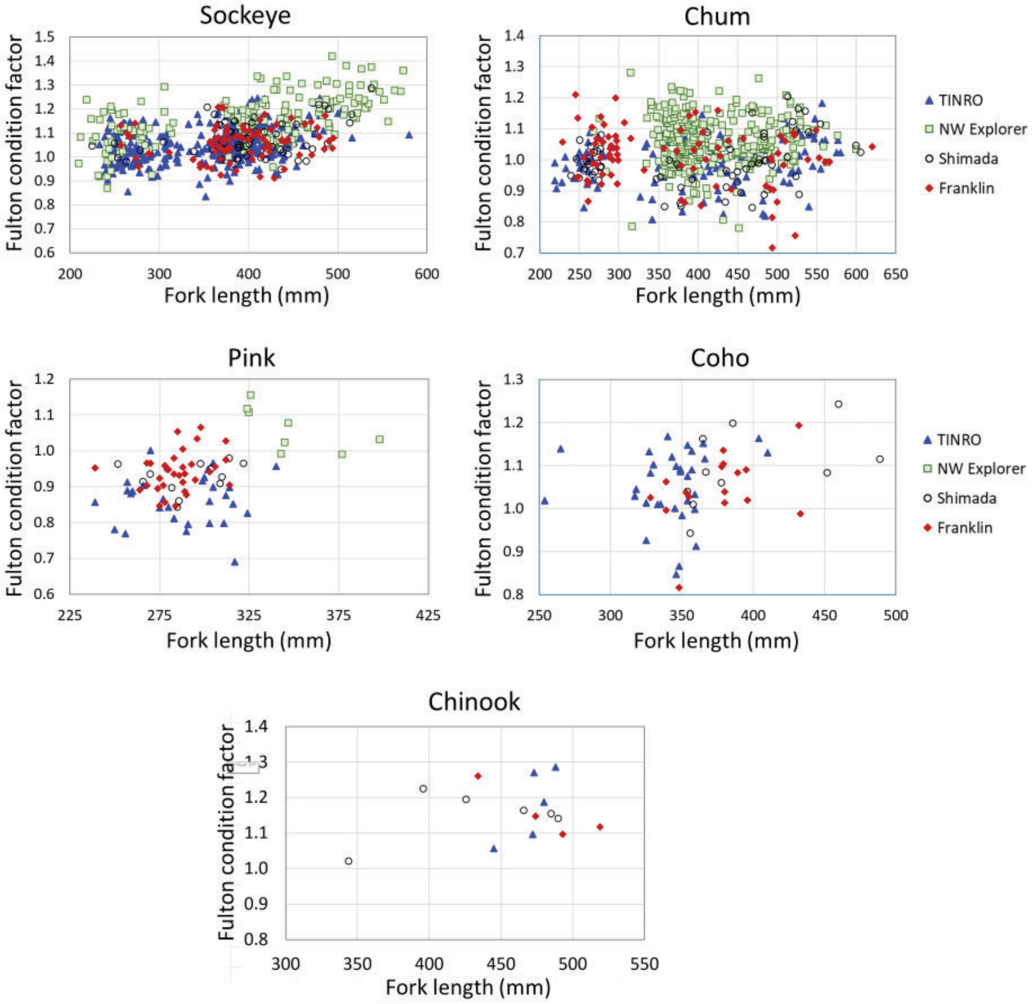

Fig. 5. Size (length, mm FL) and Fulton's Condition Factor of sockeye, chum, pink, coho, and Chinook salmon caught by trawls across the study area in 2022. The ship catching each fish is indicated.

across the study area. In all MDS plots—those using only salmon or the main taxa measured by number or weight—there was complete overlap in MDS space for the catches of each ship (Figs. 3, 4), and the term "ship" (a proxy for location) formed statistically significant but poorly defined groups ($R \leq 0.16$, $p < 0.05$). Surface water temperature was moderately correlated to the matrix of main taxa (Spearman $r = 0.29$, $p < 0.05$), indicating temperature plays a role either directly or indirectly in structuring the distributions of salmon and nekton.

The size and condition of Pacific salmon varied by species. Both sockeye and chum salmon showed distinct length modes, presumed ocean age (OA) 1 individuals, which were less than 325 mm FL (sockeye) or 300 mm FL (chum; Fig. 5). Older individuals (presumed OA > 1) of both species ranged in size from 325 to 600 mm but did not form discrete size-based groups. Although all pink and coho salmon were presumed to be OA 1, their sizes varied between 240–400 mm FL (pink salmon) and 325–485 mm FL (coho salmon). Chinook salmon displayed a surprisingly narrow size range, with all but two individuals falling between 390 and 490 mm FL. Across species, most salmon had good body condition (Fulton condition factor [CF] ≥ 0.9). Exceptions to this pattern included roughly half of pink salmon and some chum salmon in the 300–550 mm FL size range were exceptionally skinny (CF < 0.9). The size and condition of salmon caught with longlines and gillnets was similar to those caught with trawls.

Genetic assignment of individuals to reporting groups indicated Pacific salmon caught during the survey represented stocks from around the Pacific Rim. There was a general tendency for Asian and western Alaskan populations to be found in the western part of the study area (caught by F/V *Northwest Explorer* and R/V *TINRO*), and Gulf of Alaska and Pacific Northwest populations in the eastern part (caught by R/V *Bell M. Shimada*, R/V *Franklin*, and F/V *Raw Spirit*; Fig. 6). Chum and pink salmon (and to a lesser extent coho) showed the strongest clines in stock compositions moving from western to eastern samples. Most sockeye salmon originated from western Alaska and Bristol Bay, but also included fish from all other reporting groups, with fish from Russia in the western part of the study area and from British Columbia/Washington in the eastern part of the study area. Coho salmon were largely represented by North American populations. Even-year pink salmon were evenly split between Asia/Beringia and Gulf of Alaska/Pacific Northwest populations, with a strong geographic cline. Interestingly, one odd-year fish from the Asia & Beringia region was captured by the F/V *Northwest Explorer*. The few Chinook salmon captured were primarily from Bering Sea and Gulf of Alaska

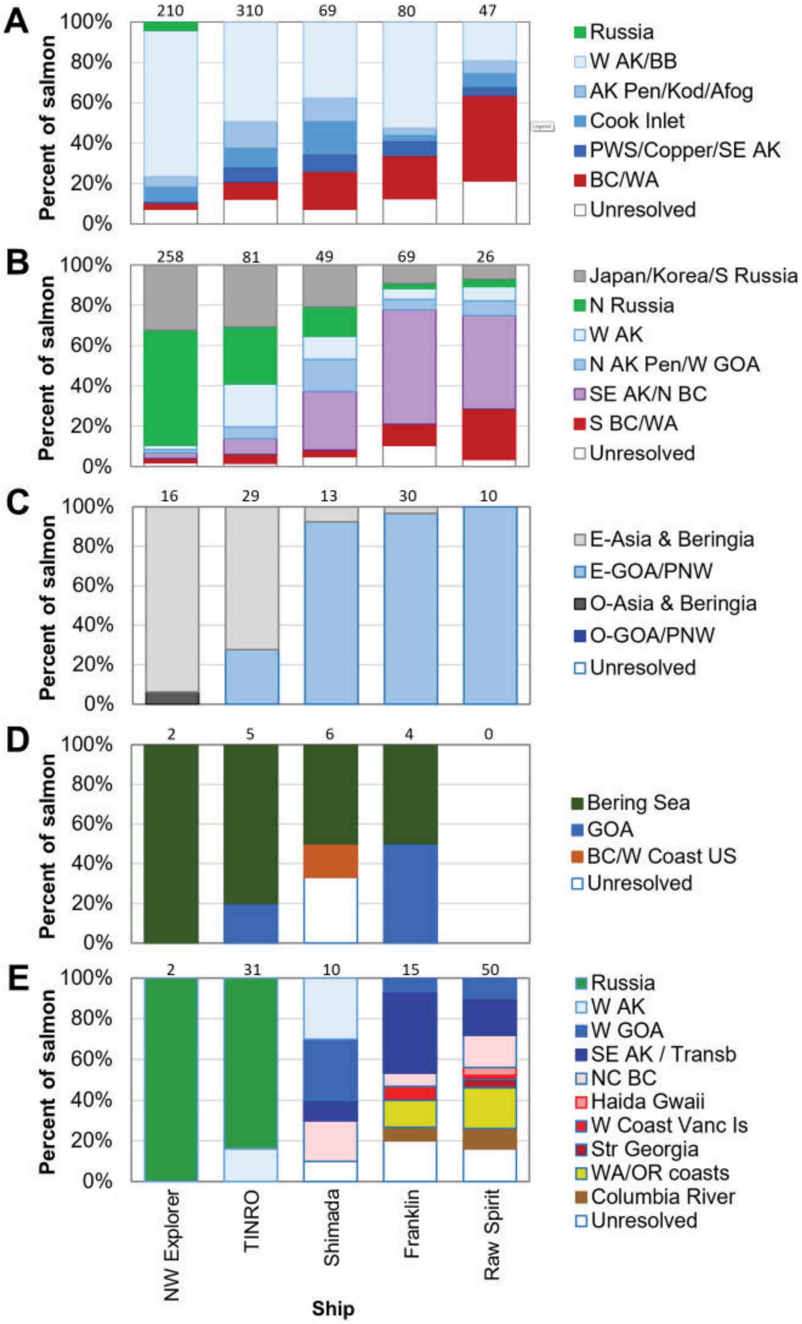

Fig. 6. Individual assignment results from the 2022 Pan-Pacific Expedition to Genetic Stock Identification (GSI) reporting groups organized by species and ship; species are: (A) sockeye; (B) chum, (C) pink, (D) Chinook, and (E) coho salmon. Numbers above each column are the number of salmon analyzed. Pink salmon stocks are separated between even (E) and odd (O) year groups. Abbreviations are AK: Alaska; BC: British Columbia; WA: Washington; OR: Oregon; S: South; N: North; W: West; E: East; SE: Southeast; Pen: Peninsula; GOA: Gulf of Alaska; BB: Bristol Bay; Kod: Kodiak; Afog: Afognak; PWS: Prince William Sound; Vanc. Is.: Vancouver Island; Str: Strait. 'W Coast US' includes salmon originating from Washington, Oregon, Idaho, and California, while 'Beringia' encompass populations originating from rivers on both shores of the Chukchi and Bering seas. Samples reported and assigned to reporting groups passed genotyping quality control and had a > 80% assignment probability or consensus assignments between labs.

populations, but the origins of two of the six fish caught by the R/V *Bell M. Shimada* could not be resolved (Fig. 6).

Preliminary salmon diet analyses from the 2019, 2020, and 2022 expeditions indicated common dominant prey items across fish sizes and years in the eastern Gulf of Alaska (Fig. 7); a full analysis is anticipated (J. King, DFO, pers. comm.). The top prey items in chum salmon stomachs were jelly-like prey (cnidarians and ctenophores), as well as euphausiids and fish. Euphausiids and fish were also top prey items found in coho, pink and sockeye salmon stomachs. Cephalopods (specifically squid) were dominant prey items found in coho (2020 and 2022) and sockeye salmon (2019 and 2020) stomachs. Across years, pink salmon had more variation in the top prey items contained in stomachs, with crustaceans (specifically decapods), fish eggs and amphipods varying in importance. Pteropods were consumed by coho, pink and sockeye salmon in the eastern Gulf of Alaska, but were not consistently among the top prey items across years.

The dominant prey items in salmon stomachs varied between the Gulf of Alaska and the central North Pacific in 2022 (Fig. 7) illustrating the importance of regional prey field variability. Ostracods (chum salmon), *Oikopleura* sp. (coho, pink and sockeye), and copepods (sockeye salmon) were dominant prey items in salmon stomachs in the central North Pacific but not dominant in the eastern Gulf of Alaska. Chinook salmon were not included in preliminary analyses due to low catches west of 135°W, but they did consume mainly fish and squid.

DISCUSSION

The five ship, 2022 winter Pan–Pacific Expedition of high seas salmon habitats successfully sampled 131 stations across 2.5 million km^2 of the central and eastern Pacific Ocean between 45° and 58°N. The expedition caught approximately 2,400 salmon, in addition to other fishes, squid, jellyfish, and other invertebrates. In general, most commonly caught taxa were patchily distributed; individuals were often caught at one station but absent at adjacent stations (Figs. 3, 4), consistent with historical high seas catch patterns (e.g., Welch and Ishida 1993). While there was clear north-south variation in the most frequently caught taxa, likely reflecting physical and biological gradients, these taxa had at least a few individuals caught across the entire east-west breadth of the study area resulting in similar catch composition throughout the study area. These results also support the concept that each species of salmon uses high seas habitats slightly differently (Myers et al. 2016; Beamish 2018).

Analysis of many types of samples and data collected during the expedition is ongoing and results generated by multiple labs have not yet been combined into study-wide datasets. Analysis of nearly 1,000 eDNA samples collected at multiple depths should shed light on taxa or individuals that were not caught. The eDNA data should indicate whether the nets simply missed individuals such as surface-oriented steelhead or diurnal vertically migrating squid and myctophids that were there or they escaped from the nets, or if they were absent from the local area (e.g., Deeg et al. 2023). Similarly, hundreds of zooplankton samples when paired with fish diets will help inform food habits and factors affecting salmon physiological status and distributions. In-depth analyses of currents, zooplankton, acoustics, eDNA, trophic biomarkers, and salmon diets, genetics, bioenergetics, and physiology are currently underway and will form the basis of future publications. These datasets will also be analyzed together to produce one or more synthesis papers.

Results from the 2022 Pan-Pacific Expedition showed both similarities and differences when compared to environmental conditions and catches from expeditions in 2019 and

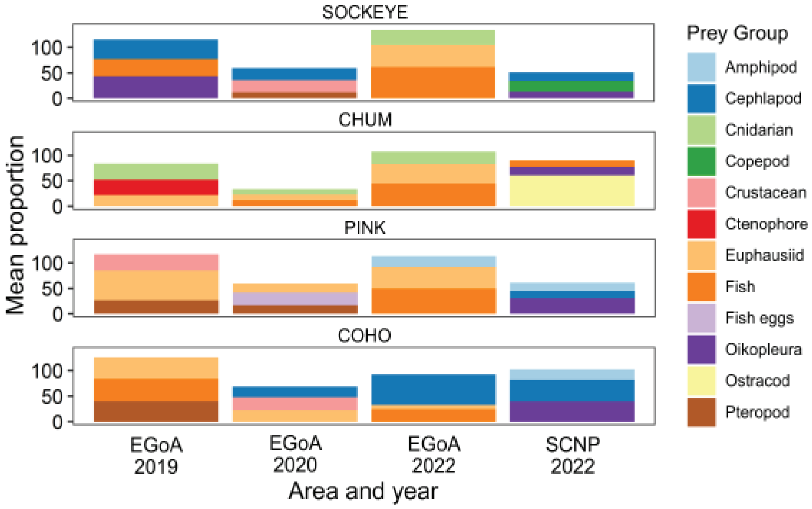

Fig. 7. The top three prey groups enumerated in sockeye, chum, pink and coho salmon stomachs in the eastern Gulf of Alaska (EGoA) in 2019 (onboard R/V *Professor Kagonovskiy*), 2020 (F/V *Pacific Legacy*) and 2022 (CCGS *Sir John Franklin*) and in the southern portion of the central North Pacific (SCNP) in 2022 (R/V *TINRO*). Top prey groups were selected using the mean proportion of prey group weight (g) to total weight of prey consumed (g) for data pooled by trawl set and salmon length.

2020 to the Gulf of Alaska and to historic winter high seas data. For example, surface water temperatures were relatively warm in 2019, average in 2020, and cool in 2022 compared to long-term averages (Table 1, Pakhomov et al. 2022a; NOAA SST Optimum Interpolation Data, coastwatch.pfeg.noaa.gov). The mean temperatures where salmon were caught also varied among years, with 2022 generally having cooler temperatures compared to 2019 and 2020 (Tables 1, 4), consistent with the overall trend in temperatures across the North Pacific Ocean. Species-specific temperature preferences (i.e., colder for sockeye, warmer for pink and coho, intermediate for chum) are consistent with historical winter catch data (Myers et al. 2016). Detailed analysis of these temperature-related catch patterns and how they might relate to thermal limits (e.g., Welch et al. 1995, 1998a,b) is ongoing (E. Lemagie, NOAA PMEL, pers. comm.)

All species of salmon were caught in all years (2019, 2020, 2022) in trawls, but the order of abundance differed by year (Table 4). In both 2019 and 2020 chum salmon were the most abundant salmon, followed by coho (2019) or pink (2020), with sockeye salmon the third (2019) or fourth (2020) most abundant salmon, and Chinook salmon the least abundant. In contrast, in 2022 sockeye were the most abundant, followed by chum, pink, coho, and Chinook salmon, although roughly half the sockeye were caught in a single tow. This order of relative abundance in 2022 (sockeye, chum, pink, coho, Chinook) was the same (but with lower abundances) if only catches by the R/V *Bell M. Shimada* and CCGS *Sir John Franklin* are considered, which have similar spatial coverage to the 2019 and 2020 expeditions. Interestingly, sockeye salmon was also the most abundant species in the 1960s in winter high seas catches while chum salmon were relatively rare (Manzer and Dodimead 1964). How these catches relate to adult abundances remains to be determined.

Also notable was the absence of likely predators of salmon, which are thought to be the primary source of mortality on the high seas (e.g., Beamish 2018). These suspected predators consist of fishes (long snouted lancetfish *Alepisaurus ferox*, daggertooth *Anotopherus pharao*, and Pacific lamprey *Entosphenus tridentatus*), sharks (salmon shark *Lamna ditropis*, spiny dogfish *Squalus suckleyi*), and marine mammals including pinnipeds and cetaceans (Bugaev and Shevlyakov 2007; Naydenko and Temnykh 2016). However, few predators were caught using trawls in 2019, 2020, and 2022 (Table 3), and eDNA analysis of water samples collected in 2019 and 2020 suggests predators were absent across much of the study areas (Deeg et al. 2023). In addition, only 5% of salmon caught in 2019 and 2020 had wounds or scars indicative of predation attempts (Weitkamp and Garcia 2022). By contrast, several salmon caught by gillnets on the F/V *Raw Spirit* (which often soaked for 12 hours) were damaged by unknown predators, indicating some predators were present. The F/V *Raw Spirit* also caught the most spiny dogfish (n = 15) and salmon sharks (n = 2, neither landed), and piscivorous seabirds and Dall's porpoise *Phocoenoides dalli* were observed several times, suggesting there were more predators at their local area than were encountered farther offshore. It is not clear at this point if concentrations of predators associated with local oceanographic features such as eddies (Arostegui et al. 2022; Deeg et al. 2023) were missed, whether predators were present, but we failed to catch them with trawls, or if they were simply absent indicating that predation on the high seas may not be a major source of mortality.

Pink salmon are the most abundant salmon across the North Pacific Ocean (Ruggerone and Irvine 2018) and show large even-odd year differences in abundance due to their two-year life span (Ruggerone et al. 2010). They are often cited as the cause of reduced productivity of other Pacific salmon in both nearshore and offshore waters by reducing prey availability through trophic cascades (Batten et al. 2018), leading to strong odd-even year variation in factors such as diets and feeding success, growth, and survival (Ruggerone and Nielsen 2004; Ruggerone and Conner 2015). Their unexpectedly low abundance in IYS surveys (8% of all salmon caught in 2019, 2020, and 2022 combined) suggests their spatial distributions may be either west or south of the study area (Morris et al. 1992), which may limit their impact on shared prey abundances. While diet data indicate some overlap between pink and other salmon, pink salmon diets were highly variable and they often consumed prey taxa that other salmon were not consuming (e.g., decapods, fish eggs, and amphipods; Fig. 7).

Low catches of pink salmon across the entire study area are not entirely consistent with expectations based on long-term average patterns and temperature preferences from historical high seas catches in April (the nearest month with ample data). These historic patterns show high pink salmon abundances in the south (largely in areas south of the IYS study area) and a near absence farther north (McKinnell and Langan, this volume; J. Langan, Univ. Alaska Fairbanks, unpubl. data). Consequently, pink salmon were more likely to be present at the southern-most stations sampled by the R/V *TINRO*, yet none were caught. Absence of pink salmon at these stations may partially reflect low abundances of Russian pink salmon in 2022; pink salmon commercial catches by Russia in 2022 (145,000 mt) were below the 10-year average (282,000 mt; 2014–2023) and well below record catches in 2018, 2019, 2021, and 2023 (326,000–507,000 mt; NPAFC 2024). The relatively low abundance of pink salmon in our survey suggests that if pink salmon affect the growth and survival of other salmon species, these interactions occur at other times or locations during ocean residence.

One important question is whether the abundance of salmon on the high seas has changed during the 60 years that winter high seas research has been conducted (e.g., Beamish 2022b). Unfortunately, direct comparisons across years are problematic due to differences in fishing gear (longlines and gillnets prior to the 1990s, surface trawls since the 1990s), which have fundamentally different units of abundance (linear versus volumetric) and catchability coefficients. Preliminary comparisons provide mixed results (S. McKinnell, pers. comm.). Using catch data expressed as presence/absence, catch of at least one salmon occurred more frequently in 2019, 2020, and 2022 (in 88% of trawl sets combined), than prior to 2019, when only 44% of net hauls caught at least one salmon. On the other hand, the median number of salmon caught by gear type from 1962–2022 was considerably higher for gillnets (29.5 salmon per set) and long lines (10 salmon per set), than trawls (1 salmon per set), a comparison likely complicated by gear-specific catchabilities. Comparing the 2022 longline and gillnet catches from the F/V *Raw Spirit* to historical catches using the same gear types may shed light on this issue (C. Neville, in prep).

Finally, genetic data indicate that all three surveys (2019, 2020, 2022) caught Pacific salmon originating from around the Pacific Rim (Beamish et al. 2022a; Deeg et al. 2022; Neville and Beamish 2022; Urawa et al. 2021, 2022; Fig. 6), consistent with historic distribution data (e.g., Myers et al. 1990). Most Pacific salmon caught in these years included individuals from Asia (Russia, Japan), Alaska, and the Pacific Northwest (British Columbia, Washington, and Oregon). This cosmopolitan stock composition demonstrates that salmon populations from throughout the North Pacific use many of the same high seas habitats and are therefore impacted by common environmental drivers. Consequently, it is critical that all Pacific salmon-producing nations work together to better understand the factors regulating salmon survival on the high seas, to ensure sustainable salmon for future generations.

CONCLUSIONS

The 2022 IYS Pan-Pacific High Seas Expedition consisted of five ships sampling salmon high seas ecosystems across 2.5 million km^2 of the central and northeast Pacific Ocean. Despite often difficult working conditions, 131 stations were sampled and nearly 2,400 salmon were caught using surface trawls, long lines, and gillnets. In addition, thousands of specimens and samples were collected and will form the basis of future analyses. Some findings from the 2022 expedition, such as temperature preferences, relative abundances, and diets, are similar to those observed in recent (2019, 2020) and during historical (1962–2009) winter high seas surveys. Other findings, such as the ability to document zonal (east-west) distributions of salmon and other nekton in winter across 42° of longitude, has previously been limited. The 2019, 2020, and 2022 expeditions also benefitted from newer technologies, including genetic stock identification, measures of salmon health (gene regulation, hormone levels) and the use of trophic biomarkers (stable isotopes and fatty acids) to document food web structure. The nearly 1,000 eDNA samples collected during the 2022 expedition will indicate the presence of many organisms that left behind DNA but were not collected by nets (Deeg et al. 2023); these eDNA samples became especially important when the weather was too rough to deploy sampling gear. Overall, the findings of the 2022 survey builds on previous research to fill key gaps in our understanding of salmon ocean distribution and migration. This should help increase our understanding of the mechanisms regulating high seas salmon production and the effects of climate change on high seas salmon and steelhead.

ACKNOWLEDGMENTS

The authors thank the officers and crew of all the ships for their professionalism during all aspects of the expedition, often working in extremely challenging conditions. They also thank the 60+ scientists who participated in the expedition and followed strict protocols to ensure all data and samples were correctly entered, labeled, and/or preserved despite rough seas. Many donors provided funds for the expeditions in 2019, 2020 and the gillnet and longline survey in 2022. The 2022 Expedition was made possible by in-kind ship time contributions from Canada and the United States, and additional financial and technical contributions from DFO, British Columbia Salmon Restoration and Innovation Fund, NOAA, North Pacific Research Board, Pacific Salmon Commission's Northern Boundary & Transboundary Rivers Restoration and Enhancement Fund, Great Pacific Foundation, Pacific Salmon Foundation, Russian Federal Research Institute of Fisheries and Oceanography, Japan Fisheries Research and Education Agency, North Pacific Anadromous Fish Commission, North Pacific Fisheries Commission, ADF&G, Washington Department of Fish and Wildlife, Tula Foundation, University of Alaska Fairbanks, University of British Columbia, Oregon State University, and University of Washington. Skip McKinnell provided comparisons between current and historical high seas data. This manuscript was improved by comments provided by Kym Jacobson, Brian Wells, Marc Trudel, and David Welch.

REFERENCES

Abdul-Aziz, O.I., N.J. Mantua, and K.W. Myers. 2011. Potential climate change impacts on thermal habitats of Pacific salmon (*Oncorhynchus* spp.) in the North Pacific Ocean and adjacent seas. Can. J. Fish. Aquat. Sci. 68:1660–1680. https://doi.org/10.1139/f2011-079

Anderson, E.C, R.S. Waples, and S.T. Kalinowski. 2008. An improved method for predicting the accuracy of genetic stock identification. Can. J. Fish. Aquat. Sci. 65: 1475–1486. https://doi.org/10.1139/F08-049

Arostegui, M.C., P. Gaube, P.A. Woodworth-Jefcoats, D.R. Kobayashi, and C.D. Braun. 2022. Anticyclonic eddies aggregate pelagic predators in a subtropical gyre. Nature 609: 535–540. https://doi.org/10.1038/s41586-022-05162-6

Batten, S., G. Ruggerone, and I. Ortiz. 2018. Pink salmon induce a trophic cascade in plankton populations in the southern Bering Sea and around the Aleutian Islands.

Fish. Oceanogr. 27: 548–559. https://doi.org/10.1111/fog.12276

Beamish, R.J. (Editor). 2018. The ocean ecology of Pacific salmon and trout. Am. Fish. Soc., Bethesda. 1099 pp.

Beamish, R.J., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Progr. Oceanogr. 49: 423–437. https://doi.org/10.1016/S0079-6611(01)00034-9

Beamish, R., C. Neville, and V. Radchenko. 2022a. Ocean ecology of coho salmon in the Gulf of Alaska in the winter. N. Pac. Anadr. Fish Comm. Tech. Rep. 18: 98–105. https://doi.org/10.23849/npafctr18/98.105.

Beamish, R.J., B.E. Riddell, and V.I. Radchenko. 2022b. Introduction. N. Pac. Anadr. Fish Comm. Tech. Rep. 18: 1–4. https://doi.org/10.23849/npafctr18/1.4.

Bond, N.A., M.F. Cronin, H. Freeland, and N. Mantua. 2015. Causes and impacts of the 2014 warm anomaly in the NE Pacific. Geophys. Res. Lett. 42: 3414–3420. https://doi.org/10.1002/2015GL063306

Bugaev, A.V., and E.A. Shevlyakov. 2007. Wounding of Pacific salmon by predators in gillnet catches in the Russian Economic Zone in 2004. N. Pac. Anadr. Fish Comm. Bull. 4: 145–154. (Available at https://npafc.org).

Clarke, K.R., and R.N. Gorley. 2006. PRIMER, version 6: user manual/tutorial. PRIMER-E, Plymouth, UK. 10 pp.

Deeg, C.M., S. Esenkulova, S. Li, B.P.V. Hunt, B.J.G. Sutherland, A. Schulze, and K.M. Miller. 2022. Environmental DNA survey of the winter salmonosphere in the Gulf of Alaska. N. Pac. Anadr. Fish Comm. Tech. Rep. 18: 37–41. https://doi.org/10.23849/npafctr17/116.120.

Deeg, C.M., S. Li, S. Esenkulova, B.P.V. Hunt, A.D. Schulze, and K.M. Miller. 2023. Environmental DNA survey of the winter salmonosphere in the Gulf of Alaska. Environ. DNA 5 (3): 519–539. https://doi.org/10.1002/edn3.404

Egger, M., R. Nijhof, L. Quiros, G. Leone, S.-J. Royer, A.C. McWhirter, G.A. Kantakov, V.I. Radchenko, E.A. Pakhomov, B.P.V. Hunt, and L. Lebreton. 2020. A spatially variable scarcity of floating microplastics in the eastern North Pacific Ocean. Environ. Res. Lett. 15: 114056. https://doi.org/10.1088/1748-9326/abbb4f

King, J.R., C. Freshwater, A.M. Tabata, T.B. Zubkowski, C. Stanley, C. Wright, E.D. Anderson, and K.L. Flynn. 2022. Eastern Gulf of Alaska Pacific salmon trawl survey, February 19–March 21, 2022 onboard the CCGS *Sir John Franklin* as contribution to the International Year of the Salmon Pan–Pacific Winter High Seas Expedition. Can. Tech. Rep. Fish. Aquat. Sci. 3502: vii + 61 pp.

Konik, M., M.A. Peña, T. Hirawake, B.P.V. Hunt, P.S. Vishnu, L.B. Eisner, A. Bracher, H. Xi, C. Marchese, and M. Costa. 2024. Bioregionalization of the subarctic Pacific based on phytoplankton phenology and composition. Prog. Oceanogr. 228: 103315. https://doi.org/10.1016/j.pocean.2024.103315

Manzer, J.I., and A.J. Dodimead. 1964. Winter distribution of salmon in the northeast Pacific Ocean, January 7 to February 7, 1964, with some reference to oceanographic conditions. Int. Pac. Salmon Fish. Comm. Doc. 748. 18 pp.

Moran, B.M., and E.C. Anderson. 2018. Bayesian inference from the conditional genetic stock identification model. Can. J. Fish. Aquatic Sci. 76: 551–560. https://doi.org/10.1139/cjfas-2018-0016

Morris, J.F.T., D.W. Welch, and O.A. Rassadnikov. 1992. Data report from the 1990 and 1991 joint USSR-Canada salmon research cruises to the north Pacific Ocean. Can. Data Rep. Fish. Aquat. Sci. 891. 175 pp.

Murphy, J., J. Dimond, E. Price, J. Lerner, T. Sheridan, M. Baker, C. Graham, E. Farley, and M. Saunders. 2022. Preliminary findings of the International Year of the Salmon Pan–Pacific Winter High Seas Expedition onboard the F/V *Northwest Explorer* during April 3–17, 2022. N. Pac. Anadr. Fish Comm. Doc. 2054. 29 pp. (Available at https://npafc.org).

Myers K.W., R.V. Walker, S. Fowler, and M.L. Dahlberg. 1990. Known ocean ranges of stocks of Pacific salmon and steelhead as shown by tagging experiments, 1956–1989. (INPFC Doc.) FRI-UW-9009, Fish. Res. Inst., Univ. Washington, Seattle. 57 pp.

Myers, K.W., J.R. Irvine, E.A. Logerwell, S. Urawa, S.V. Naydenko, A.V. Zavolokin, and N.D. Davis. 2016. Pacific salmon and steelhead: life in a changing winter ocean. N. Pac. Anadr. Fish Comm. Bull. 6: 113–138. https://doi.org/10.23849/npafcb6/113.138

Naydenko, S.V., and O.S. Temnykh. 2016. The survival of Pacific salmon in the North Pacific in the winter and spring. Russian Journal of Marine Biology 42: 527–550.

Neville, C.M., and R.J. Beamish. 2022. New information about the ocean ecology of sockeye salmon and relevance to populations in the Fraser River, British Columbia. N. Pac. Anadr. Fish Comm. Tech. Rep. 18: 72–79. https://doi.org/10.23849/npafctr18/72.79.

Neville, C., M. Banks, D. Bouillon, S. Esenkulova, R. LaForge, B. Lewis, G. Marynuik, A. Schubert, B. Riddell and R. Beamish. 2023. Expedition to study the winter ecology of Pacific salmon in Gulf of Alaska using gillnet and longline gear fished from FV *Raw Spirit*, February 25–March 25, 2022. Can. Tech. Rep. Fish. Aquat. Sci. 3524: viii + 60 pp.

NPAFC (North Pacific Anadromous Fish Commission). 2024. NPAFC Pacific salmonid catch statistics (updated June 2024). North Pacific Anadromous Fish Commission, Vancouver. Accessed August, 2024. (Available at https://www.npafc.org).

Pakhomov, E.A, C. Deeg, S. Esenkulova, G. Foley, B.P.V. Hunt, A. Ivanov, H.K. Jung, G. Kantakov, A. Kanzeparova, A. Khleborodov, C. Neville, V. Radchenko, I. Shurpa, A. Slabinsky, A. Somov, S. Urawa, A. Vazhova, P.S. Vishnu, C. Waters, L. Weitkamp, M. Zuev, and R. Beamish. 2019. Summary of preliminary findings of the International Gulf of Alaska expedition onboard the R/V *Professor Kaganovskiy* during February 16–March 18, 2019. N. Pac. Anadr. Fish Comm Doc. 1858. 25 pp. Canada, Japan, Korea, Russia, and USA (Available at https://npafc.org).

Pakhomov, E.A., R. Beamish, E. Farley, C. Freshwater, J. King, C. Neville, V. Radchenko, B. Riddell, S. Sato, A. Somov, S. Urawa, T. van der Stap, L. Weitkamp, C. Graham, and M. Saunders. 2021. Preliminary cruise plan for the NPAFC International Year of the Salmon (IYS) 2022 Pan-Pacific Winter High Seas Expedition. N. Pac. Anadr. Fish Comm. Doc. 1995. 92 pp. (Available at https://npafc.org).

Pakhomov, E.A., A. Figurkin, B.P.V. Hunt, A. Somov, N. Mahara, and International Team 2019–2020. 2022a. Oceanographic conditions during the Gulf of Alaska 2019 and 2020 expeditions. N. Pac. Anadr. Fish Comm Tech Rep 18: 20–24. https://doi.org/10.23849/npafc-tr18/20.24.

Pakhomov, E., L. Weitkamp, C. Neville, A. Somov, J. King, E. Farley, B. Hunt, C. Freshwater, J. Murphy, T. van der Stap, B. Johnson, K. Kivva, S. Esenkulova, S. Urawa, C. Waters, A. Vazhova, V. Radchenko, B. Riddel, R. Beamish, and M. Saunders. 2023. Integrated data collection from the International Year of the Salmon High Seas Expeditions (Version v4) [Data set]. N. Pac. Anadr. Fish Comm. https://doi.org/10.21966/81jn-6p63

Riddell, B., R. Beamish, and C. Neville. 2022. Third Gulf of Alaska expedition to study the winter ecology of Pacific salmon in the Gulf of Alaska. N. Pac. Anadr. Fish Comm Doc. 1996. 22 pp. (Available at https://npafc.org).

Ruggerone, G.T., and B.M. Conners. 2015. Productivity and life history of sockeye salmon in relation to competition with pink and sockeye salmon in the North Pacific Ocean. Can. J. Fish. Aquat. Sci. 72: 818–833. https://doi.org/10.1139/cjfas-2014-0134

Ruggerone, G.T., and J.L. Nielsen. 2004. Evidence for competitive dominance of pink salmon (*Oncorhynchus gorbuscha*) over other salmonids in the North Pacific Ocean. Rev. Fish Biol. Fish. 14: 371–390. https://doi.org/10.1007/s11160-004-6927-0

Ruggerone, G.T., and J.R. Irvine. 2018. Numbers and biomass of natural- and hatchery-origin pink salmon, chum salmon, and sockeye salmon in the North Pacific Ocean, 1925–2015. Mar. Coast. Fish. 10: 152–168. https://doi.org/10.1002/mcf2.10023

Ruggerone, G.T., R.M. Peterman, B. Dorner, and K.W. Myers. 2010. Magnitude and trends in abundance of hatchery and wild pink salmon, chum salmon, and sockeye salmon in the North Pacific Ocean. Mar. Coast. Fish. 2: 306–328. https://doi.org/10.1577/C09-054.1

SSC (Science Sub-Committee). 2016. North Pacific Anadromous Fish Commission Science Plan 2016–2022. N. Pac. Anadr. Fish Comm. Doc. 1665 (Rev. 1). 8 pp. The Science Sub-Committee (SSC), the Committee on Scientific Research and Statistics (CSRS) (Available at https:// npafc.org)

Somov, A., T. Blaine, C.M. Deeg, S. Esenkulova, T.J. Frost, S. Garcia, I.V. Grigorov, B.P.V. Hunt, A. Kanzeparova, R.V. LaForge, J.E. Lerner, N. Mahara, C.M. Neville, E.A. Pakhomov, B. Riddell, W.W. Strasburger, and R.J. Beamish. 2020. Preliminary findings of the second salmon Gulf of Alaska expedition onboard the R/V *Pacific Legacy* March 11–April 7, 2020 as part of the International Year of the Salmon. N. Pac. Anadr. Fish Comm. Doc. 1930. 48 pp. (Available at https://npafc.org).

Somov, A.A., A.A. Starovoytov, D.N. Chulchekov, K.K. Kivva, A.S. Khleborodov, V.I. Polyanichko, Y.Y. Korolev, A.O. Bezverkhnaya, S.V. Novokreshchennykh, V.A. Soshnina, I.N. Mukhametov, V.F. Parkhomchuk, G.A. Kantakov, and E.A. Pakhomov. 2022. Preliminary findings of the International Year of the Salmon Pan-Pacific Winter High Seas Expedition onboard the R/V *TINRO* during March 2–20, 2022. N. Pac. Anadr. Fish Comm. Doc. 2061. 25 pp. (Available at https://npafc.org).

Trudel, M., S. Tucker, J.F.T. Morris, D.A. Higgs, and D.W. Welch. 2011. Indicators of energetic status in juvenile coho salmon and Chinook salmon. North Am. J. Fish. Manag. 25: 374–390. https://doi.org/10.1577/M04-018.1

Urawa, S., T. Beacham, B. Sutherland, and S. Sato. 2021. Stock identification of chum salmon overwintering in the Gulf of Alaska by using a new SNP baseline. N. Pac. Anadr. Fish Comm. Tech. Rep. 17: 67–68. https://doi.org/10.23849/npafctr17/67.68.

Urawa, S., T. Beacham, B. Sutherland, and S. Sato. 2022. Winter distribution of chum salmon in the Gulf of Alaska: a review. N. Pac. Anadr. Fish Comm. Tech. Rep. 18: 93–97. https://doi.org/10.23849/npafctr18/93.97.

Weitkamp, L.A., and S. Garcia. 2022. Predation on Pacific salmon on the high seas. N. Pac. Anadr. Fish Comm. Tech. Rep. 18: 42–46. https://doi.org/10.23849/npafc-tr18/42.46.

Weitkamp, L., E. Farley, A. Andrews, A. Billings, B. Chasco, C. Deeg, I. Ekmanis, S. Garcia, B. Gray, K. Howard, C. Kovach, S. Lindley, M. Litz, R. McCabe, J. Moss, J. Murphy, D. Nicolls, A. Pinchuk, T. Rogers, K. Shedd, W. Strasburger, G. Troina, A. Wells, B. Wells, and E. Wisegarver. 2022. Preliminary findings of the International Year of the Salmon Pan-Pacific Winter High Seas Expedition onboard the NOAA Ship *Bell M. Shimada*, February 1–March 7, 2022. N. Pac. Anadr. Fish Comm. Doc. 2060. 30 pp. (Available at https://npafc.org).

Welch, D.W., and Y. Ishida. 1993. On the statistical distribution of salmon in the sea: application of the negative binomial distribution, and the influence sf sampling effort. Can. J. Fish. Aquat. Sci. 50: 1029–1038. https://doi.org/10.1139/f93-119

Welch, D.W., A.I. Chigirinsky, and Y. Ishida. 1995. Upper thermal limits on the oceanic distribution of Pacific salmon (*Oncorhynchus* spp.) in the spring. Can. J. Fish. and Aquat. Sci. 52: 489–503. https://doi.org/10.1139/f95-050

Welch, D.W., Y. Ishida, and K. Nagasawa. 1998a. Thermal limits and ocean migrations of sockeye salmon (*Oncorhynchus nerka*): long-term consequences of global warming. Can. J. Fish. Aquat. Sci. 55: 937–948.

Welch, D.W., Y. Ishida, K. Nagasawa and J.P. Eveson. 1998b. Thermal limits on the ocean distribution of steelhead trout (*Oncorhynchus mykiss*). N. Pac. Anadr. Fish Comm. Bull. 1: 396–404. (Available at https://npafc.org)

Wilkinson, M.D., M. Dumontier, I.J. Aalbersberg, G. Appleton, M. Axton, A. Baak, N. Blomberg, J.-W. Boiten, L.B. da Silva Santos, P.E. Bourne, J. Bouwman, A.J. Brookes, T. Clark, M. Crosas, I. Dillo, O. Dumon, S. Edmunds, C.T. Evelo, R. Finkers, A. Gonzalez-Beltran, A.J.G. Gray, P. Groth, C. Goble, J.S. Grethe, J. Heringa, P.A.C. 't Hoen, R. Hooft, T. Kuhn, R. Kok, J. Kok, S.J. Lusher, M.E. Martone, A. Mons, A.L. Packer, B. Persson, P. Rocca-Serra, M. Roos, R. van Schaik, S.A. Sansone, E. Schultes, T. Sengstag, T. Slater, G. Strawn, M.A. Swertz, M. Thompson, J. van der Lei, E. van Mulligen, J. Velterop, A. Waagmeester, P. Wittenburg, K. Wolstencroft, J. Zhao, and B. Mons. 2016. The FAIR guiding principles for scientific data management and stewardship. Sci. Data 3: 160018. https://doi.org/10.1038/sdata.2016.18

Laurie Weitkamp[1], Andrew Barclay[2], Richard J. Beamish[3], Maycira Costa[4], Ed Farley[5], Cameron Freshwater[6], Sara Gilk-Baumer[2], Caroline Graham[7,8], Kathrine Howard[2], Jackie King[6], Marta Konik[4], Jim Murphy[5], Chrys Neville[6], Evgeny A. Pakhomov[9,10], Vladimir Radchenko[7,11], Brian Riddell[12], Eric Rondeau[6], Mark Saunders[7,13], Aidan Schubert[7,14], Don Van Doornik[15], Bernard Yang[16,17], and Aleksey Somov[11]

[1]NOAA Fisheries, Northwest Fisheries Science Center,
2032 SE Marine Science Drive, Newport, OR 97365, USA
[2]Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99518, USA
[3]Fisheries and Oceans Canada, Emeritus scientist, Pacific Biological Station,
3190 Hammond Bay Road, Nanaimo, BC V9T 6N7, Canada
[4]University of Victoria, SPECTRAL Remote Sensing Laboratory,
3800 Finnerty Road, Victoria, BC V8P 5C2, Canada
[5]NOAA Fisheries, Alaska Fisheries Science Center, Ted Stevens Marine Research Institute,
17109 Point Lena Loop Road, Juneau, AK 99801, USA
[6]Fisheries and Oceans Canada, Pacific Biological Station,
3190 Hammond Bay Road, Nanaimo, BC V9T 6N7, Canada
[7]North Pacific Anadromous Fish Commission,
Suite 502, 889 West Pender Street, Vancouver, BC V6C 3B2, Canada
[8]Present address: Environment and Climate Change Canada,
401 Burrard Street, Vancouver, BC V6C 3R2, Canada
[9]Earth, Ocean and Atmospheric Sciences Department , University of British Columbia,
2207 Main Mall, Vancouver, BC V6T 1Z4, Canada
[10] Institute for the Oceans and Fisheries, University of British Columbia, AERL,
2202 Main Mall, Vancouver, BC, V6T 1Z4, Canada
[11]Pacific Branch of Russian Federal Research Institute of Fisheries and Oceanography VNIRO (TINRO),
4 Pereulok Shevchenko, Vladivostok, 690091, Russia
[12]Pacific Salmon Foundation, 320-1385 W 8th Avenue, Vancouver, BC V6H 3V9, Canada
[13]Present address: 9317 Chemainus Road, Chemainus, B.C., V0R 1K5, Canada
[14]Present address: Council of the Haida Nation, PO Box 98, Daajing Giids, Haida Gwaii V0T 1S0, Canada
[15]NOAA Fisheries, Northwest Fisheries Science Center, 7305 Beach Drive East, Port Orchard, WA 98366, USA
[16]University of Victoria, School of Earth and Ocean Sciences,
PO Box 1700 STN CSC, Victoria BC V8W 2Y2, Canada
[17]Present address: Ocean Networks Canada, 2474 Arbutus Rd, Victoria, BC V8N 1V8, Canada