

Southern resident killer whales encounter higher prey densities than northern resident killer whales during summer

Mei Sato, Andrew W. Trites, and Stéphane Gauthier

Abstract: The decline of southern resident killer whales (*Orcinus orca*) may be due to a shortage of prey, but there is little data to test this hypothesis. We compared the availability of prey (Chinook salmon, *Oncorhynchus tshawytscha*) sought by southern residents in Juan de Fuca Strait during summer with the abundance and distribution of Chinook available to the much larger and growing population of northern resident killer whales feeding in Johnstone Strait. We used ship-based multifrequency echosounders to identify differences in prey fields that may explain the dynamics of these two killer whale populations. Contrary to expectations, we found that both killer whale habitats had patchy distributions of prey that did not differ in their frequencies of occurrence, nor in the size compositions of individual fish. However, the density of fish within each patch was 4–6 times higher in the southern resident killer whale habitat. These findings do not support the hypothesis that southern resident killer whales are experiencing a prey shortage in the Salish Sea during summer and suggest a combination of other factors is affecting overall foraging success.

Résumé : Si le déclin des épaulards résidents du Sud (*Orcinus orca*) pourrait être causé par une pénurie de proies, il existe peu de données permettant de valider cette hypothèse. Nous comparons la disponibilité de proies (saumons chinooks, *Oncorhynchus tshawytscha*) recherchées par les épaulards résidents du Sud dans le détroit de Juan de Fuca durant l'été à l'abondance et la répartition des saumons chinooks disponibles pour la population beaucoup plus grande et croissante d'épaulards résidents du Nord qui s'alimentent dans le détroit de Johnstone. Nous employons des échosondeurs multifréquences embarqués pour cerner d'éventuelles différences entre les champs de proies qui pourraient expliquer la dynamique de ces deux populations d'épaulards. Contrairement aux attentes, nous constatons que les deux habitats des épaulards présentent des répartitions parcellaires de proies qui ne présentent pas de différences sur le plan de la fréquence de présences de proies ou de la composition des tailles de poissons. La densité de poissons dans chaque parcelle est cependant de quatre à six fois plus grande dans l'habitat des épaulards résidents du Sud. Ces constatations n'appuient pas l'hypothèse voulant que les épaulards résidents du Sud soient aux prises avec une pénurie de proies dans la mer des Salish durant l'été et indiqueraient qu'une combinaison d'autres facteurs influe sur le succès global de la quête de nourriture. [Traduit par la Rédaction]

Introduction

The southern residents are a seasonally migrating population of killer whales (*Orcinus orca*) that specialize in consuming salmon. They have declined in numbers since 2011, and are listed as endangered in Canada and the United States (COSEWIC 2001; NMFS 2005). Dietary analyses of stomach contents of beached carcasses, along with visual observations of prey captured, and DNA analysis of fecal samples and prey fragments, show that resident killer whales primarily consume Chinook salmon (*Oncorhynchus tshawytscha*) (Ford et al. 1998; Ford and Ellis 2006; Hanson et al. 2010, 2021), which have also declined through much of the Northwest Pacific (Yoshiyama et al. 1998; Kareiva et al. 2000; Riddell et al. 2018). Reduced numbers of Chinook are therefore thought to explain the poor body condition (Fearmbach et al. 2018) and reduced fecundity of southern resident killer whales (Ward et al. 2009, 2013) — and may explain why the southern resident population has declined. However, little is known about the abundance and accessibility of prey available to southern resident killer whales.

Previous studies that have linked declines of Chinook salmon to declines of southern resident killer whales have presumed that total annual returns of Chinook salmon averaged over wide stretches of coastal ocean are a proxy for prey availability (Ward et al. 2009; Ford et al. 2010a, 2010b). These broad-brushed studies have uncovered significant correlations that imply possible causal relationships. However, they have not been able to draw conclusions at a finer spatial scale about possible regional and seasonal differences in prey availability. Nor have the broad statistical correlations provided any insights into spatial and temporal scales of predator-prey overlap needed to manage fisheries and interactions with killer whales.

Studying animal behavior below the ocean surface presents challenges. Southern resident killer whales forage on relatively large Chinook salmon (Ford and Ellis 2006; Ford et al. 2010b) that swim fast — thus making it difficult if not impossible to use gill and trawl nets to quantitatively assess whether the availability of Chinook is sufficient to support killer whales. Such direct sampling of killer whale prey would also require integrating large

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M. Sato* and **A.W. Trites.** Marine Mammal Research Unit, Institute for the Oceans and Fisheries, The University of British Columbia, Vancouver, BC V6T 1Z4, Canada.

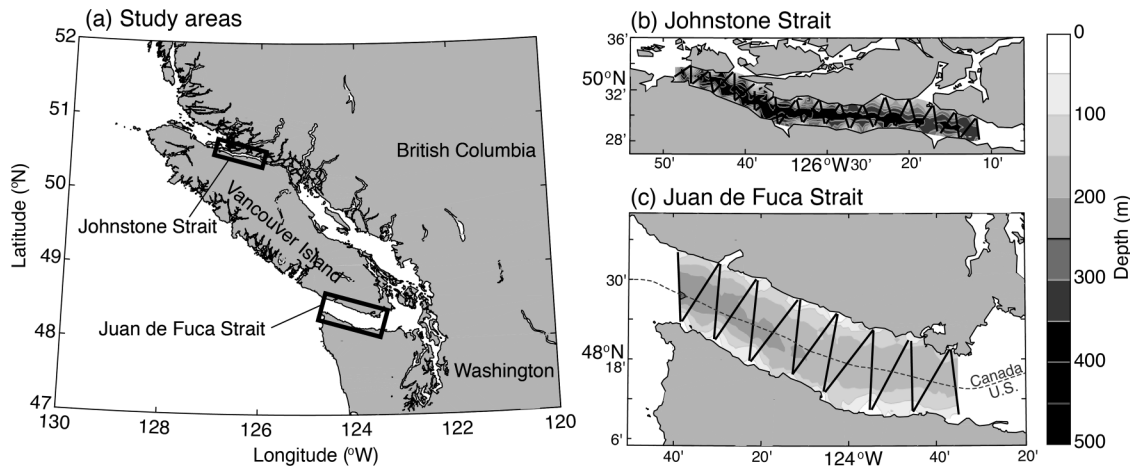
S. Gauthier. Institute of Ocean Sciences, Fisheries and Oceans Canada, Sidney, BC V8L 4B2, Canada; Department of Biology, University of Victoria, Victoria, BC V8P 5C2, Canada.

Corresponding author: Mei Sato (email: msato@whoi.edu).

*Present address: Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA.

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Fig. 1. (a) Study regions in the Northeast Pacific where southern and northern resident killer whales prey on migrating Chinook salmon. (b, c) Representative transect lines and bathymetry contours are shown for each study area. The survey area in 2018 was limited to Canadian waters. Map was generated in Matlab using the M_Map mapping software (Pawlowicz 2013).



horizontal and vertical scales, and would yield low-resolution data. Use of active acoustic sensors can overcome these sampling challenges and provide high-resolution data with wide spatial coverage over the entire water column (Kaartvedt et al. 2009; Benoit-Bird et al. 2013; Sato et al. 2016). Active acoustic techniques have been used to monitor adult salmonid escapement in rivers (Ransom et al. 1998), but have not been widely used to study salmonids in the ocean.

In this study, we used ship-based active acoustics to assess the spatial variability of prey dynamics in the coastal waters of British Columbia and Washington, where the seasonally migrating resident killer whales traditionally spend their summer months foraging. We compared two areas known to be important foraging habitats for resident killer whales — Johnstone Strait (a critical habitat of northern resident killer whales along the northeast coast of Vancouver Island) and Juan de Fuca Strait (a critical habitat of southern residents in the Salish Sea). These two sites (Fig. 1) are essential migratory corridors for Pacific salmon returning to the Salish Sea. Some of the largest salmon runs in North America move through the straits on their way to their spawning rivers in southwestern British Columbia and northwestern Washington (Quinn and Fresh 1984; Candy and Quinn 1999). Consequently, resident killer whales use these regions as primary foraging grounds during summer and fall months, selectively feeding on large Chinook salmon (Ford and Ellis 2006).

Northern and southern resident killer whales have a strong mutual reliance on Chinook salmon, but do not appear to have been equally affected by range-wide declines of Chinook salmon. The population of northern resident killer whales (which ranges from Southeast Alaska to southern British Columbia) has increased to ~300 individuals (Ward et al. 2009; Towers 2015), while southern resident killer whales (which range from southern British Columbia to California) numbered 75 individuals as of February 2021 (Orca Network 2021).

The goal of our study was to assess whether southern resident killer whales are experiencing a shortage of prey in the Salish Sea during summer. Unfortunately, there are no historic data to determine what changes may have occurred over time to the distribution and accessibility of prey available to resident killer whales. We therefore used the habitat of northern resident killer whales as a control site to test the hypothesis that prey availability, characterized by its frequency of occurrence, density, and size, was lower in southern resident killer whale habitat than in northern resident killer whale habitat. We sampled these sites using a combination of multifrequency acoustics verified by fish

sampling during summer over two years to encompass potential interannual variability.

Materials and methods

Study site and survey design

Juan de Fuca Strait is a weakly stratified, partially mixed tidal channel, connecting the inland waters of the Strait of Georgia and Puget Sound to the continental margin of British Columbia and Washington State (Fig. 1; Thomson 1981). The strait is a submarine valley ~100 km long and 20 km wide, with a maximum depth of 250 m at the mouth that decreases gradually eastward. A large volume of freshwater (mainly from the Fraser River) enters this coastal basin annually, with peak discharges occurring in early summer due to snow melt (Masson 2006). This discharge drives estuarine circulation — with relatively fresh water flowing seaward above a saltier return flow (Thomson 1981; Labrecque et al. 1994). The transition between upper-layer seaward and deep-shoreward estuarine flow is between 50 and 100 m, and is shallowest along the south margin due to Coriolis effects (Thomson 1981). Other forcing mechanisms in Juan de Fuca Strait include tides and winds. Tidal currents are about $1 \text{ m} \cdot \text{s}^{-1}$ within the strait, and have strong diurnal and semidiurnal components (Holbrook et al. 1980a, 1980b; Thomson 1994). Winds are generally along-channel, landward in the summer, and seaward during winter months (Thomson 1981).

In comparison, Johnstone Strait is a well-mixed tidal estuary located along the northeastern side of Vancouver Island (Fig. 1; Thomson 1981). Much of Johnstone Strait has a typical width of 4 km and mid-channel depths up to 400 m. While temperatures are nearly uniform throughout the entire length of Johnstone Strait, there is a weak stratification due to low-salinity surface waters originating from runoffs of the Fraser River and other various inlets and passes. The estuarine circulation consists of a net outflow of low salinity water in the upper 100 m, and a compensating inflow of more saline water at depth (Thomson 1976, 1977). Current speeds commonly reach $0.5\text{--}1.5 \text{ m} \cdot \text{s}^{-1}$ around mid-channel.

We sampled Johnstone Strait using 28, 3-km long acoustic transects for the 2018 and 2019 surveys (Fig. 1b) — and sampled Juan de Fuca Strait using 30, 10-km long transects for the 2018 survey and 15, 20-km long transects for the 2019 survey (Fig. 1c). This sampling design allowed us to examine spatial variability of the prey field between the two killer whale habitats. To examine variability within each habitat, we divided the transects into northern and southern portions based on the difference in the strength of estuarine circulation. In both locations, ebb speed is known to be

stronger than flood speed along the northern sides of the two straits (Thomson 1981). The survey in 2018 in Juan de Fuca Strait was limited to the Canadian waters due to difficulties obtaining a permit to enter and sample US waters.

Timing of the field surveys

Timing of the surveys was determined based on the long-term observations of increased foraging events on Chinook salmon by resident killer whales during July–August (Ford and Ellis 2006; Ford et al. 2010b). These summer months correspond to historic increases in sightings of the resident killer whales in our study areas based on visual observations (Nichol and Shackleton 1996; Olson et al. 2018).

We examined fishery assessment data collected by the Department of Fisheries and Oceans Canada (DFO) to assess seasonal and annual differences in the abundance of Chinook salmon migrating through our study areas. The difference in the abundance of Chinook salmon between two surveys years was examined based on annual estimates of the number of Chinook salmon returning to the Fraser watershed from the Albion test fishery. This test fishery is conducted annually from April through October, and operates every 1–2 days ~50 km upstream from the Fraser River mouth using a drifting gill net (Dempson et al. 1998). Data from the test fishery were obtained from DFO (2015).

We used recreational fishery assessment data to address the temporal offset between the timing of migrating Chinook salmon detected near the Fraser River mouth by the Albion test fishery and our survey timings in Johnstone Strait and Juan de Fuca Strait. This allowed us to assess the timing of our surveys relative to the abundance of Chinook salmon at each site. The recreational fishery assessment is used to estimate recreational angling catches in British Columbia marine waters (Schubert 1995). The monthly catch estimates of retained and released fish were obtained through angler interviews (DFO 2018, 2019). For our study, we combined the catch estimates of both retained and released Chinook salmon in Johnstone Strait — corresponding to the Pacific Fishery Management Area (PFMA) 12, and Juan de Fuca Strait (PFMA 20). These recreational fishery assessments are biased because seasonal, area-based fishery reductions and closures by DFO in 2018 and 2019 affected both retained and released catches. Because these regulations varied significantly within the study areas and over two years, and were implemented without any control site, it was impossible to evaluate its effect on the recreational catch data. Thus, we used these data sets as a qualitative measure of migration timings of Chinook salmon at each survey area.

Data collection and analysis

Ship-based sampling was conducted in the northwestern region of Johnstone Strait and Juan de Fuca Strait during 31 July – 14 August 2018 and 15 July – 5 August 2019. Simultaneous measurements of multifrequency hydroacoustics, and conductivity–temperature–depth (CTD) profiles were conducted during daylight hours on the F/V *Nordic Pearl* in 2018, and on the F/V *Carte Blanche* in 2019. Midwater trawling was carried out from the F/V *Nordic Pearl* in 2018 to identify midwater targets, while troll sampling of larger pelagic fish was carried out by the F/V *Carte Blanche* in 2019. Vessel speeds during the acoustic surveys were 4–6 knots (2.1–3.1 m·s⁻¹), and were reduced to 3–4 knots (1.5–2.1 m·s⁻¹) during midwater trawling and 2–3 knots (1.0–1.5 m·s⁻¹) during trolling.

Oceanographic data

To characterize spatial variability of water properties between the two study areas, we collected vertical profiles of temperature and conductivity (SBE 25 in 2018, SBE 19plus V2 in 2019; Sea-Bird Electronics), oxygen (SBE 43; Sea-Bird Electronics), and fluorescence (WET Labs ECO). The profiles to 5 m above the bottom depth

were taken during daytime on the semi-randomly chosen transects, resulting in 12 profiles in 2018, and 17 profiles in 2019 for Johnstone Strait — compared to 17 profiles in 2018 and 15 profiles in 2019 for Juan de Fuca Strait. CTD and oxygen data were aligned to correct for instrument lags and raw data were converted to variables of interest using factory calibrations. Each profile was averaged into 1-m depth bins. We assessed the difference between the study areas using a Mann–Whitney *U* test.

Acoustic data

Acoustic backscatter data were collected using Simrad EK80s operating at 38 and 120 kHz (7° split-beams) in 2018, and at 38 (10° split-beam), 70, 120, and 200 kHz (7° split-beams) in 2019. Transducers were hull mounted, corresponding to 4.5 m below the surface, in 2018, while the transducers were pole-mounted at 0.8 m depth on the starboard side of the vessel in 2019. Transducers were mounted as close to each other as possible to maximize the spatial overlap of the beams. During both surveys, the EK80s were configured to produce continuous wave signals with fast ramping applied. The system ran continuously at maximum ping rate (typically 0.5–1.4 pings·s⁻¹) with a pulse duration of 512 μs and a vertical resolution of 9 cm. The echosounders were calibrated using a standard sphere method (Demer et al. 2015) during the field surveys each year. To detect prey distributions as deep as 523 m, corresponding to a maximum depth in Johnstone Strait, data collected at 38 kHz were used in the analysis for single targets for 2018 survey, while 70 kHz data were used for 2019 survey due to partial failure of the 38 kHz system.

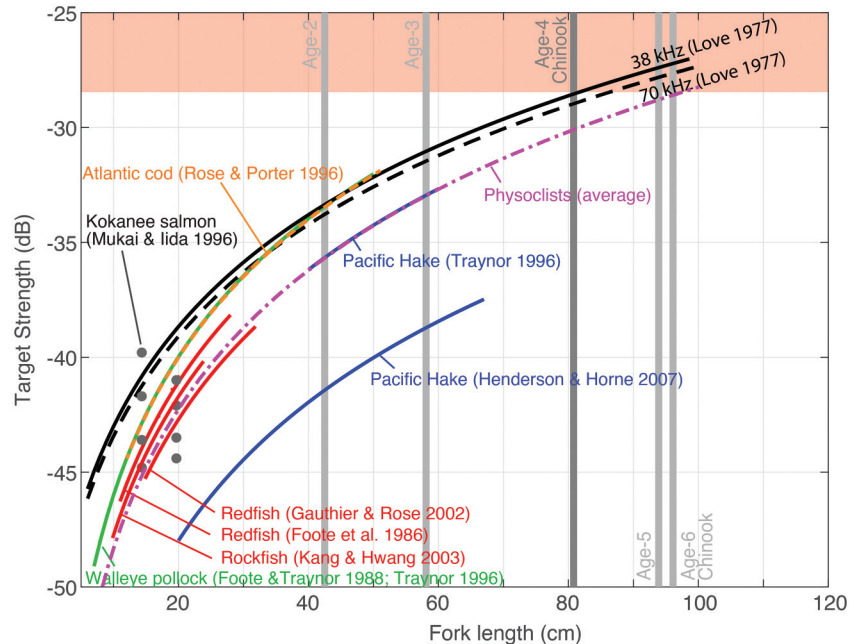
Pre-processing

Acoustic data were pre-processed using Echoview (version 9.0; Echoview Software Pty Ltd.). Data within 3 m of the transducers (shallower than 7.5 m depth) for 2018, and within 4.2 m of the transducers (shallower than 5.0 m depth) in 2019, were removed from analyses to eliminate near-field transducer effects and to reduce backscatter from surface bubbles. The echosounder-detected bottom was visually inspected, corrected if necessary, and data within 2 m of the bottom were removed from analyses. Background noise was removed using a technique developed by De Robertis and Higginbottom (2007) with a minimum signal-to-noise ratio of 6 dB and maximum noise threshold of -125 dB re 1 m⁻¹. An average of all CTD downcasts within each strait was used to estimate sound speed (Mackenzie 1981) and absorption coefficients (Francois and Garrison 1982), which were then used to calculate target strength (TS; dB) and target range. All data were visually inspected for anomalies such as false bottom and noise spikes. Fish aggregations (i.e., backscatter with discrete, closed edges) were identified using the school detection module in Echoview (Barange 1994). Detection criteria were based on those described by Sato et al. (2015) using a threshold of -60 dB re m⁻¹. The detected fish aggregations were removed from the data to avoid incorrectly identifying small fish aggregations (or parts thereof) as large individual targets.

Target strength estimates of chinook salmon

We estimated the spatial distribution, density, and size of prey based on target strength measurements using the split-beam echosounders. Since there was no dorsal aspect estimate of target strength of adult salmon, we used the empirical regressions developed by Love (1977) to determine a threshold value of target strength to isolate single targets corresponding to the typical size of killer whale prey. Instead of using the regression from the dorsal aspect corresponding to the maximum value of target strength (Love 1971), we used the equation that averages target strength over ±45° from its dorsal aspect (Fig. 2; Love 1977) since the natural orientation of fish likely diverts slightly from the dorsal aspect (Burczynski and Johnson 1986): $TS = 18.4 \log TL - 1.6 \log f - 61.6$ where *TL* is total length (cm) and *f* is frequency (kHz).

Fig. 2. Relationships between the fork length of fish and the average target strength over $\pm 45^\circ$ from its dorsal aspect of the fish (TS $\pm 45^\circ$; Love 1977) at 38 and 70 kHz, shown in black solid and dotted lines. Colour lines show target strength-length relationships of other physoclist species at 38 kHz from published sources. Filled circles show average target strength of two kokanee salmon at 50 kHz depending on their depths at 5–40 m (Mukai and Iida 1996). The vertical gray lines correspond to the mean fork lengths of 2–6-year-old Chinook salmon based on the Mark Recovery Program of Fisheries and Oceans Canada (Ford and Ellis 2006). Single targets with TS above -28 dB at 38 kHz (area highlighted in orange), corresponding to the size of age-4 Chinook, were detected as prey for killer whales in our study. [Colour online.]



Chinook salmon are the major prey for both southern and northern resident killer whales during summer months, constituting 86%–100% of their diet (Ford and Ellis 2006; Ford et al. 2010b; Hanson et al. 2021). Among Chinook salmon, resident killer whales selectively feed on adults aged 4–5 years old — constituting 83% of the Chinook salmon captured by northern residents, and 81% by southern residents (Ford et al. 2010b). Age classes of Chinook salmon were calculated by summing years in freshwater after hatching and years in marine water, then adding 1. Based on large Chinook salmon being the dominant prey of resident killer whales, we considered fish corresponding to the size of age-4 Chinook or larger to be prey. We determined the threshold values for single target analyses using (1) the mean fork lengths of Chinook salmon of different ages summarized by Ford and Ellis (2006) and (2) the empirical equations of the target strength of an individual fish developed by Love (1977). We converted fork lengths (FL; mm) to total lengths (TL; mm) using an empirical formula, $TL = 1.015FL + 39.020$ ($r^2 = 0.981$; Pahlke 1988), to apply the target strength equation by Love (1977).

Single target detection

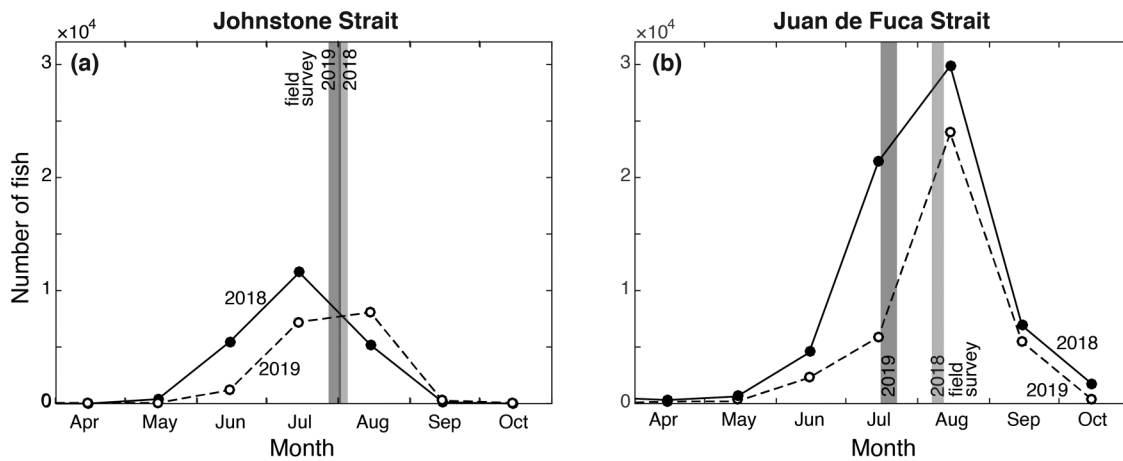
Single targets (i.e., large individual scatters at densities ≤ 1 per reverberation volume; Sawada et al. 1993) were extracted from the 38 kHz data for the 2018 survey, and from the 70 kHz data for the 2019 survey using the Echoview program. The target strength lower threshold was set to -28.5 dB at 38 kHz, and -29.0 dB at 70 kHz, corresponding to the average target strength over $\pm 45^\circ$ from the dorsal aspect of age-4 Chinook salmon (Fig. 2). A pulse length determination level (the value in dB below the peak value considered when determining the pulse length, or envelope, of a single target) of 12 dB was used. Normalized pulse lengths (the measured pulse length divided by the transmitted pulse length) were required to be between 0.8 and 2.0. The maximum beam compensation for correcting transducer directivity was set to

12 dB. To confirm all sources of scattering within the measured pulse length were from a single target, all samples within this pulse envelope had to have a standard deviation in angular position of $< 3^\circ$ in both the along and athwart ship directions of the beam.

Groups of single targets that showed a pattern of systematic movement were identified as tracks using the split-beam capabilities of the echosounders. To identify these tracks, we used the tracking algorithm in Echoview (Blackman 1986) which assumes that targets grouped into a track were generated by a single fish moving through the acoustic beam. Target strengths corresponding to multiple single targets identified as tracks were averaged and used as an estimate of the size composition of fish. Detected single targets and tracks were exported from Echoview to Matlab (Mathworks, R2018a) for further analysis.

The areal density of all single targets within the water column (i.e., the number of fish below a given surface area) was calculated by dividing the number of targets by the total volume of water, and then multiplied by the depth of the water column. To calculate the depth distribution of individual fish, we corrected the number of single-target detections for search area differences as a function of depth caused by the conical shape of the transducer’s beam. This was done by dividing the number of animals located at a particular depth by the diameter of the beam at that depth, following Levy and Cadenhead (1995). We then converted these counts to density for comparison by dividing them by the volume sampled by each beam. We examined the vertical distributions of single targets as a function of depth from the surface (i.e., the upper 50 m) and the height above the bottom in deeper waters (i.e., > 50 m) as fish are often associated with bottom bathymetry. Frequency of occurrence of single targets was estimated based on the proportion of the transect that had areal densities of single targets > 0 ind. $\cdot m^{-2}$. We compared the difference between and within the study areas using Mann–Whitney *U*

Fig. 3. Catch estimates of Chinook salmon, combining released and retained individuals, based on the recreational fishery assessments conducted by Fisheries and Oceans Canada in (a) Johnstone Strait and (b) Juan de Fuca Strait in 2018 and 2019.



test — and only considered data from the northern part of Johnstone Strait for statistical tests in 2018 to account for the limited sampling coverage in Juan de Fuca in that same year.

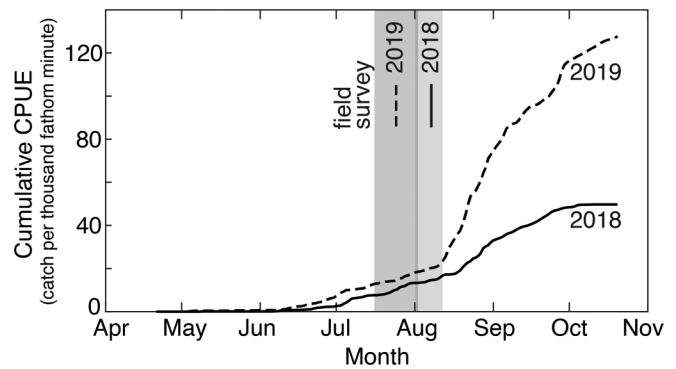
Biological samples

To identify species composition of single targets yielding high target strength values, we used both midwater trawl and commercial troll gear. Trolling was conducted to capture large fast-swimming fish which cannot be captured using midwater trawl due to its size selectivity. Using two direct sampling approaches, we targeted a wide range of pelagic species in our study areas relative to the size selectivity of each gear type. These biological samples were used solely for species composition validation of acoustic signals.

During the 2018 survey, midwater fish were sampled using a CanTrawl 250 midwater trawl (CanTrawl Nets Ltd.) fitted with a 7-mm knotless liner in the codend. The trawl was towed at a vessel speed of ~3–4 knots, targeting net opening of 50 m in horizontal and 20 m in vertical plane. The fishing depth of each trawl was selected to sample high acoustic backscatter, with trawl depth being monitored and directed using a real-time pressure sensor (SS4 CatchSensor, Scanmar) attached to the headrope of the net. Trawl duration was typically 20 min, but varied from 5 to 24 min depending on the observed density of backscatter. A total of 5 trawls in Johnstone Strait and 6 trawls in Juan de Fuca were conducted. Catches were identified, enumerated, and weighed — and a subsample of each species (up to 100 individuals) was measured for fork length or total length depending on fish species. We used the minimum and maximum lengths of fish species caught by the midwater trawl to estimate target strengths of potential single targets in our study areas. Target strengths were calculated from the published equations of the target strength – length relationship from in situ measurements, swimbladder modelling, or related species.

During the 2019 survey, line trolling was conducted at a vessel speed of ~2–3 knots. Four fishing lines were used (two on the port, and two on the starboard side of the vessel) with each line having 6–9 barbless-hook lures separated by 5.5 m. On each side of the vessel, the lures on the two fishing lines were set to target a wide range of depths (from as shallow as 6 m to as deep as 78 m). Trolling was conducted for validation purposes in areas that had single target acoustic characteristics and was only permitted in Canadian waters. Trolling locations, directions, and durations were determined based on tides, winds, marine traffic in the regions, and effective range of

Fig. 4. Estimates of the abundance (catch per unit effort; CPUE; 1 fathom = 1.8 m) of Chinook salmon returning to the Fraser watershed through the Albion test fishery located ~50 km upstream from the mouth of the Fraser River.



fishing gear deployed. The fishing lines were trolled for ~0.5–2 h depending on the catch, and the lures were usually returned to the same depths for continuous fishing. Total time of each troll-gear deployment varied between 1.5–4.5 h. A total of ~19 h was spent trolling in Johnstone Strait and ~20 h in Juan de Fuca Strait. Fish were either sacrificed for biochemical sampling immediately when they reached the surface (for collaborative research not reported here), or they were quickly transferred to a tank with seawater on deck — and subsequently released. All catches were identified and measured for fork length or total length depending on fish species. The length distributions of the troll catches between Johnstone Strait and Juan de Fuca Strait were compared using Kolmogorov–Smirnov statistics, while median values were compared using Mann–Whitney *U* tests. It was difficult to estimate the exact depth of the catch, because the depth of lures varied depending on vessel speed and tides, which often changed during trolling events. Thus, we limited the use of troll catches to inform acoustics for the presence of Chinook salmon as strong single targets in the study areas.

The Animal Care Committee of The University of British Columbia reviewed and approved the study following the Canadian Council on Animal Care (CCAC) guidelines. This work was conducted under permits issued by The University of British Columbia (A18-0037), DFO (XMMS 8 2018, XE 34 2018, XR 222 2018, XR 244 2019, XMMS 3 2019) and United States Department of State (U2019-015).

Table 1. Range of lengths and predicted target strengths of fish species caught by the midwater trawl during the 2018 survey in Johnstone Strait and Juan de Fuca Strait.

Fish species	Length (cm)		Predicted TS (dB)		Source
	Min.	Max.	Min.	Max.	
Whitebait smelt (<i>Allosmerus elongatus</i>)*	11.3 (FL)	12.3 (FL)	-46.9	-46.2	Rudstam et al. 2003
Pacific herring (<i>Clupea pallasii</i>)	7.6 (FL)	19.4 (FL)	-53.7	-45.4	Foote 1987
Grenadier (<i>Coryphaenoides</i> spp.)	5.1 (TL)	—	-64.1	—	O'Driscoll et al. 2014
Northern anchovy (<i>Engraulis mordax</i>)	11.3 (FL)	16.2 (FL)	-44.7	-42.0	Kang et al. 2009
Walleye pollock (<i>Gadus chalcogrammus</i>)	6.5 (TL)	58.3 (TL)	-49.5	-30.8	Foote and Traynor 1988; Traynor 1996
Pacific hake (<i>Merluccius productus</i>)	43.6 (TL)	95.5 (TL)	-41.4 to -35.6	-34.6 to -28.8	Traynor 1996; Henderson and Horne 2007
Lanternfish (Myctophyidae)	4.2 (TL)	11.2 (TL)	-63.2	-54.0	Yasuma et al. 2008
Pink salmon (<i>Oncorhynchus gorbuscha</i>)	11.4 (FL)	19.9 (FL)	-42.2	-38.7	Love 1977
Chum salmon (<i>Oncorhynchus keta</i>)	14.6 (FL)	21.2 (FL)	-40.7	-38.3	Love 1977
Coho salmon (<i>Oncorhynchus kisutch</i>)	13.5 (FL)	19.8 (FL)	-41.2	-38.7	Love 1977
Sockeye salmon (<i>Oncorhynchus nerka</i>)	55.5 (FL)	65.8 (FL)	-31.4	-30.1	Love 1977
Chinook salmon (<i>Oncorhynchus tshawytscha</i>)	21.5 (FL)	66.9 (FL)	-38.2	-30.0	Love 1977
Rockfish (<i>Sebastes</i> spp.)	34.5 (TL)	49.1 (TL)	-37.9 to -36.3	-34.9 to -33.3	Foote et al. 1986; Gauthier and Rose 2002; Kang and Hwang 2003
Pacific spiny dogfish (<i>Squalus suckleyi</i>)	20.6 (TL)	86.1 (TL)	-53.7	-41.3	O'Driscoll et al. 2014
Eulachon (<i>Thaleichthys pacificus</i>)	6.6 (FL)	23.6 (FL)	-66.9	-56.2	Gauthier and Horne 2004

Note: Target strengths (TS; dB) at 38 kHz were calculated from equations published in the source documents. The only exception was whitebait smelt whose TS values were estimated at 70 kHz, indicated by an asterisk (*). The equation from Love (1977) was applied for salmonids whose target strength – length relationships are unknown. Fish species without gas-filled swimbladders were also caught (sablefish, *Anoplopoma fimbria*; English sole, *Parophrys vetulus*; and northern lamprey, *Petromyzontidae*), but are not listed here because they are weak scatterers with no published information on their TS values.

Results

Timing of the field surveys

Timing of the surveys corresponded with peak or nearly peak abundance of Chinook salmon in Johnstone Strait (2018 and 2019) and in Juan de Fuca Strait (2018) based on recreational catch estimates (Fig. 3). However, peak numbers of fish returned later in Juan de Fuca Strait in 2019 than we had anticipated when planning our survey (Fig. 3b). Total abundance of spawning Chinook salmon observed at the lower Fraser River through the Albion test fishery was ~2.6 times higher in 2019 than in 2018 (Fig. 4).

Environmental conditions

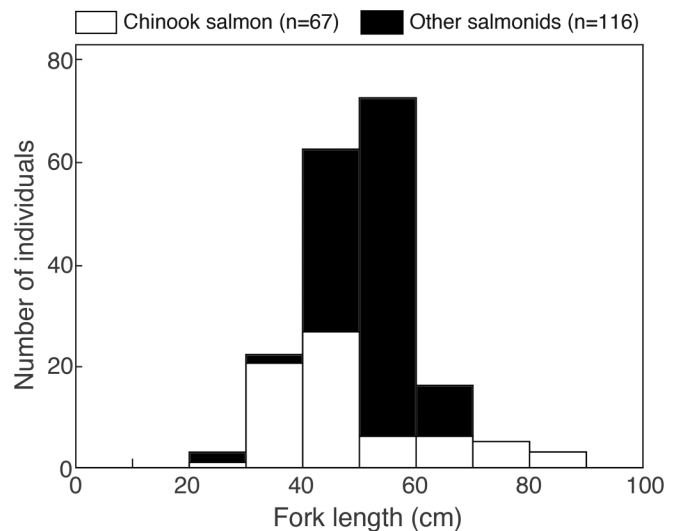
Temperature and salinity profiles showed a well-mixed water column in Johnstone Strait, having relatively consistent values throughout the water column (~11 °C and 30.5–31.5 psu near the surface and 9.3–10.5 °C and 31.0–32.1 psu at deeper depths). In Juan de Fuca Strait, the vertical structure of the water column was weakly stratified in the upper layer (<100-m depth), varying between 7–12 °C and 31–34 psu. There was little difference in physical variables within the study areas or between the survey years. Fluorescence maxima occurred at <50-m depth. Integrated fluorescence values in the upper 80 m in Juan de Fuca Strait (137.9 ± 75.8 mg·m⁻² in 2018, 54.9 ± 11.2 mg·m⁻² in 2019) were higher than in Johnstone Strait (89.8 ± 45.1 mg·m⁻² in 2018, 46.7 ± 11.0 mg·m⁻² in 2019), but the difference was statistically significant only in 2019 (p = 0.06 in 2018, p = 0.04 in 2019).

Biological samples

Various pelagic species were caught by the midwater trawls targeting acoustic scattering layers and single targets (Table 1). While two species, Pacific hake (*Merluccius productus*; TS = -28.8 dB) and Pacific spiny dogfish (*Squalus suckleyi*; TS = -53.7 to -41.3 dB), exceeded the size of 4-year-old Chinook (>81 cm FL), the predicted target strengths of all fish captured were considerably lower than those of age-4 Chinook salmon: -28.5 dB at 38 kHz and -29.0 dB at 70 kHz.

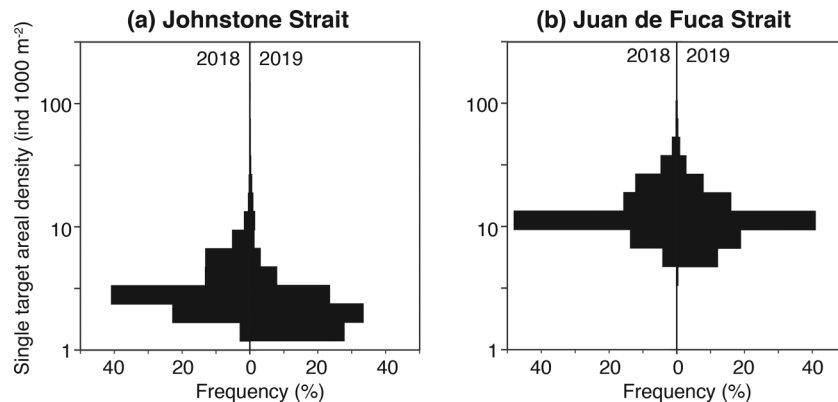
Salmonids dominated the troll catches, constituting 93% of the catch in Johnstone Strait and 95% of the catch in Juan de Fuca Strait. The remainder of the troll catches included Pacific spiny dogfish (*Squalus suckleyi*), walleye pollock (*Gadus chalcogrammus*),

Fig. 5. Size distributions of Chinook salmon and other salmonids caught by the commercial troller (hook and line) to validate acoustic signals during the 2019 survey in Johnstone Strait and Juan de Fuca Strait. Data from both regions were combined.



and rockfish (*Sebastes* spp.). Since there were no significant differences in the distribution (p = 0.09) or median size (p = 0.13) of the salmon caught between the two study areas, we combined the data from the two sites for further analyses (Fig. 5). Among the salmonids we caught, a small portion of the catch (1.6%) exceeded the size of 4-year-old Chinook (>81 cm FL) — and all were Chinook salmon (n = 3). No fish were caught larger than the size of 5-year-old Chinook (>94 cm FL). Overall, Chinook salmon — the preferred prey of resident killer whales — dominated our catch of large fish. Our troll transects were conducted in the pelagic zone, and did not target fish inhabiting deeper depths or located near the bottom.

Fig. 6. Areal densities of single targets (i.e., the numbers of large fish below 1000 m² surface areas) in Johnstone Strait and Juan de Fuca Strait in 2018 and 2019. Only data with the areal density of single targets >0 ind.·m⁻² are shown. There was little difference in the areal densities between two survey years.



Prey characteristics

Spatial distributions of prey varied considerably between and within regions, and tended to have patchy distributions of high fish densities across the two study sites. We characterized the prey distributions between and within the northern and southern resident killer whale habitats based on high temporal and spatial resolutions of acoustic measurements.

We observed regional variability in the frequency of occurrence, density, and vertical distributions of single targets (i.e., single large fish). The frequency of occurrence of single targets between study areas was similar in 2018 (median = 6.2% in Johnstone Strait and 7.9% in Juan de Fuca Strait; *p* = 0.22). However, single targets occurred more frequently in Johnstone Strait in 2019 (median = 3.5% in Johnstone Strait and 2.8% in Juan de Fuca Strait; *p* = 0.04).

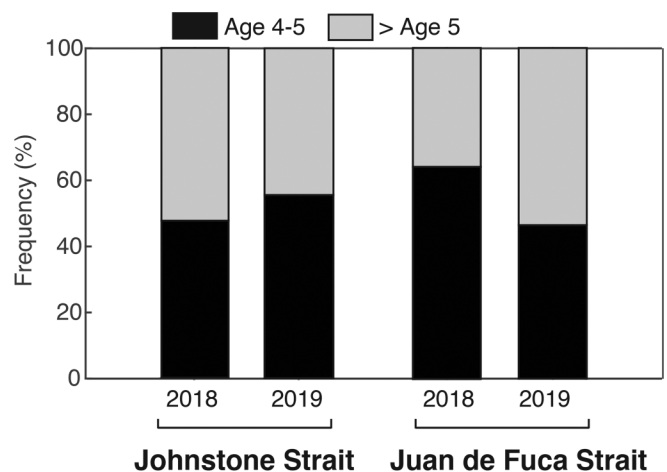
There was a notable difference in the areal densities of large fish found in the two habitats. Within transects where the areal density of single targets was >0 ind.·m⁻², densities of fish were consistently higher in Juan de Fuca Strait (mode = 11.2 ind.·1000 m⁻² in 2018 and 2019) than in Johnstone Strait (mode = 2.8 ind.·1000 m⁻² in 2018, 2.0 ind.·1000 m⁻² in 2019) over both years. Comparison of modal values between the two study areas showed that densities in Juan de Fuca Strait were 4.0 times higher in 2018, and 5.6 times higher in 2019 than in Johnstone Strait (Fig. 6).

There was no consistent difference in size composition of fish between the two habitats (Fig. 7). In Johnstone Strait, the proportion of prey within the size ranges of 4–5-year-old Chinook (81–94 cm FL) was similar to the proportion of prey deemed to be larger than 5-year-old Chinook (>94 cm FL). In Juan de Fuca Strait, the proportion of prey larger than 5-year-old Chinook was significantly less than the proportion of prey that were as large as 4–5-year-old Chinook in 2018, and was slightly higher than the proportion of 4–5-year-old Chinook present in 2019.

Prey in Juan de Fuca Strait typically occurred sub-surface (~10–30 m depth) or close to the bottom (within 50 m of the bottom), and appeared to be randomly distributed with considerable variability among the transect lines (Fig. 8b). In Johnstone Strait, however, this bimodal vertical distribution of prey appeared absent or was very small (Fig. 8a). The size distributions of prey were similar between two peaks. The average densities of fish at shallow and deep depths were significantly higher in Juan de Fuca Strait than in Johnstone Strait for both years (*p* < 0.0001).

Within each study area (Fig. 1), we found that large fish occurred at significantly higher frequencies in the northern side of each region compared to the southern side (*p* < 0.03 for all comparisons; Fig. 9). On transects where the areal density of single targets was >0 ind.·m⁻², densities of large fish were higher along the northern (mode = 11 ind.·1000 m⁻²) side of Juan de Fuca Strait compared to

Fig. 7. Size composition of single targets (large fish) in Johnstone Strait and Juan de Fuca Strait in 2018 and 2019, corresponding to the mean sizes of Chinook salmon aged 4–5 years and >5 years old.



the southern side (mode = 6 ind.·1000 m⁻²) in 2019. There was little difference in the densities of large fish observed between the north and south sides of Johnstone Strait (mode = 3 ind.·1000 m⁻² in the northern side and 2 ind.·1000 m⁻² in the southern side in 2018; mode = 2 ind.·1000 m⁻² in both the northern and southern sides in 2019). Sizes of individual fish based on target strength values were similar within our study sites.

Discussion

We assessed the spatial variability of large fish as potential prey for northern and southern resident killer whales in the Northeast Pacific. Contrary to our hypothesis, prey densities were higher in the southern resident killer whale habitat than in the northern resident killer whale habitat. However, the frequencies of occurrence of prey and sizes of fish present based on target strength analysis did not differ significantly between the two habitats. Within each habitat, large fish occurred more frequently along the northern sides of the passages (i.e., along Vancouver Island in Juan de Fuca Strait, and along the mainland side of Johnstone Strait).

The 4–6 times higher density of prey available to southern resident killer whales, when compared to northern resident killer whale habitat, suggests that they were not limited by prey during summer. This difference in prey density between the two habitats

Fig. 8. Density of single targets as a function of depth within 50 m of the surface (top panels), and within 0–250 m of the bottom (bottom panels) of Johnstone Strait and Juan de Fuca Strait in 2018 and 2019. Solid lines show medians and dotted lines show 25th and 75th percentiles. The limited single target density data corresponding to the height above the bottom of Juan de Fuca Strait reflect the shallower water depths.

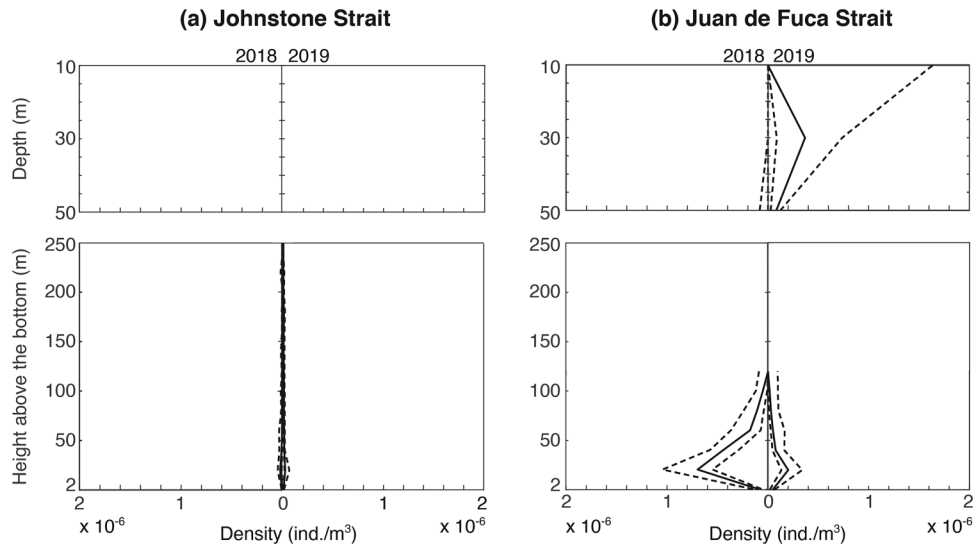
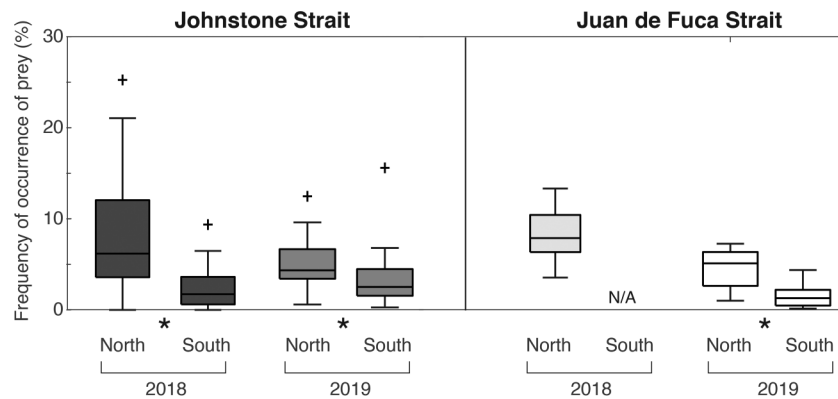


Fig. 9. Frequency of occurrence of prey, defined as the proportion of the transect with areal densities of single targets $>0 \text{ ind.}\cdot\text{m}^{-2}$, along the northern and southern sides of Johnstone Strait and Juan de Fuca Strait in 2018 and 2019. Central lines of the boxplots show the median, while boxes show 1 interquartile range, and the error bars show the range of data within 1.5 times the interquartile range from the box; plus symbols (+) indicate outliers. There were significant differences between the frequencies of occurrences along the north and south sides of Johnstone and Juan de Fuca straits as indicated by an asterisk (*) ($p < 0.05$, Mann–Whitney U test).



may reflect higher numbers of Chinook salmon using Juan de Fuca Strait instead of Johnstone Strait as a corridor to return to their natal rivers in the Salish Sea. In addition to the returning populations of Chinook salmon, some Chinook spend all or most of their marine life in the inland marine waters of British Columbia and Washington instead of feeding offshore (Pressey 1953; O'Neill and West 2009), which may also contribute to the higher density of prey present in Juan de Fuca Strait. The proportion of the lives of Chinook salmon spent in the inland waters is unknown.

The inter-annual variability we observed in the frequencies of occurrence and size composition of prey between study sites may have been due to difference in the timing of our surveys relative to the peak abundance of Chinook salmon at each study site. Since migration timing of anadromous salmonids is influenced by both genetics and environmental conditions (see reviews by Banks 1969; Dodson 1997; Quinn 2005), and our study locations are major migration corridors for multiple populations of Chinook salmon (Fraser et al. 1982), it was challenging to schedule our field surveys

to match peak migration timings. Complicating matters further was the substantial variation in life histories among populations of Chinook salmon, including variation in size at maturity and timing of spawning (Healey 1991). All of this suggests that prey availability for killer whales may be highly variable in shorter time scales (e.g., days to weeks). Long-term continuous measurements are needed to quantify such intra-seasonal variability in prey availability.

Physical processes might explain why prey occurred more frequently along the northern sides of each of the killer whale habitats. Ebb currents are stronger and last longer on the northern sides of Juan de Fuca Strait and Johnston Strait compared to the southern sides (Thomson 1981). This difference in tidal currents on each side of the channels could affect the fine-scale movements of migrating Chinook salmon that rely on olfaction as one of their primary sensory systems to find their natal streams (Dittman and Quinn 1996; Keefer and Caudill 2014). We hypothesize that salmon position themselves in stronger ebb tides to better detect natal stream odors. In contrast to physical processes, biological processes that affect prey distributions within habitats seem

unlikely to explain the northern distributions of salmon we observed, given that mature salmon largely stop feeding before they enter river systems and use stored body energy to complete their freshwater migrations (Cooke et al. 2011).

Characterizing target strength is critical for accurately assessing fish populations using acoustics (Simmonds and MacLennan 2005). One of the limitations of this study is the lack of a dorsal-aspect target strength model for salmonids, which is important for downward-looking echosounder applications. Previous studies of the relationship between target strength and body lengths of adult salmon have been undertaken to monitor fish migration in rivers, but are limited to the side- and ventral-aspects of the fish (Kubecka and Duncan 1998; Lilja et al. 2000; Knudsen et al. 2004). To our knowledge, the only published information on dorsal aspect target strengths of salmonids comes from ex-situ experiments at 50 kHz on relatively small kokanee salmon (*Oncorhynchus nerka*) (Fig. 2; Mukai and Iida 1996). For Chinook salmon, the only acoustic data currently available on target strengths are limited to a single frequency and modeling estimates, as well as simulated broadband in situ measurements (Burwen and Fleischman 1998; Au et al. 2004, 2010). The frequencies used in these previous studies are not consistent and are outside of commonly used fisheries acoustic frequencies.

In our study, we relied on empirical regressions derived from multiple fish species (Love 1977) to estimate the density and sizes of prey in the killer whale habitats. However, target strengths can vary significantly between species (Foote 1979; McClatchie et al. 1996), and we do not know the extent to which the regressions we used may have affected the accuracy of our estimates of prey density and size. To address this variability, we compared the target strength-length relationship based on Love (1977) with those of other physoclist species, which lack a duct between the swimbladder and alimentary canal (Fig. 2). We found that the regressions for walleye pollock (Foote and Traynor 1988; Traynor 1996), Atlantic cod (*Gadus morhua*) (Rose and Porter 1996), Pacific Hake (Traynor 1996), redbfish (*Sebastes marinus*) (Foote et al. 1986), and rockfish (*Sebastes schlegeli*) (Kang and Hwang 2003) provide similar results to Love's equation. Their estimated TS values corresponding to the size of age-4 Chinook salmon are within 1.5 dB of Love's estimate. However, reported target strength of redbfish is 2.0 dB lower (Gauthier and Rose 2002) and Pacific Hake is 7.3 dB lower (Henderson and Horne 2007) than the target strength estimated by Love's equation.

On average, the target strength of physoclists of age-4 Chinook size is 1.6 dB lower than the threshold value we used. Although natural variation is inherent in target strength of wild fish, it appears unlikely that values we attributed to age-4+ Chinook could be from other species which rarely reach such length (Anderson et al. 2019). Nonetheless, establishing the acoustic characteristics specific to adult Chinook salmon are needed to better assess their at-sea distributions, and to take advantage of ongoing large-scale spatial fish survey opportunities that could be simultaneously used to assess the abundance and distribution of Chinook salmon in habitats used by southern resident killer whales (e.g., acoustic-trawl surveys off the west coast of the US and Canada by NOAA and DFO).

Species identification in acoustic measurements remains a key challenge. While acoustics have long been used for fish stock assessment and management of a number of commercially important species (Simmonds and MacLennan 2005), integration of multiple, complementary sampling devices including trawls, optics, and imaging systems with acoustics is essential for accurately assessing the biomass of each species. Use of both mid-water trawl and commercial troll gear covered the majority of fish species present in the pelagic zones of our study areas — and allowed us to identify Chinook salmon as the dominant species comprising the large single targets we detected.

The range of fish sizes in the midwater trawl catches suggests that most species present were too small to produce high target

strengths comparable to those of age-4 Chinook salmon. Among the fish that have swimbladders and can get relatively large, Pacific hake and walleye pollock are typically found in aggregations that would have been excluded from our data using the school detection algorithm. Other fish, such as rockfish species, typically do not reach the size of age-4 Chinook salmon with a few exceptions (Anderson et al. 2019). By removing data within 2 m of the detected bottom, we likely excluded species with strong association to bathymetric features and the benthic environment. The only large fish species with a swimbladder that our sampling gears potentially missed is Pacific cod (*Gadus macrocephalus*). However Pacific cod are also highly demersal (Anderson et al. 2019), and would have been likely removed (if present) from our analysis of excluding the near-bottom data. Based on the sizes of fish present, exclusion of fish associated with the bottom, and the dominance of Chinook salmon caught by trolling, we conclude that the large single targets were dominated by large Chinook salmon — the preferred prey of resident killer whales.

Our study focused on the prey available to southern and northern resident killer whales during summer when peak numbers of Chinook salmon and southern resident killer whales traditionally return to the Salish Sea. Our finding that densities of Chinook were 4–6 times higher in southern resident habitat than in northern resident habitat is at odds with the few sightings of southern resident killer whales in the Salish Sea in 2018 and 2019. Our data suggest that their low frequency of summer occurrence was not due to an absence of prey in the Salish Sea. Southern resident populations have been returning later than normal to the coastal waters of British Columbia and Washington in recent years, and appear temporally and spatially mismatched with migrating Chinook salmon during summer. Whether this reflects a greater abundance of Chinook outside of our study sites is unknown.

Southern resident killer whales range from the coastal waters of central California to southern British Columbia (Ford 2006). As such, our study site occurs at the northern limit of their habitat which has traditionally been used most heavily during summer and fall (Hanson et al. 2010; Olson et al. 2018). Prey availability in other regions of their habitat remains unknown — as is knowledge about their winter and spring food sources. All of these considerations provide challenges to understanding and assessing prey availability for southern resident killer whales throughout the year.

In addition to abundance, energy content of Chinook varies among populations, and is an additional variable that affects the caloric demands of killer whales (Ford et al. 2010b; Hanson et al. 2010; Noren 2011; Williams et al. 2011). Mature Puget Sound Chinook salmon, for example, tend to be smaller and leaner than Fraser River and Columbia River Chinook salmon (O'Neill et al. 2014). Thus, the population-dependent energy content of Chinook salmon coupled with the timing of returning southern resident populations likely plays an important role in determining energy gain for this endangered species. While there are no acoustic data from the past to examine the temporal changes in prey availability, historical data suggest that Chinook salmon in the Pacific coast have become smaller and younger (Ohlberger et al. 2018). In the long term, declines in body size of Chinook salmon could reduce reproductive and survival rates of killer whales.

Our study addressed the abundance and distribution of prey available to resident killer whales, but did not address how accessible Chinook salmon are to them. The physical presence of vessels and the noise they create are two factors that could impede the ability of killer whales to successfully forage (Trites and Rosen 2018). Background noise levels increase with nearby vessel counts (Holt et al. 2009), and may mask communication between pod members and interfere with foraging and navigation (Veirs et al. 2016). Furthermore, physical presence of vessels reduces foraging effort of resident killer whales (Lusseau et al. 2009; Holt

et al. 2021). Such interference occurs more frequently in the southern than northern resident killer whale habitats, and could theoretically impact foraging abilities and survival rates.

Foraging behavior affects survival, growth, and reproduction — and is an important determinant of animal fitness (Pyke 1984). Top predators, such as marine mammals, require significant amounts of prey (Trites and Spitz 2018) and often migrate seasonally to follow their prey (Björge 2001). Understanding prey distributions is therefore essential for better understanding predator–prey interactions and ultimately how ecosystem functions. However, fine-scale variability in biological aggregations, combined with the strong swimming ability and migratory behavior of large prey make it challenging to assess prey distributions for top predators within pelagic ecosystems.

Our results show that fisheries acoustic techniques are an effective means to assess the distribution and abundance of prey available to resident killer whales in coastal waters. Using this technique, we tested the hypothesis that southern resident killer whales were more limited by prey abundance than northern resident killer whales during summer. Contrary to expectations, we found the density of potential prey available to southern resident killer whales was relatively high during summer in the coastal waters of British Columbia and Washington, where salmon restoration and enhancement management efforts including the commercial and recreational fishing regulations have been focused. This suggests that other factors such as spatial and temporal mismatches between killer whales and prey presence, shortages of prey outside of the Salish Sea, reduced energy content of individual Chinook salmon, and reduced prey accessibility due to vessel traffic may be more consequential to southern resident killer whales than previously considered.

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