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Harbour seals responded differently to pulses of out-migrating coho and Chinook smolts

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ABSTRACT: There is increasing evidence that predation by harbour seals on out-migrating salmon smolts may be responsible for the low return of adult coho and Chinook salmon in the Salish Sea. However, little attention has been given to understanding where and when this predation occurs and the extent to which it might be conducted by few or many seals in the population. We equipped 17 harbour seals with data loggers to track seal movements and used accelerometry to infer prey encounter events (PEEs) following the release of ~384 000 coho (May 4, 2015) and ~3 million Chinook (May 14, 2015) smolts into the Big Qualicum River. We found a small proportion (5.7%) of all PEEs occurred in the estuary where salmon smolts entered the ocean — and that only one-quarter of the seals actively fed there. PEE counts increased in the estuary after both species of smolts were released. However, the response of the seals was less synchronous and occurred over a greater range of depths following the release of the smaller-bodied and more abundant Chinook smolts. Harbour seals feeding in the estuary appeared to target coho smolts at the beginning of May but appeared to pursue predators of Chinook smolts in mid-May. PEE counts in the estuary increased as tide height rose and were higher at dusk and night — especially during full moonlight. Such fine-scale behavioural information about harbour seals in relation to pulses of out-migrating smolts can be used to design mitigation strategies to reduce predation pressure by seals on salmon populations.

KEY WORDS: *Phoca vitulina* · Pacific salmon smolts · Predator–prey interaction · Biologging · Accelerometry · Movement tracking

1. INTRODUCTION

Two culturally and economically valuable species of salmon — coho *Oncorhynchus kisutch* and Chinook *O. tshawytscha* — have declined to critically low numbers in the Salish Sea (i.e. Puget Sound, Strait of Juan de Fuca and Strait of Georgia; Nehlsen et al. 1991, Beamish et al. 2010, 2012). Different biotic and abiotic explanations have been proposed to explain their declines, such as overfishing (Rutter 1997), loss of vital habitat (Magnusson & Hilborn 2003), interspecific competition (Ruggerone & Nielsen 2004), changes in ocean conditions (Beamish et al. 1995) and changes in prey composition and availability (Ruzicka et al. 2011). However, none of these possible explanations are conclusively supported. Attempts to increase coho and Chinook by releasing large numbers of hatchery-raised fish and reducing commercial and recreational exploitation rates have been unsuccessful at restoring historic abundances. Both species of salmon have remained at low levels and continue to present significant economic and conservation challenges (Lindley et al. 2009).

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The recovery of harbour seals *Phoca vitulina* following intensive culling and hunting in British Columbia led to an exponential increase in harbour seal populations (Olesiuk 2010). This increase in harbour seal numbers — in addition to other environmental changes (e.g. surface temperature and wind strength) — correlates with the decline in numbers and poor marine survival rates of coho and Chinook salmon (Beamish et al. 1995, 2010, Olesiuk 2010) and led to speculation that predation by seals might be impeding recovery of these salmon species (Chasco et al. 2017, Thomas et al. 2017, Nelson et al. 2019b). Harbour seals consume both adult and juvenile salmon (smolts and subadults) but generally have not been thought to consume large amounts of them (but see Lance et al. 2012). While predation on returning adult salmon is generally low relative to numbers of returning fish, there is evidence that high mortality of coho and Chinook salmon is occurring in the early marine stage (i.e. smolt stage) as the fish move downstream and enter the ocean (Neville et al. 2015).

Harbour seals are the most abundant and the only year-round resident pinniped in the Strait of Georgia (Olesiuk 2010). They are generalist predators that feed on a variety of fish and cephalopod species but show preferences for Pacific herring *Clupea pallasii*, walleye pollock *Gadus chalcogrammus*, Pacific hake *Merluccius productus* and salmonid species (Tollit et al. 1997, Lance et al. 2012). Within seal populations, individuals exhibit distinguishable diet specialization associated with sex and size differences (Bjorkland et al. 2015, Schwarz et al. 2018). Harbour seals are also believed to vary their diet seasonally and annually according to locally abundant prey (Middlemas et al. 2006, Lance & Jeffries 2007, Luxa & Acevedo-Gutiérrez 2013).

In the Strait of Georgia, scats (faeces) of harbour seals contain the remains of many prey species — including juvenile coho, Chinook and sockeye (*O. nerka*) salmon during spring when smolts are outmigrating (Thomas et al. 2017). The seals appear to target these 3 species of salmon over the smaller-bodied juvenile chum *O. keta* and pink *O. gorbuscha* salmon (Thomas et al. 2017). Based on DNA metabarcoding and hard-part analyses of the seal scats, these 3 species of juvenile salmon seem to comprise relatively small percentages of the seal diet (~10.5% in the spring; Thomas et al. 2017). However, converting these percentages into numbers of individuals consumed suggests it may represent a significant source of mortality on salmon populations—particularly for coho and Chinook salmon that are of conservation concern (Irvine et al. 2009).

The majority of studies to date that have evaluated predation by seals on salmon smolts have focused on documenting what harbour seals eat and the potential impact this has on salmon populations (Lance et al. 2012, Howard et al. 2013, Thomas et al. 2017). Yet relatively little attention has been given to understanding where and when this predation occurs (but see Berejikian et al. 2016) and the extent to which it might be by a small or a large proportion of the harbour seal population. Documenting and assessing the temporal and spatial foraging behaviour of seals during the smolt migration is needed to fully understand predator–prey dynamics and guide the development of adequate conservation actions that may be necessary to enhance salmon numbers (Caro 2007).

The objectives of our study were to (1) track and document movements of harbour seals in the Strait of Georgia and (2) map their feeding distribution in space and time during the out-migration of coho and Chinook smolts. We predicted that harbour seals would concentrate their feeding efforts in the river mouth and estuary areas, where smolts occur in denser schools and are spatially constrained (thus, more vulnerable to predation), as opposed to open water areas (Yurk & Trites 2000). We therefore captured and equipped 20 harbour seals within 20 km of the Big Qualicum estuary (BQE) in the Strait of Georgia (British Columbia, Canada) with data loggers and tracked the seals during and after the release of thousands of coho and Chinook smolts from the Big Qualicum (BQ) hatchery. We were thereby able to map and analyze feeding intensity (particularly in the estuary area) relative to the releases of salmon smolts based on seal movements and prey encounter events (PEEs) identified from changes in body acceleration. Such information is needed to assess potential mitigation strategies designed to reduce predation pressure by harbour seals on the smolts of these salmon species of conservation concern.

2. MATERIALS AND METHODS

2.1. Study location

The study was conducted in the vicinity of the BQ River (49° 26′ 58″ N, 124° 31′ 43″ W) in the Strait of Georgia, British Columbia, Canada (Fig. 1). The BQ River is an important spawning river for Chinook *Oncorhynchus tshawytscha*, coho *O. kisutch*, pink *O. gorbuscha*, chum *O. keta* and steelhead *O. mykiss* salmon. In addition to wild Pacific salmon populations, the BQ hatchery artificially enhances the coho

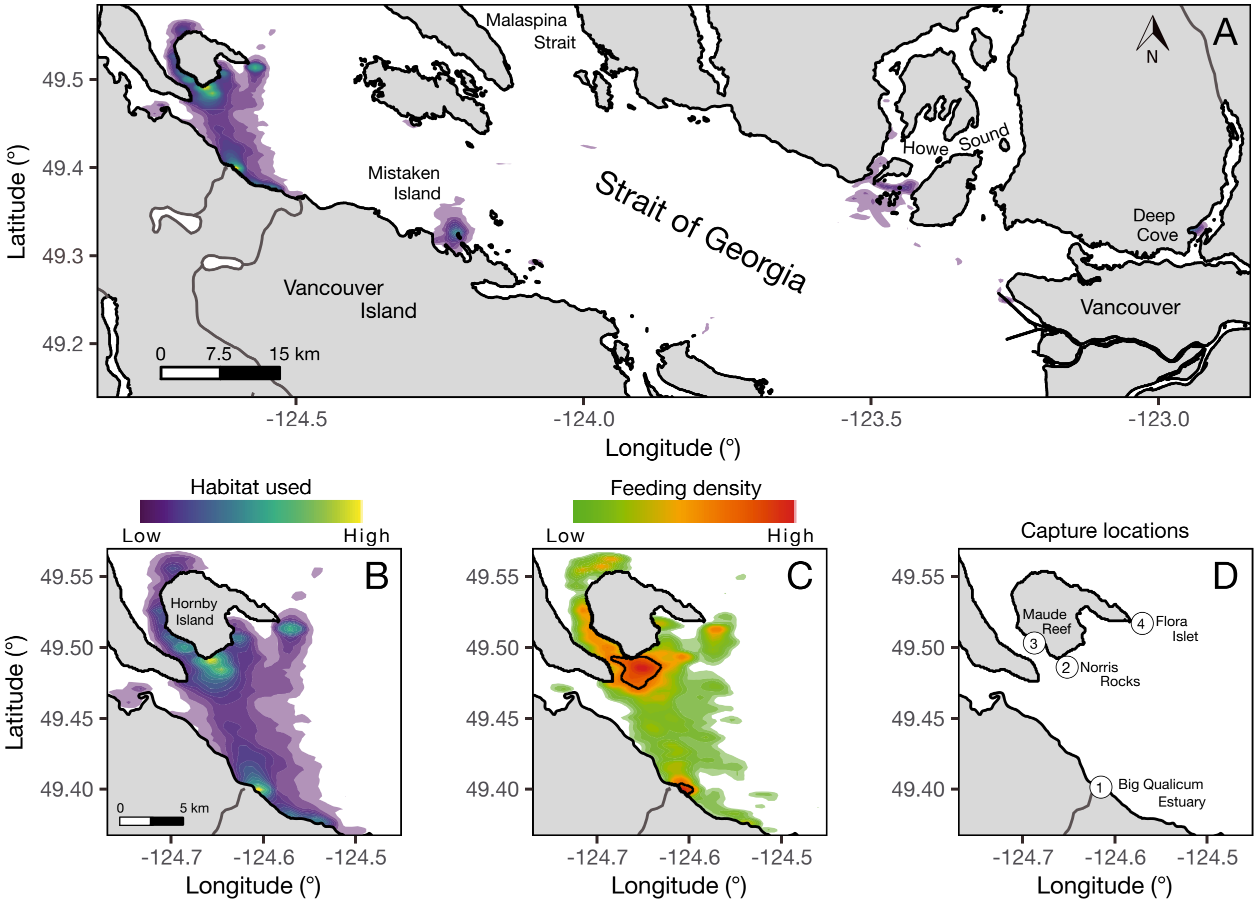

Fig. 1. (A,B) Habitat use and (C) feeding density maps of all 17 tracked harbour seals constructed from a kernel density analysis of seal locations every 15 min (A,B) and prey encounter event (PEE) locations (C) from May 2 to June 2, 2015. (A–C) Colour scale ranges from low density (95% kernel density contour) to high density (5% kernel density contour). (C) Feeding hotspot polygons (i.e. 30% kernel density contour) are delimited by black contours. (D) Locations where seals were captured: (1) Big Qualicum estuary (49.399°, –124.608°; n = 9), (2) Norris Rocks (49.484°, –124.648°; n = 9), (3) Maude Reef (49.499°, –124.684°; n = 1)

and Chinook salmon stocks in the river to increase recreational and commercial fishing opportunities (Cross et al. 1991). In the spring of 2015, when we conducted our study, the BQ hatchery passively released approximately 384 000 coho smolts on May 4 and ~3 million Chinook smolts on May 14. From all released coho smolts, the BQ hatchery tagged 37 000 individuals (i.e. 9.6%) with passive integrated transponders (PIT tags) and recorded when they left the hatchery using RFID reader antennas. Chinook smolts were not PIT-tagged due to their small body size. Several harbour seal *Phoca vitulina* haul-out sites surround the BQ area and are less than 30 km from where smolts leave the BQ River and enter the estuary (49° 23′ 55.7″ N, 124° 36′ 33.1″ W). All these haul-out sites are within foraging distance of the river mouth (Peterson et al. 2012) and are estimated to be used by over 1000 harbour seals (Olesiuk 2010).

2.2. Device deployment and data collection

We captured 20 harbour seals in the BQ area from April 21 to May 1, 2015, using either a specialized beach seine (Jeffries et al. 1993) or a low-tech boat rush method at 4 locations (Fig. 1D): BQE (n = 9), Norris Rocks (n = 9), Maude Reef (n = 1) and Flora Islet (n = 1). All seals were individually transported in hoop nets and carried to a restraining board where they were sedated with an intramuscular injection of 0.1 to 0.2 mg kg^{-1} of butorphanol. The weight (±0.2 kg) and the total length (i.e. snout to end of tail) to the nearest 0.5 cm were measured. Seals that weighed >60 kg were equipped with a floating logger package to their dorsal midline between the shoulders using a quick-drying epoxy (Devcon). The logger packages (340 g and 168.4 × 111.8 × 36.2 mm) included a GPS satellite tag (Splash 10-F; Wildlife Computers), a Daily

Diary tag (Wildlife Computers), a very high frequency (VHF) transmitter (MM190B; Advanced Telemetry Systems) and a flotation device (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m647p211_supp.pdf).

The Daily Diary tags were set to sample and archive depth at 1 Hz, earth's magnetic field at 8 Hz and acceleration at 16 Hz. The GPS satellite tags were set to sample and archive Fastloc GPS snapshots every 20 min in May and June 2015. In July and August 2015, loggers were set to transmit previously recorded GPS locations through a satellite (Argos) as a backup if they were not physically recovered. To synchronize all the data, every device was set to UTC. We located and recovered the logger packages using the VHF radio signal after they had detached and the seals were moulting (i.e. from August to October 2015). All data processing and analysis, unless mentioned, were conducted in R v.3.6.3 (R Core Team 2020).

2.3. Track reconstruction

We divided each seal's time series into either haul-out (i.e. resting on land) or at-sea state using the wet–dry sensor on the Daily Diary tag. The haul-out state started when the tag was dry for at least 10 min and ended when the tag was wet for more than 40 s (Russell et al. 2015). The seals were considered in the at-sea state the remainder of the time. Data loggers can experience memory errors during which no data are recorded. Ten of the Daily Diary tags failed to record data during <1% of the study period (except seal no. 1), which we assumed did not significantly affect the outcome of our results. Although the Daily Diary tag of seal no. 1 failed for ~2% of the study period, we also assumed it did not affect our results because this individual spent all of its time in Howe Sound outside our main study area (i.e. BQ area).

The seals were equipped with a Fastloc GPS which provided high-resolution locations even during short surface intervals (Costa et al. 2012). We applied the method outlined in Austin et al. (2003) to filter GPS locations. We used a traveling speed threshold of 2.78 m s^{-1} — the maximum swimming speed recorded by Lesage et al. (1999) in free-living harbour seals. We also conducted a final visual inspection and removed all GPS locations on land. Overall, less than 0.5% of locations were removed.

We used the dead reckoning method to reconstruct the seal pseudo-tracks between every 2 consecutive GPS locations (Wilson et al. 2007). We ran the dead reckoning pseudo-tracks using the function DeadReckoning from the R package TrackReconstruction and extracted the inclination and declination of the earth's magnetic field for May 15, 2015, and the latitude and longitude of approximately the center of the Strait of Georgia (49° 24′ 00.0″ N, 124° 06′ 00.0″ W) using the World Magnetic Model 2010 calculator from the British Geological Survey (www.geomag.bgs.ac.uk/data_service/models_compass/wmm_calc.html). We also used a 3 s running mean window to estimate the dynamic acceleration due to animal movement (Shepard et al. 2008) and 2.78 m s^{-1} for the maximum speed threshold (Lesage et al. 1999).

The raw dead reckoning tracks were generated at the magnetometer resolution of 8 Hz and then rescaled to each minute to maximize computational speed. We georeferenced the raw dead reckoning tracks by forcing them through GPS locations using the function GeoRef (from the R package TrackReconstruction), which uses the conventional bias correction equation from Wilson et al. (2007):

$$\hat{\eta}_t = x_t + \frac{y_T - x_T}{T - 1}(t - 1) \quad (1)$$

where $\hat{\eta}_t$ is the corrected path in 1 dimension (i.e. easting or northing) at time $t = 1,2,\ldots,T$ between 2 GPS locations, x_t is the dead reckoning coordinate at time $t = 1,2,\ldots,T$ and y_T is the GPS location at time T. In this equation, we assumed that $x_1 = y_1 = 0$. When georeferencing the dead reckoning tracks, we converted GPS locations from longitude and latitude to easting and northing in kilometers. While the seals were hauled out (i.e. on land), we forced their position to the GPS location recorded during that haul-out time interval. Georeferencing allows corrections for error in the dead reckoning tracks, which grows over time because each dead reckoning location depends on the previous one (Bidder et al. 2012). Although GPS tags were set to record a location every 20 min, the GPS sampling rate was on average 1 location every 65 ± 61 min (mean ± SD). We suspect that the GPS sampling rate was lower than expected because data logger packages were glued to the backs of the seals, which might not be above the water at every surface bout and therefore could increase the failure rate of GPS transmissions.

Based on visual examination of the reconstructed pseudo-tracks, we surmised that there were insufficient GPS locations to effectively correct for the error induced by the dead reckoning, especially for pseudo-tracks that lasted for more than an hour. We observed multiple pseudo-tracks crossing land. Therefore, we applied an additional custom correction algorithm to the georeferenced tracks based on geographical features constraining seal movement (i.e. land and bathymetry). This correction algorithm was run in 2 steps. First, multiple pseudo-tracks were generated between each pair of GPS locations based on the original shape of the georeferenced pseudo-track in Eq. (1). To do so, we added an extra parameter, α , into Eq. (1):

$$\hat{\eta}'_t = \alpha x_t + \frac{y_T - \alpha x_T}{T-1}(t-1) \tag{2}$$

where the parameter α proportionally modifies the original georeferenced track between 2 GPS locations while preserving its global movement shape. When $\alpha = 1$, $\hat{\eta}'_t = \hat{\eta}_t$, and the new pseudo-track is the same as the original georeferenced pseudo-track. When $\alpha = 0$, $\hat{\eta}'_t$ is a straight line between the 2 GPS locations (i.e. y_1 and y_T). We generated 21 pseudo-tracks for each interval between 2 GPS locations with an α that ranged from -1 to 1 with a step of 0.1.

The second part of our correction algorithm relied on selecting the most likely pseudo-track between 2 GPS locations. To do so, we conducted a stepwise filtering process. First, we removed all pseudo-tracks where the seals exceeded the speed threshold of 2.78 m s^{-1} (Lesage et al. 1999). Second, we selected tracks that minimized the error due to the pseudo-track passage on land while the seals were diving.

To quantify the pseudo-track error on land, we used the root mean squared error (RMSE):

$$\mathrm{RMSE}_{\mathrm{Land}} = \sqrt{\frac{\sum_{t=1}^{T} {\varepsilon_t}^2}{T}} \quad \varepsilon_t = \begin{cases} \textit{at sea}\ ,\ 0 \\ \textit{on land}\ ,\ d_t \end{cases} \tag{3}$$

where ε_t is the error difference at time t between the seal diving depth and the surface (i.e. at 0 depth) when the estimated seal location is on land, d_t is the seal diving depth at time t and T is the number of time steps between the 2 GPS locations. Finally, we selected the pseudo-tracks that minimized the error due to the seal diving below the bathymetry depth:

$$\mathrm{RMSE}_{\text{at sea}} = \sqrt{\frac{\sum_{t=1}^{T} {\delta_t}^2}{T}} \quad \delta_t = \begin{cases} b_t - d_t \geq 0\ ,\ 0 \\ \textit{else}\ ,\ d_t - b_t \end{cases} \tag{4}$$

where δ_t is the error difference at time t between the seal diving depth and the bathymetry depth, d_t is the seal diving depth at time t, b_t is the bathymetry value at time t and T is the number of time steps between the 2 GPS locations. If at this stage more than 1 pseudo-track remained, the pseudo-track with the closest α parameter to 1 (i.e. to the original georeferenced pseudo-track) was selected. We used a leave-one-out cross-validation method to estimate the accuracy of our track correction algorithm. To do so, we sequentially removed each GPS location (except the first and the last ones) for each seal and calculated the error as the distance between the estimated location and the GPS location which we considered the true value. The bathymetry data of the Strait of Georgia had a resolution of 3 arcseconds and was obtained from NOAA (https://data.noaa.gov/dataset/british-columbia-3-arc-second-bathymetric-digital-elevation-model).

2.4. PEEs

The acceleration-based method developed by Viviant et al. (2010) uses high head or jaw acceleration data to identify possible PEEs (Iwata et al. 2012, Volpov et al. 2015). In seals, this method was shown to provide similar PEE detections with head- and back-mounted accelerometers (correlation coefficient = 93%; Le Bras et al. 2016). Hence, we used the same method of PEEs from back-mounted accelerometers as a proxy to quantify feeding intensity.

First, we extracted the 3 axes (i.e. heave, surge and sway) of the dynamic acceleration (i.e. animal movement) by subtracting the static acceleration (i.e. gravity) from the total acceleration (m s^{-2}, at 16 Hz). The static acceleration was calculated from a 2 s running mean window on total acceleration. Second, we calculated the variance of the 3 dynamic accelerations over a 2 s moving window to identify high levels of acceleration variance. The 3 variance axes were combined into 1 dimension from the vector norm. Finally, we performed a k-mean clustering with 2 means on the variance data to separate it into low and high acceleration variance. We considered occurrence of a PEE when a sequence of samples, separated by <1 s, was classified into the high-variance cluster, reflecting a bout of higher body acceleration (Fig. S2). To minimize PEE false positive detections due to high body accelerations that were not related to foraging behaviour (e.g. interacting with a conspecific at the surface or mounting a rocky site to haul out), we excluded all PEEs when the wet–dry sensor was at dry and 10 min before and after the seals were hauled out.

Depth sensors commonly drift over time (Spence-Bailey et al. 2007). We applied a zero-offset correction over an hour window and with 0.5 m surface error using the software provided by the manufacturer (Wildlife Computers). We also observed quick spikes in the Daily Diary depth data caused by the Argos transmissions from the Splash tags (Wildlife Computers pers. comm.). We applied a 5 s rolling median on the depth data to remove these spikes as recommended by the manufacturer.

2.5. Feeding intensity

We considered the number of PEEs as a proxy for feeding intensity. It is important to keep in mind that PEEs were not validated in the wild. PEEs are therefore not necessarily successful feeding events but should be considered as relative proxies for prey encounters. We conducted a kernel density analysis of the locations of the PEEs to highlight geographical regions of increasing feeding intensity. We also applied the kernel density analysis to all seal locations (1 location every 10 min for each seal) to visualize the overall space used by all tagged seals. We used the R package ks to estimate the kernel density distributions for which we used an unconstrained bandwidth matrix and a smoothed cross-validation bandwidth selector as recommended by Duong (2007). We highlighted high feeding density areas (i.e. feeding hotspots) as areas encompassing the top 30% of the kernel density distribution (e.g. Kitchen et al. 2000).

As we were interested in the harbour seal response to the smolt release in the BQ River, we focused on analyzing the variability of PEEs in the BQE hotspot and its vicinity (see Section 3). Out-migrating salmon smolts more likely swim close to the surface (<50 m) as they reach estuaries, with the highest density at the top ~5 m from the surface (Beamish et al. 2000, Emmett et al. 2004). Our data showed that most of the PEE detections in the BQE area occurred within the first 5 m depth (Fig. S3). Thus, we assumed that feeding on smolts was more likely to happen in that depth range. We separated the data within the BQE hotspot into 3 depth categories (0–5, 5–80 and >80 m). Depth thresholds were extracted visually from the figure of the distribution of PEE counts over depth by separating depth ranges of high PEE density (i.e. local peaks; Fig. S3).

Using generalized linear mixed-effects models, we modeled the seal feeding intensity (counts of PEEs) in the BQE hotspot after the coho and Chinook smolts were released. First, we fitted the count of PEEs per day as a function of the post-smolt release periods to compare feeding intensity between both release periods. Second, we fitted the count of PEEs per hour as a function of the time of day, tide height and post-smolt release period. And third, we fitted the count of PEEs per hour that occurred at night as a function of tide height and fraction of moon illumination. We used a subset of the data from the day following the release of the coho smolts (May 5) to May 24 to standardize the number of days (10 d) after each smolt release period. Time periods when seals were outside the BQE hotspot were not included in the model.

As the distribution of the count of PEEs per hour is highly zero inflated, we applied a hurdle model that combines 2 distinct models. The first model fits the probability of detecting at least 1 PEE per hour (presence–absence of PEEs) following a binomial distribution with a logit link — while the second model fits the count of PEEs per hour (PEE intensity) when at least 1 PEE was detected. These counts of PEEs per hour follow a zero-truncated negative binomial distribution with a log link and a quadratic parameterization. We used a negative binomial distribution with a log link and a quadratic parameterization for the model that fits the counts of PEEs per day.

Time of day was separated into 4 periods: day, dusk, night and dawn. The daily time limits of each period were obtained from the R package maptools where twilight phases were set according to the nautical twilight (i.e. the angle of the geometric center of the sun is between 0 and 12° below the horizon). Mean hourly tide height estimates were downloaded from the Fisheries and Oceans Canada website (https://tides.gc.ca) at the Point Atkinson station. As the range of the tide height is not the same between time periods (see Fig. 5), we normalized it (i.e. rescaled to a mean of 0 and a variance of 1) within each period for a better comparison. The moon-illuminated fraction (i.e. from 0 for new moon to 1 for full moon) was downloaded from the R package oce and then normalized. We also included the seal identity as a random effect to control for repeated measurements and date and time (rounded per hour or per day) to control for temporal autocorrelation. All model analyses were fit with the R package glmmTMB (Brooks et al. 2017), and we used the Akaike's information criterion corrected for small sample sizes to select the fixed-effect combination.

3. RESULTS

3.1. Telemetry performance and general spatial distribution

Of the 20 harbour seals captured in the BQ area from April 21 to May 1, 2015, 15 were males and 5 were females. The seals weighed on average 91.7 ± 13.9 kg and were 155.3 ± 9.5 cm long (Table S1 in the Supplement). Although we were able to recover GPS locations for all 20 equipped seals either from satellite transmission (Argos; n = 1) or from the device itself (n = 19), we recovered full data for only 17 of the 20 seals. Missing data for the remaining 3 seals were due to equipment failure (n = 2) and tag loss (n = 1). Recording periods (48.2 ± 2.8 d) varied between seals due to variation in capture dates and battery life of the devices (Table S1). To keep all seal data consistent over time, we limited all our analyses from May 2 to June 2 (i.e. 32 d) during which we had complete data for 17 seals. The data from the 3 other seals were excluded from our analysis.

During the study period, we collected an average of 231 ± 14 GPS locations per day and per seal. The accuracy of the estimated locations from track reconstruction between GPS locations averaged 0.4 ± 0.57 km (median 0.26 km). Most of the seals we tracked (n = 16 of 20) limited their movements within the capture area in the BQ area (<70 km) where they generally used a primary haul-out site (e.g. Norris Rocks and Flora Islet) but also occasionally other secondary haul-out sites (e.g. Seal Bay and Mud Bay). The rest of the seals (n = 4) used the BQ area but also travelled long distances (>100 km) and used other distant areas such as the Malaspina Strait (seal no. 5), Mistaken Island (seal no. 13), Howe Sound (seal no. 1) and Deep Cove (seal no. 20; Fig. 1A).

3.2. Total feeding intensity

Based on body accelerations, harbour seals made an average of 222 ± 160 PEEs per day (Table S1) during the study period (from May 2 to June 2). The kernel density analysis of the PEE locations revealed discrete patches of increasing feeding density within the Strait of Georgia that matched with the general space use distribution (Fig. 1). Most of the detected PEEs were in the BQ area mainly around Hornby Island but also occurred in the open water up to BQE (Fig. 1C). Additional feeding patches of isolated individual seals also occurred in other areas such as Mistaken Island, Howe Sound and Deep Cove (Fig. 1).

Feeding hotspots (i.e. areas encompassing the top 30% of the kernel density distribution) occurred in 3 distinct patches. The first and largest feeding hotspot represented an area of 84.5% (5.61 km^2) of total hotspot sizes and was located around Norris Rocks where there were 20440 (24%) PEEs by 13 (76%) individual harbour seals (Table 1). These PEEs occurred throughout the water column (0–242 m) but were mainly between ~0–30 and ~120–170 m (Fig. S4). The second feeding hotspot (1.02 km^2; 15%) was in the BQE (Fig. 1C) and included 4798 (5.7%) PEEs by 8 (47%) harbour seals (Table 1). These PEEs ranged from the surface to 236 m depth but occurred primarily within the first 5 m depth (Fig. S4). Finally, the last feeding hotspot (0.01 km^2; 0.15%) was in the Deep Cove area and included 92 (0.1%) PEEs from 1 individual (Table 1). PEEs in the Deep Cove hotspot ranged from close to the surface to 52 m depth and were denser between ~20 and ~40 m (Fig. S4).

3.3. Spatiotemporal variation in feeding intensity in the BQ area

A kernel density analysis of PEE locations over time revealed temporal and spatial synchrony between the feeding intensity of the seals and the release of ~384000 coho (on May 4) and ~3 million Chinook (on May 14) smolts from the BQ hatchery (Fig. 2, Fig. S5). Overall, the area around the Norris Rocks haul-out site experienced high PEE density during the whole study period. High PEE density was also observed in the BQE area particularly following the release of the coho and Chinook smolts (Figs. 2 & 3A). Intermediate PEE patches next to the BQE in coastal and open water habitats occurred after the Chinook smolts were released and seemed to move gradually towards Norris Rocks. Two new high PEE spots appeared at the end of the study on the northern side of Hornby Island (from May 25 to June 2) and at Flora Islet (from May 30 to June 2; Fig. 2).

Table 1. Summary information on feeding hotspots accounting for the top 30% of the kernel density distribution of prey encounter events (PEEs) of 17 seals from May 2 to June 2, 2015. The number of seals (and percentage over the total number of seals) that used the hotspot, number of PEEs (and percentage over the total number of PEEs) detected inside the hotspot, area size and latitude and longitude of the polygon centroid are presented

Hotspot	No. of seals (%)	No. of PEEs (%)	Area (km^2)	Latitude (°)	Longitude (°)
Norris Rocks	13 (76)	20440 (24.2)	5.61	49.484	–124.655
Big Qualicum Estuary	8 (47)	4798 (5.7)	1.02	49.399	–124.607
Deep Cove	1 (6)	92 (0.1)	0.01	49.332	–122.936

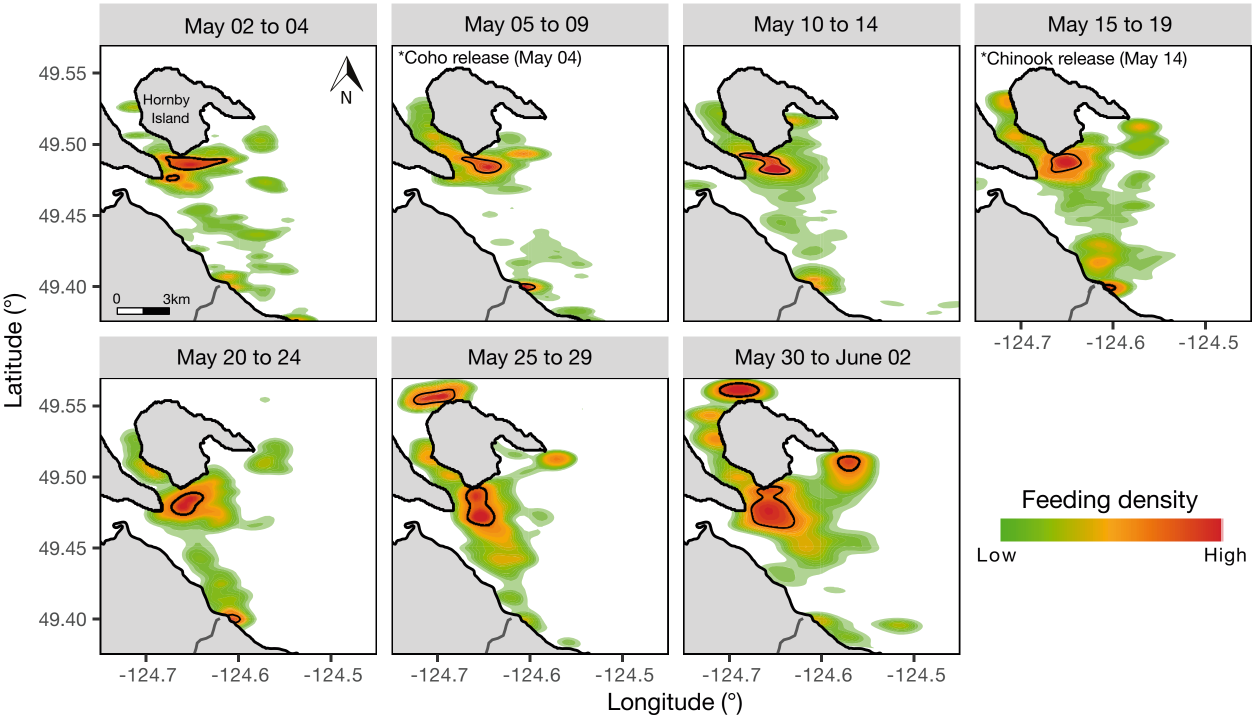

Fig. 2. Feeding density maps of harbour seals in the Big Qualicum area in 2 to 4 d intervals from May 2 to June 2. Coho (~384 000 smolts) were released on May 4 and Chinook (~3 million smolts) were released on May 14 from the Big Qualicum hatchery. Feeding densities were constructed from a kernel density analysis on all prey encounter event locations over the study period. Colour scale ranges from low density (95% kernel density contour) to high density (5% kernel density contour). Feeding hotspot polygons (i.e. 30% kernel density contour) are delimited by black contours

The BQE hotspot included 5.7% of all PEEs, of which 86% occurred <5 m from the surface. Eight (47.0%) of the 17 seals had PEEs in the BQE area, but only 4 accounted for >90% of all PEEs in that area (seal nos. 2, 11, 12 and 17; Fig. 4). The daily count of PEEs in the BQE hotspot peaked 4 d after the coho smolts were released (Fig. 3A) and can be mostly attributed to 3 seals (seal nos. 2, 11 and 17; Fig. 4) who fed within the upper 5 m of the water column. The peak in PEE counts after the release of coho smolts overlapped with the number of passive integrated transponder-tagged coho smolts that were scanned leaving the BQ hatchery. On May 14, the day of the Chinook smolt release, PEE counts increased again but were highly variable on subsequent days, with daily PEE peaks on May 16, 21 and 23 (Fig. 3A). After May 24, PEE counts remained low until the end of the study. Although most detected PEEs in the BQE area occurred within the first 5 m depth, deeper PEEs also occurred and were conducted primarily by seal no. 12 on the 4 consecutive days that followed the release of Chinook smolts (Fig. 4). Additional sporadic deeper daily PEEs were also detected by other seals, e.g. seal no. 11 on May 31 and seal no. 17 on May 23. The mean daily counts of PEEs during the post-Chinook release period (10 d) did not differ from the post-coho release period ($z = -0.9$, $p = 0.4$, Bayes factor = 1; Tables S2 & S3, Fig. S6).

The probability of detecting PEEs per hour depended on the 3-way interaction between tide height, time of day and post-smolt release period (Table 2, Table S4). After the release of coho smolts, the probability of PEEs per hour increased with the tide height at dusk and night (Figs. S7 & S8) where the highest probability occurred at high tide and at dusk (Fig. S9). After the release of Chinook smolts, tide height did not affect the probability of PEEs per hour. Compared to the post-coho release period, the post-Chinook probability of PEEs per hour was higher during the day at low and average tide and was lower at night and high tide (Fig. S9). The count of PEEs per hour increased with tide height and was higher at night and dusk during the post-coho release period but did not differ between time periods during the post-Chinook release period (Table 2, Table S5, Fig. S10). When considering PEEs only at night, the probability of PEEs per hour increased with tide height and moon illumination (Table S7, Fig. S11). The count of PEEs per hour at night did

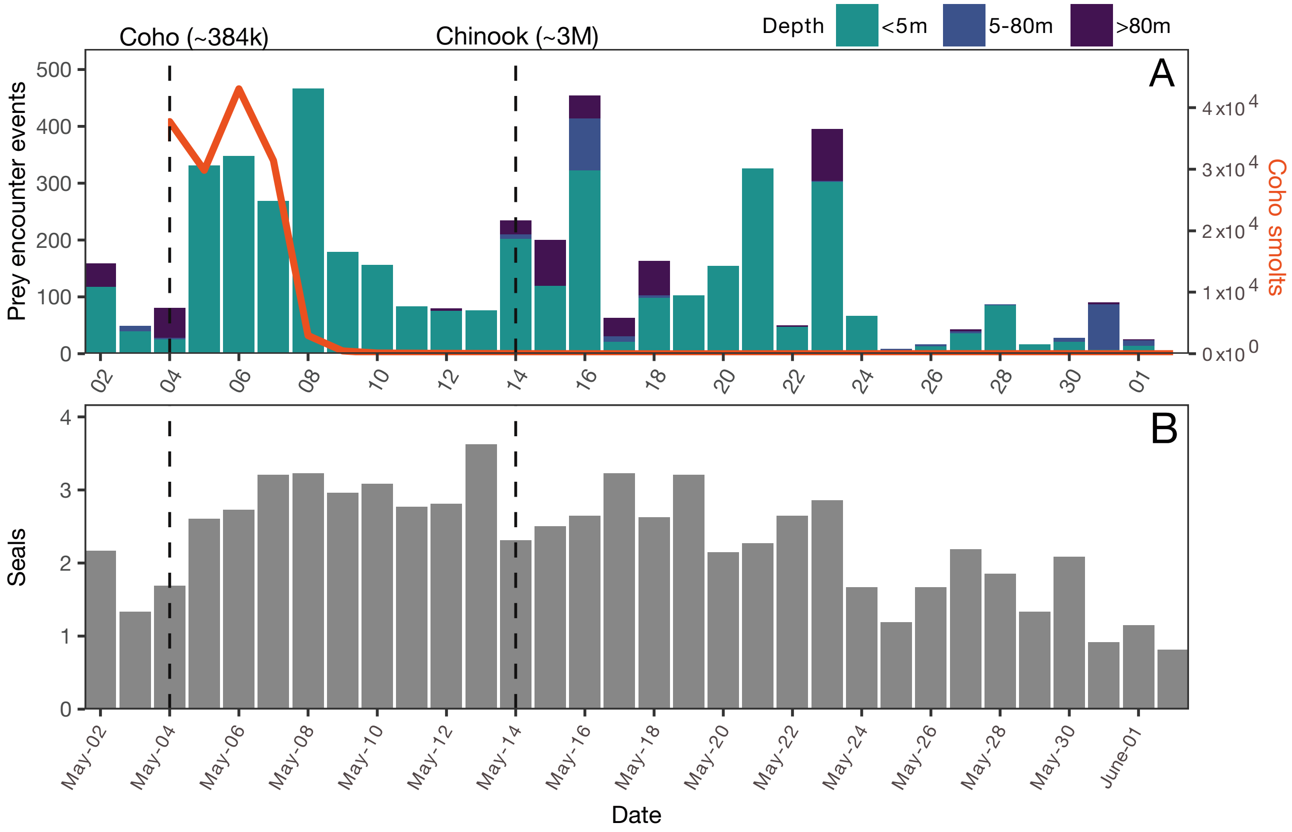

Fig. 3. (A) Daily counts of prey encounter events (PEEs; left *y*-axis) and (B) number of tagged seals inside the Big Qualicum estuary (BQE) hotspot from May 2 to June 2. (A) Daily PEE counts were tallied within 3 depth ranges: <5 m of the surface, between 5 and 80 m and >80 m. Dashed vertical lines show when ~384 000 coho smolts (on May 4) and ~3 million Chinook smolts (on May 14) were released from the Big Qualicum hatchery, while the orange line shows the numbers of passive integrated transponder (PIT)-tagged coho smolts (right *y*-axis) that left the Big Qualicum hatchery each day. Approximately 37 000 coho smolts were PIT tagged prior to release (i.e. 9.6% of all released coho smolts). (B) The number of seals in the BQE hotspot was corrected by the proportion of time seals spent each day inside that area

not change with tide height and fraction of moon illumination (Table S6).

4. DISCUSSION

We collected data from 17 harbour seals and used track reconstructions paired with body acceleration to identify areas of high feeding intensities during the out-migration of hatchery-reared coho and Chinook salmon smolts from the BQ River in the Strait of Georgia. We found high feeding patches within the BQ area but less feeding than expected within the estuary area (on average 5.7%) where smolts first enter the ocean. A second unexpected finding was that feeding intensity of harbour seals did not increase significantly in the estuary in response to the 8-fold greater numbers of Chinook released compared to coho smolts released (i.e. 3 million Chinook smolts vs. 384 000 coho smolts; Fig. 3A). These findings raise questions about factors influencing seal foraging and the relative profitability of alternative salmonid prey species.

4.1. Feeding in the BQ area

Contrary to our expectations, only a small fraction (5.7%) of all the feeding activity of all seals tracked occurred in the BQE. Approximately half of the seals (n = 8) that stayed within the BQ area conducted at least 1 PEE in the estuary. Nevertheless, the maximum number of tagged seals that used the river mouth per day was 3.6 of the 17 seals (Fig. 3B). These results suggest that out-migrating smolts entering the BQE were not a major resource pulse for the overall local harbour seal population but may have been an important source of nutrition for a small portion of the seals (<20% of the 17 tagged seals).

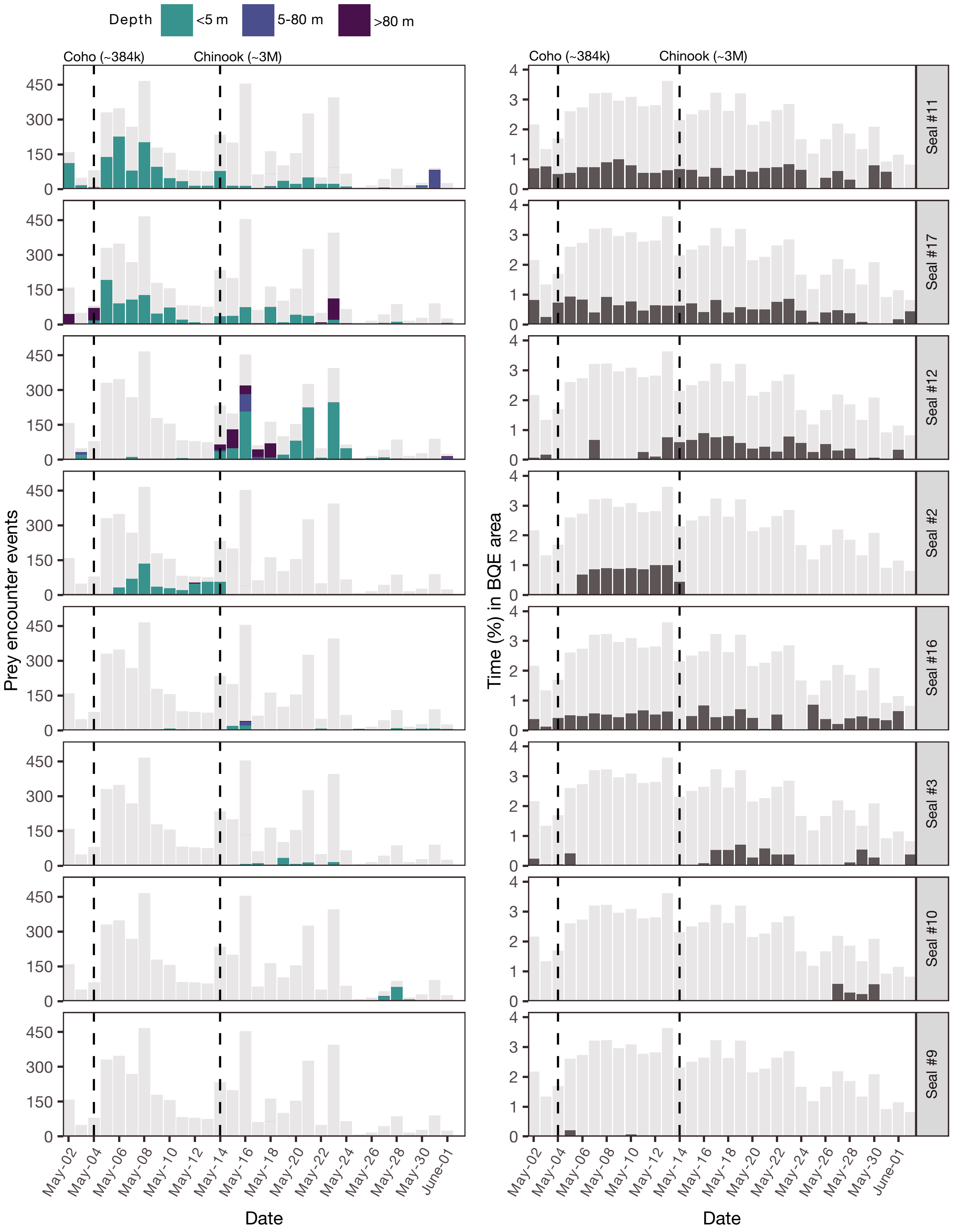

Fig. 4. Daily counts of prey encounter events (PEEs) (left panel) and proportion of time each individual seal spent inside the Big Qualicum estuary (BQE) hotspot (right panel) from May 2 to June 2, 2015. Daily PEE counts are separated into 3 depth ranges: <5 m depth, between 5 and 80 m depth and >80 m depth. Light grey bars in the background show the cumulative data for all seals. Dashed vertical lines indicate when ~384 000 coho smolts (May 4) and ~3 million Chinook smolts (May 14) were released into the river from the Big Qualicum hatchery

Table 2. Model predictors to estimate (A) the presence–absence of prey encounter events (PEEs) per hour (when at least 1 PEE is detected) in the Big Qualicum estuary hotspot. A binomial distribution with a logit link was used for model (A), and a negative binomial distribution with a log link and a quadratic parameterization was used for model (B). Only parameter estimates of the best model from Akaike's information criterion corrected for small sample sizes comparison (see Supplement at www.int-res.com/articles/suppl/m647p211_supp.pdf) are presented at the link scale. The parameters include mean tide height per hour (normalized within time periods), time periods (day, night, dawn and dusk) and post-smolt release period (post-coho from May 5 to 14 and post-Chinook from May 15 to 24). Seal identity (n = 7) and date and time (rounded per hour) were added as random effects to control for repeated measurements and temporal autocorrelation, respectively. CI: [25–95%]; BF: Bayes factor upper bound calculated as in Benjamin & Berger annexed to Wasserstein & Lazar (2016). Blank cells: parameter not selected according to the AICc model comparisons. **Bold**: significance ($p < 0.05$)

Predictor	(A) Probability of PEEs h^{-1}						(B) Count of PEEs h^{-1}					
	Log odd ratio	SE	CI	Z-score	p	BF	Log incidence rate ratio	SE	CI	Z-score	p	BF
Intercept	−1.2	0.2	[−1.6, −0.7]	−5.2	**<0.01**	1.2×10^5	1.2	0.3	[0.7, 1.8]	4.3	**<0.01**	1.7×10^3
Tide	−0.1	0.2	[−0.4, 0.2]	−0.7	0.47	1	0.2	0.1	[0.1, 0.3]	2.9	**<0.01**	17.1
Night	0.7	0.2	[0.3, 1.2]	3.0	**<0.01**	22.8	0.9	0.2	[0.5, 1.2]	4.2	**<0.01**	1.5×10^3
Dawn	−1.1	0.4	[−1.9, −0.3]	−2.6	**<0.01**	8.3	0.3	0.4	[−0.5, 1.1]	0.7	0.5	1.1
Dusk	4.5	1.4	[1.7, 7.2]	3.2	**<0.01**	39.8	1.9	0.3	[1.4, 2.4]	7.1	**<0.01**	9.7×10^9
Post-Chinook	0.9	0.2	[0.4, 1.3]	3.7	**<0.01**	1.9×10^2	0.0	0.2	[−0.4, 0.5]	0.2	0.8	2.3
Tide:Night	0.9	0.3	[0.4, 1.5]	3.6	**<0.01**	1.6×10^2						
Tide:Dawn	0.6	0.5	[−0.4, 1.5]	1.2	0.23	1.1						
Tide:Dusk	2.1	0.9	[0.2, 3.9]	2.2	**0.03**	3.5						
Tide:Post-Chinook	0.1	0.2	[−0.4, 0.5]	0.2	0.81	2.1						
Night:Post-Chinook	−1.8	0.4	[−2.5, −1.0]	−4.6	**<0.01**	5.7×10^3	−0.2	0.3	[−0.8, 0.5]	−0.5	0.6	1.3
Dawn:Post-Chinook	−0.7	0.7	[−2.2, 0.7]	−1.0	0.32	1	0.3	0.6	[−1.0, 1.5]	0.5	0.6	1.3
Dusk:Post-Chinook	−4.0	1.5	[−6.9, −1.1]	−2.7	**<0.01**	10.1	−1.4	0.5	[−2.4, −0.5]	−3.1	**<0.01**	28.6
Tide:Night:Post-Chinook	−1.1	0.4	[−1.8, −0.3]	−2.8	**<0.01**	14.8						
Tide:Dawn:Post-Chinook	−0.1	0.7	[−1.5, 1.3]	−0.2	0.86	2.9						
Tide:Dusk:Post-Chinook	−2.2	1.1	[−4.3, −0.1]	−2.0	**0.04**	2.7						

The BQE is a relatively small estuary in the Strait of Georgia compared to others such as the Fraser River estuary, the Cowichan estuary, the Puntledge River estuary or the Campbell River estuary. Thus, our results should be carefully interpreted given that seal behavioural responses may vary in larger estuaries characterized with different types of habitats. For instance, larger estuaries have longer smolt residency times compared with small ones — and are important areas for salmon growth (McCabe et al. 1986, Bottom et al. 2005). These differences in smolt time residency and body growth rates in estuaries may impact the foraging behaviour of seals.

Optimal foraging theory suggests that a predator should maximize its long-term energy gain by balancing the energy provided by the prey energy and by temporal and cognitive constraints associated with feeding on certain prey (Stephens & Krebs 1986). In our case, the seals feeding on smolts in small estuaries and rivers similar to the BQ would have had very low temporal and energy constraints associated with foraging in the confines of a shallow narrow river mouth. The seals would have avoided all energy expenditure associated with diving and time spent searching for prey, which is highly significant when foraging in the open water (Ramasco et al. 2015). In rivers, harbour seals can hold their position in the water and intercept out-migrating smolts in high numbers with minimal movements and hence minimum energy expenditure (Yurk & Trites 2000). However, feeding on smolts in rivers and estuaries may present some constraints in terms of foraging efficiency. For instance, the BQ is a relatively small estuary which may limit the number of seals feeding at one time on out-migrating smolts and consequently increase intra-specific competition. Other smolt predators such as birds (Wood 1987) are also abundant in the BQE and may increase inter-specific competition.

Although salmon smolts migrate in high numbers and densities, their energy density (~5.04 kJ g^{-1} for coho and ~3.98 kJ g^{-1} for Chinook; Roby et al. 2003) is lower than other important prey in the Strait of Georgia such as Pacific herring (~5.9 kJ g^{-1}; Anthony et al. 2000). However, energy densities of smolts are higher than those of other seal prey species such as walleye pollock (~3.5 kJ g^{-1}; Anthony et al. 2000). As a consequence of the small size and intermediate energy density of the salmon smolts relative to other prey, the seals would need to consume a large number of individuals (~100 smolts d^{-1}) to meet their daily energy requirements (Howard 2009).

In addition to feeding efficiently in the river mouth, the seals using these areas presumably need some cognitive capability to predict the migration timings if they are to take full advantage of the smolt pulses (Bell 1990, Willson & Womble 2006). How seals predict the timing of these pulses and how they assess uncertainty have presumable consequences on their foraging success and efficiency (Dall & Johnstone 2002) considering that the peak of the smolt pulses in small estuaries like the BQ may have a short time window of only a few days or weeks. Predators may use environmental (Real 1992) and social (Danchin et al. 2004) cues and information to optimize their foraging decisions, such as relying on water temperature and lunar cycles to anticipate the downstream migration of 0 yr salmon (Roper & Scarnecchia 1999) — or they may simply have learned to predict annual patterns in the release timing of hatchery salmon smolts (Nelson et al. 2019a) compared to the high interannual variability in the timing of wild salmon smolt migrations (Holtby et al. 1989). Such reduced interannual variability in the timing of hatchery smolt releases would increase the abilities of seals to exploit these pulses given that pinnipeds have high learning and memory capacities that influence their future behavioural decisions even after a long time (Reichmuth Kastak & Schusterman 2002).

A final consideration that may influence predation rates is the presence of suitable sites for the seals to haul out, which were lacking near the BQE. Time ashore (i.e. either on sand and cobble beaches, rocky shelves, tidal sand and mud bars or human-made structures) is important for harbour seals during their mating, pupping and moulting periods but also on a daily basis for resting, thermoregulation, predator avoidance, social interaction and parasite reduction (Boulva & McLaren 1979, Watts 1996). The BQE has limited haul-out space on a rocky shelf that is only available at low tide and a cobble beach that is disturbed by humans from a nearby campground. Therefore, seals that foraged in the estuary either had to use less suitable haul-out sites or had to travel back and forth between the BQE and other more distant haul-out sites (e.g. either Norris Rocks or Flora Islet). This constraint of frequently travelling in the open water, in addition to energetic constraints, increases the vulnerability of seals to predation by killer whales *Orcinus orca* (Ford et al. 1998), which presumably influences their behaviour and foraging decisions (Welton et al. 2003).

4.2. Feeding on coho vs. Chinook smolts

The number of PEEs in the BQE hotspot showed a clear peak 4 d following the release of coho smolts from the BQ hatchery (Fig. 3A), which suggests the seals were quick to detect the coho smolt arrival and preyed on them as they left the BQ River. However, there was no clear corresponding peak in the PEE counts for Chinook smolts similar to the one that occurred after the release of the coho smolts despite seals being present in that area. Instead, high numbers of PEE counts were dispersed over time. The mean daily PEE numbers did not differ between the post-coho and the post-Chinook release periods (Fig. S6) even though Chinook smolts were released in much higher numbers (~3 million) than coho smolts (~384 000). The seals did not appear to respond to the release of the Chinook smolts as they did for the release of the coho smolts. This unexpected behaviour of harbour seals could be explained in 2 ways. One is that the harbour seals preferred feeding on coho rather than Chinook smolts, and the other is that consumption of Chinook smolts was constrained by environmental factors.

The inference that the seals may prefer feeding on coho compared to Chinook smolts could be explained by differences in sizes and energy densities of the 2 species of smolts leaving the river. Measurements of smolts sampled before their release showed that the coho smolts were substantially bigger than the Chinook smolts. The coho smolts were 1.6 times longer and 3.8 times heavier than the Chinook smolts (i.e. coho averaged ~12.9 cm and ~22.6 g, while Chinook averaged ~8.0 cm and ~5.9 g). Harbour seals may prefer prey ranging between 10 and 16 cm in length (Tollit et al. 1997), which could explain the apparent preference for coho smolts over Chinook smolts. In addition, coho smolts are energy denser (~5.04 kJ g^{-1} or ~113.9 kJ ind.$^{-1}$) than Chinook smolts (~3.98 kJ g^{-1} or 23.5 kJ ind.$^{-1}$), which means that consuming 1 coho smolt was 4.8 times more energetically beneficial to a harbour seal in the estuary than consuming a Chinook smolt (Roby et al. 2003). Chinook smolts are considerably smaller than coho smolts when entering saltwater and tend to spend more time in the estuary or in nearshore habitats before reaching the open ocean (Myers & Horton 1982, Dumbauld et al. 2015). During this time, Chinook gain body mass and store lipid, which would make them a more energetically beneficial prey for predators later in the year. This is consistent with dietary and modelling studies that suggest Chinook mortality rates due to seal predation peak later in the summer (July), in contrast to the coho mortality rates that are high in May and June (Thomas et al. 2017, Nelson et al. 2019b).

The presence of the seals in the BQE hotspot and the variability in PEE counts following the release of Chinook smolts suggest that the seals may have been targeting aggregations of other Chinook smolt predators such as the Pacific hake, spiny dogfish, river lamprey, adult Chinook salmon, lingcod and walleye pollock (Beamish & Neville 2001, Emmett & Sampson 2007). Consistent with this hypothesis is that PEE intensity by the seals increased in the open water next to the estuary as the Chinook smolts were migrating and that PEEs occurred mostly below 70 m (Fig. 2). An increase in deeper PEEs (>80 m depth) was also detected in the BQE hotspot after the release of the Chinook smolts, which suggests the seals fed on other species instead of salmon smolts (Orsi & Wertheimer 1995, Emmett et al. 2004). Two of the 3 seals that contributed the most to the PEE peak following the release of the coho smolts lowered their daily PEE counts after the Chinook smolts were released, even though they seemed to spend as much time as before in the BQE hotspot (Fig. 4). The lower PEE counts could reflect satiation and consumption of larger prey but seem unlikely to be a lagged effect of having consumed the large pulse of coho smolts 10 d earlier.

The unexpected low response to Chinook smolts by harbour seals could also be explained by differences in environmental factors between the post-coho and post-Chinook smolt release periods. Out-migrating salmon smolts tend to minimize predation risk by migrating at higher numbers at night when luminosity is low (Furey et al. 2016). Harbour seals have been seen gathering in river mouths at night and using artificial lights to take advantage of out-migrating smolts (Yurk & Trites 2000). The higher probability and intensity of PEEs we observed at dusk and at night in the BQE hotspot are consistent with this, although the nearby campground provided little artificial light. Another source of light that can influence predation is moonlight. We found that PEE counts increased in the BQE hotspot as the nightly fraction of the illuminated moon increased. This suggests that moonlight might have improved seal visibility to detect their prey. Tide height is another environmental factor that affects seal predation on smolts in the river mouth. The BQ River is a relatively small river that seals cannot access at low tide. At low tide, the seals cannot take advantage of the higher densities of spatially constrained smolts (Yurk & Trites 2000). This is consistent with our finding that the probability and the intensity of PEEs in BQE hotspot increased with tide height.

As the releases of the coho and the Chinook smolts were 10 d apart, the 2 post-release periods differed in the timing of the tide height and the lunar cycle. The coho smolt release happened at full moon (i.e. the highest visibility at night) and high tide matched, with dusk and nighttime offering favorable environmental conditions to feed efficiently on coho smolts (Fig. 5). However, 10 d later, the Chinook smolt release occurred 3 d before the new moon (i.e. low visibility at night) and tide was low at dusk and night. Thus, environmental conditions were less favourable for seals to spatially constrain and visually detect the out-migrating Chinook smolts. However, as seals can detect their prey in the dark using their vibrissae (Hanke et al. 2013), we believe the temporal mismatch between the tide height and the dusk and night periods would have reduced seal foraging efficiency but not foraging attempts. One means to test this and the presumed preference for coho smolts would be to reverse the order of release.

4.3. Study limitations

Although our study brings relevant insights into the predator–prey dynamics between harbour seals and out-migrating coho and Chinook smolts in the Salish Sea, our results are limited by low sample size and methodological considerations. For instance, the behavioural feeding response we noted following the pulse of smolts entering the BQE hotspot is based on 4 of 17 tagged seals. The power to detect a difference in feeding intensity between post-coho and post-Chinook release periods was just 15% (Table S3) and would have required equipping more seals with tags to increase statistical power. The age structure and sex ratio of our tracked seals were also skewed towards older males, whose foraging ecology may differ from that of females and younger individuals (Schwarz et al. 2018).

Acceleration has become a common tool to quantify distinct behaviours in free-ranging animals—

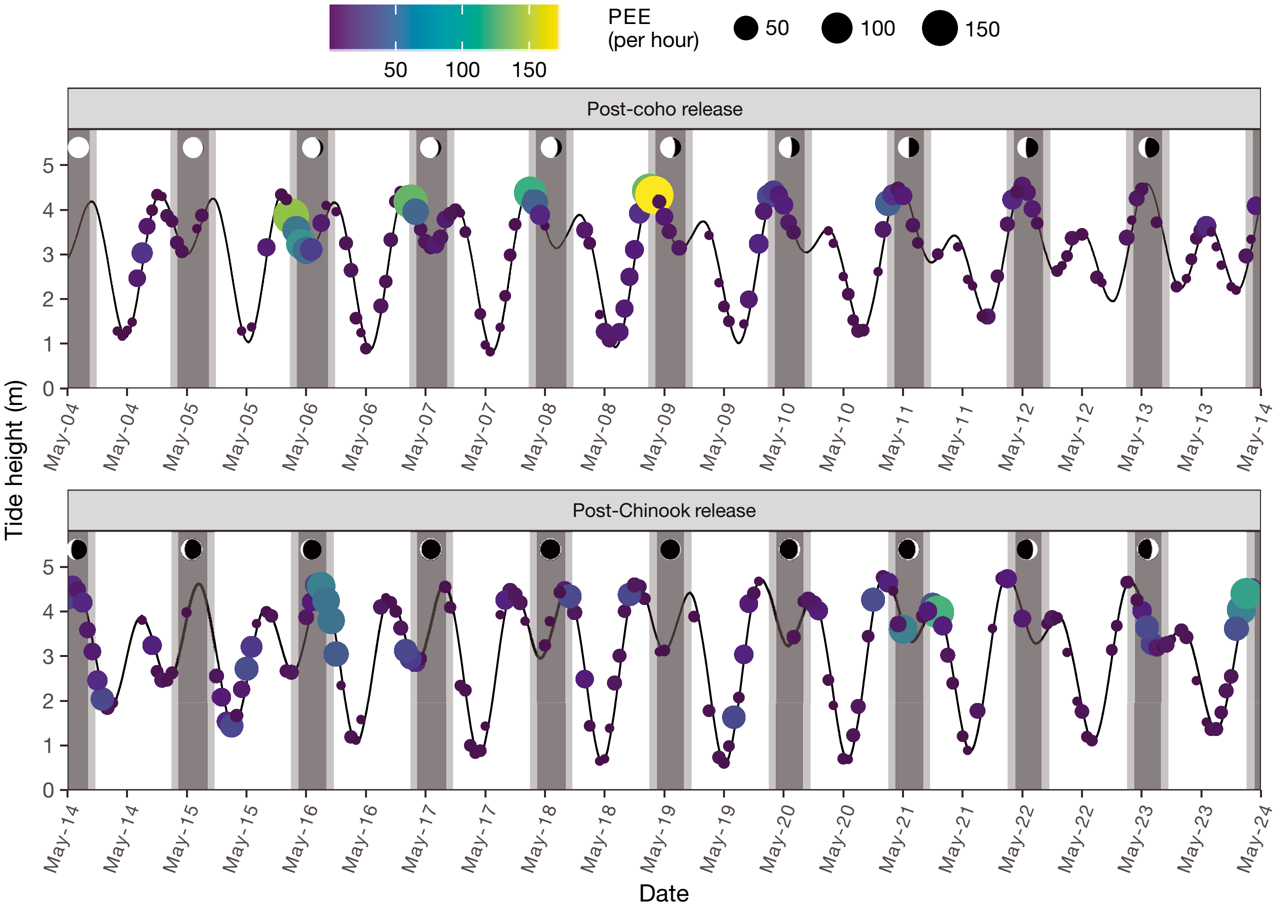

Fig. 5. Counts of prey encounter events (PEEs) per hour inside the Big Qualicum estuary hotspot over tide height (*y*-axis) and date and time (*x*-axis). Approximately ~384 000 coho smolts (on May 4) and ~3 million Chinook smolts (on May 14) were released from the Big Qualicum hatchery. The solid line shows tide height over time. Shaded time periods represent night (dark grey), dawn and dusk (light grey) and daylight (white). Within each night period, the moon phase is represented by an icon ranging from full moon (white circle) to new moon (black circle)

especially as a proxy for feeding effort (Jeanniard-du-Dot et al. 2017). However, accelerometry alone cannot determine feeding success. Additional data on diet combined with movement and diving data are needed to provide a complete understanding of harbour seal foraging response to smolt pulses.

The placement of the accelerometer on an animal is also an important consideration when using accelerometry data. Many studies have approximated foraging success with prey capture attempts by detecting head strokes (Volpov et al. 2015, Jeanniard-du-Dot et al. 2017). Due to logistical considerations, we placed the accelerometer on the backs of the seals and considered high body accelerations as PEEs to quantify feeding intensity. Given the variety of prey species consumed by harbour seals (Lance & Jeffries 2007), it is conceivable that using body acceleration instead of head acceleration led to incomplete inferences about the relative numbers of prey consumed. For example, seals swimming against river currents could hold their position in the water and use minimal movements to intercept smolts swimming towards them (Yurk & Trites 2000). Harbour seals can also consume small prey using suction feeding in addition to biting (Marshall et al. 2014). The suction feeding tactic may not be detected by the back-mounted accelerometer and could thus underestimate PEEs in rivers and estuaries. Hence, it is theoretically possible that the method we used to detect PEEs could explain the apparent low response by seals to out-migrating Chinook smolts if less seal body movement was required to catch Chinook smolts than to catch coho smolts.

5. CONCLUSIONS

Our results show that harbour seal predation on out-migrating smolts in the estuary was relatively small (23.5% of seals and 5.7% of all PEEs) compared to the foraging effort of all tracked seals within the BQ area. The most intensive feeding occurred near the southern part of Hornby Island around Norris Rocks. Those seals that travelled to the BQE responded positively to the pulse of coho smolts released from the BQ hatchery by increasing their feeding intensity. However, the seals did not respond as expected to the pulse of Chinook smolts, which were ~8 times more abundant than coho smolts. They did not appear to feed on the Chinook smolts in any significant way. Our findings suggest that the predator responses we observed were affected by the magnitude of the resource pulses as well as by other factors that impact prey profitability (e.g. prey size, relative prey energy density and availability of alternative prey) and predation efficiency (e.g. height and timing of tide level and lunar cycle).

Dietary analysis indicates that predation by harbour seals on coho and Chinook smolts likely has a substantial impact on these salmon species (Chasco et al. 2017, Thomas et al. 2017). We inferred significant predation by a few seals on coho smolts that entered the estuary, but predation pressure seemed more relaxed on Chinook smolts. Instead, we suspect the seals may have targeted predators of Chinook smolts. In all likelihood, predation pressure by harbour seals on Chinook smolts in the Strait of Georgia occurs later in the summer (July and August), once the fish have grown to a size that better fits the search image and energy requirement of harbour seals (Tollit et al. 1997).

Our findings bring new insight into the complexity of the interactions between harbour seals and outmigrating coho and Chinook smolts. They show the highly individualistic nature of seal predation and suggest that there may be complex indirect effects associated with seals consuming fish that also prey on juvenile salmon. They further suggest that the predatory impacts of seals differ substantially between juvenile coho and Chinook (at least spatiotemporally) — and question whether the survival patterns of these 2 salmonids are tightly linked (as often assumed). Such confounding factors need to be addressed when considering broad conservation measures that might be taken against harbour seals to enhance the marine survival of salmonids.

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