

Harassment and killing of porpoises (“phocoenacide”) by fish-eating Southern Resident killer whales (*Orcinus orca*)

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Abstract

Endangered Southern Resident killer whales (*Orcinus orca*) are fish-eaters that preferentially prey on adult Chinook salmon (*Oncorhynchus tshawytscha*). Despite being salmon specialists, individuals from all three killer whale pods (J, K, L) have been observed harassing and killing porpoises (family Phocoenidae) without consuming them. Retrospectively, we identified and analyzed 78 episodes of Southern Resident killer whales harassing porpoises between 1962 and 2020, of which 28 resulted in the porpoise's death (“phocoenacide”). Fifty-six episodes involved harbor porpoise (*Phocoena phocoena*), 13 involved Dall's porpoise (*Phocoenoides dalli*), and the porpoise species was unreported for nine episodes. Southern Resident killer whales often targeted young porpoises that were similar in size to adult Chinook salmon.

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Both sexes participated in porpoise harassment. Juveniles engaged in the behavior the most; however, their rates of engagement were not found to differ significantly from most other age classes. The behavior was passed through generations and social groupings, as it was first observed in L pod and spread to the other two pods. Killer whales are highly complex animals known to exhibit social learning and cultural transmission of learned behaviors, but the reason(s) for this behavior is unknown. Hypotheses include the social and developmental benefits of play, hunting practice, or displaced epimeletic behavior.

KEYWORDS

culture, killer whale, *Orcinus orca*, *Phocoena phocoena*, phocoenacide, *Phocoenoides dalli*, porpoise, Salish Sea, Southern Resident killer whale

1 | INTRODUCTION

Cetaceans exhibit diverse and complex behaviors, many of which are not yet fully understood. Differentiating predatory (consumptive) from nonpredatory (nonconsumptive) behavior during interspecies interactions between wild animals can be challenging due to observation limitations and interpretation that can be subject to observer bias (Mann & Würsig, 2014; Nowacek et al., 2016). One type of interspecific, nonpredatory aggression seen in cetaceans is the harassment and killing of porpoises (family Phocoenidae) by dolphins, a behavior termed “phocoenacide” or “porpicide.” This behavior is mainly observed in medium to small dolphins, primarily common bottlenose dolphins (*Tursiops truncatus*; Cotter et al., 2012; Gross et al., 2020; Hohn et al., 2013; Jepson & Baker, 1998; Ross & Wilson, 1996; Wilkin et al., 2012) and several species in the genus *Lagenorhynchus* (Baird, 1998; Haelters & Everaarts, 2011; Larrat et al., 2012). It is unclear why such harassment and/or phocoenacide occurs. Suggested causes include prey competition and feeding interference (Spitz et al., 2006), including kleptoparasitism (Baird, 1998; Smultea et al., 2014); practice related to fighting, predation, or infanticide (Cotter et al., 2012; Patterson et al., 1998; Weller et al., 1996); in response to a perceived threat to young or an ill conspecific (Ross & Wilson, 1996); sexual aggression or high testosterone in males (Cotter et al., 2012; Jepson & Baker, 1998; Ross & Wilson, 1996); male or conspecific bonding (Cotter et al., 2012); displaced epimeletic behavior or “mismothering” (Baird, 1998; Bearzi & Reggente, 2018); territoriality of site or resources (Cotter et al., 2012); or aberrant behavior by an individual (Gross et al., 2020). Phocoenacide has also been proposed to be a form of object-oriented “play” (Baird, 1998; Cotter et al., 2012; Haelters & Everaarts, 2011; Larrat et al., 2012; Ross & Wilson, 1996), in which the act does not contribute to the immediate survival of the individual(s), but can have cognitive, physical, or social and developmental benefits (Burghardt, 2005; Hill et al., 2017).

Harassment and killing of nonprey species by predators are not unique to marine mammals, and the hypothetical reasons for this are as varied as they are for why dolphins may kill, but not eat, porpoises. In sub-Saharan Africa, lions (*Panthera leo*), for example, kill substantial numbers of cheetahs (*Acinonyx jubatus*) and wild dogs (*Lycaon pictus*), suppressing wild dog populations, but not cheetah (Swanson et al., 2014). In fact, a review of interspecific killing among terrestrial mammal carnivores detailed 97 pairwise interactions involving 27 different killer and 54 victim species (Palomares & Caro, 1999). For the 21 killer species where information on consumption of the victim was available, killers either did or did not eat their victims in eight cases and never ate the victim in three cases (Palomares & Caro, 1999).

Killer whales (*Orcinus orca*), the largest species of dolphin, are known to have complex interactions with other species, ranging from predation to avoidance (Jefferson et al., 1991; Selbmann et al., 2022), including hunting and killing nonprey. Southern Resident killer whales (SRKW) are a small, well studied population of killer whale that range along the west coast of North America from southeastern Alaska to California with critical habitat that includes the Salish Sea, an inland sea shared by Washington State and British Columbia (National Marine Fisheries Service, 2021). The population includes three long-term, stable pods (J, K, and L) that eat exclusively fish, primarily Chinook salmon (*Oncorhynchus tshawytscha*), which constitutes 50%–100% of SRKW diet depending on the season (Hanson et al., 2021). The SRKW population is listed as endangered in Canada (Baird, 2001; Committee on the Status of Endangered Wildlife in Canada, 2001) and the United States (U.S. Federal Register, 2005) and is at risk of extinction due to the cumulative effects of three main threats (Lacy et al., 2017; Murray et al., 2021): scarcity of salmon, particularly Chinook (Couture et al., 2022; Ford et al., 2010; Hanson et al., 2021); vessel disturbance (Holt et al., 2021a,b); and legacy contaminants (Krahn et al., 2007; Mongillo et al., 2016). The impacts of these three stressors are exacerbated by an inbreeding depression (Kardos et al., 2023). Despite being fish-eaters, SRKW have been anecdotally reported to harass and kill, but not consume, harbor porpoises (*Phocoena phocoena*) and Dall's porpoises (*Phocoenoides dalli*) in the Salish Sea. These reports are not well studied, and the origins and functions of this behavior are unknown.

To understand this behavior, we collected and analyzed historical incidents of SRKW harassing and killing porpoises in the Salish Sea. We examined rates of porpoise harassment and/or phocoenacide in relation to SRKW demographics and evaluated hypotheses for the potential function(s) of the behavior. Our hypotheses about possible functions relate to which age-sex class might be responsible for the behavior. If juvenile animals have a greater rate of porpoise harassment or killing than adults, this might indicate that the behavior could serve as a form of social or developmental play for younger individuals, or as a form of practice hunting; the latter could be further evidenced by SRKW selecting for porpoise calves or neonates, which are similar in size to adult Chinook salmon. If porpoise harassment is largely performed by physically mature males, the behavior might be a sociosexual display or a form of sexual aggression. If the behavior is mainly observed in reproductive age females, it could be a form of displaced epimeletic behavior, which has been previously observed in this population (Shedd et al., 2020).

We also examine transmission of porpoise-harassing behavior within SRKW matriline and diffusion of the behavior between pods over time. The matriline is the most cohesive social unit of resident killer whale society and typically comprises an adult female, her offspring, and intervening generations that live and travel together for life (Bigg et al., 1990; Ford et al., 2000; Olesiuk et al., 2005), and share behavioral similarities, such as acoustic signatures (Ford, 1989, 1991; Ford et al., 2000; Miller & Bain, 2000; Yurk et al., 2002). The matrilineal group structure, along with an extended postmenopausal life span of killer whales, is thought to promote knowledge sharing between matriarchs and offspring and facilitate cultural transmission of information and behavior (Brent et al., 2015; Foote et al., 2016; Riesecke et al., 2012). If porpoise-harassing behavior is passed on from experience between individuals, we hypothesize the matriline would display the tightest retention of the harassment behavior. Porpoise-harassing behavior might also have diffused between pods, similar to the SRKW “fad” of carrying a dead salmon on the head, which was first observed in a female in K pod and was then repeated by members of J and L pods (Whitehead et al., 2004). Cultural inheritance involves the retention and transmission of information by communication, imitation, teaching, and learning, rather than by genetics (Peedicayil, 2001). If porpoise harassment is spread between pods, this behavior could mark the first recorded case of harassment of a nonprey species being introduced as part of the SRKW culture.

2 | METHODS

2.1 | Data collection and case definitions

We defined an incident of porpoise harassment as one in which SRKW interacted with a porpoise in a manner that could have immediately harmed the porpoise, which sometimes includes the killing of the porpoise. Reports of

porpoise harassment by SRKWs came from our own observations and were collected from other researchers, as well as whale-watch organizations and members of the public. Incident reports were queried from long-term databases (Center for Whale Research [CWR], The Whale Museum, National Oceanic and Atmospheric Administration Northwest Fisheries Science Center, Orca Network), marine mammal stranding response programs, or obtained directly from the reporting party. Reports were also identified in the literature, including peer-reviewed articles, theses, books, and newsletters. A thorough description of each event was gathered, including the SRKW individual(s) involved, health or survival outcome of the porpoise(s), and any available photographs or video. Identification of individual SRKWs involved in each incident was determined by coauthors with expertise in SRKW identification.

For this study, episodes of porpoise harassment were further classified as “confirmed kill,” “suspected kill,” or “unknown outcome.” Both confirmed kills and suspected kills were considered phocoenacide, as both were ultimately presumed to result in the killing of a porpoise by one or more SRKWs. We classified a case as a confirmed kill if it fulfilled one of two criteria: (1) when one or more SRKWs was/were observed with a live porpoise, and by the end of the observation period, the porpoise was dead; or (2) observers found a freshly deceased porpoise immediately after SRKWs were observed to have been present in an area, and no mammal-eating killer whales had been recently documented in the area. When a porpoise carcass could be collected after known or suspected phocoenacide, a complete necropsy was performed, including microscopic examination of tissues by a veterinary pathologist (Raverty et al., 2018), and in all cases the primary cause of death was determined as killer whale-induced trauma.

In incidents where the health or survival of the porpoise was not evident, cases were defined as a “suspected kill” or “unknown outcome.” Suspected kills included incidents where events suggested the porpoise ultimately died, even if the porpoise was last seen alive by observers. Examples include physical mutilation likely to have caused mortality or when the porpoise never surfaced after the interaction suggesting the carcass sank. Incidents were also called suspected kills when observers arrived on the scene while SRKWs were interacting with a dead porpoise. In such cases, SRKWs could have found a previously deceased porpoise, but SRKW behavior with the carcass suggested the porpoise died because of the actions that had recently occurred between SRKWs and the porpoise. Cases were classified as an unknown outcome when harassment was observed, but an inference could not be made about the health or survival outcome of the porpoise.

Incidents were grouped according to SRKW pod, sex, age class, individual, and matriline. Age classes included: calf (0–2 years; each sex), juvenile (3–10 years; each sex), “sprouter” male (11–19 years), physically mature or adult male (≥ 20 years), reproductive female (11–42 years), and postreproductive female (≥ 43 years; Jensen et al., 2020; Stewart et al., 2021). Sprouter refers to the growth of the male's dorsal fin as the individual becomes sexually mature. Matrilines were defined as sets of individuals with a known common maternal ancestor (Parsons et al., 2009).

2.2 | Analysis

Long-term occurrence of SRKWs in the Salish Sea has been documented by the CWR since 1976. Annual rates of porpoise harassment were computed for each SRKW pod, sex, age class, and individual. An annual rate was defined as the number of porpoise harassment or killing incidents by each SRKW grouping or individual, divided by the number of days that grouping or individual was observed by CWR over that year. Rates could not be calculated prior to 1976, the year when CWR began censusing SRKWs. Not every incident of porpoise harassment or killing was observed from CWR sighting effort, so this was not an exact measure of sampling effort for detecting porpoise incidents; further, due to the nature of CWR's data collection, the number of days SRKWs were observed by CWR does not equal the number of days the individuals were in the Salish Sea (e.g., if J pod was observed on January 1, CWR may not sample again on January 2). Despite these limitations, this method provides the most complete and reliable estimate of how often each pod and individual was in the Salish Sea and was likely to be observed. Sampling effort for porpoise-SRKW incidents during the summer months from 2005 to 2020 was likely higher than in previous years

as there were more whale-watch operations in business during this period, more research vessels in the area, and more noncommercial whale watching was occurring (Olson et al., 2018). Federal listing of SRKWs as endangered in the U.S. (2005) and Canada (2001) also resulted in more SRKW research activity and observation.

For the “by pod” analyses, we used generalized linear mixed-effect models with Poisson error-structure to compare pod engagement in harassing or killing porpoises. Models were single-term (pod; considering only the raw count of incidents) or additive (pod and the number of days each pod was observed by CWR per year), with year as a random effect. To determine how the incident rate by pods changed over time and to examine potential transmission of the behavior between pods, the total time frame available for rate calculations (1976–2020) was then divided into two periods. The justification for dividing the data into two periods was to increase statistical power for detecting a difference. Between 1976 and 2020, there were 2,441 observation days. The half-way point in terms of observation days was the year 2005, which was chosen to divide the period in two (1976–2005, 2006–2020). Poisson models were used to determine if each pod's engagement in porpoise harassment changed from period 1 (1976–2005) to period 2 (2006–2020), with the number of days CWR observed each pod per period as a fixed effect. To allow for further scrutinization of the results, analyses by pod were repeated using binomial generalized linear mixed models, such that the response variable was a two-column integer matrix with the first column giving the number of porpoise-harassing incidents per pod, per year, and the second column giving the number of days each pod was observed by CWR per year.

A binomial generalized linear mixed model was used to determine the probability that an individual whale would engage in porpoise harassing or killing, considering the number of days that CWR observed each individual. In the data for individuals, each whale is represented by the number of times it engaged in the behavior each year, accounting for variation in number of individuals within each pod. Pod-level rate analyses were repeated using the individual data, with pod as the fixed effect and year and individual whale as random effects. Repeating the analyses in this way allowed for further scrutinization of the pod-level results and to determine if one or a select few individuals were driving the results.

Binomial generalized linear models were used to examine if rates of porpoise harassment differed by SRKW sex and by age class. Here, rates were the total number of harassment incidents for the sex or age class across all years, divided by the total number of days the sex or age class was observed by CWR across all years. These models considered only individuals that could be identified.

Matrilines that were responsible for the most incidents were plotted to show the individual SRKWs involved, their sex and age, and the year of the incident. All analyses were performed using R Studio (R Core Team, 2021) and statistical significance was set at $p \leq .05$.

We gathered observations made by killer whale scientists of porpoise harassment or killing by other salmon-eating populations in the northeastern Pacific Ocean (Northern Resident killer whales [NRKW] and Alaska Resident killer whales [ARKW]) but did not calculate or analyze rates due to limited sample size. These observations were summarized and included as anecdotal comparisons.

3 | RESULTS

3.1 | Southern Resident killer whales

Between 1962 and 2020, 78 incidents of SRKW harassing or killing porpoises were observed in the Salish Sea (Table S1). Of these, 28 incidents (36%) were classified as phocoenacide (confirmed kill = 16 incidents, suspected kill = 12 incidents) and 50 (64%) were undetermined outcome. Consumption of the porpoise was never observed in any incident. Most incidents ($n = 56$, 72%) involved harbor porpoises while 13 (17%) involved Dall's porpoises. The porpoise species (harbor or Dall's) was not reported or determined for nine (11.5%) incidents. Most incidents involved a single porpoise (71/78 incidents, 91%). For incidents involving a single porpoise ($n = 71$), the porpoise's

age class was known in 40 incidents and was unreported or unknown for 31 incidents. Of those incidents involving a single porpoise and where its age class was known ($n = 40$), 80% of incidents involved neonates or calves (32/40), and 20% (8/40) were subadults or adults. Two or more porpoises were simultaneously involved in 7 of 78 incidents: this includes three incidents with two porpoises that were not a mother-offspring pair, one incident with a mother-offspring pair, one incident with three individuals that included a mother-offspring pair, and in two incidents, between five and fifteen porpoises were involved. Incidents were observed almost equally by researchers and whale-watch organizations ($n = 43$ and 39, respectively), with 14 incidents observed by both parties. Six incidents were documented in previously published literature (Table S2) and six were reported by the public to a sighting network.

Complete necropsies were performed on seven porpoises that were observed being killed by SRKWs (Table S3). This included six harbor porpoises (two neonates, one calf, and three subadults) and one Dall's porpoise neonate (see Norman et al., 2018 and Ferrero & Walker, 1999 for age class determination of harbor and Dall's porpoise, respectively). The primary cause of death for all porpoises was killer whale-induced trauma. Only one out of seven porpoises had an underlying condition (marked, multifocal verminous pneumonia) that could have contributed to reduced fitness and predisposed it to SRKW harassment and mortality. Signs of trauma ranged from severe (extensive cutaneous punctures and/or abrasions, internal hemorrhage including hemothorax and hemoperitoneum) to subtle lesions that were only discernable microscopically (e.g., only microscopic evidence of hemorrhage in brain, lung, and liver).

Most incidents (60%) of Southern Resident killer whales harassing porpoises occurred in the waters around the San Juan Islands (Washington State), where most survey effort was concentrated. Using timing that started at the onset or when observers arrived on the scene when the encounter was already in progress, harassment incidents lasted from 3 to 300 min (median = 35 min). There were consistencies in description of the behaviors between incidents, which often began with SRKWs chasing the porpoise. Once caught, behaviors included pushing the porpoise with the rostrum, holding it in the mouth (Figure 1), and carrying and balancing the porpoise above the water (Figure 2), mostly atop the rostrum or melon but occasionally on the abdomen, and sometimes between multiple SRKW individuals (Figure 3). Whale watchers reported SRKWs were "toying" with the porpoise, allowing it to escape before recapturing it and resuming behaviors such as pushing, carrying, or balancing the porpoise. Other higher activity behaviors (i.e., behaviors involving more movement and energy) were observed as well, including ramming and tossing the porpoise (Figure 4), slapping the porpoise with the flukes, thrashing the porpoise in the mouth, or raking the porpoise, any of which could have resulted in the porpoise's drowning. Two incidents involved SRKW repeatedly releasing the dead porpoise and diving to retrieve it. In six



FIGURE 1 Southern Resident killer whale L119 holding in its mouth a harbor porpoise calf that was eventually drowned by L119, L77, and L113 on September 21, 2016. Photo by Mark Malleeson, taken under DFO permit MML-001.



FIGURE 2 A harbor porpoise calf being balanced out of the water by L115 on September 21, 2019. The porpoise eventually swam away, and its survival outcome was unknown. Photo by Candice Emmons, taken under NOAA permit #21348.



FIGURE 3 Members of L pod cradling a neonate Dall's porpoise, which eventually swam away towards its mother, on September 18, 2008. Photo by Andrew Lees.

incidents the SRKWs initiated a long dive prior to the porpoise not being seen again by observers or leaving the porpoise dead at the surface.

Eighteen incidents (23%) involved a single SRKW, but most ($n = 60$, 77%) involved two or more SRKWs. Seventeen incidents (22%) involved individuals from different matriline. When more than one SRKW was involved, most (53/60) comprised between two and four SRKWs. Three times, groups of whales containing between 15 and 25 individuals were reported to have collectively engaged in the behavior.

Most incidents involved only a single pod. L pod engaged in the greatest number of incidents ($n = 39$), followed by J pod ($n = 29$), and K pod ($n = 10$). Three incidents involved individuals from two pods at once (J and K, $n = 1$; L and K, $n = 1$; J and L, $n = 1$). In three incidents, the pod was not identified. The earliest incident with an unknown SRKW pod occurred in 1962, when two killer whales, an adult male and a female, were observed chasing a porpoise in Haro Strait near San Juan Island. These killer whales were pursued with the intention to be captured for the aquarium trade, but during the operation, the female died (Hoyt, 1990). The carcass was brought back to shore and



FIGURE 4 Southern Resident killer whale J31 ramming into a harbor porpoise on September 9, 2009. J36, J39, and K37 also participated in the incident. The porpoise eventually died and was collected for necropsy by NOAA. Photo by Jeffrey Foster, taken under NOAA permit #781-1824.

dissection revealed 150 pounds (68 kg) of salmon in the stomach (Hoyt, 1990), indicating the individual was a Resident killer whale. In another incident where pods were unknown (2013), a freshly dead porpoise was found in False Bay, San Juan Island, immediately after nearly all members from all three SRKW pods had traveled through the area. In the third incident where pods were unknown (2020), members from all three pods were present in Haro Strait near San Juan Island and observers witnessed two individuals harassing a porpoise, but the pod(s) and individuals involved were not identified.

Based on the total count of incidents for the entire study period (1962–2020), L pod was seen engaging with porpoises ($\beta_0 = 0.36$, $SE = 0.19$) more than K pod ($\beta = -1.36$, $SE = 0.35$, $p < .001$) but we found no difference in the number of incidents between L pod and J pod ($\beta = -0.30$, $SE = 0.25$, $p = .23$). J pod was also seen harassing or killing porpoises ($\beta_0 = 0.06$, $SE = 0.21$) more than K pod ($\beta = -1.06$, $SE = 0.37$, $p = .004$). When considering the annual harassment rate by pod (number of porpoise-harassing incidents by the pod divided by the number of days the pod was observed by CWR that year) for each year from 1976 to 2020, L pod had a higher mean incident rate (0.063 ± 0.026 incidents/year) than either J (0.011 ± 0.003 incidents/year) or K pods (0.007 ± 0.003 incidents/year; Figure 5). Poisson models that considered the number of porpoise-harassing incidents as a function of the pod and the number of days each pod was observed by CWR per year confirmed that, between 1976 and 2020, L pod engaged in the behavior more ($\beta_0 = -1.79$, $SE = 0.39$) than either J ($\beta = -0.65$, $SE = 0.26$, $p = .013$) or K pods ($\beta = -1.00$, $SE = 0.35$, $p = .004$) (fixed effect of the number of days each pod was observed by CWR: $\beta = 0.03$, $SE = 0.007$, $p < .001$). Running this model as a binomial model made no qualitative difference to the results.

Across all years, most incidents were observed during the summer months ($n = 68$; 87%; July [$n = 24$; 31%], August [$n = 30$; 38%], September [$n = 14$; 18%]), largely reflecting SRKW presence (Olson et al., 2018), increased whale watching activity, and higher research sampling efforts by multiple organizations in the summer. The greatest number of incidents occurred in 2005 ($n = 10$), followed by 2006 and 2016 ($n = 6$ each), and then 2008, 2014, and 2015 ($n = 5$ each). A heat map of occurrence shows that L pod was the first pod to be observed engaging in this behavior, with K pod seen later, then J pod, after which all three pods or some combination of the pods were observed interacting with porpoises (Figure 6). Poisson models examining potential transmission of the behavior between pods over time, considering the number of porpoise-harassing incidents as a function of the pod and the number of days each pod was observed by CWR per year, found that in period 1 (1976–2005), L pod engaged in significantly more incidents (vs. J pod: $\beta = -1.01$, $SE = 0.43$, $p = .02$; vs. K pod: $\beta = -2.63$, $SE = 1.03$, $p = .01$; fixed effect of the number of days each pod was observed by CWR: $\beta = 0.04$, $SE = 0.01$, $p = .004$). In period

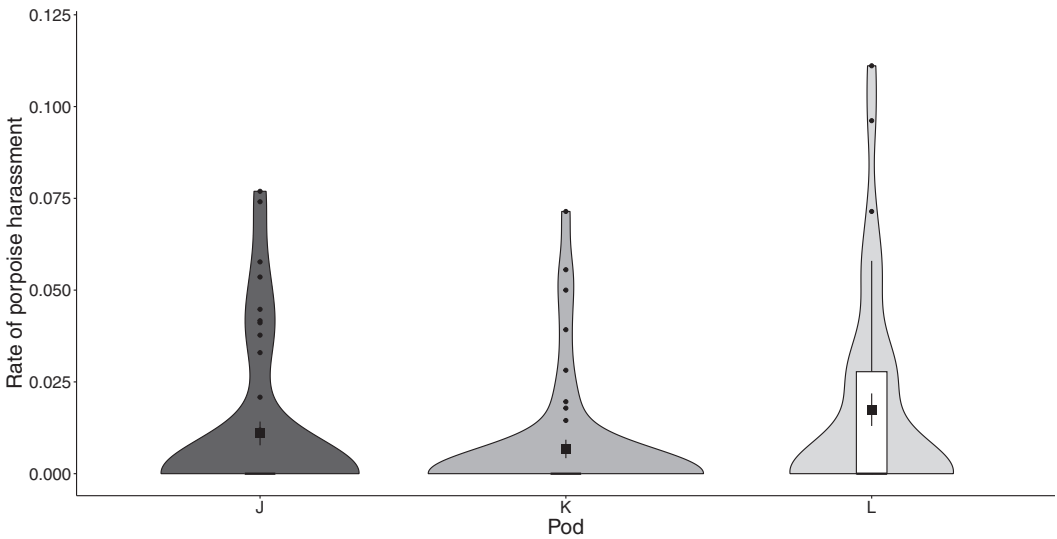


FIGURE 5 Density plots representing the full distribution of the annual rate of porpoise harassment incidents by pod over 45 years (1976–2020). The box plot (flat for J and K pods) represents the median ± interquartile range; squares represent the mean ± standard error; and dots represent the outliers. Note: Y-axis units are the pod-specific number of porpoise harassment incidents per year divided by the number of days the pod was observed by CWR per year.

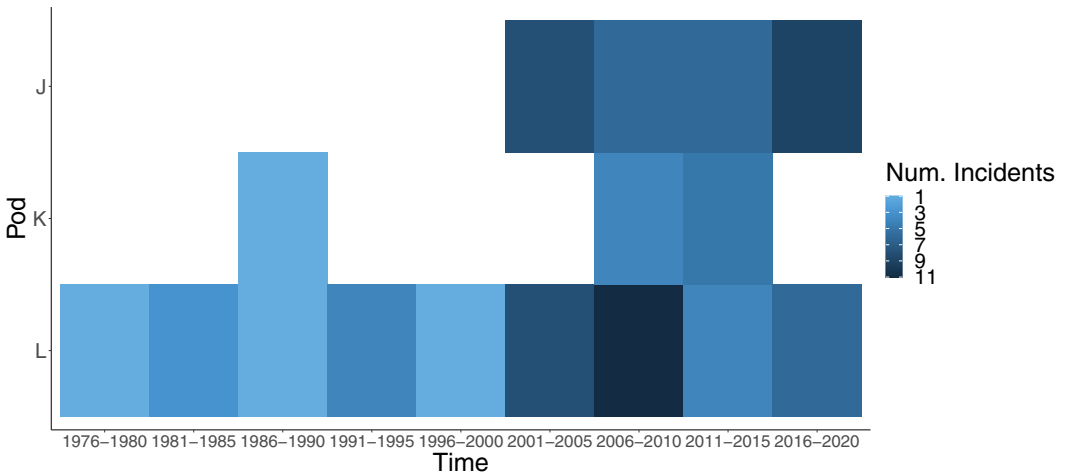


FIGURE 6 Heat map showing the number of incidents of porpoise harassment per pod over time (considering only incidents in which a pod was identified, $n = 75$).

2 (2006–2020), porpoise harassment by J or K pods were not significantly different from that by L pod (vs. J pod: $\beta = -0.14$, $SE = 0.32$, $p = .67$; vs. K pod: $\beta = -0.63$, $SE = 0.39$, $p = .11$; fixed effect of the number of days each pod was observed by CWR: $\beta = 0.01$, $SE = 0.007$, $p = .13$; Figure 7). Running these models as binomial models made little qualitative difference to the results. Similarly, changing the temporal cut-off for dividing the periods in two made little difference to the results (Figures S1 and S2). Binomial generalized linear models comparing each pod's harassment from period 1 to 2 found that K pod's harassment rate significantly increased in period 2 ($\beta = 2.298$, $SE = 1.05$, $p = .029$) and there was weak evidence that J pod's harassment rate also increased in period 2 ($\beta = 0.736$,

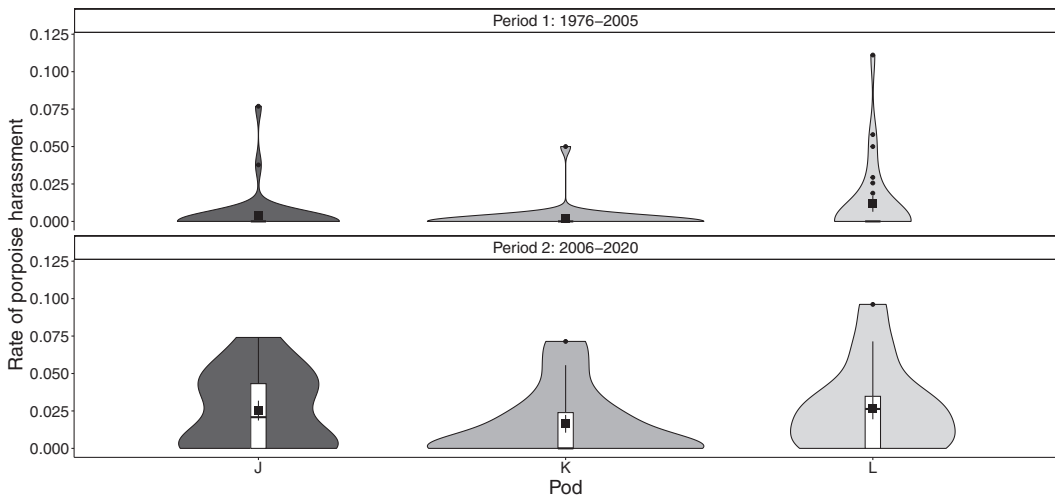


FIGURE 7 Density plots representing the full distribution of the annual rate of porpoise harassment by pod each year, in periods: 1 = 1976–2005, and 2 = 2006–2020. The box plots (flat for all pods in period 1) represent the median \pm interquartile range; squares represent the mean \pm standard error; and dots represent the outliers. Note: Y-axis units are the pod-specific number of porpoise harassment incidents per year divided by the number of days the pod was observed by CWR per year.

$SE = 0.418$, $p = .079$) but this was not statistically significant. L pod's harassment rate did not change from period 1 to 2 ($\beta = 0.047$, $SE = 0.326$, $p = .88$).

Considering only the raw incident count ($n = 78$), four whales (L5, L73, J31, and J36) interacted with porpoises most often (with five incidents per individual). In 1992, L21 was observed harassing a Dall's porpoise, and in 1992 and 1994, L5, L58, and L73 were observed harassing a Dall's porpoise. Prior to 2000, these were the only whales identified at the individual level having engaged in this behavior. Binomial models examining the rate of porpoise harassment based on individual whales revealed that no one whale engaged in the behavior more than others ($p \geq .05$ for every whale). Pod-level analyses of the rate of incidents were repeated using these individual data and confirmed that an individual of L pod had a higher probability of engaging in the behavior ($\beta_0 = -6.47$, $SE = 0.37$) than an individual in either J ($\beta = -0.81$, $SE = 0.26$, $p = .002$) or K pod ($\beta = -1.25$, $SE = 0.35$, $p < .001$).

Examining the total rate of porpoise incidents by SRKW sex (the sex-specific number of porpoise harassment incidents divided by the total number of days the sex was observed by CWR, across all years) revealed no difference between females (rate of incidents across all years: 0.00298; binomial regression: $\beta_0 = -5.82$, $SE = 0.11$) and males (rate: 0.00288; binomial regression: $\beta = -0.04$, $SE = 0.18$, $p = .8$). When examined by age class, 33% of whales of both sexes were first documented engaging in the behavior as a juvenile and 59% of females were first documented engaging when they were of reproductive age. As a raw count, reproductive females engaged in the most incidents ($n = 54$ occurrences) compared to the other female age classes (calf, $n = 4$; juvenile, $n = 16$; postreproductive female, $n = 8$). Examining the total rate of porpoise incidents by SRKW age class (the age class-specific number of porpoise harassment incidents divided by the number of days the age class was observed by CWR, across all years) found that juvenile females engaged the most (rate of incidents across all years: 0.00374; binomial regression: $\beta_0 = -5.59$, $SE = 0.25$); however, we found no difference between juvenile females and female calves (rate: 0.00304; binomial regression: $\beta = -0.21$, $SE = 0.56$, $p = .7$) or reproductive females (rate: 0.00326; binomial regression: $\beta = -0.14$, $SE = 0.29$, $p = .6$; Figure 8). Postreproductive females engaged less than juvenile females (rate = 0.00149; binomial regression: $\beta = -0.92$, $SE = 0.43$, $p = .03$). For males, the raw count showed that juvenile males engaged in the most incidents ($n = 20$ occurrences) compared to the other male age classes: calf ($n = 6$), sprouter ($n = 13$), and adult ($n = 13$). Juvenile males engaged in porpoise harassment the most within the male sex

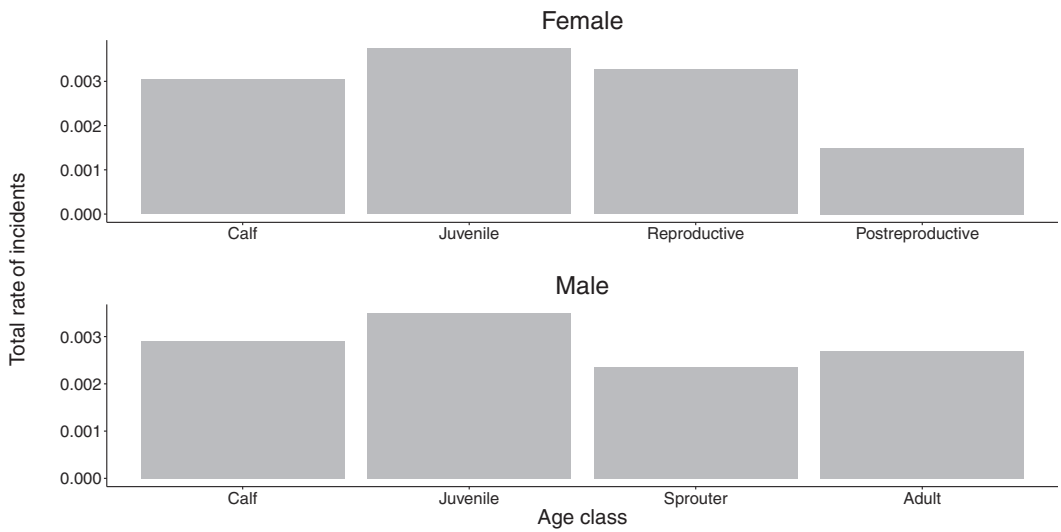


FIGURE 8 The total rate of porpoise harassment or killing incidents according to SRKW age class. Note that the total rate is the age class-specific number of porpoise harassment incidents divided by the number of days the age class was observed by the Center for Whale Research, across all years.

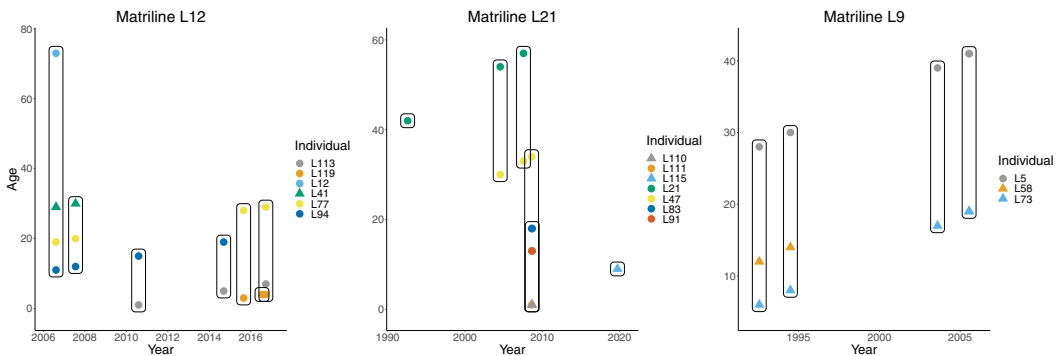


FIGURE 9 L pod matriline with the greatest number of incidents involving porpoise harassment and the distribution of incidents by individuals over time, with rectangles representing incidents, circles representing females, and triangles representing males. Only whales that could be identified were included, and individuals are represented as many times as they engaged in the behavior.

(rate of incidents across all years: 0.00351; binomial regression: $\beta_0 = -5.65$, $SE = 0.22$) but we found no significant differences between juvenile males and any other male age class (calf [rate = 0.00290, binomial regression: $\beta = -0.19$, $SE = 0.47$, $p = 0.69$]; sprouter [rate = 0.00236, binomial regression: $\beta = -0.39$, $SE = 0.36$, $p = .27$]; adult: [rate = 0.00270, binomial regression: $\beta = -0.26$, $SE = 0.36$, $p = .47$]; Figure 8).

There were 19 matriline that harassed porpoises (J pod = 4 matriline, K pod = 4, L pod = 11). Of these matriline, the majority ($n = 12$) had relatively few incidents ($n \leq 7$ incidents/matriline), but 7 matriline were responsible for ≥ 10 incidents each: matriline L12 ($n = 19$), J4 ($n = 16$), L21 ($n = 14$), L9 ($n = 12$), J7 ($n = 11$), J9 ($n = 11$), and J2 ($n = 10$). Porpoise harassing behavior appears to have been transmitted through, and retained within, matriline (Figures 9 and 10). Within matriline L9, there were three individuals which retained this behavior over time (Figure 9), while some individuals were never recorded to have participated, such as individual L84. This is in contrast

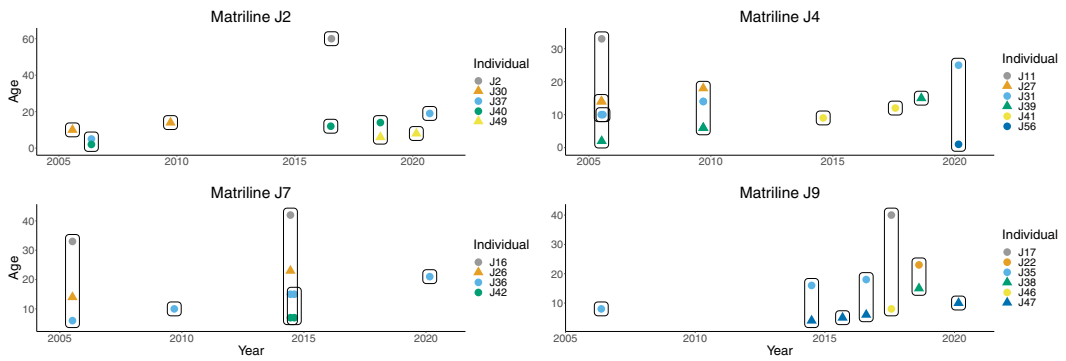


FIGURE 10 J pod matriline with the greatest number of incidents involving porpoise harassment or killing and the distribution of incidents by individuals over time, with rectangles representing incidents, circles representing females, and triangles representing males. Only whales that could be identified were included, and individuals are represented as many times as they engaged in the behavior.

with matriline L12 and L21 that had multiple new, younger individuals begin to engage in the behavior, particularly after 2005 (Figure 9). Within J pod matriline, many individuals were first observed engaging in the behavior after 2005, at a relatively young age, and often repeated the behavior over time (Figure 10). Individuals from four matriline (K30s, L15s, L25s, L28s) were never observed harassing or killing porpoises.

3.2 | Northern and Alaska Resident killer whale populations

NRKW were observed harassing porpoises five times between 1994–2017 (harbor porpoise: $n = 2$, Dall's porpoise: $n = 3$) and ARKW were twice observed harassing harbor porpoise, once each in 2002 and 2015 (Table S4). Behaviors displayed by NRKW and ARKW were like those seen in SRKW: chasing the porpoise, herding and lifting it out of the water, tossing it into the air, and cradling or squeezing it between the flanks of two individuals. Of the seven incidents, two resulted in the suspected death of the porpoise and the outcome in five incidents was unknown.

4 | DISCUSSION

Southern Resident killer whales were regularly documented harassing or killing porpoises over the last 45 years, and this behavior appears to be both increasing in frequency and spreading among the population. Even though this endangered population is prey-limited (Hanson et al., 2010; U.S. Federal Register, 2005), consumption of porpoises was never observed. We considered several hypotheses for this behavior, the most likely of which include a form of play with social or developmental benefits, practice hunting, and/or displaced epimeletic behavior for reproductive females.

Porpoise-harassing by SRKW is consistent with the definition of “play” as put forward by Burdhardt (2005) and summarized by Kuczaj and Eskelinen (2014) and Hill et al. (2017): the behavior does not contribute to immediate survival; it is spontaneous yet intentional and pleasurable; it represents a modification of an inherent behavior; it is repeated but not rigid; and it does not occur during other behavioral states such as foraging, breeding, or defense. Play is associated more with younger individuals and is thought to be developmentally significant (see Kuczaj & Eskelinen, 2014). We observed that juvenile SRKW of both sexes had the highest engagement in porpoise harassment, although this was not significantly different from the level of engagement seen in most other sex-specific age-classes, including calves, sprouters, adult males, and reproductive females (Figure 8). Porpoise harassing incidents

sometimes involved multiple age classes at once (Figures 9 and 10) and with whales acting in “cooperation” with one another. For instance, SRKWs were seen carrying the porpoise on their backs, or “shouldering” the porpoise between multiple individuals, almost appearing as a “game” where the goal was to keep the porpoise out of the water. These behaviors might be considered a form of object-oriented play and could have indirect benefits for group coordination, cohesion, and social affiliation, as was hypothesized for common bottlenose dolphins that coordinated lethal, nonconsumptive attacks on harbor porpoises (Cotter et al., 2012). The locomotor aspects of this behavior, e.g., chasing the porpoise and manipulating it or positioning it in one's mouth, could also have practical benefits for coordination or strengthening a whale's physical condition and might indirectly improve the skills required for successful hunting. Sometimes SRKWs would continue engaging with the porpoise well after it had died, indicating that the killing of the porpoise was not the goal. The extended duration of porpoise-harassing incidents, some lasting multiple hours, without the termination in a set goal or outcome (i.e., none were ever knowingly consumed) might suggest that the act of interacting with a porpoise itself is, in some way, advantageous or “pleasurable” to the whales.

Killer whales are known to engage in practice hunting: catching and playing with or manipulating prey, performed by both young individuals and adults, which may allow youngsters to learn and practice hunting skills (Baird & Dill, 1995; Coscarella et al., 2015; Guinet, 1990; Hoelzel, 1991; Lopez & Lopez, 1985; Visser et al., 2007). Porpoise harassment and phocoenacide could be a form of hunting training for SRKWs. Postreproductive females, the most experienced hunters in the population, were involved in porpoise harassment the least, whereas juveniles, calves, and adults (perhaps teaching the youngsters) were involved more (Figure 8). In incidents where a single porpoise was targeted (91% of incidents) and the porpoise's age was known and reported, 80% of incidents involved porpoise neonates or calves (compared to 20% of incidents involving subadult or adult porpoises); these younger porpoises are similar in size to SRKWs' preferred prey, adult Chinook salmon. At birth, harbor porpoises are an average 80 cm in length and weigh 7.7 kg (Norman et al., 2018), and Dall's porpoises, 100 cm and 11.3 kg (Ferrero & Walker, 1999). Adult Chinook salmon typically measure approximately 90 cm in length and weigh 13.5 kg but can surpass this (National Oceanic and Atmospheric Administration, 2022).

Differentiating killer whale hunting practice from play is not always possible, and the two are likely interrelated. In the Salish Sea, Bigg's (mammal-eating) killer whales are known to engage in the surplus killing of harbor seals (*Phoca vitulina*), likely to enable calves and juveniles to learn hunting techniques or as play (Gaydos et al., 2005). Bigg's killer whales and killer whale populations off southern South Africa, Argentina, and Antarctica also hunt and occasionally consume marine birds, presumably as play or for training of younger individuals, as these interactions are likely energetically inefficient for killer whales compared to hunting and eating marine mammals (Hoelzel, 1991; Pitman & Durban, 2010; Stacey et al., 1990; Williams et al., 1990). Bigg's killer whales have been observed harassing but not consuming salmon throughout their range (J.R.T., personal observation), nearly a direct analog to SRKWs harassing porpoises. For SRKWs, porpoise-harassing behavior could provide both practical salmon hunting practice and play that benefits group cohesion, coordination, and bonding.

Another possible explanation for porpoise-harassing is displaced epimeletic behavior, which has been hypothesized as the driver for other interactions between dolphins and porpoises (Baird, 1998; Haelters & Everaarts, 2011). Epimeletic behavior occurs when an individual shows seemingly altruistic actions towards another that is ill, dying, or dead; in cetaceans, epimeletism is often characterized by one or more adults keeping a conspecific afloat or attempting to “resuscitate” it (Bearzi et al., 2018). Recently, a killer whale off West Iceland was seen with a long-finned pilot whale (*Globicephala melas*) calf swimming in echelon position (Mruszczok et al., 2023), leading to further discussion of possible epimeletic behavior across cetacean species. Epimeletic behavior has been observed in adult females of all three SRKW pods, and that which has received the most attention was J35, when in 2018, she carried her dead neonate for 17 days and 1,600 km (Shedd et al., 2020). There were similarities in behaviors reported for cetaceans engaged in epimeletism and SRKWs harassing porpoises, such as lifting or carrying the porpoise on the back, head, or rostrum, or in the mouth, cradling the porpoise between multiple individuals, seeming to attempt to keep the porpoise above water, or swimming with the porpoise in echelon position (Bearzi et al., 2018). The majority

of female SRKWs first engaged in porpoise-harassing behavior were of reproductive age, the age most expected to engage in epimeletic behavior.

Porpoise harassment by SRKWs is likely not due to sexual aggression as there was no difference in the rates at which males and females engaged in harassment, and juveniles and calves engaged in the behavior at levels similar to adults. This is unlike other cetaceans where object-carrying can be sexual in nature (Entiaspe-Neto et al., 2022) or is performed almost exclusively by males as a sociosexual display to attract females (Martin et al., 2008). For SRKWs, neither genital contact with the porpoise nor penile protrusion by male SRKWs were observed in any incident.

Killer whales share several life history traits with other species known to commit infanticide and this behavior has been documented in the Bigg's population (Towers et al., 2018). However, it is unlikely that SRKWs use porpoises to practice infanticide, due to the style of interactions compared to the more aggressive attacks documented during cetacean infanticide (Díaz López et al., 2018; Kaplan et al., 2009; Towers et al., 2018; Zheng et al., 2016).

There is minimal dietary overlap between SRKWs (Ford et al., 2016; Hanson et al., 2021) and porpoises in the Salish Sea (Elliser et al., 2020; Nichol et al., 2013; Walker et al., 1998), largely ruling out the hypothesis that porpoise-harassment is due to prey competition. It is possible that feeding interference or kleptoparasitism by porpoises could incite SRKW attack. Dall's porpoises and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) have been observed stealing remnants of salmon from SRKWs during food-sharing behavior within matriline; while the presence of the smaller cetaceans seemingly agitated the whales, no instance of aggression towards the porpoises or dolphins was observed (G.E., personal observation). Some SRKW-porpoise interactions could have started off as a reaction to feeding interference and evolved into a form of play or hunting practice. However, foraging activity by SRKWs was never noted prior to or during any of the SRKW-porpoise harassment incidents, and the energy expended in porpoise-harassing would likely be more costly than necessary if the primary goal was in defense of foraging opportunities, perceived prey, or site.

There are several possible reasons why SRKWs appeared to target harbor porpoises more than Dall's porpoises. Dall's porpoises are faster than harbor porpoises and likely would be harder for SRKWs to catch. Further, the temporal pattern of species-specific harassment of porpoises by SRKWs reflects porpoise abundance trends in the Salish Sea. From 1994 to 2015, the harbor porpoise population increased in the Salish Sea, while Dall's have since decreased (Evenson et al., 2016; Jefferson et al., 2016). Accordingly, prior to 1994, six out of 10 harassment incidents involved Dall's porpoises, and after the early 2000s, harbor porpoises became the main target of harassment. There is an overlap between harbor porpoise calving seasonality in the Salish Sea (July–November; Norman et al., 2018) and SRKW presence in the central Salish Sea during the summer months (Olson et al., 2018), so it is possible SRKW targeted younger porpoises due to their increased availability and detection. Certainly, there is a lower cost for SRKWs to catch a young porpoise compared to an adult, perhaps partly explaining why more younger individuals were targeted; however, SRKWs were capable of catching adult or subadult porpoises, most of which had no underlying conditions that would have predisposed them to attack (Table S3). The impact of SRKW-induced mortality on porpoise populations in the Salish Sea is unknown.

Based on the few carcasses examined, porpoises killed by SRKWs were likely healthy animals. Porpoises killed by SRKWs can have traumatic lesions that are so subtle that they are only visible microscopically and can also show more severe signs of trauma. Considering this, it can be extremely difficult to differentiate a porpoise carcass as killed by SRKWs versus Bigg's killer whales unless the events were witnessed. Compared to porpoises killed by SRKW, complete necropsy findings from three porpoises that were confirmed to have been killed by Bigg's killer whales reveal more severe lesions (J.K.G., J.K.O., S.A.N., S.A.R., unpublished data). Carcasses were not fully intact, and lesions consistently included fractured bones, amputations, or degloving of the skin and subcutaneous tissue.

Porpoise harassment and killing behavior was transmitted within matriline, the tightest social unit of SRKW society. Most porpoise harassment incidents were observed involving individuals from three L pod and four J pod matriline. Within these matriline, many younger individuals engaged in the behavior multiple times and across years, suggesting the behavior is repeated and retained within matriline over time (Figures 9 and 10). The behavior appears to be widespread throughout the population: only four matriline were never observed harassing porpoises,

of which two of the four matriline (K30 and L15) had died out early in the study period (1984 and 1982, respectively) and the other two matriline (L25 and L28) are comparatively smaller in number.

Within this population, porpoise harassing or killing behavior possibly originated with L pod and was later spread to or was adopted by K and J pods (Figure 6). Individual L5 and her offspring, L58 and L73, of the L9 matriline, were the first whales identified harassing a marine mammal, a harbor seal in 1987 (Felleman 1991, The Whale Museum, 1995). Individuals L5, L58, and L73 were also the first whales identified early on harassing a porpoise (Dall's porpoise) in 1992, and again in 1994 (Table S1). The increase in the number of observed harassment incidents after 2000 likely reflects the increased effort by researchers and whale watch organizations observing SRKWs.

Based on our observations, it is possible that porpoise harassing and killing behavior was spread via social learning (observation and imitation; Caro & Hauser, 1992) between individuals. Given that porpoise harassing behavior was transmitted within SRKW matriline and diffused between pods, the behavior fits some definitions of "culture," which has been broadly defined as information that can affect individuals' behavior that is acquired from others through social learning (Foote et al., 2016; Laland et al., 2010). A similar example of cultural spread of a behavior has been documented in SRKWs, albeit over a shorter time interval. In 1987, a female from K pod began carrying dead salmon on her head; a behavior never seen prior (Whitehead et al., 2004). Within weeks, members of J and L pods had learned and repeated the same behavior, which was not observed in any pod the following summer. Some killer whales off the coast of South Africa have been recorded consuming the liver of great white sharks (*Carcharodon carcharias*), a behavior which may have spread between individuals (Towner et al., 2022). Other examples of transmission of behavior and culture in cetaceans are abundant (Garland & Rendell, 2020; Whitehead, 2009), such as the spread of humpback whale (*Megaptera novaeangliae*) songs (Schulze et al., 2022), *Tursiops* sp. signature whistles (Caldwell & Caldwell, 1965) and sponging behavior (Krützen et al., 2014), and vocal clans in sperm whales (*Physeter macrocephalus*; Rendell & Whitehead, 2003).

Porpoise-harassing behavior is not unique to SRKWs, as NRKWs and ARKWs also engage in the behavior. However, the behavior is rare in NRKWs and ARKWs compared to in SRKWs, given the relatively high observation effort (research and whale watching) within portions of the ranges of the NRKW and ARKW populations (Towers et al., 2019). The reason(s) for the differences in occurrence of the behavior between salmon-eating killer whale communities is unknown. ARKWs are known to interact nonaggressively with other marine mammals (Saulitis et al., 2000) as are NRKWs. Another fish-eating population of killer whales in Russia's Kamchatka region and Commander Islands have never been observed harassing porpoises; in the Commander Islands, Dall's porpoises, northern fur seals (*Callorhinus ursinus*), and a Pacific white-sided dolphin have been observed traveling with groups of killer whales (E. Hoyt, personal communication, March 1, 2022).

In the northeastern Pacific Ocean, killer whale ecotypes differ genetically, morphologically, and behaviorally (Riesch et al., 2012). The resident, fish-eating ecotype is believed to be a result of culturally driven ecological specialization of matrilineally based social groups, in which foraging behavior is transmitted among matriline members through social learning, followed by cultural and/or genetic mechanisms promoting reproductive isolation (Baird et al., 1992; Whitehead & Ford, 2018). The SRKWs are salmon specialists, and their dietary preference has likely been reinforced culturally and genetically over thousands of years of specialization (Foote et al., 2016; Morin et al., 2010). Specialization allows for increased prey acquisition, but once specialized, it is highly unlikely that predators will return to being generalists (Whitehead & Ford, 2018). With that in mind, SRKW phocoenacide does not suggest that SRKWs will eventually include porpoises in their diet. This is further supported by the fact that SRKWs were never observed to consume the porpoises they killed, demonstrating the strength of SRKW dietary preferences and their culture of preying upon salmon. The fact that SRKWs do not consume the porpoises they kill is dissimilar to terrestrial carnivores that kill other carnivores, where it is less common for the killers not to consume their victims (Palomares & Caro, 1999). Ultimately, like other predators, killer whales are capable of chasing animals they do not kill (intentionally or not) and killing animals they do not eat (including prey and nonprey items).

There were some limitations to this study. Using the CWR sighting database as a denominator for rate of porpoise harassment was imperfect because not all cases came from CWR observations, but generally, CWR may have

seen the whales and recorded their presence even if they were not the ones to spot the actual porpoise interactions. The comparison of porpoise harassment by age class or sex could have been influenced by low sample size (observations of harassment). Observations of SRKWs by whale watchers, researchers, and the public increased over the study period (Ettinger et al., 2022; Olson et al., 2018) and during the summer months, resulting in an effort bias; these results are based primarily on summer observations and in inland Salish Sea waters. We did not have robust enough data to include in our analyses of the SRKWs that were present but did not engage in porpoise harassing, limiting our understanding of the sociality of this behavior. Not all whales that engaged in the behavior were able to be identified to the individual level. Furthermore, we defined matriline based on a common female ancestor and do not distinguish between changing social groups over time.

In conclusion, possible explanations as to why SRKWs harass and kill porpoises include the behavior being a form of play, practice fighting, and/or displaced epimeletic behavior. Porpoise-harassing behavior appears to have been transmitted within matriline and between pods and is likely an example of culture in the SRKW population.

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In memoriam, Kenneth C. Balcomb III.

Many of the authors of this paper share one thing in common: Ken Balcomb introduced them to the Southern Resident killer whales. Largely thanks to Ken's work, more is known about this extended clan of whales than almost any other cetacean population on the planet. For over 40 years, he closely observed these whales, sharing their stories, relationships, social dynamics, and fishing culture. Research today on this population stems from Ken's carefully kept record of their lives, births, and deaths and their fight for survival. For decades, Ken was at the center of their battle. He never stopped trying to ensure that the whales' plight was in the public's eye and in the minds of the elected officials and agencies responsible for recovering these whales. His legacy lives on in the movement he inspired, dedicated to saving this unique population from extinction.

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Deborah Giles: Conceptualization; data curation; investigation; methodology; project administration; supervision; visualization; writing – original draft; writing – review and editing. **Sarah Jessica Teman:** Data curation; formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Samuel Ellis:** Formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **John K.B. Ford:** Data curation; formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Monika W. Shields:** Data curation; formal analysis; methodology; writing – original draft; writing – review and editing. **Brad Hanson:** Data curation; writing – review and editing. **Candice Kathryn Emmons:** Data curation; writing – review and editing. **Paul Cottrell:** Data curation; writing – review and editing. **Robin Baird:** Data curation; writing – review and editing. **Richard W Osborne:** Data curation; writing – review and editing. **Michael Weiss:** Data curation; writing – review and editing. **David K Ellifrit:** Data curation; writing – review and editing. **Jennifer K Olson:** Data curation; writing – review and editing. **Jared R. Towers:** Data curation;

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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