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Vessels and their sounds reduce prey capture effort by endangered killer whales (*Orcinus orca*)

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ABSTRACT

Vessel traffic is prevalent throughout marine environments. However, we often have a limited understanding of vessel impacts on marine wildlife, particularly cetaceans, due to challenges of studying fully-aquatic species. To investigate vessel and acoustic effects on cetacean foraging behavior, we attached suction-cup sound and movement tags to endangered Southern Resident killer whales in their summer habitat while collecting geo-referenced proximate vessel data. We identified prey capture dives using whale kinematic signatures and found that the probability of capturing prey increased as salmon abundance increased, but decreased as vessel speed increased. When vessels emitted navigational sonar, whales made longer dives to capture prey and descended more slowly when they initiated these dives. Finally, whales descended more quickly when noise levels were higher and vessel approaches were closer. These findings advance a growing understanding of vessel and sound impacts on marine wildlife and inform efforts to manage vessel impacts on endangered populations.

1. Introduction

Successful outcomes in conservation often hinge on identifying and effectively managing anthropogenic threats to organismal populations. However, the mechanisms by which these threats operate are often challenging to elucidate in the marine environment. Vessel traffic is a common threat to cetaceans and other marine animals globally. Vessels can strike individuals, pollute the environment, disrupt behavioral activities, and introduce broadband noise that hinders the animals' use of sound (Senigaglia et al., 2016; Lundin et al., 2018; Erbe et al., 2019; Schoeman et al., 2020). Noise can mask acoustic signals used during communication and foraging, the latter having implications for energy acquisition (Erbe et al., 2016, 2019). Furthermore, many vessels emit high frequency sonar to aid in navigation or fishing (e.g., depth sounders and fish finders) but we know little about how these signals affect cetaceans' use of sound, especially for odontocete whales that rely on similar frequencies for biosonar-based foraging (Au 1993; Au et al., 2004).

Given the particular challenges of studying the behavioral ecology of marine species, there is often ambiguity about what aspects of vessel traffic (e.g. presence, acoustic footprint, operational aspects) create the largest risks (Pirotta et al., 2015; Erbe et al., 2019). The recent development of high-resolution biologging technologies has enabled opportunities to better understand the biology and ecology of marine vertebrates and how anthropogenic activities interact with free-ranging animals in their underwater environment (Johnson et al., 2009; Bogard et al., 2010). Here, we investigate vessel and associated sound variables on the behavior of an endangered population of fish-eating killer whales, the Southern Residents, who rely on sound for biosonar-based foraging (Barrett-Lennard et al., 1996; Holt et al., 2019). These resident killer whales preferentially hunt Pacific salmonids, especially Chinook salmon (*Oncorhynchus tshawytscha*), of which many stocks are also in decline (Ford and Ellis, 2006; Hanson et al., 2010, 2021; Ford et al., 2016). Additionally, there is substantial vessel traffic from whale-watching, commercial shipping, fishing and recreation in their transboundary core summer habitat that is an important foraging area for the

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population (NOAA, 2006; Holt et al., 2009; Veirs et al., 2016; Cominelli et al., 2018).

Previous studies reported changes in surface active and vocal behavior, diving and movement patterns, and behavioral activity states of resident killer whales in response to vessels and noise (Williams et al., 2002, 2009; Holt et al., 2009, 2021, Lusseau et al., 2009; Noren et al., 2009). Reduction in foraging behavior is a commonly observed response to vessel disturbance in many cetacean species and has potential impacts on an individual's ability to meet energetic requirements (Senigaglia et al., 2016). However, most of the earlier killer whale studies inferred changes in behavior based on observations when whales surfaced, even though most behavior, especially deep diving behavior involving prey capture, occurs at depth outside of the investigators' visual range (Wright et al., 2017; Holt et al., 2019, 2021; Tennessen et al., 2019a, 2019b). Both prey availability and disturbance from vessels and sound are identified as interactive threats to the population's recovery (NMFS, 2016). We therefore focused on the foraging behavior of individuals in this population to extend an understanding of vessel threats and, in particular, to assess what aspects of vessel traffic translate into the largest risks to their endangered status.

We used high-resolution animal-borne tags that collected both acoustic and movement data from Southern Residents, along with observations of successful predation and proximate vessels during these tag deployments, to understand the relationships between vessel and sound variables and foraging outcomes. Specifically, we used kinematic signatures derived from tag data to identify foraging dives involved in prey capture (Tennessen et al., 2019a), to test a number of vessel and associated sound variables on (1) the probability of prey capture and (2) multiple parameters of prey capture dives. Our findings advance a growing understanding of the negative impacts of vessels and sound on cetacean foraging behavior, reveal further insight into interactive threats to an endangered population, and provide data necessary to inform future management actions applicable to this and other marine species.

2. Materials and methods

2.1. Data collection

In September 2010, 2012 and 2014, and in June 2011, we deployed digital acoustic recording tags (Dtags, Johnson and Tyack, 2003) to Southern Resident killer whales in their core summer habitat of the Salish Sea including waters surrounding the San Juan Islands, WA, USA and Gulf Islands, BC, Canada (approximate range: 48.2°–49.0° N, 122.7°–123.6° W). The study location and season overlapped with vessel-based viewing of killer whales by commercial whale-watching tours as well as private boaters. Under research permits (in the USA, NMFS No. 781–1824/16163 and in Canada, DFO SARA/Marine Mammal License No. MML, 2010–01/SARA-106B) and the approval of the Northwest Fisheries Science Center's Institutional Animal Care and Use Committee, we attached Dtags to Southern Resident killer whales with suction cups using a carbon fiber pole from the bow pulpit of the research vessel. We identified individuals with known sex and age from established photo-identification catalogues developed by the Center for Whale Research (Ford et al., 2000). The Dtag housed two hydrophones, temperature, pressure and triaxial accelerometer and magnetometer sensors (Johnson and Tyack, 2003). We used the version 2 tag in 2010, 2011 and 2014, which sampled audio data at 192 kHz and non-audio data at 50 Hz, and version 3 tag in 2012, which sampled audio data at 240 kHz and non-audio data at 200 Hz. We programmed the tags to release 1 h before local sunset, although some released earlier due to suction cup failure.

During tag deployments, we conducted focal follows on the tagged whale and all vessels within 1.5 km of the focal whale, including the research vessel (Holt et al., 2017). We used two customized data collection packages, each consisting of a GPS/data component, a laser range finder, and compass to store focal follow data (Giles, 2014), which included tagged whale latitude and longitude during surfacings and any evidence of successful predation. Predation events from these observations included fish brought to the surface and/or pieces left behind, such as bits of fish tissue and scales, which when possible were collected for further analysis (Hanson et al., 2010). We recorded vessel data in concentric rings starting with those closest to the focal whale at least every 5 min. Variables recorded for each vessel included its latitude and longitude position, vessel name and class (commercial whale-watching, private, research, enforcement, etc.) and estimated speed (Holt et al., 2017). Vessel speed was estimated visually and then scored as follows: 0 = stationary, shut-down or idle; 1 = slow of 1–2 knots; 2 = medium of 3–4 knots; 3 = fast of 5–6 knots; 4 = very fast of 7+ knots, as most vessels around whales were smaller vessels that did not transmit automatic identification system (AIS) signals (Houghton et al., 2015). During focal follows, the research vessel operated at distances and speeds consistent with other vessels engaged in whale-watching and we periodically monitored its speed to ground truth speed estimates of other vessels.

2.2. Data processing and calculation of variables

We downloaded, calibrated and processed tag data using the Dtag Toolbox (www.soundtags.org), along with custom scripts in Matlab (version 2017a, Mathworks, Natick, MA). We calculated the start and end times of each dive from depth data down-sampled to 5 Hz using an automated detector that identified excursions from the surface ($\leq$0.5 m) to depths $\geq$ 1 m, which were checked for error and corrected as needed (Tennessen et al., 2019a). We excluded dives within the first 5 min of each tag onset time to address potential short-term behavioral responses to tagging (Tennessen et al., 2019a). Observed responses to tagging ranged from none to moderate, which included flinching upon contact or diving and remaining submerged for a few minutes, and all individuals returned to pre-tagging surfacing behavior within 5 min of tagging.

The process used to identify prey capture dives is described elsewhere (Tennessen et al., 2019a). Briefly, we identified all dives that fit a set of stereotyped movements that preceded confirmed predation events from field observations. This involved building a prey capture dive detector using tag movement variables that significantly predicted prey capture on a dive-by-dive basis, and validating performance of the detector with acoustically confirmed predation events (feeding buzzes and prey handling crunches; Holt et al., 2019) and running the detector on all data with the exception of those collected in 2011. We excluded 2011 data as they were collected in June when little echolocation, and no prey handling sounds or predation events were observed, likely reflecting seasonal differences in the distribution of Southern Resident preferred prey in the study area (Holt et al., 2019; Tennessen et al., 2019a). The three significant predictor variables included: 1.) jerk (rate of change of acceleration) peak, defined as the maximum peak of the jerk signal, normalized by the median jerk signal, 2.) roll at jerk peak (absolute value of the roll angle at the time of jerk peak, in degrees), and 3.) circular variance in heading angle during the bottom phase of the dive (70% of maximum dive depth). We computed threshold values for the three variables, and scored all dives that met these threshold criteria as prey capture dives (Tennessen et al., 2019a). The detector had a true positive rate of 79% and a false positive rate of 0.2% (Tennessen et al., 2019a).

The methods we used to collect vessel data during focal follows are described in Holt et al. (2017). Since dive data were collected continuously whereas vessel data were collected every 5 min as possible, we aligned vessel and dive data by calculating the midpoint in time of each dive and matching it temporally (±5 min) to the vessel data. If multiple observations of the same vessel occurred within a ±5 min interval, we only used the observation closest in time to the dive midpoint. Given that prey capture typically involves a pursuit phase of individual fish at depth with the whale ascending from depth only after prey is caught

Table 1
List of explanatory variables populated by dive and tested for significance in all full models.

Explanatory Variable	Form (level)
Sex	Factor (2)
Year	Factor (3)
Salmon abundance index	Linear
Vessel Count	Linear
Mean vessel distance	Linear
Median vessel speed	Linear
Received noise level	Linear
Echosounder presence/absence	Factor (2)

Table 2
Summary of tag deployments.

Year	Deployment	Whale ID	Sex	Tag duration (h)	No. dives ≥30 m
2010	oo10_257 m	L88	M	4.50	2
2010	oo10_261 m	L72	F	0.72	3
2010	oo10_264 m	L83	F	2.72	1
2010	oo10_265 m	K33	M	6.27	16
2010	oo10_267 m	J14	F	4.00	5
2010	oo10_268 m	L86	F	7.48	5
2010	oo10_270 m	L78	M	1.13	4
2012	oo12_250 m	L22	F	6.95	17
2012	oo12_251 m	K33	M	1.67	5
2012	oo12_261 m	L84	M	2.22	2
2012	oo12_266 m	L91	F	2.65	6
2012	oo12_266n	L47	F	0.78	1
2014	oo14_249 m	L113	F	7.17	13
2014	oo14_250 m	L89	M	8.88	11
2014	oo14_263 m	L85	M	6.38	7
2014	oo14_264 m	L91	F	0.83	4
2014	oo14_265 m	K35	M	4.77	13

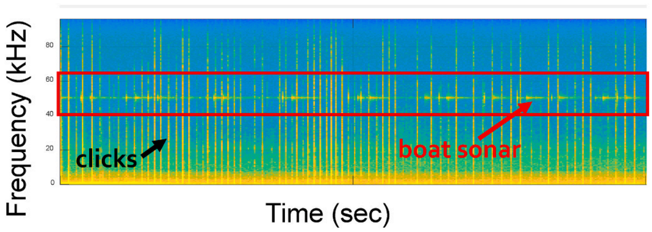

Fig. 1. Representative example of echolocation clicks of the tagged whale (black arrow) and 50 kHz navigational sonar emitted by boats (red arrow) recorded by the tag. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 3
Summaries of model results with all non-categorical model terms centered and scaled to mean 0 and SD 2 to facilitate interpretation.

Response	Model Terms	Est.	SE	*P*
Prey capture	Intercept	−0.80	0.32	
	Sex: male	1.22	0.45	0.004
	Salmon	1.27	0.45	0.003
	Vessel speed	−1.10	0.45	0.010
ln(dive duration)	Intercept	5.29	0.092	
	Sex: male	0.22	0.091	0.031
	Dive depth	0.41	0.084	<0.0001
	Echosounder	0.28	0.088	0.002
Rate of descent	Intercept	1.90	0.10	
	Dive depth	0.32	0.14	0.019
	Echosounder	−0.62	0.16	0.0001
	Vessel distance	−0.51	0.14	0.0006
	Noise level	0.33	0.16	0.041

(Wright et al., 2017; Tennessen et al., 2019a), the midpoint of a dive generally occurred when the whale was actively chasing prey at depth. Therefore, this midpoint is representative of the time at which the whale was actively pursuing prey (rather than after prey capture) on prey capture dives. The horizontal distance from whale to each unique vessel was estimated from the latitude and longitude positions of the vessel relative to the whale's latitude and longitude that was closest in time to the dive midpoint.

We measured received noise levels (dB re: 1 μPa) calculated from root-mean-squared pressure averaged over a 1-sec period for all portions of the acoustic record unaffected by flow noise or other extraneous sounds (surface splashing, killer whale sounds) following Holt et al. (2017). Specifically, for each deployment we identified intervals of the acoustic recording contaminated by flow noise in one-third octave bands using the methods of von Benda-Beckman et al. (2016) and removed these intervals from the analysis. Flow or pseudo noise from tags attached to moving whales would otherwise confound accurate characterization of broadband noise introduced by vessels (von Benda-Beckman et al., 2016; Holt et al., 2017). We then populated available noise levels for each dive, which was a different pool of noise level data than what Holt et al. (2017) reported because tag data from 2011 as well as dives with maximum depth < 30 m were not included in the current analysis (see below). We also scored the presence of echosounder signals, i.e., sonar signals emitted by vessels to aid in navigation and fishing, received by the tag (both transmitted and reflected signals) for each dive (Holt et al., 2021).

2.3. *Statistical analysis*

We tested a number of explanatory variables of vessels and associated sounds, demographics, and environmental factors on the probability of prey capture for all dives to depth of resident killer whale preferred prey (dives with a maximum depth ≥ 30 m, Candy and Quinn, 1999; Wright et al., 2017; Tennessen et al., 2019a). Dives with maximum depth <30 m were very unlikely to involve prey pursuit, attempted capture or successful capture of prey based on behavioral states characterized from acoustic and movement tag data on a dive-by dive basis; rather, dives <30 m were characterized as those involving searching for prey using echolocation with no indication of pursuing prey, or silent travel/respiratory dives (Holt et al., 2019, 2021; Tennessen et al., 2019b). We used generalized linear modeling, assuming a binomial response distribution (logit link function), to test effects on the probability of prey capture (Zuur et al., 2009). There was no evidence of temporal autocorrelation in the response variable as Southern Resident dives ≥ 30 m, including prey capture dives, do not occur in bouts (Tennessen et al., 2019a, 2019b).

The acoustic explanatory variables included received noise levels and the presence of echosounder signals received by the tag. To test for an effect of received noise levels, we first compared four candidate full models, each included all of the vessel and demographic explanatory variables (as described below, Table 1) with different bandwidths of measured noise, which were: 1.) 0.5–65 kHz, 2.) 1–65 kHz, 3.) 2–65 kHz, and 4.) 10–65 kHz. These noise metrics were compared given the trade-offs of including low frequency components of noise and flow noise contamination, as flow noise predominates at the lower frequencies and therefore including lower frequencies limits sample size. The bandwidth 10–65 kHz was particularly limited to frequencies used for biosonar-based foraging (Holt et al., 2019), which yielded the largest sample size. The upper frequency cut-off of 65 kHz was set based on the roll-off in receiving sensitivity of the hydrophones within the tags. We then tested whether the minimum, mean, median or maximum noise level calculated from all available 1 s measurements across each dive was best to include as the noise explanatory variable, selecting the one with the lowest AIC score. In this case, the best (lowest AIC score) model included the maximum received level integrated over the 10–65 kHz noise band, although delta AIC among models were all < 1.

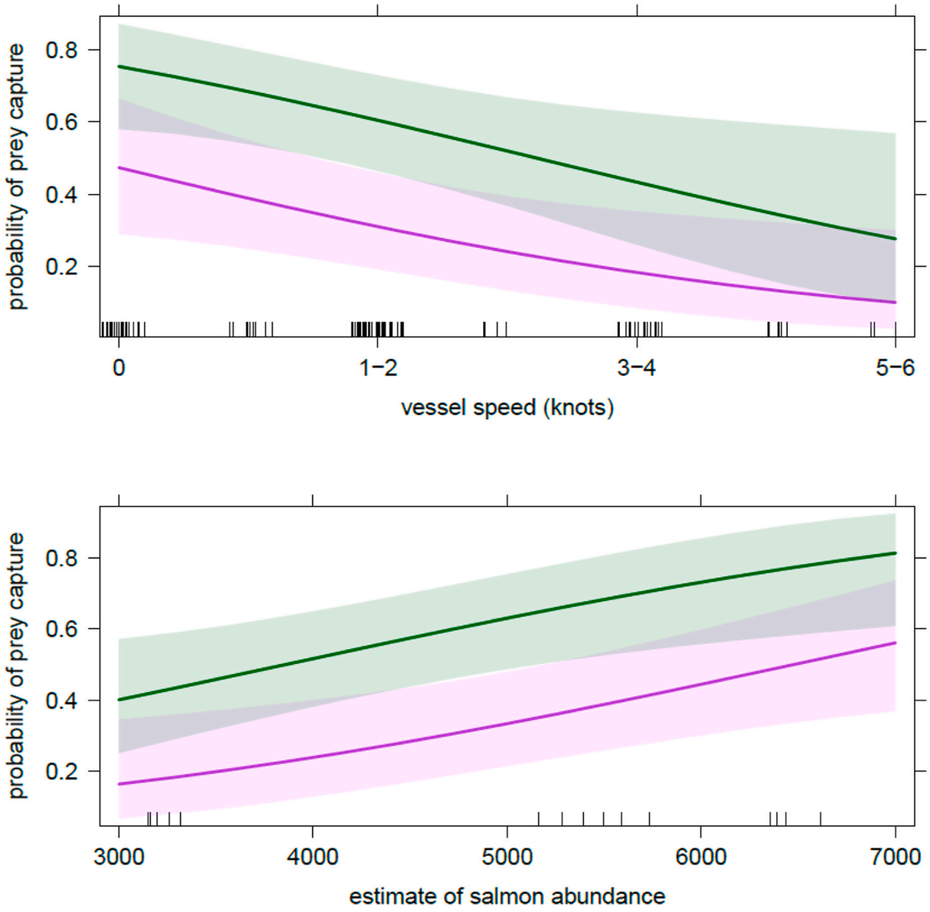

Fig. 2. Probability of prey capture as predicted by vessel speed (top) and salmon abundance (bottom) for females (purple) and males (green) when setting the other covariate to its mean value, shading indicates 95% confidence band. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Vessel explanatory variables in full models included vessel counts, average vessel distance, and median vessel speed of all unique vessels within 1.5 km (Table 1; Holt et al., 2017). We used median vessel speed as the central tendency in this case because the variable was coded as an ordinal numbered variable. We compared candidate full models with different ways to code the contribution of speed for all proximate vessels either as an unordered factor, ordered factor, or continuous variable and the model with the lowest AIC score included vessel speed as a continuous variable. We justify this choice because the numerical distance between each set of subsequent categories was equal across the range of median vessel speed in the data beyond a stationary value (see Results below).

Demographic and environmental explanatory variables in full models included sex, year and an estimate of salmon abundance in the area on the day of tagging using methods described in Ford et al. (2016). Briefly, we used data from a test fishery operated by Fisheries and Oceans Canada at the Fraser River mouth to estimate an index of daily combined Chinook and coho (*Oncorhynchus kisutch*) salmon abundance in the tag data collection area. We estimated daily abundance from catch-per-unit-effort data that were scaled by estimated total annual run size, smoothed by local polynomial regression, and adjusted for travel time between the test fishery and the tagging location (Ford et al., 2016). Stocks originating from Fraser River system make up a considerable portion of the Southern Resident summer diet in inland waters and both salmon species were approximately equally represented in the prey samples collected from tagged individuals during focal follows of the current study, consistent with September findings of other studies (Hanson et al., 2010, 2021; Ford et al., 2016). There was no evidence to include an individual-based random factor in the model structure when we compared models with and without a random factor, and interpreted the variance parameter of the random factor in the mixed effect model.

We also tested the effects of each of the explanatory variables on the parameters of prey capture dives using linear mixed effect models, with tag deployment specified as a random effect. Response variables were modeled using a Gaussian distribution and included dive duration (log transformed to meet model assumptions) and rate of descent during the descent phase (the first 70% of maximum dive depth; Arranz et al., 2016).

For all full models, we explored potential issues of collinearity among covariates, removing any as needed, and tested the significance of each explanatory variable by comparing nested models using a backward elimination process with significance defined as $\alpha < 0.05$ (Table 1, Zuur et al., 2009). We retained only the significant explanatory variables in all final models. Non-categorical explanatory variables were centered (mean subtracted) and scaled (divided by 2 SD) to facilitate comparison of effects based on parameter estimates (Gelman, 2008) but effects presented in figures are all plotted in original (un-centered and unscaled) space to aid in visual interpretation. We performed model validation following standard statistical practices including inspecting model residuals for potential issues of non-linearity and outlier data points (Zuur et al., 2009). In the case of rate of descent, we removed one potential outlier upon inspection of model residuals and re-ran model selection accordingly. We conducted all statistical analyses in R version 3.6.2 (R Core Team).

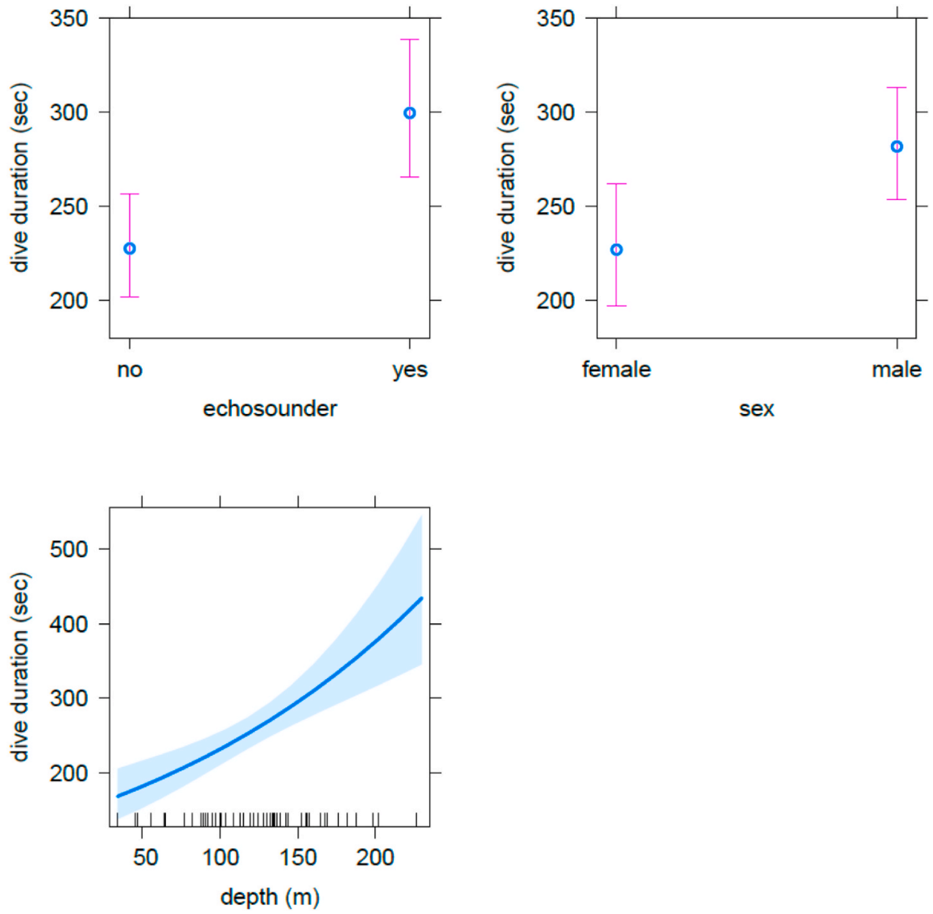

Fig. 3. Plots of marginal effects of echosounder signal (top left), sex (top right) and dive depth (bottom) on the duration of prey capture dives, when setting the other covariates to their mean values, bars and shading indicates 95% confidence band. Note that the response variable was log-transformed in the linear model but is plotted on an arithmetic scale to aid interpretation.

3. Results

Tagged Southern Residents made 115 candidate prey capture dives (≥30 m; male: n = 60, female: n = 55) in which we could measure (1) received noise levels unaffected by flow noise or other extraneous sounds in the 10–65 kHz band, and (2) all other vessel and sound variables. The dives were pooled across 17 tag deployments and 15 individuals (two individuals were tagged twice but in separate years, Table 2). Echosounder signals were detected during 52% (60/115) of these dives and the vast majority occurred at a center frequency of 50 kHz (Fig. 1), coinciding with the center frequency of killer whale outgoing echolocation clicks (Au et al., 2004). Noise level ranged between 88.3 and 138.9 dB re: 1 μPa (10–65 kHz), median vessel speed ranged between 0 (stationary) and 3 (5–6 knots), and mean vessel distance ranged between 21 and 852 m. We found that vessel speed ($\chi^2 = 6.62$, df = 1, P = 0.010), salmon abundance ($\chi^2 = 8.66$, df = 1, P = 0.003), and sex ($\chi^2 = 8.10$, df = 1, P = 0.004) were significantly associated with the probability of prey capture. In particular, the probability of prey capture was lower in females, as salmon abundance decreased, and as vessel speed increased (Table 3, Fig. 2). We also found that the duration of prey capture dives (N = 55, male: n = 35, female: n = 20) was greater in the presence of echosounder signals ($\chi^2 = 9.38$, df = 1, P = 0.002, Fig. 3), in males ($\chi^2 = 4.62$, df = 1, P = 0.031, Fig. 3), and on deeper dives ($\chi^2 = 20.6$, df = 1, P < 0.0001; Table 3, Fig. 3; deployment ID random intercept term variance = 2.03e-5, SD = 0.306). Moreover, whales also descended to depth more quickly on those prey capture dives when vessels were closer (N = 54, $\chi^2 = 11.68$, df = 1, P = 0.0006, Fig. 4), noise levels were greater ($\chi^2 = 4.18$, df = 1, P = 0.041, Fig. 4) and maximum depth was greater ($\chi^2 = 5.49$, df = 1, P = 0.019, Fig. 4), but they descended more slowly when echosounder signals were present ($\chi^2 = 14.39$, df = 1, P = 0.0001; Table 3, Fig. 4; deployment ID random intercept term variance = 2.23e-5, SD = 0.477).

4. Discussion

In this study, we investigated the relationship between environmental, demographic and vessel variables on killer whale behavior using high-resolution multi-sensor suction cup tags. Specifically, we tested whether vessel count, speed and distance, received noise level, echosounder signal presence, and salmon abundance significantly predicted the probability of prey capture. We also tested whether these vessel and sound variables were significant explanatory variables on aspects of prey capture dives.

We evaluated the probability of prey capture for all dives to depths ≥ 30 m. Approximately half (55/115) of these dives involved successful prey capture indicated by their kinematic signatures (Tennessen et al., 2019a). The remaining dives, based on maximum dive depth and behavioral state characterized in previous investigations (Holt et al., 2019, 2021; Tennessen et al., 2019a, 2019b), likely involved acoustically searching for and initiating pursuit of prey, that did not include prey capture (given the lower values of jerk, roll, heading variance and buzzing). Southern Resident killer whales had a lower predicted probability of capturing fish when estimated abundance of their preferred prey (Hanson et al., 2010; Ford et al., 2016) was lower and when nearby vessel speed increased (Table 3, Fig. 2). Females also had a lower predicted probability of capturing prey relative to males (Fig. 2), an

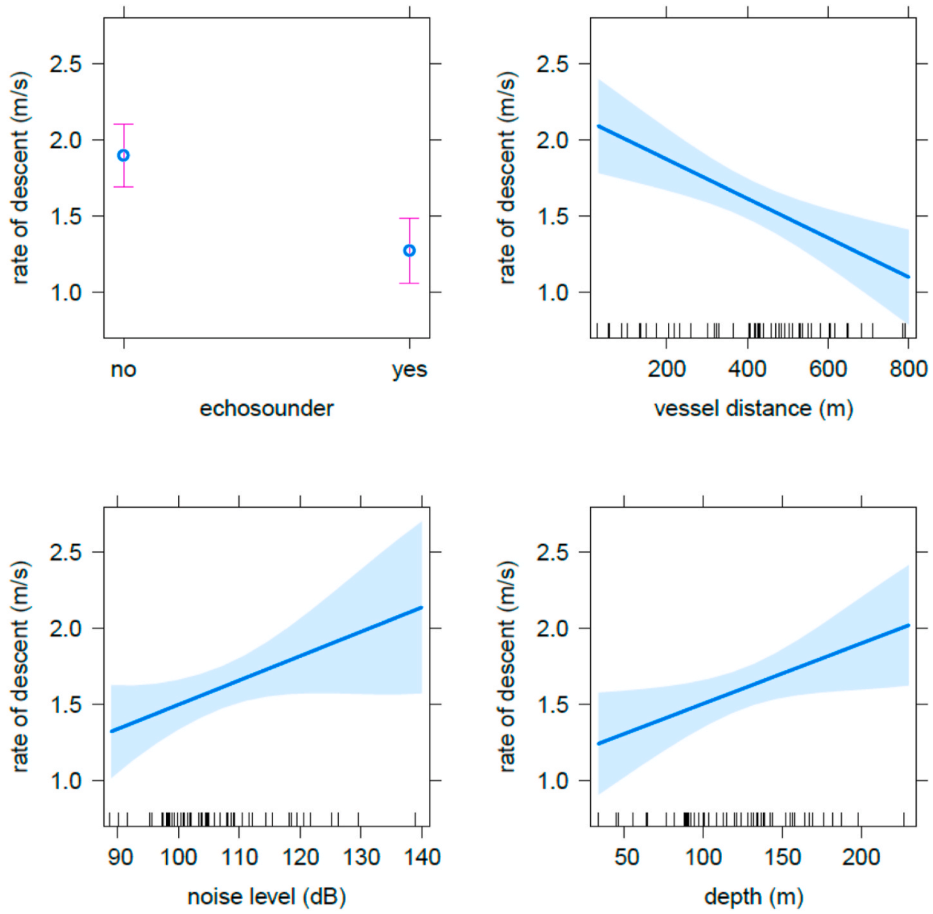

Fig. 4. Plots of marginal effects of echosounder signal (top left), vessel distance (top right), noise level (bottom left) and dive depth (bottom right) on rate of descent of prey capture dives, when setting the other covariates to their mean values, bars and shading indicates 95% confidence band. Noise levels are based on the maximum received sound pressure level (in dB re: 1 μPa) between 10 and 65 kHz.

expected sex effect based on previous work (Tennessen et al., 2019a, 2019b; Holt et al., 2021), and consistent with Williams et al. (2002) who also demonstrated differences in swimming behavior between male and female Northern Resident killer whales when approached by vessels.

There are a number of explanations for the negative relationship between probability of prey capture and vessel speed we found in the current study. Speed of nearby motorized vessels is one of the most significant positive predictors of underwater noise level introduced into the marine environment and received by killer whales (Houghton et al., 2015; Holt et al., 2017; Joy et al., 2019; MacGillivray et al., 2019). Noise could interfere with the whales' critical use of echolocation during foraging (Barrett-Lennard et al., 1996; Holt et al., 2019). Yet, unexpectedly, received noise level was not a significant effect on the probability of prey capture in the current investigation, which may be due to our restricted sample size as flow noise often contaminated the acoustic record of the tag. Another possibility is that faster vessels at the surface are less predictable and therefore require increased vigilance by an obligate air-breathing marine predator that hunts evasive fish during relatively deep and lengthy dives (Wright et al., 2017; Tennessen et al., 2019a). Moreover, resident killer whales often share prey among related group members at shallower depths (Ford and Ellis, 2006; Wright et al., 2016). Thus, the extra attention required in the presence of faster nearby vessels may result in reduced deep foraging dives involving successful capture of prey in the individuals studied here.

In addition, and importantly while accounting for effects of maximum dive depth, whales made longer dives to capture prey and descended more slowly as they initiated these dives when nearby vessels emitted sonar signals (Figs. 3 and 4). The influence of echosounder signals on dive duration and descent rate suggests potential interference with foraging behavior, or prolonged effort to successfully hunt fish prey, which might arise from acoustic masking. The vast majority of echosounder signals recorded by the tags were from 50 kHz navigational sonar, detected on approximately half of all dives, thus having high masking potential because of the overlap with the center frequency of the echolocation signals that killer whales use during foraging (Au et al., 2004; Erbe et al., 2016). Responses to echosounders might also arise from the whales' increased attention to vessels emitting sonar. For example, short-finned pilot whales varied their heading more frequently when a scientific echosounder was active during a controlled exposure study, potentially reflecting an increased awareness of the location of echosounder source (Quick et al., 2016). The current investigation provides new evidence of the consequences of prevalent navigational sonar emitted by vessels on the foraging behavior of killer whales. Additionally, when whales initiated prey capture dives, they descended to depth more quickly when broadband (10–65 kHz) noise level was higher and vessel distance decreased, on average (Fig. 4), consistent with a vertical avoidance response to noisy, close vessels.

Daily estimate of salmon abundance in the tagging area was a significant predictor of the probability of prey capture, a finding that provides experimental evidence that the rate of food intake in Southern Residents is to some extent limited by the abundance of their preferred prey. Although we used an index of salmon abundance based on estimates derived from test fisheries of the Fraser River and not all Chinook and coho salmon available to the whales in the study location originate from this system, these stocks make up a considerable portion of the Southern Resident summer and early fall diet in inland waters (Hanson et al., 2010, 2021). Moreover, analysis of prey samples collected from tagged individuals in this study indicate that selection of these salmon species matched well in space and time to results of other studies on Southern Resident diet composition (Hanson et al., 2010, 2021; Ford et al., 2016). Prey availability and disturbance from vessels and noise are identified threats that are suspected to interact given the whales' reliance on sound to hunt their declining prey in core summer habitat coinciding with ubiquitous vessel traffic (NMFS, 2016; Murray et al., 2021). Here, we provide empirical evidence of an interplay between prey abundance and disturbance that can limit access to food in a population that has failed to recover since endangered status listing (NMFS, 2016). Consequences of reduced food intake include negative impacts on the whales' ability to meet their energetic requirements to support key life functions, including growth and reproduction.

The influences of salmon abundance, vessel speed, noise and echosounder signals on prey capture dives in an endangered population has significant implications for management. In particular, vessel regulations have been implemented under various governmental jurisdictions to protect killer whales from disturbance by vessels and sound (reviewed in Holt et al., 2021). Furthermore, the consequences of underwater noise and vessel presence have been identified as an urgent research need for assessing cumulative effects of the identified threats to resident killer whale populations (Murray et al., 2021). This study contributes to a growing understanding of the consequences of vessel sounds, prey abundance, and anthropogenic disturbance on the behavior of cetaceans, and specifically extends previous findings of vessel impacts on Southern Resident killer whale foraging behavior (Lusseau et al., 2009; Friedlaender et al., 2016; Isojunno et al., 2016; Wisniewska et al., 2018; Holt et al., 2021). Here, we demonstrated that lower salmon abundance and higher vessel speed was correlated with a reduction in the probability of prey capture in an endangered population while feeding in its core summer habitat. Furthermore, we revealed vessel sound and proximity consequences on the duration and rate of descent of prey capture dives. Whales descended to depth more slowly while increasing the duration of prey capture dives when vessels emitted navigational sonar, indicating prolonged effort to successfully hunt at depth. In addition, whales descended to depth more quickly when foraging around noisier, closer vessels, consistent with a vertical avoidance response. While we offer reasonable causative explanations for our findings, some care must be taken in strictly assigning cause and effect relationships, as in any observational study it is conceivable that relationships among variables are influenced by other, unmeasured, variables. Taken together, these findings underscore the importance of conducting field-based research to inform management of endangered species, especially efforts to increase salmon abundance and amend existing vessel regulations within an adaptive management framework (NOAA, 2019; Southern Resident Orca Task Force, 2019). Moreover, these results advance a growing awareness of the negative consequences of vessels on marine wildlife in an urban coastal corridor used for a variety of human activities, confirm the prey-disturbance threat interaction in endangered killer whales, and are the first to demonstrate a potential effect of echosounder signals on foraging behavior.

CRediT authorship contribution statement

Marla M. Holt: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Visualization, Supervision, Project administration, Funding acquisition. **Jennifer B. Tennessen:** Methodology, Validation, Formal analysis, Writing – review & editing. **M. Bradley Hanson:** Conceptualization, Methodology, Investigation, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Candice K. Emmons:** Methodology, Investigation, Resources, Writing – review & editing. **Deborah A. Giles:** Methodology, Investigation, Resources, Writing – review & editing. **Jeffrey T. Hogan:** Investigation, Writing – review & editing. **Michael J. Ford:** Formal analysis, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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