










## RESEARCH ARTICLE

# Males miss and females forgo: Auditory masking from vessel noise impairs foraging efficiency and success in killer whales

Jennifer B. Tennessen<sup>1,2</sup>  | Marla M. Holt<sup>2</sup>  | Brianna M. Wright<sup>3</sup>  |  
M. Bradley Hanson<sup>2</sup>  | Candice K. Emmons<sup>2</sup>  | Deborah A. Giles<sup>4</sup>  |  
Jeffrey T. Hogan<sup>5</sup>  | Sheila J. Thornton<sup>6</sup>  | Volker B. Deecke<sup>7</sup> 

<sup>1</sup>Center for Ecosystem Sentinels, Department of Biology, University of Washington, Seattle, Washington, USA

<sup>2</sup>Conservation Biology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, Washington, USA

<sup>3</sup>Pacific Biological Station, Fisheries and Oceans Canada, Nanaimo, British Columbia, Canada

<sup>4</sup>Wild Orca, Friday Harbor, Washington, USA

<sup>5</sup>Cascadia Research Collective, Olympia, Washington, USA

<sup>6</sup>Pacific Science Enterprise Centre, Fisheries and Oceans Canada, West Vancouver, British Columbia, Canada

<sup>7</sup>Institute of Science and Environment, University of Cumbria, Ambleside, Cumbria, UK

## Correspondence

Jennifer B. Tennessen, Center for Ecosystem Sentinels, Department of Biology, University of Washington, Seattle, WA 98195, USA.  
Email: [jtenness@uw.edu](mailto:jtenness@uw.edu)

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## Abstract

Understanding how the environment mediates an organism's ability to meet basic survival requirements is a fundamental goal of ecology. Vessel noise is a global threat to marine ecosystems and is increasing in intensity and spatiotemporal extent due to growth in shipping coupled with physical changes to ocean soundscapes from ocean warming and acidification. Odontocetes rely on biosonar to forage, yet determining the consequences of vessel noise on foraging has been limited by the challenges of observing underwater foraging outcomes and measuring noise levels received by individuals. To address these challenges, we leveraged a unique acoustic and movement dataset from 25 animal-borne biologging tags temporarily attached to individuals from two populations of fish-eating killer whales (*Orcinus orca*) in highly transited coastal waters to (1) test for the effects of vessel noise on foraging behaviors—searching (slow-click echolocation), pursuit (buzzes), and capture and (2) investigate the mechanism of interference. For every 1 dB increase in maximum noise level, there was a 4% increase in the odds of searching for prey by both sexes, a 58% decrease in the odds of pursuit by females and a 12.5% decrease in the odds of prey capture by both sexes. Moreover, all but one deep ( $\geq 75$  m) foraging attempt with noise  $\geq 110$  dB re  $1 \mu\text{Pa}$  (15–45 kHz band;  $n = 6$  dives by  $n = 4$  whales) resulted in failed prey capture. These responses are consistent with an auditory masking mechanism. Our findings demonstrate the effects of vessel noise across multiple phases of odontocete

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foraging, underscoring the importance of managing anthropogenic inputs into soundscapes to achieve conservation objectives for acoustically sensitive species. While the timescales for recovering depleted prey species may span decades, these findings suggest that complementary actions to reduce ocean noise in the short term offer a critical pathway for recovering odontocete foraging opportunities.

#### KEYWORDS

anthropogenic noise, auditory masking, biologging, Dtag, echolocation, foraging behavior, foraging success, killer whale, odontocete, *Orcinus orca*

## 1 | INTRODUCTION

Rapid environmental change driven by human activities creates sensory pollutants that alter biological processes (Dominoni et al., 2020; Sih et al., 2011). Acquiring energy to meet basic needs is a fundamental requirement for all organisms. Individuals that do not take in enough energy may delay or skip reproduction in a given year, produce viable offspring but fail to finance the costs of provisioning and parental care (e.g., Gavrilchuk et al., 2021; Kershaw et al., 2021), or experience higher rates of offspring mortality (e.g., IJsseldijk et al., 2021; Wasser et al., 2017), consequently impairing population growth.

For odontocetes (toothed whales), sound plays a critical role in meeting energetic requirements, as foraging is facilitated by biosonar (Au, 1993; Moss et al., 2023). Odontocetes' sound use during foraging begins with a searching phase, during which the individual sends out broadband, high-intensity echolocation clicks and interprets the information conveyed in their returning echoes to detect prey location and distance, and to discriminate species and size information (Au et al., 2004, 2009, 2010). Once prey is detected, the animal initiates a pursuit phase during which it emits broadband, rapid burst echolocation click trains ("buzzes") with short inter-click intervals (high clicking rates) and low output levels that trade strong echoes for rapid updates about prey position to facilitate fine-scale prey targeting, pursuit, and terminal-phase prey chases (e.g., Arranz et al., 2016; Holt et al., 2019; Johnson et al., 2004; Madsen et al., 2005; Miller et al., 2004; Wisniewska et al., 2014; Wright et al., 2021). Following pursuit, the animal may capture the prey, which is often associated with incidental sound production including crunches and thumps related to shaking and positioning prey within its mouth (Holt et al., 2019; Wright et al., 2021). The individual may then consume prey alone or prepare it for subsequent sharing among group members (Baird & Dill, 1996; Ford & Ellis, 2006; Hoelzel, 1991; Lopez & Lopez, 1985; Pitman & Durban, 2012; Wright et al., 2016), which can include incidental sound production related to shaking, tearing, crunching, and repositioning prey (Holt et al., 2019; Wright et al., 2021).

Recent influxes of sound into ocean soundscapes from human-generated (anthropogenic) activities have created novel acoustic environments that interfere with odontocetes' basic activities and can threaten population growth and survival (Duarte et al., 2021; Erbe

et al., 2016, 2019; Nowacek et al., 2007; Weilgart, 2007; Wright et al., 2007). Increased noise can cause habitat loss by reducing the acoustic space through which sound-producing species send and receive intentional and incidental signals critical for survival, growth, and reproduction (Clark et al., 2009; Tennessen & Parks, 2016; Williams et al., 2014). However, empirical evidence of the impacts of noise on odontocete foraging behavior is currently limited.

Shipping is the most widespread source of anthropogenic sound in marine ecosystems and is growing rapidly (Duarte et al., 2021; Hildebrand, 2009; Kaplan & Solomon, 2016; Possenti et al., 2024). Moreover, predicted changes in ocean circulation patterns, increasing water temperatures, and acidification due to greenhouse gas emissions may change the physical properties of oceans and thus acoustic propagation efficiency. These changes may include altered sound speed profiles, reduced sound absorption at lower frequencies, and creation of subsurface ducts, further exacerbating increases in ocean noise and affecting transmission and reception of important biological signals (Affatati et al., 2022; Hester et al., 2008; Ilyina et al., 2010; Lynch et al., 2018; Possenti et al., 2024). The increase in vessel traffic and associated noise in existing shipping hotspots, as well as expansion into new areas, may catalyze new pathways for noise interference with odontocete activities including foraging (Duarte et al., 2021).

Understanding how noise affects a species' perceptual abilities is integral to predicting response severity. Anthropogenic noise can impact biological activities through at least three distinct perceptual mechanisms that link environmental stimuli to responses: masking, distracting, and misleading (Dominoni et al., 2020). These mechanistic pathways are useful for predicting how vessel noise may interfere with odontocete foraging. Anthropogenic noise can mask information conveyed in the returning echoes of echolocation clicks and buzzes, sounds produced by prey, and information communicated to conspecifics within foraging groups (Erbe et al., 2016). Anthropogenic noise can also distract foragers by diverting their attention to other stimuli or tasks (Allen et al., 2021; Branstetter et al., 2018; Luo et al., 2015), or it can mislead foragers to interpret the noise as a predator's sound and elicit antipredator responses including ceasing foraging and initiating flight behaviors (Miller et al., 2022). The conditions in which vessel noise may interfere with foraging ability (masking), cause physical/psychological disturbance (distracting), or elicit antipredator behavior (misleading) are poorly

understood. Identifying the mechanism(s) by which vessel noise impacts odontocete foraging behavior can help advance conservation efforts globally for this at-risk taxon.

Determining the relationship between vessel noise and foraging success has been limited by the challenges of distinguishing the effects of vessel noise from vessel presence, measuring the noise level received by the subject, identifying prey capture events that often occur out of sight of observers, and obtaining sufficient sample sizes of a broad range of noise levels across a range of behavioral contexts to have statistical power to detect an effect. Studies have linked some underwater noise sources, for example, military sonar, to reduction or cessation of foraging (DeRuiter et al., 2013; Isojunno et al., 2016; Miller et al., 2015, 2022; Sivle et al., 2016; Stimpert et al., 2014; Wensveen et al., 2019), and these responses may carry energetic costs (Czapanskiy et al., 2021). Limited evidence links vessel noise to altered odontocete foraging effort (Aguilar Soto et al., 2006; Azzara et al., 2013; Holt, Tennessen, Hanson, et al., 2021; Pirodda et al., 2012; Thode et al., 2007; Wisniewska et al., 2018). Models have predicted reductions in foraging time and space due to vessel noise (Joy et al., 2019; Thornton et al., 2022; Williams et al., 2014, 2021). However, the relationship between received level of vessel noise and foraging behavior for each phase of odontocete foraging and the mechanism(s) by which vessel noise interferes with foraging are unknown. Given the critical relationship between foraging, survival, and reproduction, the spectral overlap between vessel noise and echolocation sounds (Burnham et al., 2023; Veirs et al., 2016; Wladichuk et al., 2019), the positive effects of vessel quantity and speed on noise level (Holt et al., 2017), the growing intensity and spatiotemporal extent of vessel noise globally (Duarte et al., 2021; Kaplan & Solomon, 2016; Possenti et al., 2024), the at-risk status of many odontocetes worldwide (Chen et al., 2022; Davidson et al., 2012; IUCN, 2022; MacLeod, 2009), and their role as apex predators in their marine ecosystems, understanding vessel noise impacts on the foraging ecology of odontocetes is an urgent conservation priority (Duarte et al., 2021; Erbe et al., 2019).

Northern and southern resident populations of fish-eating killer whales (*Orcinus orca*) inhabit overlapping ranges along the west coast of the United States and Canada. Northern resident killer whales (NRKW) are listed as threatened under Canada's *Species at Risk Act* (SARA; DFO, 2017), and southern resident killer whales (SRKW) are endangered under SARA and the United States' *Endangered Species Act* (DFO, 2017; National Marine Fisheries Service, 2016). Reduced accessibility and availability of preferred salmonid prey, and disturbance from vessels and associated vessel noise (DFO, 2018; Murray et al., 2021) are among the risk factors threatening the recovery of resident-ecotype killer whales, who rely on acoustic information conveyed in returning echolocation clicks and buzzes (Au et al., 2010) to locate, pursue, and capture prey (Holt et al., 2019; Wright et al., 2021). Residents feed primarily on Chinook (*Oncorhynchus tshawytscha*), coho (*Oncorhynchus kisutch*), and chum (*Oncorhynchus keta*) salmon (Ford et al., 2016; Ford & Ellis, 2006; Hanson et al., 2010, 2021), which are often broken up and shared

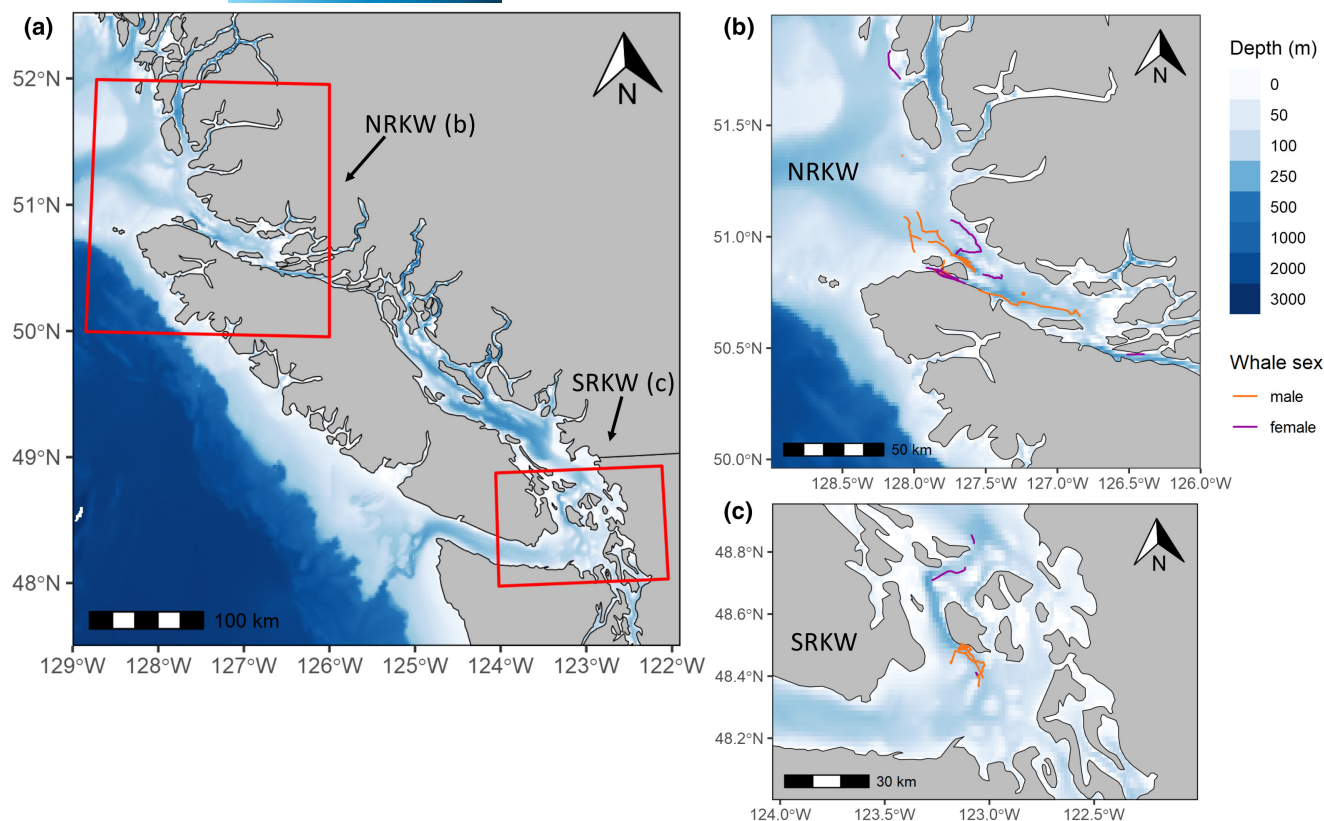
with other group members following prey capture (Holt et al., 2019; Wright et al., 2016, 2021). Vessel noise is pervasive and constant in resident killer whale critical habitat (Burnham et al., 2021, 2023) due to the proximity of three international ports and substantial recreational and commercial vessel activity. A typical modern ship passing through the core summer habitat of resident killer whales raises broadband ambient noise levels by 12–17 dB above “ancient ambient” (Clark et al., 2009) levels, measured between 20 and 70 kHz, the primary range used for echolocation (Veirs et al., 2016). Moreover, noise levels received by resident killer whales are positively correlated with the quantity and speed of nearby motorized vessels (Holt et al., 2017). Consequently, vessel noise is expected to disrupt acoustically mediated foraging in at-risk resident killer whales (Burnham et al., 2023; Holt, Tennessen, Hanson, et al., 2021; Joy et al., 2019; Veirs et al., 2016; Williams et al., 2021), but testing this hypothesis has been difficult due to limited availability of empirical data.

We used a unique acoustic and movement dataset from animal-borne biologging tags temporarily attached to individuals from two resident-ecotype killer whale populations (NRKW and SRKW) in coastal waters with high levels of industrial and recreational shipping to (1) test for the effects of vessel noise on the likelihood of occurrence of dives containing searching, pursuit, and prey capture phases of odontocete foraging behavior, as well as the likelihood of prey capture failure during deep foraging attempts, and (2) determine the mechanism of interference. We predicted that noise interferes with foraging behavior and success through acoustic masking, measured as (i) increased searching effort (e.g., Au et al., 1982), a presumed strategy to maximize foraging opportunities during masking, since echolocation clicks are metabolically cheap to produce (Noren et al., 2017) and near-continuous foraging by odontocetes incurs only small increases in field metabolic rates (Rojano-Doñate et al., 2024), and (ii) reduced likelihood of prey pursuit and prey capture within a dive, due to masking-induced interference with successful target identification and tracking (Au et al., 2004; Au & Penner, 1981).

## 2 | METHODS

### 2.1 | Study sites and data collection

We studied two overlapping populations of at-risk, fish-eating killer whales with core critical habitats within the coastal waters of British Columbia, Canada and Washington, United States. We temporarily affixed sound and movement archival biologging units ('Dtags', Johnson & Tyack, 2003) to individual whales in August (NRKW) and September (NRKW, SRKW) in 2009–2012 (NRKW) and 2010, 2012, and 2014 (SRKW) in Queen Charlotte Strait, Johnstone Strait, and the central coast of British Columbia (NRKW) and in the Salish Sea (SRKW, Figure 1; see Tennessen et al., 2023 for details). Tagging methodology details are described elsewhere (Holt et al., 2019; Tennessen, Holt, Hanson, et al., 2019; Wright et al., 2017). Briefly,



**FIGURE 1** Deployment tracks of individual killer whales from the Northern ( $n=20$ ) and southern ( $n=5$ ) resident populations (NRKW and SRKW, respectively) tagged with suction cup-attached “Dtags” along the west coast and inland coastal waterways of British Columbia and Washington. Polygons outlined within (a) larger map indicate study areas for (b) NRKW and (c) SRKW. Lines indicate female (purple) and male (orange) tracks during tag deployments. Tracks are from the subset of tags retained for analyses. Map lines delineate study areas and do not necessarily depict accepted national boundaries. NRKW, Northern Resident killer whales; SRKW, Southern Resident killer whales.

we identified individuals based on unique markings on their dorsal fins and saddle patches (Bigg, 1987) and attached Dtags at the base of the dorsal fin by suction cup, using a 7-m carbon fiber pole held by a researcher standing on the bow of a small vessel (see Johnson & Tyack, 2003 and Johnson et al., 2009 for details). We observed surface reactions to tagging that ranged from no behavioral change to flinching or diving, and all individuals returned to pre-tagging behavior within 5 min. Tags remained attached until programmed release prior to dusk or fell off prematurely due to movement or loss of suction. In total, we opportunistically affixed Dtags to 34 NRKW and 23 SRKW, while trying to achieve a balanced representation of age and sex classes within each population, and to minimize re-tagging the same individuals. We tagged three individuals (one NRKW, two SRKW) twice in different years. We omitted three NRKW deployments that fell off prematurely and were too short to be calibrated, and two deployments (one NRKW and one SRKW) due to sensor malfunctions.

We conducted focal follows of the tagged whales while tags were attached to (1) identify changes in tag orientation to facilitate calibration of sensor data, (2) validate predation events by collecting prey remains, (3) collect GPS coordinates of the whale's position at surfacings for georeferencing reconstructed tracks (see Tennessen et al., 2023 and Wright et al., 2017 for details), and (4) identify vessel

type and proximity to the tagged whale at surfacings (see Giles, 2014 for details). After release, we used a VHF receiver to locate and retrieve Dtags for downloading the data.

## 2.2 | Data processing

Dtags contained pressure (depth) and temperature sensors, tri-axial accelerometers, and magnetometers that sampled at 50–250 Hz, and stereo hydrophones that sampled at 96–240 kHz. We downloaded all tag data and calibrated sensor data using the 2014 Dtag toolbox and updates to tag tools available from the Biologging Tools Project (<https://animaltags.org>). We ran all tag calibrations in Matlab v R2016b (The MathWorks, Natick, MA; see Holt et al., 2017 and Wright et al., 2017 for details) to produce the following time-series data streams down-sampled to 50 Hz: temperature-corrected depth, triaxial orientation (pitch, roll, and heading), triaxial acceleration, and jerk (rate of change of acceleration). We used dead-reckoning of tag sensor data to estimate the whale's track using the ‘ptrack’ function from the 2014 Dtag toolbox in Matlab v R2016b (The MathWorks, Natick, MA) and constrained the accumulated spatial error by forcing tracks through known GPS coordinates (Wilson et al., 2007) to create



georeferenced tracks using the TrackReconstruction package (Battaile, 2019) in R v.3.3.3 (SRKW) and v.3.6.3 (NRKW; R Core Team, 2020).

We assigned time-series data to individual dives by identifying dive start and end cues using the 'find\_dives' function from the 2014 Dtag toolbox. We defined a dive as any excursion from the surface greater than 1 m, bounded by a return to within 0.5 m of the surface (see Tennessen, Holt, Hanson, et al., 2019 for details), and checked dives manually to confirm accuracy of time cues. We excluded (1) dives less than 4 s in duration as these are likely artifacts of fluctuations in the pressure data inherent with a high sampling rate and (2) dives that began within the first 5 min of the deployment to allow recovery from behavioral responses to the tagging event, consistent with surface observations of the time to return to pre-tagging behavior. We confirmed through visual inspection of dive profiles that 5 min was sufficient for acclimation.

### 2.3 | Quantifying foraging behavior

We audited the acoustic tag data to detect the presence of sounds associated with foraging to identify the distinct phases of foraging (searching, pursuit, and capture). Audit details are described elsewhere (Holt et al., 2019; Wright et al., 2021). Briefly, we used the 2014 Dtag toolbox in Matlab to plot spectrograms (512 point, Hann window, 50% overlap), alongside the depth profile and the angle of arrival between the two hydrophones to identify and assign sounds to the tagged whale (vs. sounds produced by nearby conspecifics). We identified the occurrence of echolocation clicks (slow clicks: inter-click interval >100 ms; fast clicks: inter-click interval 11–100 ms), buzzes (inter-click interval <11 ms), and prey handling sounds, including tearing and crunching. We used the start and end time cues of these acoustic events to assign all foraging sounds to corresponding dives. We were unable to audit nine deployments due to persistent flow noise (sound generated by water passing over the tag housing as the whale swam), presumably caused by tag placement, and we omitted these deployments (oo09\_231a, oo10\_257m, oo10\_259m, oo10\_267m, oo10\_268m, oo10\_270m, oo12\_250m, oo12\_260m, oo14\_250m) from further analysis. Additionally, we omitted one deployment (oo11\_267a) due to sensor timing errors that prevented alignment of the movement and audio data.

Movement data recorded on triaxial accelerometers and magnetometers reveal changes in body orientation, rapid body accelerations, and head movements indicative of foraging behavior. These data can provide insight into predation events when acoustic data are either absent or of poor quality (e.g., Allen et al., 2016; Del Caño et al., 2021; Jensen et al., 2023; Matika et al., 2022; Tennessen et al., 2023; Tennessen, Holt, Hanson, et al., 2019; Wright et al., 2017; Ydesen et al., 2014). We used stereotyped movement signatures detected in sensor data to identify all dives containing movements indicative of prey capture ('prey capture dives') following an established method validated with visual and

acoustic confirmation of predation events (see Tennessen, Holt, Hanson, et al., 2019 for details). Briefly, we divided dives into descent, bottom ( $\geq 70\%$  of maximum depth), and ascent phases, and computed several continuous variables for each of the phases of all dives, including jerk (rate of change of acceleration), roll (angular rotation about the whale's rostral-caudal axis), and heading (angular rotation about the whale's dorsal-ventral axis). We compressed jerk, roll, and heading vectors into single values per dive phase by computing (1) the maximum peak of the Euclidean norm of the jerk signal (jerk peak), standardized by the median of the norm jerk to account for differences in tag position on each whale, (2) the median absolute value of the roll signal at the time of jerk peak, and (3) the circular variance in the whale's heading (unitless, based on an index between 0 and 1, where 0 represents a straight path and 1 represents continuous direction changes). We filtered prey capture dives from all deployments based on minimum thresholds for each of these movement variables determined from a subset of acoustically confirmed prey capture dives (see Tennessen et al., 2023 for details). We determined filter thresholds for each population separately, by matching accuracy (true-positive rate of 100%) and specificity (false-positive rate of 26%) between populations. Since our objective was to investigate factors predicting foraging behavior, it was critical to maximize accuracy in detecting prey capture dives while, given the trade-off between accuracy and specificity, accepting a modest reduction in specificity. Additionally, we computed success or failure on a subset of dives called "foraging attempts," defined as deep dives  $\geq 75$  m that contained slow clicks. This subset of dives allowed us to quantify success by evaluating dives with presumed foraging intent.

### 2.4 | Quantifying ambient noise

We extracted all sections of recordings that were free of extraneous sounds such as echolocation clicks and communication sounds from the tagged whale or conspecifics, impacts on the tag housing, and clear instances of episodic flow noise. We computed noise level as the root-mean-square sound pressure level (SPL) over 1 s bins within these "clean" sections of recordings. We could not remove instances of flow noise during all foraging dives. To address this, we computed SPL across several successively narrower and higher frequency bands (1–45, 2–45, 5–45, 10–45, 12–45, 15–45, 17–45 and 20–45 kHz) in Matlab v R2016b and identified the optimal band that maximized bandwidth while effectively filtering out most flow noise. There is a trade-off in selecting a lower cutoff frequency that is high enough to eliminate most flow noise, yet low enough to capture contributions from anthropogenic noise. To identify the optimal lower frequency, we computed the whale's vertical speed at the time of each SPL measurement, and we inspected plots of the regression of vertical speed against SPL for each of the above frequency bands, across all deployments, to identify the lowest frequency band

at which SPL was uncorrelated with movement. Since flow noise is correlated with speed (Goldbogen et al., 2006) and most flow noise energy occurs well under 10 kHz (e.g., von Benda-Beckmann et al., 2016), we expected to see a strong positive correlation between vertical speed and SPL that weakened as the lower cutoff frequency increased. We used the Dtag pressure and pitch data and the 'kalmanspeedest' function from the 2014 Dtag toolbox in Matlab v R2016b to measure instantaneous vertical speed, and we averaged speed values over 1 s bins within each deployment. Since the vertical speed estimate is not accurate for small pitch angles, we omitted intervals for which mean pitch was  $<30^\circ$ . We selected the SPL measurement computed across the 15–45 kHz band ( $SPL_{15-45}$ ) as the optimal ambient noise metric, which is consistent with previous work (Wisniewska et al., 2018). Since noise from anthropogenic activities (including vessel sounds) often contains energy that exceeds 15 kHz (Veirs et al., 2016), this approach allowed us to effectively remove the influence of flow noise while still capturing anthropogenic noise in SPL measurements. Moreover, since killer whale hearing is most sensitive between 18 and 42 kHz (Szymanski et al., 1999), with best sensitivity at 34 kHz (Branstetter et al., 2017), this approach allowed us to measure the functionally relevant band of the noise spectrum for killer whales. Additionally, we conservatively excluded individual deployments from further analysis if, for a given deployment, the slope of the linear regression of  $SPL_{15-45}$  against vertical speed was positive and significant at  $\alpha < 0.05$ . This resulted in the removal of 10 additional deployments (oo09\_236a, oo09\_243a, oo09\_245a, oo10\_251m, oo10\_260a, oo10\_264a, oo11\_240a, oo12\_254m, oo14\_249m, oo14\_266m). We conducted regressions and visualizations in R v.3.6.3 (R Core Team, 2020).

Next, we assigned all SPLs to corresponding dives within each deployment and computed the maximum  $SPL_{rms}$  for every dive where available ( $NL_{max}$ ). Differences in hydrophone sensitivity, tag housing materials, and tag shape that likely influenced contribution of frequency-dependent flow noise of Dtags used in 2012 (version 3) and Dtags used during all other years of the study (version 2) precluded comparisons of SPL measurements across tag versions, so we excluded all 2012 (version 3) deployments (an additional six deployments: oo12\_235b, oo12\_251m, oo12\_261m, oo12\_266m, oo12\_266n, oo12\_267m).

## 2.5 | Statistical analysis

We constructed generalized estimating equations (GEEs) using the geepack package (Højsgaard et al., 2006) and generalized linear mixed models (GLMMs) using the glmmTMB package (Brooks, 2017) in R v. 4.2.2 (R Core Team, 2022) to identify predictors of the probability of occurrence of the binary response variables: (a) slow echolocation clicks, (b) buzzes, and (c) prey capture. We constructed fully saturated models with predictor variables of population, sex and SPL (hereafter "noise level,"  $NL_{max}$ ), their three-way interaction, and maximum depth. For buzz and prey

capture models, we additionally included the presence/absence of slow clicks as a predictor. We found unreasonable GEE fits and no evidence of temporal autocorrelation for the response variables, so we modeled the relationship between the response and predictor variables with GLMMs, allowing us to preserve the important inter-individual variability between tag deployments by using random effects terms. We used AIC model selection to identify the optimal random effects structure for each response variable. We considered models with random effects of (1) deployment ID, (2) deployment ID and year, (3) deployment ID and week (a proxy for temporal fluctuation in environmental conditions including prey availability), (4) deployment ID and tag ID (identifier for individual tag used), and (5) tag ID. For all response variables, the best model included deployment ID as the only random effect. Finally, we recursively dropped nonsignificant predictor variables from the optimal fully saturated model and used AIC model selection to identify the simplest model for each response variable, following established protocols (Zuur et al., 2009). Where  $\Delta AIC < 2$ , we additionally used likelihood ratio tests to facilitate interpretation (Zuur et al., 2009). For all models, we assessed significance at  $\alpha = 0.05$  and used an AIC model selection threshold of at least 2 units. We omitted one NRKW deployment (oo09\_238a) for which sex was unknown because this juvenile died before its sex could be determined. Maximum dive depth (maxdep) was a significant predictor of foraging outcomes for each of the models. Therefore, in the results, we compute probabilities of foraging outcomes for three different dive depth scenarios: shallow (5 m), mean depth (16.6 m), and deep (75 m).

## 3 | RESULTS

A total of 25 Dtag deployments (20 NRKW, 5 SRKW;  $n = 10$  females, 10–30 years;  $n = 15$  males, 6–39 years) met our criteria for inclusion (Table 1). Mean deployment duration for females was 2.6 h (range = 0.7–7.6 h). Mean deployment duration for males was 3.6 h (range = 0.3–11.7 h). Of these deployments, we were able to populate acoustic foraging variables and noise level measurements on 462 dives by females and 1265 dives by males (Figure 2a; Table 1), representing a total of 33.7 h of dive data, with an average maximum dive depth of 21.3 m by females and 14.9 m by males (Figure 2b; Table 1).

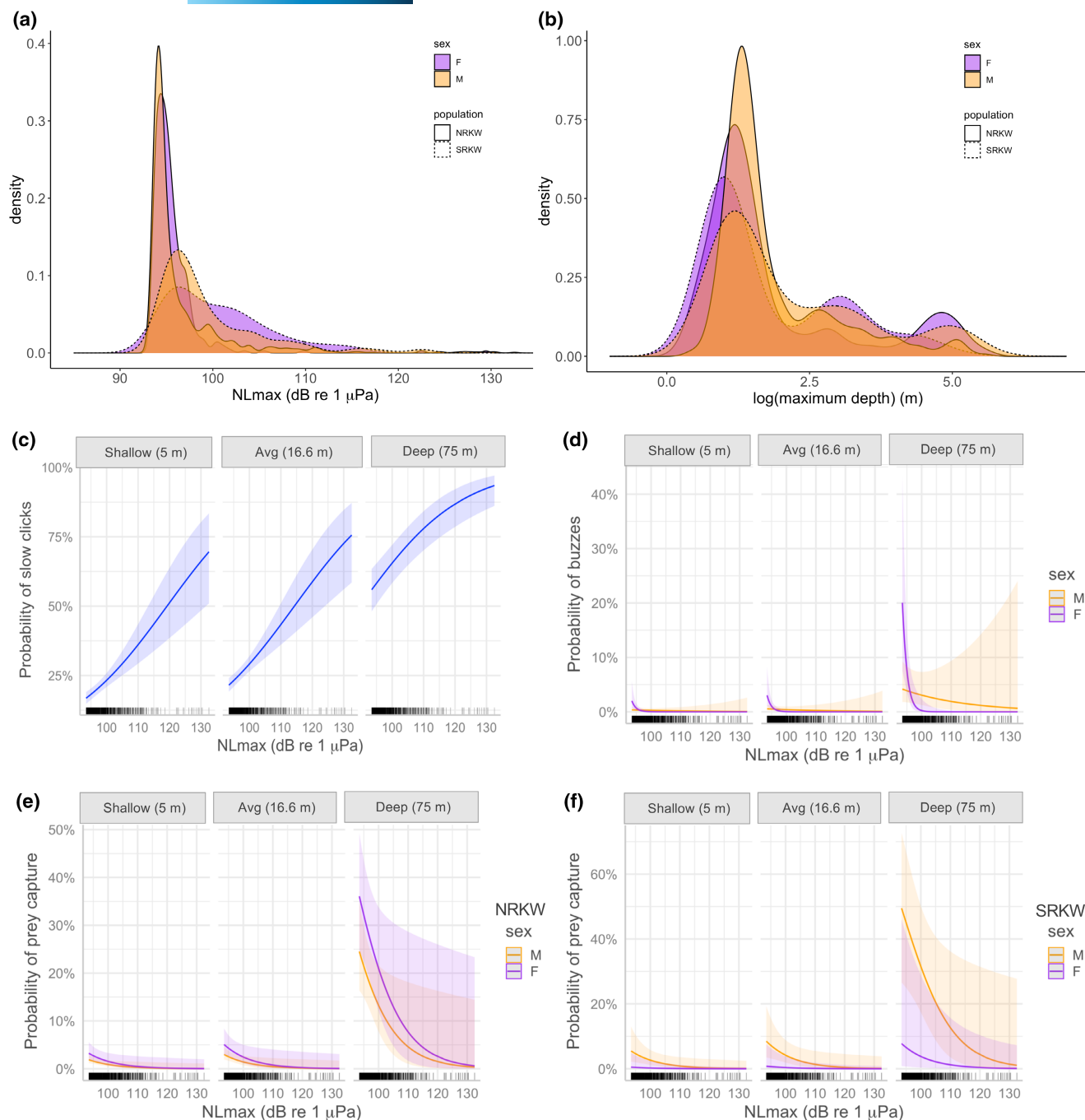
### 3.1 | Searching effort

We detected slow clicking during 96 dives (20.8%) by females and 353 dives (27.9%) by males (Table 1). There were significant effects of noise level ( $NL$ ; measured in the 15–45 kHz band) and maximum dive depth (maxdep) on the probability of slow clicking (hereafter "searching"; GLMM,  $NL_{max}$ :  $z = 2.750$ ,  $p = .0060$ ; maxdep:  $z = 10.874$ ,  $p < .0001$ ; Table 2; Figure 2c). For every 1 dB increase in  $NL_{max}$ , there was a 4% increase (odds ratio: 1.04, 95%

TABLE 1 Summary of analyzed dives from Dtag deployments on fish-eating killer whale populations between 2009 and 2014.

Deployment	DateTime (yyyy-mm-dd hh:mm:ss)	Sex	Age	Population	Dives analyzed	Duration analyzed (h)	Dives w/slow clicks	Dives w/buzzes	Dives w/prey capture
oo09_234a	2009-08-22 15:26:55	M	27	NRKW	104	1.96	59	0	5
oo09_235a	2009-08-23 14:17:32	F	10	NRKW	41	0.63	11	0	2
oo09_237c	2009-08-25 12:35:58	F	12	NRKW	28	0.39	2	0	2
oo09_237d	2009-08-25 16:09:04	M	23	NRKW	32	1.31	16	7	7
oo09_239a	2009-08-27 11:41:28	M	13	NRKW	81	1.56	5	0	2
oo09_240a	2009-08-28 11:51:51	M	32	NRKW	148	2.09	62	0	7
oo09_244a	2009-09-01 15:14:42	M	22	NRKW	78	2.10	26	3	10
oo09_245b	2009-09-02 17:51:45	M	21	NRKW	39	0.91	8	6	5
oo09_247a	2009-09-04 10:27:05	F	15	NRKW	52	0.67	0	0	2
oo10_256a	2010-09-13 11:03:10	F	10	NRKW	156	3.62	41	23	25
oo10_261a	2010-09-18 15:14:55	M	39	NRKW	66	1.04	54	5	5
oo10_261m	2010-09-18 15:32:45	F	24	SRKW	5	0.28	1	0	0
oo10_264m	2010-09-21 12:37:09	F	20	SRKW	70	1.34	0	0	0
oo10_265a	2010-09-22 15:31:15	F	20	NRKW	38	0.51	18	0	4
oo10_265m	2010-09-22 12:15:42	M	9	SRKW	73	2.86	17	14	14
oo11_224a	2011-08-12 08:51:17	F	10	NRKW	26	0.48	5	1	2
oo11_224b	2011-08-12 16:19:13	M	29	NRKW	1	0.05	1	0	0
oo11_244a	2011-09-01 09:24:22	M	26	NRKW	56	1.75	15	2	0
oo11_244b	2011-09-01 13:03:11	M	11	NRKW	6	0.17	0	0	2
oo11_245a	2011-09-02 07:58:13	M	28	NRKW	397	6.12	56	8	8
oo11_246a	2011-09-03 12:46:50	F	30	NRKW	34	0.67	13	5	9
oo11_248a	2011-09-05 13:10:15	M	6	NRKW	11	0.28	0	0	0
oo11_248b	2011-09-05 13:53:25	M	7	NRKW	112	1.39	15	0	0
oo14_263m	2014-09-20 11:57:15	M	23	SRKW	61	1.25	19	2	4
oo14_264m	2014-09-21 11:31:46	F	19	SRKW	12	0.27	5	1	1

Abbreviations: NRKW, Northern Resident killer whales; SRKW, Southern Resident killer whales.



**FIGURE 2** Noise level affects the probability of occurrence of multiple phases of foraging. Density plots display the spread of observations of (a)  $NL_{max}$  and (b) log of dive depth. Population is illustrated as solid (northern resident; NRKW) or dashed (southern resident; SRKW) lines, and sex is illustrated by purple (female) or orange (male) shading. Greater maximum received noise level (measured in the 15–45 kHz band) (c) increases the likelihood of searching for prey (occurrence of slow clicks;  $n = 1727$  dives), (d) reduces female but not male likelihood of terminal prey pursuit (occurrence of buzzes;  $n = 1727$  dives), and (e) reduces the likelihood of capturing prey within a dive for NRKW ( $n = 1506$  dives) and (f) for SRKW ( $n = 221$  dives). Probabilities of occurrence of foraging phases vary significantly by depth; here, the model is evaluated at three depth conditions: shallow (5 m), mean depth (16.6 m), and deep (75 m). Shading depicts 95% confidence intervals. Black tick marks display  $NL_{max}$  observations. Sex was not a significant predictor of the probability of slow clicks, so sex is pooled for visualization (blue lines; c). NRKW, Northern Resident killer whales; SRKW, Southern Resident killer whales.

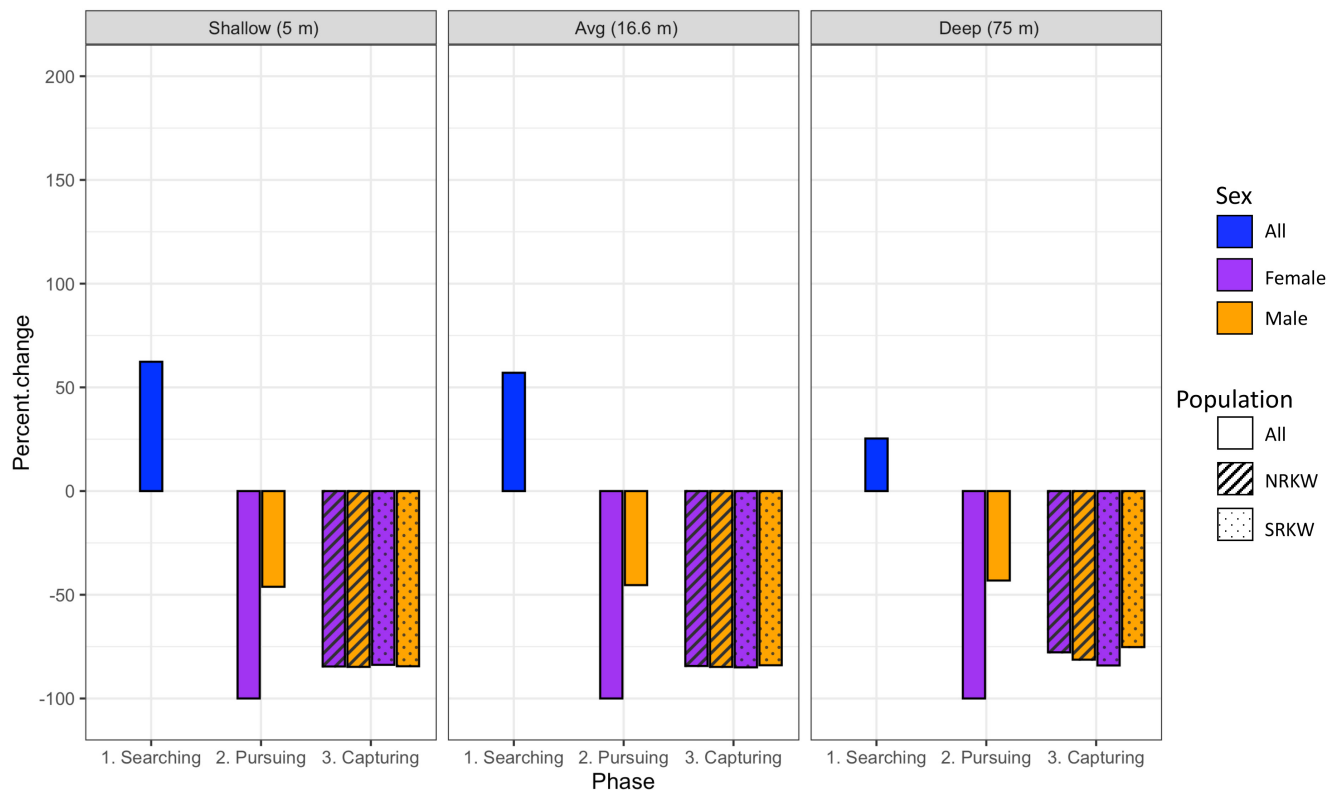
CI: [1.01, 1.07]) in the odds of searching, holding all else constant. The increase in the likelihood of searching in high (110 dB re 1  $\mu$ Pa) compared to low noise (95 dB re 1  $\mu$ Pa) varied by maximum dive depth, and ranged from 25.3% (deep, 75 m) to 62.3% (shallow, 5 m; Figure 3; Table 3).

### 3.2 | Terminal pursuit

We detected buzzes on 30 dives (6.5%) by females and 47 dives (3.7%) by males (Table 1). There were significant effects of the interaction between noise level and sex, the presence of slow clicking, and

TABLE 2 Parameter estimates of models predicting the occurrence of foraging behavior in two populations of fish-eating killer whales.

Response	Model type	Model family	Random effects	Fixed effects	n	df	Estimate	s.e.	z-value	p-value
Slow clicks	GLMM	Binomial	Deployment		1727	1726				
				Intercept			-5.6854	1.4433	-3.939	<.0001
				NL <sub>max</sub>			0.0399	0.0145	2.750	.0060
				Max. depth			0.0280	0.0026	10.874	<.0001
Buzzes	GLMM	Binomial	Deployment		1727	1726				
				Intercept			75.8044	29.5694	2.564	.0104
				NL <sub>max</sub> *sex			0.8275	0.3119	2.653	.0080
				NL <sub>max</sub>			-0.8682	0.3120	-2.783	.0054
				Sex			-78.9170	29.8075	-2.648	.0081
				Max. depth			0.0431	0.0048	8.898	<.0001
				Slow clicks			1.5248	0.4690	3.251	.0012
Prey capture	GLMM	Binomial	Deployment		1727	1726				
				Intercept			8.4349	5.5248	1.527	.1268
				NL <sub>max</sub>			-0.1265	0.0579	-2.184	.0290
				Population:sex			3.2638	1.5578	2.096	.0361
				Population			-2.2129	1.3665	-1.619	.1054
				Sex			-0.7163	0.4981	-1.438	.1504
				Max.depth			0.0414	0.0030	13.740	<.0001

FIGURE 3 Change in probability of occurrence of multiple phases of foraging between low (95 dB re 1  $\mu$ Pa) and high noise (110 dB re 1  $\mu$ Pa) for shallow, average depth (mean) and deep dives. Where significant, sex (female = purple, male = orange), and population (northern resident = diagonal stripes, southern resident = dots) are illustrated separately.

maximum depth on the probability of buzzing (GLMM, NL<sub>max</sub>\*sex:  $z=2.653$ ,  $p=.0080$ ; click:  $z=3.251$ ,  $p=.0012$ ; maxdep:  $z=8.898$ ,  $p<.0001$ ; Table 2; Figure 2d). Females produced fewer buzzes as

noise level increased. For every 1 dB increase in NL<sub>max</sub>, there was a 58% decrease in the odds of buzzing for females, holding all else constant (odds ratio: 0.42, 95% CI: [0.23, 0.77]). For females, the

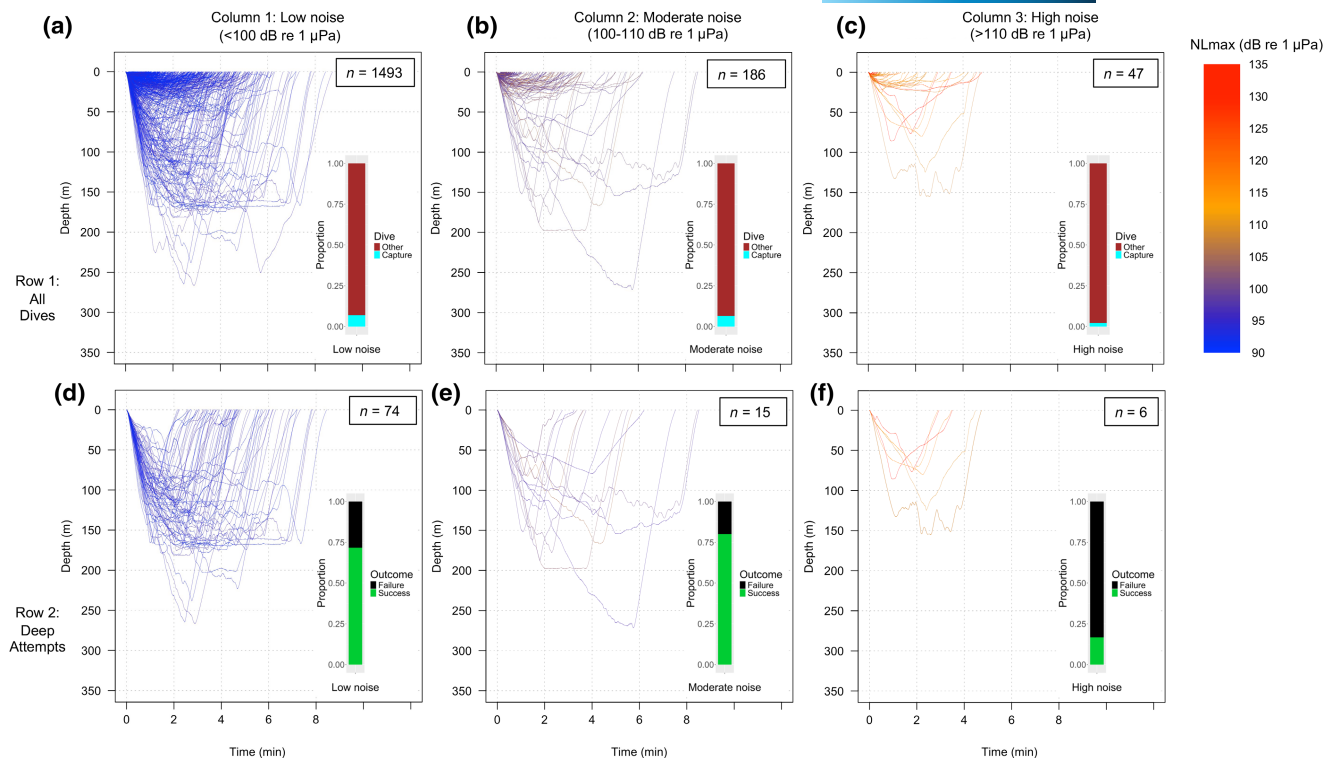


TABLE 3 Probabilities of occurrence of foraging in low (95 dB re 1  $\mu$ Pa) and high noise (110 dB re 1  $\mu$ Pa) across three depth conditions.

Probability of searching for prey							
		Shallow (5 m)		Avg. depth (16.6 m)		Deep (75 m)	
		Low noise [95% CI]	High noise [95% CI]	Low noise [95% CI]	High noise [95% CI]	Low noise [95% CI]	High noise [95% CI]
Population	Sex						
All	All	0.1474 [0.0884, 0.2366]	0.2393 [0.1377, 0.3841]	0.1932 [0.1189, 0.2994]	0.3034 [0.1817, 0.4626]	0.5511 [0.3934, 0.7011]	0.6907 [0.5184, 0.8240]
Probability of pursuing prey <sup>a</sup>							
		Shallow		Avg. depth		Deep	
		Low noise [95% CI]	High noise [95% CI]	Low noise [95% CI]	High noise [95% CI]	Low noise [95% CI]	High noise [95% CI]
Population	Sex						
All	F	0.0071 [0.0006, 0.0792]	1.5894e-08 [1.1080e-12, 0.0002]	0.0117 [0.0010, 0.1206]	2.6227e-08 [1.9222e-12, 0.0004]	0.1282 [0.0137, 0.6054]	3.2472e-07 [3.0130e-11, 0.0034]
	M	0.0052 [0.0007, 0.0377]	0.0028 [0.0003, 0.0307]	0.0086 [0.0012, 0.0580]	0.0047 [0.0005, 0.0472]	0.0969 [0.0176, 0.3938]	0.0551 [0.0067, 0.3366]
Probability of capturing prey							
		Shallow		Avg. depth		Deep	
		Low noise [95% CI]	High noise [95% CI]	Low noise [95% CI]	High noise [95% CI]	Low noise [95% CI]	High noise [95% CI]
Population	Sex						
NRKW	F	0.0331 [0.0153, 0.0699]	0.0051 [0.0008, 0.0318]	0.0524 [0.0248, 0.1070]	0.0082 [0.0013, 0.0493]	0.3828 [0.2192, 0.5774]	0.0851 [0.0159, 0.3476]
	M	0.0164 [0.0086, 0.0311]	0.0025 [0.0004, 0.0150]	0.0263 [0.0141, 0.0485]	0.0040 [0.0007, 0.0234]	0.2326 [0.1364, 0.3668]	0.0435 [0.0083, 0.1965]
SRKW	F	0.0037 [0.0003, 0.0476]	0.0006 [2.5384e-05, 0.0122]	0.0060 [0.0005, 0.0742]	0.0009 [4.1861e-05, 0.0192]	0.0635 [0.0052, 0.4674]	0.0101 [5.0537e-04, 0.1694]
	M	0.0457 [0.0122, 0.1564]	0.0071 [0.0011, 0.0439]	0.0718 [0.0196, 0.2300]	0.0115 [0.0018, 0.0678]	0.4646 [0.1783, 0.7756]	0.1151 [0.0217, 0.4320]

Abbreviations: NRKW, Northern Resident killer whales; SRKW, Southern Resident killer whales.

<sup>a</sup>Slow clicking was a significant positive predictor of the probability of prey pursuit. Probabilities are reported for the condition in which slow clicking is present.



**FIGURE 4** Noise level impairs foraging success. Prey capture dives (a–c, cyan bars) were less likely to occur in high (column 3) compared to low (column 1) or moderate noise (column 2), and deep foraging attempts were more likely to result in failure (d–f, black bars) in high (column 3) compared to low (column 1) or moderate noise (column 2). The deepest dives were observed in low and moderate noise, and the greatest  $NL_{max}$  values were generally observed in shallower dives, suggesting individuals did not initiate deep foraging attempts in high noise. All dives from all deployments are plotted and scaled to the duration (min) of the longest dive, and each dive is colored by  $NL_{max}$  from low (blue) to high (red). (a)–(c) depict all dives (prey capture = cyan bars, other dives = brown bars), and (d)–(f) depict only deep foraging attempts (defined as dives  $\geq 75$  m maximum depth, containing slow clicking; success = green bars, failure = black bars). Plots are divided into noise category, in which (a) and (d) depict low noise, (b) and (e) depict moderate noise, and (c) and (f) depict high noise.

reduction in the likelihood of buzzing in high compared to low noise conditions was 100% across shallow, average depth, and deep scenarios (Figure 3; Table 3). Holding depth constant at 75 m, in the presence of slow clicking, the likelihood of females buzzing in low noise (95 dB re 1  $\mu$ Pa) was 12.8% and reduced to 0% in high noise (110 dB re 1  $\mu$ Pa; Figures 2d and 3; Table 3). In contrast, for every 1 dB increase in  $NL_{max}$ , there was no significant change in the odds of buzzing for males, holding all else constant (odds ratio: 0.96, 95% CI: [0.28, 3.26]). The overall likelihood of buzzing increased with maximum dive depth.

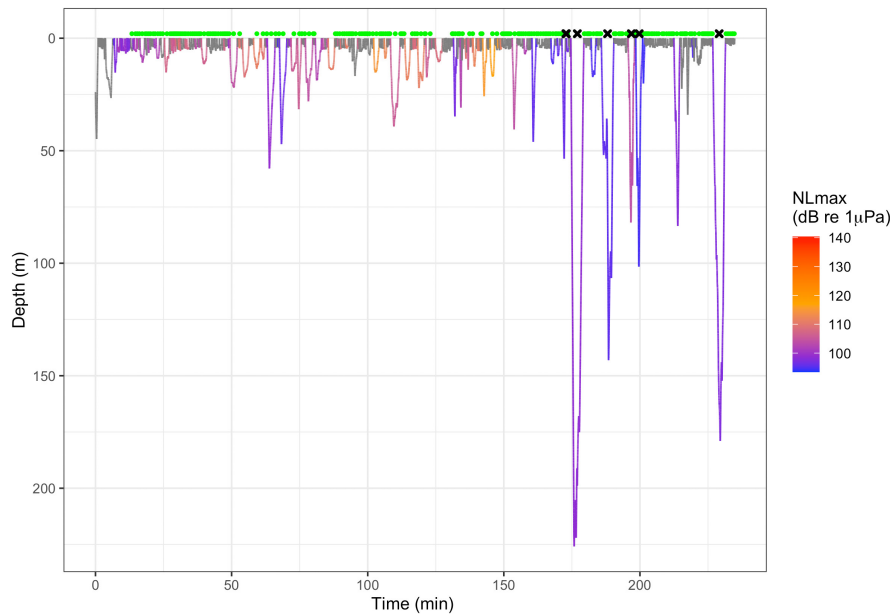
### 3.3 | Prey capture dives

We detected movement signatures of prey capture during 47 of 462 dives (10.2%) by females and 69 of 1265 dives (5.5%) by males (Table 1). There were significant effects of  $NL_{max}$ , maximum depth, and the interaction between population and sex on the probability of prey capture (GLMM,  $NL_{max}$ :  $z = -2.184$ ,  $p = .0290$ ,  $maxdep$ :  $z = 13.740$ ,  $p < .0001$ ;  $population \times sex$ :  $z = 2.096$ ,  $p = .0361$ ; Table 2; Figure 2e,f). For every 1 dB increase in  $NL_{max}$  there was an 11.9% decrease in the odds of prey capture, holding all else constant (odds ratio: 0.88, 95% CI: [0.79, 0.99]). The reduction in the likelihood of prey capture

in high-noise compared to low-noise conditions ranged from 75.2% to 85.0% and varied by population and sex (Figure 3; Table 3). Deep dives, which are associated with prey capture, tended to occur during quieter periods of a deployment (Figures 4 and 5), and deep foraging attempts were more likely to fail in high compared to low or medium levels of noise (Figures 4 and 6). Holding depth constant at 75 m, the likelihood of females capturing prey in low noise (95 dB re 1  $\mu$ Pa) was 38.3% for NRKW and 6.4% for SRKW, and reduced to 8.5% for NRKW and 1.0% for SRKW in high noise (110 dB re 1  $\mu$ Pa; Figures 2e,f and 3; Table 3). Under these same conditions, the likelihood of males capturing prey in low noise was 23.3% for NRKW and 46.5% for SRKW and reduced to 4.4% for NRKW and 11.5% for SRKW in high noise (Figures 2e,f and 3; Table 3). All but one of the deep foraging attempts (dives  $\geq 75$  m containing slow clicking) with noise levels greater than 110 dB re 1  $\mu$ Pa (15–45 kHz band;  $n = 6$  dives by  $n = 4$  whales) resulted in failure to capture prey (Figures 4 and 6).

## 4 | DISCUSSION

We used acoustic and movement data from animal-borne biologging tags to investigate whether vessel noise interferes with the



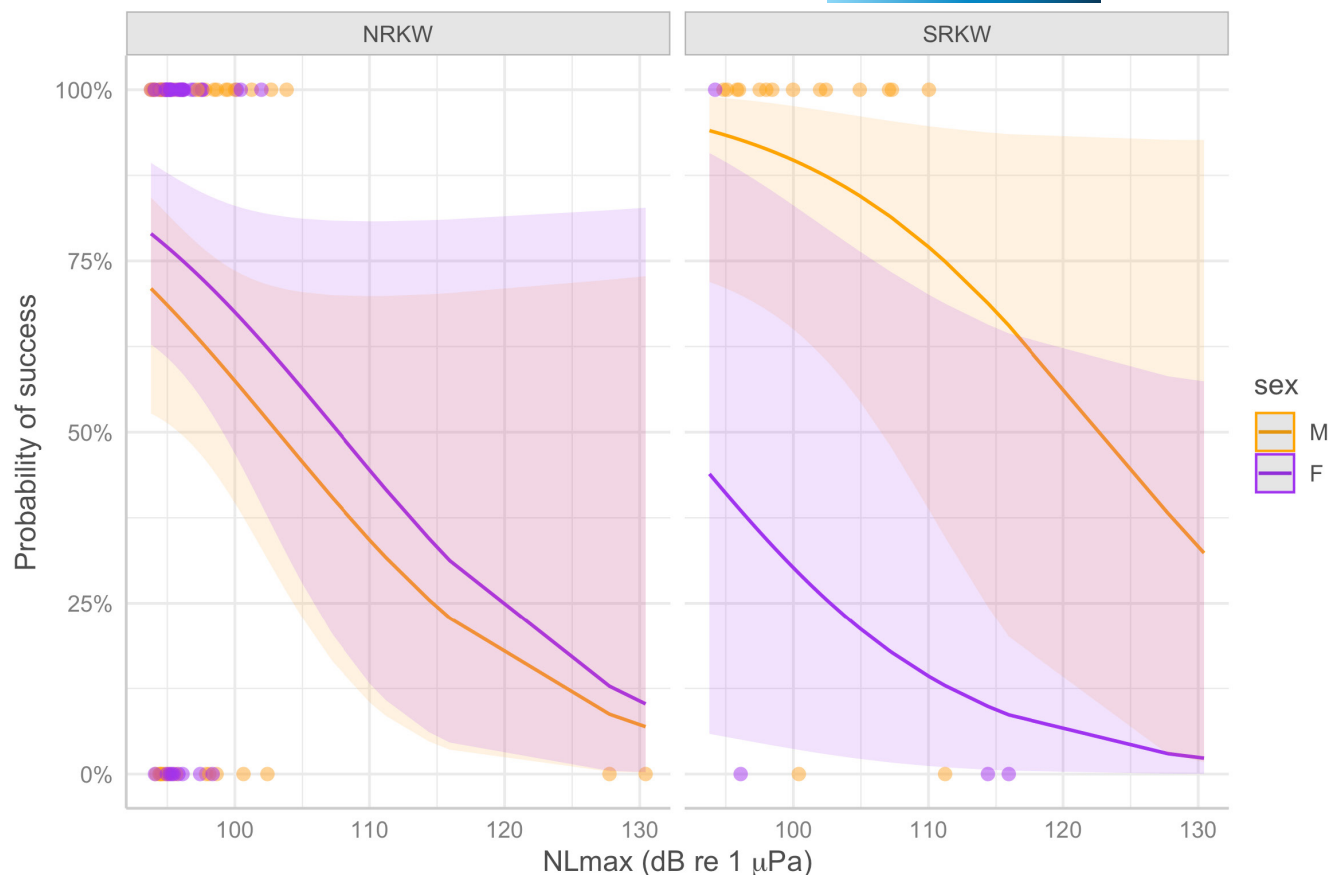
**FIGURE 5** Searching for prey (green circles) occurred throughout the deployment whereas prey capture (black Xs) occurred during quieter periods.  $NL_{max}$  is used to color dives along a gradient from low (blue) to high (red), and gray indicates dives for which we could not measure  $NL_{max}$ . Dive profile is from a representative deployment on an adult male northern resident killer whale (deployment ID oo09\_234a).

foraging behavior of fish-eating killer whales. These data were collected within an environment in which the primary source of human-generated ambient noise is from vessels, and there is a strong relationship between received noise level and vessel variables including speed and number (Holt et al., 2017; Houghton et al., 2015). We demonstrate the effects of noise level across multiple phases of foraging in two populations of fish-eating killer whales, consistent with predicted responses to auditory masking. These results reveal that vessel noise reduces foraging opportunities and that the likelihood of interference with foraging success scales positively with noise level.

The likelihood of searching for prey increased with noise level. Echolocation clicks were more likely to occur as dive depth and noise level increased. Individuals spent more time searching in noisier conditions, resulting in reduced foraging efficiency, defined as prey capture per unit effort. In chronic noise, this negative relationship between noise level and foraging efficiency could prevent individuals from consuming enough prey over time. Interestingly, the finding that individuals did not cease searching in noisy conditions, but rather increased search effort suggests that their energetic needs override the elevated cost of foraging. This finding aligns with the metabolic response theory of predator-prey relationships, where a consequence of decreasing prey density is an increase in energy expenditure required to maintain a certain level of consumption (Giacomini, 2022). Consequently, an outcome of increasing noise may be a functional decrease in prey density, resulting in adjustments in foraging effort and presumably an increase in metabolic cost, in an attempt to meet the individual's energy budget. Since click production is energetically cheap (Noren et al., 2017) and near-continuous foraging by odontocetes incurs only small increases in field metabolic rates (Rojano-Doñate et al., 2024), individuals may continue searching as a relatively inexpensive way to meet their metabolic requirements. These results suggest that inefficient, increased searching effort with

greater vessel noise may be an attempt to balance the difficulties of locating prey in noise with the urgency of consuming sufficient energy to meet metabolic demands.

We detected an interaction between noise level and sex on the likelihood of prey pursuit. Females, but not males, were significantly less likely to pursue prey (emit buzzes) as noise level increased. Given the lack of evidence of a sex difference in the source level of echolocation clicks or buzzes, it is unlikely that the observed differences in response by sex are due to an unequal ability to detect female and male buzzes in high noise. Instead, these different responses to noise may support the different foraging strategies employed by males and females in these populations (Holt, Tennessen, Ward, et al., 2021; Tennessen, Holt, Hanson, et al., 2019; Tennessen, Holt, Ward, et al., 2019; Tennessen et al., 2023; Wright et al., 2016). Females, some of whom may be lactating, need to tend to vulnerable calves. The presence of a calf reduces its mother's likelihood of prey capture (Tennessen et al., 2023), and females with vulnerable offspring often forage in shallower areas and are unlikely to continue foraging in the presence of nearby vessels (Holt, Tennessen, Ward, et al., 2021). Consequently, females may be less likely to engage in energetically costly prey pursuit that may not be successful in greater noise. In contrast, males, who generally sire offspring outside of their matriline and do not play a role in rearing their own calves (Barrett-Lennard, 2000; Ford et al., 2011; but see Kardos et al., 2023), may still attempt prey pursuit as noise level increases because their fitness-relevant costs of failure may be lower than those of females. Additionally, because oxygen storage capacity scales linearly with body size in breath-holding marine mammals (Castellini et al., 1992), adult males, which are 30% larger than adult females (Noren, 2011), can hold their breath longer, potentially enabling a riskier foraging strategy as noise increases. Moreover, since males require more energy than females due to their larger body size, the risk to males of failing to acquire prey following prey pursuit may be exceeded by the risk of forgoing opportunities to meet their greater



**FIGURE 6** Foraging success decreases with noise level. Plots depict the relationship between the maximum noise level received during a deep foraging attempt and the probability of success (foraging attempt defined as dives with maximum depth  $\geq 75$  m, containing slow clicking; northern residents: females = 36, males = 39; southern residents: females = 4, males = 16). Points represent individual outcomes. Sex is illustrated by purple (female) and orange (male). All but one of the foraging attempts that occurred in noise levels greater than 110 dB re 1  $\mu$ Pa (15–45 kHz band;  $n = 6$  dives by  $n = 4$  whales) resulted in failure. The relatively wide 95% confidence intervals (shading) are driven by the reduced sample size necessary to be reasonably certain that we evaluated only foraging attempts when computing success.

metabolic requirements (e.g., Wisniewska et al., 2016). Additionally, males typically forage in deeper waters where the payoff of larger Chinook salmon may outweigh the costs of deeper dives (Tennessen et al., 2023). Consequently, access to larger Chinook prey, coupled with greater oxygen storage capacity and release from the time and energetic constraints of rearing offspring, may enable males to use an energetically risky pursuit strategy in noisy conditions.

Both males and females were less likely to capture prey as noise level increased, but potentially for different reasons. Given that males increased searching effort and continued to pursue prey as noise level increased, the negative effect of noise level on prey capture provides evidence that noise directly reduced the success of capture attempts by males. In contrast, the reduced likelihood of females to capture prey in noisy conditions may be an outcome of their reduced prey pursuit in greater noise. These findings suggest that noise directly interferes with foraging success for males and females, but through different underlying pathways: Noise impairs males' abilities to capture prey, whereas noise causes females to forgo foraging opportunities. It is difficult to determine whether dives that did not result in prey capture were the result of engaging in other activities or were caused by failed attempts. To assess

foraging failure, we examined a subset of dives for which prey capture attempts were highly probable: dives to at least 75 m that contained slow clicking. For marine predators, diving depth has important implications for overall energy expenditure. Obligate breath holders such as cetaceans must return to the surface while foraging in order to replenish oxygen stores. Since diving bears considerable metabolic costs incurred from locomotion, drag, and breath holding (Acevedo-Gutiérrez et al., 2002; Goldbogen et al., 2008; Hazen et al., 2015; Soto et al., 2008; Williams & Noren, 2009), as well as reduced time for lactating females to nurse-dependent calves (e.g., Tennessen et al., 2023), it is unlikely that whales would engage in deep dives greater than 75 m, a conservative estimate, for purposes other than foraging. Moreover, the presence of slow clicking on these deep dives indicates that the individuals were actively searching for prey. Examining this subset of dives to at least 75 m, we found that, for both sexes, the likelihood of success during probable foraging attempts decreased as noise level increased. That is, of the subset of dives in which we can infer probable foraging intent, noise reduced the likelihood of successful prey capture. Indeed, we did not detect successful prey capture in any deep foraging attempts during which the maximum noise level within the dive exceeded 111 dB re

1  $\mu$ Pa measured within the 15–45 kHz band. Chinook are the largest and most lipid rich of salmonid prey, and adults are typically found at depths greater than 30 m (Wright et al., 2017). Our results, therefore, suggest not just a direct effect of noise on the likelihood of prey capture but also on the quality of prey consumed. These findings reveal a direct link between noise level and the likelihood of occurrence of multiple phases of foraging behavior and overall foraging success. Failed attempts at foraging that use up energy and time may exacerbate stressors to whales from reduced prey availability, especially for vulnerable individuals, including those in poor body condition (Stewart et al., 2021).

Sensory pollutants, such as ambient noise, can interfere with critical biological activities along at least three pathways: by masking, distracting, or misleading individuals from accomplishing an activity (Dominoni et al., 2020). It is unlikely that the effect of noise on foraging behavior in killer whales is due to misleading, whereby an individual confuses a stimulus for a predator's sound and elicits an antipredator response such as fleeing (e.g., Miller et al., 2022), since we did not observe cessation of searching effort that would be consistent with an antipredator response. Moreover, as apex predators, resident-ecotype killer whales are unlikely to be wary of other marine top predators. It is also unlikely that the negative relationship between vessel noise and foraging success supports the distracting hypothesis, whereby an individual ceases foraging due to cognitive interference or a startle response. According to this hypothesis, we would expect reduced searching effort as attention is diverted to competing demands for cognitive processing, such as in foraging bats (Allen et al., 2021; Luo et al., 2015) and in some bottlenose dolphins (*Tursiops truncatus*) experimentally exposed to vibratory pile-driving noise (Branstetter et al., 2018). It is possible that another interpretation of the distracting hypothesis would predict that animals would increase searching effort as noise level increases, presumably due to a shift in the function of echolocation clicks from foraging to navigation around nearby vessels. While we cannot completely rule out this prediction, it is unlikely that this alone explains the increase in searching effort as noise level increased, for two reasons. First, when resident-type killer whales are engaged in a searching behavioral state, they are more likely to continue searching on the next dive than transition to any other state (Holt, Tennessen, Ward, et al., 2021; Tennessen, Holt, Ward, et al., 2019). This high persistence in searching behavior is characteristic of foraging behavior in other cetaceans as well (e.g., Isojunno & Miller, 2018; Quick et al., 2017; Schwarz et al., 2021). When the whales do transition from searching to a different state, the most common state is deep foraging, often accompanied by prey capture (Holt, Tennessen, Ward, et al., 2021; Tennessen, Holt, Ward, et al., 2019), supporting the hypothesis that searching is used primarily for locating prey. Second, vessel speed and number of vessels, but not vessel distance to killer whale, were significant positive predictors of received noise level (Holt et al., 2017; Houghton et al., 2015). This indicates that an increase in noise level does not necessarily translate to a greater number of nearby vessels around which the whales need to navigate. Moreover, the region in which the study was conducted is frequently

transited by large commercial tankers that contribute notably to received noise level over greater spatial ranges than the active space of echolocation signals. Consequently, increases in received noise level can occur without vessels being in close proximity (i.e., echolocation range), yet we see a significant positive relationship between received noise level and the likelihood of searching, across sexes and populations.

Instead, we suggest that the increased likelihood of searching with increasing noise level best supports the auditory masking hypothesis, whereby search effort scales positively with noise level to counter the masking effect of higher levels of vessel noise on the returning echoes from echolocation clicks and buzzes as well as prey sounds, all necessary to achieve successful foraging outcomes. Indeed, there is a notable overlap of acoustic energy in the power spectral densities of foraging sounds (Au et al., 2004; Holt et al., 2019; Wright et al., 2021) and vessel noise (Veirs et al., 2016). Vessel noise routinely exceeds median background noise levels over the range of 100–40,000 Hz in SRKW critical habitat (Veirs et al., 2016). Moreover, this frequency range encompasses much of the energy contained in SRKW echolocation clicks and communication signals and overlaps the range of greatest hearing sensitivity in killer whales (18–42 kHz), which is assumed to be the frequency range most important for killer whales' biological activities (Au et al., 2004; Branstetter et al., 2017; Szymanski et al., 1999). If ambient noise from vessels in this overlapping spectral range exceeds the frequency-specific critical ratios necessary for a signal to be perceived (Branstetter et al., 2021), vessel noise will mask the detection of returning echoes from clicks and buzzes, as well as social sounds presumably necessary for facilitating prey sharing, and could impair or impede interpretation of critical information and reduce the functional range of acoustic sensory processes (Clark et al., 2009; Vagle, Burnham, O'Neill, et al., 2021). The importance of spectral robustness to signal detection versus interpretation is poorly understood in odontocetes (Branstetter et al., 2016). Experiments that test odontocetes' abilities to detect and locate objects in masking noise at frequencies that overlap with returning echolocation clicks would provide valuable information. It is important to note that we cannot rule out the possibility that noise alters prey behavior, which could indirectly lead to inefficient and unsuccessful foraging by odontocetes. Future work could explore this important possibility, including conducting vessel noise playback experiments on prey species outfitted with movement sensors to quantify potential locomotor or other behavioral responses to playback stimuli. Additionally, the maximum noise levels reported here are based on the per-dive maximum noise level measured in one-second bins over the 15–45 kHz band. Decibel measurements that are based on substantially different frequency bands or time averaging windows may not be directly comparable, representing an important consideration in the development of management strategies intended to mitigate noise impacts. Finally, the sample sizes available for our analyses are in some cases relatively small and thus contain larger margins of uncertainty. The time, resources, and environmental constraints involved in applying biologgers to



wild animals in their natural environments tend to limit sample sizes available for analyses. From the total collection of SRKW Dtag deployments, we could retain three SRKW female and two SRKW male deployments in our analyses. Thus, the patterns we have detected for SRKW are driven by the behavior of fewer individuals over a limited sampling of times and locations. We have achieved greater statistical power and a better understanding of the impact of vessel noise on killer whales by combining two related populations of the same ecotype. Future studies that can add to this dataset by including additional populations (e.g., Alaska residents) or new observations of NRKW and SRKW will advance our understanding of the patterns detected in this study.

Globally, projected increases in noise coupled with reduced populations of many species of odontocete prey may compound the effects of vessel noise on foraging. Behavioral plasticity can potentially buffer species against changing environments (Caspi et al., 2022; Johansson et al., 2024; Wong & Candolin, 2015), and life-history traits may predict which species are more resilient to rapid environmental change (Ditmer et al., 2021). Future research should explore whether odontocetes can shift foraging behavior in space and time to recoup lost foraging opportunities due to ambient noise, for example by foraging in areas with less noise (e.g., shallow or partially enclosed bays or areas away from shipping lanes and other marine traffic hotspots) or during quieter periods (e.g., during nighttime when recreational vessel traffic is reduced). Indeed, little is known about the extent to which behavioral plasticity may buffer marine apex predators and other ecosystem sentinels from the effects of noise on foraging success.

We demonstrated that vessel noise interferes with multiple phases of foraging and overall success in an apex predator that relies on sound to facilitate foraging. We revealed that vessel noise reduced searching efficiency in fish-eating killer whales, potentially causing females to forgo foraging while males still pursued but missed prey, reducing the overall likelihood of prey capture occurrence across sexes, and specifically increasing the likelihood of failed attempts. Moreover, these findings best support the hypothesis that the effects of vessel noise on foraging success in odontocetes are mediated by auditory masking interference. These results underscore the importance of managing soundscapes to achieve conservation objectives and mandates (Buxton et al., 2017; Duarte et al., 2021), which could be accomplished in part through modifications to human behaviors and activities, for example, by increasing distances between vessels and whales, reducing vessel speeds to achieve substantial reductions of noise impacts (Findlay et al., 2023; Holt et al., 2017) and increases in acoustic space (Clark et al., 2009; Tennessen & Parks, 2016; Vagle, Burnham, Thupaki, et al., 2021), and modifying mechanical components of vessels to reduce cavitation noise, which is the primary source of vessel noise (Leaper et al., 2014). While the timescales for recovering prey populations may span decades, our findings suggest that complementary actions aimed at noise mitigation and reduction over the shorter term could offer a critical pathway for bolstering odontocete foraging opportunities globally.

## AUTHOR CONTRIBUTIONS

**Jennifer B. Tennessen:** Conceptualization; formal analysis; funding acquisition; investigation; methodology; software; visualization; writing – original draft. **Marla M. Holt:** Conceptualization; data curation; formal analysis; funding acquisition; methodology; project administration. **Brianna M. Wright:** Conceptualization; software; visualization. **M. Bradley Hanson:** Funding acquisition; resources. **Candice K. Emmons:** Investigation; methodology; resources. **Deborah A. Giles:** Data curation; investigation; methodology; resources. **Jeffrey T. Hogan:** Investigation; methodology. **Sheila J. Thornton:** Funding acquisition; resources. **Volker B. Deecke:** Investigation; methodology.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at <https://doi.org/10.5281/zenodo.13333019> (2009 and

2010 audio data and raw movement data), <https://doi.org/10.5281/zenodo.13328931> (2011 and 2014 audio data and raw movement data), and <https://doi.org/10.5281/zenodo.13308835> (calibrated movement data and derived variables used in analyses).

## ORCID

Jennifer B. Tennessen  <https://orcid.org/0000-0002-1303-415X>

Marla M. Holt  <https://orcid.org/0000-0003-4153-1484>

Brianna M. Wright  <https://orcid.org/0000-0003-1243-4415>

Candice K. Emmons  <https://orcid.org/0000-0003-1326-3646>

Deborah A. Giles  <https://orcid.org/0000-0002-2701-4117>

Jeffrey T. Hogan  <https://orcid.org/0000-0002-9928-2145>

Sheila J. Thornton  <https://orcid.org/0000-0001-7996-5873>

Volker B. Deecke  <https://orcid.org/0000-0003-2781-5915>

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