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RESEARCH ARTICLE

Kinematic signatures of prey capture from archival tags reveal sex differences in killer whale foraging activity

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ABSTRACT

Studies of odontocete foraging ecology have been limited by the challenges of observing prey capture events and outcomes underwater. We sought to determine whether subsurface movement behavior recorded from archival tags could accurately identify foraging events by fish-eating killer whales. We used multisensor bio-logging tags attached by suction cups to Southern Resident killer whales (*Orcinus orca*) to: (1) identify a stereotyped movement signature that co-occurred with visually confirmed prey capture dives; (2) construct a prey capture dive detector and validate it against acoustically confirmed prey capture dives; and (3) demonstrate the utility of the detector by testing hypotheses about foraging ecology. Predation events were significantly predicted by peaks in the rate of change of acceleration ('jerk peak'), roll angle and heading variance. Detection of prey capture dives by movement signatures enabled substantially more dives to be included in subsequent analyses compared with previous surface or acoustic detection methods. Males made significantly more prey capture dives than females and more dives to the depth of their preferred prey, Chinook salmon. Additionally, only half of the tag deployments on females (5 out of 10) included a prey capture dive, whereas all tag deployments on males exhibited at least one prey capture dive (12 out of 12). This dual approach of kinematic detection of prey capture coupled with hypothesis testing can be applied across odontocetes and other marine predators to investigate the impacts of social, environmental and anthropogenic factors on foraging ecology.

KEY WORDS: Foraging behavior, Bio-logging DTAG, Accelerometer, Prey capture dive, *Orcinus orca*

INTRODUCTION

Understanding how individuals acquire sufficient food to meet their metabolic needs is a fundamental objective of behavioral ecology. Studies of foraging ecology are especially critical for threatened and endangered species when the factors threatening population persistence impact foraging success. For many species, studies quantifying feeding bouts are lacking because of the challenges in observing predation events in the wild. This is paradoxically the case for odontocetes (toothed whales) for which there is a simultaneous need for studies of foraging ecology to inform conservation efforts, and an immense challenge to acquire such data from these species that capture prey out of view, underwater. Many odontocetes are threatened by anthropogenic activities that impair foraging behavior, including acoustic masking of communication or echolocation signals from manmade sound (Nowacek et al., 2007; Weilgart, 2007), bycatch from fishing (Hamer et al., 2012) and disturbance from whale-watching vessels (Lusseau and Bejder, 2007; Senigaglia et al., 2016). Studies that reveal how odontocetes capture prey below the surface are critical for predicting anthropogenic impacts and ultimately informing conservation and management activities.

Until recently, studies of odontocete foraging behavior were generally limited to surface behavioral observations of these primarily subsurface feeding events, one-dimensional diving behavior collected by time–depth recorders (Baird et al., 2005) or acoustic behavior correlated with foraging attempts, and relied on foraging proxies such as time spent engaged in foraging behavior (e.g. Allen and Read, 2000; Laidre et al., 2003; Williams et al., 2006; Lusseau et al., 2009). Recent advances in technology have enabled the use of animal-borne bio-logging devices containing hydrophones, accelerometers, magnetometers, and in some cases, GPS loggers, to study subsurface behaviors of marine organisms (Marshall, 1998; Johnson and Tyack, 2003; Cooke et al., 2004; Block, 2005; Ropert-Coudert and Wilson, 2005; Lagarde et al., 2008; Shepard et al., 2008a; Johnson et al., 2009; Rutz and Hays, 2009; Wilson et al., 2015). These devices yield rich data streams previously unattainable (Johnson et al., 2009). Acoustic data from these tags have provided important insights into foraging behavior of odontocetes. The presence of bouts of fast, repetitive clicks with short inter-click intervals (termed 'buzzes') produced during the terminal phase of prey pursuit (Johnson et al., 2004; Miller et al., 2004; DeRuiter et al., 2009; Fais et al., 2016; Wisniewska et al., 2014) has been used to advance studies of odontocete foraging behavior, as buzzes are indicators of prey capture attempts (Fais et al., 2016). Appropriate use of tag acoustic data, however, can be limited because of masking from anthropogenic noise sources (Clark et al., 2009; Hildebrand, 2009) or the presence of excessive flow noise (water movement over the hydrophones) as a consequence of fast movements by the animal or suboptimal tag placement (Goldbogen et al., 2006; von Benda-Beckmann et al., 2016). These factors may limit the quality and availability of acoustic data recorded on animal-borne tags.

In addition to acoustic data, fine-scale movement data derived from accelerometers and magnetometers on bio-logging tags have been used to reconstruct subsurface foraging behavior of Mysticete (baleen) whales (Goldbogen et al., 2006; Hazen et al., 2009; Friedlaender et al., 2009, 2013; Wiley et al., 2011; Stimpert et al., 2014). A handful of studies have recently developed approaches to

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detect movements associated with prey capture events in some marine species with high accuracy (Skinner et al., 2009; Kokubun et al., 2011; Gallon et al., 2013; Watanabe and Takahashi, 2013; Carroll et al., 2014; Viviant et al., 2014; Ydesen et al., 2014; Allen et al., 2016). Analyses of movement data typically invoke either unsupervised classification of foraging behaviors, such as through cluster analyses (Sakamoto et al., 2009) or supervised classification such as machine learning (Carroll et al., 2014), or a hybrid approach, such as decision trees (Allen et al., 2016) to identify fine-scale movements associated with feeding events. These approaches, however, have generally required a laboratory component for validation of kinematic movement, making them impractical for large, free-swimming cetaceans (but see Allen et al., 2016). To date, movement data from accelerometers and magnetometers have not been used to develop automated detection of prey capture events in free-swimming odontocetes (but see Miller et al., 2004; Fais et al., 2016), despite the potential for such an approach to inform foraging ecology theory and to enable investigations on causal relationships between anthropogenic impacts and population declines.

We utilized suction cup-attached multisensor tags ('DTAGs'; Johnson and Tyack, 2003) that synchronously record sound, pressure and triaxial acceleration and magnetism, together with a protocol to validate feeding events (Hanson et al., 2010), to reveal how accelerometry and magnetometry data can be used to test hypotheses about odontocete foraging behavior. Specifically, we developed a method to identify prey capture events by free-swimming, piscivorous killer whales (*Orcinus orca*) with high accuracy using stereotyped signatures of movement. We validated movement (kinematic) detection using acoustic data recorded by the tag and observations of prey remains from the field, and demonstrated the utility of this method to studies of cetacean foraging ecology by testing the *a priori* hypothesis that male and female killer whales partition foraging behavior.

The southern resident killer whale (SRKW) population has been studied continuously for over 40 years by the Center for Whale Research in Friday Harbor, WA, making it an ideal case for studying foraging behavior of odontocetes because all individuals have been photo-identified and detailed records document demographic trends and group membership over this time. The SRKW population is listed as endangered in the United States and in Canada [by the National Marine Fisheries Service (NMFS, 2005) and Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2001)] with 76 individuals in May 2018, and is declining, likely as a result of reduced availability and accessibility of preferred Chinook salmon prey (Ward et al., 2009; Hanson et al., 2010; Lacy et al., 2017; NOAA, 2015), nutritional impacts on pregnancy leading to reduced fecundity and recruitment in recent years (Ward et al., 2009; Wasser et al., 2017) and exposure to toxicants and disturbance from vessel noise and presence (NOAA, 2015). This downward trend contrasts with that for northern resident killer whales, a partially sympatric piscivorous population that has exhibited net growth during the same period (Towers et al., 2015). Since male killer whales are larger than females (Clark and Odell, 1999) and have greater individual energy requirements (Noren, 2011; Williams et al., 2011), we tested the hypothesis that males and females partition foraging behavior in order to meet their biological needs. This dual approach of using kinematic detection of prey capture events to test hypotheses about foraging behavior can be applied across odontocetes and other marine foragers to investigate the impacts of social, environmental and anthropogenic factors on foraging ecology.

MATERIALS AND METHODS

Tag data collection and post-processing

We used non-invasive, multi-sensor archival tags (DTAGs; Johnson and Tyack, 2003) to record subsurface acoustic and movement behavior of southern resident killer whales [*Orcinus orca* (Linnaeus 1758)] in the Salish Sea, Washington, USA during June 2011, and September 2010, 2012 and 2014 (as in Holt et al., 2017). Version 2 DTAGs were used during 2010–2011 and 2014, and version 3 DTAGs were used during 2012. To minimize effects of seasonal differences in diet on foraging behavior, we only analyzed September deployments in this study. Each tag contained stereo hydrophones to record sound, tri-axial accelerometers and magnetometers to derive whale pitch, roll, heading and acceleration, and pressure and temperature sensors to measure depth. The tag contained flash memory for data storage, and a VHF beacon to enable tag recovery. Tags recorded acoustic data at 192 kHz (2010-2011, 2014) or 240 kHz (2012) and movement, depth and temperature data at 50 Hz (2010–2011, 2014) or 200 Hz (2012).

Tagging methodology is described elsewhere (Holt et al., 2017). Briefly, individuals were identified by unique features on the trailing edge of their dorsal fin and on the gray saddle patch immediately posterior to their dorsal fin (Bigg et al., 1987). Tagging was conducted under research permits (see Acknowledgements) from a 6.7 m rigid-hulled inflatable research vessel powered by an outboard motor with two propellers. Twenty-three DTAGs were suction cup-attached by a 7 m carbon fiber pole to the dorsal surface of 21 killer whales. Most animals displayed mild to moderate reactions to tagging, which included flinching at point of contact or diving and remaining submerged for up to a few minutes, and returned to pre-tagging surfacing behavior within 5 min of tagging, consistent with the work of others (Wright et al., 2017). Tags remained attached for up to several hours and were programmed to release before local sunset (Table 1). Effort was made to ensure an equal number of males and females were tagged, across a range of ages. All tagged animals were >1 year old. Two animals were tagged twice in different years (Table 1).

We conducted focal follows of the tagged animal to: (1) obtain GPS fixes of the tagged whale during surfacings using an integrated package consisting of a GPS system (Trimble Geo XH, GeoSpatial Innovations, Inc., Austin, TX, USA) connected to a laser range finder and a compass (for additional details, see Giles, 2014); (2) observe surface behaviors including fish brought to the surface; (3) collect prey remains when possible; (4) note changes in tag orientation, for use during tag data calibration; and (5) facilitate tag retrieval. Focal follows occurred for the duration that the tag remained on the animal, except during periods of poor visibility due to fog, or while we retrieved prey samples. After an observed predation event (i.e. a fish was observed in the focal animal's mouth or being pursued by the focal animal, followed by the presence of prey remains at the surface), prey remains (scales, tissue fragments and/or bones) were collected in a sterilized fine-meshed dip net and placed on ice for further processing at the laboratory following established protocols (Hanson et al., 2010). Prey samples were used to confirm predation events, and to identify fish species based on scale morphology and genetic analysis.

Following detachment, tags were located and retrieved using VHF radio transmission, and data were downloaded. Custom scripts in MATLAB (The MathWorks, Natick, MA, USA), including the 2014 DTAG toolbox (www.soundtags.org/dtags/dtag-toolbox), were used to: (1) calibrate movement data to correct for individual sensor characteristics and tag orientation; (2) compute three-dimensional orientation; and (3) convert pressure data to

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Table 1. Summary of analyzed DTAG deployments on southern resident killer whales, and comparison of prey capture dive detection methods

Tag ID	Date	Time (h:min:s)	Whale ID	Sex	Age (years)	Duration (h)	No. dives analyzed	Acoustic audit[b]	Detection method[c]		
									Visual	Acoustic	Kinematic
oo10_251m	2010-09-08	14:40:22	J39	M	7	1.21	117	Y	0	3	2
oo10_257m	2010-09-14	14:00:35	L88	M	17	4.51	516	N	0	–	17
oo10_259m	2010-09-16	15:50:54	K38	M	6	1.68	196	N	0	–	1
oo10_261m	2010-09-18	15:32:45	L72	F	24	0.72	36	Y	0	0	0
oo10_264m	2010-09-21	12:37:09	L83	F	20	2.72	217	Y	0	0	0
oo10_265m	2010-09-22	12:15:42	K33	M	9	6.26	517	Y	4	10	21
oo10_267m	2010-09-24	14:34:45	J14	F	36	3.99	278	N	0	–	0
oo10_268m	2010-09-25	10:53:31	L86	F	19	7.47	629	N	0	–	3
oo10_270m	2010-09-27	12:47:05	L78	M	21	1.12	111	N	0	–	5
oo12_250m	2012-09-06	10:51:13	L22	F	41	6.94	595	N	0	–	13
oo12_251m	2012-09-07	11:22:21	K33	M	11	1.66	145	Y	0	3	5
oo12_254m	2012-09-10	10:46:44	L95	M	16	7.03	574	Y	0	8	4
oo12_257m	2012-09-13	10:52:14	L109	M	5	5.13	0[a]	N	0	–	–
oo12_260m	2012-09-16	12:24:02	L116	M	2	2.76	153	N	0	–	2
oo12_261m	2012-09-17	10:11:55	L84	M	22	2.20	174	Y	1	2	2
oo12_266m	2012-09-22	10:39:21	L91	F	17	2.65	214	Y	1	5	7
oo12_266n	2012-09-22	13:45:09	L47	F	38	0.62	51	Y	0	0	0
oo12_267m	2012-09-23	14:56:07	J28	F	19	2.61	244	Y	0	0	0
oo14_249m	2014-09-06	09:55:10	L113	F	5	7.16	567	Y	2	2	8
oo14_250m	2014-09-07	09:52:25	L89	M	21	8.87	822	N	2	–	15
oo14_263m	2014-09-20	11:57:15	L85	M	23	6.61	502	Y	0	3	9
oo14_264m	2014-09-21	11:31:46	L91	F	19	0.82	60	Y	0	2	2
oo14_266m	2014-09-23	10:53:41	K35	M	12	4.76	455	Y	2	9	10

[a]Deployment oo12_257m was not included in the analysis because poor tag attachment rendered kinematic data unresolvable.
[b]For some deployments, tag placement, tag movement or excessive flow noise caused by tag placement prevented acoustic audits.
[c]Number of prey capture dives detected using either visual, acoustic or kinematic methods. Dashes within cells indicate deployments for which no data were analyzed because of poor quality.

temperature-corrected depth, following established methods (Johnson and Tyack, 2003). Acoustic data were converted to .wav files and calibrated in MATLAB following methods described in Holt et al. (2017). To identify individual dives, pressure data were down-sampled to 5 Hz and a custom dive detector was used to identify dives with maximum depth ≥1 m, bookended by a minimum depth ≤0.5 m. All dive results were manually checked for validity. Erroneous dives (i.e. false detections that appeared to meet the dive criteria due to transient fluctuations in the depth signal) were excluded. This accounted for a mean of <1% (0–4.5% per deployment) of the total dives identified. Additionally, a histogram of dive durations revealed a bimodal distribution with an outlying peak at 2–4 s, which likely represents erroneous dive detections due to fluctuations in the depth profile inherent in data sampled at a high sample rate, or incomplete surface intervals. Thus, we omitted all dives <4 s in duration. Dive start and end times were computed, and dives that began within the first 5 min of tag attachment were excluded to account for short-term behavioral reactions to tagging. Comparison of observations of surface behavior before and after tagging, along with visual inspection of dive profiles following tagging, revealed that this was a sufficient amount of time for animals to return to pre-tagging surface behavior, and to commence patterns of diving behavior that mirrored subsequent behavior recorded on tags.

Calculation of movement variables

Calibrated movement data with a 50 Hz sampling rate were used for movement analyses (version 3 DTAGs were downsampled to 50 Hz). We partitioned each dive into descent, bottom (70% of maximum depth) and ascent phases, following methods in Arranz et al. (2016). Across each dive, and within each dive phase where applicable, we computed several variables associated with subsurface movement based on those known or hypothesized to be important in describing foraging behavior (e.g. Wright et al., 2017; Ydesen et al., 2014; Table 2): maximum depth, whole dive duration, ratio of bottom to whole dive duration, rates of descent and ascent, mean vectorized dynamic body acceleration (VeDBA), median jerk, maximum jerk peak (jerk peak), median roll, roll at time of jerk peak (roll at jerk peak), and heading variance.

VeDBA is a proxy for metabolic rate (Wilson et al., 2006; Qasem et al., 2012) and was computed as the mean of the vector summation of the acceleration signal. Body acceleration is composed of both dynamic (due to motion) and static (due to gravity) acceleration (Johnson and Tyack, 2003). Dynamic acceleration contains specific acceleration (i.e. net displacement with respect to the body frame) and body rotations (i.e. angular displacement of the body) (Martín López et al., 2016). The incorporation of data from gyroscopes can enable more precise removal of body rotation from the dynamic acceleration signal (Martín López et al., 2016), but the power consumption of tags containing gyroscopes precluded their use in this study. Instead, we followed a widely used method to estimate tri-axial dynamic body acceleration (DBA; Shepard et al., 2008b; Wright et al., 2017). First, we calculated static acceleration by taking a 3 s moving mean of each axis of the tri-axial acceleration signal, and next, we subtracted this from the total acceleration signal for each axis. Then, we computed the vector sum (square root of the sum, across the three axes, of the squared DBA signal). This approach, rather than computing the summation of the DBA signal (overall DBA, ODBA) is a better proxy of animal energy expenditure when tag position has not been consistent (Qasem et al., 2012; Wright et al., 2017). Finally, we took the mean of the VeDBA vector to obtain an overall value per dive, and per dive phase.

Jerk is the rate of change of acceleration (i.e. the third derivative of position) and is a useful metric for identifying rapid movement (Allen et al., 2016). We derived jerk by computing the difference between successive values of acceleration in each axis, and then

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Table 2. Definitions of movement and acoustic variables calculated from DTAG deployments

Dive variable	Definition	Dive phase			
		Whole	Descent	Bottom	Ascent
Maximum depth (m)	Maximum depth of dive	X			
Duration (s)	Amount of time between surfacings	X	X	X	X
Bottom:whole duration	Ratio of amount of time in bottom phase versus whole dive	X			
Vertical rate of ascent (m s^{-1})	Vertical rate of change of depth				X
Mean VeDBA (m s^{-2})	Mean of the vector summation of tri-axial dynamic body acceleration (DBA)[a]	X	X	X	X
Median jerk (m s^{-3})	Median of the jerk[b] signal; jerk is the rate of change of acceleration	X	X	X	X
Jerk peak	Maximum peak of the jerk signal adjusted by the median jerk in the corresponding dive phase			X	
Median roll (deg)	Median of the absolute value of the roll signal	X	X	X	X
Roll at jerk peak (deg)	Absolute value of the roll at the time of jerk peak			X	
Heading variance	Circular variance in the heading signal	X	X	X	X
Buzz presence	Binary presence or absence of buzz sound(s)			X	
Prey handling sound presence	Binary presence or absence of prey handling sound(s)			X	X

[a]VeDBA was computed by subtracting the static acceleration from the total acceleration following methods described in Wright et al. (2017).
[b]Jerk was computed as the vector norm of the difference between successive values of the acceleration signal for each of the three axes (Ydesen et al., 2014; Allen et al., 2016; Arranz et al., 2016).

taking the vector sum across the three axes (Ydesen et al., 2014; Allen et al., 2016). We computed the median jerk over the whole dive, and over each dive phase. To derive the jerk peak during the bottom phase of a dive, we used a peak detection function in MATLAB's signal processing toolbox, with a minimum peak prominence threshold of 1, to identify all peaks in the jerk signal. Then, we selected the maximum (largest) peak and divided it by the median of the jerk signal during the bottom phase in order to apply a consistent method of adjusting for inter-individual differences that affect the magnitude of the jerk signal. We verified that a sampling rate of 50 Hz was sufficient to compute jerk peak, by comparing jerk peaks derived using 200 Hz and 50 Hz sampling rates on dives >20 m (n=50 dives), from two deployments. There was no difference between sampling rates in the peak detector's performance.

Heading is a directional quantity, measured as an angle, for which low and high values are arbitrary. Therefore, heading values require analysis with circular statistics (Berens, 2009). We used the function 'circ_var' in the package CircStat (Berens, 2009), a circular statistics package in MATLAB that utilizes equations from Zar (2010) to compute the circular variance in heading over the whole dive and during each dive phase. This approach has been used in other analyses of heading data from DTAGs (e.g. DeRuiter et al., 2013; Samarra and Miller, 2015).

Calculation of acoustic variables

Sound recordings were offloaded from each tag as wave files and post-processed using the DTAG toolbox and custom scripts in MATLAB, following methods described in Holt et al. (2017). Data were included for acoustic analysis based on quality (flow noise assessment and tag placement). Echolocation clicks from the tagged whale were distinguished from nearby conspecifics using consistent angle of arrival of each click between the two hydrophone channels in agreement with tag placement and low frequency spectral content due to near field recordings on the body (Zimmer et al., 2005; Johnson et al., 2006). Acoustic data were audited for the presence of buzzes (inter-click interval ≤10 ms) and prey handling sounds (tearing and crunching sounds, Wright et al., 2017) using scrolling displays of spectrograms (512 point, Hann window, 50% overlap), along with plots of both whale depth and angle of arrival of each sound, matched in time. Buzzes and prey handling sounds were mapped to dives, and for each dive we scored the presence or absence of buzzes and prey handling sounds (Table 2). All acoustic audits were conducted by a single experienced researcher.

Kinematic detection of prey capture dives

To identify the subset of dives that contained predation events, we employed a 4-step process consisting of: (1) assigning visually confirmed predation events to dives; (2) identifying a stereotyped movement signature of prey capture, i.e. determining the movement variables that significantly predicted the occurrence of visually confirmed predation events; (3) building a prey capture dive detector using these predictor variables and validating it against acoustically confirmed predation events; and (4) running the movement detector on all data. First, we assigned the prey samples to dives by selecting the most recent dive greater than 10 m that preceded the occurrence of the prey sample. The selection of 10 m as a threshold is supported by research on fish-eating killer whales and other cetaceans showing that deep dives are to target prey (Wright et al., 2016), and initial prey capture primarily occurs during the bottom phase of deeper dives (Arranz et al., 2016; Wright et al., 2017), after which prey (typically one prey item per dive; Ford and Ellis, 2006; Wright et al., 2016) are brought or chased to the surface and shared between pod members (Wright et al., 2016, 2017). Additionally, we required the tagged whale to be associated with the prey sample, and the dive start time to occur within the previous 15 min of collecting the prey sample (or observing a fish in the mouth). In rare cases of ambiguity about the identity of the prey capturer, we relied on acoustic cues of predation, as these are established indicators of predation events (Miller et al., 2004; Wisniewska et al., 2014, 2018; Arranz et al., 2016). If uncertainty remained about the dive assignment, or any of the conditions were not met, the event was omitted. To determine the movement variables that predicted the occurrence of visually confirmed prey capture dives we fitted generalized linear mixed effects models in R v.3.3.3 (https://www.r-project.org/) using the package lme4 (http://CRAN.R-project.org/ package=lme4), with a binomial family and logit link. The response variable was the presence or absence of a visually confirmed predation event, fixed effects were sex, jerk peak, bottom:whole duration, rate of ascent, roll at jerk peak (roll), mean vectorized dynamic body acceleration during the bottom phase of a dive (VeDBA), and heading variance in the bottom phase (heading variance). The random effects were tag deployment and year. Significant predictor variables were jerk peak, roll, and

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heading variance (Tables S1 and S2). Plots of residuals versus fitted values confirmed model validity.

We used all possible combinations of the three significant predictor variables to build several kinematic detectors of prey capture dives. The detectors classified a prey capture dive as one in which the included predictor variables met or exceeded the minimum observed value in the training set (jerk peak=14.38, roll=22.93 deg, heading variance=0.40). To validate detector performance, we compared kinematic and acoustic detections, using the subset of deployments for which acoustic audits had been possible. We defined as the response variable the binary occurrence of an acoustically confirmed prey capture event ('present' if a dive contained buzzes during the bottom phase followed by prey handling sounds during the bottom and/or ascent phases, and 'absent' if either criterion was not met). We omitted dives in which either buzzes or prey handling sounds, but not both, were detected, as their ambiguity precluded their use in the validation process. We used the acoustically confirmed prey capture event data to compute true positive (TP) and false positive (FP) rates to quantify each detector's performance. We took a conservative approach to detector selection; that is, we selected the detector that minimized the false positive rate, in order to avoid over-estimating prey capture. Finally, we ran the selected kinematic detector on the whole data set.

Statistical analyses

All statistical tests were conducted in R, using the packages lme4 (http://CRAN.R-project.org/package=lme4) or nlme (http://CRAN.R-project.org/package=nlme), with α=0.05. We validated models by visualizing residuals to confirm reasonable fit. To compare kinematics of prey capture dives to other dives, we fitted a generalized linear mixed effects model with a binomial family and logit link, dive type as the response variable, fixed effects of whole dive duration (natural log-transformed to meet model assumptions), bottom:whole duration (ratio of time spent in bottom phase of a dive to whole dive duration), jerk peak, rate of ascent, roll, mean VeDBA, and heading variance, and random effects of deployment ID and year (Table S1). Age was not included as a random effect because the model did not converge. To compare prey capture dive characteristics between sexes we fitted several independent linear mixed effects models with individual kinematic variables as the single response variable (maximum depth, jerk peak, roll, natural log-transformed dive duration, bottom:whole duration, rate of

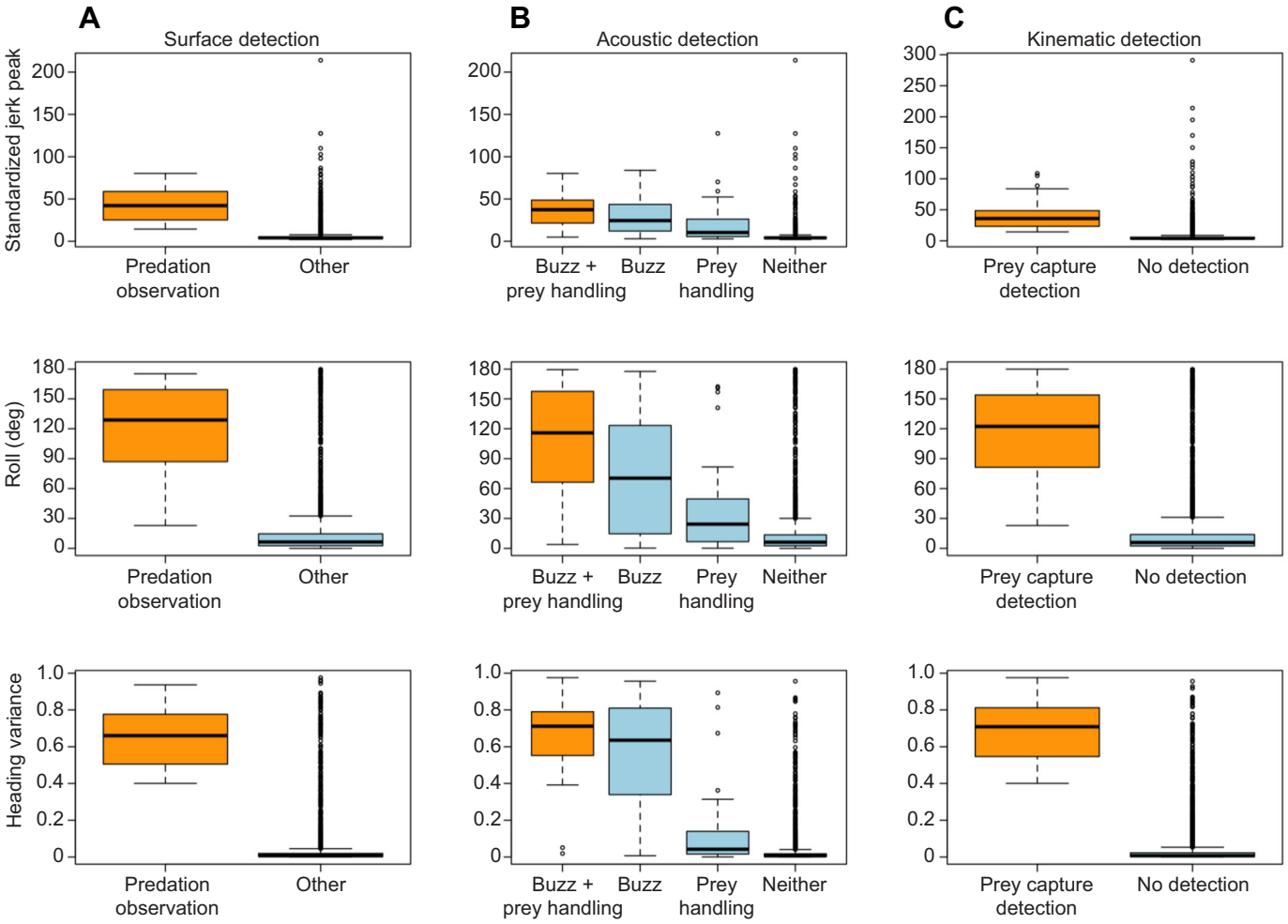

Fig. 1. Jerk peak, roll and heading variance of prey capture dives are similar across dive detection methods. Panels illustrate dive types revealed by (A) surface detection, (B) acoustic detection and (C) kinematic detection. Prey capture dives (orange shading) were defined as (A) dives associated with surface observations of confirmed prey samples (n=12), (B) dives containing the co-occurrence of buzzing and prey handling sounds (n=47), and (C) dives containing the co-occurrence of values of jerk peak, roll and heading variance above threshold values (n=126). Light blue shaded boxes indicate dives for which the criteria for prey capture dive detection were not met. Within each boxplot, boxes represent interquartile ranges, horizontal lines represent medians, whiskers indicate values within 1.5 times the interquartile range, and circles outside of the whiskers indicate outliers.

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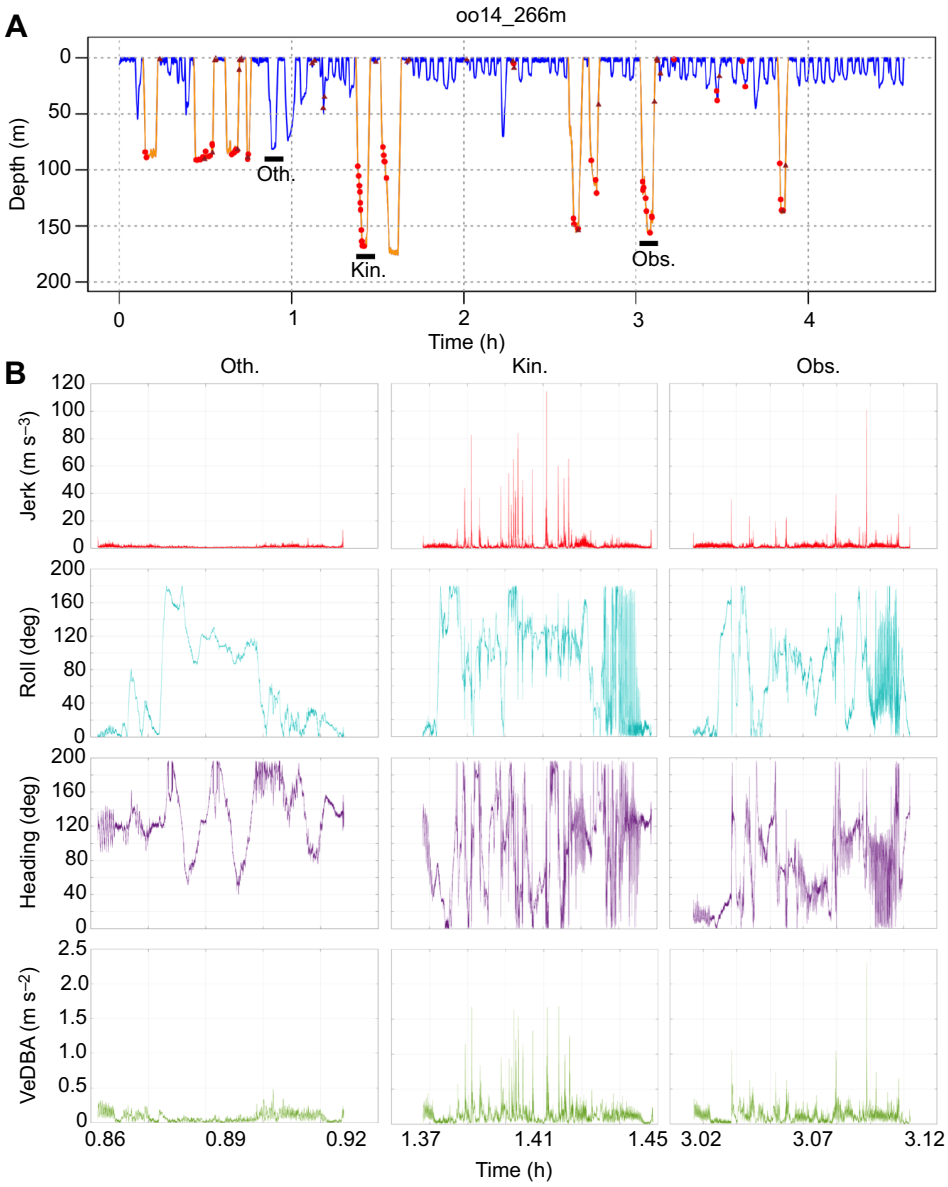

Fig. 2. Prey capture dives are kinematically distinct. (A) Plot of the dive profile for deployment oo14_266m, indicating kinematic detection of prey capture dives (orange lines), buzzes (red circles) and prey handling sounds (brown triangles). Solid horizontal black lines beneath dives identify three dive types: a non-prey capture dive (Other, 'Oth.'), a prey capture dive detected kinematically ('Kin.') and the single instance of a surface-observed prey capture dive (Observation, 'Obs.', also detected kinematically and acoustically). Kinematic detection identified more prey capture dives than either of the other methods. (B) Plots of four kinematic variables (jerk, roll, heading and VeDBA) for each of the corresponding dives (Oth., Kin., Obs.) arranged column-wise, revealing similarities in kinematics of prey capture dives, in contrast to the non-prey capture dive.

ascent, heading variance and mean VeDBA), sex as a fixed effect, and random effects of deployment ID and year (Table S1). To compare counts of prey capture dives within a deployment between males and females, we fitted a generalized linear mixed effects model with a Poisson family and log link, with dive count as the response variable, fixed effects of sex, deployment duration (in

Table 3. Descriptive statistics and model summary of the model comparing dive types identified by kinematic detection

Response	Fixed effects	Dive type* (mean±s.d.)	Estimate	s.e.	z-value	*P*-value
Dive type	ln[Duration (s)]	PC: 5.40±0.55 Other: 3.16±0.76	1.621	0.328	4.942	<0.0001
	Bottom:whole duration	PC: 0.51±0.17 Other: 0.55±0.11	−0.561	1.160	−0.484	0.6280
	Jerk peak	PC: 39.51±19.44 Other: 5.83±8.62	0.033	0.006	5.313	<0.0001
	Roll (rad)	PC: 2.03±0.76 Other: 0.24±0.42	1.107	0.204	5.438	<0.0001
	Heading variance	PC: 0.69±0.16 Other: 0.03±0.09	7.368	1.000	7.368	<0.0001
	Rate of ascent (m s^{-1})	PC: 1.65±0.67 Other: 0.57±0.25	0.323	0.326	0.991	0.3220
	Mean VeDBA (m s^{-2})	PC: 0.16±0.06 Other: 0.09±0.06	5.125	2.418	2.119	0.0341

*Abbreviations refer to binary dive types, either PC (prey capture) or other.

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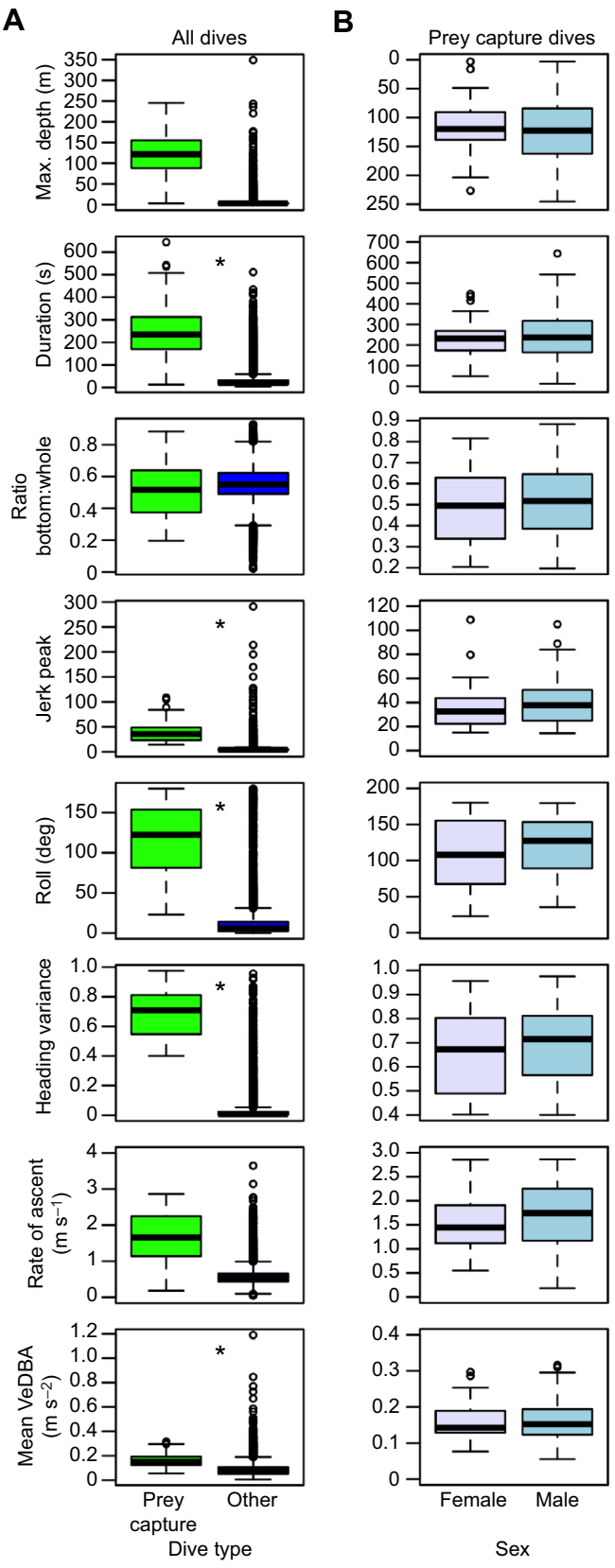

Fig. 3. Boxplots comparing descriptive and kinematic variables between dive types and sexes. (A) Prey capture dives (n=126) differed significantly from other dives (n=7047) in natural log-transformed dive duration (plotted untransformed for interpretation), jerk peak, roll, heading variance and mean VeDBA. (B) Prey capture dives by males (n=93) and females (n=33) did not differ significantly in any of the descriptive or kinematic variables measured. For both A and B, maximum depth was not included in statistical models, but is plotted for reference. Plots bearing an asterisk indicate significance; *P<0.05; generalized linear mixed effects model.

hours; natural log-transformed) and their interaction, and year as a random effect (Table S1). To compare sex differences in counts of dives to depths of preferred Chinook prey (≥30 m; Candy and Quinn, 1999; Wright et al., 2017), we fitted a generalized linear mixed effects model with a Poisson family and log link, with the number of dives as the response variable, fixed effects of sex, deployment duration (in hours; natural log-transformed) and their interaction, and year as a random effect (Table S1). Finally, to determine whether foraging effort differed between males and females, we fitted a linear mixed effects model with the response variable as the total time (in minutes; natural log-transformed) spent in dives to Chinook habitat depth (≥30 m; one deployment was omitted for which the tagged 2-year-old male did not engage in any deep dives), fixed effects of sex, deployment duration (in hours; natural log-transformed) and their interaction, and year as a random effect (Table S1). For each of the latter three models, the interaction term was not a significant effect (counts of prey capture dives, sex×deployment duration: s.e.m.=0.343, z-value=−0.933, P-value=0.351; counts of dives to Chinook depths, sex×deployment duration: s.e.m.=0.207, z-value=0.210, P-value=0.834; cumulative time diving to Chinook depths, sex×deployment duration: s.e.m.=0.501, t-value=0.268, P-value=0.792) so we excluded the interaction term from each of the final models to preserve power. Additionally, we omitted one deployment (oo12_257 m) because of improper tag attachment, which rendered the kinematic data unresolvable.

RESULTS

Summary of deployments

DTAGs recorded for a total of 117.2 h (2010=29.5 h; 2011=20.1 h; 2012=32.1 h; 2014=35.5 h). Mean deployment time was 4.19 h (range=0.69–8.87 h). We analyzed a total of 89.5 h (2010=29.7 h; 2012=31.6 h; 2014=28.2 h) from 22 deployments (2010=9; 2012=9; 2014=5; Table 1). Mean analyzed time per deployment was 4.07 h (range=0.62–8.87 h). Two of the analyzed deployments were on individuals that had been tagged once in previous years. During the analyzed portion of deployments, a total of 7173 dives met our inclusion criteria. The mean number of dives analyzed per deployment was 326 (range=36–822).

Kinematic detection of prey capture

The values of the three predictor variables for the 12 surface-confirmed prey capture events are presented in Table S2. Jerk peak, roll and heading variance of prey capture dives were significant predictors of prey sample observations (generalized linear mixed model: jerk peak: z=2.206, P=0.028; roll: z=2.481, P=0.013; heading variance: z=2.497, P=0.012) (Table S3). The detector that had the lowest false positive rate included all significant predictor variables (jerk peak, roll, and heading variance) (Table S4). Overall, this detector had a TP rate of 78.7% (females=77.8%, males=78.9%) and an FP rate of 0.2% (females=0.1%, males=0.3%). For dives ≥5 m, the detector had a TP rate of 80.4% (females=87.5%, males=78.9%) and an FP rate of 1.6% (females=1.1%, males=1.8%). Median values of jerk peak, roll and heading variance were similar between prey capture dives that were detected kinematically, those detected acoustically, and those that

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Table 4. Model summaries reporting the effect of sex on several kinematic variables of prey capture dives identified by kinematic detection

Response	Fixed effect	Mean±s.d.*	Estimate	s.e.	d.f.	*t*-value	*P*-value
Maximum depth (m)	Sex	F: 117.34±49.27 M: 119.51±59.47	−4.650	19.025	15	−0.244	0.810
Duration (s)	Sex	F: 238.31±94.27 M: 256.35±124.73	7.489	33.998	15	0.220	0.829
Bottom:whole duration	Sex	F: 0.50±0.18 M: 0.51±0.17	0.014	0.045	15	0.314	0.758
Rate of ascent (m s^{-1})	Sex	F: 1.55±0.64 M: 1.69±0.67	0.132	0.140	15	0.947	0.359
Jerk peak	Sex	F: 35.87±20.04 M: 40.81±19.17	3.620	4.612	15	0.785	0.445
Roll (deg)	Sex	F: 105.28±50.81 M: 120.19±39.96	14.549	10.178	15	1.429	0.173
Heading variance	Sex	F: 0.66±0.18 M: 0.70±0.15	0.035	0.035	15	1.009	0.329
mean VeDBA (m s^{-2})	Sex	F: 0.16±0.05 M: 0.16±0.06	0.026	0.026	15	0.991	0.338

*Abbreviations refer to binary sex class, either F (female) or M (male).

were associated with visually confirmed predation events (Fig. 1), confirming the existence of a stereotyped, kinematic signature of prey capture (Fig. 2). Kinematic detection of prey capture dives enabled substantially more dives to be included in subsequent analyses than either surface or acoustic detection methods (Table 1).

Foraging ecology

We detected 126 prey capture dives during 17 of 22 deployments. Compared with other dives, prey capture dives had significantly greater dive duration (natural log-transformed; z=4.942, P<0.0001), jerk peak (z=5.313, P<0.0001), roll (z=5.438, P<0.0001), heading variance (z=7.368, P<0.0001) and mean VeDBA (z=2.119, P=0.0341) (Table 3, Figs 2 and 3). There was no difference in bottom:whole duration or rate of ascent between prey capture and other dives. Of prey capture dives, there were no differences between males and females in any of the measured variables: maximum depth, dive duration, bottom:whole duration, rate of ascent, jerk peak, roll, heading variance or mean VeDBA (Table 4, Fig. 3).

After accounting for the effect of deployment duration, males made significantly more prey capture dives during a deployment than females (generalized linear mixed model: z=3.401, P=0.0007; Table 5, Fig. 4A). There were no prey capture dives detected during half of the deployments on females (5/10), whereas at least one prey capture dive was detected during all deployments on males (12/12; Fig. 5). Additionally, there was a significant effect of sex on the number of dives to Chinook salmon habitat (generalized linear mixed model: z=3.790, P=0.0002; Table 5, Fig. 4B) and a non-significant trend of an effect of sex on the cumulative time spent in these dives (linear mixed effects model: t=1.594, P=0.131; Table 5, Fig. 4C).

DISCUSSION

We used kinematic data derived from triaxial accelerometers and magnetometers from suction cup-attached multisensor tags to detect prey capture events by fish-eating killer whales with high true positive and low false positive rates. Additionally, we revealed overall differences in foraging effort but not foraging kinematics between males and females. Males captured more prey during a deployment than females, made more dives to Chinook habitat, and there was a trend that males spent more time engaged in deep diving.

Subsurface prey capture by killer whales was characterized by a peak in the jerk signal, a concurrent body roll to the side, and non-directional movement during the bottom phase of a dive. Peaks in jerk, the rate of change of acceleration, are the outcome of rapid, transient bursts in acceleration. These jerk peaks have been associated with terminal-phase prey capture in other cetaceans and pinnipeds (Johnson et al., 2004; Wisniewska et al., 2014; Ydesen et al., 2014; Allen et al., 2016; Arranz et al., 2016). These movements can include rapid forward motion or abrupt changes in direction (Johnson et al., 2004; Allen et al., 2016), or sudden changes in musculature in the jaw or gular region during prey suction or engulfment due to mouth opening and head shaking (Ydesen et al., 2014; Wisniewska et al., 2014, 2018). Of the deployments for which acoustic analyses were possible, the

Table 5. Descriptive statistics and summaries of models predicting number of prey capture dives per deployment, number of dives to Chinook habitat and time spent in Chinook habitat-associated dives

Response	Fixed effects	Mean±s.d.*	Estimate	s.e.	z-value	*P*-value
No. prey capture dives within deployment	Sex	F: 3.30±4.55 M: 7.75±6.70	0.691	0.203	3.401	0.0007
	ln(Deployment duration)		0.923	0.144	6.423	<0.0001
No. dives to Chinook habitat	Sex	F: 7.90±7.98 M: 15.5±12.70	0.513	0.135	3.790	0.0002
	ln(Deployment duration)		0.895	0.100	8.993	<0.0001
		Mean±s.d.*	Value	s.e.	*t*-value	*P*-value
ln[Time spent in dives to Chinook habitat (min)]	Sex	F: 6.86±1.38 M: 7.80±1.02	0.675	0.424	1.594	0.1310
	ln(Deployment duration)		0.847	0.241	3.517	0.0030

*Abbreviations refer to binary sex class, either F (female) or M (male).

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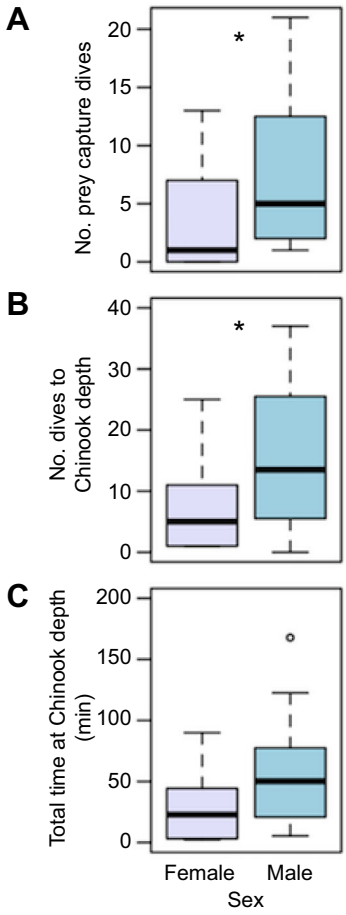

Fig. 4. Foraging behavior differs between sexes. After accounting for deployment duration, (A) males made a greater number of prey capture dives during a deployment, (B) males made more dives to Chinook depth (>30 m) and (C) there was a non-significant trend that males spent more time at Chinook depth. Plots bearing asterisks indicate significance. $P<0.05$; generalized linear mixed effects model (A,B) and linear mixed effects model (C).

majority of dives containing jerk peaks in the bottom phase above the designated detector threshold also contained buzzes, which are integral to and indicative of prey capture attempts (Miller et al., 2004; Wisniewska et al., 2014, 2018; Arranz et al., 2016). Therefore, these jerk peaks were likely due to body movements immediately prior to or during the moment of prey capture. Field studies employing video-enabled recording tags in conjunction with accelerometer-equipped tags may be able to resolve whether jerk peaks are the cause (e.g. rapid motion to intercept prey during terminal pursuit) or an outcome (e.g. muscular movement in the jaw or face to secure prey) of prey capture.

The observation of a side roll during subsurface foraging is consistent with behavior in many other cetaceans (Miller et al., 2004; Woodward and Winn, 2006; Stimpert et al., 2007, 2014; DeRuiter et al., 2009; Akamatsu et al., 2010; Aoki et al., 2012; Goldbogen et al., 2013; Blair et al., 2016; Cade et al., 2016). The function of this side roll is unclear. Inverted swimming may facilitate the use of vision during foraging, whereby prey are revealed by their silhouette against the light coming from the surface (Fristrup and Harbison, 2002). In a study on captive harbor porpoises, while there were no major differences in prey capture outcomes between foraging trials with and without eye cups that blocked vision, prey capture was slower when vision was blocked, suggesting that visual information may play a role in foraging (DeRuiter et al., 2009). Alternatively, inverted swimming during the bottom phase of a foraging dive may be acoustically efficient (Stimpert et al., 2014). A narrow, directional sonar beam may achieve a greater search area when the searcher is inverted, by changing the axis of the sonar beam (Akamatsu et al., 2010). Alternatively, it is possible that inverted swimming may help an animal maximize swimming efficiency by reducing locomotion costs of pursuing prey underwater. If so, we would expect that animals should roll during deep dives regardless of prey capture outcome, and animals of different sizes should exhibit differences in roll angle in order to minimize body size-related locomotion costs. Indeed, we often observed rolling behavior during deep dives with no kinematic or acoustic indication of prey capture (e.g. Fig. 2). Additionally, there was a non-significant trend that males, who can be up to approximately 50% longer than females and bear a dorsal fin twice the height of female fins (Clark and Odell, 1999) rolled to a greater angle than females during prey capture dives (Fig. 3). Bottom-phase rolling during prey capture attempts may help mitigate the costs of such movement. Finally, another possibility is that rolling may position an animal's mouth to facilitate prey capture; however, this has not been tested. Future studies using sound and movement tags in conjunction with video-equipped tags will be valuable in testing these hypotheses.

Heading variance during the bottom phase of a dive is an indication of the directivity of travel (e.g. DeRuiter et al., 2013). Values close to 0 indicate nearly straight paths in the lateral axis (left–right motion), whereas values close to 1 indicate circuitous, indirect paths with many changes in direction. Heading variance is partly affected by prey behavior. When being pursued by predators, salmon prey employ anti-predator responses that include evasive behaviors such as increasing swim speed, changing direction and changing depth (summarized in Wright et al., 2017). Depending on the effectiveness of these responses, prey pursuit can last seconds to minutes; thus, prey and predator behavior are tightly correlated. Since subsurface prey pursuit incurs energetic costs including from body drag and oxygen depletion due to breath-holding (Williams and Noren, 2009), larger values of heading variance during prey capture dives may be a proxy for qualitatively estimating energy expended during prey capture.

Kinematic detection of prey capture events resulted in reasonable TP and FP rates (78% and 0.2%, respectively). When we excluded dives less than 5 m, to remove any artificial dilution of the FP rate by an excess of surface-associated non-foraging dives, the TP and FP rates remained reasonable (80.4% and 1.6%, respectively). This suggests that the accuracy of kinematic detection is comparable to acoustic detection, and can additionally increase sample size because it is not affected by masking from flow noise. There is a tradeoff involved in selecting appropriate TP and FP rates. It is important to evaluate these tradeoffs when optimizing detector performance. Since endangered SRKW survival is strongly correlated with availability of their preferred prey, Chinook salmon (Ford and Ellis, 2006; Ward et al., 2009; Ford et al., 2010), and higher FP rates could result in overestimates of caloric intake, we took a precautionary approach that minimized false detections while yielding a TP rate that was sufficient to detect most prey capture dives.

We found sex differences in foraging effort of killer whales. Kinematic detection of prey capture revealed that males made more prey capture dives, and more dives to preferred prey habitat, and there was a trend that males spent more cumulative time doing so. Since diving bears an energetic cost (Williams and Noren, 2009), and 'resident'-type killer whales target Chinook salmon depths

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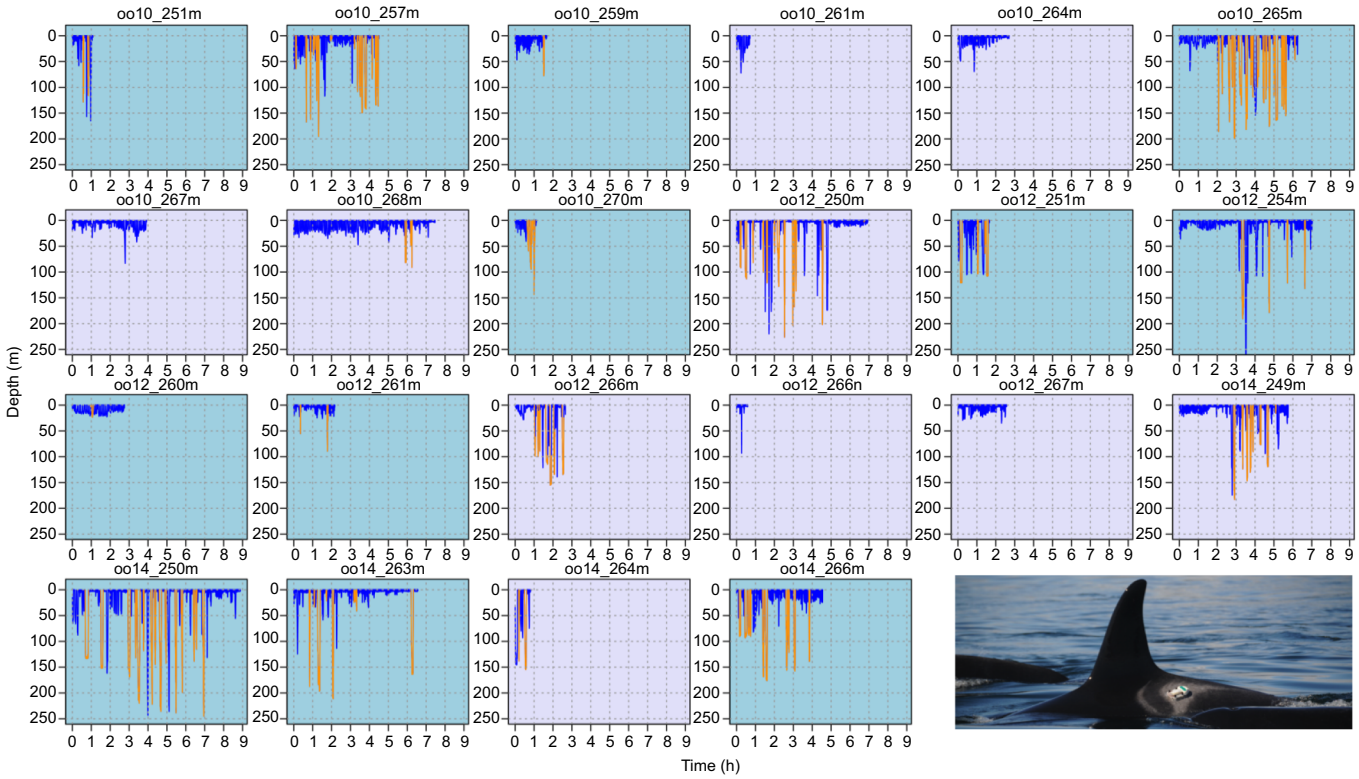

Fig. 5. Plots of dive profiles for each deployment. Prey capture dives are overlaid (orange lines), scaled to the longest deployment. There were no prey capture dives detected during half of the deployments in females (lavender), whereas at least one prey capture dive was detected during all deployments in males (light blue). Not all dives to Chinook habitat (>30 m) are prey capture dives. Image of tag in position below dorsal fin is shown on bottom right.

when foraging (Wright et al., 2017), dives below 30 m likely represent prey capture attempts. In many group-living species, foraging behavior varies between sexes (e.g. Doolan and MacDonald, 1996; Agostini and Visalberghi, 2005; Breed et al., 2006; Beck et al., 2007). One explanation for the differences in foraging behavior between male and female killer whales may be niche specialization through sexual dimorphism, to avoid intraspecific competition (Selander, 1966; Rose, 1994; Ginnett and Demment, 1997; Bearhop et al., 2006; Cook et al., 2007; Breed et al., 2006; Phillips et al., 2011). Indeed, the larger body size of male killer whales may provide a kinematic advantage for prey capture by allowing an individual to move more efficiently in pursuit of prey. However, there were no significant differences between sexes in foraging kinematics, suggesting both sexes use and orient their bodies similarly to capture prey, despite their size dimorphism. Alternatively, differences in foraging effort by males may be an adaptation to meet their greater metabolic needs resulting from their larger size. Consistent with our findings, Baird et al. (2005) used time-depth recorders to reveal that adult male SRKWs dove to depths ≥30 m more frequently than females. Males may segregate horizontally and vertically to minimize intra-pod competition (Bain, 1989; Baird et al., 2005), which is consistent with surface observations of males foraging on the periphery of a group. Indeed, greater foraging effort by males may allow them to meet their own metabolic needs while not burdening the pod nutritionally, which may enable them to remain in their natal group.

In addition to male adaptations to promote foraging efficiency, fitness-relevant factors (i.e. caring for young) may reduce the time females spent foraging. Half of the deployments on females resulted in no prey capture dives, with diving primarily confined to ≥30 m, whereas all deployments on males contained at least one prey capture dive. These results are consistent with studies showing that sperm and pilot whales engage in alloparenting, whereby adult females share the time costs of caring for kin by taking turns to remain at the surface with calves while others forage (Whitehead, 1996; Gero et al., 2009; Augusto et al., 2017). Indeed, given that SRKWs engage in non-random prey sharing (Ford and Ellis, 2006; Wright et al., 2016), and males and post-reproductive females disproportionately provision each other, particularly within their matriline (Wright et al., 2016), males and post-reproductive females may help offset the costs to the pod of additional mouths to feed, while increasing inclusive fitness through the benefits provided by post-reproductive females (Foster et al., 2012).

We demonstrate that fine-scale movement data from accelerometers and magnetometers deployed on free-swimming, wild killer whales can reveal stereotyped signatures of prey capture. This approach provides an inexpensive, minimally invasive and accurate method to estimate subsurface prey consumption in killer whales. Future studies that synchronize video and movement data will shed light on the subsurface processes that cause the stereotyped prey capture movements documented here. As we reveal with SRKWs, kinematic detection of prey capture can enable studies on foraging behavior which can advance foraging ecology theory, particularly for species that forage in social groups (e.g. Fryxell et al., 2007) and guide management efforts to conserve threatened and endangered species. Through accurate detection of prey capture, future work may explore how anthropogenic activities, including underwater noise from shipping and construction, may impact foraging outcomes. Given the global increase in the human influence on maritime patterns and processes (Halpern et al., 2007, 2008; Diaz and Rosenberg, 2008; Hoegh-Guldberg and Bruno, 2010), the time is opportune for these investigations.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
M.M.H. and M.B.H. secured funding and designed the study. M.M.H., M.B.H., C.K.E., D.A.G. and J.T.H. conducted the fieldwork. J.B.T. and M.M.H. analyzed the data. J.B.T. wrote the manuscript. All authors edited the manuscript.

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Supplementary information
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