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A R T I C L E

Marine Mammal Science

Using accelerometry tags to quantify gray whale foraging behavior

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Abstract

High-resolution tri-axial accelerometry biologging tags have quantitatively described behaviors in baleen whale species that forage using lunges and continuous ram filtration. However, detailed quantitative descriptions of foraging behaviors do not exist for gray whales, a unique baleen whale species that primarily uses benthic suction feeding with a rolling component. We deployed suction cup biologging tags on Pacific Coast Feeding Group (PCFG) gray whales to quantify foraging behavior at the broad state (dive) and foraging tactic (roll event) scales. Hidden Markov models were used to describe three distinct states using turn angle, dive duration, pseudotrack tortuosity, and presence of roll events that can be interpreted as forage, search, and transit behavior. Classification and Regression Tree

models best described foraging tactics (headstands, benthic digs, and side swims) using median pitch, depth to total length ratio, and absolute value of the median roll. On average, PCFG gray whales spent more time searching and performed more left-rolled foraging tactics at shallower depths at night compared to during the day, potentially to track prey above them in the water column. Describing foraging behavior in PCFG gray whales enables examination of links between behavioral budgets, energetics, and the physiological impact of threats facing this group.

1 | INTRODUCTION

Understanding the behavioral ecology of a species is fundamental for successful conservation because it provides a framework to assess the impact of human disturbance and overexploitation, explain the ecology of fear (i.e., how fear of predators structures communities), determine locations of critical habitat, and predict responses to climate change (Dill, 2017). However, studying the behavioral ecology of marine animals, such as cetaceans, is challenging because they perform most of their behaviors underwater, where observations require technological developments (Nowacek et al., 2016). The vulnerable state of many cetacean populations following decades of industrial whaling (Magera et al., 2013) and continued modern threats (e.g., fisheries entanglements, vessel strikes; Thomas et al., 2016) makes understanding cetacean behavioral ecology vital for interpreting their population dynamics and informing management decisions.

The development of biologging tags has revolutionized behavioral studies of cetaceans due to high-frequency sampling rates and integration of multiple sensors (i.e., accelerometers, magnetometers, and gyroscopes) that allow for fine-scale detection of behaviors and their bioenergetics implications (Crossin et al., 2014; Watanabe & Goldbogen, 2021). Biologging tags do not face the daytime-only constraint that limits visual boat–based focal follows (e.g., Schwarz et al., 2021) and allow for data collection without needing a research vessel to be near the individual, which could potentially disrupt the observed behaviors. Although the use of unoccupied aerial systems (UAS; aka drones) has progressed the study of cetacean behavior by increasing observational capacity by a factor of three (Torres et al., 2018), this method is currently constrained by limited flight time, water clarity, depth of the animal, and daylight. Additionally, given that most cetacean foraging behavior occurs at depth, the ability of biologging tags to record foraging behavior at depth provides unique and critical data that are not available from focal follows or drones (Wright et al., 2017).

High-resolution tri-axial accelerometry data from biologging tags have been used to quantify the foraging kinematics and behavior of many baleen whale species (Cade et al., 2016; Goldbogen et al., 2013; Goldbogen et al., 2017; Shadwick et al., 2019; Simon et al., 2009). Biologging instrumentation and data have elucidated the phases of lunge feeding behavior in rorquals (i.e., humpback, *Megaptera novaeangliae*, fin, *Balaenoptera physalus*, and blue, *B. musculus*, whales) (Cade et al., 2016; Shadwick et al., 2019) and showed that the ram filtration behavior of balaenids (i.e., right whale, *Eubalaena* sp., and bowhead, *Balaena mysticetus* whales) is linked to an optimal swim speed (Simon et al., 2009). Tri-axial accelerometry can thus identify behavioral patterns, which can subsequently be used to determine the corresponding energetic costs (Goldbogen et al., 2012; Potvin et al., 2012) and assess exposure to anthropogenic

threats during foraging (Constantine et al., 2015; Ware et al., 2014). Despite these demonstrated benefits, no publication has reported quantitative descriptions of the unique suction feeding behavior of gray whales (*Eschrichtius robustus*) using accelerometry data beyond an examination of lateralization patterns (Woodward & Winn, 2006).

Gray whales are a primarily benthic or epibenthic-feeding baleen whale species that inhabits the North Pacific Ocean and includes three feeding groups: (1) the Western North Pacific (WNP) population that feeds off the coast of Russia and breeds in the lagoons of Baja California, Mexico, with some individuals potentially breeding in the South China Sea (estimated population size of 230 individuals; Cooke et al., 2019); (2) the Eastern North Pacific (ENP) population that feeds in the Arctic or sub-Arctic and breeds in the Mexican lagoons (estimated population size 14,526; Eguchi et al., 2024); and (3) the Pacific Coast Feeding Group (PCFG) that is a subgroup of the ENP population, composed of whales observed in at least 2 years foraging in Pacific Northwest waters between 41 and 52°N from June 1 to November 30 (Calambokidis et al., 2002; International Whaling Commission, 2011), and also breeds in the Mexican lagoons (estimated population size 212; Harris et al., 2022). Gray whales employ suction foraging behavior that is unique in baleen whales (Goldbogen et al., 2013; Goldbogen et al., 2017; Nerini, 1984) and is characterized by rolling to one side (usually the right) during the bottom phase of the dive, often in association with a negative pitch where the mouth is angled towards the benthos (Woodward & Winn, 2006).

The dominant prey of gray whales varies between foraging grounds. Amphipods dominate the diet in the soft-bottomed foraging grounds of the WNP and ENP (Moore et al., 2022; Nerini, 1984), while epibenthic swarming mysids are thought to be the targeted prey in the Pacific Northwest foraging range of the PCFG (Feyrer & Duffus, 2011; Newell & Cowles, 2006), although this group of whales also feeds on a variety of other prey including crab larvae and amphipods (Darling et al., 1998; Hildebrand et al., 2021). PCFG gray whale foraging is often observed in association with reef habitat with and without kelp (Darling et al., 1998; Dunham & Duffus, 2002; Hildebrand et al., 2022), although observations of sediment (sand or shell) expulsions from the mouth following dives are also often recorded (C. Bird pers. comm.; Torres et al., 2018; L. Torres pers. obs.). The high diversity of prey and foraging habitats exploited by PCFG gray whales leads to a diversity of foraging tactics performed by this population.

Recent work using drones to observe the behavior of PCFG gray whales established an ethogram that includes four foraging tactics not previously observed in ENP and WNP whales (Torres et al., 2018), further illustrating the unique foraging ecology of this group of gray whales. However, due to visibility limitations, the drone ethogram does not include benthic digs, the traditional foraging tactic performed by ENP and WNP gray whales (Nerini, 1984), where the whale is rolled onto its side, suctioning up sediments to feed on benthic prey and leaving pits in the seafloor (Johnson & Nelson, 1984; Nerini, 1984). Biologging studies may be able to overcome this obstacle and detect benthic digs in the PCFG as accelerometry data are collected at depth and can be used to calculate body position metrics, such as pitch and roll (Brown et al., 2013). Body position metrics from biologging data should also be able to detect foraging tactics unique to PCFG gray whales, including headstands, where the whale is positioned vertically in the water column with head down-fluke up, and side swims, where the whale is swimming rolled on its side (Torres et al., 2018).

Drone sampling methods (Torres et al., 2018) build upon the methods of focal follow studies that have previously distinguished between gray whale broad behavior states (e.g., forage, travel, rest) (Hildebrand et al., 2022; Mallonee, 1991; Stelle et al., 2008; Sullivan & Torres, 2018; Würsig et al., 1986) by describing the fine scale details of foraging tactics performed within each dive. However, the behavioral definitions from drone and focal follow methods are not based on quantitative measurements of foraging behavior within dives, constrained to daylight hours and limited to behaviors observed at or near the surface. Biologging studies provide an opportunity to collect data during night or subsurface behaviors to contribute to assessments of diel behavioral patterns (Cade et al., 2023; Nichols et al., 2022), which are important for the construction of activity budgets and understanding the different risks whales face between day and night (Calambokidis et al., 2019). Quantification of subsurface behaviors and behavioral budgets would support bioenergetic modelling to assess the consequences of disturbance on individuals and populations (e.g., Agbayani, 2022; Villegas-Amtmann et al., 2015; Villegas-Amtmann et al., 2017). It could also be used to gain further insight into the three gray whale unusual mortality events (UMEs; 1987–1989, 1999–2000, 2019–present) in four decades (Stewart et al., 2023) that have been linked with malnutrition-caused mortalities (Christiansen et al., 2021; Le Boeuf et al., 2000; Moore et al., 2003; Perryman et al., 2002; Perryman et al., 2020; Raverty et al., 2024).

The need to obtain behavioral energetics information is exacerbated for PCFG gray whales as individuals in this group have shorter total body lengths (Bierlich et al., 2023) and lower body condition (Torres et al., 2022) than ENP gray whales. PCFG gray whales also experience high variability in their body condition (Akmajian et al., 2021; Lemos et al., 2020), all of which indicate potential nutritional stress. Additionally, PCFG gray whales are exposed to high levels of vessel traffic and noise in their nearshore foraging habitat (Haver et al., 2023) that are associated with increased concentration of glucocorticoid hormones in their feces (Lemos et al., 2022; Pirotta et al., 2023) and with changes in behavior (Sullivan & Torres, 2018). PCFG gray whales also consume high levels of microplastics through their prey and the sediments ingested during benthic foraging (Torres et al., 2023), with the contaminated prey and microparticle loads potentially reducing energy intake and causing significant health impacts. These physiological threats highlight the critical need to understand the link between the energetics of PCFG gray whale foraging behavior and fitness consequences.

To address the pressing knowledge gap in foraging behavior of gray whales, we deployed minimally invasive suction cup biologging tags equipped with tri-axial accelerometers on PCFG gray whales on their foraging grounds in coastal waters of Oregon and Washington, USA. We used hidden Markov models (HMMs) to quantitatively describe broad behavioral states (e.g., forage, search, transit) and Classification and Regression Trees (CARTs) to define within-dive foraging tactics and build upon the PCFG ethogram presented by Torres et al. (2018). We expect that the accelerometry data will inform the description of broad states and foraging tactics, revealing predominantly benthic foraging behaviors signaled by periods where the individual is rolled on its side. By using existing biologging technology, behavioral ethograms, and classification models, our analyses of the tri-axial accelerometry data we collected from gray whales add to the quantitative descriptions of baleen whale foraging behaviors that previously lacked gray whale results. Our work also provides the baseline data and activity budgets necessary for future studies to estimate the energetic cost of foraging in gray whales, as has been done in other species, and assess the effects of stressors on the foraging behavior of this unique group of gray whales.

2 | METHODS

2.1 | Data collection

Suction cup attached Custom Animal Tracking Solution (CATS; https://cats.is) video, and inertial measurement unit (IMU) tags were deployed on gray whales from rigid hulled inflatable boats using an 8-m carbon fiber pole in August 2021 and July and September 2022 off the Oregon Coast between Waldport (44.418326, −124.092222) and Depoe Bay (44.835057, −124.064164). The timing and location of tagging efforts ensured that only PCFG gray whales (International Whaling Commission, 2011) would be included in the deployments, which was confirmed through photo-identification records. CATS tags were attached to the whales using four suction cups with oxidizing releases to ensure the tags released after suction failed. Tags were recovered using very high frequency (VHF) (2021 and 2022) and Iridium (2022). CATS tags integrated a video camera, hydrophone, 400 Hz accelerometer, 50 Hz magnetometer and gyroscope sensors, and 10 Hz pressure, temperature, light, and GPS sensors. All tag deployments were carried out under National Oceanic and Atmospheric Administration/National Marine Fisheries Service (NOAA/NMFS) permit #21678 to John Calambokidis and Cascadia Research IACUC AUP-06. The University of British Columbia Animal Care Committee approved the field work under permit A21-0254. An additional CATS tag deployment from a PCFG gray whale off Cape Flattery, Washington (48.3127, −124.6858) in September 2019 was included in this analysis as this individual was a known PCFG gray whale, previously sighted in the Oregon study area between Waldport and Depoe Bay (1 sighting in 2016, 4 in 2017, 5 in 2018; L. Torres, *Unpublish. data*) and was observed to be foraging in similar nearshore reef habitat as the tags deployed in the Oregon Coast study area.

Tagged animals were identified using photo-identification through comparison to PCFG gray whale catalogs held by the Geospatial Ecology of Marine Megafauna Lab at Oregon State University (Newport, OR, USA) and Cascadia Research Collective (Olympia, WA, USA). Genetic sex information was obtained for known individuals using

previously collected tissue samples (Lang et al., 2014). A DJI Inspire 2 quadcopter with a Zenmuse X5 camera with a Micro Four Thirds (17.3 × 13 mm) sensor, 3840 × 2160-pixel resolution, a 25-mm focal length lens, and a Lightware SF11/C laser altimeter for recording altitude was used to conduct drone focal follows of tagged animals.

Drone photogrammetry was used to calculate total length (TL; in meter) and body area index (BAI) measurements of tagged animals. TL was calculated as length from rostrum to fluke notch using MorphoMetriX (Torres & Bierlich, 2020). Bierlich et al. (2023) found the asymptotic TL of PCFG gray whales ranges from 11.84 to 12.44 m for females and 11.49–12.29 m for males. We used these TL ranges to infer maturity for tagged individuals. BAI is a measure of body condition with low uncertainty that was calculated as surface area between 20% and 70% of the length and standardized by the TL of the individual (Bierlich et al., 2021; Burnett et al., 2018). Torres et al. (2022) found that BAI for PCFG gray whales in the Oregon coast feeding ground ranges from ∼22 to 32 with a median value of ∼26. We used this BAI range to make inferences about the body condition of the tagged individuals in this study. The drone was used following previously established field methods (Bierlich et al., 2023; Lemos et al., 2020; Torres et al., 2022). If a drone flight could not be conducted during tagging field work, drone photogrammetry measurements were obtained from flights within 15 days of tag deployment as gray whales do not significantly change their body condition within a 2-week period (Lemos et al., 2021).

2.2 | CATS tag data processing

All video and sensor data from the CATS tags were downloaded and imported into MATLAB (MathWorks v2021a) where they were preprocessed to align clock times, correct tag slips, and ensure sensor orientation in the whale frame (Cade et al., 2021). Pressure spikes from animals hitting the tag against the seafloor during benthic rolling behaviors were removed during this pre-processing stage and replaced with a linear interpolation of the pressure sensor data. All subsequent analysis of pre-processed data was conducted in R v4.2.3 (R Core Team, 2023).

The preprocessed data were manually audited to identify dives and periods of high roll (hereafter referred to as roll events) in the *catsr* package v0.0.0.9000 (Czapanskiy, 2022). A threshold of 25 degrees was used as this was the value at which roll events could unmistakably be determined and provided a useful visual threshold for when the animal could be described as being on its side. Audits were performed using pressure sensor data for dives and roll data calculated via three-axis accelerometry (see Figure S1 for visualization of audits). The first 15 min of each deployment was excluded to remove any influence of tagging on whale behavior (Williamson et al., 2016; Wright et al., 2017). Dives were defined as periods where the depth was >1 m for longer than 30 s, which eliminated short submergence periods during blow intervals, where the whale remained close to the surface to maximize oxygen utilization for each breath (Sumich, 1983), and there was little potential for foraging activity (Stelle et al., 2008). Periods of high roll (>25 degrees) were of interest as previous studies of gray whale foraging behavior indicate that these animals often feed on their sides (Nerini, 1984; Torres et al., 2018; Webber et al., 2024; Woodward & Winn, 2006). Co-occurring video data from the tags were used to confirm this association by looking for evidence of foraging (e.g., sediment plumes, high density of zooplankton prey) during periods of high roll. Roll event start and stop times were determined as the first and last points of inflection in the elevated roll signal to exclude transitions into the roll events. By auditing dives and roll events, a multiscale classification of behavior was conducted, with dives corresponding to broad states and roll events corresponding to foraging tactics.

Pseudotracks, with an assumed average speed of 1.5 m/s, were constructed using the *tagtools* package v0.0.0.9000 (DeRuiter et al., 2022) to create a dead-reckoned track from the biologging speed and body pointing data. The pseudotracks were used to determine the relative position of the individual at dive start times and calculate pseudotrack tortuosity (see below). The tags used for this study did not have a dedicated speed sensor. Turbulence-based methods for speed (e.g., flow noise or tag vibrations; Cade et al., 2018) are only accurate above ∼1 m/s and rely on in situ calibrations against steep descents or ascents. Because our study animals were restricted to shallow water and the behaviors of interest often involved little if any forward motion, a constant speed pseudotrack was the best

available option. The tortuosity calculated from the resulting pseudotrack is thus more of a representation of heading changes over time than true tortuosity, but still gives information to the behavioral classifier.

Descriptive summary metrics were calculated for each dive and roll event using the *tagtools* package (DeRuiter et al., 2022) to differentiate between behaviors at each scale. At the dive scale, these metrics included dive duration (in second; the amount of time spent submerged from the start of the dive to the end), maximum dive depth (in meter; the deepest depth from the pressure sensor on the CATS tag), time at surface (in second; duration of time at the surface from the end of the dive to the start of the next), ratio of surface to dive time (the ratio of the time at the surface following the dive to the dive duration), the proportion of time during the dive spent in roll events, presence of roll events (i.e., if a roll event occurred during the dive), change in heading between dive start and dive end (degrees), and pseudotrack tortuosity (a unitless ratio of the stretched-out track length during the dive duration relative to the straight-line distance between the start and end points of the dive ranging, between 0 for movement in a perfectly straight line and 1 for extremely circuitous movement).

At the roll event scale, these metrics included duration of the event (in seconds; the time from the start of the high roll period to the end), maximum depth (in meter; the deepest depth from the pressure sensor on the CATS tag), depth to TL ratio (i.e., the depth of the CATS tag divided by TL of the animal), absolute value of the median roll (degrees), absolute value of the ratio of the median roll to maximum roll, median pitch (in degrees), change in heading between start of the roll event to the end (in degrees), and relative speed of the whale (see Data S2 for further description). The depth to TL ratio used measurements of whale TL calculated from drone photogrammetry to examine the potential limitation water depth may pose to foraging tactic use by gray whales that feed where the water is often shallower than the TL of the whales.

2.3 | Behavior classification

2.3.1 | Broad states—HMMs

HMMs are a class of state-space models that use characteristics of the observed data (in this context, an animal's movement metrics) to classify a time series of underlying states while accounting for temporal autocorrelation (Morales et al., 2004). In ecology, these latent statistical states are then interpreted as the broad behavioral states of the individual. Given that the tag data provide sequential information on dives (the unit of analysis) and are thus temporally autocorrelated, we can use this information to inform multivariate HMMs and thus obtain a timeseries of behavioral states as well as the probabilities of transition from one state to another. The dive scale of analysis allowed for variable dive duration to be accounted for when determining broad behavioral states yet precluded the ability to detect surface behaviors (e.g., shallow depth, below average movement), such as a possible resting behavior, in the model. In particular, we aimed to classify forage, search, and transit states, which have been identified in previous PCFG gray whale focal follow studies (Hildebrand et al., 2022; Stelle et al., 2008; Sullivan & Torres, 2018). HMMs were fitted using the *momentuHMM* package v1.5.4 (McClintock & Michelot, 2018). See Data S2 for R code for these models.

Data streams were selected from the descriptive summary metrics calculated at the dive scale. The selection of data streams included in the model was guided by existing cetacean multivariate HMMs (DeRuiter et al., 2017) and modified in light of PCFG gray whale ecology. Specifically, we examined the histogram of each movement metric (see Data S2 for histograms) and selected those that had the most obvious breaks in their distribution, while ensuring there was no redundancy in their characterization of states (e.g., roll presence and proportion of dive spent rolling both describe the presence of a foraging tactic, so only one was included in the model). A discrete random effect of individual whale was not included due to the low number of deployments, and because it would offer little improvement in terms of state classification (McClintock, 2021).

The final set of data streams, and their distributions, were turn angle (in degrees; von Mises), dive duration (in seconds; gamma), pseudotrack tortuosity (beta), and roll presence (Bernoulli). Step length was not included in the

HMM due to its correlation with dive duration. Maximum dive depth was also excluded from the model as it failed to identify the desired broad states (see Data S2 for the results of a model including depth). Finally, the time at surface was removed from the model as we were unable to distinguish if the period at the surface was a recovery from the previous dive or preparation for the next dive. Two- and three-state HMMs were compared to determine if search behavior was distinguishable as a separate state using the biologging data. The final number of states to include in the model was chosen according to the suggestions of Pohle et al. (2017), including assessment of pseudo-residuals and biological relevance (see Data S2 for pseudo-residual plots).

To avoid convergence at local maxima, the HMMs were re-fit with random perturbations ($n = 30$) from a normal distribution in the starting parameter values. The Viterbi algorithm was used to estimate the most likely sequence of broad behavioral states (Zucchini et al., 2016).

2.3.2 | Foraging tactics—CARTs

Given that there is no a priori reason to assume a temporal structure in the choice of foraging tactic, HMMs were not deemed appropriate for the analysis of these data. Instead, we used CART models, which are supervised machine learning algorithms (Breiman et al., 1984), to define characteristics of different foraging tactics in the biologging data (see Data S2 for CART model R code). A subset of the roll event data ($n = 236$) was chosen randomly to avoid any potential dependence structure in the data and then visually classified into foraging tactics based on a previously published PCFG gray whale ethogram (Torres et al., 2018) using the TrackPlot data from the tag deployments (see Data S2 for details on visual classification methods). Headstands, benthic digs, and side swims were observed in the biologging data. These visually classified events were split 80:20 into a training and a testing data set.

Histograms of the summary metrics calculated for roll events were examined for each visually classified foraging tactic to determine the metrics with the clearest separation between tactics (see Data S2 for histograms of roll event summary metrics); these metrics were then used as variables in the CART model to simplify the model input. The chosen metrics included median pitch (degrees), absolute value of the median roll (degrees), and the depth to TL ratio. A more extreme negative median pitch indicated the individual was positioned more vertically in the water column with rostrum angled down in the sediment, while a median pitch closer to 0 indicated the individual was more horizontal. A higher absolute value of the median roll indicated that the individual was turned more on its side. A depth to TL ratio less than 1 indicated the roll event occurred at a depth that was shallower than the individual's TL. There was no need to determine correlation between the metrics as CART models account for collinearity.

The *rpart* v4.1.19 (Therneau & Atkinson, 2022) and *rpart.plot* v3.1.1 (Milborrow, 2022) packages were used to build and visualize the classification tree for the training data set. A pruned tree was also constructed using the complexity parameter that minimized cross-validation error to create a more parsimonious model as the complexity parameter imposes a penalty for each split in the CART model to prevent overfitting. The predictive accuracy of the CART model was evaluated using the testing data. If the resulting accuracy was identical between the original and the pruned model (based on a confusion matrix), the simpler model was selected. Bootstrap aggregation (bagging) with 1500 iterations of the CART model was conducted using the *ipred* package v0.9-14 (Peters & Hothorn, 2023) to calculate the out-of-bag error, or prediction error and an accuracy test on the confusion matrix was conducted to assess the ability of the best CART model to assign foraging tactics. The splitting rules from the most accurate CART model were then used to assign the nonvisually classified roll events ($n = 1654$) to a foraging tactic.

2.4 | Behavioral budgets

Proportional activity budgets were calculated at the dive and roll event scale for all deployments combined and for each individual deployment. At the dive scale, the amount of time spent at the surface was compared to the amount

of time at depth. The proportion of surface time was calculated as the sum of time at surface for each deployment divided by the total deployment duration, while the proportion of time at depth was calculated as the sum of the dive durations for each deployment, divided by the total deployment duration.

Proportional activity budgets were compared between day and night, where day was assumed to be between 06:00 and 20:00 PDT, based on the average sunrise and sunset times for Newport, OR, USA in the summer (https://weatherspark.com/y/344/Average-Weather-in-Newport-Oregon-United-States-Year-Round).

2.5 | Lateralization

Gray whales show lateralization in their foraging behaviors (Woodward & Winn, 2006). Therefore, the sidedness of foraging tactics was examined across tagged individuals. Sidedness was coded as a binary variable with 0 indicating a left-sided roll (individual's left side is down) and 1 indicating a right-sided roll (individual's right side is down). Differences in sidedness values were explored between day and night.

3 | RESULTS

3.1 | Deployment summary

Ten CATS tags were successfully deployed on PCFG gray whales in 2019 ($n = 1$), 2021 ($n = 3$), and 2022 ($n = 6$), with a mean deployment time of 9.14 h (range = .44 to 24.81 h; Table 1). Tags were deployed on six females (including a mother, G22, and her 8-year-old daughter, F22, on the same day), two males, and two whales of unknown sex.

Several malfunctions occurred during this study's tag deployments. The GPS data from the 2022 deployments could not be recovered. Data collection in deployment H22 stopped after $\sim$.5 h, despite the tag remaining on the animal. Deployment I22 showed gaps in the sensor data, and only the data following these gaps were included in the analysis.

Approximately 60.2 h of sampling occurred during the day and 31.15 h of sampling occurred at night. Four tags included behaviors performed at night—one deployment with approximately 1 h of night sampling and three deployments with 10 h of overnight sampling (Table 1). A total of 760 dives and 540 roll events occurred at night for all full overnight deployments combined, compared to 634 dives and 634 roll events during the day for these same deployments. An additional 18 dives and 20 roll events occurred at night in the deployment with 1 h of night sampling, compared to the 42 dives and 39 roll events during the day.

3.2 | Broad states

HMMs were constructed using 1856 dives from the 10 deployments. Dives were best classified into three distinct and biologically relevant states. The distribution parameters of each data stream for the three states can be found in Table S1. Adding a third state to the HMM reduced the spread of the state-dependent distributions and resulted in more normally distributed pseudo-residuals compared to a two-state model (Figure S5). A rest state was not detected by the model.

Dives classified under State 1 were characterized by turn angles close to 0°, pseudotrack tortuosity close to zero, no roll events present, and an intermediate dive duration (Figure 1). These features suggest that this dive type can be interpreted as nonforaging, transit behavior, used by whales when moving in a directed fashion.

State 2 dives had more variation in turn angle than State 1 dives, but less variation than State 3 (Figure 1a). Pseudotrack tortuosity for State 2 dives was concentrated around .1 and generally lower than .25, which was higher

TABLE 1 Biologging CATS tag deployment information.

Deploy. ID (CRC ID)	Genetic sex	Tag on	Tag off	Tag on location	Deployment length (hh:mm:ss)	TL[a] (m)	BAI[a]	No. roll events (N = 1890)	No. of dives (N = 1856)
A19 (1863)	NA	9/1/19 15:05:52	9/1/19 16:41:18	Cape Flattery, WA	01:29:17	10.2	NA	45	31
B21[b] (186)	M	8/16/21 13:01:11	8/16/21 18:20:03	Lost Creek	03:00:34	12.0	22.74	137	78
C21[b] (992)	F	8/16/21 16:04:52	8/16/21 16:31:24	Alsea River Mouth	00:26:15	11.1	25.37	3	3
D21[c] (537)	M	8/16/21 17:16:37	8/16/21 21:08:03	Alsea River Mouth	03:51:26	11.6	25.82	59	60
E22 (698)	F	7/21/22 9:50:30	7/22/22 10:38:49	Nye Beach	24:48:19	11.1	24.94	324	477
F22[d] (1753)	F	7/21/22 10:36:03	7/21/22 17:19:17	Flat Rock	06:43:14	10.4	26.94	288	141
G22 (204)	F	7/21/22 16:03:25	7/22/22 09:37:27	South Beach	17:34:02	11.6	27.39	370	298
H22 (2292)	NA	9/12/22 13:13:35	9/12/22 18:00:00	Gull Rock	00:33:25	8.9	29.45	14	7
I22 (1070)	F	9/12/22 12:49:02	9/13/22 11:54:58	Gull Rock	23:05:58	10.5	28.46	478	627
J22 (611)	F	9/12/22 11:49:02	9/12/22 19:12:53	Gull Rock	07:23:50	12.1	26.75	172	142

[a]Total length (TL; in meter) and body area index (BAI) were obtained from drone photogrammetry within 15 days of the tag deployment.
[b]Tag without audio data.
[c]Tag without video data.
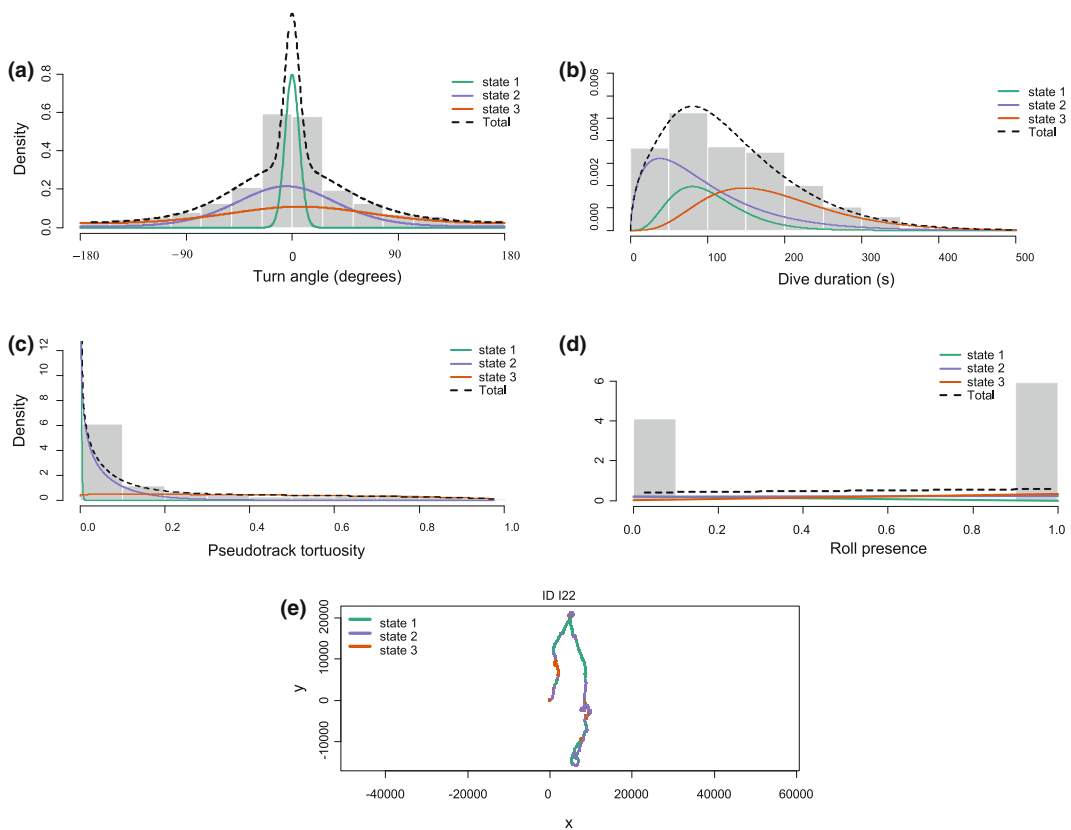[d]Individual is the known calf of G22 from 2014.

FIGURE 1 Hidden Markov model (HMM) state-dependent distributions for all dives (*n* = 1856) recorded from CATS tags deployed on PCFG gray whales based on (a) turn angle, (b) pseudotrack tortuosity, (c) dive duration, (d) roll event presence, and (e) Viterbi algorithm state assignments for one deployment's pseudotrack. State 1 likely corresponds to transit, State 2 to search, and State 3 to forage behaviors. CATS, Custom Animal Tracking Solution; PCFG, Pacific Coast Feeding Group.

than State 1 pseudotrack tortuosity but included in the distribution of pseudotrack tortuosity for State 3 dives (Figure 1b). Dives classified as State 2 had the shortest duration, albeit with high variation (Figure 1c), and were characterized by an intermediate probability of the presence of a roll event compared to the other two states (Figure 1d). The intermediate values for turn angle, pseudotrack tortuosity, and roll presence suggested that State 2 can be interpreted as search behavior.

Dives classified as State 3 had the largest variation in turn angle, being the most likely to have turn angles greater than ±90° (Figure 1a). State 3 also had the highest variation in pseudotrack tortuosity and is the state most likely to have pseudotrack tortuosity greater than .25 (Figure 1b). State 3 dives had the longest duration and the highest probability of roll presence (Figure 1c,d). Given these features, State 3 dives can be interpreted as forage behavior.

The transition probability matrix of the final HMM indicated a high likelihood for a whale to remain in its current state (Table 2), which was especially true for the State 1 transit behavior and the State 3 forage behavior. The transition probability matrix supports State 2 search behavior as an intermediate state based on the high likelihood of transition to or from both State 1 and State 3. A whale in State 1 transit behavior was more likely to transition to State 3 forage behavior than vice versa. For a whale in the State 2 search behavior, there was approximately equal probability of transitioning to State 1 transit behavior or State 3 forage behavior.

TABLE 2 Transition probability matrix for the three states estimated by the hidden Markov model (HMM) based on dives (n = 1856) recorded from CATS tag deployments on PCFG gray whales.

Current state	Proximate state		
	1	2	3
1	.853	.110	.037
2	.070	.795	.135
3	.003	.177	.820

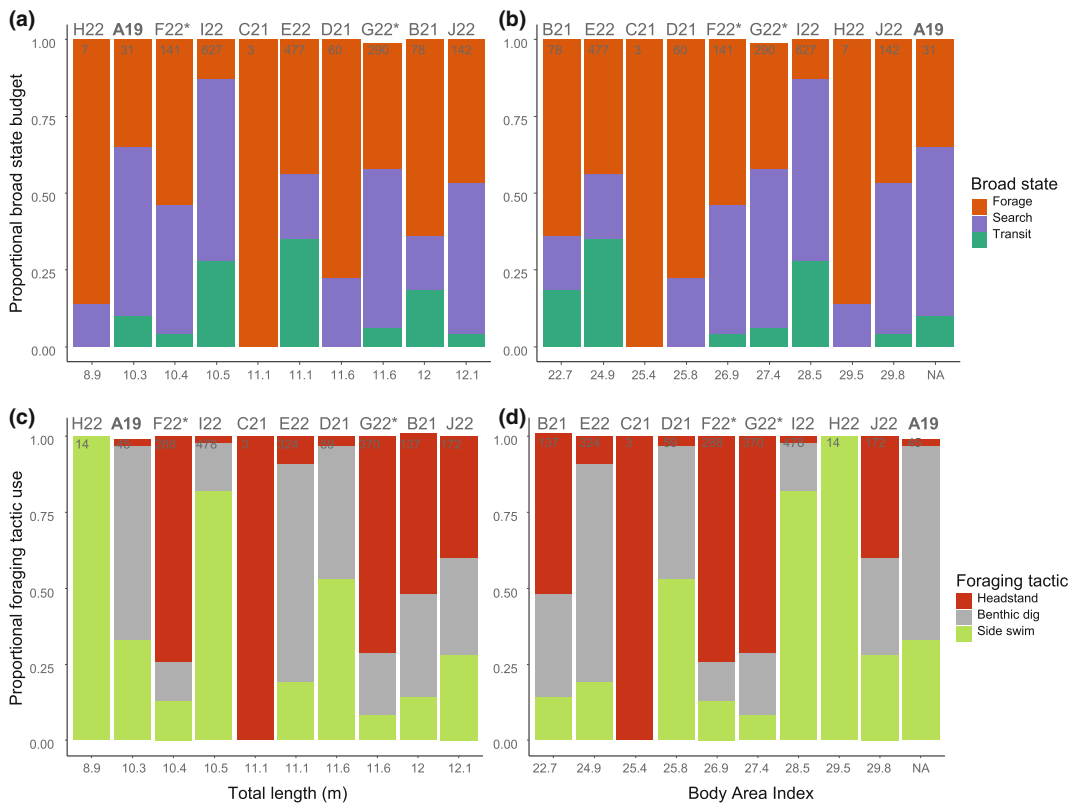*Note*: State 1 likely corresponds to transit, State 2 to search, and State 3 to forage behaviors.

FIGURE 2 Proportional activity budgets at the broad state (a, b) and foraging tactic (c, d) scales from CATS tag deployments on PCFG gray whales across total lengths (in meter; a, c) and body area index (BAI; b, d) of the whales. Each bar represents an individual deployment, labeled with deployment ID. The number of dives (a, b) and roll events (c, d) performed during the deployment is shown at the top of each bar below the deployment ID. Single asterisks denote the known mother (G22) and daughter (F22) pair, while the bolded ID is the deployment from Washington (A19). CATS, Custom Animal Tracking Solution; PCFG, Pacific Coast Feeding Group.

Across all deployments, PCFG gray whales spent 43% of their dives searching, 36% of their dives foraging, and 21% of their dives transiting (Table S7). This pattern was consistent across most individual whales, except for E22, which spent the least proportion of dives searching (Figure 2a,b; Table S7). Four individuals spent a noticeably higher proportion of time foraging (B21, C21, D21 and H22). The proportion of time spent in each state changed with time of day (Table S7). The whales also spent a higher proportion of time searching and a lower proportion of time

foraging at night compared to the day. The proportion of transiting dives remained relatively constant between day and night.

All tagged whales spent approximately 20% of their time at the surface compared to 80% at depth (Table S7). This 20:80 ratio holds for all whales except for one deployment (F22), where the individual spent 37% of time at the surface and 63% of time diving. The percentage of time spent at the surface increased to approximately 30% at night compared to 20% during the day (Table S7). This pattern was driven by one deployment (G22), where the individual spent 44% of the time at the surface at night. Only one of the other full overnight deployments (I22) showed an increase in time spent at the surface at night.

3.3 | Foraging tactics

The pruned tree (i.e., the simplified model with the optimized complexity parameter to prevent overfitting) was preferred for the classification of the training data set of visually validated roll events into foraging tactics (Figure 3), as it was more parsimonious but had the same accuracy as the unpruned tree. The pruned CART model accurately predicted 84.8% of foraging tactics in the testing data. Bagging results showed a low out-of-bag error of 16.67% and a high accuracy of 89.1%, confirming the high accuracy of the foraging tactic classification. Post hoc validation of the foraging tactics in 10 randomly selected dive series using the TrackPlot method (see Data S2 for visual classification methods) confirmed that ignoring the autocorrelation structure of the foraging tactics in the CART model did not lead to accuracy errors.

Variable importance (i.e., a scaled measure of how well a variable categorizes the roll events with each split in the decision tree) showed that median pitch was the most important variable (64.7%), followed by the depth to TL ratio (19.3%), and finally by the absolute value of the median roll (10.1%). Variable importance is evident in Figure 4, which illustrates clear breaks between foraging tactics relative to median pitch and depth to TL ratio, while the absolute value of the median roll is similar among all foraging tactics (Table S8).
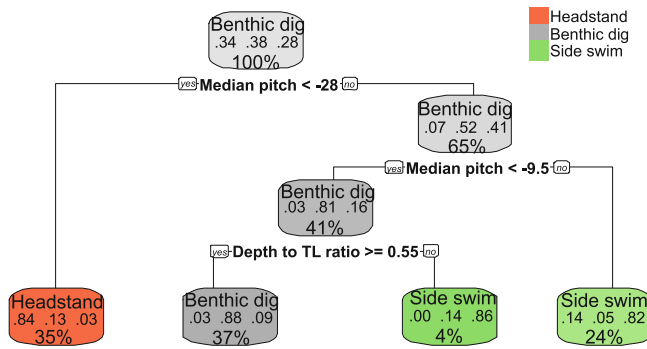

FIGURE 3 Classification and Regression Tree (CART) used to define foraging tactics for each roll event in CATS tag deployments on PCFG gray whales. The CART model was constructed using training data that were randomly selected from a subset of visually validated roll events. $N = 189$ roll events were included in the training data set used to create the CART model. A more extreme negative median pitch indicates the individual is positioned more vertically in the water column with rostrum angled down in the sediment, while a median pitch closer to 0 indicates the individual is more horizontal. A depth to total length (TL) ratio less than 1 indicates the whale is in water shallower than its body length. The top row of each box denotes the dominant foraging tactic conforming to the prior splitting rule of the decision tree. The second row denotes the proportion of data belonging to each headstand, benthic dig, and side swim foraging tactic, respectively. The last row denotes the percentage of the total data set represented in each box. CATS, Custom Animal Tracking Solution; PCFG, Pacific Coast Feeding Group.
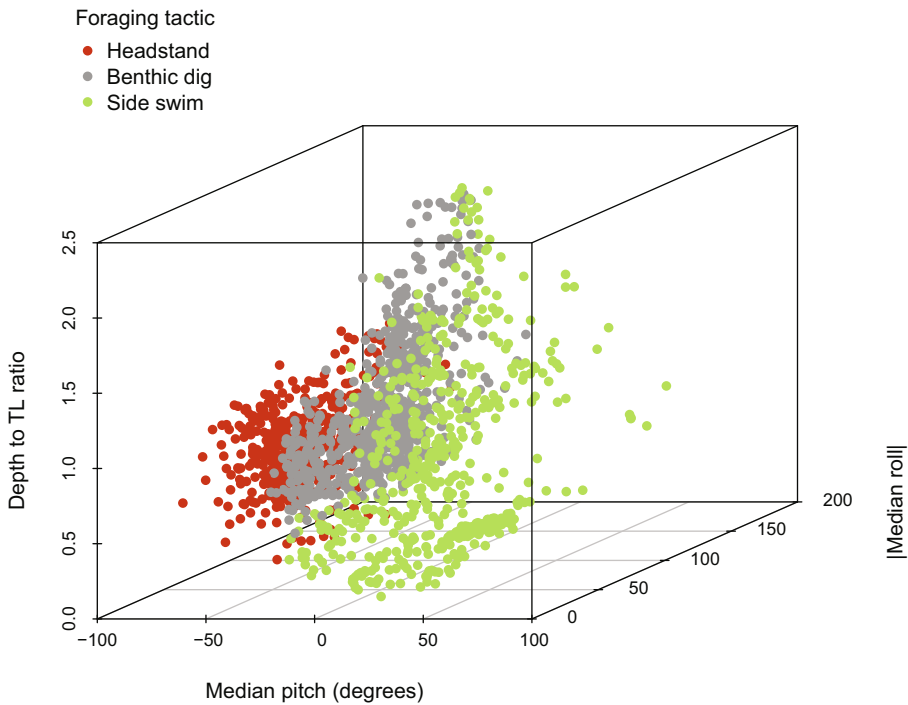
FIGURE 4 Distribution of foraging tactics relative to the variables used in the Classification and Regression Tree (CART) model calculated from CATS tag deployments on PCFG gray whales. The divisions along the median pitch axis illustrate the high importance of this variable for classifying foraging tactics, whereas the less clear separation along the absolute value of the median roll axis supports the lower importance of this variable in the CART model. The depth to total length (TL) ratio helps to separate side swim and benthic dig clusters. CATS, Custom Animal Tracking Solution; PCFG, Pacific Coast Feeding Group.

Roll events with a median pitch more extreme than $-27.9°$ were classified as headstands. Roll events with a median pitch between $-27.9°$ and $-9.5°$ and depth to TL ratio greater than or equal to .55 were classified as benthic digs. Roll events with either median pitch greater than or equal to $-9.5°$ or with median pitch between $-27.9°$ and $-9.5°$ and depth to TL ratio less than .55 were classified as side swims.

Across all deployments, the foraging tactics were present in relatively equal proportions: 31% headstands, 35% benthic digs, and 34% side swims. However, there was high individual variation between deployments (Figure 2c,d; Table S7). Three whales (A19, C21, and E22) performed headstands as their main foraging tactic. Four whales (B21, F22, G22, and J22) performed benthic digs as their main foraging tactic. One whale (D21) had relatively equal proportions of headstands and side swims as their main foraging tactics. The whales that favored headstands and benthic digs tended to be longer than 11 m (Figure 2c). Whales performing headstands as the main foraging tactic tended to have relatively low BAI (< ~25), while individuals performing benthic digs as the main foraging tactic had a mix of high and low BAI (~23–27; Figure 2d). Two whales (H22 and I22) performed side swims as their main foraging tactic and these whales were shorter than 11 m and had relatively high BAI (>28; Figure 2c,d).

Diurnal patterns in foraging tactic use are evident. Across all deployments combined, the proportion of headstands and benthic digs decreased at night while the proportion of side swims increased (Table S7). Yet, variation in foraging tactic use between day and night was largely individual specific. Deployment D21 performed almost exclusively benthic digs during the night compared to mostly side swims during the day, while deployment I22 performed almost exclusively side swims at night compared to a 60:40 split of side swims and benthic digs during the day. Deployment E22 showed little difference in foraging tactic use between the day and night, while deployment G22

shifted from a higher proportion of headstands during the day to a more balanced proportion of headstands and benthic digs at night. However, the diel differences in foraging tactic observed between individuals could also emerge from the limited time window over which each individual was observed.

Headstands and benthic digs predominantly occurred during right-sided rolls, while side swims had more variation in the sidedness of the roll event (Table S9). This pattern of right-sided headstands and benthic digs and more left-sided side swims was consistent across individuals. The depth and lateralization of foraging tactics compared across the full overnight deployments ($n = 1,172$ roll events) indicates that, at night, gray whales tended to perform foraging tactics at shallower depths (mean depth = 9.51 m, vs. 12.37 m during the day; Table S10) and roll more to the left (Figure 5). The increase in left-sided rolls was most prevalent during side swims, although deployment G22 had more right-sided side swims at night (Table S10).

4 | DISCUSSION

We successfully obtained and analyzed biologging data from suction cup tag deployments on 10 PCFG gray whales to provide the first quantitative descriptions of gray whale suction feeding behavior at both the broad behavioral state and foraging tactic scales. HMMs determined that three, reasonably distinct broad behavioral states exist at the dive scale, likely corresponding to forage, search, and transit behaviors. All whales in this study spent a higher proportion of time in the forage and search states than the transit behavior, with only two individuals spending more than 20% of their time transiting. On average, the tagged whales spent approximately 20% of their time at the surface compared to 80% diving, increased the proportion of time searching at night, and slightly increased surface time at night.

CART models indicated that the foraging tactics of headstand, benthic dig, and side swim are best defined using median pitch, the ratio of depth to TL, and the absolute value of the medial roll, with median pitch being the most important variable in the classification model. For all deployments combined, the proportion of foraging tactics used was approximately equal, but there was high individual variation in the foraging tactic with the highest percentage of occurrence. Foraging tactics were found to be shallower and include more left-sided rolls at night compared to during the day. This diurnal pattern of lateralization was most evident for side swims, which was the most frequently used tactic at night.

The HMM was able to differentiate a state that can be interpreted as search behavior in the biologging data, which supports the separation of search and forage behaviors in PCFG gray whales (Mallonee, 1991; Stelle et al., 2008). Searching has been described as a time- and distance-intensive behavior (Hildebrand et al., 2022; Sullivan & Torres, 2018) where the whale is spending a high amount of time and travelling large distances within an area. Thus, searching is a time when the whale is expending energy with no energetic gain (Norberg, 1977) and is the basis of many foraging ecology theories that aim to describe how predators optimize their foraging behavior in habitats of varying prey patch types and densities (Charnov, 1976; MacArthur & Pianka, 1966; Norberg, 1977). While there are many complexities to these theories (e.g., prey type, distance between patches, density within patches), comparisons of time spent in the search state to the time in the forage state could potentially be a useful indication of prey availability.

For the three overnight deployments included in this study, PCFG gray whales were found to slightly increase their surface time from a 20:80 (surface:dive) ratio during the day to a 30:70 ratio at night. This increase in surface time potentially indicates that whales spend more time resting at the surface during the night. This is further supported by the lack of resting dives detected by the HMM, suggesting that resting behavior may happen at the surface. Therefore, future work should focus on collecting more overnight deployments and examining when and where in the water column PCFG gray whales rest.

The HMM did not produce a state that could be described as social behavior, either reflecting a lack of social behavior in the deployments or suggesting that the movements associated with social behavior were not distinct
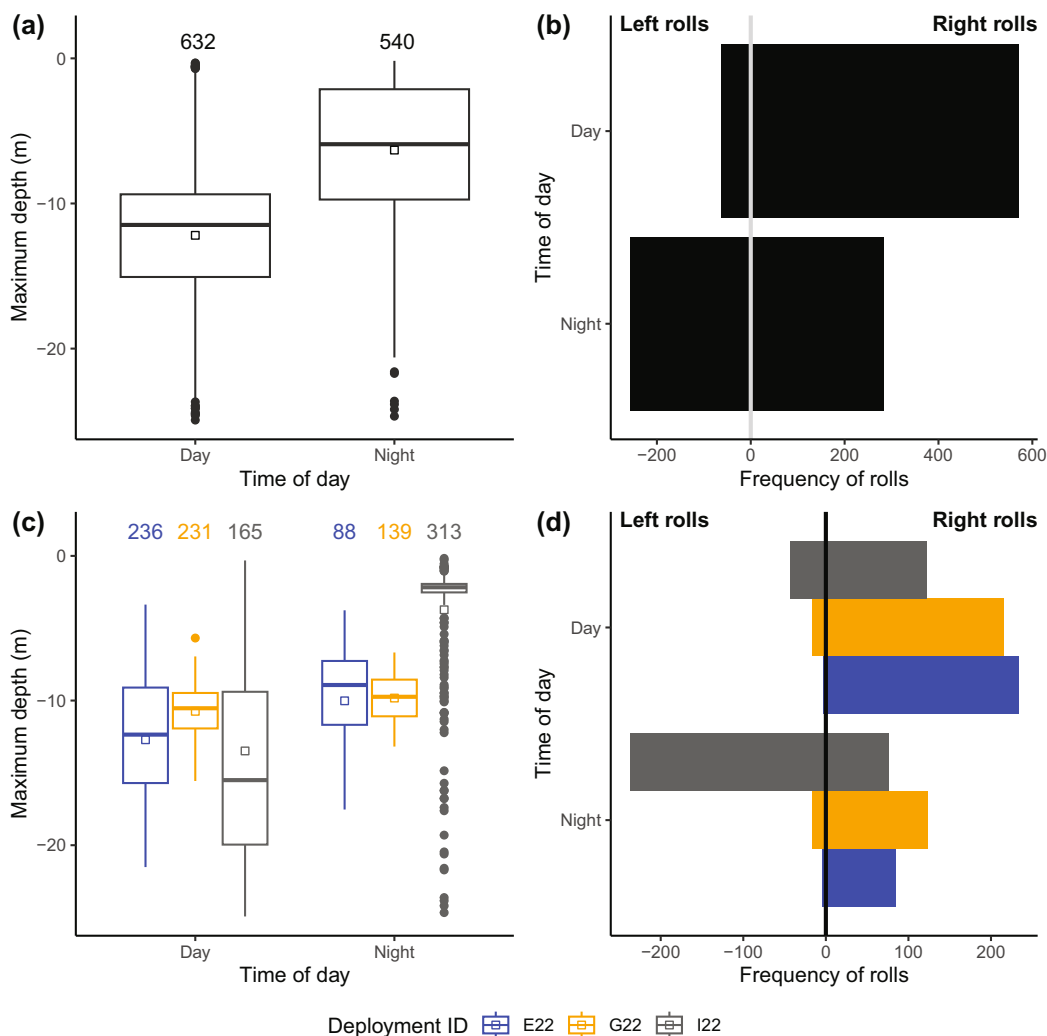
FIGURE 5 Maximum depth (in meter; a, c) and sidedness frequency (b, d) of foraging tactics from overnight CATS tag deployments on PCFG gray whales defined using a Classification and Regression Tree (CART) model during day and night for three full overnight deployments. Numbers across the top of the boxplots indicate the sample size of roll events. Day was considered to be 6 a.m. to 8 p.m. Pacific Daylight Time (PDT) based on average sunrise and sunset times in the study region. The open square represents the mean maximum depth (a, c). Frequency values to the left of the gray (b) and black (d) line indicate the number of rolls to the left, while frequency values to the right of the grey (b) and black (d) line indicate rolls to the right. Panels a and b show the distribution of values for all three overnight deployments combined. Panels c and d show the distribution of each of the full overnight deployments, with the different colors representing unique deployments.

enough to allow the model to separate it from the other broad states. It is also possible that the metrics included in the final HMM were not sufficient to indicate periods of social behavior, as surface time was excluded and there was no variable to account for the presence of other individuals. However, this study was conducted on a foraging ground with deployments occurring early in the season so it is not surprising that no social behavior was detected. These findings and explanations are supported by the rare detections of social behavior by other studies of PCFG whales, which detected slight increases in observations of social behavior later in the season (Stelle et al., 2008; Torres et al., 2018).

Body position variables—median pitch, depth to TL ratio, and median roll—were the most useful biologging metrics to quantitatively describe gray whale foraging tactics, a finding supported by their use in qualitative classification of drone focal follow data (Torres et al., 2018). Previous biologging studies on other baleen whale species used different accelerometry metrics to describe foraging behavior, including swim speed and stroke rates for continuous ram filtration (Simon et al., 2009), and signals of high accelerometry and swim speed for lunges at depth (Cade et al., 2016; Goldbogen et al., 2008; Izadi et al., 2022; Shadwick et al., 2019; Simon et al., 2012) or high horizonal accelerometry and high pitch when at the surface (Owen et al., 2016). Bottom side roll behavior of humpback whales foraging on benthic sand lance is most similar to benthic suction feeding behavior of gray whales and was detected using high roll and slow swim speed in tag accelerometry data (Ware et al., 2014). The similarity of metrics used to define bottom side roll behavior in humpback whales (Ware et al., 2014) with those used to define gray whale foraging tactics in this study supports that body position variables are useful when defining foraging behavior of baleen whales feeding on benthic prey.

The proportional activity budgets constructed from biologging data are similar to those previously constructed using other behavioral sampling techniques (e.g., theodolite focal follows, Sullivan & Torres, 2018; land-based observations, Mallonee, 1991; Stelle et al., 2008). This study found that PCFG gray whales spend 43% of their time searching, 36% of their time foraging, and 21% of their time transiting, which fall within the range of values reported for these broad states from other parts of the PCFG range (Hildebrand et al., 2022; Mallonee, 1991; Stelle et al., 2008; Sullivan & Torres, 2018). We also found that headstands, benthic digs, and side swims were present in approximately equal proportions across all deployments, which differs from the only other study that assessed foraging tactics and found headstands to be twice as common as side swims (Torres et al., 2018). This discrepancy highlights the value of collecting fine-scale data using biologging tags that capture behaviors not visible with other sampling methods, as well as the potential limitations of the small temporal and spatial scale of tag deployments to capture true behavioral variation at the population level. In agreement with Torres et al. (2018), the individual variation in tactic use we document indicates side swims are a less commonly used foraging tactic; only two deployments (H22 & I22) had side swim as the dominant foraging tactic, and these whales were shorter than 11 m, indicating that these individuals likely have not reached maturity (Bierlich et al., 2023). This finding is consistent with the ontogenetic shift noted in PCFG gray whales, which transition from side swims to headstands with increasing TL (used as a proxy for age and maturity; Bird et al., 2024).

Biologging data can be used to explore the complex relationships between behavior and body condition (Amo et al., 2007; Beale & Monaghan, 2004; Ransom et al., 2010). With our limited sample size, we documented that all gray whales with a BAI below average (i.e., less than median PCFG gray whale BAI of ~26) consistently made more foraging dives than search or transit, which aligns with previous work that found individuals in poorer body condition spent more time foraging (Allison & Conway, 2022; Ransom et al., 2010; Skogland & Grøvan, 1988; Stawski & Geiser, 2010). Body condition may also play a role in how animals respond behaviorally to disturbances, as a recent meta-analysis shows that individuals in poorer body condition are more likely to exhibit high-risk behaviors (Moran et al., 2021) that potentially increases their exposure to disturbances. Given the intensity of vessel activity in the nearshore foraging range of the PCFG gray whales (COSEWIC, 2017; Duffus, 1996; Lemos et al., 2022; Pirotta et al., 2023; Sullivan & Torres, 2018), this disturbance may reduce foraging efficiency, as seen in Sullivan and Torres (2018), and thus may negatively affect body condition. Given that PCFG body condition is negatively correlated with glucocorticoid levels (Lemos et al., 2021; Pirotta et al., 2023), decreased nutritive state may impact individual physiology and overall health, affecting the whales' energetic capacity to respond to acute threats, such as vessel strike avoidance. Biologging data can play an integral role in disentangling the relationships between behavior, body condition, and disturbance in future studies.

Biologging data can also be used to study how foraging tactics are passed through a population. For example, the tag data from a known mother (G22) and her daughter (F22) showed that they had very similar proportions of both broad states and foraging tactics. This finding suggests that there may be potential for vertical transmission of behaviors in PCFG gray whales, a group that shows high maternal recruitment (Calambokidis & Perez, 2017).

Vertical transmission of foraging tactics and tool use have been documented in bottlenose dolphins (*Tursiops aduncus*) from mothers to primarily female offspring (Wild et al., 2019) and the importance of female-kinship for shared prey preferences has been demonstrated in humpback whales (Rendell et al., 2019). While there is limited data documenting maternal kinship in baleen whales (Rendell et al., 2019), and only two of our study animals had a known maternal relationship, this finding demonstrates how our study system of PCFG gray whales with strong site-fidelity and maternal recruitment (Calambokidis & Perez, 2017) presents a viable opportunity for future research to examine vertical transmission of foraging behavior in baleen whales.

Diurnal changes in behavior from the three overnight deployment's biologging data paired with diurnal prey dynamics from published literature suggest that gray whales are visual predators (Torres, 2017). While PCFG gray whales have been documented to have a broad diet (Darling et al., 1998; Hildebrand et al., 2021), their primary prey in the study region is likely mysids (Allyn et al., 2024; Newell & Cowles, 2006). Therefore, while we were unable to document the exact prey the tagged whales were feeding on, it is likely they were targeting mysids, which have been documented to undergo a vertical expansion of their depth range at night (Alldredge & King, 1980; Mauchline, 1980). More dispersed prey and the inability to rely on visual cues at night potentially require gray whales to use more exploratory behavior to detect prey in the dark, leading to a higher proportion of the search state and lower proportion of foraging behavior at night. The higher dispersion of prey might also explain the increased proportion of side swims at night, as this foraging tactic is performed in the mid-water column (Bird et al., 2024; Torres et al., 2018). Decreased foraging depth and higher number of rolls to the left (right-eye up) during nighttime could also potentially result from an increased vertical distribution of prey and indicate that whales may track prey above them (Jaakkola et al., 2021). The increase in left-sided rolls with decreased foraging depth is consistent with patterns of lateralization observed in foraging blue whales (Friedlaender et al., 2017), further supporting the hypothesis that the right-eye is important for prey tracking in baleen whales. The overnight deployment with the most extreme change in depth and sidedness occurred when the moon was 97.58% illuminated (https://nineplanets.org/moon/phase/9-12-2022/), supporting the idea that, with high moonlight, the whale may have been looking for the shadow of prey above them. The two other overnight deployments were when the moon was only 44.36% illuminated (https://nineplanets.org/moon/phase/7-21-2022/), which might explain why there were less notable changes in sidedness of foraging tactics between day and night.

The impact of prey on behavior supports the importance of integrating prey data with the behavioral biologging data to not only understand drivers of behavior choice but investigate the energetic gain and foraging efficiency of each foraging tactic (e.g., Savoca et al., 2021; Volpov et al., 2015; Ydesen et al., 2014). The bioenergetic implications of foraging tactics has not been examined in gray whales, but can be obtained from combining prey densities, foraging energetics, and measurements of prey quality (Hildebrand et al., 2021). Additionally, tagging studies are inherently limited by sample size and individual variation when generalizing to the larger population (Hays et al., 2016). However, this study illustrated the feasibility of using biologging data to describe broad behavioral states and foraging tactics of PCFG gray whales along the Oregon and Washington coasts. Collection of a larger sample size of biologging data from PCFG gray whales would help account for individual variability in behavioral classifications and increase the sample period covered to account for more variability in prey and environmental conditions. Therefore, future research should focus on collecting biologging data from gray whales throughout the PCFG foraging range, as well as the from the WNP and ENP populations foraging in the Arctic. Also, the whales included in this study were predominantly females; other demographic units should be targeted in future tagging efforts to ensure that any behavioral differences in age and sex are captured in the biologging data.

Overall, our quantification of gray whale broad behavioral states and foraging tactics fills a knowledge gap in detection and quantitative description of foraging signals in this species, adding to the thorough description of feeding methods by other baleen whales (Goldbogen et al., 2017). The newly established quantitative methods to detect and describe foraging in PCFG gray whales can enable other analyses that require information on foraging behavior. For example, bioenergetic models for ENP and WNP gray whale populations have been developed to assess the population consequences of disturbance (McHuron et al., 2021; Villegas-Amtmann et al., 2015;

Villegas-Amtmann et al., 2017). The quantification of PCFG gray whale foraging behavior could support a similar analysis to inform management decisions on the multiple threats facing this subgroup.

AUTHOR CONTRIBUTIONS

Kate M. Colson: Conceptualization; formal analysis; investigation; methodology; visualization; writing – original draft. **Enrico Pirotta:** Methodology; writing – review and editing. **Leslie New:** Funding acquisition; methodology; writing – review and editing. **David E. Cade:** Investigation; methodology; resources; writing – review and editing. **John Calambokidis:** Investigation; resources; writing – review and editing. **Kevin Bierlich:** Investigation; writing – review and editing. **Clara N. Bird:** Investigation; writing – review and editing. **Alejandro Fernandez Ajó:** Investigation; writing – review and editing. **Lisa Hildebrand:** Investigation; writing – review and editing. **Andrew W. Trites:** Conceptualization; supervision; writing – review and editing. **Leigh G. Torres:** Conceptualization; funding acquisition; investigation; methodology; resources; supervision; writing – review and editing.

ACKNOWLEDGMENTS

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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REFERENCES

Agbayani, S. V. (2022). *Energy requirements of grey whales*. [Master's thesis]. University of British Columbia.

Akmajian, A. M., Scordino, J. J., Gearin, P. J., & Gosho, M. (2021). Body condition of gray whales (*Eschrichtius robustus*) feeding on the Pacific Coast reflects local and basin-wide environmental drivers and biological parameters. *Journal of Cetacean Research and Management*, *22*(232), 87–110.

Alldredge, A. L., & King, J. M. (1980). Effects of moonlight on the vertical migration patterns of demersal zooplankton. *Journal of Experimental Marine Biology and Ecology*, *44*(2), 133–156. https://doi.org/10.1016/0022-0981(80)90150-1

Allison, A. Z. T., & Conway, C. J. (2022). Daily foraging activity of an imperiled ground squirrel: effects of hibernation, thermal environment, body condition, and conspecific density. *Behavioral Ecology and Sociobiology*, *76*. https://doi.org/10.1007/s00265-022-03142-4

Allyn, E. M., Scordino, J. J., & Akmajian, A. M. (2024). Distribution and demographics of mysids (Crustacea: Mysida) as prey for gray whales (*Eschrichtius robustus*) in northwest Washington state. *PeerJ*, *12*, e16587. https://doi.org/10.7717/peerj.16587

Amo, L., López, P., & Martín, J. (2007). Habitat deterioration affects body condition of lizards: A behavioral approach with *Iberolacerta cyreni* lizards inhabiting ski resorts. *Biological Conservation*, *135*(1), 77–85. https://doi.org/10.1016/j.biocon.2006.09.020

Beale, C. M., & Monaghan, P. (2004). Behavioural responses to human disturbance: A matter of choice? *Animal Behaviour*, *68*(5), 1065–1069. https://doi.org/10.1016/j.anbehav.2004.07.002

Bierlich, K. C., Hewitt, J., Bird, C. N., Schick, R. S., Friedlaender, A., Torres, L. G., Date, J., Goldbogen, J., Read, A. J., Calambokidis, J., & Johnston, D. W. (2021). Comparing uncertainty associated with 1-, 2-, and 3D aerial photogrammetry-based body condition measurements of baleen whales. *Frontiers in Marine Science*, *8*, 1–16. https://doi.org/10.3389/fmars.2021.749943

Bierlich, K. C., Kane, A., Hildebrand, L., Hildebrand, I., Bird, C. N., Fernandez Ajo, A., Stewart, J. D., Hewitt, J., Hildebrand, I., Sumich, J., & Torres, L. G. (2023). Downsized: Gray whales using an alternative foraging ground have smaller bodies. *Biology Letters*, *19*, 20230043. https://doi.org/10.1098/rsbl.2023.0043

Bird, C., Pirotta, E., New, L., Bierlich, K., Donnelly, M., Hildebrand, L., Ajo, A. F., & Torres, L. (2024). Growing into it: Evidence of an ontogenetic shift in gray whale use of foraging tactics. *Animal Behaviour*, *214*, 121–135. https://doi.org/10.1016/j.anbehav.2024.06.004

Breiman, L., Friedman, J., Olshen, R., & Stone, C. (1984). *Classification and regression trees*. CRC Press.

Brown, D. D., Kays, R., Wikelski, M., Wilson, R., & Klimley, A. P. (2013). Observing the unwatchable through acceleration logging of animal behavior. *Animal Biotelemetry*, *1*, 20. https://doi.org/10.1186/2050-3385-1-20

Burnett, J. D., Lemos, L., Barlow, D., Wing, M. G., Chandler, T., & Torres, L. G. (2018). Estimating morphometric attributes of baleen whales with photogrammetry from small UASs: A case study with blue and gray whales. *Marine Mammal Science*, *35*(1), 108–139. https://doi.org/10.1111/mms.12527

Cade, D. E., Barr, K. R., Calambokidis, J., Friedlaender, A. S., & Goldbogen, J. A. (2018). Determining forward speed from accelerometer jiggle in aquatic nvironments. *Journal of Experimental Biology*, *221*(2). https://doi.org/10.1242/jeb.170449

Cade, D. E., Friedlaender, A. S., Calambokidis, J., & Goldbogen, J. A. (2016). Kinematic diversity in rorqual whale feeding mechanisms. *Current Biology*, *26*(19), 2617–2624. https://doi.org/10.1016/j.cub.2016.07.037

Cade, D. E., Gough, W. T., Czapanskiy, M. F., Fahlbusch, J. A., Kahane-Rapport, S. R., Linsky, J. M. J., Nichols, R. C., Oestreich, W. K., Wisniewska, D. M., Friedlaender, A. S., & Goldbogen, J. A. (2021). Tools for integrating inertial sensor data with video bio-loggers, including estimation of animal orientation, motion, and position. *Animal Biotelemetry*, *9*, 34. https://doi.org/10.1186/s40317-021-00256-w

Cade, D. E., Kahane-Rapport, S. R., Gough, W. T., Bierlich, K. C., Linsky, J. M. J., Calambokidis, J., Johnston, D. W., Goldbogen, J. A., & Friedlaender, A. S. (2023). Minke whale feeding rate limitations suggest constraints on the minimum body size for engulfment filtration feeding. *Nature Ecology and Evolution*, *7*(4), 535–546. https://doi.org/10.1038/s41559-023-01993-2

Calambokidis, J., Darling, J., Deeke, V., Gearin, P., Gosho, M., Megill, W., Wright, C. T., Goley, D., Toropova, C., Gisborne, B., & Gisborne, B. (2002). Abundance, range and movements of a feeding aggregation of gray whales (*Eschrictius robustus*) from California to southeastern Alaska in 1998. *Journal of Cetacean Research and Management*, *4*(3), 267–276.

Calambokidis, J., Fahlbusch, J. A., Szesciorka, A. R., Southall, B. L., Cade, D. E., Friedlaender, A. S., & Goldbogen, J. A. (2019). Differential vulnerability to ship strikes between day and night for blue, fin, and humpback whales based on dive and movement data from medium duration archival tags. *Frontiers in Marine Science*, *6*. https://doi.org/10.3389/fmars.2019.00543

Calambokidis, J., & Perez, A. (2017). Sightings and follow-up of mothers and calves in the PCFG and implications for internal recruitment. Paper SC/A17/GW/04 Presented to International Whaling Commission Scientific Committee, Olympia, WA.

Charnov, E. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, *9*, 739–752.

Christiansen, F., Rodríguez-González, F., Martínez-Aguilar, S., Urbán, J., Swartz, S., Warick, H., Vivier, F., & Bejder, L. (2021). Poor body condition associated with an unusual mortality event in gray whales. *Marine Ecology Progress Series*, *658*, 237–252. https://doi.org/10.3354/meps13585

Constantine, R., Johnson, M., Riekkola, L., Jervis, S., Kozmian-Ledward, L., Dennis, T., Torres, L. G., & Aguilar de Soto, N. (2015). Mitigation of vessel-strike mortality of endangered Bryde's whales in the Hauraki Gulf, New Zealand. *Biological Conservation*, *186*, 149–157. https://doi.org/10.1016/j.biocon.2015.03.008

Cooke, J. G., Sychenko, O., Burdin, A., Weller, D., Bradford, A., Lang, A., & Brownell, R. L. (2019). Population assessment update for Sakhalin gray whales. Western Gray Whale Advisory Panel, 20th Panel.

COSEWIC. (2017). COSEWIC assessment and status report on the Grey Whale Eschrichtius robustus, Northern Pacific Migratory population, Pacific Coast Feeding Group population and the Western Pacific population, in Canada. www.sararegistry.gc.ca/status/status_e.cfm

Crossin, G. T., Cooke, S. J., Goldbogen, J. A., & Phillips, R. A. (2014). Tracking fitness in marine vertebrates: Current knowledge and opportunities for future research. *Marine Ecology Progress Series*, *496*, 1–17. https://doi.org/10.3354/meps10691

Czapanskiy, M. (2022). catsr: Tools for using CATS PRH files in R.

Darling, J. D., Keogh, K. E., & Steeves, T. E. (1998). Gray whale (*Eschrichtius robustus*) habitat utilization and prey species off Vancouver Island, B.C. *Marine Mammal Science*, *14*(4), 692–720. https://doi.org/10.1111/j.1748-7692.1998.tb00757.x

DeRuiter, S. L., Johnson, M., Sweeney, D., McNamara-Oh, Y. J., Fynewever, S., Tejevbo, R., & Marques, T. (2022). tagtools: Tools for Working with Data from High-Resolution Biologging Tags. https://github.com/animaltags/tagtools_r

DeRuiter, S. L., Langrock, R., Skirbutas, T., Goldbogen, J. A., Calambokidis, J., Friedlaender, A. S., & Southall, B. L. (2017). A multivariate mixed Hidden Markov Model for blue whale behaviour and responses to sound exposure. *Annals of Applied Statistics*, *11*(1), 362–392. https://doi.org/10.1214/16-AOAS1008

Dill, L. M. (2017). Behavioural ecology and marine conservation: A bridge over troubled water? *ICES Journal of Marine Science*, *74*(6), 1514–1521. https://doi.org/10.1093/icesjms/fsx034

Duffus, D. A. (1996). The recreational use of grey whales in southern Clayoquot Sound, Canada. *Applied Geography*, *16*(3), 179–190. https://doi.org/10.1016/0143-6228(96)00002-1

Dunham, J. S., & Duffus, D. A. (2002). Diet of gray whales (*Eschrichtius robustus*) in Clayoquot Sound, British Columbia, Canada. *Marine Mammal Science*, *18*(2), 419–437. https://doi.org/10.1111/j.1748-7692.2002.tb01046.x

Eguchi, T., Lang, A., & Weller, D. W. (2024). ABundance of Eastern North Pacific gray whales 2023/2024. https://doi.org/10.25923/bmam-pe91

Feyrer, L. J., & Duffus, D. A. (2011). Predatory disturbance and prey species diversity: The case of gray whale (*Eschrichtius robustus*) foraging on a multi-species mysid (family *Mysidae*) community. *Hydrobiologia*, *678*(1), 37–47. https://doi.org/10.1007/s10750-011-0816-z

Friedlaender, A. S., Herbert-Read, J. E., Hazen, E. L., Cade, D. E., Calambokidis, J., Southall, B. L., Stimpert, A. K., & Goldbogen, J. A. (2017). Context-dependent lateralized feeding strategies in blue whales. *Current Biology*, *27*(22), R1206–R1208. https://doi.org/10.1016/j.cub.2017.10.023

Goldbogen, J. A., Cade, D. E., Calambokidis, J., Friedlaender, A. S., Potvin, J., Segre, P. S., & Werth, A. J. (2017). How baleen whales feed: The biomechanics of engulfment and filtration. *Annual Review of Marine Science*, *9*, 367–386. https://doi.org/10.1146/annurev-marine-122414-033905

Goldbogen, J. A., Calambokidis, J., Croll, D. A., Harvey, J. T., Newton, K. M., Oleson, E. M., Schorr, G., & Shadwick, R. E. (2008). Foraging behavior of humpback whales: Kinematic and respiratory patterns suggest a high cost for a lunge. *Journal of Experimental Biology*, *211*(23), 3712–3719. https://doi.org/10.1242/jeb.023366

Goldbogen, J. A., Calambokidis, J., Croll, D. A., Mckenna, M. F., Oleson, E., Potvin, J., Pyenson, N. D., Schorr, G., Shadwick, R. E., & Tershy, B. R. (2012). Scaling of lunge-feeding performance in rorqual whales: Mass-specific energy expenditure increases with body size and progressively limits diving capacity. *Functional Ecology*, *26*(1), 216–226. https://doi.org/10.1111/j.1365-2435.2011.01905.x

Goldbogen, J. A., Friedlaender, A. S., Calambokidis, J., McKenna, M. F., Simon, M., & Nowacek, D. P. (2013). Integrative approaches to the study of baleen whale diving behavior, feeding performance, and foraging ecology. *BioScience*, *63*(2), 90–100. https://doi.org/10.1525/bio.2013.63.2.5

Harris, J., Calambokidis, J., Perez, A., & Mahoney, P. J. (2022). Recent trends in the abundance of seasonal gray whales (*Eschrichtius robustus*) in the Pacific Northwest, 1996–2020. https://repository.library.noaa.gov/

Haver, S. M., Haxel, J., Dziak, R. P., Roche, L., Matsumoto, H., Hvidsten, C., & Torres, L. G. (2023). The variable influence of anthropogenic noise on summer season coastal underwater soundscapes near a port and marine reserve. *Marine Pollution Bulletin*, *194*, 115406. https://doi.org/10.1016/j.marpolbul.2023.115406

Hays, G. C., Ferreira, L. C., Sequeira, A. M. M., Meekan, M. G., Duarte, C. M., Bailey, H., Bailleul, F., Don Bowen, W., Julian Caley, M., Costa, D. P., Eguíluz, V. M., Fossette, S., Friedlaender, A. S., Gales, N., Gleiss, A. C., Gunn, J., Harcourt, R., Hazen, E. L., Heithaus, M. R., ... Thums, M. (2016). Key questions in marine megafauna movement ecology. *Trends in Ecology and Evolution*, *31*(6), 463–475. https://doi.org/10.1016/j.tree.2016.02.015

Hildebrand, L., Bernard, K. S., & Torres, L. G. (2021). Do gray whales count calories? Comparing energetics values of gray whale prey across two different feeding grounds in the Eastern North Pacific. *Frontiers in Marine Science*, *8*, 683634. https://doi.org/10.3389/fmars.2021.683634

Hildebrand, L., Sullivan, F. A., Orben, R. A., Derville, S., & Torres, L. G. (2022). Trade-offs in prey quantity and quality in gray whale foraging. *Marine Ecology Progress Series*, *695*, 189–201. https://doi.org/10.3354/meps14115

International Whaling Commission. (2011). Report of the Scientific Committee. *Journal of Cetacean Research Management*, *12*, 1–75.

Izadi, S., Aguilar de Soto, N., Constantine, R., & Johnson, M. (2022). Feeding tactics of resident Bryde's whales in New Zealand. *Marine Mammal Science*, *38*, 1104–1117. https://doi.org/10.1111/mms.12918

Jaakkola, K., Loyer, C., Guarino, E., Donegan, K., & McMullen, C. (2021). Do dolphins really have a rightward lateralization for action? The importance of behavior-specific and orientation-neutral coding. *Behavioural Brain Research*, *401*. https://doi.org/10.1016/j.bbr.2020.113083

Johnson, K. R., & Nelson, C. H. (1984). Side-scan sonar assessment of gray whale feeding in the Bering Sea. *Science*, *225*(4667), 1150–1152. https://doi.org/10.1126/science.225.4667.1150

Lang, A. R., Calambokidis, J., Scordino, J., Pease, V. L., Klimek, A., Burkanov, V. N., Gearin, P., Litovka, D. I., Robertson, K. M., Mate, B. R., Jacobsen, J. K., & Taylor, B. L. (2014). Assessment of genetic structure among eastern North Pacific gray whales on their feeding grounds. *Marine Mammal Science*, *30*(4), 1473–1493. https://doi.org/10.1111/mms.12129

Le Boeuf, B. J., Perez-Cortes, M. H., Urban, R. J., Mate, B. R., & Ollervides, U. F. (2000). High gray whale mortality and low recruitment in 1999: potential causes and implications. *Journal of Cetacean Research and Management*, *2*, 85–99.

Lemos, L. S., Burnett, J. D., Chandler, T. E., Sumich, J. L., & Torres, L. G. (2020). Intra- and inter-annual variation in gray whale body condition on a foraging ground. *Ecosphere*, *11*(4), e03094. https://doi.org/10.1002/ecs2.3094

Lemos, L. S., Haxel, J. H., Olsen, A., Burnett, J. D., Smith, A., Chandler, T. E., Nieukirk, S. L., Larson, S. E., Hunt, K. E., & Torres, L. G. (2022). Effects of vessel traffic and ocean noise on gray whale stress hormones. *Scientific Reports*, *12*, 18580. https://doi.org/10.1038/s41598-022-14510-5

Lemos, L. S., Olsen, A., Smith, A., Burnett, J. D., Chandler, T. E., Larson, S., Hunt, K. E., & Torres, L. G. (2021). Stressed and slim or relaxed and chubby? A simultaneous assessment of gray whale body condition and hormone variability. *Marine Mammal Science*, *38*, 801–811. https://doi.org/10.1111/mms.12877

MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*, *100*(916), 603–609.

Magera, A. M., Mills Flemming, J. E., Kaschner, K., Christensen, L. B., & Lotze, H. K. (2013). Recovery trends in marine mammal populations. *PloS One*, *8*(10). https://doi.org/10.1371/journal.pone.0077908

Mallonee, J. S. (1991). Behaviour of gray whales (*Eschrichtius robustus*) summering off the northern California coast, from Patrick's Point to Crescent City. *Canadian Journal of Zoology*, *69*(3), 681–690. https://doi.org/10.1139/z91-100

Mauchline, J. (1980). The biology of mysids and euphausiids. *Advances in Marine Biology*, *18*, 1–681.

McClintock, B. T. (2021). Worth the effort? A practical examination of random effects in hidden Markov models for animal telemetry data. *Methods in Ecology and Evolution*, *12*(8), 1475–1497. https://doi.org/10.1111/2041-210X.13619

McClintock, B. T., & Michelot, T. (2018). momentuHMM: R package for generalized hidden Markov models of animal movement. *Methods in Ecology and Evolution*, *9*(6), 1518–1530. https://doi.org/10.1111/2041-210X.12995

McHuron, E. A., Aerts, L., Gailey, G., Sychenko, O., Costa, D. P., Mangel, M., & Schwarz, L. K. (2021). Predicting the population consequences of acoustic disturbance, with application to an endangered gray whale population. *Ecological Applications*, *31*(8), e02440. https://doi.org/10.1002/eap.2440

Milborrow, S. (2022). rpart.plot: Plot "rpart" models: An enhanced version of "plot.rpart.". https://cran.r-project.org/package=rpart.plot

Moore, S. E., Clarke, J. T., Okkonen, S. R., Grebmeier, J. M., Berchok, C. L., & Stafford, K. M. (2022). Changes in gray whale phenology and distribution related to prey variability and ocean biophysics in the northern Bering and eastern Chukchi seas. *Plos One*, *17*(4), e0265934. https://doi.org/10.1371/journal.pone.0265934

Moore, S. E., Grebmeier, J. M., & Davies, J. R. (2003). Gray whale distribution relative to forage habitat in the northern Bering Sea: Current conditions and retrospective summary. *Canadian Journal of Zoology*, *81*(4), 734–742. https://doi.org/10.1139/z03-043

Morales, J. M., Haydon, D. T., Frair, J., Holsinger, K. E., & Fryxell, J. M. (2004). Extracting more out of relocation data: Building movement models as mixtures of random walks. *Ecology*, *85*(9), 2436–2445. https://doi.org/10.1890/03-0269

Moran, N. P., Sánchez-Tójar, A., Schielzeth, H., & Reinhold, K. (2021). Poor nutritional condition promotes high-risk behaviours: a systematic review and meta-analysis. *Biological Reviews*, *96*, 269–288. https://doi.org/10.1111/brv.12655

Nerini, M. (1984). A review of gray whale feeding ecology. In M. L. Jones, S. L. Swartz, & S. Leatherwood (Eds.), *The gray whale: Eschrichtius robustus* (pp. 423–450). Academic Press. 10.1016/B978-0-08-092372-7.50024-8

Newell, C. L., & Cowles, T. J. (2006). Unusual gray whale *Eschrichtius robustus* feeding in the summer of 2005 off the central Oregon coast. *Geophysical Research Letters*, *33*(22). https://doi.org/10.1029/2006GL027189

Nichols, R. C., Cade, D. E., Kahane-Rapport, S., Goldbogen, J., Stimpert, A., Nowacek, D., Read, A. J., Johnston, D. W., & Friedlaender, A. (2022). Intra-seasonal variation in feeding rates and diel foraging behaviour in a seasonally fasting mammal, the humpback whale. *Royal Society Open Science*, *9*. https://doi.org/10.1098/rsos.211674

Norberg, R. A. (1977). An ecological theory on foraging time and energetics and choice of optimal food-searching method. *Journal of Animal Ecology*, *46*(2), 511–529.

Nowacek, D. P., Christiansen, F., Bejder, L., Goldbogen, J. A., & Friedlaender, A. S. (2016). Studying cetacean behaviour: New technological approaches and conservation applications. *Animal Behaviour*, *120*, 235–244. https://doi.org/10.1016/j.anbehav.2016.07.019

Owen, K., Dunlop, R. A., Monty, J. P., Chung, D., Noad, M. J., Donnelly, D., Goldizen, A. W., & Mackenzie, T. (2016). Detecting surface-feeding behavior by rorqual whales in accelerometer data. *Marine Mammal Science*, *32*(1), 327–348. https://doi.org/10.1111/mms.12271

Perryman, W. L., Donahue, M. A., Perkins, P. C., & Reilly, S. B. (2002). Gray whale calf production 1994–2000: Are observed fluctuations related to changes in seasonal ice cover? *Marine Mammal Science*, *18*(1), 121–144. https://doi.org/10.1111/j.1748-7692.2002.tb01023.x

Perryman, W. L., Joyce, T., Weller, D. W., & Durban, J. W. (2020). Environmental factors influencing eastern North Pacific gray whale calf production 1994–2016. *Marine Mammal Science*, *37*(2), 448–462. 10.1111/mms.12755

Peters, A., & Hothorn, T. (2023). ipred: Improved predictors. https://cran.r-project.org/package=ipred

Pirotta, E., Fernandez Ajo, A., Bierlich, K. C., Bird, C. N., Buck, C. L., Haver, S. M., Haxel, J. H., Hildebrand, L., Hunt, K. E., Lemos, L. S., New, L., & Torres, L. G. (2023). Assessing variation in faecal glucocorticoid concentrations in gray whales exposed to anthropogenic stressors. *Conservation Physiology*, *11*, coad082. https://doi.org/10.1093/conphys/coad082

Pohle, J., Langrock, R., van Beest, F. M., & Schmidt, N. M. (2017). Selecting the number of states in Hidden Markov Models: Pragmatic solutions illustrated using animal movement. *Journal of Agricultural, Biological, and Environmental Statistics*, *22*(3), 270–293. https://doi.org/10.1007/s13253-017-0283-8

Potvin, J., Goldbogen, J. A., & Shadwick, R. E. (2012). Metabolic expenditures of lunge feeding rorquals across scale: Implications for the evolution of filter feeding and the limits of maximum body size. *PLoS ONE*, *7*(9), e44854. https://doi.org/10.1371/journal.pone.0044854

R Core Team. (2023). *R: A language and environment for statistical computing*. R Core Team. https://www.r-project.org/

Ransom, J. I., Cade, B. S., & Hobbs, N. T. (2010). Influences of immunocontraception on time budgets, social behavior, and body condition in feral horses. *Applied Animal Behaviour Science*, *124*(1–2), 51–60. https://doi.org/10.1016/j.applanim.2010.01.015

Raverty, S., Duignan, P., Greig, D., Huggins, J. L., Huntington, K. B., Garner, M., Calambokidis, J., Cottrell, P., Danil, K., D'Alessandro, D., Duffield, D., Flannery, M., Gulland, F. M., Halaska, B., Lambourn, D. M., Lehnhart, T., Urbán, R. J., Rowles, T., Rice, J., … Fauquier, D. (2024). Gray whale (*Eschrichtius robustus*) postmortem findings from December 2018 through 2021 during the Unusual Mortality Event in the Eastern North Pacific. *PLoS ONE*, *19*(3), e0295861. https://doi.org/10.1371/journal.pone.0295861

Rendell, L., Cantor, M., Gero, S., Whitehead, H., & Mann, J. (2019). Causes and consequences of female centrality in cetacean societies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *374*(1780). https://doi.org/10.1098/rstb.2018.0066

Savoca, M. S., Czapanskiy, M. F., Kahane-Rapport, S. R., Gough, W. T., Fahlbusch, J. A., Bierlich, K. C., Bierlich, K. C., Segre, P. S., Di Clemente, J., Penry, G. S., Wiley, D. N., Calambokidis, J., Nowacek, D. P., Johnston, D. W., Pyenson, N. D., Friedlaender, A. S., Hazen, E. L., & Goldbogen, J. A. (2021). Baleen whale prey consumption based on high resolution foraging measurements. *Nature*, *599*, 85–90. https://doi.org/10.1038/s41586-021-03991-5

Schwarz, J. F. L., Mews, S., DeRango, E. J., Langrock, R., Piedrahita, P., Páez-Rosas, D., & Krüger, O. (2021). Individuality counts: A new comprehensive approach to foraging strategies of a tropical marine predator. *Oecologia*, *195*(2), 313–325. https://doi.org/10.1007/s00442-021-04850-w

Shadwick, R. E., Potvin, J., & Goldbogen, J. A. (2019). Lunge feeding in rorqual whales. *Physiology*, *34*, 409–418. https://doi.org/10.1152/physiol.00010.2019

Simon, M., Johnson, M., & Madsen, P. T. T. (2012). Keeping momentum with a mouthful of water: Behavior and kinematics of humpback whale lunge feeding. *Journal of Experimental Biology*, *215*(21), 3786–3798. https://doi.org/10.1242/jeb.071092

Simon, M., Johnson, M., Tyack, P., & Madsen, P. T. (2009). Behaviour and kinematics of continuous ram filtration in bowhead whales (*Balaena mysticetus*). *Proceedings of the Royal Society B: Biological Sciences*, *276*(1674), 3819–3828. https://doi.org/10.1098/rspb.2009.1135

Skogland, T., & Grøvan, B. (1988). The effects of human disturbance on the activity of wild reindeer in different physical condition. *Rangifer*, *8*(1), 11–19. https://doi.org/10.7557/2.8.1.726

Stawski, C., & Geiser, F. (2010). Fat and fed: Frequent use of summer torpor in a subtropical bat. *Naturwissenschaften*, *97*, 29–35. https://doi.org/10.1007/s00114-009-0606-x

Stelle, L. L., Megill, W. M., & Kinzel, M. R. (2008). Activity budget and diving behavior of gray whales (*Eschrichtius robustus*) in feeding grounds off coastal British Columbia. *Marine Mammal Science*, *24*(3), 462–478. https://doi.org/10.1111/j.1748-7692.2008.00205.x

Stewart, J. D., Joyce, T. W., Durban, J. W., Calambokidis, J., Fauquier, D., Fearnbach, H., Grebmeier, J. M., Lynn, M., Manizza, M., Perryman, W. L., Tinker, M. T., & Weller, D. W. (2023). Boom-bust cycles in gray whales associated with dynamic and changing Arctic conditions. *Science*, *382*, 207–211. https://doi.org/10.1126/science.adi1847

Sullivan, F. A., & Torres, L. G. (2018). Assessment of vessel disturbance to gray whales to inform sustainable ecotourism. *Journal of Wildlife Management*, *82*(5), 896–905. https://doi.org/10.1002/jwmg.21462

Sumich, J. L. (1983). Swimming velocities, breathing patterns, and estimated costs of locomotion in migrating gray whales, *Eschrichtius robustus*. *Canadian Journal of Zoology*, *61*(3), 647–652. https://doi.org/10.1139/z83-086

Therneau, T., & Atkinson, B. (2022). rpart: Recursive partitioning and regression trees. https://cran.r-project.org/package=rpart

Thomas, P. O., Reeves, R. R., & Brownell, R. L. (2016). Status of the world's baleen whales. *Marine Mammal Science*, *32*(2), 682–734. https://doi.org/10.1111/mms.12281

Torres, L. G. (2017). A sense of scale: Foraging cetaceans' use of scale-dependent multimodal sensory systems. *Marine Mammal Science*, *33*(4), 1170–1193. https://doi.org/10.1111/mms.12426

Torres, L. G., Bird, C. N., Rodriguez-Gonzalez, F., Christiansen, F., Bejder, L., Lemos, L., Urban, R. J., Swartz, S., Willoughby, A., Hewitt, J., & Bierlich, K. C. (2022). Range-wide comparison of gray whale body condition reveals contrasting sub-population health characteristics and vulnerability to environmental change. *Frontiers in Marine Science*, *9*, 867258. https://doi.org/10.3389/fmars.2022.867258

Torres, L. G., Brander, S. M., Parker, J. I., Bloom, E. M., Norman, R., Van Brocklin, J. E., Lasdin, K. S., & Hildebrand, L. (2023). Zoop to poop: Assessment of microparticle loads in gray whale zooplankton prey and fecal matter reveal high daily consumption rates. *Frontiers in Marine Science*, *10*. https://doi.org/10.3389/fmars.2023.1201078

Torres, L. G., Nieukirk, S. L., Lemos, L., & Chandler, T. E. (2018). Drone up! Quantifying whale behavior from a new perspective improves observational capacity. *Frontiers in Marine Science*, *5*, 319. https://doi.org/10.3389/fmars.2018.00319

Torres, W., & Bierlich, K. (2020). MorphoMetriX: a photogrammetric measurement GUI for morphometric analysis of megafauna. *Journal of Open Source Software*, *5*(45), 1825 10.21105/joss.01825

Villegas-Amtmann, S., Schwarz, L. K., Gailey, G., Sychenko, O., & Costa, D. P. (2017). East or west: The energetic cost of being a gray whale and the consequence of losing energy to disturbance. *Endangered Species Research*, *34*, 167–183. https://doi.org/10.3354/esr00843

Villegas-Amtmann, S., Schwarz, L. K., Sumich, J. L., Costa, D. P., & Peters, D. P. C. (2015). A bioenergetics model to evaluate demographic consequences of disturbance in marine mammals applied to gray whales. *Ecosphere*, *6*(10), 183. https://doi.org/10.1890/ES15-00146.1

Volpov, B. L., Hoskins, A. J., Battaile, B. C., Viviant, M., Wheatley, K. E., Marshall, G., Abernathy, K., & Arnould, J. P. Y. (2015). Identification of prey captures in Australian fur seals (*Arctocephalus pusillus* doriferus) using head-mounted accelerometers: Field validation with animal-borne video cameras. *PLoS ONE*, *10*(6). https://doi.org/10.1371/journal.pone.0128789

Ware, C., Wiley, D. N., Friedlaender, A. S., Weinrich, M., Hazen, E. L., Bocconcelli, A., Parks, S. E., Stimpert, A. K., Thompson, M. A., & Abernathy, K. (2014). Bottom side-roll feeding by humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine, U.S.A. *Marine Mammal Science*, *30*(2), 494–511. https://doi.org/10.1111/mms.12053

Watanabe, Y. Y., & Goldbogen, J. A. (2021). Too big to study? The biologging approach to understanding the behavioural energetics of ocean giants. *Journal of Experimental Biology*, *224*, 202747. https://doi.org/10.1242/jeb.202747

Webber, M. A., Keener, W., Markowitz, T. M., Chamberlin, D., Allen, D., Lane, R. S., Slaathaug, J. M., Rodriguez, P. N., George, K., & O'Hern, J. E. (2024). Fish feeding and rapid foraging behavior switching by gray whales (*Eschrichtius robustus*) in California. *Aquatic Mammals*, *50*(2), 132–151. https://doi.org/10.1578/AM.50.2.2024.132

Wild, S., Allen, S. J., Krutzen, M., King, S. L., Gerber, L., & Hoppitt, W. J. E. (2019). Multi-network-based diffusion analysis reveals vertical cultural transmission of sponge tool use within dolphin matrilines. *Biology Letters*, *15*(7). https://doi.org/10.1098/rsbl.2019.0227

Williamson, M. J., Kavanagh, A. S., Noad, M. J., Kniest, E., & Dunlop, R. A. (2016). The effect of close approaches for tagging activities by small research vessels on the behavior of humpback whales (*Megaptera novaeangliae*). *Marine Mammal Science*, *32*(4), 1234–1253. https://doi.org/10.1111/mms.12324

Woodward, B. L., & Winn, J. P. (2006). Apparent lateralized behavior in gray whales feeding off the Central British Columbia coast. *Marine Mammal Science*, *22*(1), 64–73. https://doi.org/10.1111/j.1748-7692.2006.00006.x

Wright, B. M., Ford, J. K. B., Ellis, G. M., Deecke, V. B., Shapiro, A. D., Battaile, B. C., & Trites, A. W. (2017). Fine-scale foraging movements by fish-eating killer whales (*Orcinus orca*) relate to the vertical distributions and escape responses of salmonid prey (*Oncorhyncus* spp.). *Movement Ecology*, *5*. https://doi.org/10.1186/s40462-017-0094-0

Würsig, B., Wells, R. S., & Croll, D. A. (1986). Behavior of gray whales summering near St. Lawrence Island, Bering Sea. *Canadian Journal of Zoology*, *64*(3), 611–621. https://doi.org/10.1139/z86-091

Ydesen, K. S., Wisniewska, D. M., Hansen, J. D., Beedholm, K., Johnson, M., & Madsen, P. T. (2014). What a jerk: Prey engulfment revealed by high-rate, super-cranial accelerometry on a harbour seal (*Phoca vitulina*). *Journal of Experimental Biology*, *217*(15). https://doi.org/10.1242/jeb.111070

Zucchini, W., MacDonald, I. L., & Langrock, R. (2016). *Hidden Markov models for time series* (2nd ed.). CRC Press.

SUPPORTING INFORMATION

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How to cite this article: Colson, K. M., Pirotta, E., New, L., Cade, D. E., Calambokidis, J., Bierlich, K. C., Bird, C. N., Ajó, A. F., Hildebrand, L., Trites, A. W., & Torres, L. G. (2025). Using accelerometry tags to quantify gray whale foraging behavior. *Marine Mammal Science*, *41*(2), e13210. https://doi.org/10.1111/mms.13210