



Growing into it: evidence of an ontogenetic shift in grey whale use of foraging tactics

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Individual specialization may occur relative to diet, behaviour or spatial distribution, potentially leading to differential resource and space use within a population. While specializations have been documented across many animal populations, the underlying causes of individual specialization (e.g. morphology, age or sex) are not always identified. Causes of specialization can be especially challenging to uncover for large, long-lived marine animals. We used a Bayesian multilevel, multinomial logistic regression model to study the relationships between grey whale, *Eschrichtius robustus*, use of foraging tactics and morphology (body length and condition), while accounting for habitat characteristics and individual variation in tactic use. The model was informed by a 7-year longitudinal data set of concurrent morphology and foraging behaviour collected using drones. We found evidence of an ontogenetic shift in the use of foraging tactics associated with body length (a proxy for age). Individual specialization in behaviour was also associated with water depth and habitat. After accounting for the effects of these covariates, there was some residual individual level variation in the use of different foraging tactics. Our findings demonstrate variation in resource and habitat use within a baleen whale population at the individual level relative to body length and habitat, suggesting that individual spatial distribution and access to prey may vary by age class. Our results can be applied to investigate whether juveniles and adults differ in their foraging success and resilience to stressors.

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Variation in individual traits (e.g. morphology, behaviour) can affect a population's diet, abundance, distribution, evolutionary potential and vulnerability to environmental change and disturbance events (Wennersten & Forsman, 2012). Understanding individual variation and its drivers improves population models and conservation efforts by acknowledging that there may be intra-population differences in resource use, competition and energetic success.

The term 'individual specialization' broadly refers to any individual level variation in resource use (Dall et al., 2012). Specialization includes variation in diet composition, behaviour or habitat use, and it can be caused by a variety of genetic, phenotypic and environmental differences. Both optimal foraging theory (Emlen,

1966; Schoener, 1971) and niche partitioning theory (Pianka, 1974) posit that resource availability is a major driver of individual specialization, although they disagree about whether this relationship is positive or negative. When resource availability decreases, either because of increasing population density (i.e. resource consumption) or changing environmental conditions, then competition for that resource subsequently increases. Under limited resource conditions, optimal foraging theory predicts that individuals will generalize their diet to increase the likelihood of encountering prey, whereas niche partitioning theory predicts that individuals will specialize to avoid competition (Emlen, 1966; Pianka, 1974).

When considering foraging success, resource availability is not only the quantity or quality of prey in an area, but also the accessibility of prey to an individual. Accessibility includes the ability to capture and consume the resource and the ability to access the habitat where the resource is present (Halsey, 2016; Keen & Qualls,

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2018; Schoener, 1971). The cost of consuming prey varies with individual ability (Krebs et al., 1977), and variation in individual ability to access and capture prey is often driven by morphological differences. Skull and body morphology affect prey capture and consumption ability, which are linked to diet specialization in insects (Cisneros & Rosenheim, 1997), amphibians (Cucherousset et al., 2011) and fish (Araújo et al., 2008; Ward-Campbell & Beamish, 2005). Body morphology also affects habitat accessibility, consequently affecting prey type availability. As an animal grows, this increase in size can enable access to, or improved manoeuvrability in, new habitats (Adams, 1997; Gustafsson, 1988; Jegliński et al., 2013). Furthermore, shared morphologies within a population often lead to shared specializations, emphasizing the importance of determining morphological groupings associated with specialization.

Common sources of phenotypic variation linked with individual specialization include sexual dimorphism, resource polymorphism and ontogenetic shifts (Dall et al., 2012). Sexual dimorphism, i.e. differences between sexes, has been linked to spatial segregation in pinnipeds (Kernaléguen et al., 2016; Kienle et al., 2022) and seabirds (Orgeret et al., 2021), causing differential threat exposure. In contrast, resource polymorphism, which occurs when behavioural or diet variation emerges from differences between distinct morphs, can lead to variable foraging efficiency and pollutant consumption associated with different specializations (Cucherousset et al., 2011; De Meyer et al., 2018). Finally, ontogenetic niche shifts, resulting from size, shape and behaviour changes that occur as an individual grows, often occur when individuals tend to consume larger prey or access different habitats as they grow (Adams, 1997; Newland et al., 2009). This differential prey consumption, driven by age structure, can affect the ecosystem community through density-dependent predation rates on prey (Cisneros & Rosenheim, 1997). The consequences of specialization (i.e. differential threat and pollutant exposure, variable foraging success, effects on other populations) can be shared across groups, emphasizing the need to document individual specialization and its link with phenotypic variation (often meaning morphology). However, collection of concurrent morphology and behaviour data can be challenging in wild populations, particularly for larger and less accessible organisms such as cetaceans.

Diet and foraging behaviour specializations have been identified in both odontocete (Remili et al., 2021) and baleen whale (Pontbriand et al., 2023) populations, with some specializations linked to specific habitat characteristics (Hoelzel et al., 1989; Torres & Read, 2009). However, these studies did not address the drivers behind the development of the specialist behaviours. Several studies identified social learning as a driver of tactic use development in cetaceans, including vertical (parent to offspring) and social (nonvertical) transmission (Allen et al., 2013; Wild et al., 2019, 2020). Ontogenetic diet shifts have also been identified in several odontocete populations through stable isotope analysis (Mendes et al., 2007; Riccialdelli et al., 2013; Rossman et al., 2015; Samarra et al., 2022). These studies suggest a shift towards consumption of larger prey driven by individual growth, but the mechanism underpinning this shift remains unknown without concurrent data on morphology, behaviour, habitat and diet.

Behavioural patterns of cetaceans are particularly hard to study as these species spend most of their time underwater and can travel great distances. Furthermore, it has been historically challenging to obtain morphological measurements of free-living individuals in the wild and difficult to collect repeat samples of individuals over a long period. Unoccupied Aircraft Systems (UASs, or drones) have revolutionized the study of marine mammals, particularly large cetaceans. Drones increase observation time and enable the

detection and identification of behaviours in greater detail (Torres et al., 2018). Drones are effective for studying a range of cetacean behaviours including foraging and social interactions (Frouin-Mouy et al., 2020; Hartman et al., 2020; Nielsen et al., 2019; Torres et al., 2020). Drone imagery also provides photogrammetric measurements of body length and condition (Bierlich, Hewitt, et al., 2021; Burnett et al., 2018; Christiansen et al., 2016). Overall, drones enable collection of high-frequency replicate data noninvasively, contributing to significant longitudinal data sets of variable morphology (Lemos et al., 2020).

Pacific Coast Feeding Group (PCFG) grey whales, *Eschrichtius robustus*, comprising ~212 individuals (Harris et al., 2022), constitute a subgroup of the eastern North Pacific (ENP) population of grey whales (~14 526; Eguchi et al., 2023). PCFG grey whales forage in coastal waters typically of <20 m depth (Hildebrand et al., 2021) between northern California, U.S.A. and southern British Columbia, Canada, where individuals are often resighted and show high site fidelity (Calambokidis et al., 2019; Lagerquist et al., 2019). Grey whales are considered generalists. They forage using suction feeding, a technique distinct from those used by other baleen whales, to consume a range of prey types (Nerini, 1984). ENP whales forage primarily in the Bering Sea and the Chukchi Sea on benthic amphipods (family Ampeliscidae) in soft sediment, using a benthic dig tactic (Brower et al., 2017; Nerini, 1984). In contrast, PCFG whales forage on a variety of prey types, including mysids (Mysidae), crab larvae (*Cancer magister*, Porcellanidae sp.), bay ghost shrimp, *Neotrypaea californiensis*, and benthic amphipods (Darling et al., 1998; Dunham & Duffus, 2001, 2002; Hildebrand et al., 2021), using a range of epibenthic and benthic feeding tactics (Torres et al., 2018). While there are no data linking feeding tactics to prey types, observations indicate that mysids are a predominant prey found in reef, kelp and rocky habitats where grey whales often forage and that benthic amphipods are associated with sandy bottom habitat (Hildebrand et al., 2022). Although the microsatellite allele frequencies of the PCFG overlap with those of the ENP (Lang et al., 2021), PCFG whales are skinnier and shorter than ENP whales, with smaller flukes and shorter skulls (Bierlich et al., 2023; Torres et al., 2022). While the drivers and consequences of these morphological differences are not yet identified, physical size may influence a PCFG whale's ability to perform shallow water feeding tactics.

The nearshore foraging habitat of PCFG grey whales exposes them to diverse anthropogenic threats, including high microplastic loads (Torres et al., 2023), entanglements in fishing gear (Scordino et al., 2017), behavioural disturbance from vessel traffic (Sullivan & Torres, 2018) and ocean sound and vessel traffic levels, which are positively correlated with glucocorticoid hormone levels (Lemos et al., 2022; Pirotta et al., 2023). Moreover, broad-scale environmental changes in PCFG whale habitat have caused significant declines in kelp habitat, with an associated indirect effect that impacts prey availability (Hildebrand et al., 2024). While these threats have been documented to occur at the population level, it is unknown whether there are differences in exposure and impact among individuals of different sex, age or reproductive status, potentially caused by specialization, that affect population dynamics.

The high resight rate and shallow water foraging habits of PCFG grey whales provide an excellent opportunity for drone-based assessment of individual behavioural specialization with concurrent morphological data in a baleen whale population. Here we use a 7-year longitudinal data set to investigate the hypothesis that foraging tactic specialization is driven by morphological differences, i.e. body length and condition, and is associated with habitat characteristics.

METHODS

Study Site and Survey Design

We conducted boat-based surveys near Newport ($44^{\circ}36'28''\text{N}$, $124^{\circ}4'54''\text{W}$) and Port Orford ($42^{\circ}44'15''\text{N}$, $124^{\circ}30'19''\text{W}$), Oregon, U.S.A., between May and October 2016–2022 (Fig. 1). Survey effort was conducted in good weather (<22 km/h, swell <1.5 m, minimal fog or rain) by teams of three to four people in a small (5.4 m) rigid-hull inflatable boat. When a whale was spotted, a sighting was considered to have started, representing the start of an observation event during which multiple whales could be observed and multiple drone flights could occur. The whale was then approached (at 30–80 m) to collect images for photo-identification, information on behavioural state and to conduct drone operations.

Ethical Note

Data were collected noninvasively using drones. Research was conducted under NOAA/NMFS permits 16011 and 21678. UAS operations were conducted by a Federal Aviation Authority (FAA) certified private pilot with a Part107 license. During field work, behaviour was observed for indications of a behavioural response to disturbance (changes in direction, increased swim speed, sudden dives) and none were observed. Disturbance potential was minimized by maintaining a slow boat speed when near whales and maintaining each drone at a minimum altitude of 20 m.

Drone Data

Drone operations

Drone flights were conducted in good weather conditions (wind <18.5 km/h, no fog or rain, cloud ceiling >300 m). Four drones were used during the study period: DJI Phantom 3 Pro; DJI Phantom 4 Advanced; DJI Phantom 4 Pro; DJI Inspire 2. Starting in 2020, a laser altimeter (e.g. 'LidarBoX') was mounted on the drone to collect more accurate altitude data and reduce uncertainty in photogrammetric measurements (Bierlich et al., 2024; Dawson et al., 2017). Further details are provided in the Supplementary

material. Once a whale was located by the pilot, the drone approached the whale at an altitude between 20 and 40 m and then followed the whale as long as it was visible at the surface and underwater. Video footage was recorded continuously during flight.

Drone video processing and coding

Drone footage was first clipped into periods where a whale was visible. The whale(s) observed in each clip were identified using the footage and concurrent photo-identification images taken from the boat during the flight. Clips were then reviewed multiple times and behaviours were annotated by a single experienced analyst using the open-source software Behavioural Observation Research Interactive Software (BORIS; Friard & Gamba, 2016). If two or more whales were in a clip, the clip was reviewed once per individual. Periods when the drone was directly over the whale were annotated so that the GPS location of the drone could be used to extract GPS locations for each behaviour observation.

While an overall primary behaviour state (foraging, travel, social, rest) was assigned in the field to the whale(s) observed at each sighting (Table 1), behaviours observed in the video clips were annotated following our developed ethogram containing 49 behaviours (tactics: Table 1, complete ethogram included in the Supplementary material, Table S1). We started with the ethogram developed by Torres et al. (2018) and added behaviours as additional years were reviewed for this project. While the ethogram contains all observed behaviours, here we focus on the eight foraging tactics: headstand, side-swim (stationary), side-swim (forward), upside-down swim (forward), subsurface swim (forward), subsurface stationary, surface feeding and skim feeding. As several of these tactics tended to co-occur and were mechanically similar, they were grouped for subsequent analysis to reduce the categories and increase sample size, yielding five behavioural tactic groups. Specifically, the forward moving tactics of side, upside-down and subsurface swimming were grouped together as the 'forward swimming tactics' and surface and skim feeding were grouped as the 'surface tactics'. For this analysis, behaviour observations were grouped by sighting, which could include multiple flights.

Morphology

We estimated total length (TL) and body area index (BAI) from snapshots extracted from drone footage using MorphoMetriX (W. Torres & Bierlich, 2020) and CollatriX (Bird & Bierlich, 2020) following photogrammetry methods described in Torres et al. (2022). BAI is a length-normalized measure of body condition that allows for comparison between whales of different sizes (Bierlich, Hewitt, et al., 2021; Burnett et al., 2018). Photogrammetric uncertainty associated with each measurement was incorporated by applying Bayesian methods to generate a posterior predictive distribution for each measurement (Bierlich, Schick, et al., 2021). The mean and standard deviation of each distribution were extracted for input into the model. TL data were filtered to one value per individual per year, as TL would not be expected to change within the 5-month period of each year in this study; if multiple estimates were available within a year, the latest data point was chosen. However, due to increased uncertainty associated with older drone models without a mounted laser altimeter (Bierlich, Schick, et al., 2021), we applied additional quality filtering (see Appendix, Total Length Quality Filtering). If there was no available BAI measurement from the date of the individual behaviour observation, we selected the nearest BAI measurement within a 2-week window (on either side).

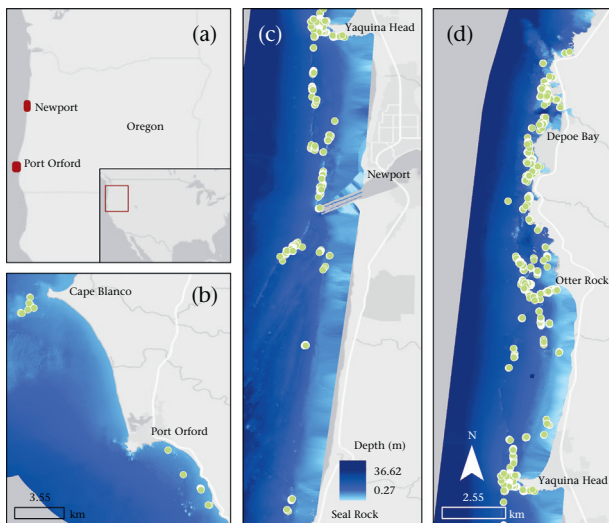


Figure 1. Map showing the bathymetry of the study area and the locations of foraging tactic observations (green points). (a) Locations of Newport and Port Orford, Oregon, U.S.A., with inset showing location of Oregon. (b) Southern region of Newport study area. (c) Northern region of Newport study area. (d) Northern region of Newport study area.

Table 1
Descriptions of behaviours identified in the drone footage

Primary behaviour state	Tactic group	Sub-behaviour tactics	Definition
Foraging	Headstand	Headstand	Whale is positioned head down with fluke up, or if in water depths less than one body length, it may be more horizontal in water column. With both body positions, the whale pushes its head/mouth into substrate
	Side-swim (stationary)	Side-swim (stationary)	Whale swims on its side but does not move forward. Characterized by frequent jaw snapping
	Forward swimming tactics	Side-swim (forward)	Whale swims on its side, moving forward. Characterized by frequent jaw snapping
		Upside-down swim (forward)	Whale swims upside down, moving forward. Characterized by frequent jaw snapping
	Subsurface (stationary)	Subsurface swim (forward)	Whale swims subsurface while feeding. Characterized by frequent jaw snapping
		Subsurface (stationary)	Subsurface (stationary)
Surface tactics	Surface feeding	Whale feeds at the surface, frequently breaking the surface but without breathing. Characterized by frequent turning and frequent jaw snapping/flexing	
	Skim feeding	Whale swims at the surface with mouth open for an extended period. Characterized by moving forward in a straight line	
Social			Whales interact with each other; usually involves some form of tactile interaction
Rest			Logging type behaviour observed where the whale remains in the same location, lying at or just below the surface, and with minimal to no active fluking to promote movement. Surfacing are generally slow and at regular intervals
Travel			Whale shows directed travel in a consistent direction, with regular surfacing intervals

Complete ethogram is available in the Supplementary material (Table S1). The ethogram used in this study was derived from the ethogram presented in Torres et al. (2018).

Bathymetry and Habitat Maps

Bathymetry map

A bathymetry map for the Newport study area was created using water depth measured approximately every 6 s by the onboard Garmin GPSMAP 722xs (259 352 points across ~160 km²) and corrected for tide using mean low low water (MLLW) tide data extracted from the NOAA tides and currents Web site (<https://tidesandcurrents.noaa.gov/stations.html?type=Water+Levels>).

The tide-corrected depth values were then interpolated into a raster. A NOAA coastal bathymetry layer was used to extract depth for the area around Port Orford as it was surveyed less frequently and therefore lacked sufficient coverage to generate a bathymetry map.

To match depth with behaviour data, we overlaid the GPS location of behavioural observations derived from the drone's location onto the bathymetry map and extracted depth values at each point. Points were then grouped by sighting, individual and behaviour, and depth was averaged by group. Then, the tide at that hour was added back to calculate the actual depth at the time the behaviour was performed (see the Appendix for further details).

Benthic habitat map

Benthic substrate data were collected through GoPro camera drops. The GoPro was used to collect brief videos of benthic habitat, by dropping it on a weighted rope to the seafloor and bringing it back up after ~30 s. The footage was then reviewed to classify benthic habitat type as reef, sandy bottom, hard bottom, mixed hard bottom and sandy, boulders, boulder with reef, sand dollars or shelly (example GoPro images of each type are included in the Supplementary material, Fig. S1). Additional benthic habitat data were sourced from a substrate classification layer collected by multibeam in 2010 and provided by C. Goldfinger and C. Romos (Active Tectonics and Seafloor Mapping Lab, Oregon State University).

The final habitat layer was created by integrating the substrate classification layer, GoPro footage and reef identification extracted

from the bathymetry map. The substrate classification layer provided information on the presence of rock and sand habitat but lacked identification of finer resolution reef and boulder habitat. Reef locations in Newport were extracted from the high-resolution bathymetry map developed from our Garmin sounder data; using rugosity and image segmentation methods, reef polygons were identified and then overlaid onto the broad habitat classification map. Boulder locations were extrapolated from the GoPro points by creating 50 m buffers around each point and then adding them to the integrated broad habitat classification and reef map. For the Port Orford behavioural observations ($N = 12$), habitat was identified using the substrate classification layer or through visual identification of habitat from the drone footage (reef or sand). Further details are available in the Appendix (also see Supplementary Fig. S1).

Statistical Analysis

We used a Bayesian multilevel, multinomial logistic regression model (Koster & McElreath, 2017) to explore the relationship between the use of different tactics, individual morphometry and habitat type. This approach allowed us to directly accommodate the structure of the observational data, in which the tactic observed fell into one of multiple categories at any given time (i.e. the observational data had a multinomial distribution), while simultaneously accounting for repeated observations of individuals through an individual level random effect. The variance and correlations of this random effect could be used to explore individual specialization after accounting for the effects of other covariates (Koster & McElreath, 2017). Sighting identity (ID) was also included as a random effect to account for potential observation bias associated with the conditions at each sighting. The multinomial response variable comprised the five foraging tactics, with headstanding set as the reference tactic. We included TL, BAI, depth and habitat type as fixed effects. True BAI and TL values for each individual observation were imputed in the Bayesian analysis from a normal distribution centred on the posterior mean and standard deviation to

incorporate photogrammetric uncertainty. We did not include age as a fixed effect because of the strong relationship between age and TL (Bierlich et al., 2023; Rice & Wolman, 1971). Age estimates based on sighting history are also less accurate. Therefore, TL served as a proxy for age. Sex was only known for a subset of whales and was not included as a covariate in the models, but we evaluated known sexual dimorphism through post hoc assessment of the relationship between sex-specific asymptotic body lengths and tactic probability. All continuous variables were z-score standardized. We considered including year and observation duration (i.e. the time the whale was visible in the drone footage) as random effects to account for differences in environmental conditions across years and for potential bias resulting from prolonged versus short observation time. However, exploratory data analysis indicated no relationship between the number of unique tactics used by an individual and either observation duration or the year of the observation, so these variables were not included in the model (see Appendix, Fig. A4, for additional information). We used weakly informative priors for all model parameters, which are reported in the Appendix (Table A1).

We ran three chains of 30 000 iterations, with the first 10 000 used as warm-up. Model convergence was assessed using effective sample size, \hat{R} values and visual examination of trace plots (McElreath, 2020). The estimated posterior distributions for the regression coefficients represent the effect of the predictors on the probability of tactic occurrence relative to the reference category. However, from a biological perspective it is more informative to interpret these effects using the predicted posterior probabilities of each tactic without orienting on the reference tactic (Koster & McElreath, 2017). Therefore, using the generalized logit link function (Koster & McElreath, 2017), we predicted the probabilities of engaging in each tactic as a function of each fixed effect while holding all others constant. To interpret the effect size of each fixed variable, we calculated differences in predicted probabilities at specific values of that variable and used the distribution of the difference for inference. Analyses were performed in R version 4.1.2 (R Core Team, 2021) using ‘RStan’ (Stan Development Team, 2020) and ‘rethinking’ (McElreath, 2020). All data and code are available at <https://figshare.com/s/8038a48c2b9a77989343>.

RESULTS

Over 7 years, we analysed 287 observations of 78 individual grey whales foraging across 160 sightings (Table 2, Fig. 2). Headstanding was the most frequently observed tactic (56.4%), while the forward swimming tactics accounted for 26.5% of observations, side-swim stationary for 10.1%, subsurface stationary for 4.53% and the surface tactics accounted for 2.44%.

Total Length

The probability of headstanding, side-swim (stationary) and the forward swimming tactics varied with TL, whereas there was no detectable change in the probability of subsurface stationary or

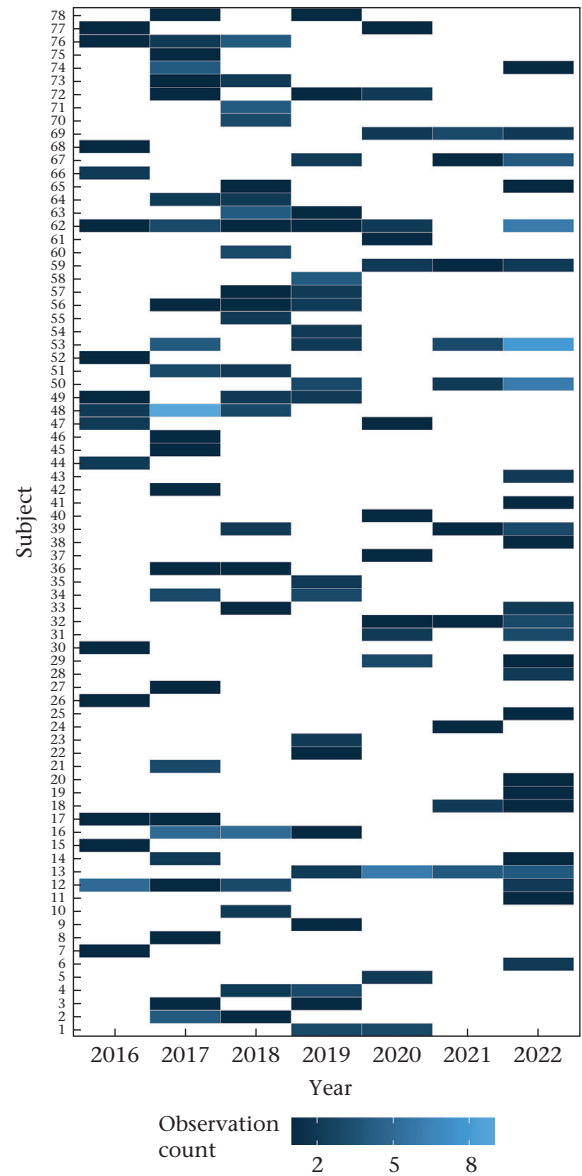


Figure 2. Heat map showing the number of observations per individual per year.

surface tactics (Fig. 3). The probability of headstanding steadily increased from the minimum TL (7.69 m) to the maximum TL (13.83 m) by 0.424 (95% credible interval, CI_{95} : 0.014, 0.763). However, there was no difference between the probabilities of headstanding at either the male asymptotic TL (0.016, CI_{95} : -0.236, 0.224) or the female asymptotic TL (0.001, CI_{95} : -0.227, 0.186), at 11.88 m and 12.11 m, respectively, as determined by Bierlich et al. (2023). The probability of side-swim (stationary) also increased with TL (0.296, CI_{95} : 0.054, 0.675).

Table 2
Number of tactic observations per year

	2016	2017	2018	2019	2020	2021	2022
Headstand	15 (0.625)	26 (0.448)	26 (0.500)	28 (0.667)	15 (0.500)	14 (0.737)	38 (0.613)
Side-swim (stationary)	2 (0.083)	10 (0.172)	9 (0.173)	1 (0.024)	4 (0.133)	0 (0.000)	3 (0.048)
Fwd swim tactics	7 (0.292)	16 (0.276)	13 (0.250)	10 (0.238)	11 (0.367)	4 (0.211)	15 (0.242)
Subsurface stationary	0 (0.000)	6 (0.103)	4 (0.077)	2 (0.048)	0 (0.000)	1 (0.053)	0 (0.000)
Surface tactics	0 (0.000)	0 (0.000)	0 (0.000)	1 (0.024)	0 (0.000)	0 (0.000)	6 (0.097)

Values in parentheses represent the proportion of times that each tactic was observed in each year.

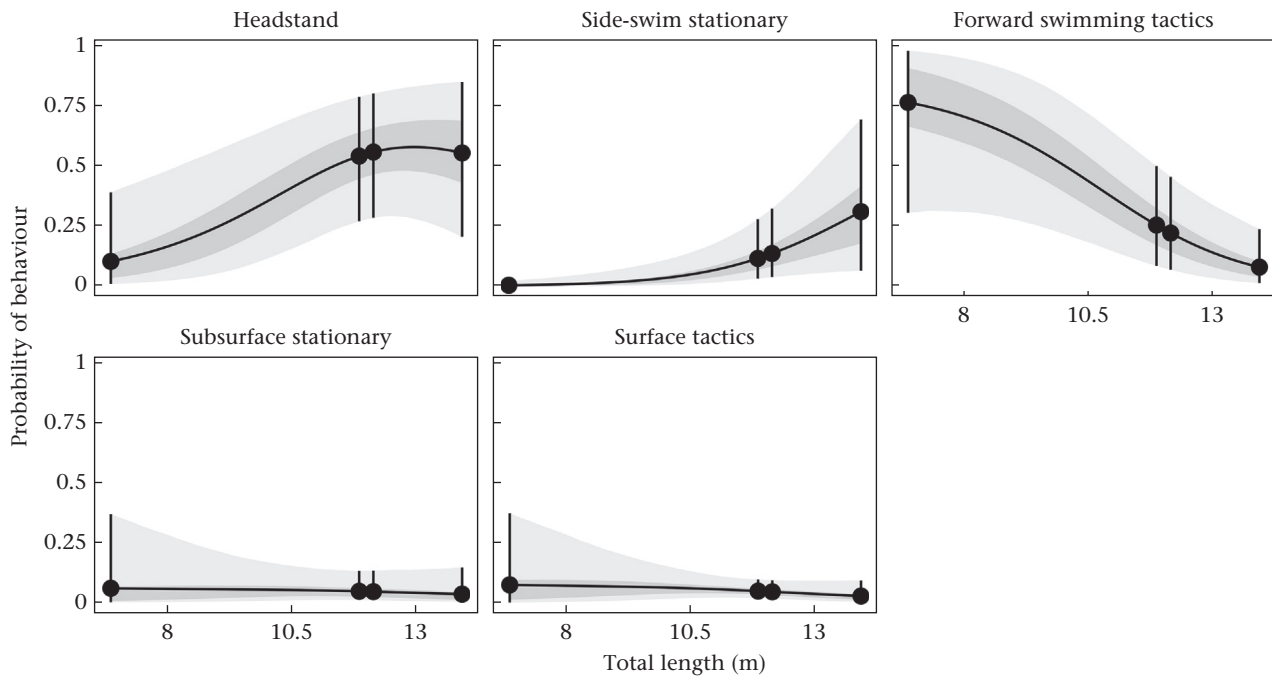


Figure 3. Model predictions of the effect of total length (TL) on the probability of a tactic occurring. In each panel, the line represents the mean probability, the darker shaded region represents 50% credible interval and the lighter shaded region represents 95% credible interval. Points with bars represent the mean probability and 95% credible interval at the minimum (7.69 m), male asymptotic (11.88 m), female asymptotic (12.11 m) and maximum (13.83 m) TLs. The TL asymptotes for male and female PCFG whales were taken from Bierlich et al. (2023).

Conversely, the probability of the forward swimming tactics decreased with TL (-0.653 , CI_{95} : -0.925 , -0.208).

Depth

Depth was related to the probability of all tactics except subsurface stationary (Fig. 4). The probability of headstanding increased by 0.341 (CI_{95} : 0.085, 0.584), from 1.88 m (the minimum depth) to 11.82 m depth, and then decreased by 0.200 (CI_{95} : -0.098 , 0.479), from 11.82 m to 20.10 m (the maximum depth), although the 95% credible interval of the decrease included zero. The probability of side-swim (stationary) decreased with depth (-0.337 , CI_{95} : -0.634 , -0.081), although the 95% credible interval included zero. The probability of the forward swimming tactics also decreased with depth (-0.303 , CI_{95} : -0.058 , -0.609); the maximum probability occurred near the minimum depth at 3.17 m. The probability of the surface tactics increased substantially with depth (0.530, CI_{95} : 0.111, 0.896).

Body Area Index (BAI)

BAI had no clear effect on the probability of any tactic occurring, as the 95% credible intervals of all calculated differences included zero (Fig. 5).

Benthic Habitat Type

Benthic habitat type was associated with the probability of headstanding, side-swim (stationary) and subsurface stationary (Fig. 6). The probability of headstanding was highest in reef habitat (0.705, CI_{95} : 0.595, 0.805) and it was greater than the probability of headstanding in rock habitat (0.272, CI_{95} : 0.083, 0.450). The probability of side-swim (stationary) was highest in rock habitat (0.135, CI_{95} : 0.052, 0.257); this probability was notably higher than the probability of side-swim (stationary) in reef habitat (0.085, CI_{95} :

0.003, 0.202). The probability of subsurface stationary was also highest in rock habitat (0.076, CI_{95} : 0.018, 0.173), with a higher probability than the probability of subsurface stationary in reef habitat (0.059, CI_{95} : 0.006, 0.151).

Individual Level Variance

The variance estimates for the individual level random effects were not consistent across tactics, indicating that some behaviours were used by most individuals (low variance estimates) while other behaviours were used only by a small subset of individuals (high variance estimates). Subsurface stationary had the greatest variance (1.09, CI_{95} : 0.437, 1.793), followed by side-swim stationary (0.58, CI_{95} : 0.068, 1.162) and surface tactics (0.53, CI_{95} : 0.049, 1.317), and forward swimming tactics had the smallest variance (0.35, CI_{95} : 0.021, 0.905). Note that there is no variance estimate for headstanding because it was our reference category. The correlations of the individual level random effects across tactics were negligible, as the 95% credible intervals all included zero (Table 3), indicating that a whale's use of any one foraging tactic was not associated with the probability of using another tactic.

DISCUSSION

Our study investigated the effects of morphology, body condition, water depth and habitat type on individual behaviour specialization in grey whales, which represents a unique study of a free-living cetacean species. We found evidence of an ontogenetic shift in foraging tactic use related to growth in body length; the probability of headstanding increased with body length, while the probability of the forward swimming tactics concurrently decreased, suggesting a switch between the two behaviours as whales age. We also found that water depth, habitat type and individual ID were associated with variable tactic use. Foraging theory posits that differential access to resources can lead to

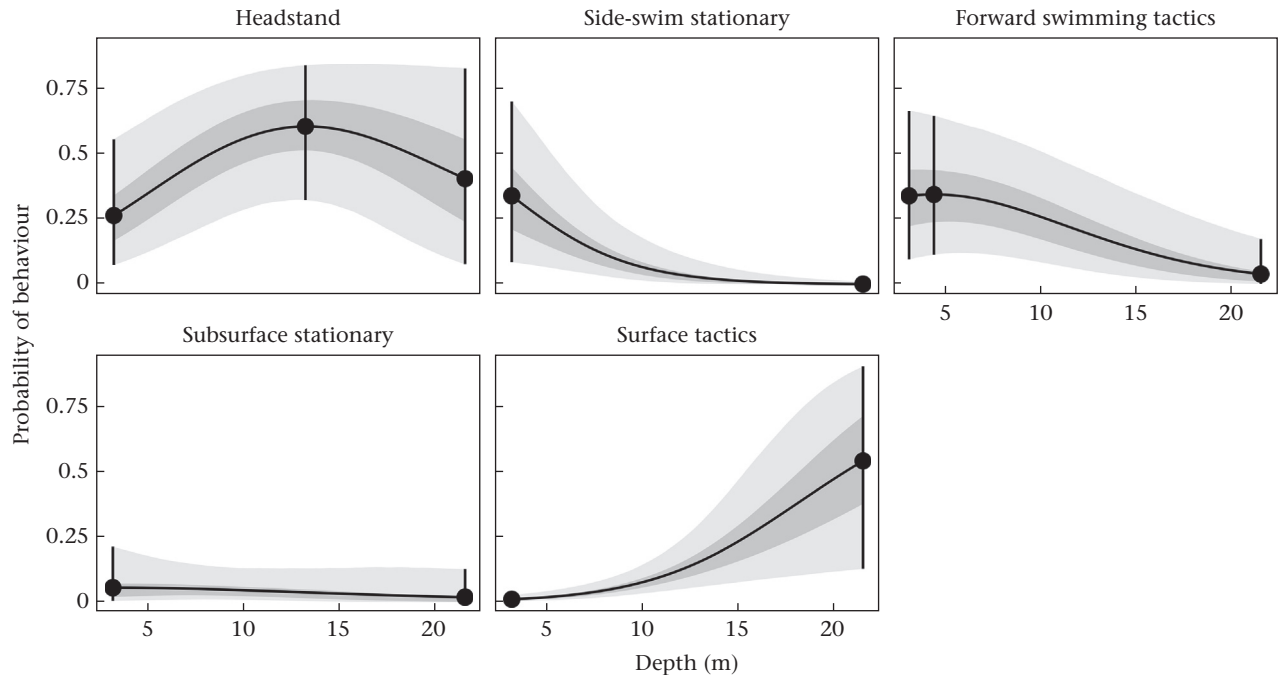


Figure 4. Model predictions of the effect of depth on the probability of a tactic occurring. In each panel, the line represents the mean probability, the darker shaded region represents 50% credible interval and the lighter shaded region represents 95% credible interval. Points with bars represent the mean probability and 95% credible interval at the minimum and maximum depth. The headstanding and forward swimming tactic plots also display a point at the maximum probabilities.

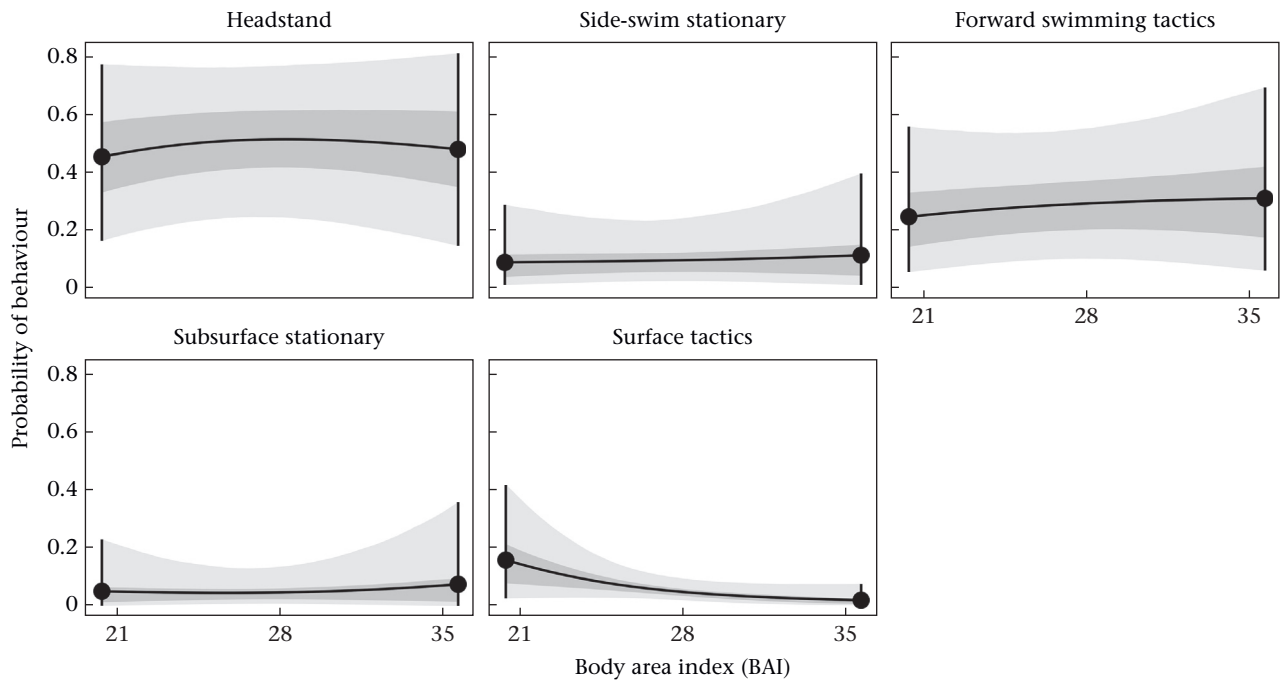


Figure 5. Model predictions of the effect of body area index (BAI) on the probability of a tactic occurring. In each panel, the line represents mean probability, the darker shaded region represents 50% credible interval and the lighter shaded region represents 95% credible interval. Points with bars represent the mean probability and 95% credible interval at the minimum (20.17) and maximum (35.61) BAI.

specializations that facilitate partitioning, thus reducing competition and potentially causing disproportionate foraging success across individuals and demographic classes (Emlen, 1966; Pianka, 1974). Hence, we contend that our results demonstrate how PCFG grey whale morphology and age affect foraging tactic use and subsequently causes differential access to profitable habitat and prey resources, likely structured by age class.

The probability of headstanding increased with both TL and water depth and was highest in reef habitat. Together, these results suggest that headstanding is a tactic that requires learning, either through experience and/or cultural transmission, or physical size or strength to enable access to prey that aggregate on reefs. Furthermore, the increased probability of headstanding with water depths up to 11.82 m may be due to depth limitations for headstanding by

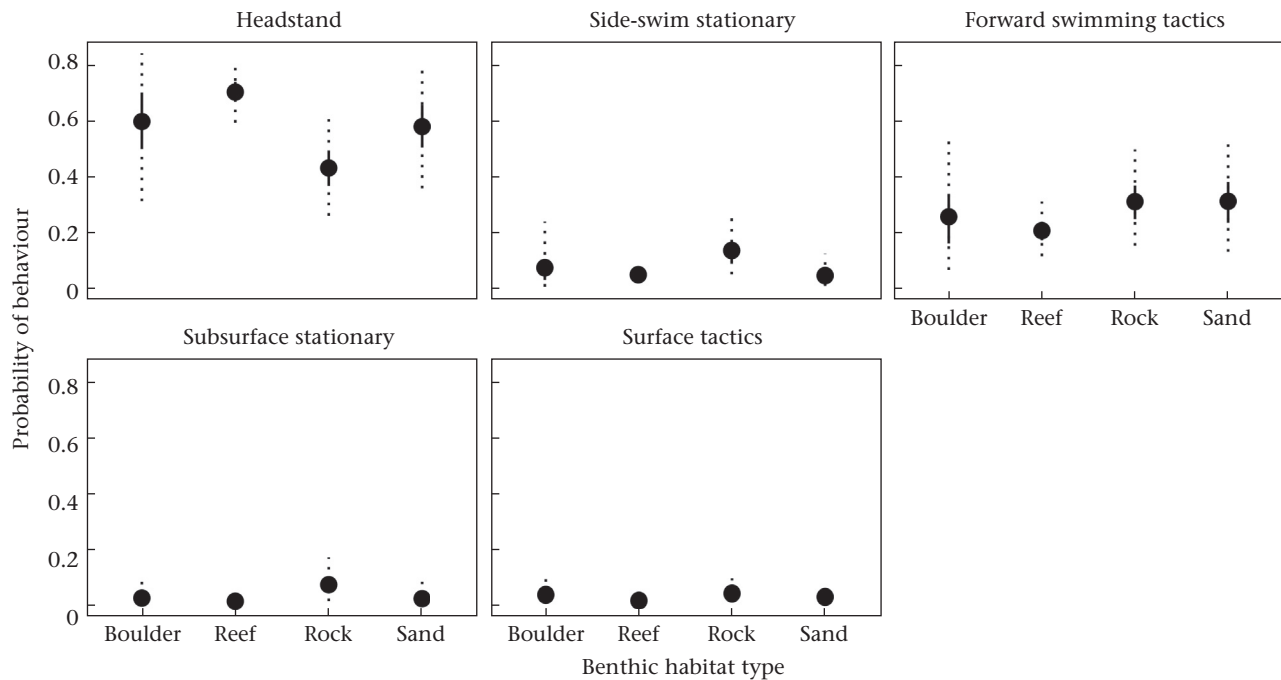


Figure 6. Model predictions of the effect of benthic habitat type on the probability of a tactic occurring. In each panel, the points represent the mean probability, the solid lines represent the 50% credible intervals and the dashed lines represent 95% credible intervals. Note that the Y-axis scale varies by tactic; a fixed-scale version is available in the Appendix (Fig. A3).

Table 3
Correlations of individual level random effects (other than the reference category)

	(1)	(2)	(3)	(4)
(1) Side-swim stationary		0.060 (−0.560, 0.660)	−0.114 (−0.632, 0.421)	−0.038 (−0.632, 0.603)
(2) Forward swimming tactics			−0.145 (−0.657, 0.417)	0.064 (−0.588, 0.675)
(3) Subsurface stationary				−0.061 (−0.649, 0.534)
(4) Surface tactics				

Values are the mean of the posterior samples with the 95% credible interval in parentheses.

larger whales (i.e. an 11.5 m whale cannot physically headstand in 5 m of water). Comparably, the probability of side-swim (stationary) increased with TL, but decreased with depth, and was highest in rock habitat, suggesting that this tactic is used by longer, older whales to access prey in shallow, rocky habitat. Both headstanding and side-swim (stationary) involve the whale maintaining position in the water without moving forward, potentially indicating that it is the ability to maintain position that develops with age. Conversely, the probability of the forward swimming tactics decreased with both TL and depth and had no notable relationship with habitat type. These relationships suggest that the forward swimming tactics are performed by smaller, younger whales in shallow water, over a variety of benthic habitat types. This result suggests that these are the only tactics young whales are capable of or that these tactics become unprofitable when whales grow beyond a certain body length. The forward swimming tactics had the lowest individual level variance, suggesting that these behaviours were relatively common. Subsurface stationary was one of the rarer tactics and only had a notable relationship with benthic habitat type, with the highest probability in rock habitat. It appears to be a specialized tactic as it had the highest individual level variance. The probability of the surface tactics, the other rare tactic, only increased with depth, suggesting that this tactic is used to target a prey type that aggregates in deep water.

As an individual grows it gains physical maturity and experience, with both mechanisms potentially driving an ontogenetic

shift. As the overall habitat of the study area was relatively shallow for a baleen whale (<20 m), this shift is unlikely to depend on an individual's improved deep-diving ability with age, as is common in other marine mammals (Jeglinski et al., 2013). A similar trend was found in Western North Pacific (WNP) grey whales foraging near Sakhalin Island (Bröker et al., 2020), where younger whales foraged in the shallow (<20 m), nearshore habitat before ultimately switching to deeper offshore habitat (~35–60 m). Comparably, juvenile humpback whales, *Megaptera novaeangliae*, in the New York Bight forage in shallower habitat than adults, putting them at higher risk of vessel strikes (Stepanuk et al., 2021). In contrast, the trend here is likely related to improved manoeuvrability and locomotion as whales age, allowing them to access different habitat and prey aggregations more effectively. Similar patterns have been documented in largemouth bass, *Micropterus salmoides*, where ontogenetic shifts in diet were associated with improved locomotive ability (Zhao et al., 2014). Headstanding involves an individual holding its large body in place with its head down and tail up and typically includes sculling of the pectoral fins and beating of the fluke to maintain position. These manoeuvres are highly different from the typical grey whale swimming motion; therefore, headstanding may be a physically challenging tactic that requires a higher level of manoeuvrability, dexterity and strength than smaller individuals are capable of. Additionally, experiential and social learning may play a role in the ability to use this dextrous tactic and therefore the ontogenetic shift may reflect the time

required for learning. Experience and social learning, both vertical and horizontal, affect specializations in sea otters, *Enhydra lutris* (Tinker et al., 2009), and bottlenose dolphins, *Tursiops truncatus* (Mann & Sargeant, 2003). While this shift to headstanding appears to be most closely related to growth and ageing, the documented sexual dimorphism in body size of PCFG grey whales (Bierlich et al., 2023; Rice & Wolman, 1971), where females reach a longer asymptotic length than males, could mean that females are able to switch to the headstanding tactic at a younger age than males.

Interestingly, BAI was not associated with the probability of any tactic occurring, which was unexpected, as increased buoyancy with better body condition can make it more challenging for cetaceans to dive in shallow water (Aoki et al., 2021; Rosen et al., 2007). Additionally, energy reserves can affect foraging behaviour; for example, fasted sheep, *Ovis aries*, use different grazing behaviours and consume different diets compared to nonfasted sheep (Newman et al., 1994). Therefore, the lack of a relationship suggests that these whales either do not encounter buoyancy challenges or have the capacity to overcome them, and that their level of energy reserves does not affect tactic use, at least not at the scale of this study. Grey whales may vary foraging frequency or intake rate in response to energy reserves, as opposed to tactic use (Junnian et al., 2007).

We found variable relationships between water depth and four of the five foraging tactics. As side-swimming and the forward swimming tactics occur mid-water column, this relationship is likely not driven by the physical ability to perform the tactic at that depth, but rather the depths at which the target prey of these tactics are available (Kaltenberg & Benoit-Bird, 2013). Importantly, however, this relationship could also mean that our ability to detect behaviours from the drone decreased when a whale was feeding in deeper water due to water clarity and visibility limitations. Although surface tactics occur at the water surface, they are only observed in deep water areas. In all our observations of surface tactics, the whales were feeding on large aggregations of porcelain crab larvae that may require these deep water habitats to form (Hameed et al., 2016). The relationship between water depth and headstanding echoed the relationship between TL and headstanding up until a depth of 11.82 m, when the probability decreased. The increase in probability with depth likely reflects that headstanding requires the whale to be vertical in the water column, making this manoeuvre challenging to perform in shallow water. Interestingly, the peak in probability of headstanding was close to the male asymptotic length (11.88 m; Bierlich et al., 2023), so there may be some benefit to feeding in water not much deeper than one body length. The decline in probability after 11.82 m was minor, and the credible interval crossed zero, but could suggest that headstanding does not occur in deeper water or that our ability to detect behaviours occurring at deeper depths decreased due to reduced visibility.

The relationships between benthic habitat type and each tactic's probability likely reflects associations between tactics and prey types found in different habitats, more than whale manoeuvrability. Furthermore, several of the tactics occur mid-water column and therefore are unlikely to be related to a specialization necessary for the type of benthic substrate. The highest probability of headstanding occurred in reef habitat, suggesting that the whales use this tactic to feed on mysids, which are often found in reef habitat in high densities (Dunham & Duffus, 2002; Hildebrand et al., 2022; Murison et al., 1984). Headstanding also occurred with higher probability in sand habitat than in boulder or rock habitat, indicating that headstanding can also be used for benthic feeding on benthic amphipods that burrow in this substrate (Burnham & Duffus, 2016). The associations of side-swim stationary and sub-surface stationary with rock habitat are also probably linked to prey

availability, but knowledge regarding the distribution and ecology of these nearshore prey items is limited.

In optimal foraging theory, prey are identified as discrete items that a forager captures and consumes, and prey types are characterized by their energetic value and handling time (Emlen, 1966; MacArthur & Pianka, 1966; Stephens & Krebs, 1986). Prey types are often thought of as prey species; however, for a large whale feeding on relatively small prey, different aggregation types of the same species within distinct habitats that influence accessibility could be considered separate 'prey types', given the different energetic cost–benefit trade-offs. Foraging tactics also have different energetic costs and benefits, due to their associated locomotion costs, target prey types or prey capture abilities (Norberg, 1977). Mysids represent a calorically rich prey source for PCFG grey whales (Hildebrand et al., 2021) and often swarm in dense epibenthic aggregations near reefs (Hildebrand et al., 2022; Kaltenberg & Benoit-Bird, 2013). We hypothesize that these dense reef-associated aggregations of prey have a different energetic value and cost to a whale than a diffuse aggregation of mysids spread through the water column. Thus, once the headstanding foraging tactic is learned or mastered as a whale ages and grows, it could provide increased accessibility to dense prey patches with increased capture efficiency. Alternatively, as PCFG grey whales grow they may lose the ability to manoeuvre effectively through reef systems using forward swimming tactics, so they are forced to utilize another foraging tactic (i.e. headstanding). A comparison of the energetics of different tactics and target prey items is needed to fully understand the consequences of these specializations.

We document variance in the individual level random effects, indicating that some behaviours are consistently used by more individuals than other behaviours (Koster & McElreath, 2017). While we have shown evidence of an ontogenetic shift, there are factors unaccounted for in our analysis that may be driving additional specialization, such as skull or fluke size (Bierlich et al., 2023) or learning (Tinker et al., 2009). Animal personality, or 'behavioural syndromes', may also be related to variation in preferred foraging strategies, although that is challenging to quantify in wild studies (Dall et al., 2012; Sih et al., 2004). This result could also be partly affected by the limitations associated with our sampling methods. Drones are limited by their battery life and the ability of the pilot to track the whale underwater; therefore, our behaviour observation times were short (<20 min) and limited by water clarity. While there was no relationship between observation time and the unique number of tactics observed per individual, residual individual variation may be a function of the short observation window. Furthermore, there may be tactics, including the traditional benthic dig (Nerini, 1984), that were not documented from drone footage due to water depth and clarity and the position of the whale's body. Lastly, we did not have a high number of replicates for every individual, meaning that a larger sample size would be necessary to better ascertain the degree of residual individual niche specialization in this study group (Bolnick et al., 2003; Dall et al., 2012).

Our documented ontogenetic shift in the use of foraging tactics by PCFG grey whales has important implications for understanding their ecology. For example, there may be differences in space use or prey consumption patterns associated with age class. Additionally, the effect of TL on behaviour is particularly relevant in the context of the recent finding by Bierlich et al. (2023) that PCFG grey whales are significantly smaller than ENP grey whales. Our finding that the probability of headstanding peaks at 11.82 m depth builds upon Bierlich et al.'s hypothesis that the PCFG foraging range provides an ecological opportunity, whereby behaviourally and morphologically adapted whales (i.e. shorter, with smaller skulls and flukes) are able to forage effectively. These findings also suggest that age classes could be differentially affected by environmental variability

or anthropogenic disturbance in this system. For example, the PCFG range has experienced environmental variability in recent years, with documented impacts on body condition (Torres et al., 2022). Given our results, it is possible that these impacts were differentially distributed across age classes (Bolnick et al., 2003). It is unknown whether this interannual variation in PCFG whale body condition is distributed differently across age classes, tactic use and space use, warranting further investigation. Furthermore, the relationships between this behavioural ontogenetic shift and space use should be examined to better inform spatial management efforts aimed at protecting critical foraging habitat and reducing overlap between grey whales and anthropogenic threats.

In conclusion, we document an ontogenetic shift in foraging tactic use in a baleen whale, demonstrating how a long-term drone data set can be successfully applied to study specialization in a previously hard to study species. These results also highlight the importance of assessing specialization within a generalist population. Grey whales have long been considered individual generalists within a generalist population, yet the specialization we documented may influence the future grey whale research and management, as well as highlight the potential presence of specialization in other baleen whale populations. The effects of size, age and habitat on behaviour are not only interesting in the context of culture (Cantor & Whitehead, 2013) but also because they can affect population dynamics, a population's role within its community (Araújo et al., 2008) and exposure and resilience to disturbance (Pirota et al., 2019). Within the context of foraging theory, we propose that length, manoeuvrability and learning associated with age affect the profitability of foraging tactics due to changing accessibility to prey, leading to behavioural variability and specialization in a population.

Data Availability

Data and code available from FigShare: <https://figshare.com/s/8038a48c2b9a77989343>.

Author Contributions

Clara N. Bird: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Enrico Pirota:** Formal analysis, Methodology, Supervision, Writing – review & editing. **Leslie New:** Formal analysis, Funding acquisition, Methodology, Supervision, Writing – review & editing. **K.C. Bierlich:** Data curation, Investigation, Writing – review & editing. **Marc Donnelly:** Data curation, Methodology, Writing – review & editing. **Lisa Hildebrand:** Data curation, Investigation, Writing – review & editing. **Alejandro Fernandez Ajó:** Investigation, Writing – review & editing. **Leigh G. Torres:** Conceptualization, Data curation, Funding acquisition, Investigation, Project administration, Resources, Supervision, Writing – review & editing.

Declaration of Interest

The authors declare no conflict of interest.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <https://doi.org/10.1016/j.anbehav.2024.06.004>.

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Appendix

Total Length Quality Filtering

Some of the older drone models (DJI Phantom 3 Pro, Phantom 4 Pro) had greater measurement uncertainty compared to the newer drone models (DJI Inspire 2) (see [Supplementary Table S2](#)). If an individual whale's total length (TL) was greater than the value of a subsequent year (suggesting the whale had shrunk in size), we assumed the value to be an overestimation due to this greater photogrammetric error and instead replaced the value with the most temporally proximate value with the lowest standard deviation of its posterior distribution for TL. Similarly, if a TL value was more than 1 m larger than a value from the previous year and the individual had not been a calf, we assumed it to be an overestimation and replaced the value with the most temporally proximate value with the lowest standard deviation of its posterior distribution for TL.

Potential Impacts of Total Length Time Point Selection

To check that selecting the last TL measurement in a season per individual did not bias the results, we ran the model using the TL per year with the lowest uncertainty and found no significant difference in the posterior distributions of the coefficients when compared to the results reported in the main manuscript (mean difference = 0.03, CI_{95%}: –1.67, 1.75).

Bathymetry and Habitat Maps

Bathymetry map

We created a fine-scale bathymetry map using point measures of depth extracted from the onboard Garmin GPSMAP 722xs track line data ([Fig. A1](#)). Data from May to October 2016–2021 were used to create the bathymetry layer. Points were first corrected for tide using tide data downloaded from NOAA Tides and Currents. Tide data was downloaded in the mean low low water (MLLW) datum at 1 h intervals. The tide at the corresponding date and hour was then subtracted from the recorded depth at each point. The points were then loaded into ArcGIS PRO version 2.9.2. The points were interpolated using the Empirical Bayesian Kriging tool to a cell size of 0.0001 (<10 m²). Kriging interpolation was used because it has been found to be a reliable method for interpolating single point bathymetric data into a layer ([Parente & Vallario, 2019](#)).

Benthic habitat map

We created a fine-scale benthic substrate map using a combination of classifications from GoPro footage, image segmentation of the bathymetry layer and a substrate classification layer collected by multibeam in 2010 and provided by C. Goldfinger and C. Romsos,

Active Tectonics and Seafloor Mapping Lab, Oregon State University (see Fig. A2).

The Goldfinger layer was first manually clipped to our study region. Reefs were extracted using image segmentation. First, Focal Statistics was run on the bathymetry layer to calculate the mean value across three window sizes (5 × 5, 10 × 10, 25 × 25). Next, each of these layers was subtracted from the original bathymetry layer using Raster Calculator. Then, a Natural Jenks Break classification with two classes was applied to all three subtracted layers and the ‘Con’ tool was used to pull out the class that represented the reefs. Lastly, the filtered rasters were converted to polygons, aggregated using a 30 m radius, and dissolved to create the reef polygon layer. The reef layer was added to the Goldfinger layer using the ‘Update’ tool (see Fig. A3).

Boulder habitat was identified using GoPro footage. The benthic substrate of each GoPro drop was classified as either reef, sandy bottom or boulder with reef (see Supplementary Fig. S1). To

create the boulder layer, we selected points classified as boulder habitat, then created a buffer with a 50 m radius around each point. The buffers were then aggregated using a 50 m radius. Overlapping polygons were then merged and dissolved. The boulder layer was then added to the habitat layer using the ‘Update’ tool.

Relationship between Depth and Benthic Habitat Type

An ANOVA found no significant difference in depth between the habitat types ($F_{3,283} = 1.73, P = 0.162$; Fig. A5).

Table A1
Posterior distributions of all coefficients

Name	Coefficient	Prior	Mean	SD
Intercept	a[1]	Normal(0,1)	2.327	0.571
Intercept	a[2]	Normal(0,1)	0.536	0.577
Intercept	a[3]	Normal(0,1)	1.705	0.558
Intercept	a[4]	Normal(0,1)	-0.217	0.636
Depth	bD[1]	Normal(0,1)	-0.580	0.231
Depth	bD[2]	Normal(0,1)	-1.610	0.360
Depth	bD[3]	Normal(0,1)	-1.031	0.273
Depth	bD[4]	Normal(0,1)	-0.926	0.387
Body area index (BAI)	bB[1]	Normal(0,1)	0.388	0.290
BAI	bB[2]	Normal(0,1)	0.410	0.337
BAI	bB[3]	Normal(0,1)	0.415	0.309
BAI	bB[4]	Normal(0,1)	0.416	0.397
Total length (TL)	bT[1]	Normal(0,1)	0.415	0.341
TL	bT[2]	Normal(0,1)	0.949	0.412
TL	bT[3]	Normal(0,1)	-0.338	0.371
TL	bT[4]	Normal(0,1)	0.087	0.459
Julian day	bJD[1]	Normal(0,1)	0.055	0.285
Julian day	bJD[2]	Normal(0,1)	0.513	0.359
Julian day	bJD[3]	Normal(0,1)	0.001	0.310
Julian day	bJD[4]	Normal(0,1)	0.834	0.516
Habitat - Reef	bHR[1]	Normal(0,1)	1.275	0.579
Habitat - Reef	bHR[2]	Normal(0,1)	0.363	0.617
Habitat - Reef	bHR[3]	Normal(0,1)	0.645	0.577
Habitat - Reef	bHR[4]	Normal(0,1)	-0.053	0.686
Habitat - Sand	bHS[1]	Normal(0,1)	0.649	0.660
Habitat - Sand	bHS[2]	Normal(0,1)	-0.240	0.712
Habitat - Sand	bHS[3]	Normal(0,1)	0.608	0.676
Habitat - Sand	bHS[4]	Normal(0,1)	-0.220	0.760
Habitat - Rock	bHK[1]	Normal(0,1)	0.016	0.634
Habitat - Rock	bHK[2]	Normal(0,1)	0.586	0.644
Habitat - Rock	bHK[3]	Normal(0,1)	0.286	0.637
Habitat - Rock	bHK[4]	Normal(0,1)	0.691	0.672
Habitat - Boulder	bHB[1]	Normal(0,1)	0.497	0.708
Habitat - Boulder	bHB[2]	Normal(0,1)	-0.083	0.818
Habitat - Boulder	bHB[3]	Normal(0,1)	0.171	0.739
Habitat - Boulder	bHB[4]	Normal(0,1)	-0.459	0.896
Individual level random effect	sigma_id[1]	Exponential(1)	0.580	0.336
Individual level random effect	sigma_id[2]	Exponential(1)	0.349	0.282
Individual level random effect	sigma_id[3]	Exponential(1)	1.091	0.413
Individual level random effect	sigma_id[4]	Exponential(1)	0.529	0.405
Sighting random effect	sigma_dtst[1]	Exponential(1)	0.268	0.201
Sighting random effect	sigma_dtst[2]	Exponential(1)	0.262	0.224
Sighting random effect	sigma_dtst[3]	Exponential(1)	0.256	0.192
Sighting random effect	sigma_dtst[4]	Exponential(1)	0.462	0.378

There is one coefficient per variable per behaviour. Behaviour (1) is side-swim stationary, (2) is forward swimming tactic, (3) is subsurface stationary and (4) is surface-feeding tactic.

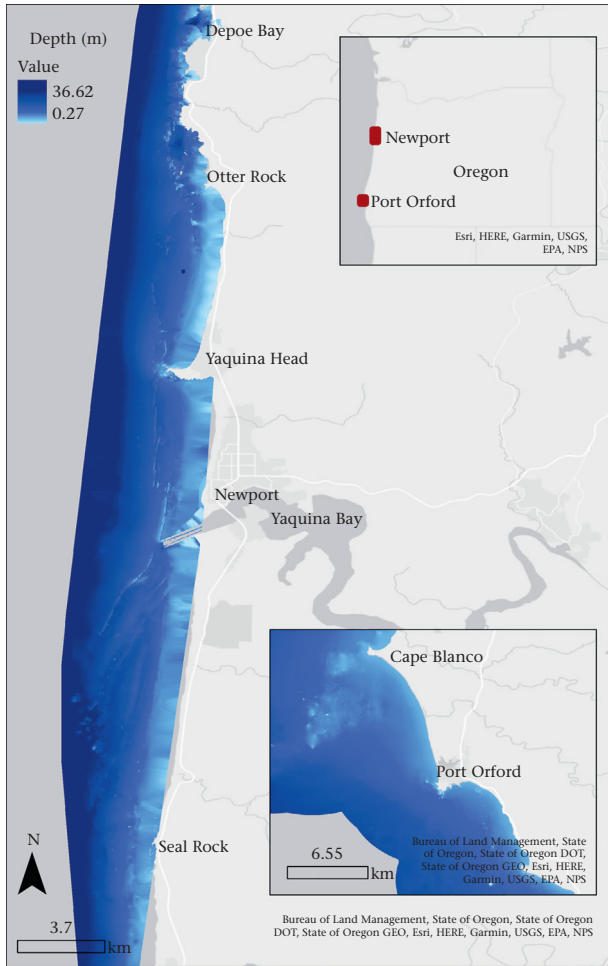


Figure A1. Bathymetry map for Newport and Port Orford, Oregon, U.S.A. study regions. Darker colours indicate deeper water. The Newport map was developed for this study. Bottom right inset map shows bathymetry for Port Orford sourced from NOAA. Upper right inset map displays the locations of Newport and Port Orford.

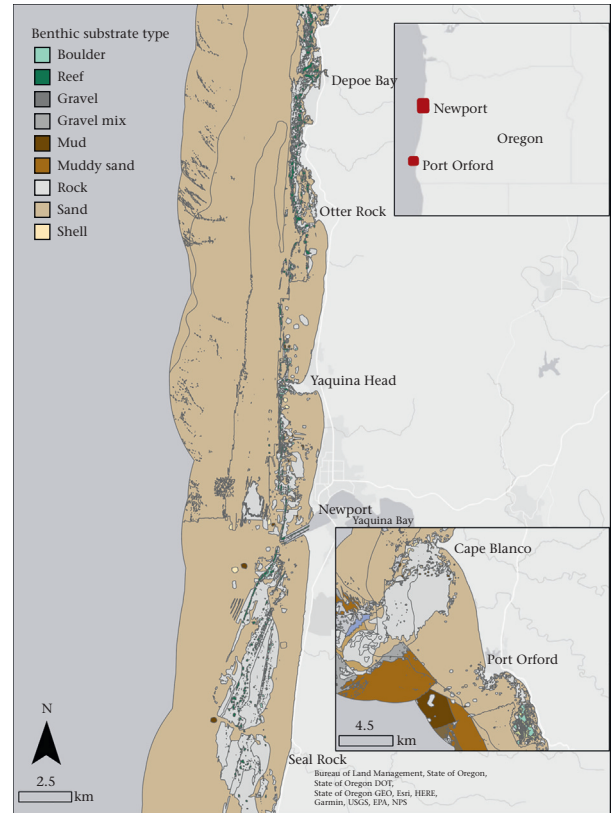


Figure A2. Bathymetry map for Newport and Port Orford, Oregon, U.S.A. study regions. Polygons are coloured by benthic substrate type. The Newport map was developed for this study. Bottom right inset map shows habitat for Port Orford from the Goldfinger map. Upper right inset map displays the locations of Newport and Port Orford.

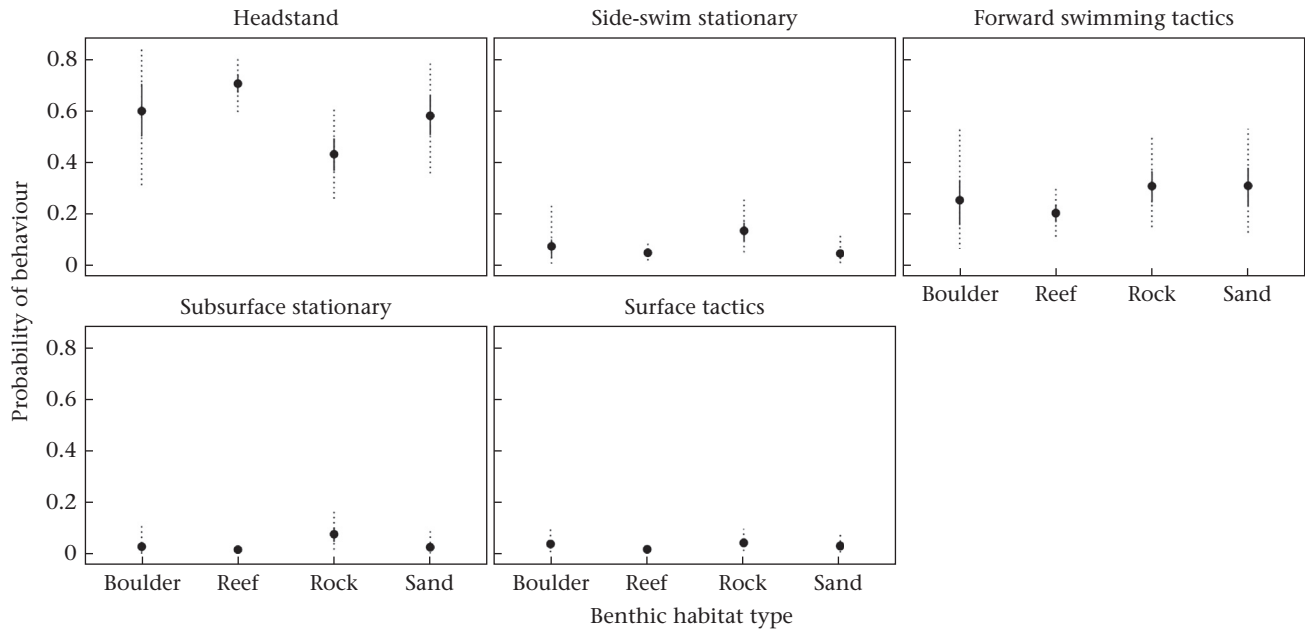


Figure A3. Model predictions of the effect of benthic habitat type on the probability of a tactic occurring. In each panel, points represent the mean probability, solid lines represent the 50% credible intervals and dashed lines represent 95% credible intervals.

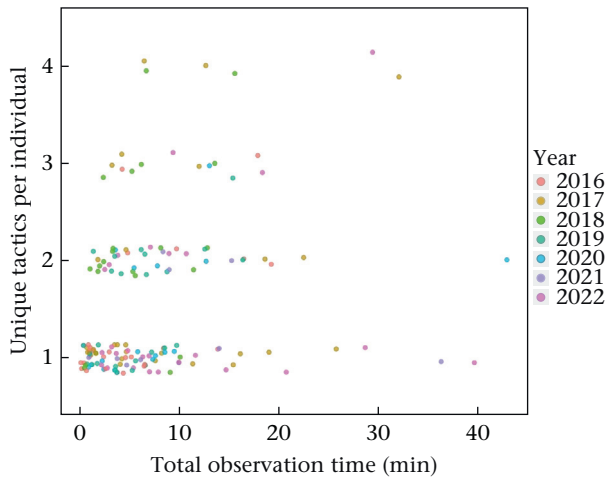


Figure A4. Relationship between total observation time and number of unique tactics performed by each individual during each year.

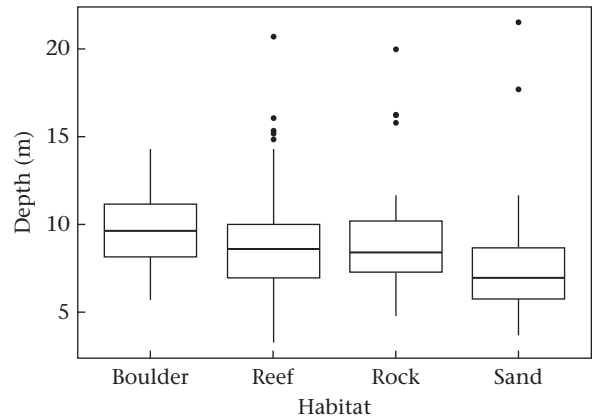


Figure A5. Relationship between benthic habitat type and depth (m).