



Trade-offs in prey quantity and quality in gray whale foraging

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ABSTRACT: To forage optimally, predators face complex decisions regarding target prey distribution, quantity, and quality. We paired theodolite tracking of gray whales *Eschrichtius robustus* in Port Orford, Oregon, USA, with concurrent sampling of their zooplankton prey to examine foraging decisions relative to prey quantity (abundance) and quality (caloric content). We tested the hypotheses that whales (1) feed more than search or transit in areas with high quantity and quality prey and (2) select foraging habitat dominated by the calorically rich mysid *Neomysis rayii*. Relative prey abundance was assessed through standardized image analysis of camera drops, and zooplankton prey community was determined from net tows. These data were spatially interpolated and modeled to generate daily layers of species-specific prey abundance and calories (20 m grid) for comparison to whale behavior derived from tracking data. Whales fed significantly more in areas with higher prey abundance and calories than where they searched and transited. Whales increased foraging effort as overall prey availability increased, yet foraging probability was significantly correlated with the quantity and quality of the mysid *Holmesimysis sculpta*, which has significantly lower calories than *N. rayii*. However, during the study period, the maximum abundance of *N. rayii* was 4 times lower than that of *H. sculpta* and never reached the quantity threshold determined by a logistic regression needed to support whale foraging behavior. Hence, gray whale prey selection involves trade-offs between prey quantity and quality to maximize energetic gain, and prey quality should be considered alongside abundance in ecological studies investigating predator decision-making.

KEY WORDS: Energetic trade-off · Optimal foraging · Prey quality · Foraging ecology · Gray whale · *Eschrichtius robustus* · Marine mammal · Zooplankton · Theodolite tracking

1. INTRODUCTION

Obtaining enough food is crucial for predators to ensure adequate energy gain for maintenance of vital functions and support for energetically costly life history events. Foraging involves decisions at every step of the process, including prey selection, capture, and consumption, all of which should be as efficient as possible. Optimal foraging theory (OFT)

predicts that predators should pursue prey that will provide maximum returns for minimal energetic input (MacArthur & Pianka 1966). Yet concentrated foraging in one area will eventually result in diminishing returns, requiring a predator to decide when to abandon a prey patch. The marginal value theorem (MVT) posits that a predator should leave its current prey patch when the gain from the patch falls below the average capture rate of the surrounding

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habitat (Charnov 1976). Poor foraging decisions regarding OFT and MVT can have long-term repercussions on reproductive success and population dynamics (Harris et al. 2007, 2008, Grémillet et al. 2008), and for marine predators that rely on prey that is spatially and temporally dynamic and notoriously patchy (Hyrenbach et al. 2000), these decisions can be especially challenging.

Prey abundance and density are frequently used as predictors of marine predator distribution, movement, and foraging effort, with predators often selecting highly abundant or dense prey patches (e.g. Goldbogen et al. 2011, Cohen et al. 2014, Armstrong et al. 2016, Torres et al. 2020). However, there is increased recognition that prey quality is also an important factor to consider when assessing a predator's ecology and habitat use (Spitz et al. 2012), and marine predators do show a preference for higher quality prey items (e.g. Haug et al. 2002, Meynier et al. 2008, Spitz et al. 2010, Cade et al. 2022). Moreover, negative impacts of low quality prey on the health and breeding success of top marine predators (Österblom et al. 2008, Ludynia et al. 2010), including marine mammals (Rosen & Trites 2000, Trites & Donnelly 2003), have been documented. Most studies regarding prey choice by marine mammals occur at broad spatio-temporal scales and/or the population level, creating a knowledge gap concerning individual predator choice between prey quality and quantity at finer scales. For instance, analysis of whale blubber indicates prey preferences over broad scales (Fleming et al. 2016, Groß et al. 2020) or relative to background prey availability (Nickels et al. 2018), but efforts to link individual whale movements with real-time prey species choice and quality are rare.

Concurrent predator and prey sampling at appropriate spatial scales is logistically challenging for studies on marine mammals, as they forage in highly dynamic ecosystems (Torres et al. 2008). Oceanographic predictors are commonly used as proxies for prey availability in marine mammal foraging ecology studies at meso (5–100 km; e.g. Citta et al. 2018, Barlow et al. 2020) or large (100–500 km; e.g. Moore et al. 2002, Palacios et al. 2019) scales, yet this method may falter at finer scales where prey patchiness exceeds detectable variability in oceanographic features. Although relatively little is definitively known about the scales at which whales perceive and react to prey (Torres 2017), studies that concurrently relate whale behavior and movement to *in situ* measurements of prey availability (e.g. hydroacoustics, net sampling) at the fine (100 m–5 km) or micro (0–100 m) scales are more likely to elucidate foraging

choices relative to prey quantity (e.g. Feyrer & Duffus 2015) and quality (e.g. Owen et al. 2015).

The Pacific Coast Feeding Group (PCFG) of gray whales are a sub-group of the larger Eastern North Pacific (ENP) population of gray whales that migrate from breeding grounds in Baja California, Mexico, to the Arctic where they feed (Rice & Wolman 1971). The PCFG diverges from this migration pattern by primarily foraging in coastal habitats from northern California, USA, to northern British Columbia, Canada (IWC 2011). PCFG whales are generalist feeders, with reported prey including benthic amphipods, mysids, cumaceans, crab larvae, ghost shrimp, and herring roe (Darling et al. 1998, Dunham & Duffus 2001, 2002). This breadth in diet adds complexity to the decision-making of foraging PCFG gray whales, as several of these prey species have significantly different caloric values (Hildebrand et al. 2021). Ideally, the prey species with the highest caloric value would also be the most ubiquitous and least energetically expensive prey item to capture and consume, such that predators like gray whales truly could expend very little energy to secure high energetic rewards (OFT; MacArthur & Pianka 1966). However, foraging opportunities and decisions are rarely this straightforward. PCFG whales must make frequent decisions amidst fluctuating prey availability, quantity, and quality to ensure they acquire the energy reserves needed for migration, reproduction, and the winter fast (Villegas-Amtmann et al. 2015).

In this study, we paired movement and behavior data of PCFG gray whales tracked by theodolite with concurrent zooplankton prey quantity and quality data collected from a research kayak. Our objective was to determine whether PCFG gray whale foraging decisions are driven by prey quantity (abundance) or quality (caloric content) at a scale of 20 m (<2 adult gray whale body lengths). To our knowledge, individual baleen whale foraging decisions relative to available prey quality and quantity have not been addressed previously at this micro scale. We address fundamental hypotheses regarding OFT including (1) gray whale foraging behavior will be higher in areas of high relative prey quantity and quality compared to areas used for search and transit behavior states, and (2) individual whales will select areas where the prey community is dominated by the mysid *Neomysis rayii*, which is significantly higher in caloric content (Hildebrand et al. 2021), rather than areas dominated by other zooplankton species. Foraging behavior and habitat use are often assessed through prey quantity metrics, which may not reveal the entire ecological picture (Österblom et al. 2008).

Evaluating multiple prey metrics, including prey quality, when investigating a predator's foraging ecology is therefore valuable and necessary.

2. MATERIALS AND METHODS

2.1. Fieldwork

We simultaneously monitored gray whale behaviors and their zooplankton prey during the month of August for 3 consecutive years (2018–2020) in Port Orford, Oregon, USA (Fig. 1). Fieldwork was conducted

by 2 teams of 2 individuals each: one team collected whale identification and movement data while the other team was responsible for conducting zooplankton sampling. All field sampling was conducted during daylight hours (barring fog), beginning in the morning (~06:30 h) and continuing until ocean conditions compromised accurate data collection (Beaufort sea state >3) or the whale observation team had surveyed for 8 h, whichever came first. If conditions were unfavorable (e.g. wind speed >10 knots and swell >3 ft [~1 m]), then field sampling was not conducted. The whale tracking team recorded whale locations using a theodolite (Sokkia DT210) and the tracking

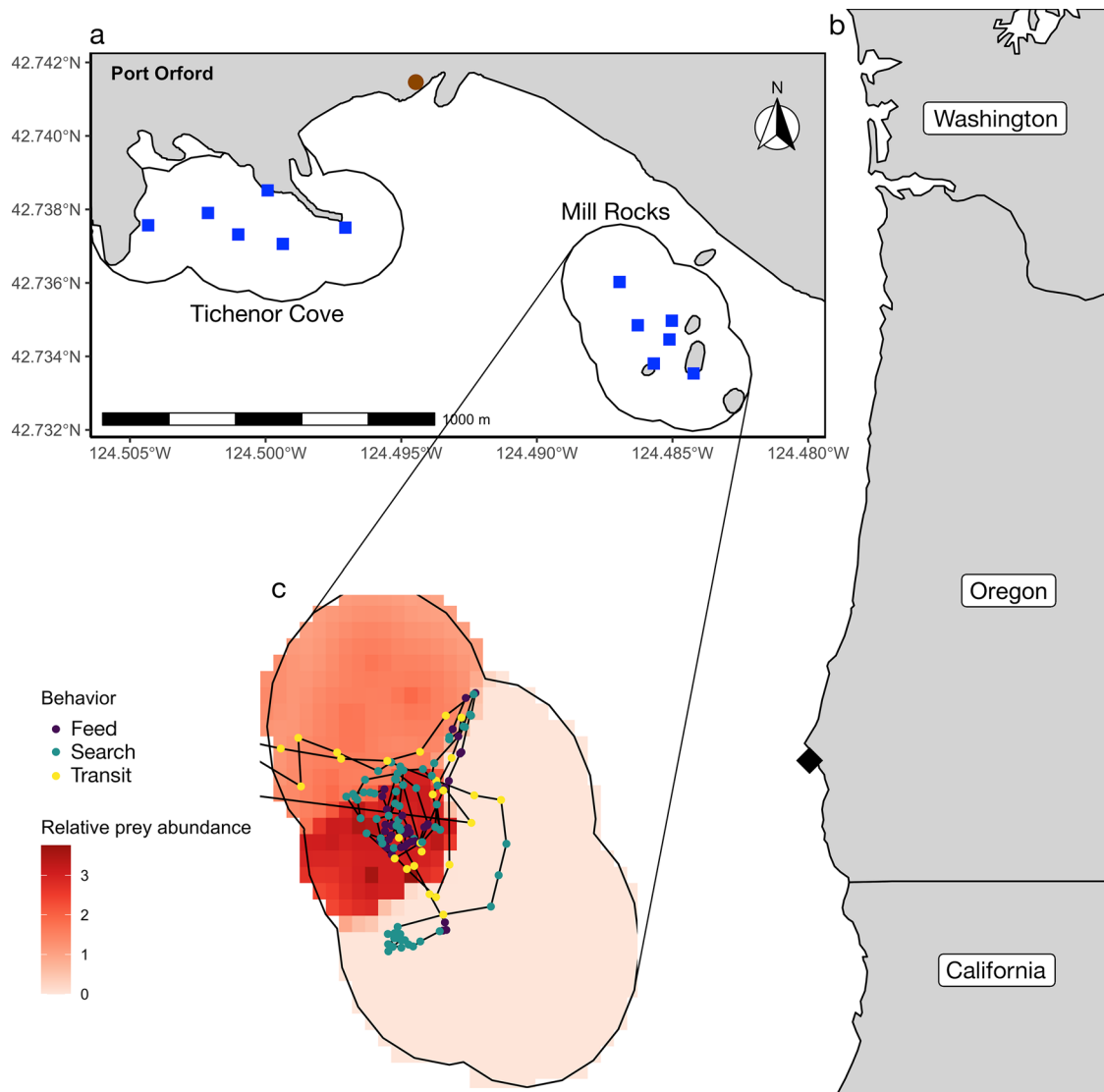


Fig. 1. Location of (a) the 12 sampling stations (blue squares) within the 2 study sites (site boundaries demarcated with black lines) in (b) the nearshore region of Port Orford, Oregon, USA (black diamond). Brown dot in (a): cliff-top observation site where theodolite tracking occurred. (c) An example daily layer of relative prey abundance (increasing color darkness corresponds with increasing abundance) in Mill Rocks with a whale theodolite trackline recorded on the same day overlaid and color-coded by behavioral state

software Pythagoras (Gailey & Ortega-Ortiz 2002), from a cliff-top observation site with an elevation of 33 m (Fig. 1a). Two areas of high whale foraging activity were viewable from this observation point where zooplankton sampling was also conducted: Mill Rocks (MR) and Tichenor Cove (TC). Whales were tracked with the theodolite as far as ~8 km away; however, our analyses in this study are limited to where whale tracklines co-occurred with zooplankton sampling in MR and TC. Whales were only tracked if a single whale was present within MR or TC to ensure that the same whale was being tracked. Binoculars were used to aid the cliff team in spotting whales and qualitatively assign 3 behavior states (feed, search, or transit) at each surfacing. Behavioral state was determined through consensus by the 2 observers at each whale surfacing. 'Feed' was assigned when a whale repeatedly surfaced in a small, restricted area (<20 m²). 'Search' was assigned when a whale moved short distances between surfacings (<100 m) with frequent changes of direction and duration of dives. 'Transit' was assigned when an individual moved at a consistent speed and direction between surfacings. Photo-identification of all tracked whales was performed using a Canon EOS 70D camera.

Zooplankton sampling was conducted at 12 established sampling stations within MR and TC (Fig. 1a) once a day from a 16 ft (~4.9 m) tandem, sit-on-top, research kayak (Ocean Kayak, Zest 2 EXP), which was launched at ~06:45 h (Fig. 1). These sampling stations were selected based on previous observations of whales foraging in the area (Sullivan & Torres 2018), with the inclusion of 2 null sites. Whales were avoided by the kayak team, so the order or timing of station sampling was occasionally altered. The person in the stern position of the kayak (sampler) conducted the zooplankton sampling. At each station, the sampler used a Secchi disk to measure water clarity. Data on relative prey abundance were collected using a paired GoPro and time–depth recorder (TDR; Solinst Levellogger 3001 F100/30) system deployed from a downrigger. The GoPro/TDR was lowered through the water column to the bottom and then pulled up at a speed of $0.1 \pm 0.05 \text{ m s}^{-1}$. Subsequently, zooplankton were captured for species identification using a zooplankton net (Fieldmaster, 8 inch [~20 cm] diameter, 363 μm mesh). Using the downrigger, the sampler lowered the net to the bottom and then raised it as quickly as possible to maximize zooplankton catch before they scattered to evade the net. Captured zooplankton samples were frozen at -20°C prior to sorting of all individuals to species level, and the proportion of each species captured was calculated to de-

scribe prey community availability. The person in the bow position of the kayak (navigator) maintained the kayak's position on station during each sampling event using a handheld GPS unit that had the target sampling locations stored for reference. The navigator actively paddled to counteract any movement of the kayak due to wind or currents. The kayak was repositioned in between sampling events (Secchi disk, GoPro/TDR, and zooplankton net) if it had drifted away from the sampling location. A location was marked on the handheld GPS when the GoPro/TDR system reached the bottom to ensure that drift from the reference station location was less than 20.3 m (the cell size extent for spatial grid; see Section 2.3). The coordinates of these true sampling locations were used in further analyses, rather than the coordinates of the target sampling locations.

2.2. Relative prey abundance

We quantified relative prey abundance through analysis of the GoPro cast imagery collected at each sampling station. Still images were extracted at 5 s intervals during the retrieval cast of the GoPro video and matched to the water column depth using data from the TDR. Each still image was divided into a 3×3 cell grid (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m695p189_supp.pdf). Each grid cell was then scored on a scale of 0–5 relative to the number of zooplankton present in the cell, using reference images (Fig. S1). A score of 0 indicated absence of zooplankton and 5 represented the highest zooplankton abundance. Grid cells that were obscured due to high turbidity, low lighting, or obstructions by kelp and/or rocks were assigned a value of NA. A single image analyst (L.H.) scored the photos to ensure consistency across years. The mean of all 9 grid cell values (excluding NAs) was calculated, providing a single relative abundance score for each image (full methods available in Text S1). The mean values of all images within a cast were summed, resulting in a relative prey abundance value for each station per sampling day. We describe relative abundance (summed values) rather than relative density (summed values / depth of GoPro cast) due to (1) variability in the depth of GoPro casts (mean \pm SD depth: $8.29 \pm 2.91 \text{ m}$), (2) the propensity for zooplankton to be benthically biased (ANOVA by binned depth, $F_{2,10674} = 124.8$, $p < 0.001$), and (3) the accessibility of all surveyed habitat to whales for foraging based on observations of whales across the whole extent during the study period.

2.3. Spatial prey layers

For spatial analysis, the boundaries of MR and TC were defined using the mean distance between sampling stations (475.50 m). A buffer of half this distance (237.75 m) was drawn around each sampling station and merged to form the boundaries (Fig. 1a). The spatial extent of the survey area outside of MR and TC was calculated by creating a minimum convex polygon around all theodolite points. A resolution of 20.3×20.3 m grid cell size was applied for all spatial analyses because this value was half the size of the radius used to classify whale behavior state (see Section 2.4).

Spatial layers of relative prey abundance for MR and TC were created for each prey sampling day. Given the patchiness of zooplankton, we incorporated *a priori* knowledge of zooplankton ecology and distribution through implementation of a generalized additive model (GAM; using the 'mgcv' R-package, version 1.8-39; Wood 2018) in each inverse-distance weighting (IDW) daily interpolation of zooplankton abundance. The GAM assessed daily zooplankton abundance relative to an annual distance to kelp layer (mapped as a polygon using the theodolite at the end of each field season), benthic substrate (classes: reef with kelp, reef with no kelp, and sandy bottom), and Secchi disk depth (m) (full methods available in Text S2). Species-specific abundance preyscapes were generated by multiplying these daily abundance preyscapes (produced by GAM-informed IDW interpolation) by the proportions of each prey species at each sampling station (determined from the net tows; Fig. 1c).

Daily caloric preyscapes for MR and TC were then created by multiplying species-specific abundance preyscapes by the mean caloric value for each species (2.42, 1.60, and 1.25 kJ g⁻¹ wet weight for *Neomysis rayii*, *Holmesimysis sculpta*, and *Atylus tridens*, respectively; Hildebrand et al. 2021). A total caloric layer was calculated by summing the daily species-specific caloric layers together. Caloric content of zooplankton species relevant in this study did not differ between study years (Hildebrand et al. 2021), and therefore we did not account for annual caloric differences in our daily caloric preyscapes.

2.4. Whale behavior classification

We used residence in space and time (RST; Torres et al. 2017) to quantitatively assign behavioral states to each location of a whale trackline. Prior to applica-

tion of RST, all theodolite locations ($n = 4233$) were corrected for height of station (33 m), tide level, and azimuth. A speed filter of 9.57 km h⁻¹ was applied to tracklines to exclude erroneous points ($n = 317$, based on the fastest recorded transit speed of PCFG gray whales from state-space modeled locations of tagged whales; Lagerquist et al. 2019, B. Lagerquist pers. comm.). Speed-filtered tracklines were then discretized at 1 min intervals to approximate movement underwater. RST is scale-dependent and assigns a behavioral state based on occupancy patterns in space (distance traveled) and time within a given radius. The applied radius (R) is flexible but can be determined through the following formula:

$$R = (\text{mean transit speed} \times \text{sampling interval}) / 2 \quad (1)$$

which requires *a priori* knowledge of an animal's mean transit speed. Based on the broad behavioral classifications by the cliff team, whales consistently transited between MR and TC without engaging in foraging or searching behavior, which allowed us to calculate a mean transit speed of 1.36 ± 0.50 m s⁻¹ ($n = 107$ track points) by using those portions of trackline. Using this value, a radius of 40.7 m was derived and deemed ecologically appropriate, as it is slightly greater than 3 body lengths of an average adult gray whale (Agbayani et al. 2020) and falls within the range of baleen whale visual acuity (Mass & Supin 1997, Torres 2017). RST analysis relates the residence time and residence distance metrics within the radius of each location to produce a normalized residual value that scales from -1 to 1. Feeding (the engulfment of prey) is a time-intensive behavioral state represented by negative residual values because the animal spends a long time in the radius without covering much distance. Searching is a time- and distance-intensive behavioral state represented by positive residual values because the animal spends a long time within the radius but also covers a large distance. Transit behavior is represented by residual values equal to zero because the animal spends little time and space within the radius.

2.5. Whale behavior relative to prey availability

Since it is unknown whether gray whales are able to discriminate between prey species, we conducted analyses in 2 ways: (1) with all prey species combined (representing the total abundance and calories available within the preyscape; hereinafter referred to as 'overall prey/preyscapes') and (2) at a species level through assessment of areas where each zoo-

plankton species dominated the prey community. We considered an area to be dominated by one zooplankton species if that species comprised >60% of the prey community in a net tow. This approach allowed us to disentangle the strong correlation between prey abundance and calories (more prey results in more calories) to understand prey choice by whales.

First, we evaluated differences in whale behavioral patterns within and outside of MR and TC using a chi-squared contingency table. Next, we assessed the relationships between whale behavioral state (feed, search, transit) and prey abundance and calories using ANCOVAs (followed by post hoc Tukey tests and calculated mean effect size [partial η^2]) with the 'multcomp' R-package (version 1.4-18; Hothorn et al. 2016) on data points from all whale tracklines that had corresponding prey data. To do so, we assigned log-transformed abundance and caloric values extracted from daily spatial layers to each whale location. Trackline was included as a covariate to account for variability across tracks. Then, we used generalized linear models (GLMs; 'stats' R-package, version 4.0.2) with a Poisson distribution to determine if whales increase the amount of forage (feed and search points combined) behavior within a site relative to increasing prey abundance or calories. With the GLMs, we assessed the relationship between the number of forage points from each trackline relative to the sum log-transformed prey abundance and calories available within MR or TC. The prey metrics (abundance and calories) were included as an interaction term with site in the GLMs to account for differences in area of the 2 sites (see Table 1). Since habitat through which whales transited had a median prey availability of 0 for both abundance and calories (see Fig. 2), we did not include transit behavior in this analysis or subsequent analyses. Furthermore, since whales did not select areas dominated by *A. tridens* for feeding (see Fig. 2), we focused this analysis and further analyses on the mysid shrimp species *N. rayii* and *H. sculpta*.

Since the GLMs revealed a significant relationship between foraging activity and increasing prey availability in MR but not in TC (see Fig. 3), we investigated prey selection drivers of foraging whales in MR at a finer scale. To do this, we gridded the MR site at a 20.3 × 20.3 m cell size resolution aligned with the prey spatial layers; then, for each track, we assigned a value of 1 to cells that included at least one whale forage point (feed or search behavior). Cells that were not visited by whales or through which whales only transited were assigned a value of 0. We then fitted generalized linear mixed models

(GLMMs) using the 'lme4' R-package (version 0.99875-9; Bates & Sarkar 2007) with the probability of foraging as a binomial response variable relative to prey abundance and calories (both as overall prey and split by the 2 mysid shrimp prey species). Hence, 4 GLMMs were conducted, including separate models for prey abundance and calories given the correlation of these 2 metrics. We restricted this analysis to tracklines where whales spent a significant amount of time (e.g. ≥40 min) within MR. Individuals contributed an uneven number of tracks in this subset (range: 1–6); we treated each track independently (rather than grouped by unique individual) since whales encountered a new preyscape within each trackline and these tracklines were recorded across the 3 yr study period. Therefore, we included trackline as a random effect to account for the non-independence of points within a trackline. GLMM parameters were estimated using Laplace approximations, and models were evaluated using Akaike's information criterion (AIC) and deviance explained. We generated a null model and a random effect only (track) model to evaluate the performance of our GLMMs. We used the R-package 'inflection' (version 1.3.5; Christopoulos 2016) to calculate the inflection points (i.e. points in the curve at which the curvature changes sign) of each of the logistic regression curves generated by the best-performing GLMM to identify relative prey thresholds for the probability of gray whales to switch from non-foraging to foraging behavior. We summarized these values by calculating the mean, minimum, and maximum from the 14 inflection points.

All statistical analyses were conducted using R (version 4.0.2; R Core Team 2020).

3. RESULTS

3.1. Prey sampling

Across all 3 yr, a total of 681 GoPro casts (which equates to 11 854 still images extracted and scored) and 677 zooplankton net tows were conducted over 70 sampling days. Identification of zooplankton net tow samples revealed that the mysids *Neomysis rayii* and *Holmesimysis sculpta* and the amphipod *Atylus tridens* were the 3 dominant prey species, accounting for 95.5% of all individual prey items identified. *H. sculpta* was significantly more abundant than the other zooplankton species across all sampling years (ANOVA, $F_{2,4055} = 472.2$, $p < 0.001$; Fig. S2).

3.2. Spatial prey layers

The best performing GAM included distance to kelp, habitat type, and Secchi disk depth as significant predictor variables of zooplankton abundance (Table S1 in the Supplement, Model 2). Zooplankton abundance decreased with increasing distance from kelp and decreasing Secchi disk depth (Fig. S3a,b). It should be noted that the negative relationship between zooplankton abundance and Secchi disk depth is likely due to reduced visibility making it more difficult to detect prey in the GoPro still images. Furthermore, zooplankton abundance was highest in reef with kelp habitat, followed by reef with no kelp habitat, and was lowest in sandy bottom habitat (Fig. S3c). Therefore, this model was implemented in IDW analysis to produce the daily abundance preyscapes.

3.3. Whale behavior

Whales were observed in the study area on 59 of the 70 prey sampling days, with a total of 94 tracks recorded (127 h) from 24 unique individuals. RST activity budgets of whales differed significantly within and outside of MR and TC ($\chi^2 = 348.99$, $df = 4$, $p < 0.001$; Table 1), with more transit behavior out-

side of MR and TC and more searching within both MR and TC. Additionally, whales spent more time feeding inside MR (21 h) than outside (16 h). Whales spent less time feeding in TC than in MR or outside. Overall, whales spent 61 % of their time (78 h) within MR and TC despite being comparatively smaller in area than the surveyed area outside of the site boundaries (Table 1). All subsequent analyses were carried out only for whale locations within MR and TC that had concurrent daily prey data (30 h).

The 3 different whale behavioral states were associated with significantly different mean log-transformed zooplankton abundance and calories (Table 2; mean effect size = 0.0076). Feeding points were significantly more associated with higher prey abundance than transiting points (post hoc Tukey, $p = 0.003$; Fig. 2a). Searching and transiting points were also significantly different from one another (post hoc Tukey, $p = 0.02$), with searching points more associated with higher prey abundance than transiting points (Fig. 2a). Although feeding and searching points were not significantly different from one another (post hoc Tukey, $p = 0.694$), prey abundance was higher at feeding points than searching points (Fig. 2a). These same patterns were also evident between behavior states and prey calories (Fig. 2b). Trackline was a significant covariate in all of the ANCOVAs (Table 2).

Table 1. Gray whale activity budget in the Port Orford study area by site and behavior state determined by residence in space and time analysis. Absolute number of points included in parentheses after each percentage

Site	Area (km ²)	Feed	Search	Transit
Mill Rocks (MR)	0.24	37.7 % (1237)	40.8 % (1336)	21.5 % (705)
Tichenor Cove (TC)	0.34	23.2 % (320)	53.4 % (735)	23.4 % (322)
Outside	4.12	32.3 % (963)	30.3 % (906)	37.4 % (1116)

Table 2. ANCOVA results between the 2 prey metrics (relative abundance and calories), overall and by individual prey species (*Neomysis rayii*, *Holmesimysis sculpta*, *Atylus tridens*) compared to gray whale behavioral state (feed, search, transit) and trackline. Only one test result is shown for each prey species because results of species-specific ANCOVAs for abundance and calories produced the same results due to correlation between these 2 metrics. Statistically significant ($p < 0.05$) results are in **bold**

Prey metric	Behavior				Trackline			
	df	Adj. SS	F	p	df	Adj. SS	F	p
Abundance	2	4.58	5.67	0.003	60	560.48	23.14	<0.001
Calories	2	7.46	5.96	0.003	60	733.61	20.23	<0.001
<i>N. rayii</i>	2	0.17	2.47	0.087	19	32.67	51.85	<0.001
<i>H. sculpta</i>	2	3.13	7.05	<0.001	34	167.37	22.19	<0.001
<i>A. tridens</i>	1	0.02	1.47	0.255	5	4.85	68.1	<0.001

When examining each prey species individually, no significant differences were found between abundance and calories associated with different whale behavior states (Table 2), except between feeding and searching points in *H. sculpta*-dominated preyscapes (post hoc Tukey, $p < 0.001$; Fig. 2c). No feeding points occurred in areas where the amphipod *A. tridens* dominated the prey community even though whales searched and transited through these areas (Figs. 2c,d).

Despite spending relatively similar amounts of time in the 2 study sites (MR: 21 h; TC: 16 h), whales significantly increased foraging effort as prey availability (both abundance and calories) increased in MR (GLM, abundance: $z = 6.92$, $p < 0.001$; calories: $z = 6.14$, $p < 0.001$; Fig. 3) but not in TC (GLM, abundance: $z = 0.679$, $p = 0.497$; calories: $z = 0.408$, $p = 0.683$; Fig. 3).

All GLMMs that examined prey selection by whales during long (≥ 40 min)

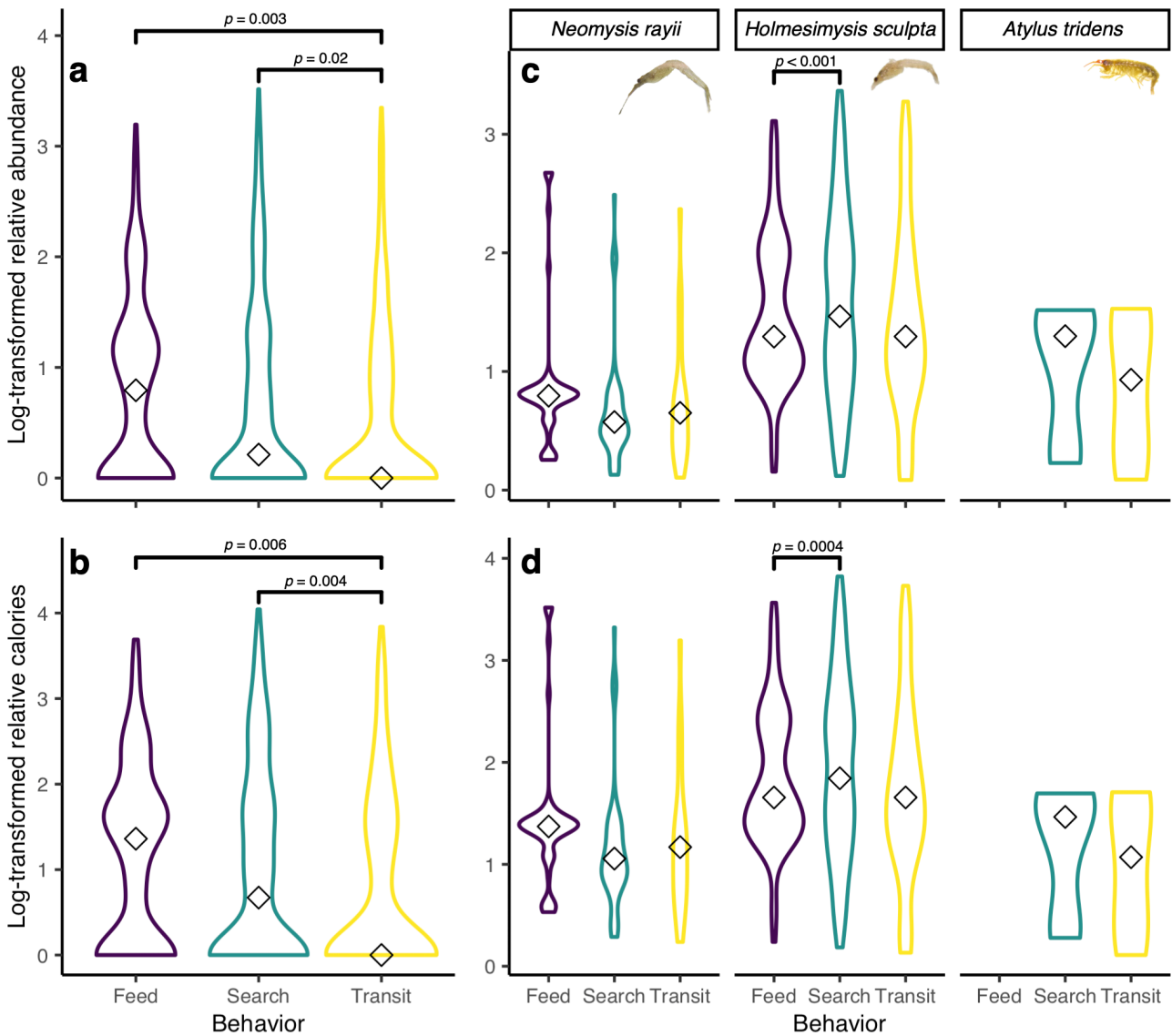


Fig. 2. (a,b) Overall and (c,d) species-specific log-transformed relative prey abundance (a,c) and log-transformed relative prey calories (b,d) by gray whale behavioral state (feed, search, transit). Black diamonds: median values. Bars with p-values indicate significant differences between behaviors

tracklines (n = 14) in MR included significant prey predictor variables (Table 3, Models 1–4). The models that best explained the probability of gray whale foraging were the prey species-specific GLMMs (Models 3 and 4), with the abundance and calories of *H. sculpta* being the influential predictor variables (Table 3). Model 3 had the lowest AIC and was therefore used to identify the inflection points of the logistic regression curves of gray whale foraging probability (Fig. 4). The mean inflection point for the *H. sculpta* relative abundance curves was 12.0, with a minimum value of 7.2 and a maximum value of 15.3. Inflection points could not be derived for the *N. rayii* abundance curves (Fig. 4).

4. DISCUSSION

Our study expands the field of foraging ecology by investigating large marine predator foraging decisions at a micro scale (0–100 m; Torres 2017) relative to both prey quantity and quality and by incorporating individual behavioral data. We demonstrated that PCFG gray whales select areas with high relative prey abundance and that a prey quantity threshold initiates foraging behavior. While whales never selected areas dominated by the low-calorie species *Atylus tridens*, the abundance of the highest caloric prey identified in this study, *Neomysis rayii*, was low throughout our study period and area, appearing

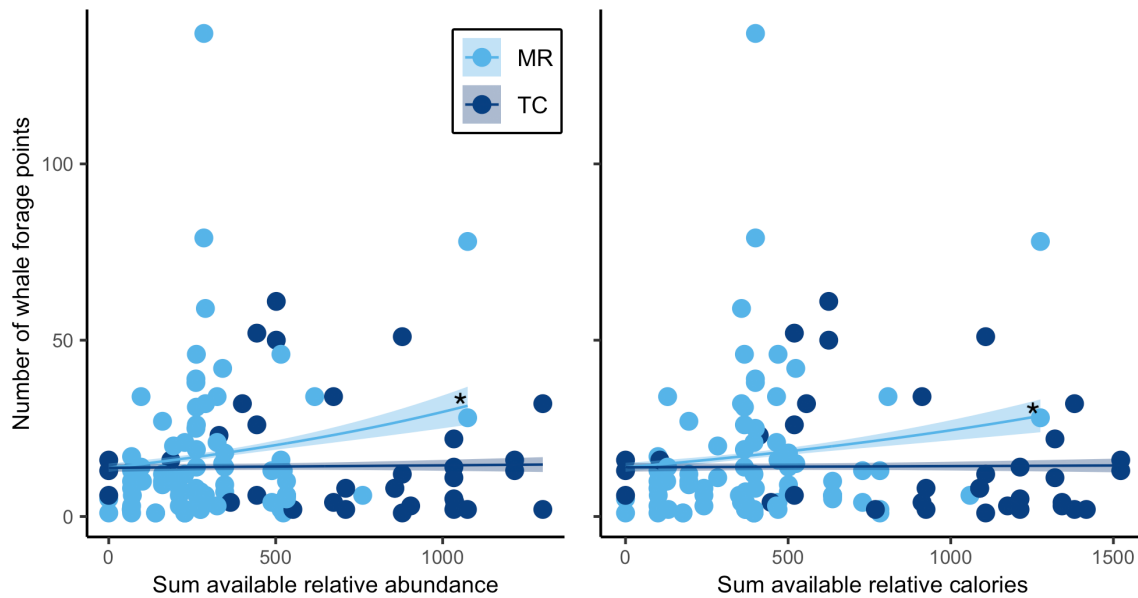


Fig. 3. Number of gray whale points by site (MR: Mill Rocks; TC: Tichenor Cove) along tracks interpolated at 1 min intervals compared to the sum available relative abundance (left panel) and calories (right panel) of prey. Curves with asterisks: statistically significant ($p < 0.05$) relationship as determined by generalized linear models

Table 3. Generalized linear mixed-effects models run on all 14 long (>40 min) tracklines in Mill Rocks, between the binomial response variable of gray whale foraging compared to the 2 prey metrics (relative abundance and calories) overall and by individual prey species (*Neomysis rayii*, *Holmesimysis sculpta*). Statistically significant ($p < 0.05$) predictor variables are in **bold**. Model 3 was the best-performing model in terms of Akaike's information criterion (AIC) and deviance explained (%) and was therefore implemented for logistic regression curves displayed in Fig. 4

Model	AIC	Deviance explained (%)	Prey metrics	Coefficient	SE	z-value	p
Null	3702.2						
Track	3576.3	3.46					
1	3469.7	6.39	Abundance	0.26	0.03	10.3	<0.001
2	3483.3	6.03	Calories	0.15	0.02	9.57	<0.001
3	3455.5	6.83	<i>N. rayii</i> abundance	-0.07	0.08	-0.93	0.351
			<i>H. sculpta</i> abundance	0.28	0.03	11.1	<0.001
4	3459.3	6.73	<i>N. rayii</i> calories	0.01	0.03	0.38	0.705
			<i>H. sculpta</i> calories	0.18	0.02	10.7	<0.001

never to reach a threshold needed to elicit foraging behavior (Piatt & Methven 1992). These results reveal that while prey quality impacts baleen whale foraging decisions, trade-offs between prey quality and quantity are made by whales to achieve optimal foraging. Thus, we highlight the importance of considering the quality of prey, alongside prey quantity metrics such as abundance or density, in studies of predator foraging ecology.

Of the prey species identified in this study period and area, *N. rayii* and *A. tridens* represent opposite ends of the caloric quality spectrum, with *Holmesimysis sculpta* as a caloric intermediary (Hildebrand et al. 2021). Despite not having the highest quality, *H. sculpta* did have the highest abundance and showed

a significant positive relationship with foraging behavior, unlike the other prey items. These results demonstrate trade-off choices by whales for this abundant, medium-quality prey. Moreover, although our prey abundance metric is relative, we determined that a threshold of *H. sculpta* abundance is required to initiate the probability of gray whale foraging behavior. If we multiply the mean *H. sculpta* threshold (12.0) by the mean caloric value of *H. sculpta* (1.60 kJ g^{-1} wet weight; Hildebrand et al. 2021), we can estimate a theoretical relative caloric value required to initiate gray whale foraging behavior (19.2 kJ g^{-1} of relative abundance). Dividing this theoretical relative caloric value by the mean *N. rayii* caloric value (2.42 kJ g^{-1} wet weight; Hildebrand et

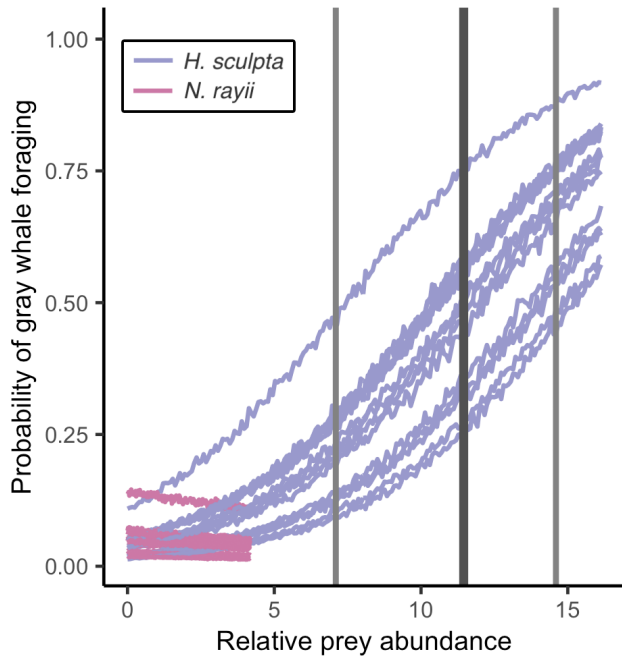


Fig. 4. Logistic regression curves of each analyzed gray whale trackline generated from the generalized linear mixed-effects model of the binary response of whale foraging probability compared to the species-specific relative abundance for the mysid shrimp prey *Holmesimysis sculpta* and *Neomysis rayii*. Dark grey vertical line: mean inflection point for the *H. sculpta* curves (12.0); light grey vertical lines: minimum (7.2) and maximum (15.3) inflection points for the *H. sculpta* curves. Inflection points could not be calculated for the *N. rayii* curves

al. 2021) indicates that a relative *N. rayii* abundance of 7.93 would be required for gray whales to initiate foraging behavior; this relative abundance was never reached for *N. rayii* in our study (Fig. 4). While these calculations are theoretical and relative, they may explain why high gray whale foraging effort is observed in areas of low prey density, and likewise why lower foraging effort can be observed in areas of high prey density (Feyrer & Duffus 2015). These non-intuitive observations may be driven by significant caloric differences (Hildebrand et al. 2021) between zooplankton species available to foraging PCFG whales across space and time. Therefore, we posit that while *N. rayii* abundance did not reach the threshold at which foraging is beneficial in our study, this threshold can be achieved across the PCFG foraging range, leading PCFG whales to forage in areas of lower *N. rayii* abundance than nearby areas of higher *H. sculpta* abundance. This trade-off between prey quantity and quality has also been detected in humpback whales foraging in Antarctica that feed at depths deeper than where the densest krill patches occur in order to exploit less dense krill patches that are likely composed of larger, gravid krill (Cade et al.

2022). While it is unclear how baleen whales differentiate between prey species or reproductive stages, several mechanisms have been suggested, including visual and auditory identification (Torres 2017) or detection via vibrissae (Pyenson et al. 2012). We assume here that gray whales, and other baleen whale species, can differentiate between prey species. Thus, our results showcase the importance of knowing the quality (such as caloric content) of prey items available to predators to understand their foraging ecology (Spitz et al. 2012).

We attempted to overcome the inherent correlation in the relative estimates of prey abundance and calories through an assessment of gray whale prey selection by prey species individually and with all prey grouped together. However, a more fine-scale approach could also be achieved through assessment of prey by reproductive stage since the caloric content of gravid female mysids examined in this study are significantly more calorically rich (Hildebrand et al. 2021). Given that mysids aggregate by size class and reproductive stage (Kaltenberg & Benoit-Bird 2013), prey patches of gravid individuals are likely more profitable to foraging gray whales. Furthermore, our daily prey sampling scale could also have affected our results, as we acknowledge that the prey community, distribution, and availability may have changed between the time of prey sampling and the tracked movements of whales. Therefore, future efforts should attempt (1) a more refined classification of reproductive stage or age–size class and/or (2) to sample twice a day, as these improvements could reveal a more nuanced understanding of whale prey selection.

Our findings of gray whale foraging preferences relative to prey quality and quantity at a micro scale could help explain documented variation in PCFG gray whale body condition (Newell & Cowles 2006, Lemos et al. 2020, Akmajian et al. 2021), which was attributed to variable environmental conditions that can reduce prey abundance (Brodeur et al. 2019) or quality (Peterson et al. 2017). Furthermore, gray whales in poor body condition have higher fecal cortisol stress levels (Lemos et al. 2022), showcasing the physiological consequences of foraging success. Decreased prey quality has resulted in reduced body condition and fitness (Trites & Donnelly 2003, Cohen et al. 2014), reproductive failure (Harris et al. 2007, 2008, Grémillet et al. 2008), and population declines (Crawford et al. 1995, Trites & Donnelly 2003, Ludyria et al. 2010) in a number of other marine predators and is one of the hypothesized causes of the unusual mortality event for ENP gray whales (2019–present; Christiansen et al. 2021, Torres et al. 2022). Variation

in the quality and quantity of prey available to PCFG gray whales may be associated with ongoing declines in kelp forests along the US west coast triggered by a marine heatwave that occurred from 2013–2015 (Rogers-Bennett & Catton 2019, Starko et al. 2019). While the effects of kelp declines on zooplankton, particularly mysids, are unknown, reduced kelp habitat frequently causes altered community species composition (Sanford et al. 2019) and lasting ecological impacts (Rogers-Bennett & Catton 2019). Indeed, we noted a sharp decline in kelp abundance across years in the study area, particularly in the TC site (L. Torres pers. obs.), which may influence the zooplankton community given the significant relationship we documented between zooplankton abundance and kelp habitats. We expect that the null relationship we found between whale foraging and prey in TC, which contrasts the relationship documented in MR, is due to kelp declines in TC causing prey abundance to be reduced below the threshold needed for whales to initiate foraging behavior.

Although our study examined the foraging decisions of PCFG gray whales in a small area (4.7 km²), the study environment and available prey species are typical of PCFG foraging habitat across much of their range (Jenkinson 2001, Feyrer & Duffus 2015, Scordino et al. 2017), indicating that our results may extend to the larger region and sub-group. With marine heatwaves predicted to increase in frequency due to climate change (Frölicher et al. 2018), and our documented preference of gray whales for feeding on patches of high relative mysid prey abundance, it is important to understand how mysid species are affected by perturbations like marine heatwaves and kelp losses and the subsequent impacts on gray whale health (Spitz et al. 2012).

Predator foraging ecology studies often aim to inform conservation management efforts through improved knowledge of habitat use and movement patterns in both terrestrial (e.g. Pettorelli et al. 2010, Lantschner et al. 2012, Moss et al. 2016) and marine (e.g. Wells et al. 2018, Southall et al. 2019, Barlow et al. 2020) systems. Since predators distribute themselves in space and time relative to their prey, improving our understanding of predator choices based on prey availability metrics, such as selection for higher quality or quantity, can ultimately improve spatial management efforts. While simultaneous sampling of marine predators and multiple prey metrics is often not feasible at meso or large scales, results from fine- or micro-scale studies can guide prioritization of research questions and methods in other studies. For instance, if gray whales make trade-offs between

prey quality and quantity, as our results suggest, the availability of calorically rich mysid species such as *N. rayii* and *H. sculpta* should be studied and monitored across the whole range to understand impacts on PCFG gray whale population health and dynamics. Our findings illustrate that prey quality plays a role in shaping foraging decisions of gray whales and therefore should not be overlooked in foraging ecology studies aimed at understanding movement and habitat use patterns, especially in the context of conservation management applications. The variability of prey quality and quantity are particularly salient when considering the resilience of marine megafauna faced with shifting marine ecosystem dynamics due to climate change (Harley et al. 2006, Hazen et al. 2013).

Data availability. The data set used in this study is available upon request to the corresponding author.

Acknowledgements. Funding for this research was provided by Oregon Coast STEM Hub, Wild Rivers Coast Alliance, Oregon State University (OSU) Marine Mammal Institute, OSU Port Orford Field Station, OSU Marine Studies Initiative, and the American Cetacean Society—Oregon Chapter. Data collected for this study were derived from an integrated student and community engagement program to increase STEM learning and career paths. We thank all high school, undergraduate, and graduate interns who participated in this project and worked diligently to help collect data for this study. Finally, thank you to Barney Eredia for kindly providing access to his property for whale shore-surveys and to Dave Lacey and South Coast Tours for their generosity with kayak equipment, training, and expertise.

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Editorial responsibility: Peter Corkeron,
Woods Hole, Massachusetts, USA

Reviewed by: C. Ryan and 1 anonymous referee;
a previous version was reviewed in MEPS by
L. Feyrer, J. Scordino and 1 anonymous referee

Submitted: April 18, 2022

Accepted: June 29, 2022

Proofs received from author(s): August 9, 2022