



Do Gray Whales Count Calories? Comparing Energetic Values of Gray Whale Prey Across Two Different Feeding Grounds in the Eastern North Pacific

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Predators must consume enough prey to support costly events, such as reproduction. Meeting high energetic requirements is particularly challenging for migrating baleen whales as their feeding seasons are typically restricted to a limited temporal window and marine prey are notoriously patchy. We assessed the energetic value of the six most common nearshore zooplankton species collected within the Oregon, United States range of the Pacific Coast Feeding Group (PCFG) gray whale (*Eschrichtius robustus*) feeding grounds, and compared these results to the energetic value of the predominant amphipod species fed on by Eastern North Pacific (ENP) gray whales in the Arctic. Energetic values of Oregon zooplankton differed significantly between species (Kruskal–Wallis $\chi^2 = 123.38$, $df = 5$, $p < 0.0001$), with Dungeness crab (*Cancer magister*) megalopae displaying the highest mean caloric content of all tested species (4.21 ± 1.27 kJ g⁻¹). This value, as well as the mean energetic value of the mysid *Neomysis rayii* (2.42 ± 1.06 kJ g⁻¹), are higher than the mean caloric content of *Ampelisca macrocephala*, the predominant Arctic amphipod. Extrapolations of these results to daily energetic requirements of gray whales indicate that lactating and pregnant gray whales feeding in the PCFG range would require between 0.7–1.03 and 0.22–0.33 metric tons of prey less per day if they fed on Dungeness crab megalopae or *N. rayii*, respectively, than a whale feeding on *A. macrocephala* in the Arctic. Yet, these results do not account for differences in availability of these prey species to foraging gray whales. We therefore suggest that other factors, such as prey density, energetic costs of feeding, or natal philopatry and foraging site fidelity play a role in the differences in population sizes between the PCFG and ENP gray whales. Climate change is implicated in causing reduced body condition and increased mortality of both PCFG and ENP gray whales due to decreased prey availability and abundance. Therefore, improved understanding of prey dynamics in response to environmental variability in both regions is critical.

Keywords: gray whales, eastern North Pacific, caloric content, Oregon, energetic trade-off, zooplankton

INTRODUCTION

Foraging efficiency is key to predator success. This efficiency must balance energetic cost with energetic reward, forcing predators to make decisions regarding target prey type, size, location, and behavioral effort. To maximize the net energy gained, optimal foraging theory (OFT) posits that an individual should target prey with the most benefit (energy) for the lowest possible cost (MacArthur and Pianka, 1966). Moreover, the marginal value theorem (MVT) illustrates that patch choice requires predators to consider the potential value of future patches relative to a current foraging patch, as well as the time and energy required to search for a new patch (Charnov, 1976). These energetic trade-offs impact predator distribution patterns and population dynamics (Owen-Smith et al., 2010; Louzao et al., 2014), and can be particularly challenging in marine ecosystems where prey is patchy and spatially and temporally dynamic (Hyrenbach et al., 2000).

Foraging decisions by baleen whales cannot afford much error as they are capital breeders with large energetic demands that must be met within a limited temporal window while on feeding grounds. Energy acquired during the foraging period must support the majority of their energetic requirements needed for foraging effort, migration, and reproduction for the subsequent year (Lockyer, 1984). For instance, it is estimated that gray whales (*Eschrichtius robustus*) must regain 11–29% of their body mass on the feeding grounds (Villegas-Amtmann et al., 2015); hence, finding enough prey is crucial. Prey patch selection by baleen whales is strongly associated with patch density and capture efficiency (Piatt and Methven, 1992; Croll et al., 2005; Goldbogen et al., 2011; Feyrer and Duffus, 2015; Hazen et al., 2015), where whales prioritize the densest patches in the most accessible areas (e.g., shallow to minimize diving costs) to achieve the highest energetic gain for the lowest cost (Croll et al., 2001; Doniol-Valcroze et al., 2011; Goldbogen et al., 2013; Torres et al., 2020).

Additionally, there is increased recognition that prey quality, such as caloric content, is important for the foraging ecology of cetaceans, including baleen whales (Spitz et al., 2012). Variability in the caloric value of zooplankton can occur within and between species, across seasons and between years, and by region (Mauchline, 1980). This variability may be due to differences in lipid composition and storage (Lee et al., 2006), diet (Mauchline, 1980), or reproductive stage (Schaafsma et al., 2018). Foraging decisions by baleen whales can be influenced by prey caloric content. For example, it has been shown that blue whales (*Balaenoptera musculus*) preferentially feed on a more calorically rich species of krill (Nickels et al., 2018). Caloric decisions may also be an important element in prey patch selection of generalist baleen whales that have multiple prey options. These generalists must maximize both density and caloric intake while minimizing the cost of capture associated with the energetic requirements of behavioral foraging adaptations fit to prey characteristics. For instance, gray whales in the Bering, Chukchi, and Beaufort Seas (hereafter referred to as Arctic) feed predominantly on benthic amphipods (Nerini, 1984; Moore et al., 2003; Coyle et al., 2007a), yet they feed on epibenthic and pelagic zooplankton along the

North American west coast (Nerini, 1984; Nelson et al., 2008; Feyrer and Duffus, 2011; Gosho et al., 2011).

Gray whales in the eastern North Pacific Ocean migrate from breeding grounds in Baja California, Mexico to their feeding grounds in the Arctic during the summer (Rice and Wolman, 1971). The benthic amphipod community in this region is dominated by the ampeliscid amphipod, *Ampelisca macrocephala*, which comprises over 70% of the benthic community (Coyle and Highsmith, 1994) and is the primary prey of the Eastern North Pacific (ENP) gray whale population (Nerini, 1984). ENP individuals feed benthically by diving to the seafloor at mean depths of 40–50 m (Schonberg et al., 2014) and sucking up benthic infauna in the soft sediment (Nerini and Oliver, 1983). A sub-group of this population of gray whales, termed the Pacific Coast Feeding Group (PCFG), does not migrate to the Arctic feeding grounds but rather stops approximately halfway up the North American west coast and utilizes the region from northern California, United States to northern British Columbia, Canada as their foraging ground (Calambokidis et al., 2002). PCFG gray whales are well-known as generalist feeders (Nerini, 1984) based on evidence of feeding on benthic amphipods (Burnham and Duffus, 2016), mysids (Newell and Cowles, 2006; Feyrer and Duffus, 2011), cumaceans (Gosho et al., 2011), crab larvae (Nelson et al., 2008), ghost shrimp (Duffus, 1996; Darling et al., 1998), and herring roe (Darling et al., 1998). The ability to feed on such a wide variety of zooplankton prey requires different feeding behaviors adapted to successfully capture variable prey in a diversity of habitats. Torres et al. (2018) used an unoccupied aerial system (UAS; a.k.a. “drone”) to describe and quantify a variety of foraging tactics employed by PCFG individuals along the Oregon, United States coast, including “headstands,” “bubble blasts,” and “sharking” on reefs, as well as documentation of whales expelling sediment from their mouths.

Abundance estimates of the ENP and PCFG indicate the population sizes are two orders of magnitude different, with the ENP estimated at ~20,000 individuals (Stewart and Weller, 2021), while the PCFG contains only ~250 individuals (Weller et al., 2013; Calambokidis et al., 2017). Genetic analysis has yet to resolve the degree of reproductive mixing between the ENP and PCFG sub-groups. Mitochondrial genetic data indicates low genetic exchange between sub-groups, yet microsatellite analysis showed no evidence that whales from the two different feeding grounds are reproductively isolated (Frasier et al., 2011; Lang et al., 2014). The relatively large size of the ENP population suggests that migrating all the way to the Arctic feeding grounds is advantageous despite the longer, and therefore more costly, migration. Increased prey quantity, quality, and availability in the Arctic potentially outweigh the trade-off of increased migration costs. Yet, PCFG whales are also able to gain critical energetic mass throughout a foraging season (Soledade Lemos et al., 2020) and successfully recruit calves (Calambokidis and Perez, 2017), all while migrating half as far. Hence, the mystery of the PCFG persists: Why would a gray whale not join the PCFG? Or is life as a PCFG gray whale harder than perceived, perhaps due to reduced prey quality?

To help unravel the mystery of the PCFG, this study aims to (1) assess the quality (caloric content) of different potential zooplankton prey on the Oregon coast, and (2) compare the quality of prey on the Oregon coast (as a proxy for the entire PCFG range) to the quality of prey in the Arctic ENP feeding grounds through extrapolations of gray whale energetic needs using published values in the literature. We hypothesize that Oregon coast prey will vary by species, reproductive stage, and time of year. Furthermore, we anticipate that Arctic prey (amphipods) will be more calorically rich than Oregon prey, contributing to the fact that the majority of ENP gray whales migrate to the Arctic to feed during the summer rather than traveling half as far to feed in the PCFG range. Our aim is to inform the foraging energetics of the PCFG through comparisons to the larger population of ENP gray whales and thus elucidate the existence of this small sub-group and inform population management efforts.

MATERIALS AND METHODS

Sample Collection and Preparation

Collection of zooplankton samples was conducted near the coast of Newport (44°38'12" N, 124°03'08" W), Oregon, United States, between June and October from 2017 to 2019 as part of a larger study on gray whale ecology (Soledade Lemos et al., 2020). Collection occurred using a simple, low-cost light trap, which was a modified plastic water jug with an LED light placed inside to attract zooplankton (adapted from design in Chan et al., 2016). The light trap was deployed overnight at randomly selected nearshore sites where gray whales were observed foraging previously that day (Figure 1). The bottom habitat of the collection sites was rocky reef, with and without kelp. The trap was deployed overnight with an anchor and float line to keep the trap just above the seafloor. This system is effective at sampling epibenthic species associated with the benthos in rocky coastal habitats where it is difficult to sample using towed nets (Chan et al., 2016). The light trap was collected the subsequent day. In addition, Dungeness (*Cancer magister*) and porcelain (*Porcellanidae* sp.) crab larvae were opportunistically sampled in the Newport study area with nets where gray whales were observed feeding on surface swarms (Figure 1).

Once collected, all samples were transferred to sterile jars and frozen at -20°C until subsequent sorting and calorimetric analysis. All samples were sorted to species level and separated by reproductive stage. All sorted samples were blotted and wet-weighted prior to being dried in a desiccating oven at 60°C between 48 and 72 h until they reached a constant mass. After reweighing, the dried samples were ground into a homogenous powder and, using a pellet press (Parr Instruments, Moline, IL, United States), were made into 2–100 mg pellets, depending on the amount of sample available each day. Pellet weights were recorded for each sample prior to calorimetry. Where possible, a minimum of three replicate pellets were made per sample. However, the small sample number of certain species or reproductive stages on some sampling days limited replication (Table 1).

Calorimetry

Pellets were combusted using a semi-micro bomb calorimeter (Model 6725, Parr Instruments, Moline, IL, United States). Calibrations of energetic density estimates were performed using 0.2 g benzoic acid ($\text{C}_6\text{H}_5\text{COOH}$) pellets and resultant caloric densities were corrected for uncombusted fuse wire and/or sample (Parr Instruments Company, 2010). Caloric densities with standard deviations (SD) are reported here in kilojoules per gram wet weight ($\text{kJ g}^{-1}\text{ WW}$).

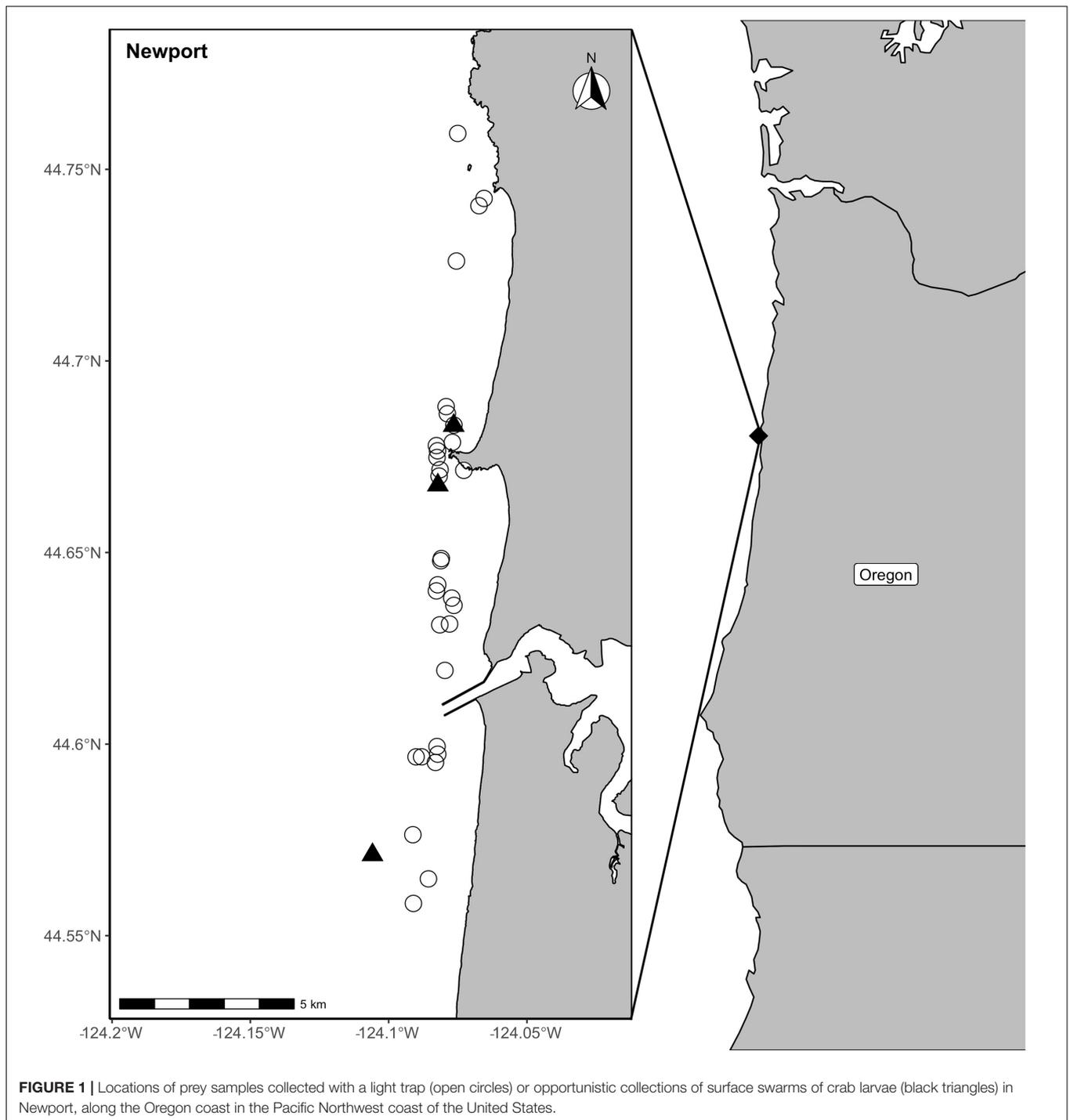
Statistical Analysis

All statistical analyses were conducted using R (version 4.0.2; R Core Team 2020). Data did not meet the assumptions of normality and homogeneity of variance, therefore Kruskal–Wallis rank sum tests were performed to assess differences in energetic value between species, reproductive stage, and time (month and year). If significant differences were detected, pairwise comparisons with the Dunn's test were carried out. A Bonferroni correction was applied to account for multiple comparisons (Dunn, 1961). A total of eight Kruskal–Wallis tests were performed, resulting in a new Bonferroni-adjusted alpha value of 0.006 (0.05/8). Linear regressions were conducted to test for the effect of reproductive stage on caloric content with day of year (DOY).

Extrapolations to Daily Whale Energetic Needs

Although PCFG gray whales show varying degrees of site fidelity to specific foraging sites within their range (Calambokidis et al., 2017), they also move between foraging sites within and between foraging seasons (Lagerquist et al., 2019). Hence, PCFG whales may gain their annual energetic needs from a variety of locations within the PCFG range. The nearshore bottom habitat along the central Oregon coast is predominantly rocky reef, with interspersed sedimentary areas (Romsos et al., 2007; L. Torres, pers. obs.). The prey associated with this habitat type (Table 1) are similar to those described for British Columbia (Dunham and Duffus, 2002; Feyrer, 2010; Feyrer and Duffus, 2011, 2015), Washington (Scordino et al., 2017), and northern California (Jenkinson, 2001). Therefore, for our extrapolations of PCFG gray whale caloric requirements from prey, we assume that (1) a similar suite of prey species is available to gray whales across the PCFG range as we captured off central Oregon, and (2) caloric estimates by species and reproductive stage documented in our analysis are similar across the PCFG range. However, we recognize that we did not measure the caloric content of all prey types known to be fed on by gray whales in this range, such as herring roe (Darling et al., 1998) and benthic amphipods (Burnham and Duffus, 2016), but these have never been captured in our study's field site (Oregon). Since it is unlikely that gray whales feeding in the PCFG range exclusively consume one species of prey during the whole foraging season, we created a PCFG composite prey caloric value by calculating the mean caloric value of the six Oregon prey species tested in this study.

Caloric values of *A. macrocephala*, the predominant amphipod species in the Arctic feeding grounds of ENP gray whales



(Nerini, 1984), were compiled from the published literature (Highsmith and Coyle, 1990, 1992; Hondolero et al., 2012; Wilt et al., 2014). These studies report the caloric content of *A. macrocephala* as dry weight values. In contrast, we have reported wet weight values of caloric content because this unit is relevant to foraging whales, as this is the form in which prey is consumed. Therefore, to facilitate comparison of the number of individual zooplankton by species needed to be

consumed by a gray whale to meet their daily energetic needs, we converted the published average dry weight caloric content for *A. macrocephala* ($4.473 \text{ kcal g}^{-1}$; Hondolero et al., 2012) to average wet weight caloric content (2.021 kJ g^{-1}) after obtaining the dry and wet weights of the samples used in that study (K. Iken, unpublished data).

Prey caloric values were extrapolated by species to the daily energetic requirements (MJ day^{-1}) for pregnant and lactating

TABLE 1 | Energetic values (wet weight) and sample sizes by zooplankton species and reproductive group collected from June to October in 2017 to 2019 in central Oregon.

Species	Number of energetic values	Mean energetic value (kJ g ⁻¹)	Minimum energetic value (kJ g ⁻¹)	Maximum energetic value (kJ g ⁻¹)	Standard deviation
<i>Atylus tridens</i>	28	1.25	0.47	2.93	0.57
Gravid	2	0.78	0.60	0.97	0.26
No brood pouch	25	1.31	0.47	2.93	0.58
Empty brood pouch	1	0.71	–	–	–
Dungeness crab megalopae	13	4.21	2.61	6.14	1.27
<i>Holmesimysis sculpta</i>	100	1.60	0.47	5.21	0.66
Gravid	33	1.74	0.83	3.04	0.58
No brood pouch	48	1.65	0.83	5.21	0.73
Empty brood pouch	19	1.23	0.47	2.36	0.49
<i>Neomysis rayii</i>	128	2.42	0.59	7.96	1.06
Gravid	37	2.50	1.27	7.96	1.04
No brood pouch	67	2.59	0.86	5.54	1.12
Empty brood pouch	24	1.86	0.59	3.47	0.75
<i>Polycheria osborni</i>	11	0.83	0.53	1.14	0.21
Porcelain crab larvae	4	1.17	1.00	1.31	0.14
PCFG composite prey	284	1.91	–	–	–
<i>Ampelisca macrocephala</i>	–	2.02	–	–	–

Mean energetic value (wet weight) of all Oregon prey species tested in this study (PCFG composite prey) and Arctic amphipod species *Ampelisca macrocephala* (obtained from Hondolero et al., 2012 and K. Iken, unpublished data) are also included in the table.

female ENP gray whales based on the results of Villegas-Amtmann et al. (2017) to estimate the requirements per day of (1) the biomass of prey, in metric tons, and (2) the number of individual prey items. Villegas-Amtmann et al. (2017) calculated daily energetic requirements for self-maintenance and costs of reproduction over a female's 2-year reproductive cycle. Biomass (metric tons) of prey required per day was calculated by dividing the daily energetic requirement by the mean caloric value (MJ g⁻¹) of each prey species, divided by 1 million. Number of individual prey items required per day was calculated by dividing the biomass of prey required per day by the mean wet weight per individual of each prey species.

RESULTS

Sample Collection and Preparation

Light trap deployment depth was 11.2 ± SD 2.98 m. A total of 36 light traps were deployed, however, following recovery, five traps did not contain any zooplankton, likely due to a malfunction of the light used to attract zooplankton to the trap.

Therefore, 31 light trap samples and three opportunistic surface samples were analyzed.

In total, nine zooplankton species were identified: the mysids *Alienacanthomysis macropsis*, *Exacanthomysis davisii*, *Holmesimysis sculpta*, and *Neomysis rayii*, the amphipods *Atylus tridens*, and *Polycheria osborni*, Dungeness crab megalopae and porcelain crab larvae, and an unknown species of *Caprellidae*. *A. macropsis*, *Caprellidae* sp., and *E. davisii* were rare, only being identified in 1, 1, and 4 light trap samples, respectively. These occurrences were represented by a single specimen, which prevented successful calorimetric determination for these three species.

For the mysids, gravid females were identified through the presence of a brood pouch that contained any developmental stage of offspring (from eggs to larvae). Individuals that had a brood pouch without any contents were classed as empty brood pouch females and considered to have already released their young. For *A. tridens*, gravid females were identified by a clutch of eggs in their pereopods. Reproductive stages could not be discerned for *P. osborni* due to its small size.

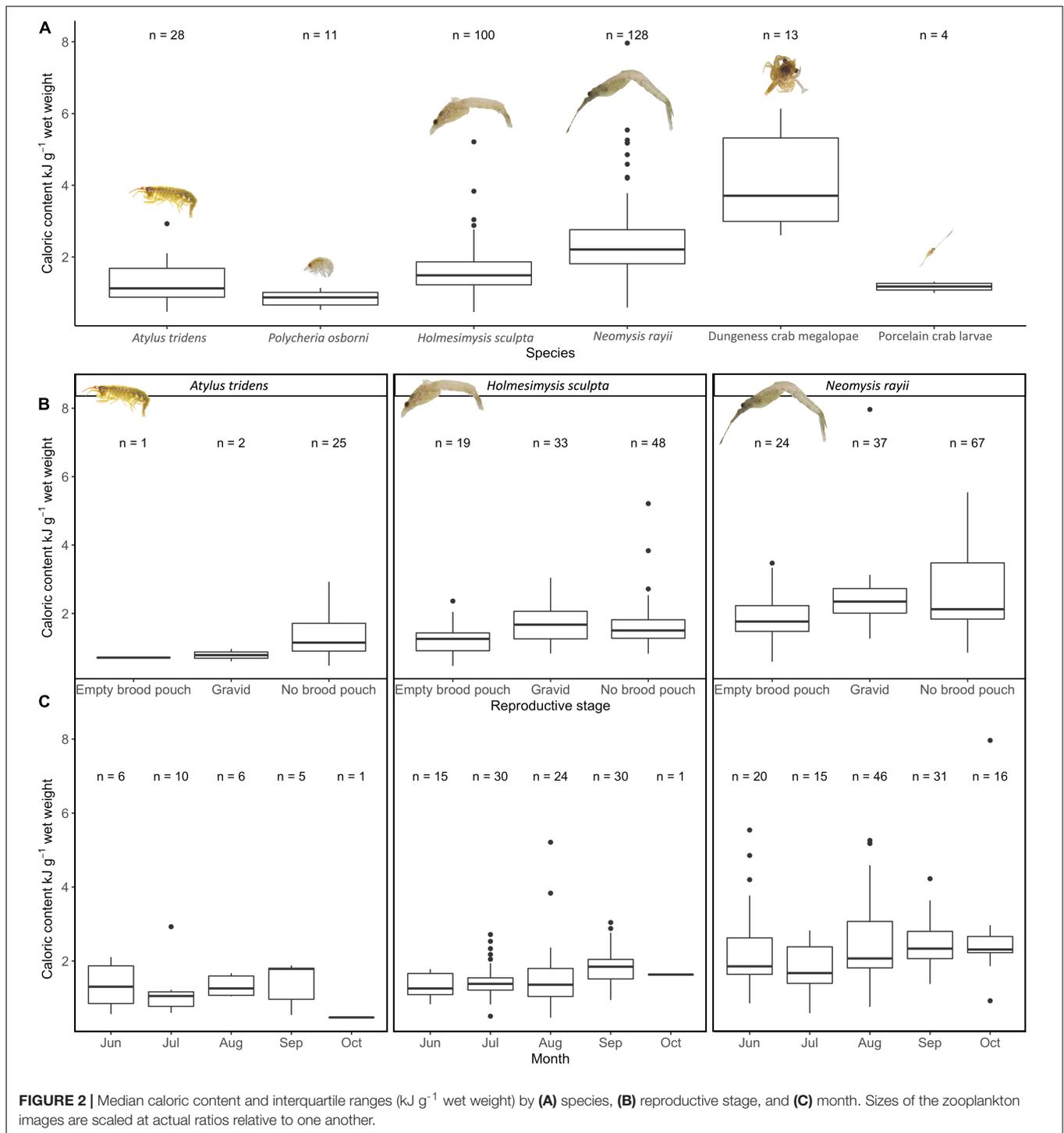
Energetic Value

A total of 284 energetic values were determined (Table 1). Caloric content did not vary significantly between years (Kruskal–Wallis $\chi^2 = 3.20$, $df = 2$, $p = 0.202$). Therefore, samples were pooled across years for all subsequent analyses.

The energetic density between species (pooled across reproductive stage and month) varied significantly (Kruskal–Wallis $\chi^2 = 123.38$, $df = 5$, $p \geq 0.0001$; Figure 2A). Dungeness crab megalopae ($n = 13$) had the highest mean energetic density (4.21 ± 1.27 kJ g⁻¹) and the amphipod *P. osborni* ($n = 11$) had the lowest mean energetic density (0.83 ± 0.21 kJ g⁻¹). Caloric values of Dungeness crab megalopae and the mysid *N. rayii* (2.42 ± 1.06 kJ g⁻¹) were significantly higher than those of the mysid *H. sculpta* (1.60 ± 0.66 kJ g⁻¹), porcelain crab larvae (1.17 ± 0.14 kJ g⁻¹), and the amphipods *A. tridens* (1.25 ± 0.57 kJ g⁻¹) and *P. osborni* (Dunn's test, $p < 0.001$). Dungeness crab megalopae and *N. rayii* caloric contents were also significantly different from one another, with the former having the higher caloric value (Dunn's test, $p = 0.0006$). The caloric contents of *H. sculpta* and *P. osborni* differed significantly (Dunn's test, $p = 0.0006$), with *H. sculpta* having a higher caloric content. All other pairwise comparisons were not significant (Dunn's test, $p > 0.006$). Comparison of the mean caloric values of the prey species tested in this study to the mean caloric value of Arctic amphipod *A. macrocephala* (2.02 kJ g⁻¹) showed that two Oregon zooplankton species have higher caloric contents, namely Dungeness crab megalopae and *N. rayii* (Table 1). The PCFG composite prey caloric value was 1.91 kJ g⁻¹.

Since significant differences between species were found, analyses to determine whether energetic values vary by reproductive stage and month were carried out within each species. Sufficient replicate samples for different reproductive stages and months were only obtained for the two mysid species (*N. rayii* and *H. sculpta*) and the amphipod *A. tridens*.

Reproductive stages had significantly different caloric values for *H. sculpta* (Kruskal–Wallis $\chi^2 = 10.34$, $df = 2$, $p = 0.005$),



however, not for *N. rayii* (Kruskal–Wallis $\chi^2 = 9.49$, $p = 0.008$) nor *A. tridens* (Kruskal–Wallis $\chi^2 = 3.35$, $p = 0.187$) (Figure 2B). For *H. sculpta*, females with empty brood pouches had significantly lower caloric values ($1.23 \pm 0.49 \text{ kJ g}^{-1}$) than gravid females ($1.74 \pm 0.58 \text{ kJ g}^{-1}$; Dunn’s test, $p = 0.0007$), but not than individuals with no brood pouch ($1.65 \pm 0.73 \text{ kJ g}^{-1}$; Dunn’s test, $p = 0.008$). No significant differences were identified between

H. sculpta gravid females and individuals without a brood pouch (Dunn’s test, $p > 0.1$).

Significant differences in energetic content between months were only detected for *H. sculpta* (Kruskal–Wallis $\chi^2 = 15.38$, $\text{df} = 4$, $p = 0.004$; Figure 2C), whereby September was significantly higher than all other months (June, July, August; Dunn’s test, $p < 0.002$), except October (Dunn’s test, $p > 0.4$).

Linear regressions of caloric content by reproductive stage within each species over time (DOY) revealed that the energetic value of the gravid reproductive stage increased significantly throughout the season for both mysids, *H. sculpta* ($F_{1,31} = 15.71$, $p = 0.0004$, $R^2 = 0.32$) and *N. rayii* ($F_{1,35} = 6.138$, $p = 0.0182$, $R^2 = 0.12$) (Figure 3). All other linear regressions conducted were not significant ($p > 0.2$; Figure 3).

Energetic Extrapolation

A gray whale feeding exclusively on Dungeness crab megalopae, the highest caloric prey tested in this study (Table 1), would meet its daily energetic requirements by consuming 0.95 or 0.64 (pregnant or lactating, respectively) metric tons day⁻¹ (Figure 4A). In contrast, a gray whale feeding exclusively on the amphipod *P. osborni*, the lowest caloric prey tested in this study (Table 1), would meet its daily energetic requirements by consuming 4.82 or 3.25 (pregnant or lactating, respectively) metric tons day⁻¹ (Figure 4A). A pregnant female would need to consume 1.65, 1.98, 2.50, 3.20, and 3.42 metric tons day⁻¹, while a lactating female would require 1.12, 1.34, 1.69, 2.16, and 2.31 metric tons day⁻¹ of *N. rayii*, *A. macrocephala*, *H. sculpta*, *A. tridens*, and porcelain crab larvae, respectively (Figure 4A). A gray whale feeding on the PCFG composite prey would meet its daily energetic requirements by consuming 2.09 or 1.41 (pregnant or lactating, respectively) metric tons day⁻¹ (Figure 4A).

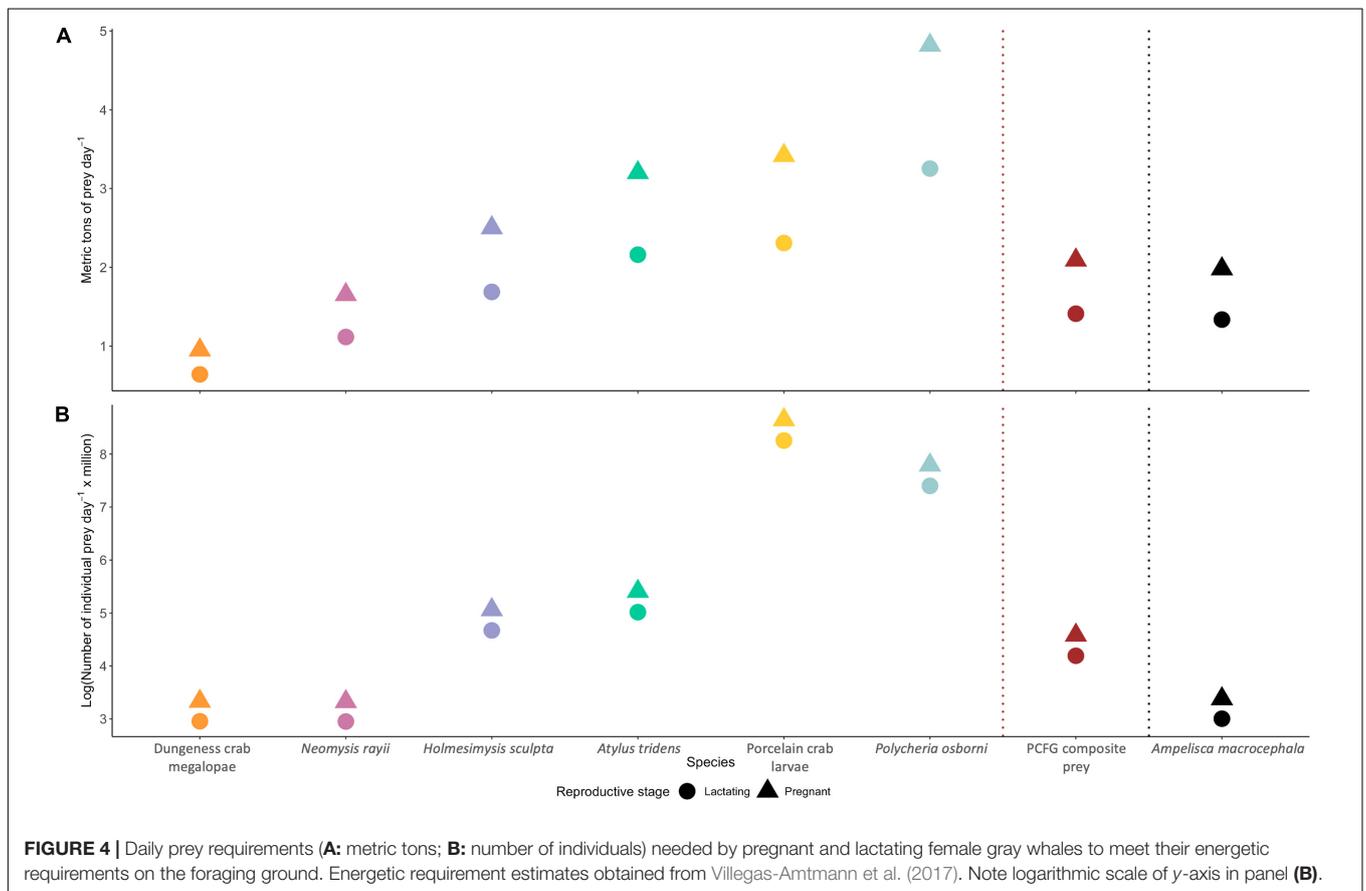
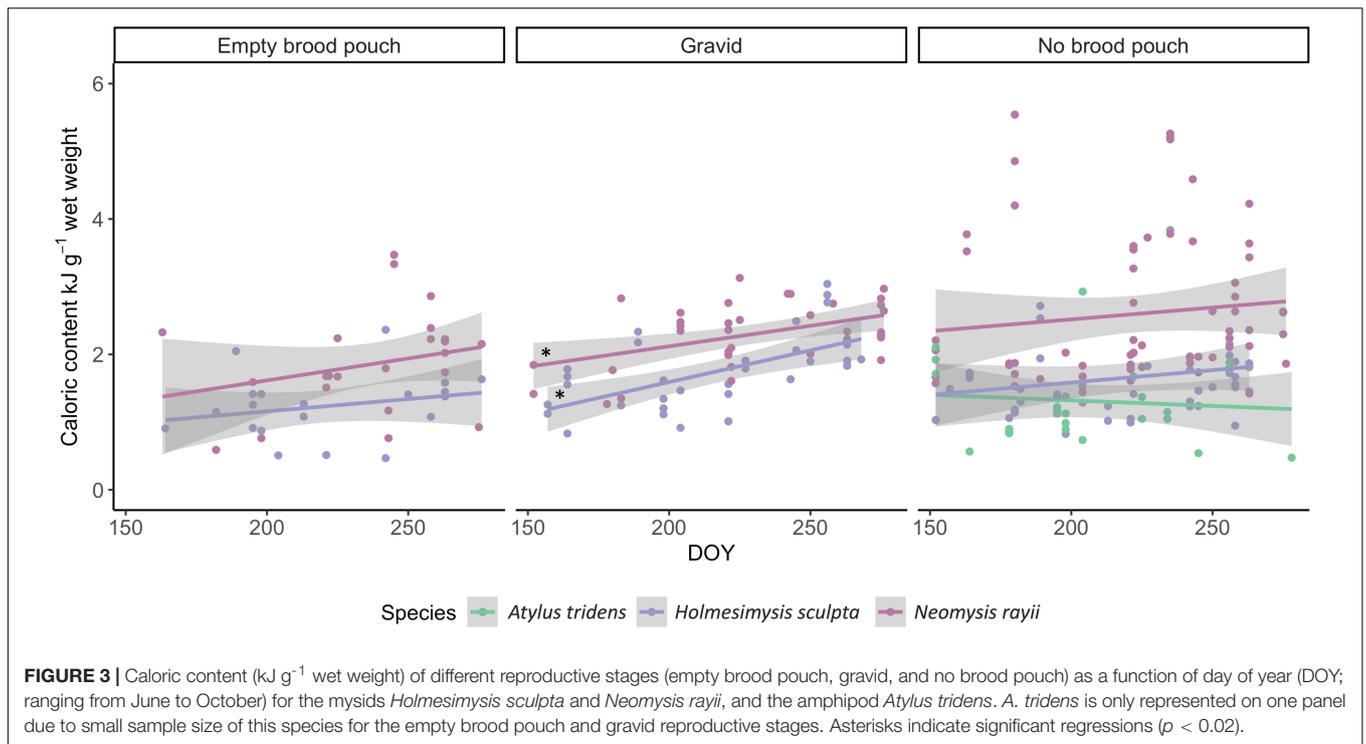
The number of individual zooplankton a gray whale needs to consume to achieve its daily energetic requirement varies widely by prey species (Figure 4B). The smallest total number of individual prey a gray whale would need daily is 26.8 or 18.1 million individuals of *N. rayii*, depending on if the gray whale is a pregnant or lactating individual, respectively (Figure 4B). In contrast, if a gray whale fed solely on porcelain crab larvae, the greatest number of individual prey items would be needed, totaling 5,698 or 3,846 million individuals day⁻¹, depending on the stage of the gray whale (pregnant or lactating, respectively; Figure 4B). A pregnant female would need to consume 26.9, 28.4, 156.9, 222.2, and 2,421 million individuals day⁻¹, while a lactating female would require 18.2, 19.1, 105.9, 150.0, and 1,634 million individuals day⁻¹ of Dungeness crab megalopae, *A. macrocephala*, *H. sculpta*, *A. tridens*, and *P. osborni*, respectively (Figure 4B). A gray whale feeding on the PCFG composite prey would need to capture 96.6 or 65.2 (pregnant or lactating, respectively) million individuals day⁻¹ (Figure 4B) to meet its daily energetic requirements.

DISCUSSION

Contrary to our hypothesis, Arctic prey (ampelisid amphipods) are not the most calorically rich prey species available to gray whales in the eastern North Pacific (of the seven species considered in this study). Rather, two prey species collected in the PCFG range along the Oregon coast, Dungeness crab megalopae and the mysid *N. rayii*, had higher caloric values than *A. macrocephala*, which is the predominant ampelisid amphipod species in the Arctic ENP feeding grounds. Given that

the PCFG sub-group of gray whales is considerably smaller (~250 individuals; Calambokidis et al., 2017) than the ENP (~20,000; Stewart and Weller, 2021), our comparative results suggest that caloric value of prey may not be a driver in the larger population size of the ENP, but rather prey abundance, depth, habitat, and patch density may influence gray whale foraging ground use.

Baleen whales must hold their breath while diving to search for, locate and consume their prey, making foraging behavior energetically costly for rorqual whales (e.g., blue and humpback whales; Acevedo-Gutiérrez et al., 2002) and likely for gray whales too, which spend only 17% of their time at the surface while feeding (Stelle et al., 2008). Hence, whales must ensure they target prey patches that are dense enough to compensate for these costs (Goldbogen et al., 2012; Torres et al., 2020). Historically, ENP gray whales foraged in high abundances in the northern Bering Sea, particularly in the Chirikov Basin (Johnson and Nelson, 1984), where the benthic amphipod community is considered one of the most productive in the world, with the predominant species, *A. macrocephala*, reported as being the most productive benthic marine amphipod species (Highsmith and Coyle, 1990). In the 1980s the mean abundance of *A. macrocephala* was $2,499 \pm 1,183$ individuals m⁻² (Highsmith and Coyle, 1990), however, recent density estimates demonstrate a large reduction, of up to 50% in some areas (Moore et al., 2003; Coyle et al., 2007b). This reduction in benthic prey populations has occurred simultaneously to increased pelagic fish populations, a reduction of sea ice, and increased air and ocean temperatures, and it is believed that a major ecosystem shift from arctic to subarctic conditions is occurring in the northern Bering Sea (Grebmeier et al., 2006). Coincident with this decline in primary prey and ecosystem change, the foraging habitat of ENP gray whales has shifted further north into the Chukchi Sea to an area where water depths range from 40 to 60 m (Moore et al., 2003; Bluhm et al., 2007; Brower et al., 2017, 2018), which is markedly deeper than where gray whale foraging was previously concentrated in the shelf waters of the northern Bering Sea (20–40 m; Coachman et al., 1975). The increased depth range means that benthically feeding ENP gray whales must dive deeper than previously, which may increase the energetic cost of foraging. In contrast, along the Oregon coast, PCFG gray whales typically forage in water depths that are on average four times shallower (mean = 12.7 m, SD = 3.98 m, $n = 345$ sightings, L. Torres unpublished data) than feeding habitat in the Chukchi Sea. The shallow depth of PCFG foraging habitat not only reduces dive time and associated energetic costs, but likely also reduces the amount of surface recovery time needed in between dives, thereby increasing the amount of foraging time available to PCFG whales. However, foraging depth does not account for prey availability and therefore is not directly related to consumption rates or energetic costs. Thus, empirical data of foraging gray whale bioenergetics (i.e., kinematics, respiratory patterns) paired with prey availability information are needed to evaluate these hypotheses regarding cost-benefit trade-offs between PCFG and ENP gray whales. Nevertheless, it appears that PCFG whales have three advantages over ENP whales: a considerably shorter migration (Calambokidis et al., 2002), greater or equal prey caloric value, and possible behavioral energetic advantages of



shallow foraging habitat. Despite this, the vast majority of gray whales in the North Pacific forage in the Arctic, not the PCFG range. Therefore, we hypothesize that prey within the PCFG range have reduced availability, predictability, and patch density compared to ENP foraging grounds in the Arctic.

Dungeness crab megalopae were the most calorically rich prey tested in this study. A gray whale, regardless of reproductive stage, would need less than half of the required amount of *A. macrocephala* to reach its daily energetic requirements if it only consumed Dungeness crab megalopae. However, Dungeness crab megalopae occurrence on the Oregon coast is not consistent throughout the summer due to the seasonality of Dungeness crab reproduction (Roegner et al., 2007), with the megalopae larvae only available to nearshore foraging gray whales in the late spring and early summer (Shanks and Roegner, 2007). Therefore, while Dungeness crab megalopae can be considered caloric “gold mines,” they are an ephemeral prey resource for foraging gray whales. Consequently, PCFG gray whales must be flexible foragers with a diverse diet and the ability to switch between prey types as availability dictates.

In contrast to Dungeness crab megalopae, the mysid species *N. rayii* and *H. sculpta* are more consistently available throughout the summer along the PCFG range due to their continuous iteroparous reproduction (Mauchline, 1980). While the energetic benefit of feeding on *N. rayii* is not as large of a benefit as feeding on Dungeness crab megalopae, a diet of the former would result in a gray whale in either reproductive stage requiring approximately one million less individual prey items a day than if it fed on *A. macrocephala* in the Arctic (Figure 4B). Sighting rates of PCFG whales peak toward the end of the feeding season in August and October (Scordino et al., 2017) and may be explained by the concurrent seasonal increase in caloric content of prey, particularly of gravid mysids (Figure 3). Mysids aggregate by size class and reproductive stage (Kaltenberg and Benoit-Bird, 2013), making patches of gravid individuals with high caloric content even more profitable to foraging gray whales. However, little is known about mysid patch density and distribution due to their preferred shallow, rocky, often kelp-dominated, habitat that makes net-tow and hydroacoustic measurements challenging. The wide range of mysid density estimates within the PCFG range (714–15,541 individuals m^{-3}) illustrate the high variability and patchiness of this prey resource to gray whales (Kaltenberg and Benoit-Bird, 2013; Feyrer and Duffus, 2015). At small scales, fluctuating oceanographic conditions, such as internal waves, currents, and tides (Prairie et al., 2012), and swarming behaviors, including antipredator responses (Folt and Burns, 1999; Kaltenberg and Benoit-Bird, 2013), drive mysid patch dynamics. These factors make fine-scale mysid density hard to measure since patches may form and disperse faster than they can be quantified (Feyrer and Duffus, 2015).

While caloric content and patch density impact the energetic benefit of foraging decisions, whale foraging behavior can significantly impact the energetic cost side of the equation. Mysid species may be more continuously available throughout the foraging season in the PCFG range, but their patchy distribution may require a gray whale to search harder and/or longer before it finds a suitably dense prey patch to offset foraging

costs, as compared to a potentially more stable distribution of *A. macrocephala* in the Arctic. Two previous studies have associated poor body condition of PCFG gray whales with unfavorable environmental conditions linked with poor prey availability and the costs associated with increased time spent searching (Newell and Cowles, 2006; Soledade Lemos et al., 2020). When mysid patches become less dense and/or abundant, PCFG gray whales may have to work harder to find enough prey to meet their energetic demands. However, the risk of this patchier prey availability in the PCFG range relative to *A. macrocephala* in the Arctic region may be compensated for by the elevated caloric content of *N. rayii* and especially Dungeness crab megalopae.

Furthermore, the energetic input required of a gray whale to capture surface swarms of crab larvae, including both Dungeness crab megalopae and porcelain crab larvae, appears to be very low based on field observations and drone footage (L. Torres, pers obs). When feeding on both species of crab larvae, gray whales appear to exert little energy as they lay at the surface, with minor forward movement, and repeatedly open and close their mouths to capture and filter prey (Supplementary Video). In contrast, PCFG whales are often observed working harder (qualitative assessment based on body dynamics and breathing rates) when foraging on mysids that are commonly found in rock crevices of reef systems and kelp forests (Torres et al., 2018; L. Torres, pers obs). Torres et al. (2018) documented several unique behaviors displayed by PCFG gray whales while foraging in reef habitat, including “bubble blasts” where whales release air while underwater presumably to access or aggregate prey, and “headstands” where whales position themselves head down, flukes up in the water column to push their head/mouth region into the substrate to capture prey. While these qualitative assessments do not account for any variation of internal biomechanics of prey consumption (i.e., gular and tongue pumping), it does suggest that foraging on mysids and benthic amphipods may be more energetically costly than feeding on surface crab larvae. However, quantitative assessments of the energetic requirements of these different foraging behaviors are required to confirm this hypothesis.

It is possible that PCFG whales do not exclusively feed along the West Coast range, but perhaps switch foraging ground use relative to environmental and prey conditions. Classification of a PCFG whale is defined as an individual documented in the range between northern California to northern British Columbia (from 41°N to 52°N) between June 1 and November 30 in at least two different years (International Whaling Commission (IWC), 2012). While this definition requires an individual to show some degree of site fidelity to the PCFG range, it does not preclude PCFG whales from utilizing areas outside of the PCFG range. In fact, satellite tag and photo identification data demonstrate that PCFG individuals utilize areas outside of the PCFG range (i.e., Icy Strait and Kodiak Island, Alaska, United States) in the late spring and early summer, before spending the majority of the summer feeding within the PCFG range (Mate et al., 2010; Gosho et al., 2011; Ford et al., 2013). The PCFG’s small abundance estimate and evidence of matrilineal fidelity (Calambokidis and Perez, 2017) suggests that knowledge of this alternative foraging ground could be culturally transmitted (e.g., Valenzuela et al., 2009;

Baker et al., 2013), and, as our study demonstrates, potentially advantageous. Comparative assessments of recruitment rates and population dynamics between the PCFG and ENP relative to oceanographic factors and prey availability may elucidate the relative advantage of this cultural group, and reveal whether feeding in the PCFG range is an exclusive behavior or used as an ecological safety net during unfavorable conditions in the Arctic.

Although our study demonstrates that some prey species found in the PCFG gray whale range have greater caloric value than the predominant prey in ENP feeding grounds in the Arctic, thus enabling PCFG whales to potentially meet their daily energetic requirements faster, the vast majority of gray whales in the North Pacific feed on amphipod amphipods in the Arctic. If we assume that gray whales forage optimally (MacArthur and Pianka, 1966; Charnov, 1976), this conundrum indicates that prey patch density and predictability, and behavioral cost of capture likely play a significant role in the trade-offs of foraging ground use. However, reduction of amphipod amphipod biomass from the 1980s to the 2000s (Moore et al., 2003; Coyle et al., 2007b) and rapidly changing environmental conditions in the Arctic (Johannessen et al., 2004; Overland and Stabeno, 2004; Wang et al., 2012; Box et al., 2019), raise questions about the stability of this Arctic food resource to gray whales. In fact, ENP gray whales have undergone two unusual mortality events (UME) in the last two decades (1999–2000 and 2019–present), with elevated strandings of emaciated whales likely due to reduced prey availability as a function of the population exceeding carrying capacity (Rugh et al., 2005; Coyle et al., 2007b) and/or environmental change (Le Boeuf et al., 2000; Moore et al., 2001, 2003; Stewart and Weller, 2021). Furthermore, ENP calf production is correlated with spring sea ice conditions in the Arctic, with early access to prey by gestating females resulting in higher calf production in the subsequent year (Perryman et al., 2020). Yet, ongoing climate change is predicted to alter this pattern in the future (Perryman et al., 2020). Even though the abundance estimates for the PCFG have remained relatively stable since 2002 (Calambokidis et al., 2017), environmental changes are also occurring within the PCFG range, with increased occurrence of marine heat waves (Gentemann et al., 2017; Joh and Di Lorenzo, 2017; Frölicher et al., 2018) and resultant changes in prey communities (Peterson et al., 2017; Brodeur et al., 2019). To understand and anticipate gray whale population response to these impacts of climate change, it is important to monitor their prey availability, foraging ecology, and health (i.e., body condition) at both foraging grounds. Addressing these topics will enhance management of both the ENP and PCFG gray whale

populations and further our understanding of the factors that limit the carrying capacity of the PCFG region.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

LH contributed to project development, data collection, data processing, led data analysis, and led manuscript writing. KB provided access to lab and calorimetry instruments, oversaw caloric lab and data analysis, and provided edits to the manuscript. LT conceived the project, acquired funding for fieldwork, oversaw data collection and analysis, and contributed to manuscript preparation. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.683634/full#supplementary-material>

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