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INTRA-SEASONAL VARIATION IN FEEDING RATES AND DIEL FORAGING BEHAVIOR IN A SEASONALLY FASTING MAMMAL, THE HUMPBACK WHALE (*MEGAPTERA NOVAEANGLIAE*)

A thesis submitted in partial satisfaction
of the requirements for the degree of

MASTER OF SCIENCE

in

OCEAN SCIENCES

by

Ross C. Nichols

December 2020

The thesis of Ross C. Nichols is approved:

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ABSTRACT

Intra-seasonal variation in feeding rates and diel foraging behavior in a seasonally fasting mammal, the humpback whale (*Megaptera novaeangliae*)

by Ross C. Nichols

Southern hemisphere humpbacks whales are seasonally fasting mammals who concentrate foraging in summer when Southern Ocean waters are most productive, coincident when their primary prey, the Antarctic krill, are most accessible. To accumulate blubber energy stores necessary to fuel energetically costly migrations and breeding events during the winter fasting period, humpbacks optimize foraging behaviors to exploit the ephemeral distribution and behavior of their prey. While humpback foraging in fall, prior to a northward migration, is well described, foraging upon arrival to the foraging grounds in summer is poorly understood. Between 2010-2019 we deployed suction cup attached biologgers onto 83 adult humpbacks along the Western Antarctic Peninsula throughout the austral summer and early fall. Tags remained attached for 18 hours on average, recording high resolution motion, depth and audio of the animal. Using idiosyncratic motion signals, we manually detected feeding lunges for each deployment, yielding 33,246 total detected lunge events between depths of 0 – 461 meters. Our results did not support previous hypotheses of increased humpback foraging from summer to fall along the WAP, conversely, we found a 51% reduction in daily feeding rates over the same period. There was nearly continuous daylight during the early summer period where whales fed during all hours of the day, this changed such that foraging occurred mostly during nighttime hours in the fall. Changes in lunge depths observed over the season indicate that humpbacks track the diel vertical migrations of krill that appear to change over the foraging season. Our results provide novel information on seasonal changes in foraging behavior of humpback whales and demonstrate that these animals, contrary to nearly all other animals that seasonally fast, likely maximize their food intake immediately upon exiting the fasting period. More direct information on krill densities concurrent to whale foraging would allow quantification of food intake to better test this hypothesis.

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INTRODUCTION

Foraging, or the process by which an organism captures energy from its environment, is necessary for fueling biological processes. Within a habitat, animals forage on discrete patches of prey that vary in space and time, and efficient acquisition of these variable resources is necessary to maximize the probability of reproductive success and survival *(Charnov 1976; Stephens and Dunlap 2017).* Animals must therefore exhibit plasticity in their foraging behavior in order to maximize energy gain while minimizing energetic cost (Charnov 1976). Food intake, a unit of foraging, is the rate of calorie consumption, or in other words, the rate at which an animal removes energy from its environment. Food intake does not describe animals' net energy gain, as determining net gain requires detailed knowledge of both an animal's metabolic costs and the absorption efficiency of the food consumed (Costa and Gales 2003; Gomez-Amaro et al. 2015). Rather, food intake is a measure of foraging effort, and the spatiotemporal patterns of an animal's resource acquisition are a vital metric in the investigation of energetics and ecology (Croll et al. 1998; Florant and Healy 2012; Schneider et al. 2013; Rigano et al. 2016).

In seasonally variable systems, resources are unevenly distributed throughout the year. This results in periodic resource limitations caused, in part, by reductions in primary production, spatiotemporal resource fluctuations, inclement conditions that preclude foraging, or an animal’s intrinsic induction through costly biological processes (Millar and Hickling 1990). Fasting mammals circumvent this by accumulating excess energy as internal (e.g., fat, blubber) or external (e.g., food hoarding) energy caches (Florant and Healy 2012). Animals can then utilize these energy reserves when resources in the environment are insufficient to maintain homeostasis or fuel energetically costly life history events (e.g., gestation, migration, moult, arousal) (Humphries, Thomas, and Kramer 2003; Dark 2005; Kumar and Mishra 2018). The accumulation of caches, however, relies on the efficient consumption of resources through optimal decision making and the precise timing of phenological events to synchronize foraging effort with periods when resources are most efficiently available (Armstrong et al. 2016; Visser and Gienapp 2019). Often, fasting animals express a period of hyperphagia, concentrating food intake over a relatively short period of time during the foraging season (Dark 2005; Florant and Healy 2012). This highlights a critical foraging period when resources are acquired from the environment at peak efficiency, and signaling potential mass gain paramount for an animal’s successful development of energy caches. Efficient foraging on these fugacious resources is thus paramount to accumulating sufficient energy to ensure a fasting mammal’s survival and growth.

Food intake is the product of intrinsic and extrinsic factors that simultaneously influence foraging (Schneider et al. 2013). In many terrestrial fasting animals, food intake is dependent on intrinsic signals of body condition and metabolic state (e.g. torpor, activity) (Florant and Healy 2012; Dark 2005). Food intake is also driven by the external environment, where prey availability, predation threat, and environmental factors influence an animal's ability to acquire prey (Stephens and Dunlap 2017). To optimize food intake, animals maximize overlap between intrinsic needs and extrinsic availability of resources (Ramakers, Gienapp, and Visser 2019; Visser and Gienapp 2019). They achieve this through the timing of major phenological events such as migration, hyperphagia, or hibernation, which are heavily influenced by both intrinsic and extrinsic factors (Saino et al. 2010; Evans et al. 2016; Oliver et al. 2020). Thus, by measuring food intake in free-living animals, one inherently receives information on animals' internal and external state and can draw hypotheses regarding the environmental conditions and phenological timings influencing food intake. However, disentangling the interactions between intrinsic and extrinsic factors requires specific investigation and has been subject to recent study (Daunt et al. 2005; De Pascalis et al. 2020; M. Humphreys, Wanless, and M. Bryant 2006).

Food intake is notoriously difficult to measure in free-living animals, requiring measurements of both foraging event frequency (i.e. feeding rate) and the caloric value associated with each event (i.e. prey quality) (Burns, Pond, and Fisher 1994; Chivers 1998). These measurements are especially arduous to obtain in cryptic species or those inhabiting remote or inaccessible environments. Marine environments prove exceptionally difficult to investigate, as consumers and resources are distributed ephemerally over vast spatial and temporal scales and can be logistically difficult for researchers to quantify. To overcome this obstacle, recent research has gained insight into marine systems via biologging the behavior of air-breathing diving predators (e.g. seabirds, marine mammals), using them as surveyors of the remote environments they inhabit (Simmons et al. 2007; Charrassin et al. 2002; Miller et al. 2004; Jaud et al. 2012; Guinet et al. 2014; Benoit-Bird et al. 2013; Saijo et al. 2017)

Biologgers are a critical tool for studying food acquisition in marine predators (Wilson et al. 1993; Ropert-Coudert and Wilson 2005; Williams et al. 2020; Wilmers et al. 2015). However, the difficulty of discerning individual foraging events using biologgers has resulted in a plethora of techniques used to best measure and quantify fine-scale foraging, each with varying resolution, limitations, and assumptions (Simeone and Wilson 2003; Ropert-Coudert and Wilson 2005; Naito et al. 2013; Horsburgh et al. 2008; Liebsch et al. 2007). Many biologgers are capable of estimating coarse animal behavioral states at broad spatio-temporal scales, such as satellite tags estimating animal foraging through ‘area-restricted search’ (ARS) (Jonsen, Flemming, and Myers 2005; Gurarie et al. 2016). However, most satellite tags lack precise measurements that question accuracy of behavioral classification on scales relevant to the species in question (Weimerskirch et al. 2007; Hebblewhite and Haydon 2010; Williams et al. 2020). More recent studies have overcome this methodological hurdle by using tags equipped with high resolution accelerometer sensors, as seen in pinniped and cetacean species, minimizing previous resolution limits in detecting foraging events (Iwata et al. 2012; Naito et al. 2010; Naito et al. 2013; Gallon et al. 2013; Cade et al. 2016).

Rorqual whales (*Balaenopteridae*), a family of the baleen whales (*Mysticete*), are ideal research candidates of fine-scale foraging using motion sensing tags, as their unique foraging strategy has defined jerk ($\frac{m}{s^3}$), speed ($\frac{m}{s}$), and body orientation signals. This 'lunge feeding', named for its abrupt thrust of forward motion, begins with a whale's rapid acceleration upon approaching a dense prey patch before opening its mouth for capture. During this behavior, the water's dynamic pressure inflates the buccal cavity, comprised of an accordion-like arrangement of spring-like blubber (i.e. ventral groove blubber)(Shadwick et al. 2013), enabling engulfment of enormous volumes of prey-laden water (Goldbogen et al. 2017; Goldbogen et al. 2011b). This incurs high drag forces, resulting in a pronounced deceleration of the whale. The engulfed prey-laden water, up to 160% of the whale's body mass, is then sieved through keratinous baleen filters, expelling water and extracting prey for consumption (Goldbogen et al. 2017). The high signal to noise ratio of foraging events in rorquals provides a unique opportunity to precisely measure individual foraging events in a freely-moving marine mammal. These behavioral classifications can be made with high confidence, due to recent tag deployments collecting synchronous motion and video data on rorqual whales. This allows researchers to validate movement signatures with concurrent direct observations of foraging behavior (Cade et al. 2016; Cade et al. 2018). Such tactics have often been employed with humpback whales (*Megaptera novangliea*), a cornerstone species for biologging research.

Humpback whales are large-bodied rorqual whales that partition each year between low latitude breeding and calving sites in the winter, and high latitude foraging sites between spring and fall, with migrations between each site spanning thousands of miles (Dawbin 1966; Rasmussen et al. 2007). Humpbacks fast during the breeding season and surrounding migrations, where all metabolic needs are satisfied solely by the breakdown of internal adipose stores (i.e. blubber). Humpbacks are estimated to lose 25 – 50% of their body mass over this period (Lockyer 1981; Christiansen et al. 2020). Humpback whales, and other migratory baleen whales, are unlike terrestrial fasting animals that reduce energy expenditure through torpor. Rather, humpbacks incur increased metabolic costs while fasting by engaging in costly physiological and behavioral processes associated with reproduction and migration (Félix and Haase 2001). Humpbacks meet this energy demand through efficient foraging, as humpbacks target prey patches yielding the highest net energy gain, maximizing patch density while minimizing the cost to attain it (Goldbogen et al. 2013; Goldbogen et al. 2015; Friedlaender et al. 2016; Tyson, Friedlaender, and Nowacek 2016; Friedlaender et al. 2017). Additionally, humpbacks modify foraging behavior to adapt to the diel vertical migrations (DVM) of prey (Friedlaender et al. 2009; Espinasse et al. 2012), concentrating foraging effort when prey are shallowest to maximize net energy gain (Friedlaender et al. 2013). Targeting this dense, shallow prey minimizes their inter-lunge intervals, thus increasing feeding rate and foraging efficiency (Ware, Friedlaender, and Nowacek 2011; Tyson, Friedlaender, and Nowacek 2016; Friedlaender et al. 2016). Thus, in the absence of prey data, the presence of humpback foraging can serve as an indicator of dense prey distributions.

Humpback foraging in the Southern Hemisphere exploits the highly productive Antarctic and sub-Antarctic waters, coincident with the summer retreat of annual sea ice and the spawning season of Antarctic krill (*Euphausia superba*), their primary prey (Kawamura 1980; Lockyer 1981; Nicol 2006). The Western Antarctic Peninsula (WAP) serves as a summer foraging ground for a subpopulation (breeding stock G) of humpbacks that migrate from winter breeding grounds off the coast of Ecuador and Colombia ("Annual Reports of the International Whaling Commission" 2006; Albertson et al. 2017). While the timing of migration is dependent upon sex, age, and reproductive status, humpbacks generally arrive to the WAP in late spring to early summer (Nov-Jan) (Lockyer 1981; Craig et al. 2003). Upon arrival in early summer, krill are broadly distributed across the neritic and oceanic waters, foraging on phytoplankton growth enhanced by the extended solar period and incursions of nutrient-rich circumpolar deep water (Nicol 2006; Prézelin et al. 2000; Dinniman, Klinck, and Smith 2011). As the season progresses towards fall, krill aggregations shift into the sheltered bays and fjords close to shore (Nicol

2006; Cleary et al. 2016; Nowacek et al. 2011; Espinasse et al. 2012). Coincident with a horizontal shift, krill patch density and vertical distributions also fluctuate over the humpback foraging season. Krill appear to be distributed in lower densities and at shallower depths in the spring, progressively becoming deeper and more densely aggregated into nearshore areas in the fall (Lascara et al. 1999; Nicol 2006; Atkinson et al. 2008; Lawson et al. 2008). Surveys in the WAP bays and fjords have found deep and highly dense patches of large-bodied krill in the late foraging season (Cleary et al. 2016; Nowacek et al. 2011). However, these studies were temporally restricted and may not be representative of typical late-season environments. Another factor influencing the distributions of krill species along the WAP is the presence of a DVM, with shallow krill aggregations during the nighttime becoming deeper during the day (Espinasse et al. 2012; Cleary et al. 2016; Friedlaender et al. 2016). Seasonal fluctuation in solar period, food abundance and predation risk have been hypothesized to abate the amplitude of the migration in the summer period, resulting in lower magnitude DVMs in the summer and becoming progressively more extreme into fall (Lascara et al. 1999; Cleary et al. 2016; Cresswell et al. 2009; Conroy et al. 2020). Variation in prey density and depth over the foraging season can massively impact humpback food intake, yet prey information on the spatio-temporal scales relevant to humpbacks is lacking along the WAP, curtailing accurate prediction of seasonal humpback foraging behavior and food intake.

Summer – fall humpback foraging inferred from ARS suggests a continuous increase in time spent foraging as the season progresses, peaking in fall (Weinstein and Friedlaender 2017). If foraging inferred from time spent in ARS is assumed to be a reasonable approximation of food intake, it can be hypothesized that humpback food intake increases throughout the foraging season with a fall maximum. Early studies estimating humpback weight gain using harvesting records from industrial whaling predicted that by February, body mass would be at a seasonal asymptote; contradictory to ARS estimates, this would require peak food intake in January or earlier (Lockyer 1981). However, humpbacks are known to stay on the foraging grounds until May or June, three to four months post-Lockyer's (1981) predicted mass peak. Why animals would remain on the foraging grounds long after peak mass also remains uncertain. To resolve these inconsistencies and improve our understanding of humpback food intake requires continuous and accurate measures of feeding rates throughout the course of the entire feeding season. To date, however, the only published literature on fine-scale foraging behavior comes from the fall (May – June), showing that humpbacks exhibit extreme diel foraging patterns, foraging solely during night periods and mostly at depths >50 meters (Ware, Friedlaender, and Nowacek 2011; Friedlaender et al. 2013).

As fasting animals, humpback food intake over their foraging period is of critical ecological importance. Understanding intra-seasonal foraging dynamics of humpbacks can reveal novel information about cryptic prey environments. In the absence of prey data, humpback foraging can identify spatiotemporal fluctuation in suitable quality prey distributions. Using high-resolution accelerometer tags, this thesis will investigate humpback predation dynamics over the foraging season to test both novel and existing hypotheses. Specifically, we test the ARS derived hypothesis that humpback food intake (measured by feeding rates) increases as the foraging season progresses from January -June, peaking in June. Additionally, we test the hypothesis that krill perform an abated DVM in the summer, and that diel differences in vertical and temporal distribution become more extreme into the fall by measuring the relative distribution of humpback foraging by time of day and depth over the foraging season.

MATERIALS AND METHODS

Suction Cup Tag Deployment

We deployed two types of high-resolution, archival, non-invasive, digital recording motion-sensing tags to study the foraging behavior of humpback whales:

- DTAGs – (https://www.soundtags.org/) capable of recording depth (pressure transducer), a triaxial magnetometer and accelerometer sampled at 50 Hz, and audio (stereo-hydrophone; sampling rate: 64 kHz) (Johnson and Tyack 2003).
- CATS (Customized Animal Tracking Solutions; http://www.cats.is/) – capable of recording depth (pressure transducer), motion (triaxial

magnetometer and accelerometer) sampled between 40 – 400 Hz, and audio (stereo hydrophone; sampling rate: 64 kHz) (Cade et al. 2016).

All deployments were on adult humpback whales in nearshore waters on the continental shelf of the WAP between 64°32'7.74"S and 65° 6'44.83"S latitude and 61°29'2.70"W and 64°50'47.12"W longitude. Tags were deployed between 2009-2019 spanning the months of January-June. Data collection was performed under multiple projects, including the cetacean ecology component of the Palmer Station Long Term Ecological Research Project on the Antarctic peninsula (https://pal.lternet.edu/). Although deployments occurred over a long period of time with multiple tag types, data processing methodologies remained consistent across deployments. Deployments were conducted aboard 6 – 7 m inflatable vessels, equipped with a bow pulpit. Tags were deployed using a 3 – 4 m carbon fiber pole with a friction-fit housing; tags are deployed on the back of the whale adhering via four silicon suction cups. Tags are designed to remain on the whale for up to 48 hours and all data are archived on the tag. GPS locations were taken immediately after deployment to record time and location of animal attachment. After detaching from the animal and floating to the surface, a GPS location and VHF transmitters were used to relocate the tag for retrieval and data download. All tagging procedures were conducted under NMFS marine mammal research permits, Antarctic Conservation Act Permits, and certified Institutional Animal Care and Use Committee protocols in conformance with the Animal Welfare Act.

Raw Data Processing and Lunge Detection

Post-recovery, raw data was extracted using proprietary software developed by the respective tag companies. Sensor data processing for use in further analysis used custom MATLAB (Natick, Massachusetts: The MathWorks Inc., ver. 2014a) scripts (Cade et al. 2016). Individual feeding lunges were manually identified through a combination of accelerometer data, magnetometer data, and speed similar to previous work (Goldbogen et al. 2017; Goldbogen et al. 2019; Shadwick, Potvin, and Goldbogen 2019). Changes in animal speed, a primary metric used to identify lunges, was calculated from accelerometer jiggle and flow noise (Cade et al. 2018). Expert auditors experienced in identifying characteristic kinematic signals of foraging manually discriminated lunges for each deployment. Idiosyncratic signals of lunges included episodic fluctuations in body orientation (roll, pitch and heading), peaks in jerk ($\frac{\mathrm{m}}{\mathrm{s}^3}$) and speed ($\frac{\mathrm{m}}{\mathrm{s}}$) as the whale accelerates towards its prey before opening its mouth to engulfing a large volume of prey-laden water. Baleen whale lunge feeding produces an extraordinary kinematic signature because of the rapid acceleration and deceleration signal (Shadwick, Potvin, and Goldbogen 2019). Because of this and the suite of other sensors to help corroborate these signals, we have high accuracy when determining individual feeding events (Cade et al. 2016; Goldbogen et al. 2017). For each feeding lunge, we also recorded the time of day and depth.

Normalized Feeding Rates

Feeding rate, or the number of feeding lunges over a given period of time, was calculated for each tag deployment (**Equation 1**). Where FR_t is the feeding rate of time period (*t*) of which the rate is being calculated. L_t is the number of detected lunges within the time period (*t*), and S_t is the number of periods (*t*) sampled with recorded tag data. We calculated both hourly and half-hourly feeding rates for all individuals in our analysis.

Equation 1.

$$FR_t = \frac{L_t}{S_t}$$

Diel Period and Solar Elevation

For hours where tag data was present*,* each hour of the day was classified into one of two diel periods: day or night. Due to the extreme fluctuation in solar period across the austral summer, hour of the day could not be used as consistent delineators throughout the course of the entire feeding season. Rather, we used solar position relative to time of day, measured as solar elevation in degrees above the horizon. Boundaries between these periods were set to: Day > 0° ≥ Night; where 0° represents sunset. While the solar elevations between 0° (sunset) and -6° (civil twilight) are typically more associated with a crepuscular period; elevations below -6° were not present in the early summer thus there was no true 'night' during these periods. In essence, what we refer to as 'night' is more accurately a combination of night and crepuscular periods. Solar elevation was calculated using "*The Climate Data Toolbox for MatLab*" (Greene et al. 2019); these values were equivalent to those generated by the NOAA solar calculator (https://www.esrl.noaa.gov/gmd/grad/solcalc). Solar elevations were calculated for each detected lunge and for each hour of the day where tag data was present. For each tag, GPS coordinates taken immediately post-tag deployment were used as the location for their respective solar calculations.

We calculated the ratio of daytime to nighttime feeding rates (henceforth referred to as "diel feeding ratio") for each analysis period. This was calculated by dividing the number of lunges by the number of sampled hours separately for both daytime and nighttime hours, producing a mean daytime and nighttime feeding rate. The mean daytime rates were then divided by the mean nighttime rates to produce a diel feeding ratio value. A ratio value larger than 1 indicates higher daytime rates while values lower than 1 indicate relatively higher nighttime feeding rate.

Seasonal Foraging Analysis

To test for seasonal changes in feeding rates and foraging behavior, data was pooled into 20-day analysis periods to estimate foraging metrics characteristic of each period. 20-day period lengths were chosen to balance sample size and ecologically relevant seasonal resolution. Six 20-day analysis periods were created from January 1st – June 9th or ordinal date 1 and 160 respectively. March 22nd – April 30th (ordinal date 81 – 120) was excluded from this analysis due to insufficient data. Analysis periods (**Figure 1 & Table 1**) were labelled A – F and encompass the following 20-day calendar periods: A.) January 1st – January 20th, B.) January 21st – February 9th, C.) February 10th – March 1st, D.) March 2nd – March 21st , (Excluded; March 22nd – April 30th), E.) May 1st - May 20th, F.) May 21st – June 9th. Refer to table 1 for sample sizes, deployment locations and statistics by analysis period. Daily feeding rates were calculated for each analysis period (**Equation 2***)*. Where the FR_{h} is the calculated feeding rate for hour of the day (*h*), and the estimated daily feeding rate is the summation of FR_{h} across all hours of a 24-hour period day.

Equation 2.

$$Est. Daily\ Feeding\ Rate = \sum_{\mathrm{h}=1}^{24} FR_{\mathrm{h}}$$

Statistics and Figures

To test the hypothesis that humpback whale foraging increases from summer to fall along the WAP, for each individual deployment we calculated hourly feeding rates for every hour of the day. then calculated estimated daily feeding rates using equation 2 for each analysis period. A linear regression analysis was then performed on estimated daily feeding rates compared to analysis period. A linear regression analysis was also performed on lunge depth by analysis period to test for linear trends in foraging depth over the foraging season.

We also tested the hypothesis that diel differences in humpback foraging behavior increase in magnitude from summer to fall. We used two distinct methods to assess this comparison: categorical (day versus night) and by hour of the day. First, to investigate and assess the categorical differences in diel foraging behavior over the foraging season we used a single sample Kolmogorov-Smirnov test to test our samples against normal distributions. We performed this on both lunge depths and feeding rates for each sampled day and night period by each analysis period. We then performed a Student's two-sample t-test between day and night samples of feeding rate and lunge depth for each analysis period. Next, we calculated the diel feeding ratio for each analysis period. A linear regression analysis was then applied, comparing day:night ratios of feeding rate to analysis period.

Using a secondary method to test for changes in diel foraging behavior over the study period, we compared feeding rates and foraging depth by hour of the day. We performed a linear regression analysis on lunge depth and individual hourly feeding rates by ordinal date segregated for each hour of the day in which the foraging occurred.

All figures and statistical analysis were generated using statistical software *MATLAB* (Natick, Massachusetts: The MathWorks Inc., ver. 2019b). All linear regressions were calculated using the least-squares method. The significance threshold was set at 0.05 for all p-values.

RESULTS

We deployed 83 tags between January 5th and June 4th during the years 2009, 2010, and 2016 – 2020. 16 deployments were DTAGS deployed in 2009 and 2010; the remaining 67 were CATS tags deployed between 2016 – 2020. 14 deployments with less than one full hour of data were excluded from analysis. Of the 69 remaining deployments a total of 1276.4 hours of recorded sensor data were usable for analysis. The length of deployments ranged from 2.1 – 56.9 hours with a mean (mean ± s.d.) duration of 18.49 ± 10.39 hours. A total of 33,246 lunge feeding events were detected across all deployments. Conversely, two deployments had no detectable lunges, whose mean deployment lengths were 3.63 ± 2.19 hours. The lack of detected lunges on these deployments may have been due to their short duration. Lunges were detected at depths between 0 and 461 m (62.0 ± 81.28 m). Depths of lunges were predominantly shallow with 65% of all detected lunges occurring $\geq$ 50 meters.

Intra-Seasonal Variation in Feeding Rate and Depth

To evaluate variation in feeding rates over the foraging season, we calculated estimated daily feeding rates (lunges day^{-1} $whale^{-1}$) for each analysis period (**Figure 2, top & Table 2**). Period A: 770.8, B: 699.4, C: 752.0, D: 628.8, E: 359.9, F: 394.8. Daily feeding rates were highest during period A with an estimated rate of 770.8 lunges day^{-1} $whale^{-1}$ while the lowest rates were present in period E at 359.9 lunges day^{-1} $whale^{-1}$. A linear regression analysis on daily feeding rate by analysis period found a significant decrease throughout the season ($R^2 = 0.91$, $p = 0.0027$). Feeding rates declined significantly as the season progressed with rates 51.2% lower during the terminal study period (Period F, 394.8 lunges day^{-1} $whale^{-1}$) in contrast with the initial period (A, 770.8 lunges day^{-1} $whale^{-1}$).

For each analysis period, we also calculated mean hourly feeding rates (lunges $hour^{-1}$ $whale^{-1}$) (**Table 2**). Reported here as: mean ± sd (range); period A: 32.1 ± 11.1 (11.8 – 48.5); B: 29.1 ± 12.9 (11.7 – 55.2); C: 31.3 ± 24.2 (5.7 – 75.2); D: 26.2 ± 23.8 (0.5 – 65.8); E: 15.0 ± 12.3 (0 – 38.8); F: 16.4 ± 11.9 (0 – 34.6). Maximum mean hourly rates were found in period A with 32.1 lunges $hour^{-1}$ $whale^{-1}$ with minimum rates in E with 15.0 lunges $hour^{-1}$ $whale^{-1}$.

Mean feeding depths (m) for each analysis period, (**Figure 2, center & Table 2**); reported here as: mean ± sd (range); period A: 16.1 ± 17.4 (0.4 – 157.3); B: 12.1 ± 8.9 (0.2 – 111.8); C: 55.4 ± 63.1 (0.7 – 301.1); D: 101.0 ± 107.8 (0.5 – 461.1); E: 96.3 ±

65.6 (3.0 – 339.5); F: 116.5 ± 91.5 (1.4 – 387.7). Maximum mean foraging depths were in period D at 101.0 m with minimum feeding depths occurring in period B with 12.1 m. A linear regression analysis (**Figure 2, center**) on feeding depth with ordinal date showed a significant increase in foraging depth over the study period ($R^2 = 0.18083$, $p < 0.001$, $N = 33246$). We saw significant variation in foraging depths over the study period with near surface (<30m), unimodal foraging occurring primarily in the beginning of the study period shifting to a bimodal distribution in foraging with predominantly deeper lunges (>50m) later in the season (**Figure 3**).

Intra-Seasonal Variation in Diel Foraging Behavior

Feeding depths between day and night periods were significantly different for every analysis period (two-sample t-test; **Table 3**). Comparisons were most significant in period C (t-stat: 26.58, df: 9240, $p < 0.001$) and least significant in period F (t-stat: -2.32, df: 2757, $p = 0.02$). However, it should be noted that period F recorded only 4 total lunges during daytime hours. Minimum mean feeding depths occurred in period B (9.2 ± 4.2, N = 1581) during the night. Daytime minimum depths were recorded in period F (10.4 ± 1.9, N = 4), however, only 4 lunges were detected and is likely not representative of typical feeding depths (**Figure 4**). Maximum foraging depths were found in period E during the daytime (223.6 ± 92.5, N = 69) which also had very few total lunges detected during this period. We also found significant differences in hourly feeding rates between day and night for every analysis period (**Table 4**). Comparisons were most significant in period C (t-stat: -16.6, df: 273, p <0.001) and least significant in period F (t-stat: -4.74, df: 138, p <0.001). Minimum hourly feeding rates were recorded in periods E (1.2 ± 4.9, N = 24) and F (2.0 ± 5.8, N = 32) during the daytime with a maximum in period C (59.3 ± 28.9, N = 93) during the night (**Figure 5**).

To test seasonal differences in diel foraging using categorical assignments of day and night, we calculated the diel feeding ratio for each analysis period (**Figure 2, bottom**). A: 0.51, B: 0.34, C: 0.23, D: 0.27, E: 0.10, F: 0.04 We found that the highest diel feeing ratio occurred in period A with a value of 0.51, meaning that average daytime hourly feeding rates were 51% that of nighttime rates. The smallest ratio occurred in period F with a value of 0.04, indicating very low daytime feeding rates compared to nighttime in the terminal study period. We performed a linear regression analysis of the diel feeding ratio by the analysis period and found a significant negative trend ($R^2 = 0.91$, p = 0.003).

As a secondary method of investigation into seasonal changes in diel foraging behavior instead using continuous variables, we compared both feeding rates and depths by local hour of the day for each analysis period. For reporting of foraging depths, see **Figures 6 & 8**. For reporting on feeding rates, see **Figures 7 & 8**. Extremely low mean hourly feeding rates (<5 lunges hour^{-1} whale^{-1}) were present during select hours of analysis periods D (0900 – 1500), E (0800 – 1400) and F (0900

– 1400). No foraging was detected during select hours of period E (0800, 0900, 1100) and F (1000, 1100, 1300, 1400). Especially high mean feeding rates (>60 lunges hour^{-1} whale^{-1}) were present during periods C (2200 – 0300) and D (0000 – 0200) with our reported maximum during 2300 of period C (75.2 lunges hour^{-1} whale^{-1}). Feeding occurred at all hours of the day at shallow depths in the early study period, before becoming progressively deeper and at lower rates as the season progressed; except for the hours surrounding midnight, which saw a peak in feeding rates in the mid-study period. See **Figure 9** for an integrated view of diel feeding depth and rates for each analysis period.

We tested for seasonal changes in diel feeding depths and feeding rates by performing a linear regression analysis on both lunge depths and individual mean feeding rates by ordinal date for each hour of the day (**Figures 10 & 11**). Our results found a significant increase in feeding depth for each hour of the day throughout the study period ($p < 0.001$) (**Figure 10**). The most significant increase in foraging depth over the study period took place during the hour of 0200 ($p < 0.001$). The least significant increase took place during 1100 ($p < 0.001$). For additional reporting of linear regression results, refer to figure 10. Our results for feeding rates by hour of the day over the study period found heterogenous trends and significance between hours (**Figure 11**). Over the course of the season, no significant trend in feeding rates were seen during the hours of 0000, 0200 – 0700, 1700, 2000 – 2200. While feeding rates significantly decreased during the hours of 0800 – 1500. Conversely, significant increases in feeding rate were seen in hours 1600, 1800, and 1900. The most significant trend was found at 1900 ($R^2 = 0.30$, $p < 0.001$, $N = 55$), the least significant was at 0700 ($R^2 < 0.001$, $p = 0.98$, $N = 57$) and 2100 ($R^2 < 0.001$, $p = 0.98$, $N = 41$). For additional reporting of linear regressions, refer to figure 11.

DISCUSSION

Our results provide the first evaluation of intra-seasonal variation in foraging behavior of an Antarctic cetacean. We found that in early summer, humpback whales exhibited extremely high feeding rates on shallow prey. As the foraging season progressed into fall, whales subsequently fed deeper and at lower rates. We also found that whales fed over more hours of the day and at twice the rates early in the season versus late in the season. We posit that these changes in foraging behavior are largely in response to shifting prey distribution (shallow versus deep prey availability), however, humpbacks' intrinsic signals such as energy gain also likely play a crucial role that is worthy of future investigation. Humpback whales have been shown to modify their behavior to maximize net-energy gain and our results display the clear behavioral plasticity required to do so in a seasonally variable environment. High feeding rates in the early summer were likely enhanced by the consistent availability of shallow prey, allowing humpbacks to maximize foraging efficiency, as has previously been recorded (Ware, Friedlaender, and Nowacek 2011; Friedlaender et al. 2016).

Intra-seasonal Variation in Humpback Foraging Behavior

Our results do not support the hypotheses proposed by satellite telemetry studies, which suggest that whales spend more time feeding later in the season than earlier in the season. Along the WAP, Weinstein and Friedlaender (2017) measured an increasing trend in inferred foraging between January to June derived from ARS. Our results show that feeding rates exhibit the opposite trend, with estimated daily feeding rates declining as the season progressed. We believe that the satellite tag data clearly detect a shift in the distribution of whales and their prey (and therefore foraging), and that the changes in ARS do not reflect true feeding rates and effort. In the early season, the targeting of shallow, but horizontally dispersed prey could attenuate the ARS signal as humpbacks forage over broader areas (Curtice et al. 2015), despite our results indicating the foraging occurring at higher rates. Furthermore, our results also indicate that the late season ARS signal could be inflated. As fall approaches, krill concentrate within bays and fjords along the WAP and whales distribute themselves relative to this change (Nowacek et al. 2011; Curtice et al. 2015). Coincidentally, extreme diel segregation of humpback foraging behavior becomes more prominent later in the season, when low movement behaviors (e.g. resting) become common during the daylight hours. Humpbacks also appear to target much deeper prey later in the season than earlier in the season, presumably increasing vertical prey search during the fall (Friedlaender et al. 2013; Friedlaender et al. 2016). The combination of resting during daytime periods and foraging in concentrated areas at night contribute to the increased amount of time whales spend in ARS but the relatively low feeding rates observed during this time of year.

Geophysical features and prey distributions may influence humpback foraging strategy and its interpretation through ARS on the WAP. Interestingly, ARS of humpbacks in Eastern Antarctica peaked in the center of the foraging season in February and March (Riekkola et al. 2019), two months earlier than estimates on the WAP, and two months later than our reported peak in feeding rates (analysis period A). While our peaks in daily feeding rates did not correspond, select crepuscular hours in late February (analysis period C) marked our recorded maximum mean hourly feeding rates (75 lunges hour^{-1} whale^{-1}), coincident to the ARS peaks found in Riekkola et al. (2019). Eastern Antarctic humpbacks forage following a retreating ice edge in open water systems throughout the season where krill may be subject to advection or large horizontal variation in areas of oceanographic retention (Nicol 2003; Bestley et al. 2019; Riekkola et al. 2019). This contrasts with the fall, when krill are horizontally restricted into embayments and retained through consistent low velocity surface currents and mesoscale eddies that could offer consistent inter-annual foraging habitats (Zhou, Niiler, and Hu 2002; Beardsley, Limeburner, and Owens 2004; Nowacek et al. 2011; Espinasse et al. 2012) Other marine mammals have been shown to disproportionately express ARS in areas exhibiting historically consistent prey availability rather than in open ocean habitats, irrespective of actual foraging success between the habitats (Thums, Bradshaw, and Hindell 2011). Thus, these habitat differences likely require differing optimal foraging strategies to which our results may not necessarily apply and the relationship between ARS to both feeding rates and foraging success may differ between them.

Foraging Behavior and its Relation to the Prey Environment

Our results describing the feeding behavior of the WAP's largest krill consumer indicate that humpback foraging changes in multiple dimensions throughout the summer – fall, signaling clear shifts in seasonal prey availability. The distribution and abundance of the Antarctic krill at large spatial or temporal scales are notoriously difficult to measure in the Southern Ocean. However, models of the multi-dimensional shifts in krill behavior have been enhanced through large scale survey efforts, comprehensive databases and independent proxy measures (Siegel and Watkins 2016). Our study contributes to a framework of estimating prey dynamics in remote areas by measuring the foraging of air-breathing diving predators (Guinet et al. 2014; Chimienti et al. 2017; Saijo et al. 2017; Green et al. 2020). Humpback whale foraging depth increases from summer to fall, with early season feeding occurring primarily in the upper 30m of the water column, transitioning into a bimodal distribution in May and June surrounding depths of 60m and 225m (**Figure 3**). Humpbacks have been shown to optimize feeding efficiency during shallow feeding by incorporating filtration into their surface intervals (Ware, Friedlaender, and Nowacek 2011; Friedlaender et al. 2016; Tyson, Friedlaender, and Nowacek 2016) allowing them to incorporate non-feeding activities into prey handling times. It is reasonable then, to suggest that the abatement of shallow forging in the fall indicates a significant reduction in availability of dense prey in the upper water column in comparison to the early summer along the WAP.

In addition to the vertical variability in foraging, we also found pronounced trends in the diel foraging activity of humpbacks from summer to fall. Diel variability in foraging behavior that mirrors prey behavior has been observed in multiple humpback populations (Friedlaender et al. 2009; Stimpert et al. 2007) including along the WAP (Friedlaender et al. 2013). DVM of Antarctic krill in the Southern Ocean is regionally and seasonally variable (Lascara et al. 1999). Evidence of DVM in Antarctic krill along the WAP suggests more extreme vertical movements in fall compared to summer (Zhou and Dorland 2004; Espinasse et al. 2012; Cleary et al. 2016). However, the timing of the transition between these DVM phases has not been measured from summer to fall, nor has the rate of change between them. Our results found significant differences in both feeding rate and foraging depth between night and day during all analysis periods and suggest that a component of diel variability in foraging behavior persists throughout the entire study period. Additionally, our results report that the diel feeding ratio (day:night) declined significantly from early summer (0.51) to fall (0.04). These results suggest that humpbacks transition between two behavioral modes of diel foraging effort; from an early summer mode of foraging occurring at all hours of the day with relatively moderate diel differences, to a diel pattern in the fall with foraging occurring almost exclusively at night.

Our results show similarity to previous reports of diel krill abundance in the summer and fall, indicating that seasonal fluctuations in shallow prey availability are a likely driver of shifts in humpback foraging behavior. In the summer along the WAP, krill express shallow distributions (<60m) throughout the night and day, with relatively higher abundance of shallow krill occurring at night (Cresswell et al. 2009). These observations are parallel to our results of foraging throughout the day in the summer, but at relatively higher rates in the night. This suggests that the relative diel abundance of krill influence the rate at which humpbacks are foraging in the upper water column. However, additional information on krill densities is needed to assess this, as prey abundance must be accompanied with a minimum threshold patch density for foraging to be energetically beneficial for baleen whales (Goldbogen et al. 2015). In the fall, a more pronounced DVM has been observed, with Antarctic krill descending at dawn, at roughly 0800 (Zhou and Dorland 2004). This corresponds precisely with the descent in mean foraging depth and major reduction in feeding rates during the fall that our analysis revealed (analysis periods E and F). Zhou and Dorland (2004) also recorded upward movement of krill occurring at about 1600-1700, corresponding to our results showing major increases in feeding rates during this period at increasingly shallow depths (**Figure 8 and 9**).

The humpback foraging patterns reported here likely reflect intra-seasonal availabilities of dense krill in the upper water column. We believe the increasing diel differences in humpback foraging is likely driven by a more dramatic diel vertical migration made by Antarctic krill from summer into fall. Our results indicate a flexibility in humpback behaviors that enables them to efficiently acquire energy from the environment across seasons/throughout seasonal cycles through the exploitation of their prey's cyclic behaviors. These results illustrate the temporal periods critical to humpback foraging and their variation throughout the foraging season, which should be taken into consideration in future assessments of humpback food intake.

Seasonal Food Intake

Estimating humpback whale food intake is a critical component of understanding the structure and functioning of Southern Ocean marine ecosystems. When baleen whales forage on zooplankton at depth, they enable remineralization of limited nutrients, such as iron, into the photic zone through defecation. In nutrient-limited regions, such as the Southern Ocean, humpbacks serve as a unique nutrient recycler promoting phytoplankton growth (Nicol et al. 2010; Roman and McCarthy 2010; Roman et al. 2014). While the extent to which humpbacks contribute to primary production remains under investigation (Ratnarajah, Nicol, and Bowie 2018), any trophic effects will increase in magnitude as Southern Ocean baleen whale populations continue to recover from industrial whaling. Estimates of nutrient remineralization, however, could be vastly improved by measuring food intake rates on the foraging grounds. Additionally, food intake is highlighted as desired research for ecosystem management as factors such as climate change, an expanding krill fishery and tourism driven vessel traffic all threaten whale's access to their primary prey (Williams and Crosbie 2007; Montes-Hugo et al. 2009; Flores et al. 2012; Childerhouse 2011; Weinstein et al. 2017).

Indirect methods of calculating food intake rely on estimations through allometric scaling of annual metabolic costs to generate average daily intake rates given a 120-day foraging period (Innes et al. 1986; Boyd and Hoelzel 2002; Reilly et al. 2004; Leaper and Lavigne 2007). However, we believe these methods give unrealistic predictions of daily feeding as homogenous daily events across the foraging period by neglecting to incorporate or validate with *in situ* measurements of feeding rate and prey density. Previous *in situ* measurements by Owens et al. (2017) of Southern Ocean humpbacks prior to their arrival at Antarctic feeding grounds estimated ingestion rates of 1.2 to 3.4x humpback daily energetic requirements. However, daily ingestion was based on short daytime measurements, which likely biased these reported daily feeding rates to the specific hours recorded. Our results suggest that the hour of day and time of year should be considered when extrapolating fine-scale foraging resolution to daily rates for humpbacks.

A simple model of *in situ* estimates of food intake rates can be calculated using the following equation:

$$\text{food intake rate } \left(\frac{\text{kg of prey consumed}}{\text{time}}\right) = \text{feeding rate } \left(\frac{\text{number of lunges}}{\text{time}}\right) \times$$
$$\text{captured prey density [prey patch biomass density (kg m}^{-3}\text{)} \times \text{capture efficiency (\% of biomass captured)]} \times \text{engulfment volume (m}^{3}\text{)}$$

While absolute values of food intake or caloric intake are beyond the scope of our study, relative intra-seasonal trends in food intake rates can be theorized given a set of assumptions. If we assume that engulfment volumes and capture efficiency are constant, then food intake rates would be a function of feeding rates and prey biomass density. Given our results in intra-seasonal lunge rates, we estimate theoretical krill biomass densities necessary to sustain the following three theoretical distributions of intra-seasonal food intake rates: 1.) Constant food intake rates: If food intake rates were to remain constant over the foraging season, prey biomass density would be predicted to increase relative to the gradual decrease in feeding rates, eventually doubling from summer to fall. For example, if mean prey biomass densities in the early summer were 1.0 kg m^{-3} at a rate of 771 lunges day^{-1}, fall densities of 1.9 kg m^{-3} would be necessary for food intake rates to be equivalent given our reported rates of 395 lunges day^{-1}. While we believe a constant food intake rate is unlikely given the high variability in feeding rates; if food intake were limited not by prey availability but by an unidentified limit on daily ingestion or satiation, seasonally constant food intake would be advantageous. 2.) Unimodal food intake rates: As in many terrestrial fasting animals (Florant and Healy 2012) and as we report in our feeding rates, food intake could also express a unimodal peak in distribution. If targeted prey biomass densities were to decrease over the foraging season or remain constant, peak food intakes would correspond with peak feeding rate in the early summer. For a unimodal peak in food intake to occur outside that of peak feeding rate, targeted prey biomass density must increase over the foraging season. The greater the difference between feeding rates between two points in the season, subsequently would require a greater magnitude in prey density difference to facilitate a peak in food intake. 3.) Multi-modal food intake rates: As with other marine predators (Bost et al. 1997; Thums, Bradshaw, and Hindell 2011; O'Toole et al. 2015), humpbacks may express multi-modal peaks in food intake rates over the foraging period. Periodic travel and subsequent arrival to horizontally distributed high-quality local foraging grounds would be observed as pulses in food intake rates over the foraging season and display a multi-modal distribution. However, the prey density threshold for peak food intake would nonetheless increase over the foraging season given the decreasing daily feeding rates we observed.

Predictions regarding the seasonal modal distribution of humpback food intake would be vastly improved through *in situ* measurements. However, these measurements are currently limited by variability in estimations of prey capture efficiency, engulfment volumes and prey dynamics on seasonal scales. Our prior assumptions of seasonally constant engulfment volume and capture efficiency can easily be challenged. Engulfment volume is highly dependent on body length and lunge speeds (Cade et al. 2016; Kahane-Rapport and Goldbogen 2018) and thus will likely differ based on individual and foraging strategy, a factor worth integrating into future consideration of seasonal variability. Capture efficiency also likely varies over the foraging season, as humpback's reliance on visual prey detection is likely hindered by reduced light availability into the fall season and at depth. Thus, late season foraging conditions may reduce capture efficiency, and thus could partly counteract the effect of increased prey densities. Foraging strategy may also affect capture efficiency, but varies with changing seasonal prey characteristics. For example, humpback bubble net feeding is capable of manipulating prey in ways that may alter targeted patch density and capture efficiency, however, this strategy is only possible when prey are available in the upper water column (>20m, (Wiley et al. 2011)) and thus a bubble netting strategy will be overrepresented in the early season. Intra-seasonal variability in capture efficiency is a likely factor affecting the efficient intake of food across the foraging season and warrants further investigation. Capture efficiency and caloric intake could also be influenced by a changing distribution in krill sizes over the foraging season, with larger and more calorically dense individual krill generally becoming more available in the fall. Although the effect of this on humpback foraging is unclear, it has the potential to influence humpback food intake (Ruck, Steinberg, and Canuel 2014). As humpbacks target ever-deepening prey fields throughout the season, the targeted densities also likely increase (Friedlaender et al. 2016). This is substantiated from previous reporting indicating increased densities of krill swarms at greater depths throughout the season (Nowacek et al. 2011; Espinasse et al. 2012; Cleary et al. 2016) and aligns with the marginal value theorem, as increased travel time should be compensated with increased prey quality or time within a patch (Charnov 1976). However, current literature reporting krill distributions and densities over the summer and fall season prevent proper capture density estimates. This is in part due to the patchiness and temporally limited surveys in neritic waters along the WAP, but also due to the scales used to report biomass in the literature. Spatial scales of prey density and distribution relevant to humpback foraging must account for the spatial scale of a foraging event, or the ‘gulp’ (Cade et al. in review). The gulp acts as a minimum vertical and horizontal resolution at which to assess prey availability, also referred to as the “whale-scale”, which should be considered in future reporting of prey metrics for applications in assessing predator bioavailability.

Indirect methods of measuring food intake rates are likely oversimplified, as they neglect to consider impacts of variable feeding rates, relevant scales of prey densities, temporal variation of prey distribution, and the feedbacks on optimal foraging behavior. These estimates could be improved through *in situ* validation. However, many there are uncertainties in assessing seasonal-scale food intake using *in situ* methods that should be a focus of future work in an effort to establishing more precise models of trophic energy flow in the Southern Ocean.

Optimal Foraging and Migration Timing

Humpback arrival to the seasonal foraging grounds necessitates precise timing of migration to capitalize on the productive summer season in the Southern Ocean. Humpbacks migrate from low latitude breeding sites with no information on foraging ground conditions; reliance of timing is based solely on historical information engrained in previous experience and genotype to synchronize foraging periods with the presence of available prey fields. Fasting animals attempt to maximize overlap between foraging effort and presence of resource availability (Visser and Gienapp 2019); if humpbacks behave in a similar way, food intake efficiency would be increased by maximizing their presence on the foraging grounds with the availability of shallow, dense prey fields. Thus, historical information about humpback migration timings could be used to indicate larger temporal shifts in prey availability where prey data are lacking. In a similar vein, the WAP continues to experience increasingly variable ice conditions (Clarke et al. 2007; Stammerjohn et al. 2008), shifts in phytoplankton distributions (Montes-Hugo et al. 2009) zooplankton demography and community structure (Fraser and Hofmann 2003; Steinberg et al. 2015; Atkinson et al. 2004), and distribution of sympatric krill predators populations (Ainley 2002; Fraser et al. 2013) due to climate change. Thus, the inherit information lag between migration timing and foraging ground conditions allows variability due to climate change the potential to impact the overlap of humpback foraging effort with efficient prey fields. Future research would benefit to better understand the historical and future implications of the phenological mismatch between prey fields and feedbacks in humpback migratory timing.

In Relation to the Fasting Animal Framework

Our results indicate that a critical period of humpback foraging effort takes place in the early summer, soon after their arrival at the WAP foraging grounds. The high daily feeding rates measured during this period were facilitated by suitable prey patches being available shallow in the water column throughout the entire day. Interestingly, in terrestrial systems, peak food intake at the beginning of a feeding season is atypical for most fasting animals. However, humpbacks lack the common burdens that limit early acquisition of mass energy gain in terrestrial fasting animals, and thus may express differing distributions of seasonal food intake and hyperphagia. Terrestrial fasting animals typically express a hyperphagic period near the temporal midpoint between emergence and immergence from torpor (Dark 2005; Florant and Healy 2012). This is the case in golden mantled ground squirrels (*Callospermophilus lateralis*) and yellow-bellied marmots (*Marmota flaviventris*) (Florant et al. 1991; Mrosovsky and Boshes 1986; Davis 1976) The hyperphagic period can also occur near the end of the foraging season, as in some bear species

(Hilderbrand et al. 1999). The timing of the hyperphagic period in terrestrial mammals has been attributed to two main mechanisms. First, the necessary increasing of metabolism after emergence from torpor results in muted behavior for a period after emergence, also called “walking hibernation” in bears, which limits activity and forging motivation (Toien et al. 2011; Evans et al. 2016). The second being the trade-off between the ability to accumulate sufficient energy caches before immergence into torpor with the detrimental costs of carrying those caches. Carrying internal adipose tissues incurs an increased cost of transport, limits mobility, increases predation risk and makes heat dissipation more difficult (Millar and Hickling 1990). Thus, many terrestrial animals will optimize the acquisition of energy stores by modulating food intake to minimize the time spent carrying them while maximizing the energy accumulated before undergoing torpor. Humpback whales are largely unconstrained by these limitations due to an absence of metabolic suppression (Brodie 1975), a low cost of transport (Williams 1999; Goldbogen et al. 2011a; Gough et al. 2019) and lack of adult predation (Steiger et al. 2008; Pitman et al. 2015). Therefore, it is advantageous for humpbacks to regain energy stores as soon as possible by maximizing foraging effort when prey is most efficient to consume. This early hyperphagic hypothesis is supported by our results of humpback feeding rates and depths, however, future research would benefit to test this through better measures of food intake by also estimating captured prey quality.

There are few marine examples of comparison to humpback foraging outside of other baleen whales, however, a worthy species for contrasting foraging behavior is the Southern elephant seal (SES) (*Mirounga leonina*) which shares similar life history characteristics, including extended periods of seasonal fasting and foraging (Laws 1956). SES show similar trends with foraging effort and success peaking near the beginning of their foraging periods (O'Toole et al. 2015). While foraging success is relatively consistent when foraging within productive areas, seasonal variability may be due to increasingly patchy distributions of prey as the foraging season progresses (Cotté et al. 2015; Guinet et al. 2014; O'Toole et al. 2015). SES forage on mesopelagic and benthic prey fields, where seasonal variability may act at differing dimensions and scales than epipelagic systems such as in humpbacks and Antarctic krill (Dall'Olmo et al. 2016). Similarities in foraging phenology seem to favor early-season foraging in both marine predators, however, differing foraging modalities (engulfment feeding versus single target feeding), prey field variabilities and associated foraging pressures likely result in differing optimal foraging strategies worthy of more detailed comparison. These comparisons could be improved with future research into humpback seasonal mass gain rates and the development of long-term tags capable of detecting individual fine-scale foraging variability across a season.

CONCLUSION

Our results challenge a previously established hypothesis of late season humpback hyperphagia by demonstrating that daily feeding rates peak in summer with a subsequent decline into fall. Our reported humpback foraging indicates that Antarctic krill are available during all hours of the day at shallow depths, becoming deeper and unavailable during the day in the late fall. How these seasonal changes in feeding rates affect food intake is uncertain, but likely indicates that the early foraging period is critical for establishing fat reserves. An early hyperphagic period is unique among fasting mammals and is likely enabled by the precise phenological timing of migration on the availability of high-quality prey and an unsuppressed metabolism that enables high foraging activity in the early foraging period.

Our results demonstrate a method of incorporating fine-scale foraging measures of an air-breathing predator into greater frameworks of fasting animal phenology, prey distributions, and a conceptual model of Southern Ocean systems from a predator's perspective. However, our results have limitations that should be considered. Although Antarctic krill appear to be the preferred prey of humpback whales, there are reports of Southern Ocean humpbacks and Antarctic minke whales feeding on crystal krill (*Euphausia crystallorophias*) (Lockyer 1981; Konishi et al. 2013); and it is an assumption that the foraging reported here is representative of foraging on Antarctic krill (*Euphasia superba*). Sampling bias of tagged humpbacks may also influence these results, as humpbacks were tagged on known foraging grounds where they potentially exhibit foraging patterns consistent with historically available prey, rather than any random point along the WAP. Likely, sample size is also a metric that could influence our results through interannual variability, individual variability in foraging behaviors (Wiley et al. 2011; Acevedo et al. 2011), and demographic influence that could determine energetic requirements (Kooijman 2009) and thus foraging strategy. However, these results represent the largest fine-scale cetacean foraging datasets in the Southern Ocean, and we believe that future work is critical to improve our understanding of these considerations on the foraging behavior of humpback whales.

We hope these results contribute to a holistic approach toward a better understanding of seasonal variability in humpback foraging behavior. While our results are critical in bringing humpbacks into a larger ecological framework of foraging phenology, additional work is needed in a few key areas. First, estimations of seasonal mass gain rates are needed for assessing seasonal changes in food intake and the translation of foraging effort into a physiological response. This could be done using existing methods through UAS photogrammetry (Gray et al. 2019) or tag derived buoyancy models (Nousek-McGregor et al. 2014; Robinson et al. 2010). Second, establishing endocrine relationships with adult body condition is vital towards developing biopsy-derived health assessments of individuals. Investigation should focus on common mammalian chemical signals of adipose tissue levels such as leptin, free-fatty acids, ghrelin, and insulin. Comparisons between endocrine relationships on the feeding grounds versus the breeding grounds should also be considered, as the response in the arcuate nucleus of the hypothalamus likely varies between physiological states, as it does in terrestrial fasting animals (Florant and Healy 2012). Third, future research should also consider seasonal variability in specific foraging strategies such as bubble net feeding and the role in efficient foraging. Bubble net feeding, a common strategy of humpbacks (Hain et al. 1981; Wiley et al. 2011; Goldbogen et al. 2017) that has only recently been observed at high frequencies on the WAP (Friedlaender, personal communication, November, 2020), has unique features that allow humpbacks to manipulate prey in the upper water column. This may allow humpbacks to increase krill swarm densities prior to consumption, thus acoustically measured concurrent prey fields would yield underestimates of consumption densities and food intakes calculations and should be considered in future investigation. These suggested research prospects are critical measures in modeling the energetics and ultimate costs of survival of baleen whales and efforts should continue towards innovative approaches to these questions.

Humpback whale foraging contributes a unique perspective on Southern Ocean ecosystems and fasting animal phenology. Measuring a predator's foraging behavior spotlights critical periods of resource acquisition necessary for the accumulation of energy caches from ephemeral resources. Top-down influences of humpback feeding cycles and the interconnected behavior of predator and prey emphasizes investigating humpbacks as a mechanism of ecosystem infrastructure and as an ecosystem indicator. Improvement in disentangling the mechanisms driving foraging variability and its relation to energy acquisition will benefit greatly for better ecosystem monitoring and management of a rapidly changing Southern Ocean.

FIGURES

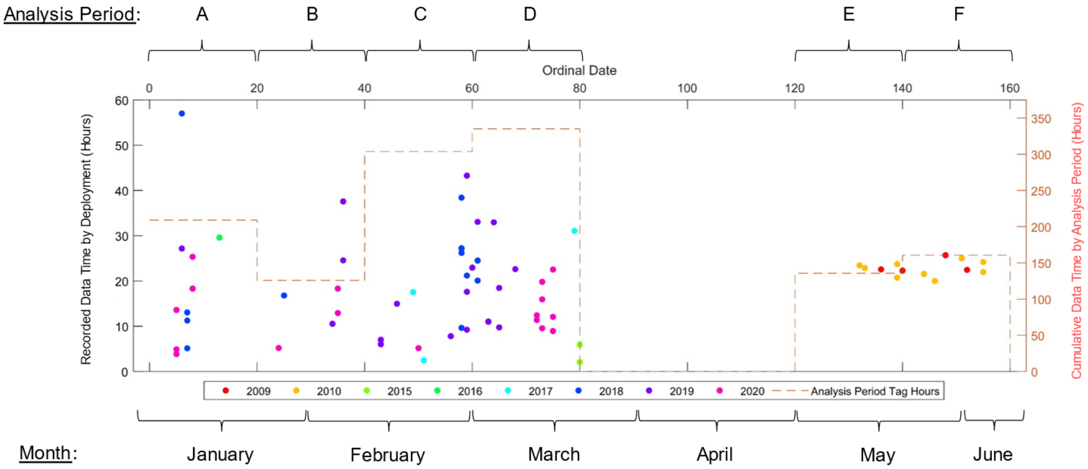


Figure 1 – Study Period Data Summary: A visualization of the study period, deployments and analysis periods. 20-day analysis periods can be seen on the upper x-axis ranging from A – F. Scatter points represent deployments, with year represented as color. The red dashed line represents the cumulative data time from each deployment within respective analysis periods. Calendar months are labeled beneath the x-axis for reference.

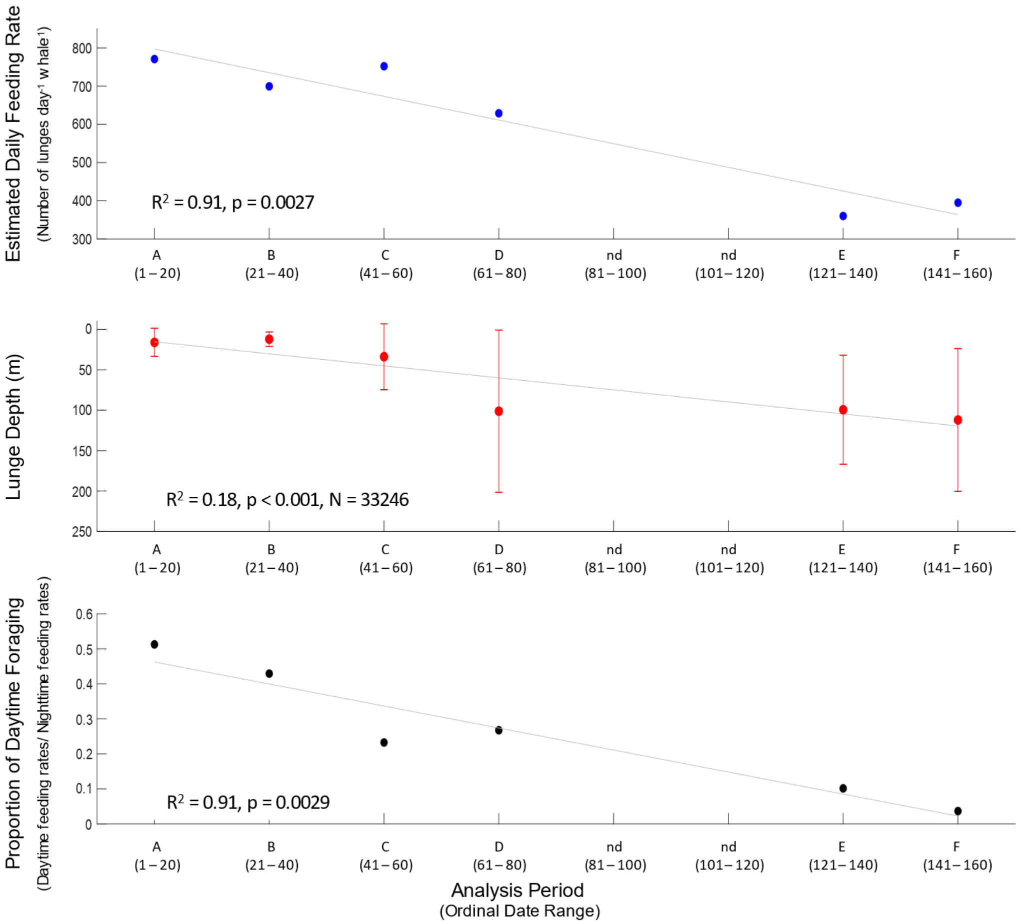


Figure 2 – Linear Regressions in Seasonal Trends of Foraging Metrics: Top.) Estimated daily feeding rates by analysis period. The solid grey line represents the linear regression (R^2 = 0.91, p = 0.0027). Center.) Foraging depth by analysis period. The solid grey line represents the linear regression (R^2 = 0.18, p = <0.001, N = 33246). Error bars extend to the standard deviation for each analysis period. Bottom.) Day to night proportion of feeding rates for each analysis period, the solid grey line represents the linear regression (R^2 = 0.91, p = 0.003).

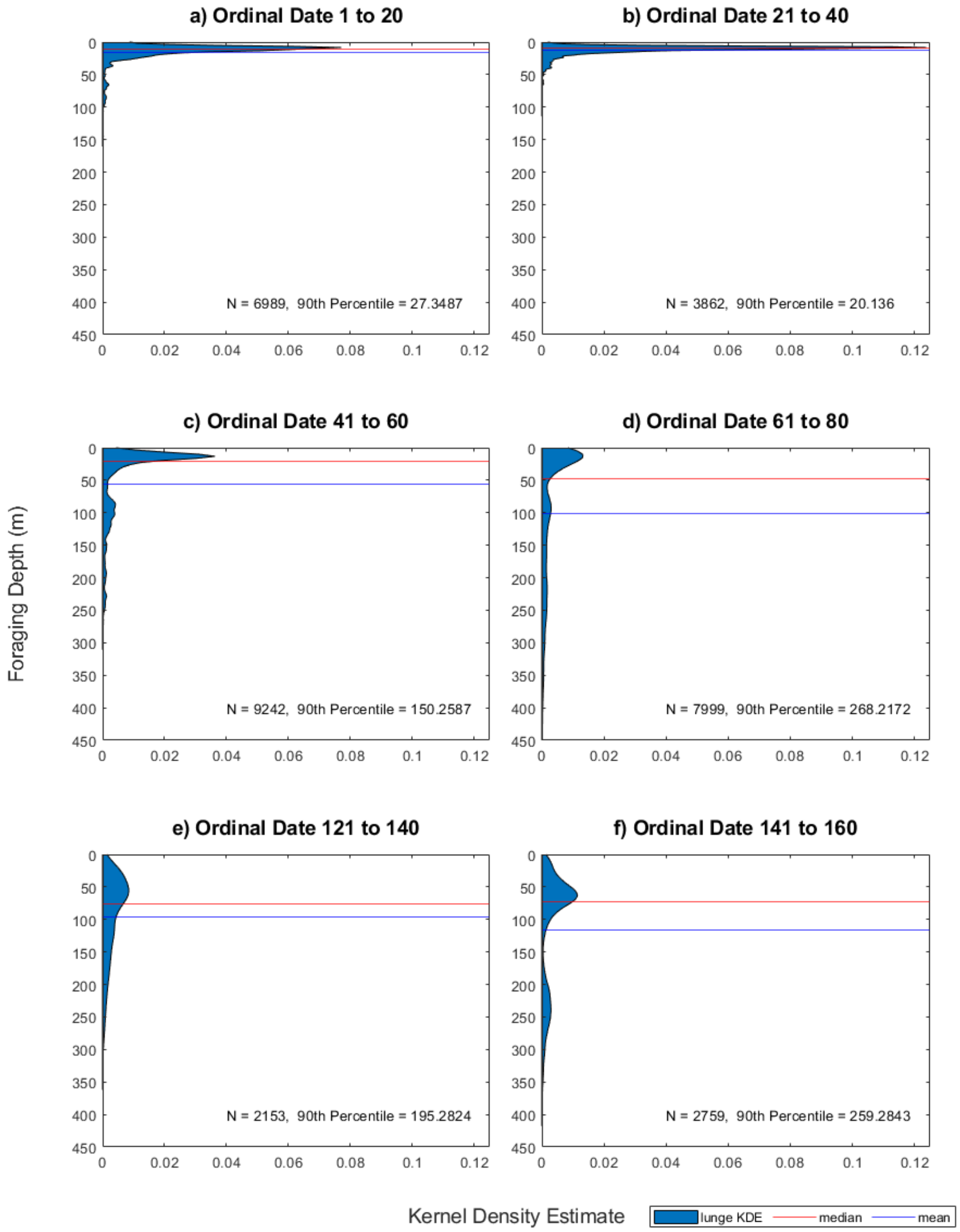


Figure 3 – Kernel Density Estimates of Lunge Depths by Analysis Period: Each plot represents foraging depths detected for each 20-day analysis periods (A – F). Medians of each analysis period is represented by a solid red line. Means are represented by a solid blue line.

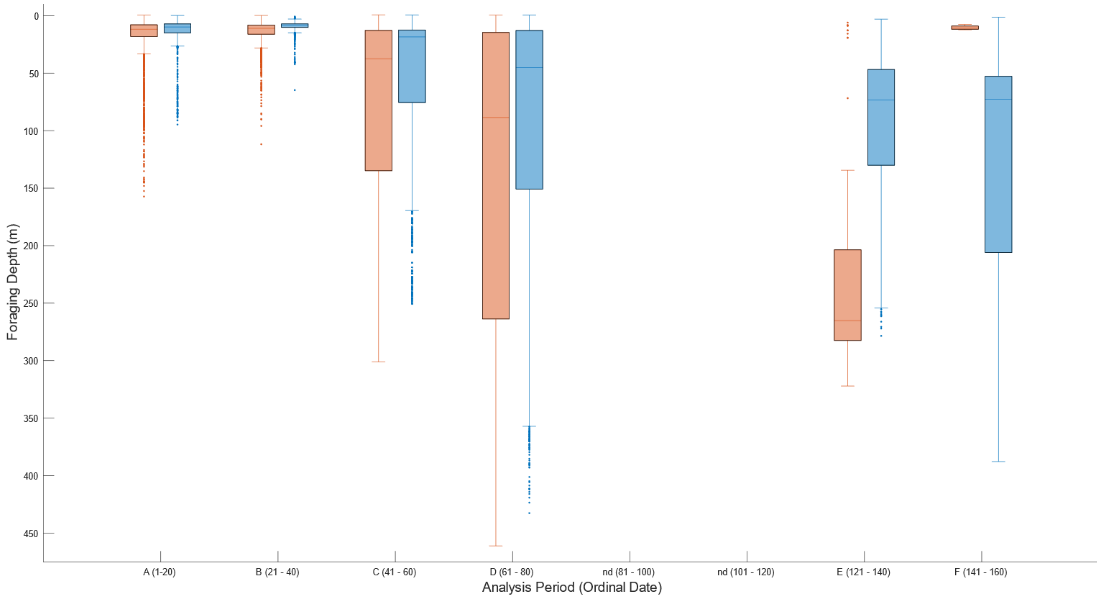


Figure 4 – Boxplot of Diel Period Lunge Depths by Analysis Periods: Red: daytime; Blue: nighttime. Horizontal lines within the boxes indicate median values. Box edges indicate the 25th and 75th percentiles. The whiskers extend to the most extreme values not designated as an outlier (‘•’). Ordinal dates 81 – 120 were excluded from analysis due to lack of sufficient data, signified by ‘nd’ (no data).

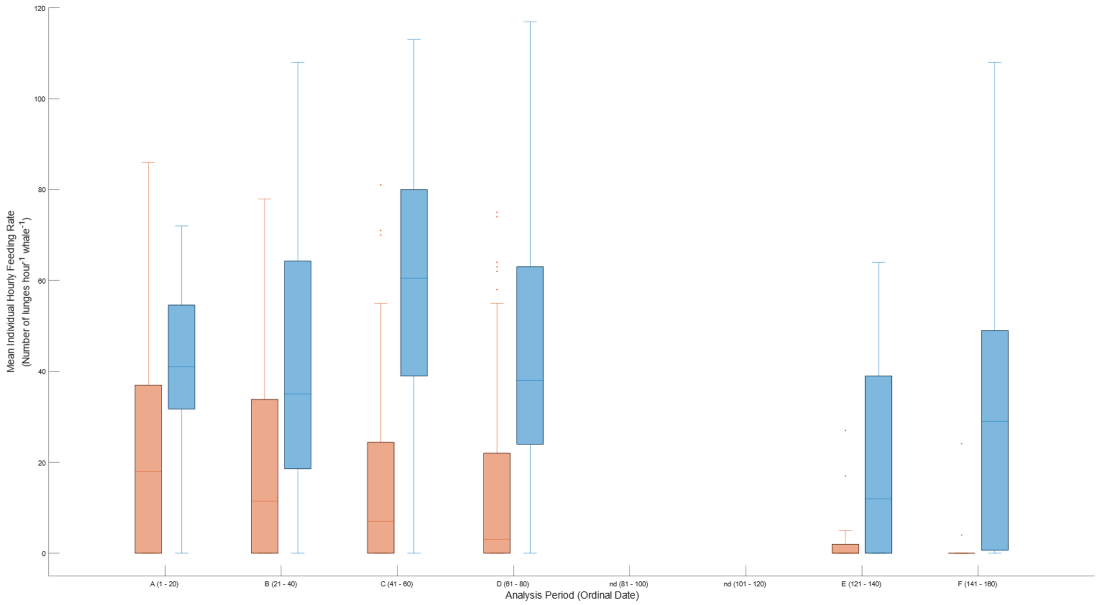


Figure 5 – Boxplot of Diel Period Feeding Rates by Analysis Periods: Red: day; Blue: night. Horizontal lines within the boxes indicate median values. Box edges indicate the 25th and 75th percentiles. The whiskers extend to the most extreme values not designated as an outlier (‘•’). Ordinal dates 81 – 120 were excluded from analysis due to lack of sufficient data, signified by ‘nd’ (no data).

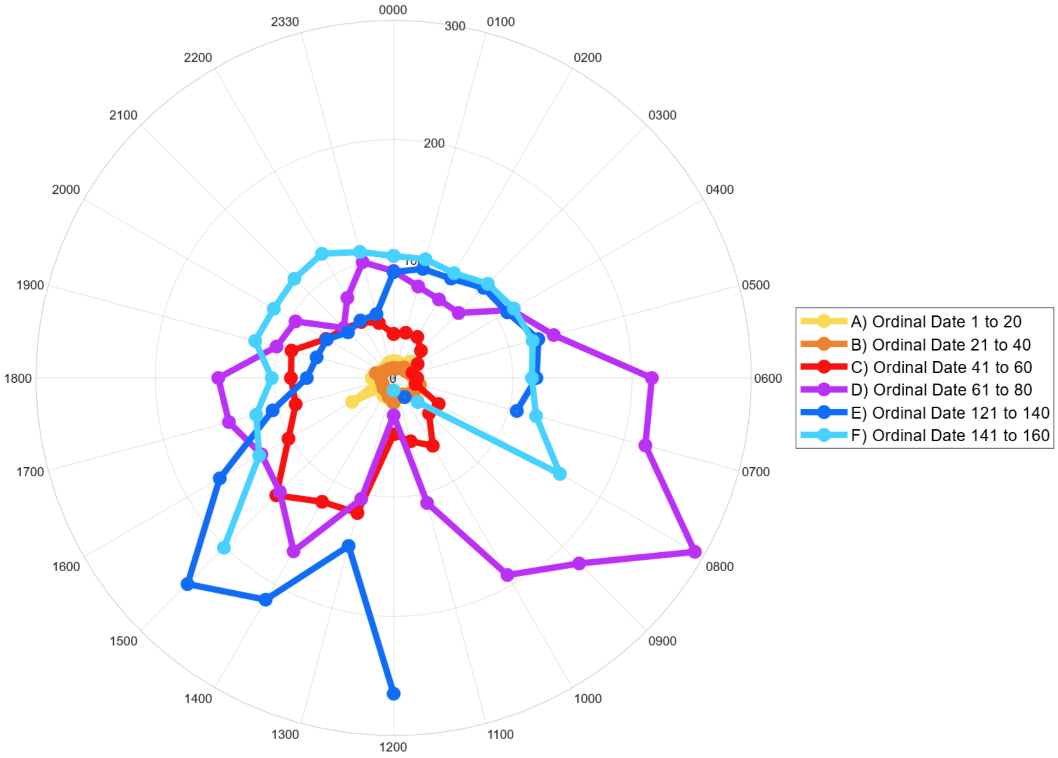


Figure 6 – Polar Plot of Lunge Depths by Time of Day for each Analysis Period: Mean foraging depths by hour of the day, each line representing an analysis period. The circular axis indicates the hour of the day. The radial axis indicates the mean foraging depth (m). Points closest to the center of the circle indicate shallower foraging, with the center of the circle indicating the surface. Line gaps indicate hours where no foraging was detected. Lines for ordinal date 81 – 120 are absent due to insufficient data.

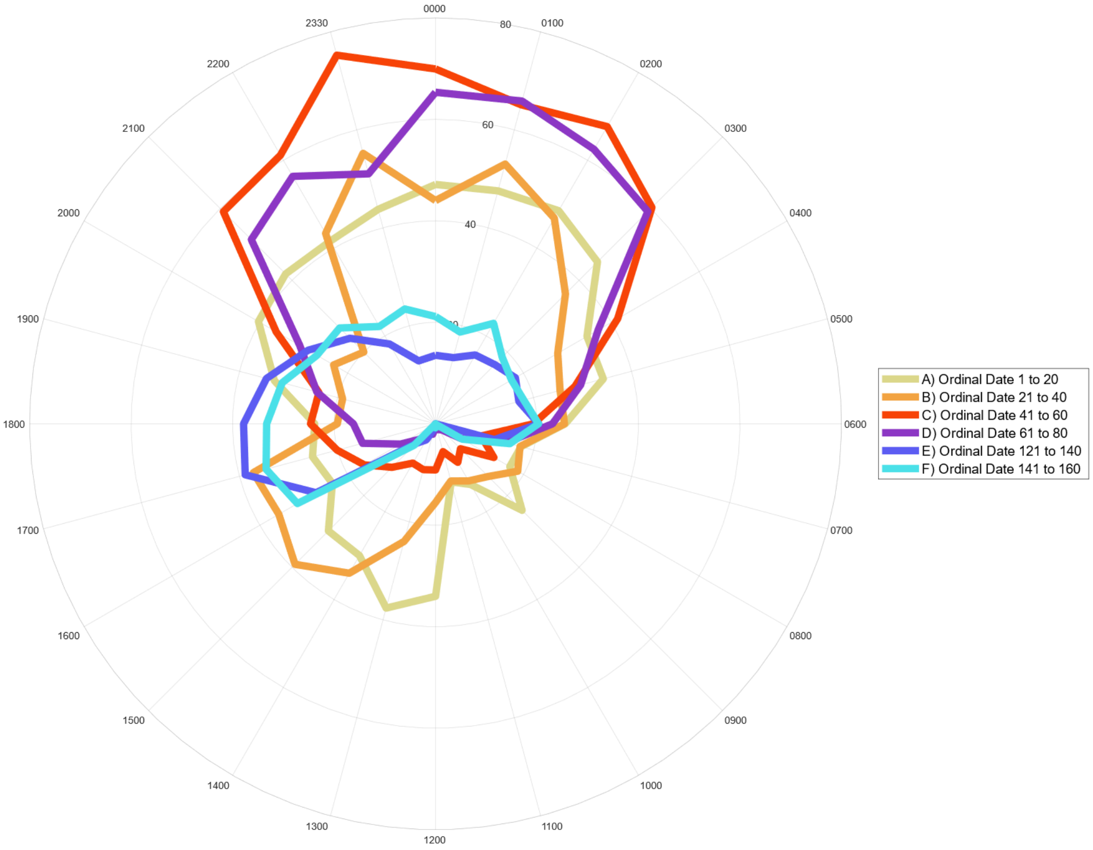
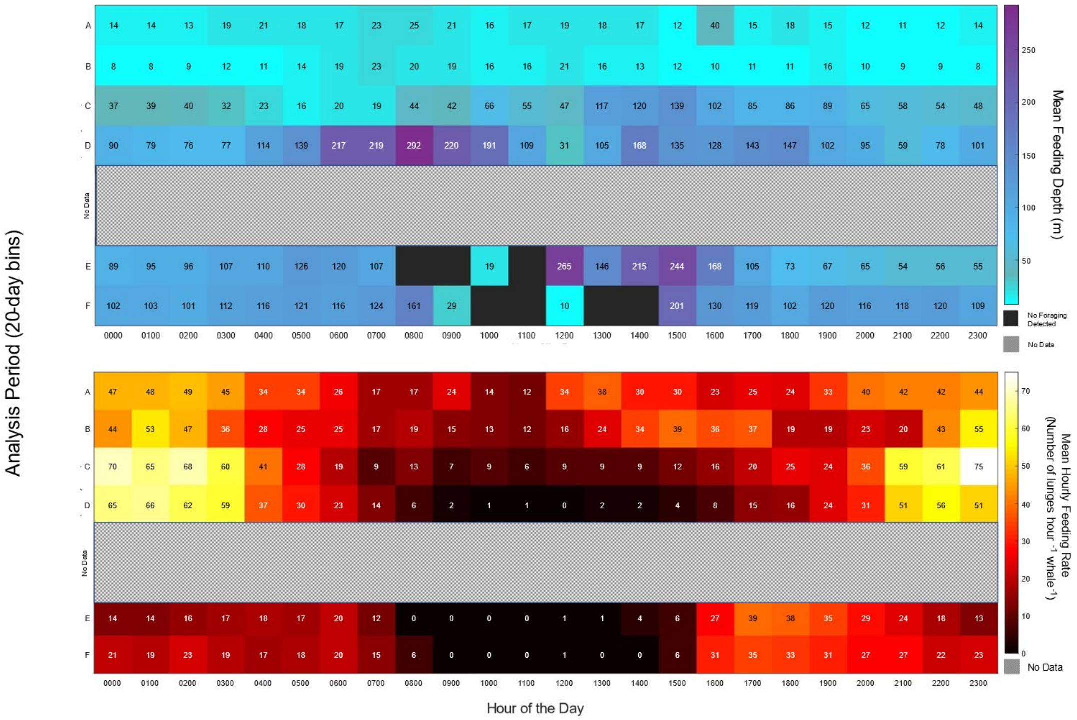


Figure 7 – Polar Plot of Feeding Rates by Time of Day for each Analysis Period: Mean feeding rates by hour of the day, each line representing an analysis period. The circular axis indicates the local hour of the day. The radial axis indicates the mean hourly feeding rate (lunges hour^{-1} whale^{-1}). Values near the center of the circle indicate lower feeding rates with the center being zero. Lines for ordinal date 81 – 120 are absent due to insufficient data.



	0000	0100	0200	0300	0400	0500	0600	0700	0800	0900	1000	1100	1200	1300	1400	1500	1600	1700	1800	1900	2000	2100	2200	2300
A	14	14	13	19	21	18	17	23	25	21	16	17	19	18	17	12	40	15	18	15	12	11	12	14
B	8	8	9	12	11	14	19	23	20	19	16	16	21	16	13	12	10	11	11	16	10	9	9	8
C	37	39	40	32	23	16	20	19	44	42	66	55	47	117	120	139	102	85	86	89	65	58	54	48
D	90	79	76	77	114	139	217	219	292	220	191	109	31	105	168	135	128	143	147	102	95	59	78	101
No Data																								
E	89	95	96	107	110	126	120	107	■	■	19	■	265	146	215	244	168	105	73	67	65	54	56	55
F	102	103	101	112	116	121	116	124	161	29	■	■	10	■	■	201	130	119	102	120	116	118	120	109

	0000	0100	0200	0300	0400	0500	0600	0700	0800	0900	1000	1100	1200	1300	1400	1500	1600	1700	1800	1900	2000	2100	2200	2300
A	47	48	49	45	34	34	26	17	17	24	14	12	34	38	30	30	23	25	24	33	40	42	42	44
B	44	53	47	36	28	25	25	17	19	15	13	12	16	24	34	39	36	37	19	19	23	20	43	55
C	70	65	68	60	41	28	19	9	13	7	9	6	9	9	9	12	16	20	25	24	36	59	61	75
D	65	66	62	59	37	30	23	14	6	2	1	1	0	2	2	4	8	15	16	24	31	51	56	51
No Data																								
E	14	14	16	17	18	17	20	12	0	0	0	0	1	1	4	6	27	39	38	35	29	24	18	13
F	21	19	23	19	17	18	20	15	6	0	0	0	1	0	0	6	31	35	33	31	27	27	22	23

Figure 8 – Data Heatmap Table of Lunge Depths and Feeding Rates by Hour of the Day and Analysis Period: Top: Heatmap and data table of mean foraging depths (m) for each hour of the day (x-axis) and analysis period (y-axis). Darker colors (dark blue/purple) represent deeper foraging depths, lighter colors (cyan) represent shallower foraging. Black sections represent periods where data was present, but no foraging was detected. Grey crosshatched sections indicate periods with insufficient data. Bottom: Heatmap and data table of mean hourly foraging rates (number of lunges hour^{-1} whale^{-1}) for each hour of the day (x-axis) and analysis period (y-axis). Darker colors (dark red/black) represent lower feeding rates; lighter colors (white/yellow) represent higher feeding rates during that period. Grey crosshatched sections indicate periods with insufficient data.

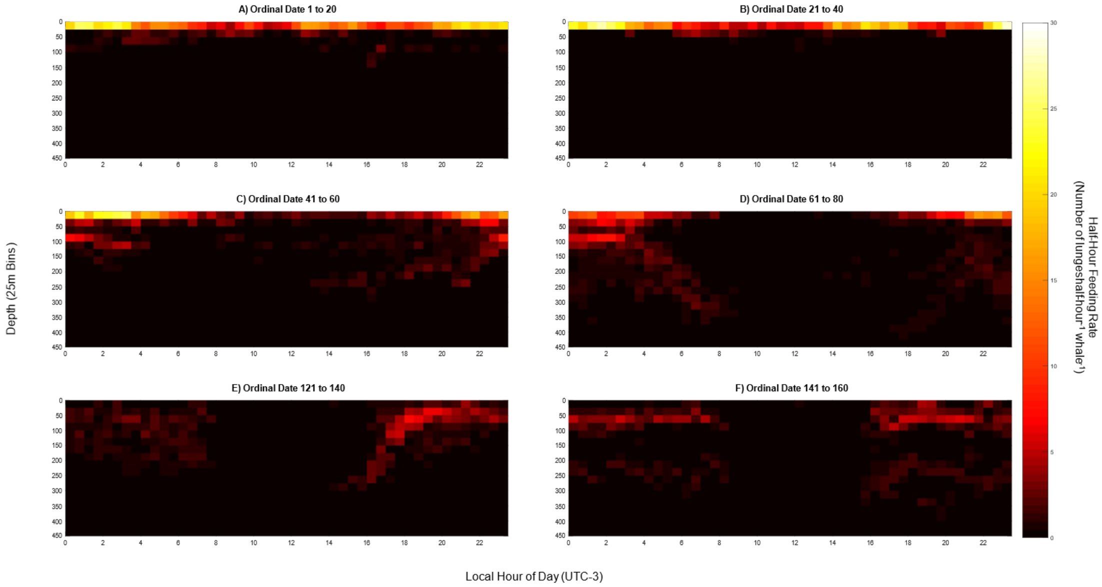


Figure 9 – Heatmap of Feeding Rates by Depth and Time of Day for each Analysis Period: Heatmaps of half-hour feeding rates over the diel period discretized by 25-meter depth bins on the y-axis and by half-hour bins on the x-axis. Each plot represents the average half-hour feeding rates at depths across 20-day analysis periods (A – F). Lighter colors indicate higher feeding rates, as where black indicates a feeding rate of near zero, or no detected foraging. Figures for ordinal dates 81 – 120 are absent due to insufficient data.

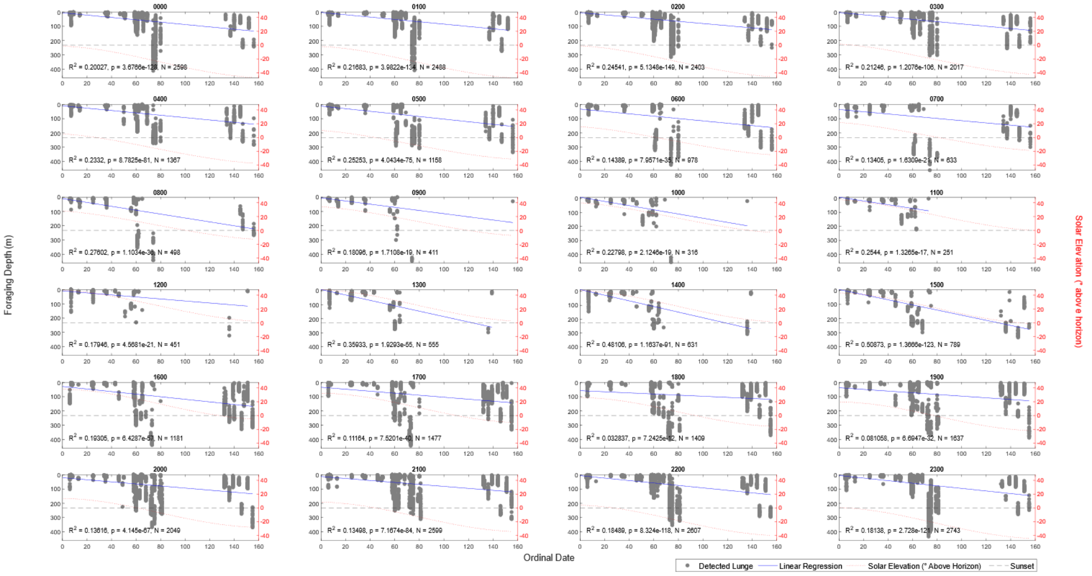


Figure 10 – Linear Regression Analysis of Lunge Depth by Time of Day: Each plot represents one hour of the local time of day (UTC -3). Detected lunges from all deployments are plotted against ordinal date and depth, denoted by grey circles. A linear regression was applied to each plot as represented by the solid blue line. The average solar elevation for each hour is plotted on the secondary y-axis by ordinal date and is represented by a dotted red line. Sunset (0° solar elevation) is denoted by the grey dashed. The intersect of the red dotted and grey dashed line indicates the transitional ordinal date of the subject hour being classified as a day or night hour.

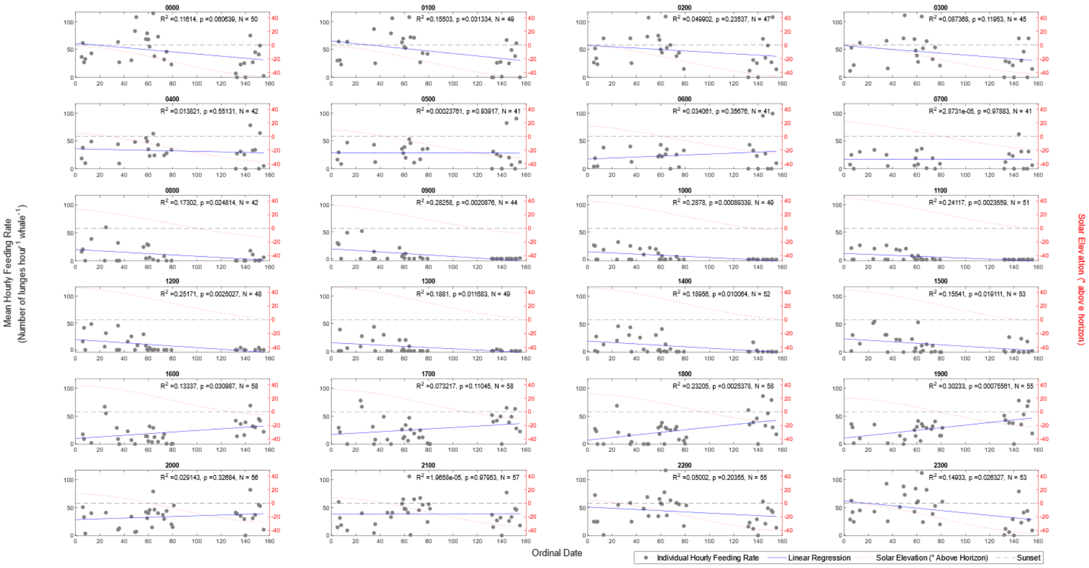


Figure 11 – Linear Regression Analysis of Feeding Rate by Time of Day: Each plot represents one hour of the local time of day (UTC -3). Grey circles indicate an hourly rate for each recorded hour of data across all deployments. A linear regression was applied to each plot as represented by the solid blue line. The average solar elevation for each hour is plotted on the secondary y-axis by ordinal date and is represented as a dotted red line. Sunset, which is 0° in solar elevation is denoted by the grey dashed line as a delineator between night and day. The intersect of the red dotted and grey dashed line indicates the transitional ordinal date of the subject hour being classified as a day or night hour.

TABLES

Table 1 – **Deployment information summary by analysis period:** All values taken after deployment exclusions – See Results.

	Analysis Period					
	A	**B**	**C**	**D**	**E**	**F**
Ordinal Date Range	1–20	21–40	41–60	61–80	121–140	141–160
Number of Deployments	11	7	17	20	6	7
Tag Data Hours	209.1	125.8	303.7	335.0	135.5	160.7
Deployment Locations	Bismark Straight, Palmer Canyon, Wiley Bay	Lamaire Channel, Palmer Canyon, Wiley Bay	Anvord Bay, Wiley Bay	Anvord Bay, Charlotte Bay, Wilhelmina Bay	Flanders Bay, Wilhelmina Bay	Flanders Bay, Wilhelmina Bay
Detected Lunges	6989	3862	9242	7999	2153	2759

Table 2 – **Foraging Metric Statistics by Analysis Period:** Estimated daily feeding rates are reported as number of lunges day^{-1} whale^{-1}. Mean hourly feeding rates are reported as number of lunges hour^{-1} whale^{-1}.

	Analysis Period					
	A	**B**	**C**	**D**	**E**	**F**
Ordinal Date Range	1-20	21-40	41-60	61-80	121-140	141-160
Num. of Detected Lunges	6989	3862	9242	7999	2153	2759
Est. Daily Feeding Rate	770.8	699.4	752.0	628.8	359.9	394.8
Mean Hourly Feeding Rate	32.1	29.1	31.3	26.2	15.0	16.4
SD	11.1	12.9	24.2	23.8	12.3	11.9
Range (min – max)	11.8 – 48.5	11.7 – 55.2	5.7 – 75.2	0.5 – 65.8	0 – 38.8	0 – 34.6
Mean Feeding Depth (m)	16.1	12.1	55.4	101.0	96.3	116.5
SD	17.4	8.9	63.1	107.8	65.6	91.5
Range (min – max)	0.4 – 157.3	0.2 – 111.8	0.7 – 301.1	0.5 – 461.1	3.0 – 339.5	1.4 – 387.7

Table 3 – Feeding Depth Statistics by Diel Category and Analysis Period: Lunge depth (m) statistics by diel category compared between analysis periods (A – F). Bolded values are maximum values within a diel category. N represents the number of lunge depth values per statistical measure.

Analysis Period (Ordinal Date Range)	Day			Night			Two-sample t-test		
	N	Mean (Range)	SD	N	Mean (Range)	SD	t	df	p
A (1 – 20)	4944	16.9 (0.4 – 157.3)	18.4	2045	14.0 (0.1 – 94.7)	14.3	6.34	6987	<0.001
B (21 – 40)	2281	14.1 (0.2 – 111.8)	10.6	1581	9.2 (0.8 – 64.7)	4.2	17.37	3860	<0.001
C (41 – 60)	2840	80.6 (0.7 – 301.1)	81.2	6402	44.2 (0.7 – 250.6)	49.1	26.58	9240	<0.001
D (61 – 80)	1648	139.8 (0.4 – 461.1)	140.3	6351	90.9 (0.5 – 432.6)	95.1	16.68	7997	<0.001
E (121 – 140)	**69**	**223.6** **(6.0 – 322.1)**	**92.5**	2084	92.1 (3.0 – 278.4)	60.1	17.49	2151	<0.001
F (141 – 160)	4	10.4 (7.7 – 12.3)	1.9	**2755**	**116.6** **(1.4 – 387.7)**	**91.5**	-2.32	2757	0.020

Table 4 – **Feeding Rates Statistics by Diel Category and Analysis Period:** Feeding rate (lunges hour^{-1} whale^{-1}) statistics by diel category compared between analysis periods (A – F). Bolded values are maximum values within a diel period. N represents the number of individual hourly feeding rates per statistical measure.

Analysis Period (Ordinal Date Range)	Day			Night			Two-sample t-test		
	N	Mean (Range)	SD	N	Mean (Range)	SD	t	df	p
A (1 – 20)	138	**20.3** (0 – 86)	**19.9**	36	40.1 (0 – 72)	18.4	-5.39	174	<0.001
B (21 – 40)	93	19.4 (0 – 78)	21.4	28	45.5 (0 – 108)	29.5	-5.17	121	<0.001
C (41 – 60)	180	13.8 (0 – 81)	16.7	93	**59.3** (0 – 113)	**28.9**	-16.60	273	<0.001
D (61 – 80)	177	11.9 (0 – 75)	16.8	132	44.4 (0 – 117)	26.7	-13.07	309	<0.001
E (121 – 140)	32	2.0 (0 – 27)	5.8	106	19.6 (0 – 64)	21.2	-4.74	138	<0.001
F (141 – 160)	24	1.2 (0 – 24)	4.9	136	30.5 (0 – 108)	28.3	-5.18	160	<0.001

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