RESEARCH ARTICLE

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The advantages of diving deep: Fin whales quadruple their energy intake when targeting deep krill patches

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Abstract

1. How predators maximize energetic gains while minimizing the costs associated with exploiting heterogeneous prey remains a difficult ecological principle to test in natural systems.

2. Deep-diving, air-breathing predators face conflicting demands of oxygen conservation to extend dive time and oxygen usage from the exercise required to find and capture prey. How predators balance these opposing factors is additionally complicated by prey patches that are heterogeneous spatially, temporally and in quality.

3. Tags deployed on foraging fin whales revealed that deeper dives consisted of higher feeding rates (lunges/hr), as generally predicted by optimal foraging theory. By simultaneously measuring prey density and distribution in the local environment, we show that whales increased their dive depths in order to forage on the densest prey patches.

4. Despite the increased travel time needed to find deeper prey during a breath-hold dive, the increase in feeding rates of fin whales and modelled prey consumption quadrupled compared to shallow foraging. Because the cost of transport is low at this extreme in body size, we posit that feeding on the deep prey patches significantly increases the energetic efficiency of foraging.

5. Given the increasing recognition that anthropogenic disturbance can curtail deep foraging dives in many cetacean species, endangered fin whales may be susceptible to significant energetic losses that may impact individual fitness and population health in some areas.

KEYWORDS
air-breathing divers, feeding efficiency, optimal foraging

1 | INTRODUCTION

Air-breathing diving predators face the conflicting demands of oxygen conservation during a breath-hold and the maximization of energy gain from prey capture at depth (Mori, 2002). The oxygen located at the sea surface can be considered the 'central place' in an optimal foraging theoretical (OFT) framework, which predicts foraging to be dictated mainly as a function of feeding depth. Within this framework, feeding rates (lunges/hr) on a given dive are expected to increase as the distance to the sea surface increases (Doniol-Valcroze, Lesage, Giard, & Michaud, 2011). This relationship has been both modelled and experimentally tested (Sparling, Georges, Gallon, Fedak, & Thompson, 2007; Thompson & Fedak, 2001; Watanabe, Ito, & Takahashi, 2014), and it is generally understood that many animals exhibit a suite of optimal foraging behaviours (Tyson, Friedlaender, & Nowacek, 2016). However, most field-based studies of diving behaviour are conducted independent of direct prey measurements and rely largely on models that are specific only to oxygen consumption. Therefore, how diving animals respond to changes in prey availability at depth and how this affects foraging performance has been difficult to evaluate.

One mechanism that has been used to interpret complex feeding behaviour is the marginal value theorem (MVT), which is predicated on the assumption that animals will move between patches when the rate of energy gain falls below the costs of foraging in a specific patch (Charnov, 1976). In marine systems, this is a difficult theory to test in the field because it is logistically challenging to quantify predatory feeding rates and prey patch quality at comparable scales. Watanabe et al. (2014) tested the MVT in penguins through a combination of multi-sensor tags and a qualitative visual measure of patch quality. Unlike in most other systems, the abundance and distribution of rorqual whale (Balaenopteridae) prey can be quantified concurrently and at appropriate scales using echosounders mounted on small boats that follow tagged whales (e.g. Cotté & Simard, 2005; Friedlaender, Tyson, Stimpert, Read, & Nowacek, 2013; Hazen et al., 2009). Therefore, studies of rorqual whale foraging provide new opportunities to test fundamental ecological questions.

Diving animals utilize a vast three-dimensional environment and can feed throughout the water column. Most baleen whales are known to feed at the surface as well as to depth of up to 400 m (e.g. Friedlaender et al., 2013; Goldbogen et al., 2013). However, how divers modulate their feeding behaviour in response to prey availability across a depth gradient remains poorly understood in most natural systems. Knowledge of how species and taxonomic groups with different feeding strategies and physiological limitations solve these issues is critical to a better understanding of predator–prey dynamics, ecosystem function and the potential for disturbance. Differences in feeding strategies and energetic needs will dictate the relationships between predators and their prey. Seals, birds, toothed whales, dolphins and porpoises feed on single prey targets, while many of the largest marine predators are bulk-filter feeders (e.g. baleen whales, manta rays, whale sharks, basking sharks), and capturing large quantities of food (i.e. high-density prey patches) is

critical to support the increased energetic demands of large body size (Goldbogen & Madsen, 2018). As prey is ephemeral, patchy and affected by environmental conditions across a range of spatial and temporal scales, animals such as baleen whales have adapted feeding strategies to maximize energetic gains where high-quality (e.g. high density) prey is located (e.g. Friedlaender, Hazen, et al., 2016a; Hazen, Friedlaender, & Goldbogen, 2015). Furthermore, obligate filter feeders may decide to conform or deviate from OFT or MVT when using these divergent foraging strategies, particularly when prey density is high. Large baleen whales, which exhibit an extremely low cost of transport (Williams, 1999), may be able to exploit higher quality prey at depth relative to smaller predators.

Here, we use fine-scale movement tags to study fin whale, *Balaenoptera physalus*, foraging ecology. In order to provide context to the foraging behaviour of the whales, it is critical to have information on prey to test how its availability influences foraging. We use tag data to first define the foraging ranges of fin whales and the relative frequency of feeding that occurs throughout the water column. We then test whether fin whales increase their feeding rates as a function of depth in order to maximize feeding opportunities on deep dives. We then use a subset of tag deployments with concurrent quantitative measurements of prey to test for evidence of how the vertical distribution of prey affects feeding performance, and if foraging rates change primarily as a function of prey patch depth (Doniol-Valcroze et al., 2011). These relationships between feeding rates and prey quality have rarely been studied in diving animals despite their ubiquity and will provide critical insights into the functional relationships between predators and prey and the behaviours that regulate these interactions in air-breathing diving animals. This information is also essential when considering not only normal behaviour and ecological relationships, but the impacts of disturbance and the consequences that can result from anthropogenic activities.

2 | MATERIALS AND METHODS

We deployed motion-sensing and acoustic recording suction-cup tags: DTAGs (Johnson & Tyack, 2003), CATS tags (Cade, Friedlaender, Calambokidis, & Goldbogen, 2016) and Acousonde tags (Friedlaender et al., 2014) on fin whales off the coast of California and Cape Cod, USA, the Azores and Greenland to evaluate the diving and foraging behaviour of the species.

High sample rate accelerometer data (40–500 Hz) were used to manually detect lunge feeding events (Cade et al., 2016; Simon, Johnson, & Madsen, 2012) on each tag deployment. Similar to Allen et al. (2016), experts in tag data analysis used a suite of known features that together indicate foraging to mark individual feeding events on dive records. Lunges were determined by locating episodes of rapid acceleration, changes in body orientation (Cade, Barr, Calambokidis, Friedlaender, & Goldbogen, 2018) and associated strong fluke strokes as whales approached prey and a marked deceleration that occurs when the whale opens its mouth to engulf a large volume of prey-laden water. For each foraging dive, we determined

the number of observed lunges and the depth at which each occurred and used this to calculate averages for lunge frequency at a given depth. Additionally, for each animal tagged we calculated the maximum number of feeding lunges and the associated maximum dive depth.

GPS positions of whale surfacing locations were used to georeference the tracks of tagged whales and link them to prey data for a subset of animals (Friedlaender, Johnston, et al., 2016b). For all tagged whales where prey mapping occurred, focal animal follows were also conducted and data on location, behaviour and environmental conditions were collected on each surfacing to link with the spatio-temporal distribution of prey. We then calculated the proportion of feeding lunges in 10-m vertical bins for the subset of animals for which concurrent prey were measured. Similarly, we calculated the number and mean density of prey patches in each given depth bin. To test for relationships between feeding depth, rates and prey, we only considered patches measured proximate to whales in both space and time (<1 km, <10 min). Most whales in this study from southern California were part of a behavioural response project (Southall et al., 2012) and tag data during a 30-min experimental sound exposure and 60-min recovery phase were not included, but all other data before and after were used for our analyses.

In order to assess foraging efficiency between shallow and deep feeding dives, we calculated rates of foraging (lunges/hr) for each individual tagged whale. Lunges were counted per hour from the start of the first foraging dive recorded on the tag after deployment. We plotted these rates against the mean lunge depth for the hour of lunges to test whether fin whale feeding rates increase as a function of dive depth.

During 11 of the tag deployments off of California, prey was measured using calibrated dual-frequency Simrad EK60 echo sounders (38 and 120 kHz) mounted on a towfish at 2 m depth. Acoustic data were analysed using ECHOVIEW software (V5) partitioned into 250 m by 10 m bins (horizontal by vertical), and individual prey patches were determined using the SHAPES school detection method with a 5-m linking distance (Coetzee, 2000). 38 kHz data were then subtracted from the 120 kHz data and assigned as krill when there was a 2–18 dB difference. We converted from volumetric backscatter to number of krill/m^3 using a swarming krill ($\theta = 11° \pm 4°$) target strength estimate of −85.0 dB re 1 m^{-1} (Conti & Demer, 2006) for a patch concentration of 80% *Thysanoessa spinifera* (mean length: 19.3 ± 1.53 mm) and 20% *Euphausia pacifica* (mean length: 16 ± 2.05 mm) as found in sympatric blue whale diets in central California (Croll et al., 2005). The TS (target strength) of the distribution was calculated (Jarvis, Kelly, Kawaguchi, Wijk, & Nicol, 2010), and krill number was converted to biomass using a multi-species length–weight regression (Mauchline, 1967).

3 | RESULTS

A total of 29 fin whales were tagged around the world between 2010 and 2018. From these deployments, we measured a total of 771 feeding dives (Table 1), the median feeding depth was 130 m,

and the maximum feeding depths recorded for each individual whale ranged from 22 to 359 m. The number of lunge feeding events per dive ranged from 1 to 12, with a median of 6.5. We found a significant relationship between the maximum number of feeding lunges and the maximum dive depth for fin whales (R^2 = .66, p < .0001). Maximum lunge counts increased linearly to a depth of approximately 300 m and then reached an average of 8 per dive at depth (Figure 1).

Eleven of the fin whales had prey mapping surveys concurrent to tag deployments. From these tags we measured 787 lunges on 156 foraging dives (Table 2). The number of lunges per dive increased significantly from shallow to deep feeding depths (p < .001, t test), averaging 4.5 ± 0.453 from 20–110 m where feeding occurred in all depth bins and 7.7 ± 0.213 from 190 to 280 m where feeding again was continuous (Figure 1a). Between 120 and 180 m, we measured very little feeding with some depth bins being void of any feeding effort. The feeding rates across all whales increased from 15.15 ± 4.9 lunges/hr at depths less than 190 m to 29.33 ± 1.5 at depths deeper than 190 m, as predicted by Doniol-Valcroze et al. (2011) (Figure 2). Krill density in the vicinity of feeding whales varied from 3–117 g/m^3, and while the number of patches decreased with depth, patch density increased with depth (Figure 1b) suggesting fewer but denser high-quality patches occurring at greater depth.

We fit a 2-segment linear regression based on the bi-modal distribution of whale foraging effort (Segmented package, R Development Core 2016 (Muggeo, 2003)) to determine whether whales targeted different densities of prey in the two depth ranges where foraging was measured. The regression identified one break point with a narrow confidence interval (233 m ± 33 m) (Figure 3a), consistent with the distribution of lunges and changes in lunge frequency with depth from the tagged whales. The first slope of the segmented regression was insignificant (β = .1189 (95% CI = −0.2842, 0.5219), indicating no change in patch density from the surface to the breakpoint, while the second slope indicated increasingly and significantly (p = .05) denser patches targeted at greater depths (β = .9376; CI = 0.3282, 2.1920).

We estimated foraging efficiency, approximated by prey intake per unit time. We assumed that the cost of transport did not vary significantly for whales diving to different depths, and we also assumed consistent prey capture rates (i.e. the proportion of prey captured did not change with prey patch density) and feeding costs. Prey intake was calculated by multiplying the average krill density encountered by the number of lunges/hr in a given 10-m depth bin by the engulfment capacity of a 20-m fin whale (37.7 m^3 calculated by Goldbogen et al., 2013). We evaluated this in shallow (<200 m) and deep (>200 m) feeding. We chose 200 m to distinguish between shallow and deep feeding based on the lower bound of the standard error on the break point in krill density shown in Figure 3a. This also coincided with a break in vertical distribution of feeding lunge frequency and the number of feeding lunges observed per dive (see Figure 1a). We found fin whale foraging efficiency was 4.0 times greater when whales fed on deep and denser prey patches (118,194 g/hr) versus shallow and less-dense patches (29,593 g/hr) (Figure 3b).

TABLE 1 All tagged fin whales used in the study including the location and measured foraging and diving behaviour of each whale

ID	Location	# of feeding dives	Maximum feeding dive depth (m)	Median feeding dive depth (m)	Maximum dive time (min)	Maximum feeding lunges per dive	Median feeding lunges per dive
bp10_236a	CA	1	193.26	193.26	8.57	8	8
bp10_236b	CA	2	169.45	112.77	6.67	6	4.5
bp10_239a	CA	18	200.18	147.52	9.13	6	3.5
bp10_244a	CA	8	290.98	282.4	11.98	9	8
bp10_245a	CA	8	219.62	28.9	10.88	6	1
bp12_217a	CA	41	279.36	230.04	9.82	9	6
bp12_294a	CA	9	87.2	38.5	13.52	3	2
bp13_193a	CA	6	320.78	301.91	10.1	9	7
bp13_216a	CA	11	284.39	249.44	11.56	8	7
bp13_257a	CA	14	47.99	25.69	6.29	5	3
bp13_257b	CA	26	62.49	27.01	4.61	4	2
bp13_258a	CA	7	68.69	31.25	2.69	4	2
bp13_258b	CA	1	22.1	22.1	3	1	1
bp13_258C	CA	20	42.52	20.58	3.25	1	1
bp13_265a	CA	19	118.07	99.4	8.24	9	5
bp14_259a	CA	4	172.84	30.25	10.12	2	1
bp150619-3a	MA	2	85.62	85.61	4.07	3	2
bp15_075a	CA	23	57.44	41.2	7.48	6	4
bp15_229a	CA	33	97.8	57.83	8.59	6	3
bp15_235a	CA	6	67.52	50.39	6.87	4	2.5
bp15_236a	CA	18	107.51	72.77	7.97	6	2
bp160609-36	Azores	2	106.64	86.29	8.12	4	3
bp160614-3b	Azores	5	76.5	55.83	5.16	3	3
bp160615-3c	Azores	1	59.68	59.68	8.92	2	2
bp160728-25	CA	25	148.42	108.35	8.39	8	6
bp160912	CA	219	359.31	40.57	13.53	9	3
bp160914	CA	157	340.21	195.08	12.9	12	5
bp16_256a	CA	13	297.43	271.87	10.77	9	6
bp170907-41b	Greenland	152	305.33	188.35	10.09	6	4

4 | DISCUSSION

Our results demonstrate that fin whale foraging in this study is not constant with respect to depth, showing a bi-modal distribution of shallow and deep feeding. This variation leads to significant differences in feeding rates and energy gain, mediated by changes in prey availability. Our data suggest that fin whales in this study maximized foraging performance and food intake by modulating their behaviour in response to foraging depth in two fundamental ways. By increasing feeding rates with increasing dive depth (in the absence of direct prey measurements) fin whales would increase their overall intake rates if prey remained at a constant density. Specifically when targeting deep, dense and larger prey patches measured in the field, fin whales increased their estimated prey consumption per unit time by a factor of four relative to feeding on shallow, smaller and less-dense prey patches. This may explain why whales dive deeper even if prey

is found throughout the water column: denser prey patches can be exploited to enhance foraging efficiency despite the increased travel and diving time needed to reach those depths. The large body size of fin whales likely confers very low transport costs, which should enhance their ability to exploit the best prey patches that are far from the sea surface. Moreover, marine mammals can modulate their buoyancy and exhibit gliding gaits during dives that save energy and reduce locomotor costs (Williams et al., 2000). Therefore, we posit that diving for the best prey does not significantly increase locomotor costs relative to foraging on shallow prey. Consequently, the observed increase in feeding rates and krill intake per unit time should substantially increase the energetic efficiency of foraging.

In contrast to blue and fin whale populations in the Eastern North Pacific, Antarctic humpback whales similarly modulated their foraging behaviour by increasing feeding rates (Ware, Friedlaender, & Nowacek, 2011) but fed preferentially when krill formed larger
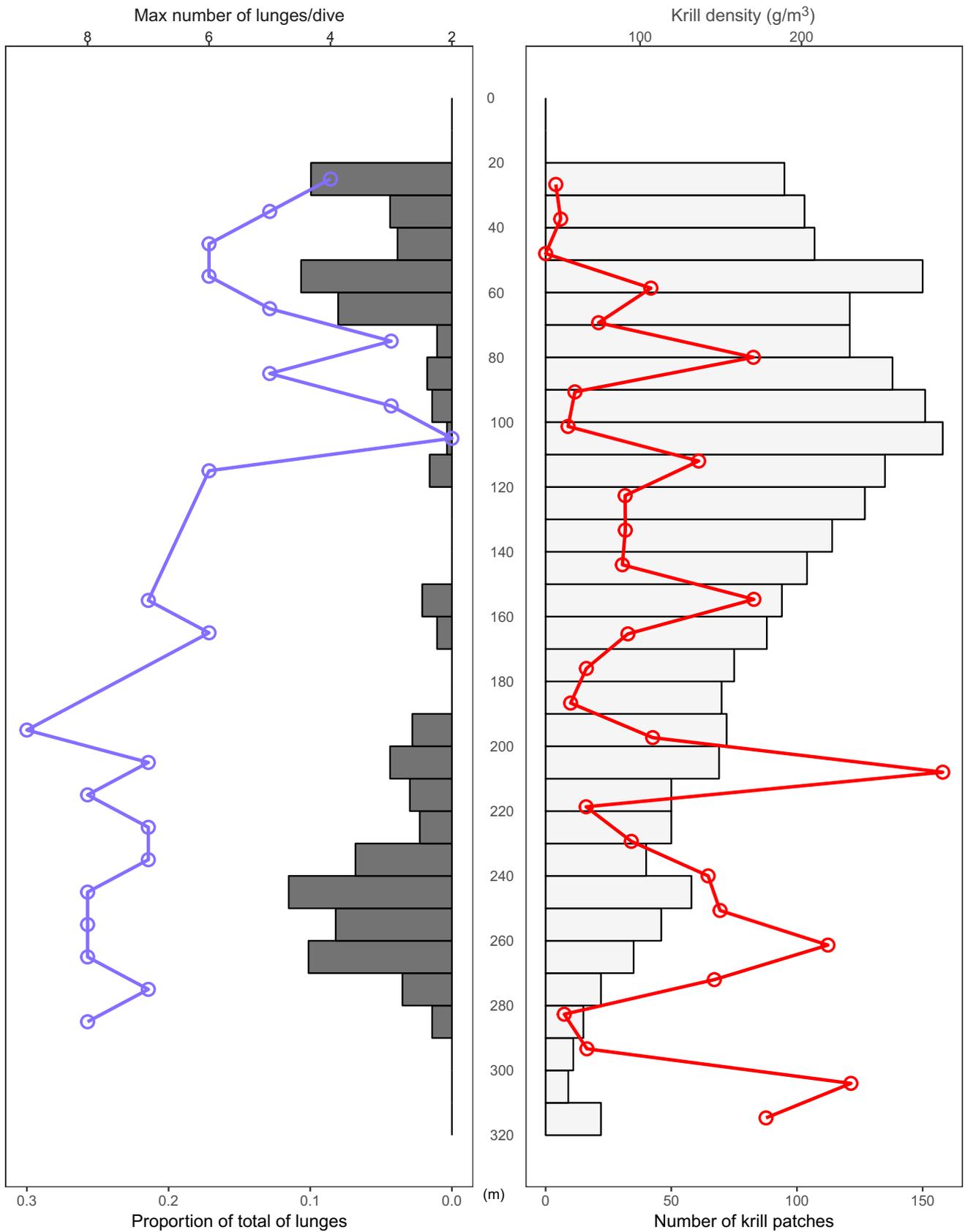
FIGURE 1 (a) The maximum number of feeding lunges observed in each 10-m depth bin (blue points and blue line is smoothed moving average with standard error) and the proportion of feeding lunges occurring in each 10-m depth bin shown as a histogram for the 11 fin whales tagged with concurrent prey data. (b) The total number of krill patches in each 10-m depth bin shown as a histogram and red points and line showing the average krill density (g/m³) for all measured krill patches in each 10-m depth bin (red points and line)

TABLE 2 Tag data including dive and feeding parameters for the subset with concurrent prey mapping surveys

Animal ID	Date	Tag on (local)	Tag off (local)	Duration (hr:mm)	Lunges	Average depth/dive (m)	Average lunges per dive	Max lunges per dive	Max feeding depth (m)
bp12_217a	8/4/12	11:58	7:17	19:18	260	213.8	5.9	9	279
bp12_294a	8/20/12	11:40	17:50	6:10	14	50.6	1.2	2	96
bp13_216a	8/4/13	13:50	18:42	4:52	86	255.5	6.6	8	284
bp13_257a	9/14/13	13:24	15:44	2:20	38	26.5	2.7	5	38
bp13_257b	9/14/13	13:00	18:10	5:10	89	32.0	1.2	4	63
bp13_258a	9/15/13	10:43	16:38	5:55	23	0.0	1.0	1	0
bp13_258b	9/15/13	10:57	16:27	5:03	41	18.5	1.0	1	33
bp13_258c	9/15/13	11:37	17:51	6:14	20	21.2	1.0	1	43
bp13_259a	9/16/13	9:09	14:23	5:14	63	24.4	1.0	1	50
bp15_229a	8/17/15	10:30	16:11	5:41	134	56.5	3.3	6	98
bp15_235a	8/24/15	12:41	16:47	4:06	19	43.0	2.0	4	68

less-dense prey aggregations near the surface at night rather than smaller, more dispersed but denser patches at depth during the day (Friedlaender, Johnston, et al., 2016b). This difference may be due to changes in prey behaviour between the two regions, that humpback whales display an alternate foraging strategy based on differences in body condition (e.g. buoyancy) that affects diving performance (Narazaki et al., 2018), or a combination of the two. The observation that humpback whales feed on less-dense prey near the surface in the Antarctic may also relate to their smaller size, lower energetic demands and a capacity to therefore forage successfully on a lower threshold of prey density (e.g. Piatt & Methven, 1992) than larger fin and blue whales.

The capacity for fin whales to respond to a heterogeneous prey environment and maximize energetic gains is similar to blue whales using a similar habitat and prey type. However, in our dataset the number of feeding lunges did not increase with depth as much as was observed for blue whales in Southern California (Hazen et al., 2015; Figure 2). Species-specific differences in energetic demands and behaviour may account for some of these observed dissimilarities even though in some locations like California the whales are sympatric (Friedlaender, Goldbogen, Hazen, Calambokidis, & Southall, 2015). Blue whales have larger energetic demands than fin whales and they rely on dense krill patches for energetic gain (Hazen et al., 2015), reduce their manoeuverability when feeding on deep, dense patches relative to shallow, less-dense patches (Goldbogen et al., 2013, Friedlaender, Johnston, et al., 2016b) and feed exclusively on krill rather than switching prey (Fiedler et al., 1998). Understanding the energetic requirements and kinematic signatures of foraging fin

R^2 = .39326 Intercept = 11.713 Slope = 0.060775 p = .00027206
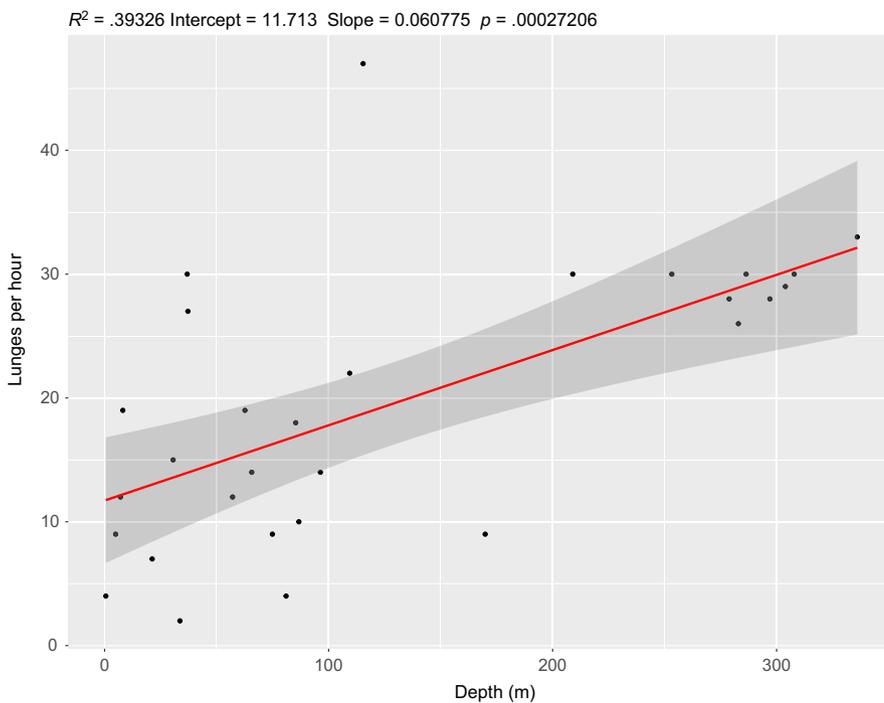
FIGURE 2 Regression analysis of lunges/hr and mean depth for each individual shows a linear trend in red with 95% confidence interval in dark grey. The relationship is significant (p < .0001, R^2 = .39, n = 23) and shows an increased foraging rate as a function of depth

FIGURE 3 (a) Segmented regression analysis of krill patch density (black points) and krill depth with linear trend in red and the break point occurring at 233 (±33 m) meters. Error bars are shown in red on the *x*-axis. Overlaid is the depth-stratified maximum lunge frequency (blue). (b) Calculated krill consumption was 4.0× greater for deep foraging dives (>200 m) compared to shallow dives (<200 m)
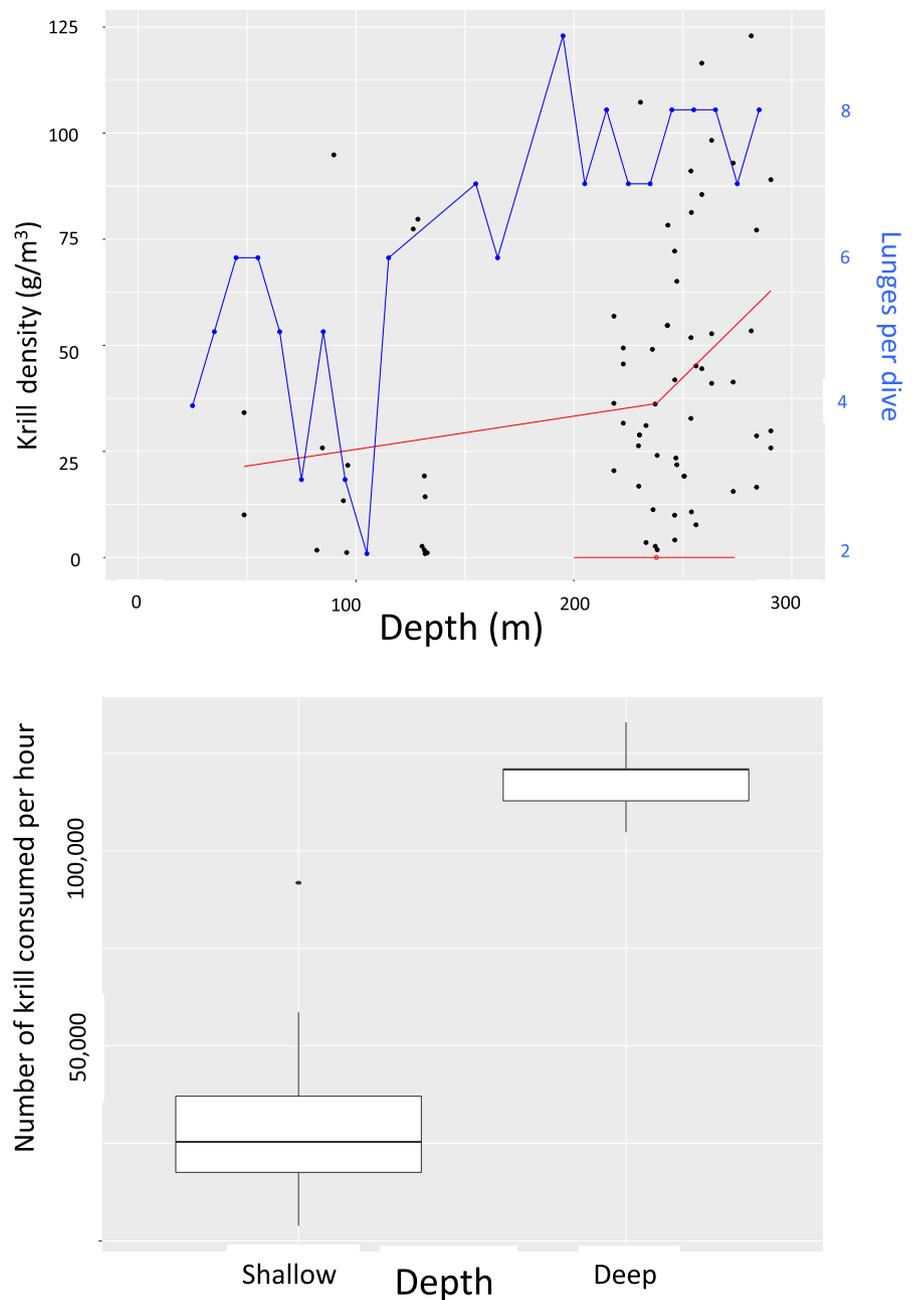
whales would help us understand why their diving behaviour differs from blue whales yet is able to still be profitable and sustainable.

While the number of deep feeding fin whales with simultaneously measured prey data was relatively small (2 of 11, see Table 2), the foraging patterns were consistent across the complete dataset of fin whales from multiple oceans (*n* = 23). The bi-modal distribution of feeding depths in our data supports active modulation of feeding by the whales in response to changes in prey density. From the surface to 200 m depth, fin whales decreased their foraging effort in terms of frequency of feeding dives, likely influenced by a relatively consistent (and low) prey density throughout this portion of the water column. As dive depth increases, so does transit time during which whales do not feed and whales need to somehow account for this time spent not gaining energy on deep dives. We and previous other

studies thus point to increased feeding rates with increased dive depth as a means for whales to overcome this (e.g. Friedlaender et al., 2013; Hazen et al., 2015). While transiting on dives incurs a cost in terms of time spent feeding, lunge feeding is one of the most energetically costly behaviours measured in animals (Potvin, Goldbogen, & Shadwick, 2012), and for whales to even initiate feeding requires a marginal threshold for energy gain to be reached (Goldbogen et al., 2011). The observation that fin whales feed less frequently and at lower rates on shallow versus deep dives supports the notion that the densities of prey found in shallow water are not frequently high enough to support the energetic demands of the whales. In contrast, whales feeding on deeper and denser patches likely maximized energy gain despite the increased transit time. Our results provide new evidence and a framework for further more dedicated studies of

how diving animals modulate their feeding rates and performance in environments with patchy and heterogeneous prey. This information could then provide valuable metrics for comparative studies of optimal foraging strategies among predators with differing foraging strategies, body sizes, energetic demands, physiological limitations and variable preyscapes. Furthermore, given the diverse feeding mechanisms found across central-place foragers, understanding differences in optimal foraging strategies can lead to greater knowledge of the functional relationships between predators and prey across ecosystems.

Our findings provide new information on the functional mechanisms that govern feeding in air-breathing divers, but also have important implications for understanding the consequences of disturbance to animals. Our results demonstrate that deep-diving fin whales deviate from theoretical oxygen-conservation strategies particularly when prey patches are dense and far from their oxygen source. This is further support for patterns observed in blue whales, where energetic efficiency was greatest when diving deep on dense prey (Hazen et al., 2015). In particular, these deep dives are where whales are greatly surpassing their baseline energetic requirements and are proposed to be important for building up energy stores that are used to fuel ocean-scale migrations that in turn may enhance overall fitness. Recent experimental work has shown context-dependent responses by blue whales to navy sonar: deep feeding blue whales were more likely to respond to this disturbance and did so by cessation of feeding (Goldbogen et al., 2013; DeRuiter et al., 2016; Southall et al., 2019). Although similar analyses have not yet been performed for sympatric fin whales, we suspect that they would similarly be at greatest risk from missed foraging opportunities due to non-lethal acoustic disturbance during their most efficient and critical foraging bouts at depth (Friedlaender et al., 2015). Thus, if fin whales respond to sonar similarly, aborting deep dives of high energetic gain, they would represent another endangered baleen whale species at risk from noise disturbance, particularly in areas of Navy sonar such as in the Northeast Pacific and areas of high human activity generally.

While blue whales are obligate krill specialists and fin whales are generalist feeders known to switch between fish and zooplankton, coastal California fin whales have only been observed feeding on krill (Flinn, Trites, Gregr, & Perry, 2002). Generalist predators often sacrifice efficiency on one prey type to maximize generality, so fin whales may not be as efficient feeding on krill as blue whales despite them being sympatric and likely targeting similar prey patches (Friedlaender et al., 2015), thus further research is needed to understand the population impacts of chronic stress that has been identified as a threat to other baleen whale species. Understanding the basic foraging ecology of a recovering predator combined with short-term response to acoustic disturbance (Goldbogen et al., 2013) is a critical first step in understanding how these effects may accumulate to affect individual fitness and ultimately population health (Pirotta et al., 2018). Our study represents an effective and informative step forward to better understanding the ecology of air-breathing diving animals. This information may help form the foundation for conservation action and mitigating anthropogenic threats on this endangered species.

CONFLICT OF INTEREST

We have no competing interests.

AUTHORS' CONTRIBUTIONS

A.S.F. collected data, participated in analysis, designed the experiment and drafted the manuscript with J.A.G. M.T.B. conducted data analysis and drafted the manuscript. D.C., E.L.H., A.K.S., A.N.A., J.C., J.F., P.S., F.V. and J.A.G. collected data, participated in data analysis and edited text. B.L.S. collected data, coordinated the study and edited text. All co-authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available at: https://purl.stanford.edu/fh584sg8391 subject to Office of Naval Research data sharing guidelines relative to grants.

ETHICAL APPROVAL

Research in the US was conducted under NOAA/NMFS permit 14534 and 19116 and multiple IACUC protocols, including ACUP fried1706 for fieldwork and tagging involving whales.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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