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Prey density and distribution drive the three-dimensional foraging strategies of the largest filter feeder

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Summary

1. Despite their importance in determining the rate of both energy gain and expenditure, how the fine-scale kinematics of foraging are modified in response to changes in prey abundance and distribution remain poorly understood in many animal ecosystems.

2. In the marine environment, bulk-filter feeders rely on dense aggregations of prey for energetically efficient foraging. Rorqual whales (Balaenopteridae) exhibit a unique form of filter feeding called lunge feeding, a process whereby discrete volumes of prey-laden water are intermittently engulfed and filtered. In many large rorqual species the size of engulfed water mass is commensurate with the whale's body size, yet is engulfed in just a few seconds. This filter-feeding mode thus requires precise coordination of the body and enlarged engulfment apparatus to maximize capture efficiency.

3. Previous studies from whale-borne tags revealed that many rorqual species perform rolling behaviours when foraging. It has been hypothesized that such acrobatic manoeuvres may be required for efficient prey capture when prey manifest in small discrete patches, but to date there has been no comprehensive analysis of prey patch characteristics during lunge feeding events. We developed a null hypothesis that blue whale kinematics are independent of prey patch characteristics.

4. To test this hypothesis, we investigated the foraging performance of blue whales, the largest filter-feeding predator and their functional response to variability in their sole prey source, krill using a generalized additive mixed model framework. We used a combination of animal-borne movement sensors and hydroacoustic prey mapping to simultaneously quantify the three-dimensional foraging kinematics of blue whales (*Balaenoptera musculus*) and the characteristics of targeted krill patches.

5. Our analyses rejected our null hypothesis, showing that blue whales performed more acrobatic manoeuvres, including 180° and 360° rolling lunges, when foraging on low-density krill patches. In contrast, whales targeting high-density krill patches involved less manoeuvring during lunges and higher lunge feeding rates.

6. These data demonstrate that blue whales exhibit a range of adaptive foraging strategies that maximize prey capture in different ecological contexts. Because first principles indicate that manoeuvres require more energy compared with straight trajectories, our data reveal a previously unrecognized level of complexity in predator–prey interactions that are not accounted for in optimal foraging and energetic efficiency models.

Key-words: baleen whales, bulk-filter feeding, foraging ecology, physiological ecology, predator–prey interactions

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Introduction

Predators modify foraging strategies to efficiently exploit spatially and temporally ephemeral prey resources. The overall efficiency of foraging is largely determined by the ratio of energy assimilated from ingested prey to the energy expended for locomotion, prey capture and basal metabolism. In aquatic vertebrates, previous research has identified a suite of behaviours that minimize energy expenditure, including low swimming speed to reduce drag (Sato *et al.* 2007; Watanabe *et al.* 2011), intermittent loco-motion and gliding gaits (Williams *et al.* 2000), and choice of dive trajectory (Gleiss, Norman & Wilson 2011). In contrast, prey capture often requires rapid changes in speed and body orientation that predictably incur high-energy use (Miller, Johnson & Tyack 2004; Soto *et al.* 2008; Aoki *et al.* 2012; Potvin, Goldbogen & Shadwick 2012). It has been hypothesized that predators modulate the magnitude and frequency of these costly manoeuvres to maximize intake when prey density is high or minimize energy expenditure in low prey quality conditions (Hindell 2008; Thums, Bradshaw & Hindell 2011; Wilson *et al.* 2011; Thums *et al.* 2013; Watanabe, Ito & Takahashi 2014). However, researchers have only begun to simultaneously measure both predator and prey at proximate scales to assess the physiological and ecological processes that determine foraging performance and its energetic consequences.

Compared with predators that target and capture single prey items (Soto *et al.* 2008; Watanabe & Takahashi 2013; Watanabe, Ito & Takahashi 2014), bulk-filter feeders are predictably more dependent on dense aggregations of zoo-plankton or schooling fish for energetically efficient forag-ing (Sims 1999; Goldbogen *et al.* 2011). The ability to engulf and process large quantities of small-bodied prey is important for supporting the energetic demands of the gigantic body sizes exhibited by many filter-feeding verte-brates (Friedman *et al.* 2010; Goldbogen, Potvin & Shad-wick 2010). High energetic efficiency also provides a means for rapidly developing large lipid reserves required to fuel ocean-scale migrations to breeding grounds where prey resources may be less reliable (Brodie 1975; Lockyer 2007; Bailey *et al.* 2009). Moreover, the abundant marine resources targeted by many bulk-filter feeders are largely ephemeral, fluctuating in patch size, shape, biomass and density over multiple spatial and temporal scales as a result of both environmental and ecological factors (Piatt & Methven 1992; Hazen *et al.* 2013). Therefore, bulk-filter feeders must be able to respond to changes in the prey field through adaptable foraging strategies that maximize ener-getic efficiency across different ecological scenarios.

There are different modes of bulk-filter feeding observed in aquatic vertebrates that require either suction- or flow-induced pressure to transport water and prey into the mouth (Sanderson & Wassersug 1993). During continuous ram filter feeding, animals use swimming-induced pressure to hydraulically drive water past the filtration apparatus, a mechanism that requires slow swimming speeds (Sims

2000; Simon *et al.* 2009). Bowhead and right whales (Bala-enidae), a family of baleen whales that exhibit enlarged mouth apertures, employ this type of continuous ram feed-ing mechanism to filter prey-laden water at an estimated rate of 3–5 m^3 s^{-1} (Werth 2004; Simon *et al.* 2009). The functional trade-off of this high-throughput feeding strat-egy is that it must occur at slow swimming speeds to mini-mize drag, thereby limiting prey options to slower moving zooplankton (Werth 2012). In contrast, rorqual whales (Balaenopteridae) use a unique lunge feeding strategy that involves the intermittent engulfment and subsequent filtra-tion of large volumes of prey-laden water that are com-mensurate with the animal's body size (Goldbogen, Pyenson & Shadwick 2007). During a lunge, rorquals accelerate to high speed and rapidly open and close their jaws around a target volume of water and prey, followed by a purging phase with the mouth closed except for a rela-tively small area of baleen that acts as the filtering surface.

The extreme gape angles, high speed and unsteady forces required for lunge feeding increase drag and the cost of a lunge (Potvin, Goldbogen & Shadwick 2009), but the over-all energetic efficiency can be high because of the large amounts of prey that can be captured (Goldbogen *et al.* 2011). Moreover, the ability to engulf and process prey in a short period of time predictably enables rorquals to effi-ciently exploit more agile prey (Simon, Johnson & Madsen 2012). Recent research has revealed a wide range of dynamic foraging strategies in several of the largest ror-qual species including blue, fin and humpback whales (Friedlaender *et al.* 2009; Doniol-Valcroze *et al.* 2011; Wi-ley *et al.* 2011; Simon, Johnson & Madsen 2012; Goldbo-gen *et al.* 2013a; Kot *et al.* 2014; Ware *et al.* 2014). Tag studies have revealed that subsurface lunge feeding behav-iour in fin whales (*Balaenoptera physalus*) and humpback whales (*Megaptera novaeangliae*) involves significant roll-ing moments, although the extent of the roll is typically 90-degrees (Wiley *et al.* 2011; Ware *et al.* 2014). Lunge feeding at the sea surface, which to date has only been analysed from ship observations, often involves a greater range of manoeuvring strategies (Kot *et al.* 2014). Com-pared with continuous ram feeding balaenids (Simon *et al.* 2009), we hypothesized that balaenopterids are capable of more adaptable foraging strategies because of their inter-mittent lunge feeding mechanism. There are clear differ-ences in lunge feeding strategies of rorquals when targeting different prey types (Ware, Friedlaender & Nowacek 2011; Wiley *et al.* 2011; Simon, Johnson & Madsen 2012) which we hypothesized is driven by prey patch characteristics such as density and distribution.

Data obtained from whale-borne video tags have recently shown that blue whales perform 360-degree barrel rolls when lunge feeding on krill patches (Goldbogen *et al.* 2013a). This rare glimpse into the visual ecology of rorqual foraging indicated that the krill patches targeted by these acrobatic lunges were relatively small, shallow and less dense compared with those encountered during deep forag-ing lunges (Calambokidis *et al.* 2007; Goldbogen *et al.*

2011). However, what is lacking is a quantitative assessment of prey density and distribution where tagged whales are actively foraging. Such data are needed to explicitly test the hypothesis that more extensive foraging manoeuvres are required for exploiting lower-density, more patchily distributed prey thereby rejecting the null hypothesis that whale kinematics are independent of prey patch characteristics. Here, we tested the hypothesis by measuring the three-dimensional kinematics and foraging performance of the largest-ever bulk-filter feeder, blue whales (*Baleanoptera musculus*), lunge feeding on krill patches that varied widely in density, patch size and depth distribution off the coast of Southern California.

Materials and methods

WHALE KINEMATICS

We used suction-cup-attached multi-sensor DTAGs (Johnson & Tyack 2003) to quantify the fine-scale movement and acoustic behaviour of foraging blue whales during the summer months of 2011 in the Southern California Bight, using a protocol described previously (Goldbogen *et al*. 2012). These deployments were conducted in the context of behavioural response studies on blue whales and other marine mammals (see Southall *et al*. 2012), but the data collected for this study were during periods outside sound exposure. The DTAGs recorded acoustic pressure (sampling rate: 64 kHz) and motion (tri-axial accelerometers and magnetometers sampling at 50 Hz, decimated to 5 Hz in post-processing). We used the motion sensor data to estimate whale orientation and stroking activity, and the level of flow noise recorded by the hydrophone was used to estimate the speed during lunges (Johnson & Tyack 2003; Goldbogen *et al*. 2006; Simon, Johnson & Madsen 2012). We defined the occurrence of lunges using a combination of kinematic parameters. A lunge feeding event is characterized by a distinct kinematic signature including acceleration to high speed, involving a high rate of acceleration or jerk, followed by a rapid decrease in speed (Simon, Johnson & Madsen 2012). The bout of fluking that initiates the lunge also continues through the deceleration phase of the lunge (Goldbogen *et al*. 2006), indicating the substantial increase in drag experienced as the mouth opens to engulf the prey-laden water (Goldbogen, Pyenson & Shadwick 2007). After a lunge, there is relatively little fluking as the water is purged from the expanded oropharyngeal cavity (Goldbogen *et al*. 2012). For each lunge, from the acceleration phase to the end of the purging (filtering) phase, we measured the following kinematic parameters: peak-to-peak change (Δ) in pitch, Δroll, Δheading, inter-lunge interval and the vertical depth deviation during the lunge (peak-to-peak change in depth).

PREY PATCH METRICS

We quantified the prey field in the vicinity (<1 km) of tagged and foraging blue whales using dual frequency Simrad EK 60 echosounders (38 and 120 kHz) (Friedlaender *et al*. 2009; Hazen *et al*. 2009) that were calibrated following standardized methods (Demer, Soule & Hewitt 1999). The acoustic backscatter was sampled at 10 Hz with pulse widths of 512 and 256 μs for the 38 and 120 kHz echosounders, respectively, which were used to measure scattering volumes (S_V) for specific prey patches. We used net tow samples when possible, combined with published krill size distributions in this region, to estimate krill density in grams per cubic metre of seawater as described previously (Lawson *et al*. 2006; Santora *et al*.

2011; Friedlaender *et al*. 2014a). The echosounders were continuously towed between 2 and 5 knots in a clover-leaf or zig-zag sampling protocol described by Hazen *et al*. (Hazen *et al*. 2009, 2011). Mapped prey schools were detected using the SHAPES school detection algorithm within Echoview 5 (www.myriax.com) incorporating a −75 dB threshold and 5 m linking distance (Coetzee 2000). We used a mean adult krill length of 28 mm (Santora *et al*. 2011) and published target strength–length relationships (Lawson *et al*. 2006) to calculate a krill target strength estimate of −75·0 dB (Watkins & Brierley 2002) [Correction added after online publication date 10 June 2015: − 5·0 dB changed to − 75·0 dB] which we used to convert acoustic backscatter to estimates of krill density (Simmonds & MacLennan 2005). We also examined the difference in s_v between the 120 kHz and 38 kHz data to ensure schools were consistent with krill scattering properties (Watkins & Brierley 2002). For each krill patch detected by the echosounders, we measured krill density, patch height and mean patch depth in addition to number of patches per 10 minutes of survey time. We tracked tagged whales and estimated their position during each surfacing series using a combination of boat-based GPS position and distance to whale from a laser range finder. We only used data for prey patches that were <1 km from foraging whales for statistical analyses.

STATISTICS

Prey patch metrics and lunge feeding kinematics were assessed on a dive-by-dive basis. If multiple lunges occurred during a dive, we calculated the average value for each kinematic parameter described above and assigned that value to the dive. We used Generalized Additive Mixed Models (GAMMs) to test for significant relationships among kinematic (Table 1) and prey field parameters, with individual whale as a random variable (Wood 2006). GAMMs were fitted using the 'mgcv' package in the statistical software R (version 3.0.2, R Core Team 2014) with 5 knots, and using a Gaussian distribution with an identity link function. A total of seven models were run with krill patch metrics as the predictor variables and kinematic data from the tag as response variables (Table 1). GAMM results are presented for the full models, including all predictor variables. To test for correlation among response variables, we calculated the variance inflation factor (VIF). All VIF values were <3 indicating collinearity would not bias the model results (Zuur *et al*. 2009). We used the full models in a biological hypothesis testing framework (Johnson & Omland 2004) to conservatively estimate which parameters of prey patch metrics were significantly correlated with foraging kinematics (H_0: Blue whale kinematics are independent of prey patch metrics, H_1: Blue whale kinematics are significantly affected by prey patch metrics).

Results

We collected data on the kinematics of lunge feeding and proximate krill characteristics for 11 blue whales. Krill aggregations targeted by blue whales exhibited a continuum of density, depth and patchiness across individuals. Patch density varied from 30 to over 500 krill m^{-3}, with patch depths from 15 to 280 m, and distance from the seafloor as 3–800 m. In general, deeper and bottom-associated krill patches (up to 280 m) tended to be larger and denser ($r^2 = 0\cdot047$, $P = 0\cdot041$; Fig. 1a), whereas shallow mid-water krill patches were smaller, more numerous and less dense ($r^2 = 0\cdot11$, $P = 0\cdot002$; Fig. 1b). However, we observed a significant amount of variation in krill density throughout the water column, as indicated by the weak

Table 1. GAMM analyses with individual models as a column

	Δroll	ΔHeading	Δpitch	Depth deviation lunge	Inter-lunge interval	No. of lunges per hour	No. of lunges per dive
s(Krill Density)	**4·59E-05**	**0·029**	**0·00891**	7.7×10^{-8}	0·069	**0·0012**	0·054
s(School Depth)	0·432	0·35	**0·00713**	0·5	0·69	**0·04**	0·88
s(School Height)	0·959	0·39	0·73133	0·86	0·72	0·63	0·58
S(# Schools)	0·826	0·11	0·35157	0·36	0·072	0·94	0·66
s(Bottom Depth)	0·188	0·37	0·8806	0·87	0·72	0·76	0·61
r^2	0·35	0·11	0·17	0·47	0·117	0·152	0·041

The significance of each term in the full model is included and bolded when P is <0·05. The overall model r^2 is included as the last row.
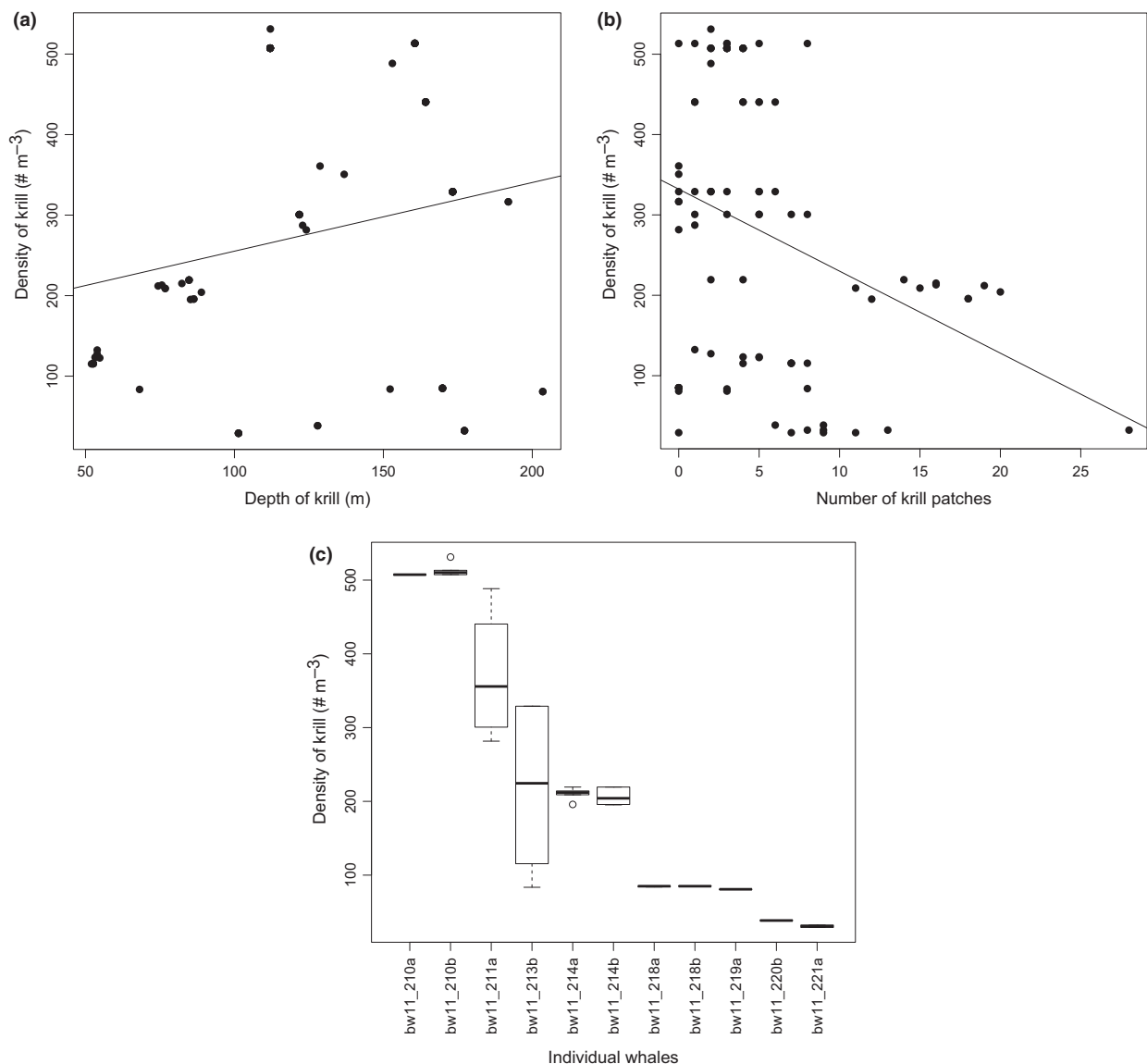

Fig. 1. Krill patch characteristics. (a) Krill density generally increases with patch depth ($r^2 = 0.047$, $P = 0.041$). (b) Krill density and the number of krill patches were inversely related ($r^2 = 0.11$, $P = 0.002$). Over the course of our study, krill density progressively decreased (c). Notation for individual whales: bw11 = blue whale, year 2011; three-digit number represents Julian day.

relationship between these parameters. Throughout the 12 consecutive days of our study, we found that krill density steadily decreased over time (Fig. 1c).

We recorded a total of 261 feeding lunges across 89 foraging dives that ranged in maximum depth from 49 to 283 m and dive durations of 1·6–11·0 min. From the

GAMM output, mean lunges increased with krill density, but not with patch depth (Table 1; Fig. 2a). Lunge feeding rate (number of lunges per hour) increased with patch depth (Table 1; Fig. 2b). We found a negative relationship between the changes in body orientation (Δpitch, Δroll, Δheading,) and krill density (Fig. 3a). In addition, the depth deviation during each lunge (DDL) and inter-lunge interval (ILI) were both negatively related to krill density (Table 1; Fig. 3b). Overall, whales were more likely to increase kinematic variability and lunge less frequently when feeding on less dense, mid-water prey patches com-

pared with more lunges and less kinematic deviation when feeding on deeper, bottom-oriented prey patches (Fig. 4).

Discussion

Prey density is a primary driver of foraging behaviour on various temporal and spatial scales in the marine environment. Not only is prey density a strong predictor of predator habitat use in horizontal space (Friedlaender *et al.* 2006; Friedlaender, Lawson & Halpin 2009; Hazen *et al.* 2009; Benoit-Bird *et al.* 2011, 2013a), it also largely
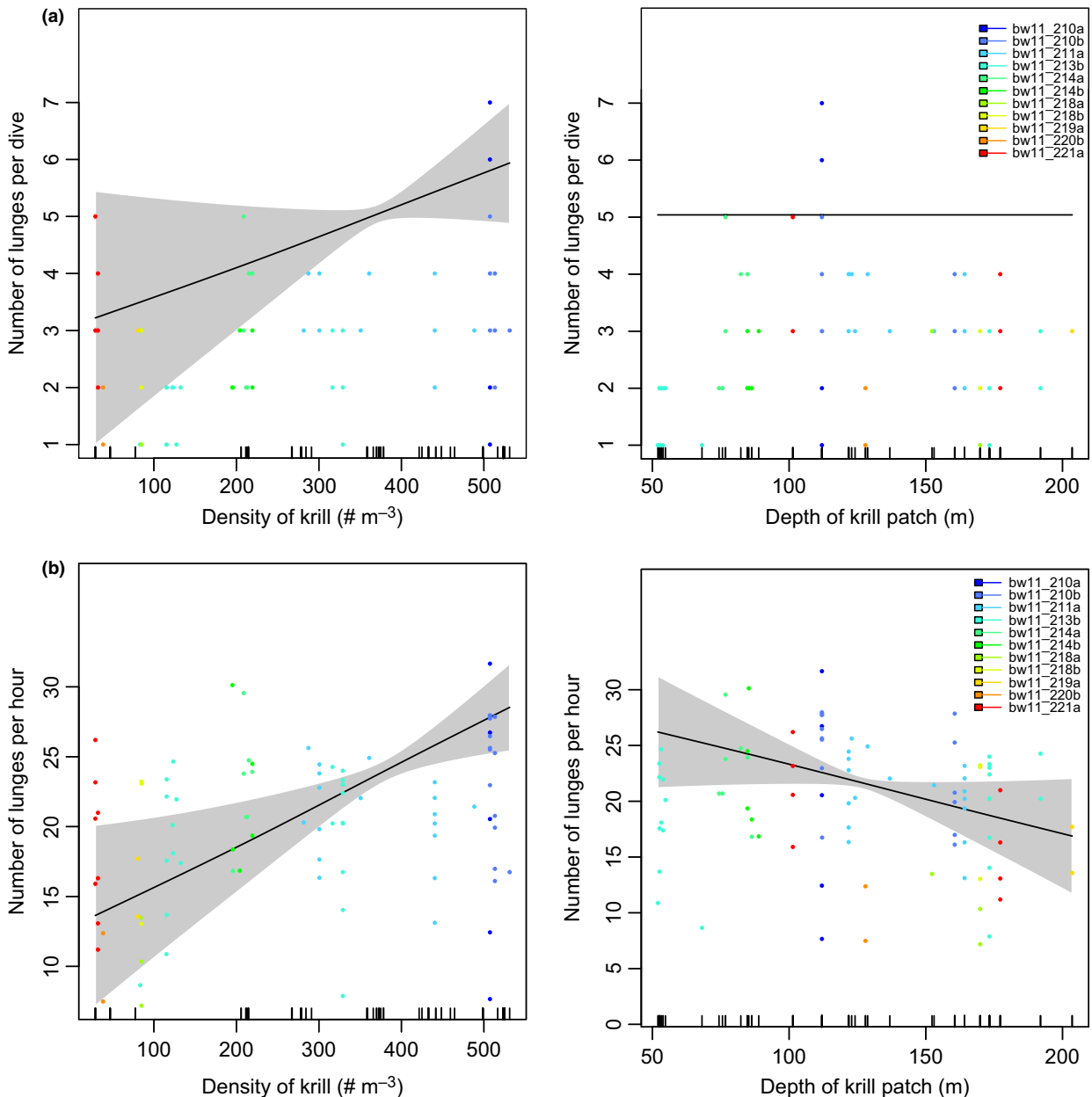

Fig. 2. Foraging performance correlates with krill patch characteristics. Lunge frequency (a, number of lunges per dive) and feeding rate (b, number of lunges per unit time) as a function of krill density and patch depth. Figures show Generalized Additive Mixed Model partial plots, with mean and error represented by black and grey, respectively. Coloured dots indicate observed data points among individuals.
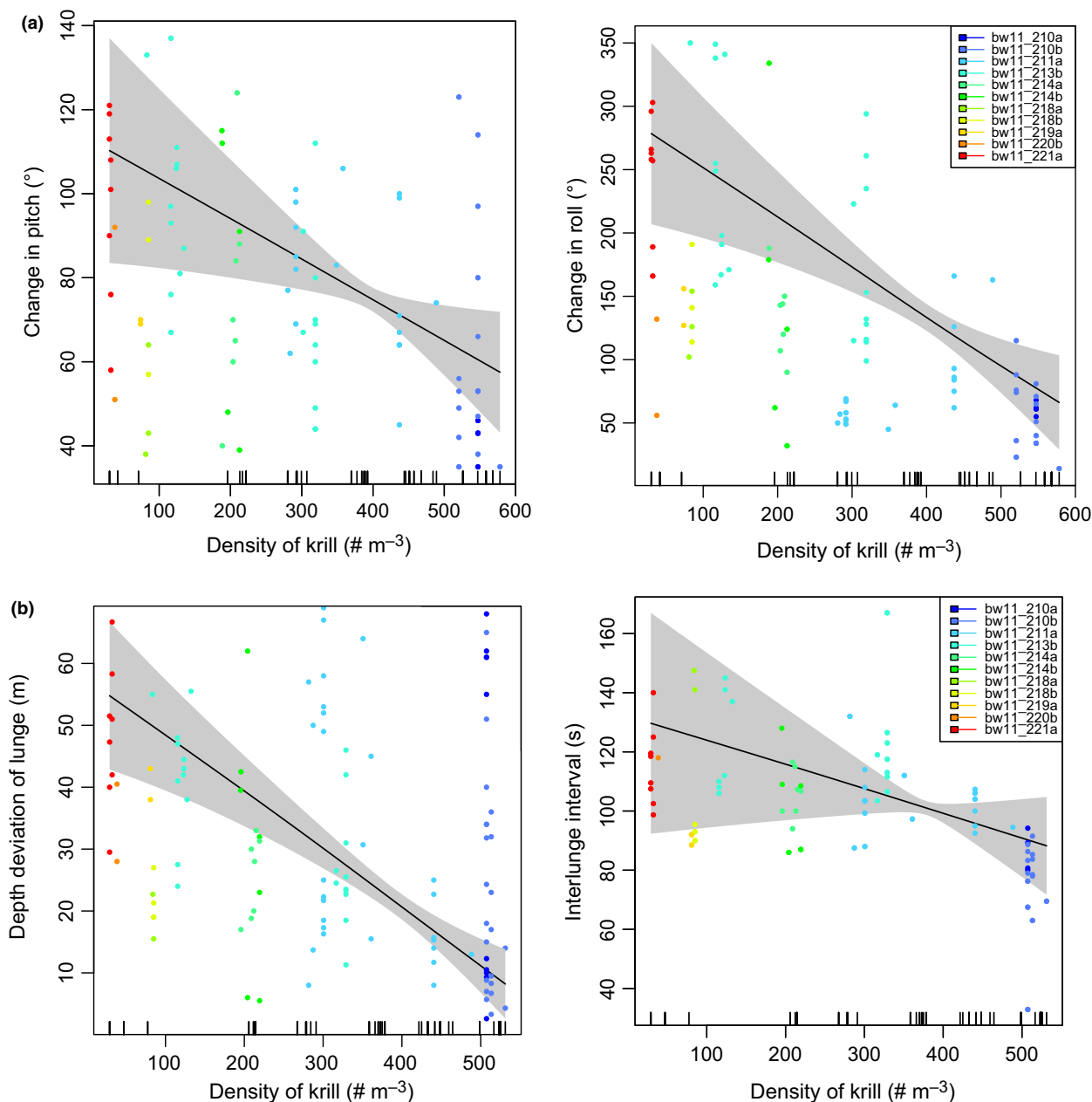
Fig. 3. Lunge feeding kinematics as a function of krill density. Each data point represents the mean value across all lunges performed during a foraging dive for changes in body orientation (a) and vertical displacement and temporal separation between consecutive lunges (b).

determines the depth where foraging occurs (Croll *et al.* 2005). For predators that target dense aggregations of fish or zooplankton, foraging effort often tracks the diel vertical movement of these prey resources (Fiedler *et al.* 1998; Friedlaender *et al.* 2013). For krill, an important prey type for a wide range of predators, it is thought that the density of aggregations will vary largely with depth during these vertical excursions (Hewitt & Demer 2000; Sourisseau, Simard & Saucier 2008; Simard & Sourisseau 2009). However, krill density can also be affected through environmental factors such as the physical forcing of ocean currents and interactions with seafloor topography, and these phenomena can manifest seasonally, tidally or in

response to other geophysical forces (Hamner 1984; Hamner & Hamner 2000). As a result, many marine resources, including krill, are often patchily distributed in hierarchical spatial scales (Benoit-Bird *et al.* 2013b), yielding a wide dynamic range in density that predators must respond to with adaptable foraging strategies.

Our analyses indicate that blue whales significantly modify the kinematics of foraging behaviours in response to changes in krill density and distribution (Figs 2–4). Specifically, our data show a continuum of foraging strategies that are characterized by changes in body orientation and deviation in depth during lunges. When foraging on shallow, low-density krill aggregations that were distributed in
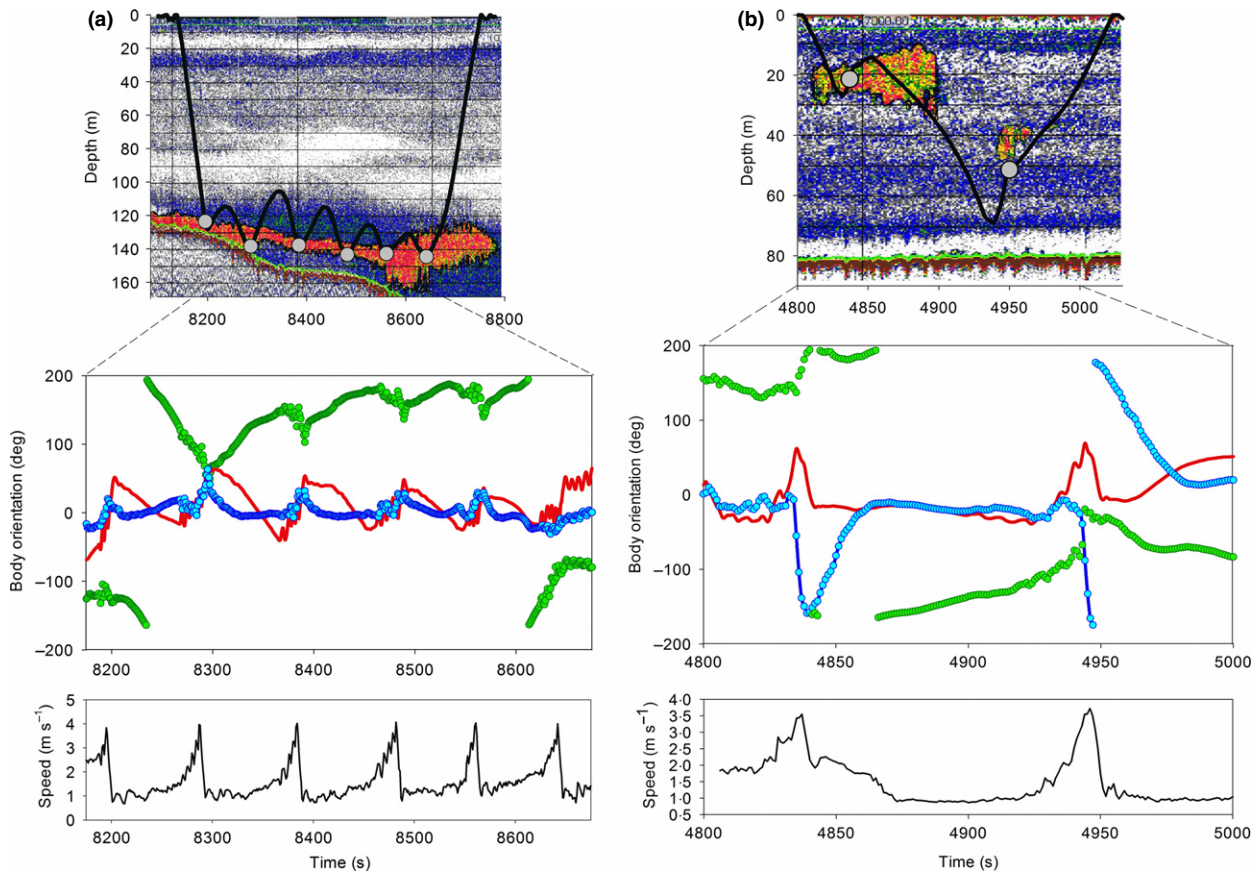
Fig. 4. Divergent foraging strategies driven by differences in prey density. Foraging dives that targeted deeper, denser krill patches exhibited lunges with less manoeuvring and higher lunge frequencies (a). Foraging dives on shallower, lower-density krill patches involved lunges that had much more extensive manoeuvring, including 180 degree rolling inverted lunges and complete 360 degree rolling lunges (b). In each panel, the depth profile from tag data was superimposed on prey field maps from hydroacoustic data that were temporally and spatially synchronized. Grey circles indicate the timing of lunge feeding events. In the middle panel red, blue, green represent body pitch, roll, and heading respectively.

multiple patches, blue whales exhibited more acrobatic manoeuvres during lunges and relatively high lunge feeding rates. In contrast, blue whales manoeuvred less when foraging on deep, high-density krill, more sparsely distributed patches. Although both the mean and maximum number of lunges per dive increased with krill density, the overall feeding rate decreased as blue whales targeted deeper patches. We attributed this difference to the extra time required for vertical transit, post-dive surface recovery and searching for prey patches, all of which do not typically involve feeding events. Our results support previous hypotheses that suggest the number of feeding events during a dive reflects the quality or density of a prey patch (Goldbogen *et al.* 2008). Foraging dives with high feeding rates (and thus an extended bottom phase of the dive) typically exhibit steep dive ascents and descents, whereas dives with less foraging activity tend to have shallower dive angles that increase horizontal transit and the probability of finding a better prey patch at a different location (Sato *et al.* 2004; Goldbogen *et al.* 2008). Our data suggest that blue whales use a variety of different foraging strategies in

response to prey conditions that not only maximize prey capture during each lunge feeding event (by modulating body orientation), but also to optimize overall energetic efficiency under different prey conditions (through control of feeding rate and dive trajectory). These empirical data on the characteristics of foraging strategies in response to environmental variables directly inform the interpretation of behavioural responses to disturbance, including acoustic exposure during controlled exposure experiments (Goldbogen *et al.* 2013b), and energetic models of the consequences of disturbance.

Among all the prey characteristics measured in our study, krill density was the primary factor influencing the behaviour and kinematics of foraging blue whales. The distinctive foraging strategy defined by large changes in body angle about all three body axes (roll, pitch, and heading) may be required to exploit small, low-density krill patches, presumably to search, manoeuvre and reorient the body so that the whale is optimally positioned to maximize prey engulfment. Here, we provide a mechanistic hypothesis consistent with previous research on blue whales using

animal-borne video tags that documented a 360° rolling lunge towards an isolated krill patch in the upper 50 m of the water column (Goldbogen *et al.* 2013a). Rorqual whales lunge feed using a wide variety of body rotations and translations (Kot *et al.* 2014), and certain combinations of each kinematic degree-of-freedom may be optimally efficient for specific prey types, densities or locations (seafloor, mid-water, or sea surface). Among all the rorqual species, humpback whales exhibit the most flexible of these foraging strategies, from bottom side-roll and deep feeding to bubble-net and near-surface feeding (Friedlaender *et al.* 2009; Hazen *et al.* 2009; Ware, Friedlaender & Nowacek 2011; Wiley *et al.* 2011; Ware *et al.* 2014). The specialized morphology of humpback whales, including high aspect ratio flippers and low aspect ratio flukes, likely facilitates the high-speed manoeuvres required for many of these complex foraging strategies (Woodward, Winn & Fish 2006). However, the mechanisms that drive the relationship between morphology, performance and ecological niche across rorqual species remains poorly understood.

Ultimately, mechanical scaling effects may strongly influence and in many ways limit the performance of these species-specific foraging strategies. Body size is a prime determinant of locomotor performance and metabolic rate, and therefore scale has a major influence on predator–prey interactions, foraging performance and efficiency (Domenici 2001; Williams 2006). In addition to the widely recognized advantages of large body size, such as efficient metabolic rate and low cost of transport, rorqual whales exhibit tremendously large engulfment apparatuses due to the positive allometry of the skull and oropharyngeal cavity (Goldbogen, Potvin & Shadwick 2010). As a result, larger rorquals have greater mass-specific engulfment capacity, but at the expense of progressively limiting dive duration and feeding rates (Goldbogen *et al.* 2012). Across the entire body size range of rorqual species, from 5-m-long minke whales to over-30-m-long blue whales, there is a continuum of foraging strategies that is characterized by an inverse relationship between engulfment capacity and lunge frequency (Friedlaender *et al.* 2014b). At the upper extreme of this scale-dependent foraging envelope, blue whales may benefit from a large gulp, low lunge frequency strategy that confers high energetic efficiency if dense prey patches can be exploited. At the other extreme, smaller rorquals like minke whales may be better equipped to exploit small and more widely distributed prey patches through a small gulp, high lunge frequency strategy.

Despite their massive body size, blue whales exhibit extraordinary manoeuvrability during lunge feeding events (Goldbogen *et al.* 2013a), particularly when foraging on patchily distributed, low-density krill (Fig. 2). Although our analyses provide a broad perspective on different manoeuvring strategies as a function of prey density, they do not elucidate the mechanisms that govern unsteady locomotor performance, nor do they clarify the energetic consequences of the broad suite of foraging strategies. Blue whales should realize greater energetic efficiency when targeting higher density krill patches (Fig. 2) and first principles indicate that manoeuvres and turns should incur a greater energetic cost compared with maintaining a linear trajectory (Wilson *et al.* 2013). Because we found a correlation between the degree of manoeuvring and lower krill densities, it begs the question of how the balance of energy varies across the observed spectrum of foraging strategies. There are multiple, interconnected processes that influence the overall energy balance for the different foraging modes we observed in this study (Table 2). Our data underscore the importance of simultaneously quantifying the fine-scale kinematics and prey patch characteristics to fully understand the energetics of foraging animals. Future studies should directly assess the energetic efficiency of different foraging behaviours through a combination of feeding rates (Simon, Johnson & Madsen 2012), prey density measures (Hazen *et al.* 2011), animal-borne accelerometry (Gleiss, Wilson & Shepard 2011) and hydromechanical models (Potvin, Goldbogen & Shadwick 2012).

To increase our understanding of the biomechanical drivers of foraging energetics and ecology, additional studies are needed that quantify all six kinematic degrees of freedom (rotations about and translations along three orthogonal body axes) to fully characterize the manoeuvrability of free-ranging marine animals. Novel tag sensor suites will be required to quantify these processes, including gyroscopes and video cameras to understand how control and propulsive surfaces are used to facilitate different manoeuvres. Furthermore, we do not yet have the ability to assess the very fine-scale features of the prey field at multiple scales relative to the foraging animal. With the progressive miniaturization of electronic sensors, future

Table 2. Summary of energy balance parameters for blue whale foraging ecology

Parameter	Shallow feeding	Deep feeding	Energy balance	Figures
Manoeuvring	+	−	Expenditure	3
Diving costs	−	+	Expenditure	1 and 2
Feeding rate	+	−	Gain	2
Prey density	−	+	Gain	2 and 3

Plus and minus symbols indicate a predicted increase and decrease, respectively, for each parameter that contributes to the overall energy balance of foraging.

studies could potentially use animal-borne echosounders or stereo video systems that quantify prey at a scale that is directly in front of the predator, but these approaches still need to be combined with broader prey patch metrics to understand prey patch selection, foraging bout duration and migration among patches. Finally, our study assessed foraging behaviour of individual blue whales foraging on krill that varied by only one order of magnitude, but krill can aggregate at much greater densities (Nicol 1986; Simard & Lavoie 1999; Nowacek *et al.* 2011). Longer tag deployments that measure body kinematics are critically needed to provide multi-day and weekly daily diaries of foraging performance, prey patch selection and energetic efficiency.

Acknowledgements

Data accessibility

Data for this paper are deposited in the Stanford Digital Repository. Available at: http://purl.stanford.edu/zr202wj1976 (Goldbogen *et al.* 2015).

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