

RESEARCH ARTICLE

Functional Ecology



Predator-scale spatial analysis of intra-patch prey distribution reveals the energetic drivers of rorqual whale super-group formation

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Abstract

1. Animals are distributed relative to the resources they rely upon, often scaling in abundance relative to available resources. Yet, in heterogeneously distributed environments, describing resource availability at relevant spatial scales remains a challenge in ecology, inhibiting understanding of predator distribution and foraging decisions.
2. We investigated the foraging behaviour of two species of rorqual whales within spatially limited and numerically extraordinary super-aggregations in two oceans. We additionally described the lognormal distribution of prey data at species-specific spatial scales that matched the predator's unique lunge-feeding strategy.
3. Here we show that both humpback whales off South Africa's west coast and blue whales off the US west coast perform more lunges per unit time within these aggregations than when foraging individually, and that the biomass within gulp-sized parcels was on average higher and more tightly distributed within super-group-associated prey patches, facilitating greater energy intake per feeding event as well as increased feeding rates.
4. Prey analysis at predator-specific spatial scales revealed a stronger association of super-groups with patches containing relatively high geometric mean biomass and low geometric standard deviations than with arithmetic mean biomass, suggesting that the foraging decisions of rorqual whales may be more influenced by the distribution of high-biomass portions of a patch than total biomass. The hierarchical distribution of prey in spatially restricted, temporally transient, super-group-associated

[Correction note added on 25-February 2021, after first online publication: The second author in the How to cite this article box has been amended.]

patches demonstrated high biomass and less variable distributions that facilitated what are likely near-minimum intervals between feeding events.

5. Combining increased biomass with increased foraging rates implied that overall intake rates of whales foraging within super-groups were approximately double those of whales foraging in other environments. Locating large, high-quality prey patches via the detection of aggregation hotspots may be an important aspect of rorqual whale foraging, one that may have been suppressed when population sizes were anthropogenically reduced in the 20th century to critical lows.

KEYWORDS

blue whales and humpback whales, fisheries acoustics, foraging ecology, gulp-sized cell, lognormal prey distribution, patchiness, raptorial filter-feeding, whale scale

1 | INTRODUCTION

Both the density of foraging predators and the types of collective behaviours displayed by groups are strongly driven across taxa by the heterogeneity, or patchiness, of resources in the environment (Gordon, 2014; Piatt & Methven, 1992), but effectively describing the availability of patchy resources to foragers is a fundamental challenge in ecology (Benoit-Bird et al., 2013; Chave, 2013; Levin, 1992). Baleen whale (parvorder: Mysticeti) predator/prey systems are ideal for investigating the physiological drivers and ecological limits related to patchiness because, as capital-breeding bulk filter-feeders, baleen whales require dense concentrations of seasonally available prey; essentially, their life history is driven by both spatial (Hazen et al., 2009, 2015; van der Hoop et al., 2019; Piatt & Methven, 1992) and temporal patchiness (Abrahms et al., 2019; Fossette et al., 2017). Additionally, unusually in pelagic systems it is possible to study both the behaviour of baleen whales and the distribution of their euphausiid (krill) prey quantitatively and simultaneously in situ via the use of bio-logging tags and hydroacoustic echosounders (e.g. Baumgartner & Mate, 2003; Goldbogen et al., 2019; Guilpin et al., 2019; Owen et al., 2017).

Baleen whales are the largest predators of all time, and rorqual whales (in the clade Balaenopteroidea) including blue whales *Balaenoptera musculus* and humpback whales *Megaptera novaeangliae* can engulf volumes of water (means ~130 and 15 m³ respectively) that approach or exceed their own body masses (Goldbogen et al., 2012; Kahane-Rapport & Goldbogen, 2018). Most typically, lunge-filter-feeding whales forage singly or in small groups (≤ 3 animals), and large groups of up to 10–20 animals, often fish-feeding humpback whales, have also been reported in some ecosystems (Jurasz & Jurasz, 1979; Kirchner et al., 2018; Whitehead, 1983). Group membership can be defined spatially or behaviourally according to the process under study (Mann, 2000); here we refer to groups as spatially cohesive aggregations, regardless of social, temporal or behavioural affiliations, such that individuals must interact with each other (constructively or destructively) when accessing prey. Topographical or transient oceanographic features (i.e. bays, fronts and upwelling regions) are sometimes associated with very large numbers (200+) of animals distributed over large (10–70 km) spatial extents that can generally be considered to

be foraging independently of each other (e.g. Jaquet, 1996; Nowacek et al., 2011). In contrast, our study involves dense aggregations such that individuals could be in direct conflict for the same resource.

The formation of spatially constricted, large aggregations of humpback whales in close proximity (numbering upwards of 100 whales within five body lengths) have been observed since 2011 in the Benguela Current upwelling region off the west coast of South Africa in a region where previous studies reported only loose aggregations up to 20 animals (Findlay et al., 2017). Known as super-groups, similarly large aggregations have been reported historically (e.g. Bruce, 1915), and the contemporary re-emergence of this behaviour may be related to the recovery of regional large whale populations above critical thresholds. Findlay et al. (2017) relate that animals in these super-groups are likely foraging; however, group behaviour does not necessarily imply optimal behaviour (Przybylski et al., 2013), and the proximate causes that inspire such large aggregations have not before been explained.

In this study, we examined the prey conditions near, and the foraging behaviour of, large aggregations of rorqual whales in two environments: humpback whales in South Africa and blue whales in Monterey Bay off the US west coast (Figure 1). We hypothesized that the whales observed in super-groups were foraging throughout the environment in which they were observed, but that foraging conditions were of higher quality proximal to super-group observations, suggesting that prey availability is an underlying driver of super-group aggregation. To test this hypothesis, we characterized the prey fields in both environments proximal to foraging whales that were both loosely and densely aggregated by analysing fisheries acoustics data at spatial scales that match the foraging style of the predators. We show how this method can be used to reveal differences between heavily foraged patches proximal to large predator aggregations and other patches in the environment that also appear to contain abundant biomass. We additionally used bio-logging tags in both environments to test whether whales in super-groups demonstrated higher feeding rates than whales not aggregated in super-groups. Illuminating the differences in prey conditions between aggregated and non-aggregated whales may not only explain why super-groups form,

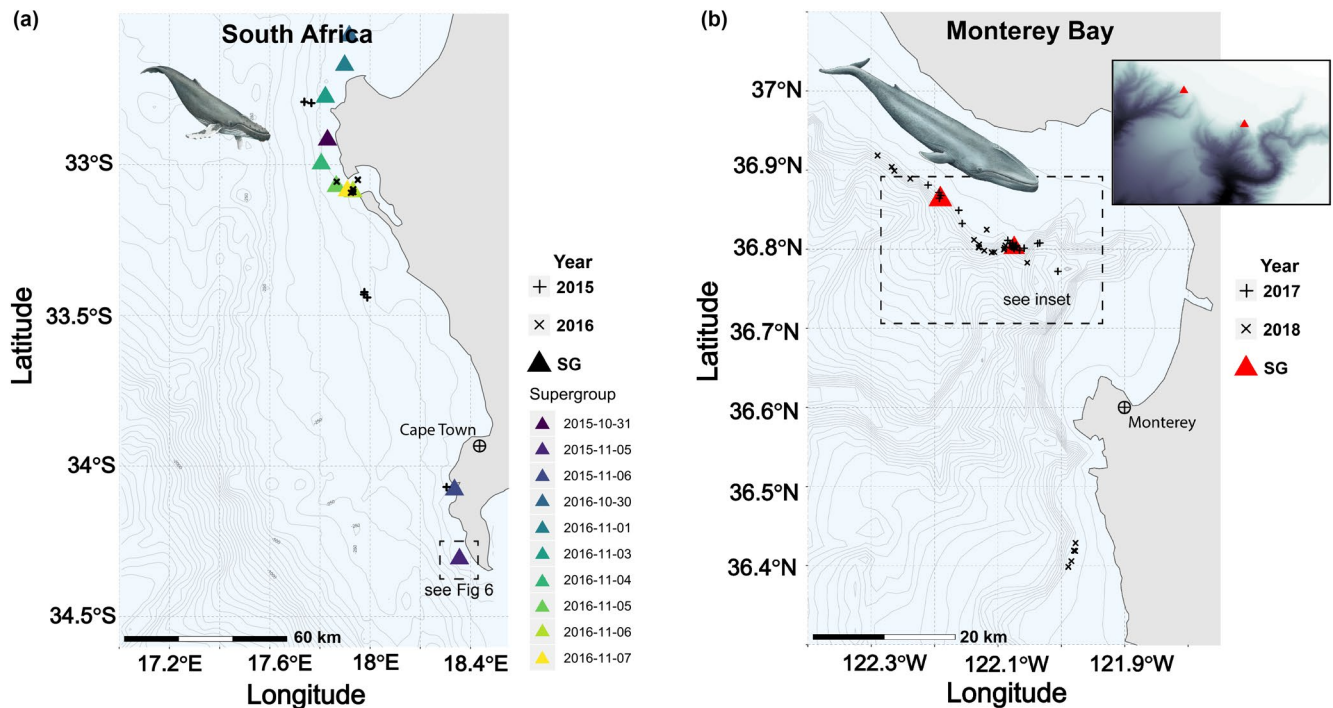


FIGURE 1 Field locations in South Africa (a) and Monterey Bay (b). Depth contour lines are separated by 50 m until the 500-m isobath and then 100 m thereafter. Triangles show observed super-group (SG) locations, and + and x mark the deployment locations of suction-attached bio-loggers on humpback (a) and blue whales (b). Data collected near each super-group are collated in Table S1

but may aid understanding about how predators foraging in a patchy environment make decisions about where and when to expend foraging effort.

2 | MATERIALS AND METHODS

We investigated aggregations of rorqual whales in two eastern boundary current upwelling ecosystems: humpback whales in the Benguela Current off South Africa's west coast in 2015 and 2016, and blue whales in Monterey Bay off the US west coast in 2017 and 2018 (Figure 1). These aggregations are distinct from other contemporary descriptions of large baleen whale groups in the extraordinary density of animals within a small region of open ocean—in the case of humpback whales including up to 200 individuals within regions as small as 200 m on a side (Findlay et al., 2017)—such that animals must interact with each other as they are foraging (Figure 2, Video S1). While humpback whale super-groups were the specific focus of research efforts in South Africa, large aggregations of blue whales were encountered only twice opportunistically during Monterey Bay field efforts. For detailed field methods, see Appendix S1.

2.1 | Foraging behaviour

In both locations, to examine foraging behaviour within and outside of super-groups, we attached integrated 3D accelerometer

and video tags to whales for time periods of ~2–20 hr. Individual feeding events that involve engulfing a mass of water and krill that can exceed the size of the whale (hereafter, 'lunges' or 'gulps', see Goldbogen et al., 2017) were identified via their kinematic signatures (as in Cade et al., 2016). Foraging behaviours including feeding rate (lunges/hr), inter-lunge interval, foraging bout length and foraging depth were compared within species between super-group and non-super-group times (details in Appendix S1), as well as between the two study ecosystems and among other ecosystems with krill-feeding whales of the same species (total of 112 blue whales and 45 humpback whales, Table 1).

To determine the significance of comparisons between super-group and non-super-group foraging of tagged animals, both t-tests and generalized linear mixed effects (GLME) models were used. Foraging of tagged whales when they were and were not in super-groups was compared, and super-group foraging was additionally compared to other whales in the same environment but not in super-groups. Finally, super-group foraging was compared to a larger population of whales outside the specific tagging period. For humpback whales, this was all krill-feeding whales from California, the Antarctic and South Africa. For blue whales, this was a comparison with blue whales in the same region as the super-group (Monterey Bay) but a year later. T-tests were used to test for significant differences between mean feeding rates (lunges/hr during foraging bouts) of super-group whales and mean feeding rates of whales foraging when not aggregated in super-groups (Table 2; Table S2). For both species, foraging bouts were defined as the time period that included all foraging dives with <5.5 min (see Appendix S1 and

FIGURE 2 Investigating super aggregations of predators and prey. (a) UAV image of at least 60 humpback whales off South Africa's west coast, scale is estimated from mean humpback whale length (image© Jean Tresfon). (b) UAV image of four blue whales in an aggregation of ~15 whales in Monterey Bay, CA (image© Duke Marine Robotics and Remote Sensing). Inset: map of super-group region with tracks of tagged whales; the green track represents the topmost whale in the image. (c, d) Underwater views of multiple humpback and blue whales, respectively, feeding simultaneously. (e, f) Acoustic backscatter near super-group in South Africa and Monterey Bay, respectively, overlaid with the time-synched depth profiles and lunges (green circles) of whales tagged nearby. Grid lines are sized to match the dive-scale unit of analysis for each species

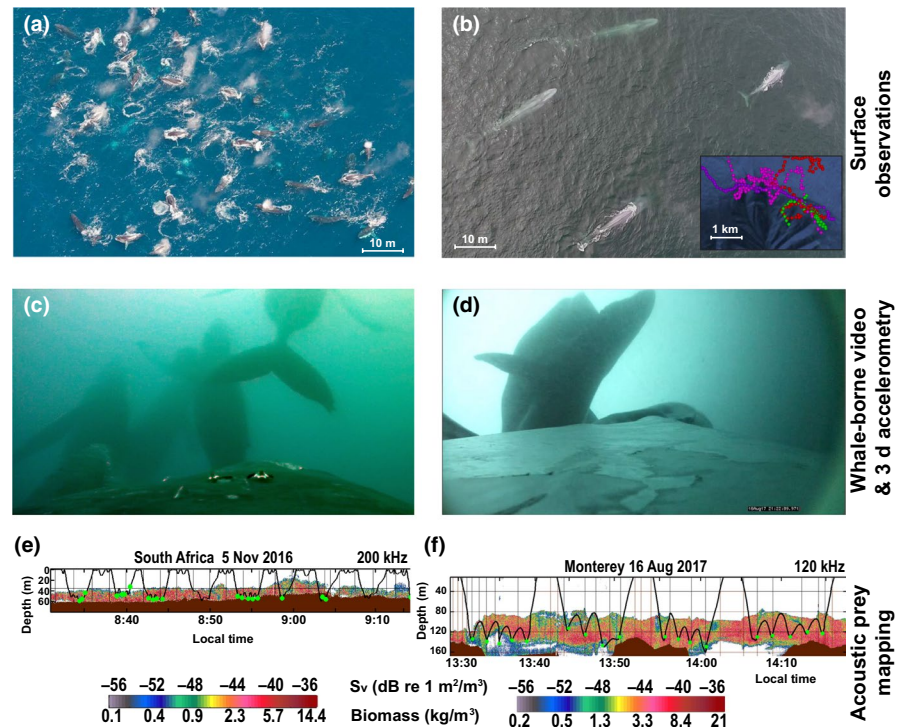


TABLE 1 Morphometric and feeding parameters that informed analysis, using all krill-feeding whales from (Goldbogen et al., 2019). Body lengths are representative of whales in the region. Ventral Groove Blubber length (VGB_L) and jaw length (Jaw_L) were allometrically determined (Kahane-Rapport & Goldbogen, 2018) and used to create the gulp-size cell (Figures 3 and 4). Search areas were used to calculate the size of the dive-sized cells

Species	Length	VGB_L	Jaw_L	Vertical search area	Horizontal search area	Inter-lunge interval	Lunges per dive	Deployments
<i>Balaenoptera musculus</i>	22.5 m	12.8 m	4.25 m	$44 \pm 16 \text{ m}^a$	$240 \pm 119 \text{ m}^a$	$108 \pm 254 \text{ s}$	3.3 ± 2.0	112
<i>Megaptera novaeangliae</i>	10.5 m	6.0 m	2.25 m	$35 \pm 20 \text{ m}$	$125 \pm 99 \text{ m}$	$43 \pm 12 \text{ s}$	3.2 ± 1.1	45

^aSearch areas for *B. m.* were limited to deployments with georeferenced pseudotracks ($n = 51$).

Figure S4) from the return to the surface of one foraging dive to the start of the next foraging dive. GLME models were constructed in Matlab 2019a for inter-lunge interval (ILI), lunges per dive, dive duration and search area from all data using super-group status as a fixed effect and individual whale as a random effect. For dive duration and lunges per dive, factors known to be influenced by dive depth, mean lunge depth for each dive was binned into 50-m depth bins and used as an additional random effect.

2.2 | Prey data collection and initial processing

Prey data were collected using multi-frequency (38 and either 120 or 200 kHz), split-beam fisheries acoustic systems (Simrad EK60s or EK80s) ensonifying the water column below a vessel within an estimated 500 m of foraging whales in both ecosystems, a distance we considered proximal given the size of observed patches. Data collected near super-groups were compared to data collected near feeding whales not aggregated into super-groups on each observation day and in aggregate as described below. Krill biomass at each

analysed spatial scale was estimated from the mean volume back-scattering strength (S_v in $\text{dB re } 1 \text{ m}^2/\text{m}^3$, Table 3) of pings aggregated into cells in Echoview v9 with heights and lengths as detailed below. The acoustic set-up, the calculation of target strength for small krill and the conversion of acoustic units to biomass units are all detailed in Appendix S1. Aggregations of krill, dominated by large swarms >10 m thick and 1 km across, were identified in acoustic echograms using the SHAPES school detection algorithm (Barange, 1994; Coetzee, 2000) and dB differencing techniques (Jarvis et al., 2010, additional details in Appendix S1).

2.3 | Predator-scale prey analysis

Rorqual whales utilize a unique foraging style, lunge-filter-feeding, characterized by raptorial targeting of discrete parcels of water followed by filtration through baleen plates and retention of prey (Goldbogen et al., 2017; Pivorunas, 1979). Typically this behaviour consists of diving to depths ranging from the surface to >300 m, performing one to ten lunges, and then returning to the surface to

TABLE 2 Mean feeding parameters derived from tag data for whales foraging in super groups (SG) and not in super groups (NSG). Feeding bout definition described in Figure S4. Data for individual whales foraging in super-groups ($n = 6$ in both ecosystems) in Table S2. *M. n.* = *M. novaeangliae* (humpback whales), *B. m.* = *B. musculus* (blue whales)

	Feeding rate (lunges per hr within a foraging bout)		Inter lunge interval (ILI, s)		Inter lunge search area (10^2 m^2)		Lunges per dive	
	SG	NSG	SG	NSG	SG	NSG	SG	NSG
<i>Megaptera novaeangliae</i> (South Africa)								
SG animals	55 ± 15	37 ± 18	32 ± 10	40 ± 18	3.4 ± 2.5	8.1 ± 11	4.5 ± 1.5	3.6 ± 2.2
(<i>p</i> -value)	(0.078)		*** (0.000)		*** (0.000)		(0.516)	
Number of animals	6	5	6	5	6	3	6	5
All SA <i>M. n.</i>	55 ± 15	39 ± 15	32 ± 10	36 ± 16	3.4 ± 2.5	6.6 ± 10	4.5 ± 1.5	4.1 ± 2.5
(<i>p</i> -value)	(0.086)		*** (0.000)		*** (0.000)		(0.492)	
Number of animals	6	7	6	7	6	5	6	7
All <i>M. n.</i>	55 ± 15	38 ± 16	32 ± 10	44 ± 18	3.4 ± 2.5	11 ± 26	4.5 ± 1.5	4.4 ± 2.1
(<i>p</i> -value)	*(0.028)		*** (0.000)		** (0.006)		(0.913)	
Number of animals	6	17	6	33	6	30	6	33
<i>Balaenoptera musculus</i> (Monterey Bay)								
SG animals	24 ± 2.9	21 ± 5.1	95 ± 17	102 ± 19	36 ± 34	42 ± 40	4.0 ± 0.9	3.3 ± 1.3
(<i>p</i> -value)	(0.214)		(0.187)		(0.083)		(0.387)	
Number of animals	6	5	6	5	6	5	6	5
All MRY 2017 <i>B. m.</i>	24 ± 2.9	22 ± 3.9	95 ± 17	101 ± 16	36 ± 34	42 ± 32	4.0 ± 0.9	3.3 ± 1.3
(<i>p</i> -value)	(0.200)		(0.126)		*(0.028)		*(0.038)	
Number of animals	6	17	6	17	6	17	6	17
SG <i>B. m.</i> versus 2018 <i>B. m.</i>	24 ± 2.9	18 ± 3.1	95 ± 17	108 ± 22	36 ± 34	57 ± 85	4.0 ± 0.9	4.8 ± 1.4
(<i>p</i> -value)	*** (0.000)		*(0.014)		(0.124)		(0.886)	
Number of animals	6	22	6	22	6	22	6	22

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

breathe before diving again. To match the spatial scale of prey analysis to the spatial scale utilized by diving whales, we first used tag data to identify the mean horizontal and vertical distances travelled by foraging whales of both study species from 10 s before the first lunge in a dive to 10 s after the last lunge in a dive (distances in Table 1, details in Appendix S1). We then divided the acoustically identified prey patches (Figures 3a and 4c–d) into these dive-sized cells (Figures 3b and 4e–f).

To examine the distribution of krill within dive-sized cells (Figure 3c and 4h), we used Echoview to calculate S_v within analytical cells the size of an average whale engulfment volume (S_{v_gulp} , symbol definitions in Table 3) as calculated from the morphology of an intermediately sized representative of each species of interest (blue whale total length = 22.5 m, humpback whale = 10.5 m). Jaw length was used for the vertical size of the cell (blue whale = 4.3 m, humpback whale = 2.3 m), and the ventral groove blubber length (blue whale = 12.8 m, humpback whale = 6.0 m) was used for the horizontal cell size (lengths calculated from ordinary least squares regression relationships in Kahane-Rapport & Goldbogen, 2018). At the observed prey patch depths, all return echoes had y-axis values larger than the head width, so the extracted cells represented a 2D projection of the gulp size. The engulfed water volume of

rorqual whales is a good spatial match for the analysis of acoustic data since the large size of engulfed water parcels allows multiple acoustic returns to be processed even at our smallest desired spatial scale. Gulp-sized cells contained a minimum of two pings, and in Monterey, blue whale gulp-sized cells averaged 9.4 ± 12.5 pings (mean \pm SD), while in South Africa humpback whale gulp-sized cells averaged 8.4 ± 6.8 pings (details in Appendix S1). The variation in the number of pings per gulp is a product of variable speeds by the survey vessel and variable ping rates set to maximize the number of samples without introducing acoustic artefacts like false bottoms. When such variation is present in a survey, data that are averaged into patches without first accounting for survey distance can potentially be biased. We report whole patch S_v (e.g. Figure 4c,d; Table S3) for comparison to the spatially averaged approach described above.

2.4 | Characterizing patchy prey

In both marine (Bennett & Denman, 1985; Campbell, 1995) and terrestrial (White, 1978) environments, both inter- (Magurran & Henderson, 2003; Pagel et al., 1991; Preston, 1948, 1962) and intra- (Anand & Li, 2001; Barnes, 1952) species abundances tend to be

TABLE 3 Definitions of symbols and abbreviations. See Figure 3 for schematic representation of hierarchical prey distribution calculations. Subscripts LN or N before the variable denote lognormal or normal distributions respectively. See MacLennan et al. (2002) for further descriptions of S_v and TS. For further discussion of the calculation of \hat{B} or \hat{S}_v , see Appendix S1 section 'Estimating overall intake'. See equation 1 in Appendix S1 for information on calculating B from S_v

Symbol	Definition	Units	Scale
\cdot	Multiply or divide (the multiplicative correlate to \pm)	—	—
B_{gulp}	Biomass density within a gulp-sized cell	kg/m ³	Gulp
B_{patch}	Arithmetic mean biomass density within a patch (estimated from $S_{v_{\text{patch}}}$)	kg/m ³	Patch
${}^{\text{LN}}B_{\text{ws}}$	Whale scale biomass: the distribution of B_{gulp} within a dive-sized cell, estimated from ${}^{\text{N}}S_{v_{\text{ws}}}$ and equivalent to $\text{geomean}(B_{\text{gulp}}) \cdot \text{GSD}(B_{\text{gulp}})$	kg/m ³	Dive
$\overline{{}^{\text{LN}}B_{\text{ws}}}$	Distribution of ${}^{\text{LN}}B_{\text{ws}}$ within a patch or region, estimated from $\overline{{}^{\text{N}}S_{v_{\text{ws}}}}$ and equivalent to $\text{geomean}({}^{\text{LN}}B_{\text{ws}}) \cdot \text{GSD}({}^{\text{LN}}B_{\text{ws}})$	kg/m ³	Patch or region
\hat{B}	Estimated arithmetic mean biomass (mean biomass consumed over time) calculated the summary variables $\text{geomean}(B_{\text{ws}})$ and $\text{GSD}(B_{\text{ws}})$	kg/m ³	Dive, patch or region
geomean	Geometric mean	—	—
GSD	Geometric standard deviation	—	—
SD	Standard deviation	—	—
S_v	Mean volume back scatter strength (MVBS)	dB re 1 m ² / m ³	—
$S_{v_{\text{gulp}}}$ or $S_{v_{\text{gulp}}}$	MVBS within a gulp-sized cell	dB re 1 m ² / m ³	Gulp
$S_{v_{\text{patch}}}$ or $S_{v_{\text{patch}}}$	MVBS within a patch	dB re 1 m ² / m ³	Patch
$S_{v_{\text{dive}}}$ or $S_{v_{\text{dive}}}$	MVBS within a dive-sized cell	dB re 1 m ² / m ³	Dive
${}^{\text{N}}S_{v_{\text{ws}}}$ or ${}^{\text{N}}S_{v_{\text{ws}}}$	Whale scale S_v : the distribution of $S_{v_{\text{gulp}}}$ within a dive-sized cell, presented as $\text{mean}(S_{v_{\text{gulp}}}) \pm \text{SD}(S_{v_{\text{gulp}}})$	dB re 1 m ² / m ³	Dive
$\overline{{}^{\text{N}}S_{v_{\text{ws}}}}$ or $\overline{{}^{\text{N}}S_{v_{\text{ws}}}}$	Distribution of $\text{mean}({}^{\text{N}}S_{v_{\text{ws}}})$ of all dive-sized cells within a patch or region, presented as $\text{mean}({}^{\text{N}}S_{v_{\text{ws}}}) \pm \text{SD}({}^{\text{N}}S_{v_{\text{ws}}})$	dB re 1 m ² / m ³	Patch or region
\hat{S}_v	Estimated MVBS from a dive, patch or region, calculated from the summary variables $\text{mean}(S_v)$ and $\text{SD}(S_v)$	dB re 1 m ² / m ³	Dive, patch or region
TS	Target strength (see equation 1 in Appendix S1)	dB re 1 m ²	—

distributed heterogeneously and can often be characterized by log-normal distributions (Dennis & Patil, 1987). That is, the log of abundance data is typically normally distributed and can be characterized by the mean and standard deviation of logged data, or, equivalently, the geometric mean and geometric standard deviation of the unlogged data. Fisheries acoustics data, however, are typically reported as overall mean abundance integrated over broad areas (e.g. Benson et al., 2002; Cox et al., 2009; Croll et al., 1998; Nickels et al., 2019) or mean volumetric density within patches (e.g. Hazen et al., 2015; Nowacek et al., 2011; Owen et al., 2017). Prey patches can be heterogeneously distributed in space (Benoit-Bird et al., 2019; Kaartvedt et al., 2005; Watkins & Murray, 1998), however, and aggregations themselves can have variable structure (Benoit-Bird et al., 2017), implying that using a single number to characterize the biomass density of a large patch may not represent what a foraging animal encounters

(Stephens & Krebs, 1986). Additionally, averaging the biomass densities among patches with variable sizes may misrepresent mean availability if biomass is not weighted by patch size, or if acoustic surveys with variable ping rates or vessel speeds are not first averaged into spatially consistent regions.

When prey patches are small such that a lunge-feeding whale feeds on it only once, describing patch density with a single number for each krill patch would be an appropriate strategy. However, the krill swarms we observed in this study were several kilometres across (Figure 2) such that predators could be considered to be foraging within a patch rather than among patches. Consequently, to better represent the prey biomass available to foraging rorqual whales, we characterized the prey fields proximal to feeding whales at predator-specific spatial scales, dividing large patches into analytical cells the size of an individual whale's gulp and then examining how those gulp-sized cells are

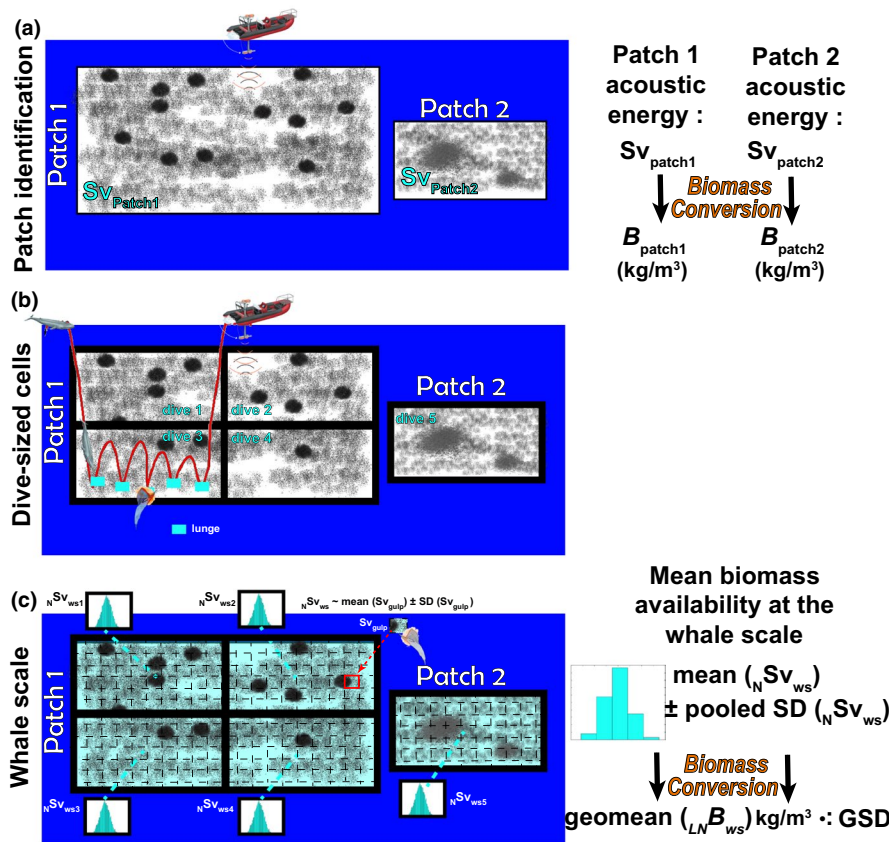


FIGURE 3 Schematic illustrating the analytical technique for two acoustically detected prey patches. (a) The patch scale is commonly reported in acoustics literature, looking at the linearly averaged mean biomass within each patch. (b) In the whale-scale approach, patches are first divided into cells the size of an average whale foraging dive (Table 1). (c) The whale scale looks at the distribution of the biomass of gulp-sized cells within dives and then pools results for a representation of the mean availability of biomass at the scale experienced by the predator. Biomass conversion equation in Appendix S1, equation 1. SD = standard deviation, geomean = geometric mean = $\text{antilog}(\text{mean}(\log(\text{biomass})))$, GSD = geometric standard deviation = $\text{antilog}(SD(\log(\text{biomass})))$. Other symbols defined in Table 3

distributed within cells of a size likely experienced by whales on a foraging dive (Figures 3 and 4). These gulp-sized cells are distributed, as in patchy prey in other aquatic and terrestrial systems, lognormally (more details in Appendix S1, Figure S1). Details for estimating mean intake from lognormal distributions are also reported in the Appendix S1 section 'Estimating overall intake'.

2.5 | The whale scale

For each dive-sized cell in a region of interest (e.g. all dive-sized cells proximal to a super-group on a specific day), we first summarized the distribution of biomasses likely to be experienced by a foraging whale on a dive by calculating the mean and standard deviation (SD) of Sv_{gulp} within each dive-sized cell. To ensure sufficient statistical power, only cells that had at least 30 gulp-sized cells were included in analysis. We then summarized the overall distribution in super-group-associated patches and patches not associated with super-groups by averaging all dive summary values (Nsv_{ws}) in a region and calculating the pooled SD of all dives within the region of interest (Figure 3c). We refer to this summarized analysis of prey as the mean 'whale scale' (Nsv_{ws} in acoustic units, $LN B_{ws}$ in estimated biomass units, Table 3).

All statistical comparisons were done on the acoustic units which have approximately normal distributions, and then Sv was converted to estimated biomass (generally following Jarvis et al., 2010, with study-system-specific calculation details in Appendix S1). Because biomass estimation is subject to model enhancements over time, we report Sv

(as mean \pm pooled SD) throughout the text in addition to biomass (B , Table 3). Biomass of gulp-sized cells (B_{gulp}) was lognormally distributed at larger scales (Figure S1), so for whale-scale summary values we present the geometric mean (geomean) and the geometric standard deviation (GSD) of gulp-sized cells (B_{gulp}). The geo

mean and GSD are equivalent to the antilog of the mean and SD of $\log(\text{biomass})$. There are several advantages to summarizing data using lognormal distributions instead of reporting mean biomass including less sensitivity to outliers and a better ability to characterize the spread of data. We report lognormal summary statistics as 'biomass in kg/m^3 ∴ a multiplicative scalar', where ∴ is read 'multiplied or divided by' and is a combination of the multiplication (\cdot) and division ($:$) symbols introduced by Leibniz (1684). ∴ can be interpreted as the multiplicative complement to the commonly used \pm .

The whale scale analytical scale—the distribution of gulp-sized cells within their containing dive-sized cell (Figures 3c and 4e,f)—can be thought of as the spread of biomass around a dive's median biomass. We developed this scale because of its link to the spatial scale of prey experienced by foraging rorqual whales on any given foraging dive. This analytical technique gives a representation of what a foraging rorqual could encounter on a dive and would represent what it is likely to forage on if it forages indiscriminately during its dive. However, to account for the likelihood that rorquals employ an active selection strategy to maximize their prey intake, we additionally analysed the distribution of only the top 50% of gulp-sized cells within dive-sized cells. The choice of 50% as a threshold was selected as a compromise between indiscriminate feeding centred

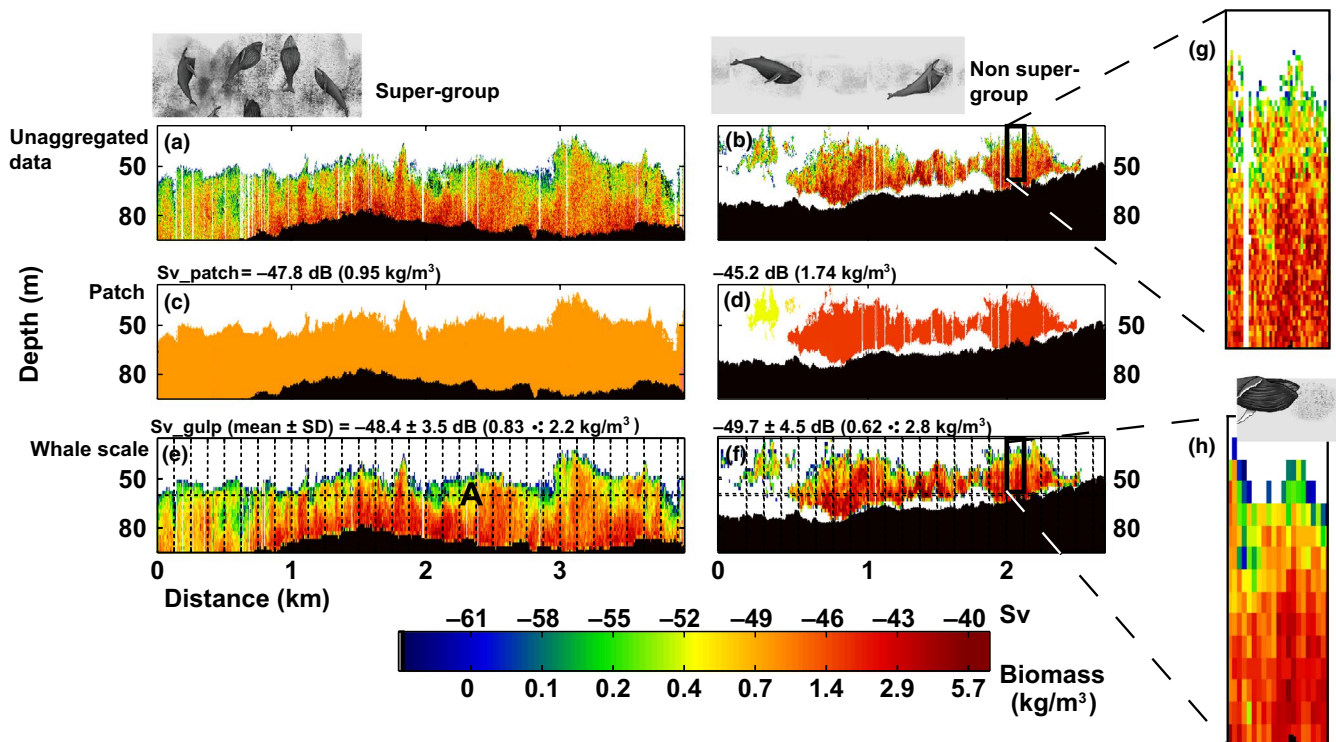


FIGURE 4 Matching the spatial scale of rorqual whale feeding with acoustic analysis can illuminate differences between patches that appear to be of similar quality. (a, b) Hydroacoustic data from super-group and non-super-group regions on 5 November 2015, averaged into 1 m × 1 m cells (for display purposes along a consistently sized x-axis). (c, d) The mean density of each identified krill swarm as exported from Echoview. The large non-super-group krill swarm in d had nearly double the krill density overall than the swarm in c proximate to a super-group, suggesting that the mean density of krill swarms may not be an appropriate metric to describe prey availability here since at this scale the super-group patch would appear to be lower quality. (e, f) The whale scale: the patch is divided into cells the average size of a (2D) humpback whale foraging dive (125 m × 35 m) and then further divided into gulp-sized cells. The geometric mean of the gulp-sized cells within dive-sized cells is higher in the super-group proximal patch. (g) Acoustic data in a dive-sized cell at fine resolution. (h) Acoustic data in a dive-sized cell averaged into gulp-sized cells, demonstrating how at this resolution the distribution of krill within the patch is preserved

around a patch's median and precise selection of gulps with maximum density given how much is unknown about the behavioural patch selection algorithm employed by rorqual whales. We refer to this technique as the 'informed whale-scale' analysis and it can be thought of as the distribution of biomass around the 75th percentile of biomass in a dive-sized cell.

3 | RESULTS

Humpback whale super-groups off South Africa's west coast are described in detail in Findlay et al. (2017) and consist of 20–200 whales surfacing haphazardly in an area as restricted as 200 m on a side (Figure 2a; Video S1). Super-groups were observed on 10 of 20 ship days in 2015–2016 (Figure 1). The duration of super-group cohesiveness is unknown as none were observed from formation to dispersal, but all were observed for at least 1 hr and in all five instances where group dispersion was observed, emigration was sequential. Unlike in other environments where humpback whales have been observed coordinating their fish-feeding behaviour (Jurasz & Jurasz, 1979; Mastick, 2016; Wiley et al., 2011), underwater video evidence suggests that lunge feeding within these krill patches is uncoordinated

(e.g. Video S1). Two blue whale super-groups were encountered in 4 field days in 2017 in Monterey Bay, California, USA and consisted of an estimated 15–40 whales surfacing within sight of an observer at sea level (~1 km range); no super-groups were encountered in 9 field days in 2018. Blue whales generally forage in singles or in pairs and the super-groups we observed consisted of many singles and pairs feeding in the same area in an apparently uncoordinated fashion. Due to the similarities in behaviour and the much larger sizes of blue whales (blue whales are ~2× the length, 4× the mass and have 8× the engulfment capacity of humpback whales, Kahane-Rapport & Goldbogen, 2018), we propose that the observed group sizes are comparable despite their differences in individual predator abundances. The blue whale super-group encountered on August 14 (25–40 whales estimated) was encountered at 08:30 and had begun to decrease in density at ~11:15. On August 16, the group (15–20 whales estimated) was encountered at 13:30 and our vessels left the area at 14:20.

3.1 | Foraging behaviour

All whales fed continuously (accounting for surface recovery and transit time) while in super-groups. Humpback whales fed at a mean

depth of 43 ± 13 m while blue whales fed at 109 ± 30 m (e.g. Figure 2). In both cases, whales in super-groups had similar lunges per dive as non-super-group whales (Table 2), but the smaller ILI and area traversed between lunges for whales in super-groups compared to non-super-groups (Table 2) led to shorter dive durations (model estimates accounting for foraging depth differences, blue whale 95% confidence interval (CI): 197 to 391 s shorter, humpback whale 95% CI: 60 to 112 s shorter). These factors combined to influence the overall feeding rate, as measured in lunges/hr during feeding bouts, which were 49 and 14% higher, respectively, in humpback whale and blue whale super-groups versus feeding rates when these same whales were not feeding in super-groups, and were 45 and 34% higher, respectively, when super-group whales were compared to krill-feeding whales more generally (Table 2). The increased feeding rates in super-groups suggested that we would find that prey near super-groups were distributed in such a way as to facilitate decreased search times.

3.2 | Prey analysis

Analysis of prey abundance and distribution revealed high-quality foraging conditions in both super-group and non-super-group behaviour states in each ecosystem. Identified prey patches near foraging whales were typically tens of metres thick and hundreds of metres wide, regardless of group size, such that whales could be described as foraging within a patch rather than among patches (Figure 2; Video S1). Examination of the distribution of the biomass of gulp-sized cells from all identified patches on each survey day revealed that the biomass density was distributed lognormally (Figure S1,

Appendix S1), suggesting the appropriateness of the 'whale scale' analytical technique for describing the prey field experienced by these large predators. Describing skewed data using the lognormal parameters (geomean and GSD) has the additional advantage of being less sensitive to outliers in the data, and summarizing acoustic data into spatially determined cells has the advantage of matching the spatial scale of collection with the spatial scale experienced by the predator under study.

In comparing the prey fields in super-group and non-super-group regions, we found that prey density was generally higher in super-group than in non-super-group regions. On 10 of 11 observation days (Table S3; Figure 5), geomean prey density at the whale scale ($\overline{B_{WS}}$) was higher near super-groups than near foraging whales not in super-groups ($p < 0.001$ in both environments): blue whale gulps in super-groups averaged 1.5 ± 1.6 kg/m³ (-47.5 ± 2.2 dB) while gulps in non-super-groups averaged 1.2 ± 1.8 kg/m³ (-48.5 ± 2.6 dB), and humpback whale gulps in super-groups averaged 0.49 ± 2.0 kg/m³ (-50.7 ± 3.0 dB) while non-super-group gulps averaged 0.31 ± 2.1 kg/m³ (-52.7 ± 3.3 dB). In 3 of 11 days, prey density was lower near super-groups if prey was described using whole patch means (further discussed below). Patches were additionally substantially and significantly thicker near super-groups in all cases (mean in South Africa: 22 ± 14 m vs. 8 ± 9 m, mean in Monterey: 33 ± 27 m vs. 15 ± 15 m, Figure 5; Table S3).

The GSD of gulps at the mean whale scale was not significantly different between super-group and non-super-group patches on any given day (Table S3). In 9 of 10 cases, the mean gulp at the mean informed whale scale (i.e. the mean gulp within the denser half of dive-sized cells) was significantly higher in super-groups, and in all

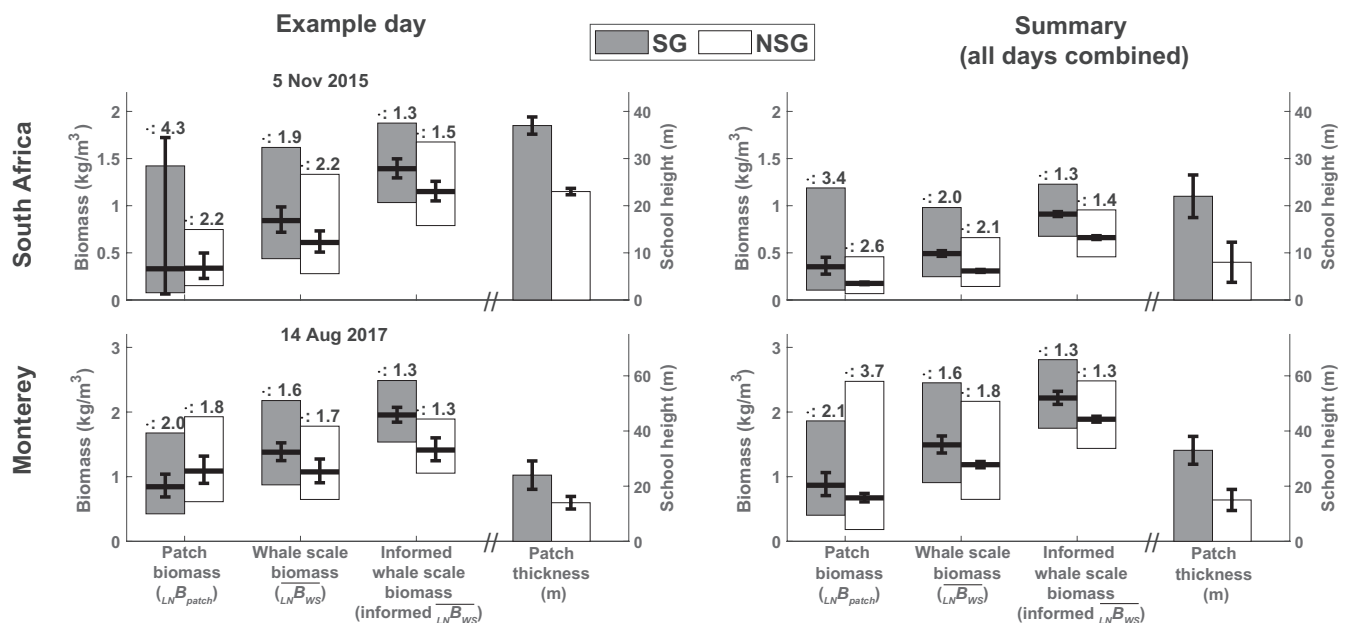


FIGURE 5 Summary prey data from an example day and in aggregate for both South Africa and Monterey. Summary data for all days are displayed in Table S3. Symbol definitions in Table 3, SG = super-group, NSG = non-super-group. Prey patch geometric means are the thick horizontal bars, and the shaded bars represent the GSD with the multiplicative factor listed above each bar. Error bars around the geometric means are the 95% confidence intervals (calculated in acoustic units and converted to biomass). Patch thickness error bars are 95% confidence intervals

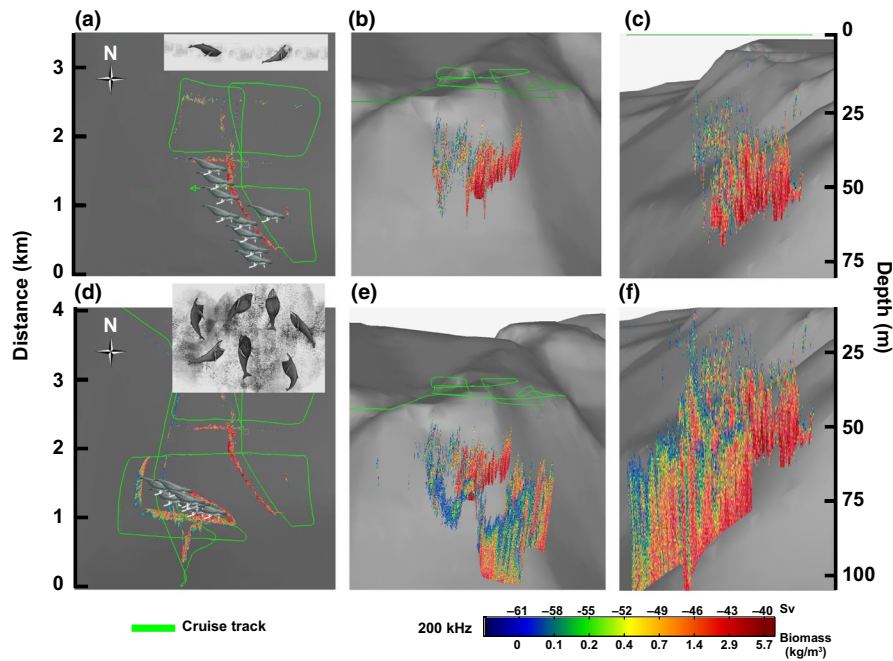


FIGURE 6 3D view of super-group-associated prey patch on 5 November 2015 in South Africa (the southernmost group in Figure 1). These are the same data from which Figure 4 was created. (a–c) Prey and whales spread out before super-group formation (prey data shown until 17:00 local time). (a) Overhead view. (b) Oblique view (from the northwest), highlighting the prey in relation to submarine canyon bathymetry. (c) Side-on view, looking from the south. (d–f) Same views now including super-group-associated data when 150–200 whales converged into a region ~200 m on a side at ~17:00. Bad weather on this day precluded suction-cup tag deployment. Whale illustrations by Alex Boersma. Bathymetry courtesy of the South Africa Navy Hydrographic Office. Data plotted in Echoview v10 using a 50x vertical exaggeration

cases the SD of gulp density at the mean informed whale scale was 0.1–0.6 dB lower in super-groups than non-super-groups.

Prey conditions in the same region both before and during super-group formation were observed just once in South Africa on 5 November 2015 (Figures 4 and 6). In that case, 150–200 whales were spread out along a shelf break before coming together into a single aggregation (Figure 6). Prey density in patch averages was not significantly different before or during super-group formation ($p > 0.9$, Figure 5). However, the geomean of gulps at the mean whale scale was 38% higher ($p = 0.010$) in super-group-associated patches and was 21% higher at the mean informed whale scale ($p = 0.002$). Additionally, mean patch thickness was estimated to be 14 m larger in super-groups ($p < 0.001$), and gulp GSD at both the whale scale and the informed whale scale was smaller in super-groups, though only significantly so at the informed whale scale (Figure 5; Table S3).

In Monterey Bay, the blue whale super-group on 14 August 2017 demonstrated a similar pattern as the 5 November 2015 humpback whale super-group (Figure 5). While the geomean of patch biomass was smaller (but not significantly different) in the prey field near the observed super-group, geomean gulp biomass at the mean whale scale and the mean informed whale scale were both significantly and substantially higher (Figure 5; Table S3), and patch thickness and gulp GSD at the informed whale scale were significantly higher and lower respectively ($p < 0.001$ in both cases, Table S3). While the super-group associated-patch on 16 August 2017 had slightly higher

geomean biomass at both the whale scale and in patches, results were non-significant (Table S3). Instead, prey around this super-group was characterized by a 2.5-fold increase in patch thickness as well as both a significant increase in geomean gulp biomass density and significant reduction in gulp GSD at the informed whale scale (Table S3).

Patches near super-groups thus had more available biomass on average than patches near whales not in super-groups. In both environments, better quality of super-group patches was indicated by higher geomean gulp density, thicker patches and indications that the prey at the informed whale scale (the denser half of the prey in each dive-sized cell) was more uniform in distribution (i.e. displayed smaller variance).

4 | DISCUSSION

Our results suggest that the formation of super-groups of two species of rorqual whales was largely influenced by high-quality foraging conditions. Gulp-sized cells analysed at the whale scale had higher geomean biomass and lower variability within prey patches associated with super-groups of humpback and blue whales, and whales within super-groups demonstrated higher feeding rates than more dispersed individuals. Furthermore, characterizing the intra-patch distribution of krill biomass appears to offer an explanation for the higher feeding rates observed in super-groups. Specifically, we found that super-groups were strongly associated with patches

characterized by high geomeans and low GSD of biomass, particularly in the densest half of gulps within dive-sized cells (the informed whale scale). Higher geomeans imply that even a naïvely foraging whale would benefit from increased energy intake at each feeding event, and a lower GSD (when paired with a high geomean) implies that a greater proportion of gulp-sized parcels would be of sufficient quality to feed (i.e. a greater proportion of gulps were above a threshold at which it would be beneficial to feed), enabling the observed increase in lunge-feeding events per unit time by decreasing search time. The match of predator behaviour (increased feeding rates) with our findings of higher density with less variance in cells the size of what a predator will experience on a foraging dive additionally supports the whale-scale level of analysis.

In ecological models of foraging in patchy environments, patch quality is often assessed as the overall intake (per unit time) enabled by an ecosystem (Giraldeau & Caraco, 2000). To improve the efficacy of such models, the intake rate parameter, λ , could further be decomposed into two component parts: 1) the energetic quality of each captured prey parcel and 2) the rate at which prey are captured. In rorqual whale foraging systems, these quantities are represented by the mean biomass density in each gulp (λ_p) and the lunge rate per unit time (λ_f), respectively, such that $\lambda = \lambda_p \times \lambda_f$. We found that prey patches associated with super-groups not only had 40%–50% more biomass in the median (geomean) gulp than patches not associated with super-groups, implying higher λ_p , but also had smaller GSD. The small GSD implied that prey was of more uniform quality proximal to super-groups, making it easier for whales to maximize consumption without spending time between lunges searching for the best nearby parcel. This reduction in search time likely facilitated the observed increases in super-group λ_f by decreasing the inter-lunge interval as well as the spatial distance travelled between lunges (Table 2). Indeed, the reported super-group feeding rates in both study areas (humpback whales: 55 ± 15 lunges/hr, blue whales: 24 ± 2.9 lunges/hr, Table 2) are comparable to the highest reported rates for whales in other studies: Goldbogen et al. (2008) report that one tagged humpback whale fed at a rate of 45 lunges/hr over 8 hr, Owen et al. (2017) report humpback feeding rates of 49 lunges/hr, while Southall et al. (2019) report blue whale feeding rates over 10-min bins that range from 5 to 30 lunges/hr when foraging, with mean rates typically <20 lunges/hr and max rates over foraging bout-comparable time-scales of approximately 25 lunges/hr. The high rates of foraging in super-groups suggest that these whales are feeding at rates close to their biomechanical limits.

The analysis of prey at the nested scales we describe is particularly well-suited for describing prey conditions available to krill-feeding rorqual whales because their foraging style utilizes characteristics of both filter-feeding, where energy cost per foraging event is independent of the quality of the prey, and raptorial feeding in which prey (i.e. in bulk patches) are engulfed in discrete units. The combination of these feeding modes distinguishes rorquals from right whales *Eubalaena glacialis*, whale sharks *Rhincodon typus* and other continuous ram filtration feeders. From our meta-analysis of data from 45 blue whales and 21 humpback whales that

lunged multiple times per dive and for which georeferenced tracks could be calculated, we found that those two species traverse an average of 177 ± 51 and 73 ± 34 horizontal metres between lunges and average 4.1 ± 1.4 and 5.2 ± 2.3 lunges per dive, respectively, yet the distance travelled for one lunge is only the length of the buccal cavity (12.8 and 6.0 m, respectively, for a 22.5 m blue whale and 10.5 m humpback whale). Right whales, approximately the same length as humpback whales, are continuous ram filtration filters that filter an average of 670 m^3 of water on every dive (van der Hoop et al., 2019). At 14 m^3 of water engulfed per lunge (Kahane-Rapport & Goldbogen, 2018), a humpback whale would have to lunge 48 times per dive (an order of magnitude more than their average) to filter an equivalent volume. These factors, combined with the ability to feed on more manoeuvrable prey enabled by high-speed, raptorial approaches (Cade et al., 2020), imply that rorqual whales may be energetically required to make active choices regarding what patch and what part of a patch to feed on, further supporting analysis at the informed whale scale.

Matching the spatial scale of analysis to the scale of the event under study is particularly critical in patchy environments (Benoit-Bird et al., 2013; Levin, 1992). Although the sensory mechanisms by which rorqual whales determine patch quality in the environment are currently unknown, insights into the process can be gleaned by proposing and examining potential behavioural algorithms used by whales to maximize their energy intake (Hein et al., 2020). Prior work has proposed that baleen whales initiate foraging when prey is available above a certain density (Cotté & Simard, 2005; Feyrer & Duffus, 2015; Hazen et al., 2009; Kirchner et al., 2018; Mayo & Marx, 1990). Our findings extend these ideas by suggesting that the density and distribution of encountered prey is a better indicator of where whales forage than overall patch or regional abundance. Future work may be able to refine this general principle into a prediction for a behavioural algorithm that would describe under what conditions a whale would give up foraging in one environment to take advantage of an environment it perceives as more favourable.

Better matching the scale of prey distribution to the scale of predator foraging effort could also be used to better predict overall intake rates (λ). Considering that super-groups of two species of whales aggregated in regions with less variability in the densest half of the cell, and given that rorquals are likely not feeding indiscriminately, we suggest that the actual prey consumed by foraging rorqual whales would likely be reflected by the biomass of prey available at the whale scale as a lower bound, but be even better reflected by analysis at the informed whale scale, and we include suggestions for the calculation of these bounds in Appendix S1. Additional studies to quantify a more precise threshold for the informed whale scale could eventually shed light on how rorquals maximize their foraging efficiency in a given environment.

Although humpback and blue whale super-groups have only been recently described, abnormally large densities of krill do not appear to be a new phenomenon. Nicol et al. (1987) report surface swarms of *E. lucens* near our study area in South Africa of up to 35 kg/m^3 . The historical record of super-groups (Bruce, 1915) followed by a

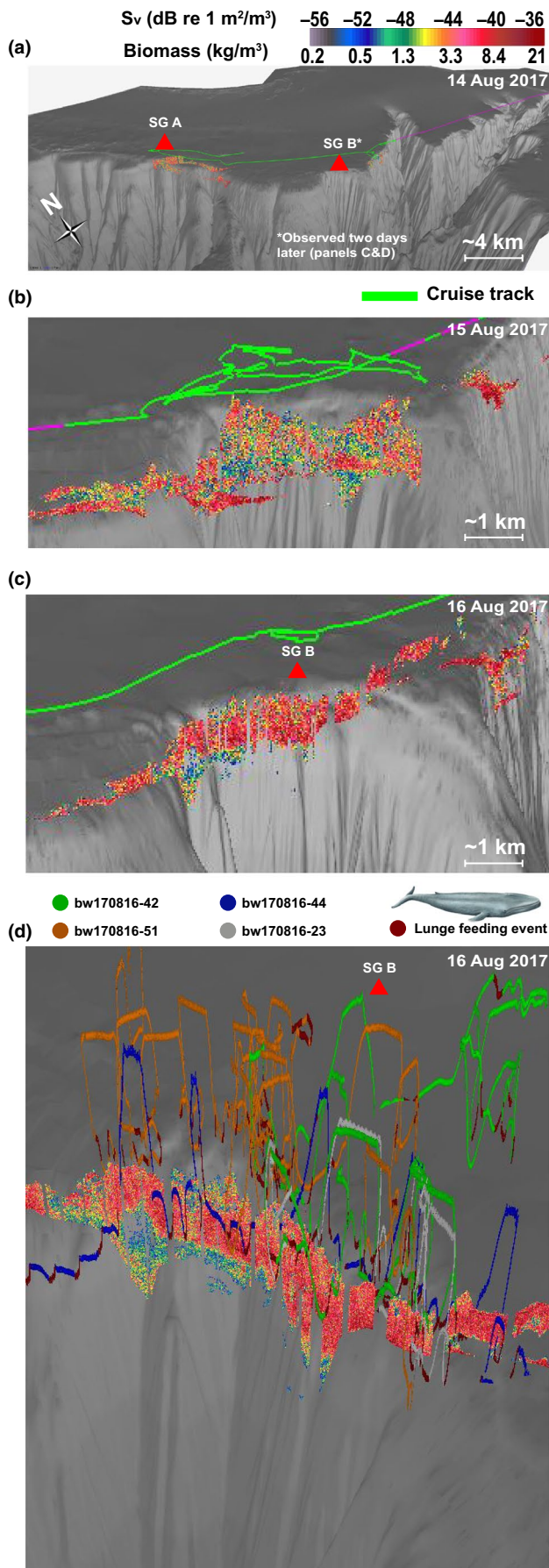


FIGURE 7 3D view of super-group (SG) associated prey patches in Monterey Bay, CA, USA. (a) Overall layout of the north Monterey Canyon edge with prey data near SG A on 14 August 2017. (b) Zoomed-in plot of the SG B location, but the day before the SG was noticed. There were scattered blue whales feeding in this area, but it is noticeable how much less uniform and diffuse the high-quality parts of this large patch are. (c) Zoomed-in plot of the SG B associated patch on 16 August 2017. (d) View from the southeast of the same patch, overlain with tracks from the four tagged whales feeding within SG B. Data plotted in Echoview v10 using a 10× vertical exaggeration

lack of observed occurrences during periods of low cetacean abundance combined with consistent aggregations of krill suggest that rorqual whale super-groups were once a more common occurrence. Given the 20%–60% increase in geomean prey density we found in super-groups and the concurrent 33%–45% increase in feeding rates compared to non-super-group environments, it is likely that super-groups were once an important part of rorqual whale foraging ecology before anthropogenic hunting removed more than three million whales globally (Rocha et al., 2014). It is plausible, therefore, that recovering populations benefit from a positive feedback loop whereby increasing population sizes increase the likelihood of discovering extensive but ephemeral (Figure 7) patches since concentrations of calling whales, even if calling is not directly related to patch quality or extent, could serve as a signpost for wanderers about the location of ephemeral, high-quality foraging grounds (Wilson et al., 2018). This socially mediated information exchange would decrease the search time of individuals who might not otherwise find the highest quality regions within a foraging ground (Hein & Martin, 2020; LaScala-Gruenewald et al., 2019).

The spatial collocation of the observed super-group-associated patches with bathymetric features, including small scale (1–5 km wide) canyons that incise typical rorqual foraging habitat regions off the edges of continental shelves (Figures 1, 6 and 7), suggests that the two environments in our study may have a specific proclivity to support large, dense prey patches due to the interaction of bathymetry and local oceanographic process that have been shown to aggregate zooplankton (e.g. Benoit-Bird et al., 2019; Santora et al., 2018). Future work examining the spatiotemporal links between mesoscale oceanographic processes, local bathymetry and temporally transient prey conditions may better help explain how these large predators effectively exploit prey in spatially and temporally complex habitats.

It was not until relatively recently in the fossil record (5–7 Ma) that baleen whales developed gigantic body sizes (>10 m), and it is likely that this large change came about in concert with oceanic conditions that favoured annually consistent upwelling zones that brought nutrient-rich water to the surface in specific areas, creating natural aggregation areas (Slater et al., 2017). Locating and exploiting these prey hotspots is essential to the foraging strategy of rorqual whales, and we found that differentiating the highest quality prey areas (as characterized by high geometric means and low GSD) from merely good prey areas can result in a doubling of intake rates

(λ) when increased feeding rates (λ_f) are combined with increased prey density (λ_p). We have described two disparate environments in which predator patchiness—indicated by temporally transient and spatially limited super-group formation—is driven by prey patchiness, and we utilize predator-specific prey density metrics to characterize high-quality whale habitat. Our results suggest that foregoing local foraging within good prey environments in favour of traversing to great prey environments where conspecifics are aggregating may be an evolutionarily stable strategy when such prey patches are extensive and ephemeral, and future research may reveal the specific social drivers that cue whales into the locations of these high-quality foraging hotspots.

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AUTHORS' CONTRIBUTIONS











D.E.C., S.M.S., K.P.F., J.C., A.S.F., E.L.H. and J.A.G. drove investigation; J.D.W. calculated TS of *E. lucens* and *T. spinifera*; D.E.C., J.F. and J.A.G. prepared hydroacoustic data for processing; D.E.C. and S.R.K.-R. analysed feeding rates from tag data; D.E.C., S.M.S., K.P.F., D.K., S.M., M.M., M.G.O., C.W., J.C., A.S.F., J.A.F., E.L.H., S.R.K.-R., W.K.O. and J.A.G. collected field data; D.E.C. processed the hydroacoustic and tag data, performed statistical analyses and led the writing of the manuscript. All the authors contributed substantially to revisions and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Prey and tag data have been deposited at Stanford University's digital repository: <https://purl.stanford.edu/rq794kc6747>. Monterey Bay bathymetric NAVD88 data at 1/3 arc-second resolution used for Figure 7 was downloaded from www.ncei.noaa.gov.

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SUPPORTING INFORMATION

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

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