

Social exploitation of extensive, ephemeral, environmentally controlled prey patches by supergroups of rorqual whales

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Large groups of animals aggregate around resource hotspots, with group size often influenced by the heterogeneity of the environment. In most cases, the foraging success of individuals within groups is interdependent, scaling either constructively or destructively with group size. Here we used biologging tags, acoustic prey mapping, passive acoustic recording of social cues and remote sensing of surface currents to investigate an alternative scenario in which large, dense aggregations of southeast Atlantic humpback whales, *Megaptera novaeangliae*, and northeast Pacific blue whales, *Balaenoptera musculus*, were each associated with ephemeral krill aggregations large enough such that their availability to predators appeared to be influenced more by environmental features than by consumption, implying independence of group size and consumption rates. We found that the temporal scale and spatial extent of oceanographic drivers were consistent with the temporal scale and locations of predator aggregations, and additionally found that groups formed above bathymetric features known to promote zooplankton concentration. Additionally, we found calling behaviour counter-indicative of competition: blue whale foraging calls were anomalously high during observed aggregation time periods, suggesting signalling behaviour that could alert conspecifics to the location of high-quality resources. Modelled results suggest that the use of social information reduces the time required for individuals to discover and exploit high-quality resources, allowing for more efficient foraging without apparent costs to the caller. Thus, rorqual whales foraging in these environments appear to exhibit a social foraging strategy whereby a behaviour with negligible individual costs (signalling) provides information that enhances group foraging efficiency. The population density dependence of this social foraging strategy may help explain why some rorqual species were at first slow to recover from human exploitation, but have since increased more rapidly.

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Animals are distributed relative to the resources they rely upon, often scaling in number with resource availability (Bernstein et al., 1991; Johnson et al., 2002; McNamara & Houston, 1990) and with the spatial and temporal heterogeneity of resource distribution (Johnson et al., 2002). Large aggregations of animals form for a wide

variety of reasons including mating (Johannes et al., 1999; Swartz & Jones, 1981), proximity to a limiting resource (Valeix et al., 2007), physical forcing (Hofmann & Murphy, 2004), increased foraging opportunities (Brown, 1988; Giraldeau & Caraco, 2000) and either active predator defence (Clark & Robertson, 1979; Magurran, 1990) or passive predator avoidance (Laundré, 2010); generally these benefits result in an increased evolutionary fitness that outweighs the costs associated with dividing available resources among the group (Lang & Farine, 2017; Parrish & Edelman-Keshet, 1999).

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Social foraging frameworks typically model depletable (i.e. consumable) patches of various sizes and have been shown to apply in systems as diverse as bats (Egert-Berg et al., 2018), ants (Flanagan et al., 2011; Gordon et al., 1992), finches (Livoreil & Giraldeau, 1997) and seabirds (Buckley, 1997; Pöysä, 1992). An underlying assumption of these frameworks is that an individual's resource intake is reduced by the presence of interacting conspecifics that compete for a resource pool that is depleted more rapidly as group size increases.

Baleen whales (parvorder: Mysticeti) are the world's largest predators, exhibit both individual and group foraging behaviour, have large vocal repertoires (Dunlop et al., 2008; Fournet et al., 2015) that can be detected over large ranges (Miller et al., 2019; Stafford et al., 1998), and, as capital-breeding bulk filter feeders, require dense concentrations of seasonally available prey that exhibit both spatial (Friedlaender et al., 2020; Hazen et al., 2009; Irvine et al., 2019; Kirchner et al., 2018; Piatt & Methven, 1992; van der Hoop et al., 2019) and temporal patchiness (Abrahms et al., 2019; Becker et al., 2014; Dodson et al., 2020; Fossette et al., 2017). Social foraging frameworks would thus be expected to apply to baleen whale predator/prey systems, and the development of biologging devices and hydroacoustic prey mapping have recently made it possible to study both the behaviour of these enigmatic predators and the distribution of their prey quantitatively and simultaneously in situ (e.g. Goldbogen et al., 2019; Owen et al., 2017).

Various sized aggregations of baleen whales around patchy resources are commonly reported at a wide variety of spatial scales and with varying degrees of temporal cohesion (e.g. Baines et al., 2017; Fiedler et al., 1998; Findlay et al., 2017; Huckle-Gaete et al., 2004; Jurasz & Jurasz, 1979; Littaye et al., 2004; Lomac-MacNair & Smultea, 2016; Mastick, 2016; Newton & DeVogelaere, 2013; Nowacek et al., 2011; Piatt & Methven, 1992; Schoenherr, 1991; Visser et al., 2011; Whitehead, 1983). Humpback whales, *Megaptera novaeangliae*, for example, are flexible foragers that commonly prey on both relatively static patches of krill (euphausiids) as well as mobile schooling fish. Humpback whales have been observed feeding both alone and in large groups with synchronized and apparently coordinated behaviours that serve to concentrate schools of fish before individuals lunge into the school to capture as many fish as possible in a single mouthful. The size of fish schools can influence the size of the foraging groups (Fig. 1) – individuals foraging in the same region can pursue one small school, engulf it and move on to the next (e.g. Cade et al., 2020; Weinrich et al., 1992), or a group of individuals can lunge several times on the same large school of fish (e.g. Cade et al., 2020; Jurasz & Jurasz, 1979; Kirchner et al., 2018; Wiley et al., 2011). Although rigorous tests of social foraging theories in these systems have yet to be completed, both of these strategies appear to fit model assumptions (e.g. Giraldeau & Caraco, 2000), with patches that are depleted over time and individual decisions driven by the trade-offs involved in resource sharing.

In marine environments, however, the heterogeneity of the ecosystem and its resource availability can be controlled by rapid turnover of nutrients and cyclical physical processes (Hauray et al., 1978). This leads to spatially and temporally restricted blooms in resource availability and encourages aggregations of mid-trophic level animals to form and disperse under the influence of cyclical environmental processes such as upwelling (Benoit-Bird et al., 2019), currents (Lévy et al., 2018), surface winds (Blukacz et al., 2009) and tides (Cotté & Simard, 2005; Dustan & Pinckney, 1989; Johnston et al., 2005). The ocean, then, is a likely environment in which to find ephemeral patches of prey whose foraging quality is driven more strongly by the environment than by predation (Benoit-Bird & McManus, 2012). These conditions suggest an

additional social foraging scenario in which patch quality and resource availability are not affected by group size, encouraging alternative social foraging strategies wherein it is advantageous for individuals to cooperate by communicating the location of ephemeral resources when they are available (Torney et al., 2011; Wilson et al., 2018). In this scenario, alerting conspecifics to the

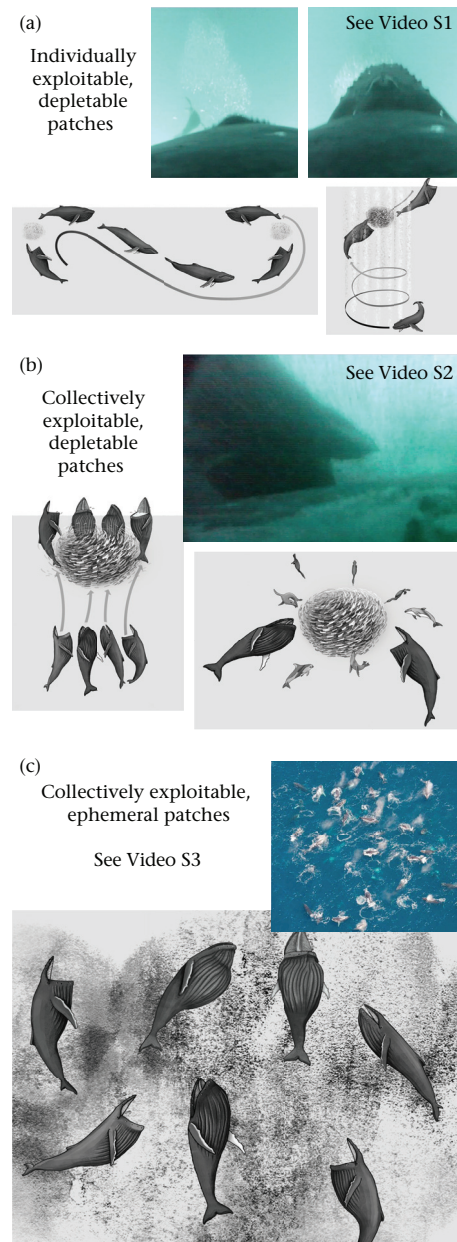


Figure 1. Social patch and prey models (Giraldeau & Caraco, 2000) in humpback whale predator–prey systems. (a) Individually exploitable, depletable patches that are consumed after a single gulp by an individual whale. Images are from a camera attached to a humpback whale approaching an anchovy school in the Santa Barbara Channel, U.S.A. Drawings are schematics of a humpback whale foraging on krill schools and an individual whale blowing a bubble net to herd herring or sand lance. (b) Collectively exploitable, depletable patches. These fish schools are larger and break apart easily. They generally are kept together either by multiple species of predators, or by groups of humpback whales blowing bubbles and then lunging synchronously through the school. (c) Collectively exploitable, ephemeral patches. ‘Ephemeral’ in this context means the patch size is so large that it is not meaningfully depleted by foraging whales, but its diminishment is environmentally controlled. Aerial image © Jean Trefson, cropped from Figure 2 of Findlay et al. (2017) under creative commons CC-BY 4.0 (<https://creativecommons.org/licenses/by/4.0/>), illustrations by Alex Boersma.

location of extensive, ephemeral resources would have low individual costs but high collective advantages. We refer to this scenario as ‘environmentally controlled’ and examine evidence that large aggregations of two species of rorqual whales foraging within extensive but ephemeral krill patches could be an exemplar of this ephemeral prey patch model.

Beginning in 2011, spatially constricted, numerically dense concentrations of humpback whales have been reported seasonally in the Benguela Current region off South Africa's west coast (Findlay et al., 2017). Known as ‘supergroups’, these aggregations consist of 20 to >200 whales, each of which is within five body lengths of a conspecific. These aggregations were shown to be associated with extraordinarily dense, abundant and thick aggregations of prey that were more uniform in distribution than nearby prey patches, leading to a doubling of intake rates for animals foraging in those patches (Cade et al., 2021). Here we investigate the bathymetry and surface currents surrounding these groups, hypothesizing that surface currents interact with bathymetric features in the region on spatial and temporal scales consistent with those of each observed group.

In contrast to humpback whales, blue whales, *Balaenoptera musculus*, are typically observed singly or in pairs, forage almost exclusively on krill (Kawamura, 1980) and are not known to engage in behaviours, such as prey herding, that may be more effective in larger groups (Mastick, 2016). These predators, which are the world's largest, are also rarely observed in close proximity: 21 out of 22 studies synthesized by Ramm (2018, see Tble 2 therein) observed mean blue whale group sizes of one to two individuals, and in 963 field surveys over 20 years by our field team, less than 6% encountered at least 25 blue whales over the course of the day, most of which involved separate encounters separated by several miles. However, on 14 and 16 August 2017, dense aggregations of 15–40 blue whales were observed surfacing within a 1 km radius area, in Monterey Bay, California, U.S.A., that were associated with thick, dense, evenly distributed prey patches (Cade et al., 2021). As with the humpback whale groups off South Africa, we hypothesized that the observed blue whale aggregations were located near constrictive bathymetric features that would serve to aggregate prey on multi-hour temporal scales consistent with the observed timescales of group formation.

The prey intake rate (λ) of blue whales (and other rorqual whales) is constrained biomechanically, physiologically and environmentally (Fig. 2). While prey processing time is a biomechanical constraint that appears to depend on engulfment volume (regardless of prey density in the volume, Kahane-Rapport et al., 2020) and surface time is a physiological constraint that depends on the characteristics of an individual patch (Hazen et al., 2015), the search time required to find appropriately dense prey is limited by the animal's ability to find and detect food (Wilson et al., 2018) that can be dispersed across a home range that spans hundreds of kilometres (Abrahms et al., 2019; Mate, Lagerquist, & Calambokidis, 1999), making the time to find high-quality patches the dominant temporal factor influencing λ . While it is not known which sensory systems blue whales use to locate good forage areas, it has been shown that signalling behaviour that recruits conspecifics to a food resource can be an evolutionarily stable strategy in spatially and temporally dynamic environments like those in marine krill ecosystems (Torney et al., 2011). We thus hypothesized that we would detect increased signalling behaviour from blue whales during the observed aggregation events. To test this hypothesis, we used data from a continuously recording hydrophone in Monterey Bay, and we constructed models to examine how such signalling behaviour would affect overall prey intake and influence the timescales of group formation.

METHODS

Supergroup Predator/Prey Dynamics

We investigated aggregations of rorqual whales in two eastern boundary-current upwelling ecosystems: 11 instances of humpback whale supergroups in the Benguela Current off South Africa's west coast in 2015 and 2016 and two instances of blue whale supergroups in Monterey Bay off the U.S. west coast in 2017 (Fig. 3). These aggregations are distinct from other contemporary descriptions of large groups in the extraordinary density of animals within a small region of open ocean such that animals must interact with each other as they are foraging (Video S3). Specifics of both types of aggregations are detailed in Cade et al. (2021).

Formation and dispersion of whale aggregations were observed opportunistically from research vessels in each ecosystem. To examine foraging behaviour within and outside of supergroups, we attached 17 integrated 3D accelerometer and video tags to individual blue whales for time periods of ~2–20 h, six of which were whales foraging within supergroups in 2017, and we tagged an additional 22 blue whales in the same region in 2018 (no supergroups were observed in 2018). Prey data were collected using a multifrequency, split-beam fisheries acoustic system (Simrad EK60s or EK80s) ensonifying the water column below a vessel within 500 m of foraging whales in both ecosystems, and data collected near supergroups were compared to data collected near feeding whales not aggregated into supergroups. Aggregations of krill, dominated by large patches > 10 m thick and 1 km across, were identified in acoustic echograms using the SHAPES school detection algorithm (Barange, 1994; Coetzee, 2000) and decibel differencing techniques (Jarvis et al., 2010), and were analysed at predator-specific spatial scales relevant to the unique foraging mechanisms of lunge-feeding rorqual whales (detailed description of the ‘whale-scale’ method, including conversion from acoustic units to estimated biomass in Cade et al., 2021).

Bathymetry

Bathymetric data for the inset Monterey Bay map in Fig. 3a and Fig. 4a were gridded to 25 m resolution (from source data sets having variable resolutions) and provided by the Monterey Bay Aquarium Research Institute (MBARI). Remaining Monterey Bay data were derived from a one-third arcsecond digital elevation model from the NOAA National Geophysical Data Center, accessed at: <https://www.ncei.noaa.gov/metadata/geoportal/rest/metadata/item/gov.noaa.ngdc.mgg.dem:3544/html>. Data in Fig. 3a were plotted in R with contours from 50 m to 1600 m depth at 50 m intervals, and data in Fig. 3b as well as all three-dimensional plots were based on contours generated by the contour function in MatLab v.2014a (Mathworks, Natick, MA, U.S.A.) at 3 m intervals to 120 m, at 10 m intervals to 1000 m, then at 50 m after that. Three-dimensional data were plotted in Echoview v.10 (<https://echoview.com>) from the MatLab-generated contours using a 10 × vertical exaggeration and the Echoview 1xx colour scheme coloured for greyscale display (minimum depth: -1000 m; maximum depth: 7000 m).

Depth soundings in the South African study region at approximately 5 km resolution (ungridded) were provided by the South African Naval Hydrographic Office for exclusive use of this project. Data were gridded using the geoloc2grid function in MatLab at 22.5 arcsecond resolution, then contoured and plotted as above except with vertical exaggerations as noted in the figure legends for clarity. The coastline depicted in Fig. 3b is from Wessel and Smith (1996).

Social Cue Production

We utilized a continuous passive acoustic monitoring system from the Monterey Accelerated Research Station (MARS) cabled observatory hydrophone (Oestreich et al., 2020; Ryan et al., 2016) to examine the production of acoustic cues by blue whales temporally proximate to supergroup observations. This omnidirectional hydrophone has a bandwidth of 10 Hz–200 kHz and has been sampling nearly continuously at 256 kHz from late July 2015 to the present. The hydrophone is situated on Smooth Ridge (36°42.75'N, 122°11.21'W; depth 891 m), spatially located both in blue whale foraging habitat generally (Croll et al., 2005) as well as in the field effort for this study specifically (Fig. 3). Blue whale calls are of low frequency and have been recorded at distances of hundreds of kilometres (Miller et al., 2019; Stafford et al., 1998), so any calls produced by the whales in our study (supergroup distances were 16.8 and 14.0 km while the maximum distance from any feeding whale was 48.9 km) were likely to be recorded. Sound propagation loss modelling results for blue whale B calls (Oestreich et al., 2020) and humpback song (Ryan et al., 2019) at the same instrument

indicate that the locations of observed supergroups are well within the sampling radius of the MARS hydrophone. Blue whale calls have the bulk of their energy below 200 Hz (Oleson, Wiggins et al., 2007), so acoustic data were decimated by a factor of 128 to produce a 2 kHz product (via software available at: <https://bitbucket.org/mbari/soundscape-decimate-notebook/src/master/>).

D calls in blue whales, which are thought to be associated with feeding (Oleson, Calambokidis, et al., 2007), are characterized by a steep downsweep in frequency in the 20–120 Hz range over ~2–7 s (Oleson, Wiggins, et al., 2007), and high calling rates have been associated with aggregating blue whales (Miller et al., 2019). We manually audited spectrograms (FFT window size = 1024, Hann window, overlap = 95%) from data recorded 1 August through 15 September in both 2017 and 2018 to identify D calls, distinguishable from fin whale, *Balaenoptera physalus*, calls by the length of the signal (Huang et al., 2016) and from downsweeping humpback whale song segments by the context within the spectrograms (see Results, Fig. 5a). We aggregated D call counts into 1 h bins to calculate a mean diel cycle during this time period (Fig. 5b). We calculated D call rate anomalies (Fig. 5c) by subtracting the mean

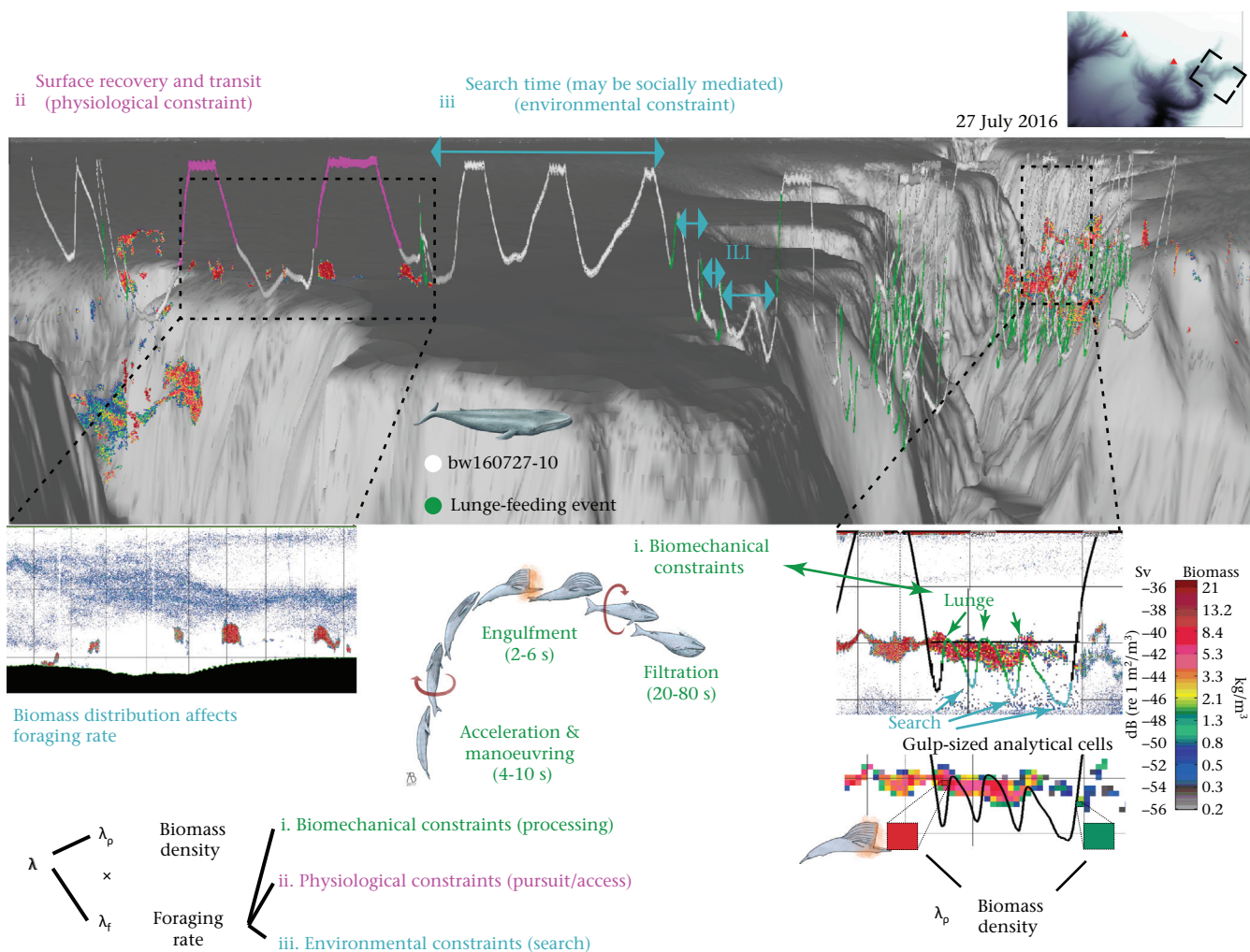


Figure 2. As a modelling parameter, λ links the patch quality to a predator's intake rate. In rorqual whales, the environment is represented by krill biomass and distribution, which affects the transit time between lunge-feeding events such that it controls both λ_p and λ_f . λ_f may also be influenced by social information that decreases patch detection time. Foraging rate is also a result of individual parameters including biomechanical and physiological constraints such that larger animals spend a larger portion of their foraging time processing food (Kahane-Rappoport et al., 2020). Three-dimensional plot crafted in Echoview v.10 using a 10× vertical exaggeration and 120 kHz data, with the spatially matched track of a tagged blue whale. Biomass estimated as in Cade et al. (2021). Two-dimensional plots are temporally linked echosounding data with the tagged whale's depth profile. Illustrations by Alex Boersma.

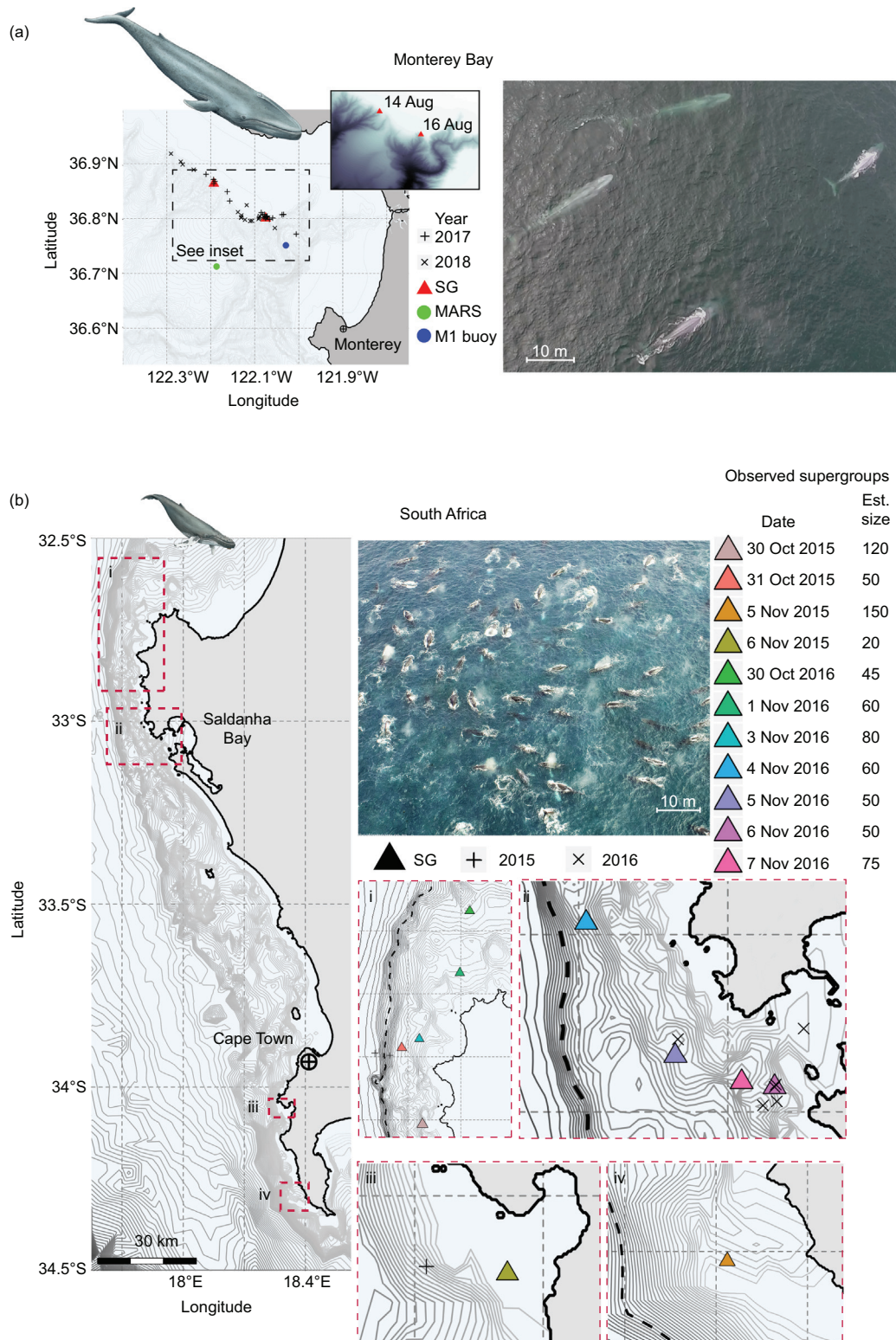


Figure 3. Supergroup locations in each study area. Triangles show observed supergroup (SG) locations, and + and x mark the deployment locations of suction-attached biologgers. (a) In Monterey Bay, blue whale supergroups were observed at the heads of small slope-incising canyons (see also Fig. 4). Aerial image is from supergroup B on 16 August 2017, image © Duke Marine Robotics and Remote Sensing. Depth contour lines are separated by 50 m. (b) In South Africa, supergroups were found associated with complex bathymetry. Depth contour lines are separated by 3 m from 30 m to 120 m, then 10 m thereafter. Dotted line in insets is the 99 m isobath. Aerial image © Dave Hurwitz.

24 h trend from the hourly binned D call counts and then reduced noise by averaging these hourly anomalies into 4 h bins.

Oceanographic Features

We examined the oceanographic conditions temporally proximate to blue whale supergroup observations in Monterey Bay in three ways: (1) using backwards-in-time finite-time Lyapunov exponents (FTLE) to perform a Lagrangian analysis of predicted particle accumulation based on surface currents measured by the high-frequency (HF) radar data along the California coast (Paduan

& Rosenfeld, 1996); (2) examining hourly plots of surface current rotation rates (vorticity), also derived from HF radar; and (3) assessing in situ Acoustic Doppler Current Profiler (ADCP) data from a mooring at the mouth of Monterey Bay over Monterey Canyon (Fig. 3a; 36.755°N, 122.03°W).

Surface current data for deriving FTLE and vorticity data were downloaded from the Southern California Coastal Ocean Observing System (SCCOOS, <http://www.sccoos.org/data/hfrnet/>) at hourly resolution (cells 6 km on a side) using a polygon bounded by parallels and meridians at 37.25°N, 36.0°N, 123.0°W and 121.5°W. This polygon encompasses all feeding areas utilized by tagged blue

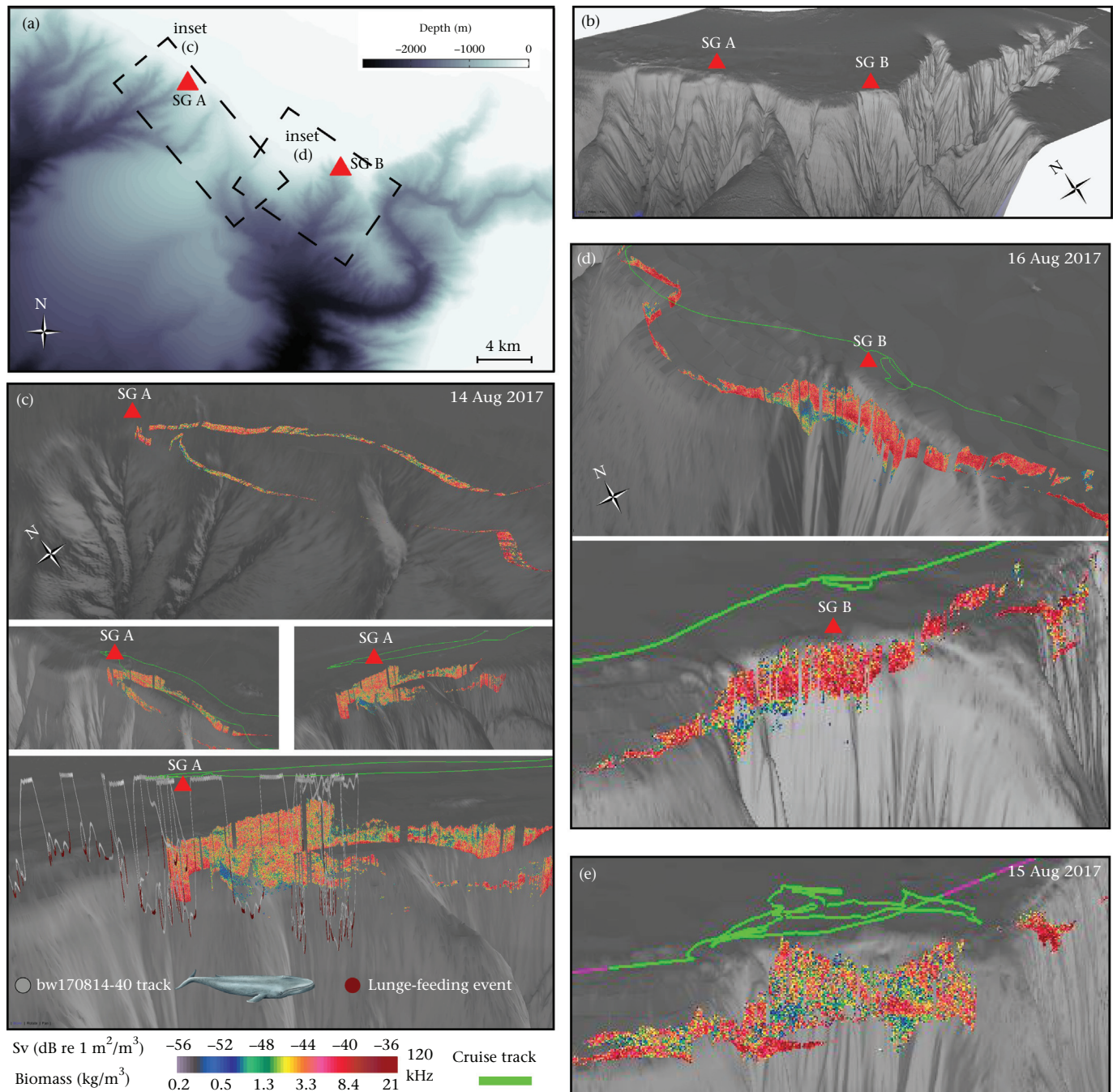


Figure 4. Topographic context of observed blue whale supergroups (SG) and SG-associated prey patches. (a) General bathymetry of Monterey Canyons, where SG A (25–40 whales) was observed on 14 August 2017 and SG B was observed on 16 August 2017 (15–20 whales). (b) Three-dimensional plot of Monterey Canyon. (c) Several views of the prey field around SG A. Bottom panel includes the track of tagged whale bw170814-40 showing concentrated foraging at the heads of small narrow canyons. (d) Two views of SG B. (e) Comparison plot of the prey field in the same location as SG B but 1 day earlier. All three-dimensional plots crafted in Echoview v.10 using a 10× vertical exaggeration.

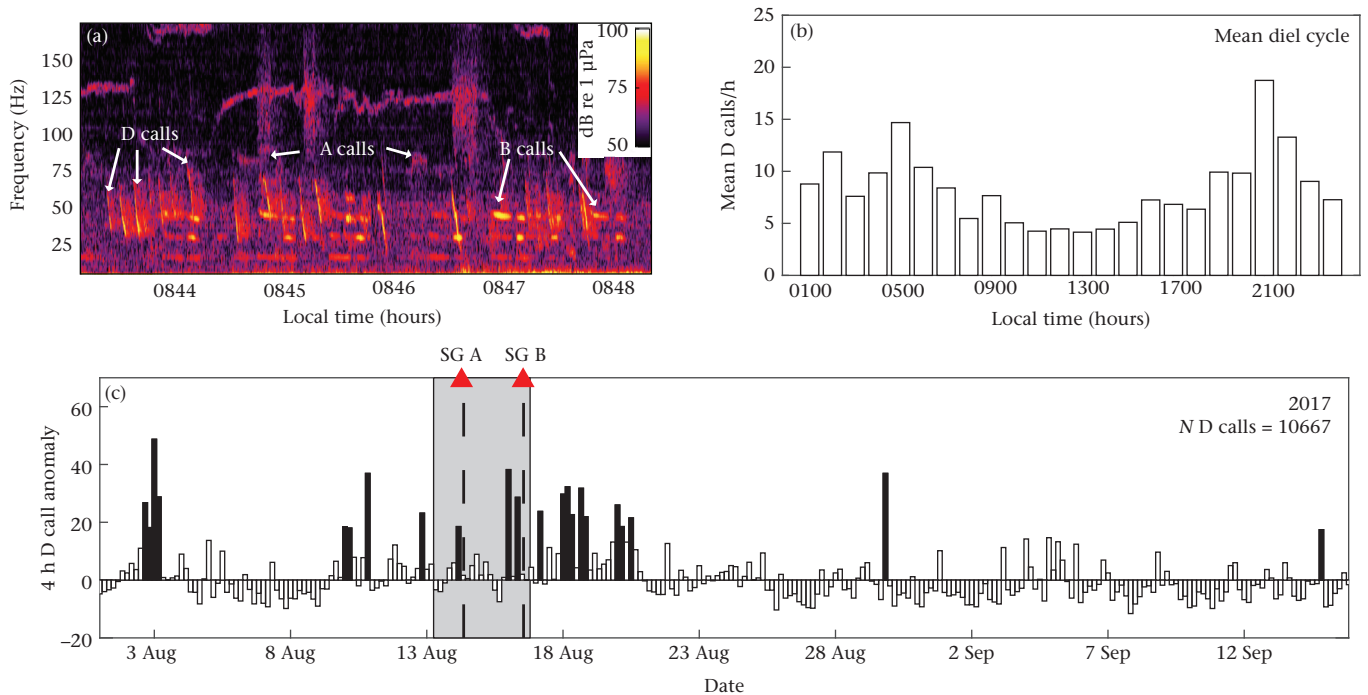


Figure 5. Blue whale D calls recorded during the 2017 field season at the MARS hydrophone. (a) Spectrogram display (FFT parameters: Hann window, 1024 samples, 95% overlap, Raven Pro v.1.5, Cornell Lab of Ornithology, Ithaca, NY, U.S.A.) of passive acoustic data from 16 August 2017. Northeast Pacific blue whale D calls are prevalent, and A and B calls are also labelled. (b) Mean diel cycle of D call counts during 1 August – 15 September 2017 and 2018. (c) Time series of 4 h D call anomalies recorded in 2017 (defined as the number of calls above or below the mean diel value for that 4 h bin). Dark bars indicate outlier 4 h periods exceeding the median anomaly by more than 2 SD. Dashed lines and red triangles indicate the times of observed blue whale supergroups (SG). Shading indicates field effort during 2017.

whales from 2017 and 2018 in Monterey Bay and is within the coverage range of HF radar platforms. HF radar, a terrestrial-based remote-sensing platform, overcomes the spatial and temporal resolution constraints of traditional remote-sensing platforms (e.g. satellites, buoys) by providing fine-scale measurements of surface current movements (hourly, 2–6 km resolution) in areas that overlap with typical blue whale habitat (up to 200 km offshore). It works by reflecting electromagnetic waves off the surface of the ocean to determine the two-dimensional speed and direction of water moving at the surface (Chapman et al., 1997), and it has been used to look at the relationship between foraging behaviour and surface convergent features (Abrahms et al., 2018; Oliver et al., 2019; Scales et al., 2014; Scales et al., 2017).

To facilitate a Lagrangian analysis in the calculation of FTLE, we restored data gaps in the HF radar surface current measurements using the algorithms described in Ameli and Shadden (2019), selecting a concave hull (alpha shape radius of 10 km) and excluding land. Using the restored surface current data, we calculated the backward-in-time FTLE using TRACE (<http://transport.berkeley.edu/trace/>), a Lagrangian analysis tool that follows the methodology described in Shadden et al. (2005, 2009). We used a tracer resolution of 10 times the spatial resolution of the HF radar data (sensu Shadden et al., 2009) and applied a free-slip boundary condition to tracers near land. Tracer advection used a bilinear spatial interpolation and an adaptive fourth-order Runge-Kutta-Fehlberg integration method. At every hourly time step, the trajectories of the evenly spaced grid of tracers were integrated for the preceding 6, 12, 24 or 96 h period and FTLE was calculated from the time-dependent movement of tracer trajectories. Similar to finite-size Lyapunov exponents (FSLE) (Peikert et al., 2014), FTLE calculates areas of potential particle accumulation – including zooplankton – based on the movement of surface currents and has been shown to correlate with foraging animal movement patterns (Abrahms et al., 2018; Scales et al., 2014; Scales et al., 2017). A time-

series visualization of the FTLE values in the study region was created to assess both the size and temporal persistence of Lagrangian coherent structures (LCS), which were visually identified ridges of high FTLE values (Shadden et al., 2005; Video S4). Detailed plots of the regional FTLE values temporally proximal to the observed supergroups were made in R (v.3.5).

We additionally calculated a time series of surface vorticity in the 6×6 km data cell that encompassed each Monterey supergroup (see Results, Fig. 6b, e) for the period 10–20 August 2017. We also calculated surface vorticity in the surrounding study area (25×24 cells, Video S5). The raw data were imported and processed in R (v.3.5) using the *ncdf4* package (v.1.16). Raw surface current data consist of a time vector and two arrays (U and V) representing surface current velocities at each time step in the eastward (x) and northward (y) directions, respectively. Vorticity was calculated as the difference in the derivative of V with respect to x and the difference in the derivative of U with respect to y using the focal function in R raster package v.2.7–15: $\text{vorticity} = dV/dx - dU/dy$. This package utilizes a moving window (e.g. convolution matrix) that passes over each cell and performs an addition of values based on the weights provided in the window to determine a rate of change between neighbouring values in a grid. The 3×3 cell convolution matrices used were:

$$x = \begin{bmatrix} -0.25 & 0.00 & 0.25 \\ -0.50 & 0.00 & 0.50 \\ -0.25 & 0.00 & 0.25 \end{bmatrix}, \text{ and } y = \begin{bmatrix} 0.25 & 0.50 & 0.25 \\ 0.00 & 0.00 & 0.00 \\ -0.25 & -0.50 & -0.25 \end{bmatrix}$$

The derivative matrices ($\frac{dV}{dx}$ and $\frac{dU}{dy}$) were combined to calculate vorticity for each grid cell in the time series, resulting in an array of vorticity raster layers of the same dimensions as the original U and V arrays. A time-series visualization of the vorticity in the study region was created to assess both the size and temporal persistence of coherent features over time (Video S5), and

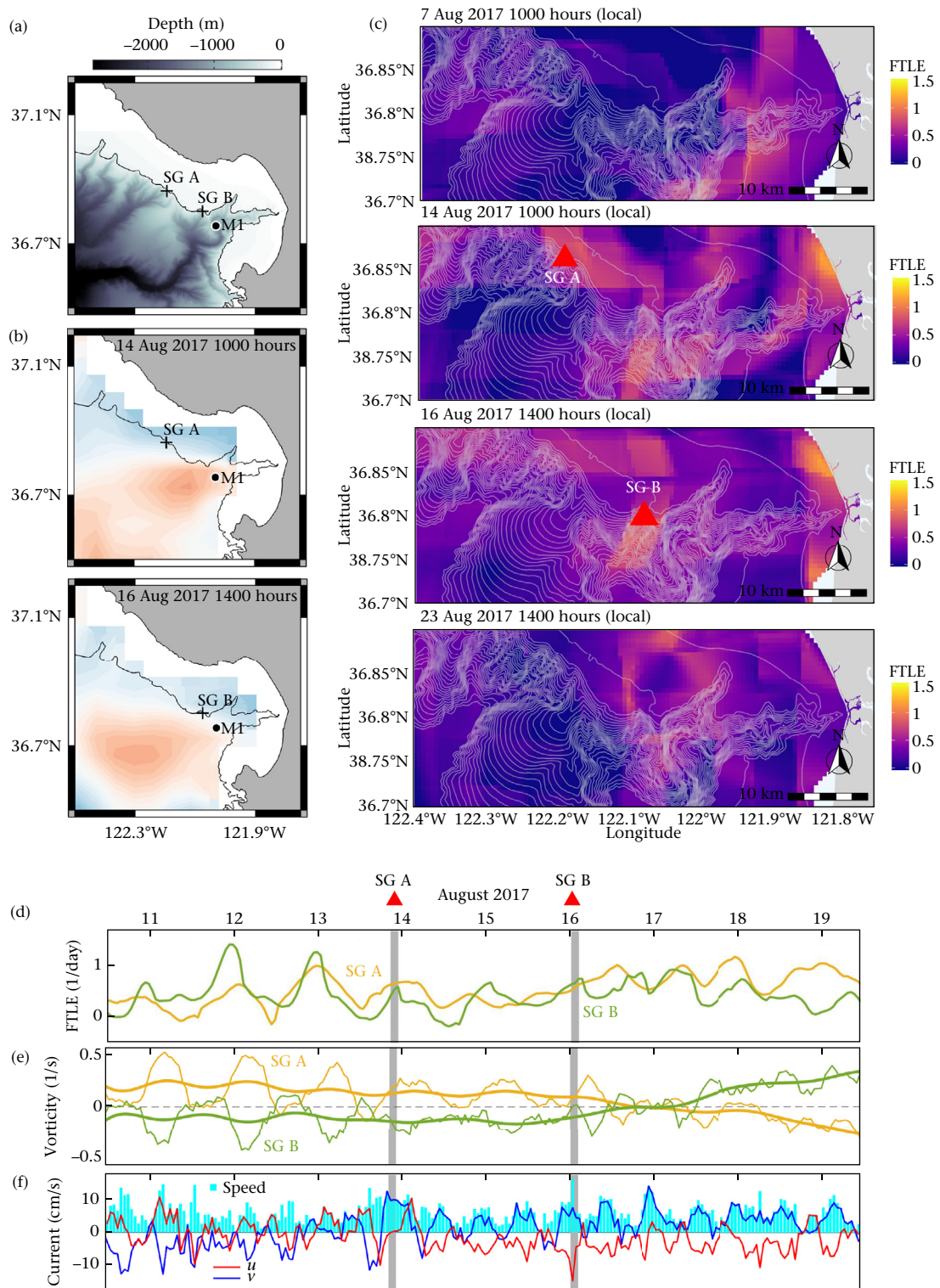


Figure 6. Oceanographic processes interacting with topography. (a) High-resolution bathymetry map; overlaid are the 200 m isobath, locations of supergroup (SG) encounters and the location of environmental mooring M1 (36.755°N, 122.03°W; 18.9 and 6.4 km from the supergroup observation locations), (b) Vorticity maps coincident with each supergroup encounter. Boundaries between surface vorticity features could indicate a subsurface front known to aggregate prey. (c) Selected spatial maps of 12 h backwards-in-time integrated finite-time Lyapunov exponent (FTLE) values 1 week before the first SG encounter, at the times of each SG, and 1 week after the second SG encounter. FTLE is a metric of simulated particle aggregation based on measured surface currents. (d, e) Time series of FTLE and vorticity, respectively, of the grid cell containing the observed supergroup; thick lines in (e) are 33 h low-pass filtered. (f) Time series of average currents in the depth range of 100–200 m at the M1 mooring.

the vorticity at each supergroup location was plotted over time (Fig. 6e).

Subsurface current data were available near the observed supergroups (M1 in Fig. 3a). The RDI/Teledyne Workhorse Long Ranger ADCP at M1 measures water velocity in the upper 500 m. Currents across the depth range of the shelf break (100–200 m) were averaged and plotted as a time series (Fig. 6f).

Off South Africa, oceanographic data were more limited in spatial and temporal resolution. Daily FSLE, similar in their ability to define LCS as FTLE described above (see, e.g.: Abrahms et al., 2018; Scales et al., 2017; Shadden et al., 2005), are an AVISO data product (<https://www.aviso.altimetry.fr/en/data/products/value-added-products/fsle-finite-size-lyapunov-exponents.html>) calculated following the method of d'Ovidio et al. (2004) at $1/25^\circ \times 1/25^\circ$ spatial resolution. We plotted daily values from -0.2 to 0 in the region where supergroups were observed, from 17.4° to 18.8° E and 32.4° to 34.7° S. We analysed a 3×3 grid surrounding each observed supergroup on its observed day and calculated the minimum FSLE in the grid. We also determined whether the grid overlapped with the boundary of an LCS by determining whether the grid contained both zero and nonzero FSLE values. For calculating the probability of a randomly chosen point being on an LCS boundary, we also determined the boundary status of every point located in the study region in 20–100 m of water.

Aggregation and Intake Model

To test the likelihood of blue whales independently encountering the high-quality prey patch and aggregating there independently of social information use, we created a simple model comparing random discovery of a prey hotspot to two social cue scenarios using a Monte Carlo simulation with 1000 iterations. MatLab code to construct the model is available at the repository listed in the Data Availability section. In all models, the habitat was assumed to be the 54 km region of the linear north canyon edge over which we observed blue whales in August 2017 (Fig. 3a), whales were assumed to transit the canyon edge at 5.6 km/h while actively foraging (the mean linear transit speed of the two whales foraging towards the supergroup on 16 August 2017), the hotspot was assumed to be 2 km long (matching the spatial extent of the observed patch) and located 43 km from the northwestern edge of the habitat (the approximate location of the second supergroup). In all scenarios, once a whale entered the hotspot, it would stay there until the end of the simulation. The random foraging model assumed that whales would transit along the canyon edge, but every 10 min (approximately the length of a blue whale foraging dive), the whale would randomly move in the same direction or turn back where it came from with equal probability. In the first social cue scenario, we assumed that all whales called continuously and that each whale would have a $P\%$ chance of travelling in the direction where $P\%$ of the whales were located. In the second social cue scenario, we assumed that whales only called once they were in the hotspot, and that if $P\%$ of the population were located in the hotspot, individuals had a $(50 + P/2)\%$ chance of turning towards the hotspot. Cumulative intake is the total amount of food consumed by all whales assuming a representative environmental intake rate (λ_{env}) of 1 and a hotspot intake rate (λ_2) of double the environmental rate.

Ethical Note

All cetacean data were collected under National Marine Fisheries Service (NMFS) permits 16111, 20430 and South African permits RES2015/DEA and RES2016/DEA. All procedures were approved by the Institutional Animal Care and Use Committee of Stanford University (IACUC protocol number 30123). All tagging of

wild animals involved noninvasive suction-cup attached tags that detached within 48 h. Candidate animals were only chosen if they did not have signs of additional stress (e.g. extreme malnourishment). Tagged animals were monitored upon return to the surface for signs of reactions to tagging, but no unusual behaviour was noted. The lowest frequency of our prey-mapping system (38 kHz) was much higher than the threshold of crustacean hearing (which generally have sensitivity peaks < 2 kHz, see Budelmann, 1992), and prior studies have not noted significant differences between quiet vessels and louder research vessels that would indicate behavioural responses to fisheries acoustics systems in krill (Brierley et al., 2003).

RESULTS

Supergroup Formation and Dispersion

Humpback whale supergroups off South Africa are described in Findlay et al. (2017) and consist of 30–180 whales surfacing in an area as restricted as 100 m on a side (Figs 1c, 3b). Supergroups were observed relatively commonly on 10 of 20 ship-days in 2015–2016. The precise duration of supergroup cohesiveness was unknown as none were observed from formation to dispersal, but all were observed for at least 1 h and were not in the same place the following day. In all five instances where group dispersion was observed in these two observation years, emigration from the group was sequential.

Blue whales were observed and tagged along the Monterey canyon edge during 13–16 August 2017. Across the three research vessels, a total of 289 blue whale sightings were recorded, 133 of which were successfully photographed for later identification. Of these 133 photographed encounters, 50 were unique individuals. Applying the known resighting ratio (50/133) to the total sighting record suggests an approximate local population of 109 individuals, so this value was used as our approximate population size in model results. Blue whale abundances of this size are relatively uncommonly reported: small boat surveys in the California Current from 1988 to 2018 encountered at least 25 blue whales in a single day fewer than 6% of the days in which blue whales were sighted (55 out of 963 field-days).

Two blue whale supergroups were observed in 2017 (Figs 3, 4) and consisted of an estimated 15–40 whales surfacing within sight of an observer at sea level (~ 1 km range). Blue whales are $\sim 2\times$ the length and $4\times$ the mass of humpback whales (Kahane-Rappoport & Goldbogen, 2018), so we considered the observed blue whale group sizes to be ecologically comparable to the humpback whale supergroup sizes. On 14 August, the group (25–40 whales estimated) was encountered at 0830 hours and had begun to decrease in size at ~ 1115 hours. On August 16, the group (15–20 whales estimated) was encountered at 1330 hours and our vessels left the area at 1420 hours. On August 15, approximately 8–10 blue whales were feeding in the vicinity of the supergroup observed on 16 August, but during the 15 August encounter, whales were spread out with hundreds of metres separating individuals. Cade et al. (2021) related how humpback whales and blue whales within supergroups feed at rates 45% and 34% higher, respectively, compared to feeding rates of whales not in supergroups, and they attributed this increase in effort to the less variable distribution of high-quality prey patches within the larger prey patches proximate to supergroups that facilitate shorter transits between high-biomass gulps.

Physical Environmental Features

Thirty-seven of 39 blue whales were tagged along the Monterey Canyon shelf break along the ~ 200 m isobath (Fig. 3a), a feature

known to directly influence ocean circulation and krill distributions (Benoit-Bird et al., 2019; Croll et al., 2005; Santora et al., 2018; Witte et al., 1988). Lunge feeding was predominantly observed above the 200 m bathymetric contour, and both observed blue whale supergroup locations were spatially located at krill aggregation hotspots at the heads of narrow, steeply sloping canyons (Fig. 4). Off South Africa, bathymetric data were of lower resolution but observed aggregations were located near similarly steep features (Fig. 3b).

Prey

Prey patches associated with supergroups were more than two times thicker (mean thickness 33 ± 27 versus 15 ± 15 m in Monterey Bay, 22 ± 14 versus 8 ± 9 m off South Africa), approximately 50% denser, and the denser biomass portions were more evenly distributed than the krill layer along the shelf break (further details in Cade et al., 2021). Prey patches associated with supergroups were also always found near topographic features (Fig. 4). Prey mapping at the canyon head associated with the supergroup observed on 16 August was also conducted on 15 August. The biomass density measured at the informed whale-scale (the top 50% of gulp-sized cells in the patch) on 15 August was $1.87 \pm 1.32 \text{ kg/m}^3$ ($-46.5 \pm 1.22 \text{ dB}$), where ‘ $\pm$ ’ is read ‘multiplied or divided by’ and is the corollary of $\pm$ but is used to describe the mean and standard deviation of lognormally distributed biomass in the region of interest (parentheses indicate the raw acoustic units). This was significantly less biomass per gulp-sized cell ($P = 0.039$) with a higher variance than the patch associated with the supergroup on the following day, which had a mean biomass density of $2.05 \pm 1.26 \text{ kg/m}^3$ ($-46.1 \pm 1.0 \text{ dB}$).

Acoustic Call Detection

Manual audits in Monterey Bay for blue whale D calls (Fig. 5a, Audio S1), which are thought to be associated with both foraging and aggregations (Miller et al., 2019; Oleson, Calambokidis, et al., 2007), yielded 10 667 detections over 1 August 2017–15 September 2017. The 4 h bin directly preceding the supergroup on 14 August had a higher D-call anomaly than 94% of the other 4 h bins, and the bin preceding the supergroup on 16 August had a higher anomaly than 97% of bins (Fig. 5c). Bars in Fig. 5c were coloured black if they exceeded the median anomaly + 2 SD, equivalent to the 93rd percentile. The probability that both supergroups would be associated with D-call rates of this magnitude or higher strictly by chance was 0.0049.

Oceanographic Features

Temporally, both blue whale supergroups in Monterey Bay were observed when Lagrangian coherent structures (LCS) characterized by spatially coherent regions of enhanced FTLE intersected the supergroup locations (Fig. 6, Video S4). While 24 h and 96 h integrations appeared to smooth over LCS features associated with the supergroups (Video S4), both 6 h and 12 h integrations predicted enhanced particle aggregation temporally and spatially coincident with both supergroup observations. In the $6 \times 6 \text{ km}$ region surrounding each supergroup location, FTLE cycled on approximately daily cycles, with both supergroup observations occurring when local FTLE was at a local maximum.

Both blue whale supergroups also coincided with a boundary between circulation features, specifically the boundary between cyclonic flow over the shelf (blue in Fig. 6b) and anticyclonic flow

over the slope and deeper offshore waters (red in Fig. 6b). Each supergroup was observed after periods of increasing surface vorticity in the $6 \times 6 \text{ km}$ analysis region surrounding each supergroup location (Fig. 6e, Video S5). Offshore (westward) transport at 100–200 m depth at the M1 buoy exhibited local maxima during or immediately preceding the observed supergroup events (Fig. 6f), indicating an unusually strong flow that may have interacted with the canyon topography.

Ten of 11 observed humpback whale supergroups off South Africa were associated with the edges of LCS (Video S6). The 10 groups that did coincide with LCS edges were substantially larger (45–150 estimated whales) than the group observed on 6 November 2015 that did not (20 whales). FSLE values associated with supergroups ranged from 0 (on 6 November 2015) to -0.17 , with a mean ($\pm$ SD) of -0.08 ± 0.07 . Within the identified habitat, the percentage of nonsupergroup gridded FSLE cells on the boundary of an LCS ranged from 44% to 78% (mean $\pm$ SD: $63 \pm 13\%$). The probability that at least 10 of 11 randomly chosen points from each day would be on the boundary of an LCS was 0.04, and the probability that all 10 large group observations would be on an LCS boundary was 0.01.

Modelling the Effects of Social Cue Production

Our random foraging model (Fig. 7) predicted that 15 blue whales (our lowest estimate for supergroup size) would independently locate the prey hotspot in 3.4 h, 25 whales (our median estimate) would take 11.2 h and 40 whales (our high estimate) would take longer than 1 day. The recruitment rate in the random foraging scenario decreased over time. In the all-calling scenario, recruitment was at first rapid, but then levelled off as the population divided into a southeast contingent in the hotspot and a northwest contingent that slowly moved towards the hotspot until it was close enough such that an individual 10 min step would put whales in the hotspot. In the hotspot calling scenario, recruitment rate increased for 13 h before declining, and the model predicted that 15 whales would reach the hotspot in 2.3 h, 25 whales would arrive in 4.5 h and 40 whales would arrive in 8.0 h.

DISCUSSION

Social foraging theory (Giraldeau & Caraco, 2000; Parker & Stuart, 1976) describes two scenarios in which multiple predators exploit a patch of resources (Fig. 1). If the resource is finite and thus depletes faster as the size of the group of foragers increases (i.e. a ‘dispersion economy’), conditions favour direct competition whereby all foragers would leave the patch nearly simultaneously once the patch is consumed. In such a scenario, and in the absence of some other advantage to maintaining group cohesion, it is to a predator's disadvantage if conspecifics know its location when it finds a high-quality patch (Fournet et al., 2018; Page & Bernal, 2020). Echolocating bats, for instance, form large groups of foragers around what are described as ‘ephemeral’ resources (Egert-Berg et al., 2018), and some species have been shown to eavesdrop on the foraging sounds of conspecifics (Page & Bernal, 2020; Roelke et al., 2020). We use Giraldeau and Caraco's (2000) definition of ‘ephemeral’ to mean not only that the patch is limited in its temporal availability, but also that its quality is driven more strongly by the environment than consumption; that is, the resource declines (or persists) at a rate independent of exploitation. This scenario is particularly relevant for engulfment feeders like rorqual whales, for whom the energetic cost and processing time of each individual foraging event depends on the engulfment volume

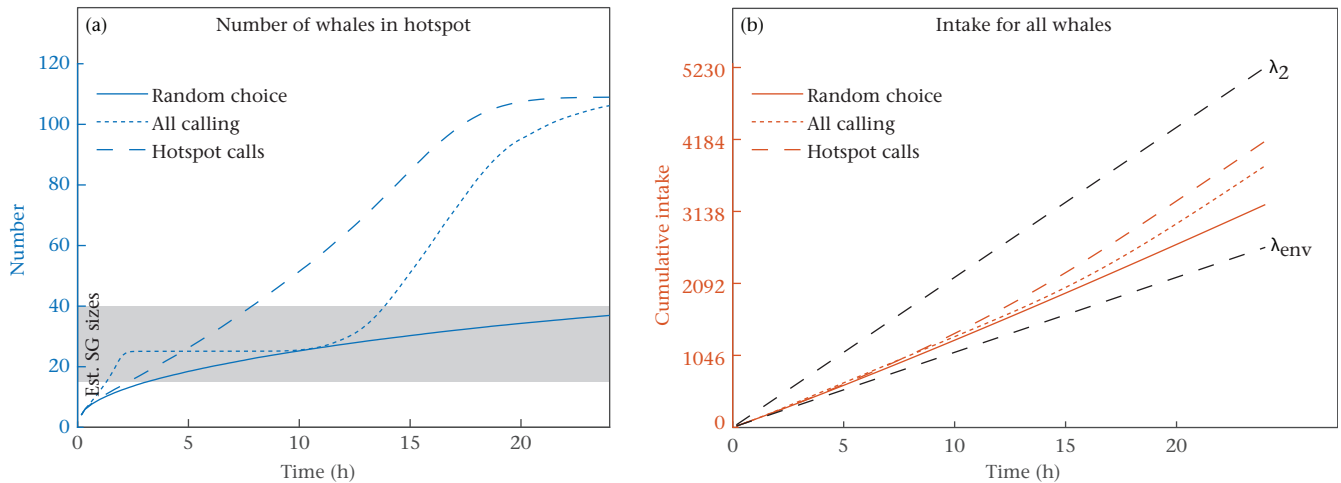


Figure 7. Simple model results from 1000 trials given random foraging for two social information scenarios predicting (a) the number of whales to find a prey hotspot and (b) the cumulative intake of all whales. λ_{env} is a representative intake rate, while λ_2 is the representative hotspot intake rate.

(Potvin et al., 2020) and will thus be approximately the same regardless of the amount of food in each mouthful, so the packing density of organisms within a swarm can be just as important as overall abundance (Boswell et al., 2016; Burrows et al., 2016; Cade et al., 2021; Hazen et al., 2015).

When resources are locally abundant, as in a prey hotspot, but temporally or spatially ephemeral, Torney et al. (2011) demonstrated that signalling that helps a population track resources can be an evolutionarily stable strategy, even if the recipients are not direct kin and even if signalling has a cost (directly or indirectly through competitive exclusion). If both the direct and indirect costs of signalling are low, it would imply that information sharing would be even more strongly selected for. We thus propose that a predator–prey system characterized by extensive, ephemeral, environmentally controlled prey patches exploited by predators with low costs of transport and the ability to produce social cues detectable over large distances would be expected to utilize an information-sharing strategy to increase environmental information and avoid the pitfalls associated with finding patches individually (Hein & Martin, 2020; Wilson et al., 2018). We propose four reasons that this scenario characterizes orca whale supergroups.

Extensive, Ephemeral, Environmentally Controlled Prey Patches

The patches we observed coincident with supergroups contained more biomass than could be consumed by the observed whales over relevant timescales. The densest 50% of gulp-sized cells (the 'informed whale-scale' described in Cade et al., 2021) in the measured portion of the supergroup associated prey patch from 16 August 2017 (SG B in Fig. 4), which is only a slice of the overall patch, were echo returns from organisms in 1.1 million m³ of water (accounting for overlap between pings). This slice alone would take 40 blue whales 9 h to consume at their supergroup feeding rates. Additionally, Cade et al. (2021) showed that prey patches associated with supergroups were not only higher in biomass (higher λ_p , Fig. 2), but also were distributed in such a way as to increase foraging rates (λ_f), resulting in an overall higher patch quality (λ) than nearby krill layers in which whales were also observed foraging prior to or subsequently to supergroup observations.

Secondly, although the sizes of prey patches associated with supergroups exceeded 1 km, the highest-quality areas were spatially restricted by topographically constrictive bathymetric

features (Figs 3, 4). Monterey Canyon, the largest submarine canyon along the U.S. west coast, is known to be a krill hotspot and essential foraging habitat for blue whales (Croll et al., 2005; Santora et al., 2012; Schoenherr, 1991). Submarine canyons and other physical features such as island wake eddies (Johnston et al., 2005), tidal flow (Cotté & Simard, 2005) and internal waves (Hazen et al., 2009; Pineda et al., 2015) can create prey aggregation hotspots on hourly or daily timescales by disrupting flow patterns and creating hydrodynamic structures that advect, entrain or attract freely swimming micronekton to local areas (Allen et al., 2001; Benoit-Bird et al., 2019; Santora et al., 2018). These fine-scale ocean features have been shown to be associated with prey aggregations and, in turn, result in increased predator foraging opportunities. Our observations of both blue whale supergroups at the heads of small canyons incising the slope support the importance of canyons and flow–topography interactions and imply that the observed spatially restricted blue whale aggregations were related to the spatial scale of prey aggregations.

Thirdly, physical oceanographic features aligned spatially and temporally with observed krill patches and blue whale supergroups. Krill are known to aggregate along oceanographic barriers and near submarine canyons like the ones we observed near supergroups (Santora et al., 2018; Warren & Demer, 2010) but to become more diffuse in the absence of strong circulatory patterns like upwelling that often act on subdaily timescales in relation to diel wind patterns and semidiurnal tides (Benoit-Bird et al., 2019; Johnston et al., 2005). Specifically, areas where currents form features that interact with one another, such as fronts, jets or eddies, have been linked to animal habitat selection in multiple systems (Abrahms et al., 2019; Oliver et al., 2019) due to their potential to aggregate biomass (Abrahms et al., 2018; Scales et al., 2014). Off South Africa, observed supergroups were associated with the boundaries of LCS, and in 2016 a strong feature (mean FSLE < -0.1) formed outside of Saldanha Bay (Fig. 3b, inset ii, Video S6) that was not present in 2015 when no aggregations were observed there. In Monterey Bay, water velocity across the shelf break depth range at the M1 buoy indicated circulation patterns that may have influenced foraging conditions, as supergroup encounters coincided with two periods of high current speeds in the shelf break depth range: strong northward flow during and preceding each supergroup observation (Fig. 6f) may have accumulated krill swarms while transporting them on-shelf along the upward-sloping seafloor, while sharp pulses of strong westward flow may have rapidly

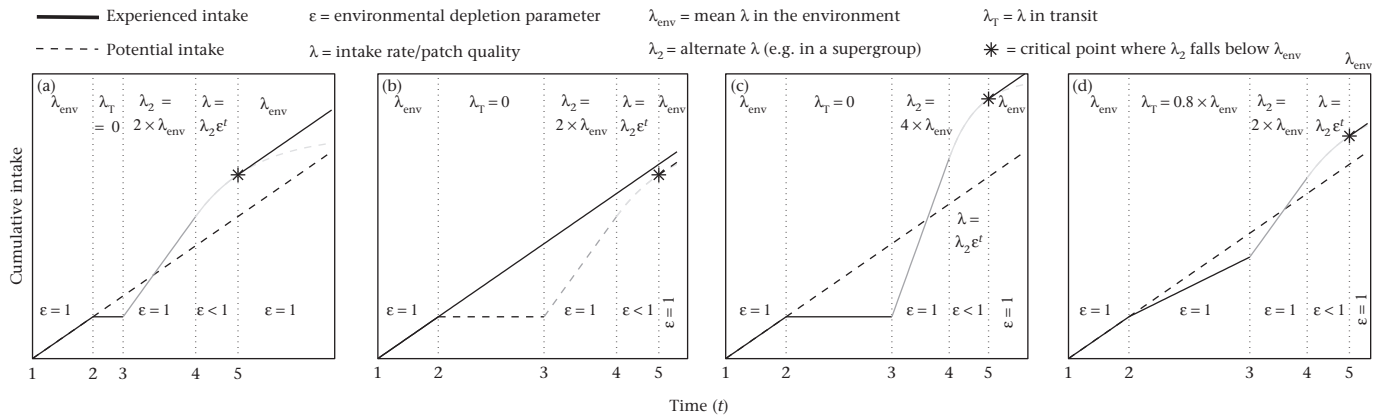


Figure 8. A model of resource intake (λ) in an environmentally controlled, ephemeral, noncompetitive social foraging scenario. λ = instantaneous intake rate (patch quality) represented by the slope at any given time t . The time steps are (1) animal foraging with an environmentally influenced intake rate λ_{env} , (2) animal detects conspecific cues and either continues foraging or breaks off foraging to transit to the conspecific aggregation, (3) animal arrives at aggregation and begins foraging at λ_2 , the new intake rate, (4) the intake rate at the patch begins to decline as a result of environmental controls until (5) the point when the slope of the intake function reaches λ_{env} and the forager is motivated to leave the patch. (a) An animal foraging at λ_{env} when it detects a cue and transits without feeding to the source, the increased intake rate results in a higher overall intake than if the individual had stayed in its original environment. (b) An animal detects a similar aggregation, but its distance is far enough such that increased foraging would not make up for the loss of intake during transit, in this scenario the optimal foraging strategy is not to transit. (c) A forager detects cues the same distance as the prior scenario, but the strength of the cues (e.g. calling rate) is such that it implies that λ_2 would be high enough to account for the long transit time. (d) When prey are arranged in long layers (e.g. along a shelf break), it could be optimal to continue foraging but towards the direction of the cue source such that transit is longer but overall intake is still higher. This appears to be what we observed with two tagged blue whales that fed along the shelf break to the southeast towards the direction of supergroup B (Video S7).

ejected near-bottom krill swarms into the shelf break water column, transporting them seaward into deeper water. Both blue whale supergroup encounters were temporally coincident with observable surface FTLE and vorticity features that persisted on the scale of hours and were not present 1 week prior or 1 week past when the aggregations were observed (Fig. 6, Videos S4 and S5), suggesting that the size and density of the observed prey patches were environmentally influenced. Observations of the prey patch associated with supergroup B over two successive days (Fig. 4d and e) support these interpretations. On 15 August, when the patch was large but not as uniformly dense as the patch associated with supergroup B on 16 August, there were 8–10 blue whales feeding in the area, with hundreds of metres separating them (i.e. not aggregated into a supergroup). It should be noted that the surface features intersecting the canyon edge were also observable at other times during the study period, but it is not known whether large prey patches, and large predator aggregations, formed at those times in those locations. Future studies will be needed to more closely link the prey field along the shelf break to surface features.

Finally, we also found evidence that supergroup formation may be socially mediated. Rorqual whales forage across large expanses of the ocean, a consummate acoustic medium (Au & Hastings, 2008), and their low-frequency vocalizations can be perceived over tens to hundreds of kilometres (Stafford et al., 1998). We recorded anomalously high rates (> 94th percentile) of D calls – thought to be associated with foraging behaviour in blue whales (Barlow et al., 2021; Miller et al., 2019; Oleson, Calambokidis, et al., 2007) – at the MARS hydrophone in the 4 h bins preceding both observations of supergroups in Monterey Bay, suggesting that blue whales may increase calling activity near high-quality foraging grounds. Anomalously high D call production was also recorded in subsequent days (17, 18 August), and although field efforts had concluded (so aggregations could not be confirmed), high-magnitude LCS continued to form around the Monterey Canyon edge over the same time period (Video S4), suggesting that conditions for superpatch creation remained in place through the period of observed anomalously high social cue production. Modelled results (Fig. 7) demonstrate that the observed blue whale group sizes, which were likely more than 25 and as high as 40

animals, formed much more rapidly if social information informed travel direction. The increase in cumulative resource intake in the population that was assumed to use social information provides additional evidence of a benefit that could result in an evolutionarily stable foraging strategy. Our observations during the study period support these models: two blue whales tagged prior to observations of the 16 August supergroup both traversed along the shelf break and joined the forming aggregation (Video S7), suggesting knowledge about the environment that presumably exceeded their sensory perception (as modelled in Fig. 8d). Although we did not have equivalent recordings off South Africa, prior studies found evidence of song production near supergroups (Gridley et al., 2018; Ross-Marsh et al., 2020). Although it is more typically associated with breeding grounds, song is among the loudest humpback whale vocalizations. This contrasts with other regions characterized by foraging on depletable fish schools, like southeastern Alaska, where humpback whale vocalizations have been noted to be quieter than expected (Fournet et al., 2018), likely to avoid alerting conspecifics.

The implications of the environmentally controlled social foraging scenario we propose are modelled in Fig. 8. In these models, we propose that the mean intake rate for any individual (λ) – for modelling purposes equivalent to the environmental patch quality that facilitates an individual's intake rate (Giraldeau & Caraco, 2000) – can be described by $\lambda = \lambda_0 e^t$, where ϵ represents the environmental input such that the patch declines if $\epsilon < 1$, stays constant at $\epsilon = 1$ and grows if $\epsilon > 1$, where λ_0 is the initial intake rate and t is time. The plots show cumulative intake of an individual over time, such that the slope of the line at any point is the intake rate λ . The scenarios described in Fig. 8 differ from the ephemeral prey patch model in Giraldeau and Caraco (2000) in that they do not assume that the intake of a solitary forager differs from that of a forager in a group. The Fig. 8 scenarios also allow both for search/exploitation cycle durations that vary and for values of λ that remain steady within a patch for some nontrivial period of time. To effectively characterize the environment in which krill-feeding rorqual whales forage, the environmentally controlled, ephemeral, noncompetitive social foraging scenario we propose rests on four assumptions that could be tested in systems that exhibit

similar environmental characteristics: (1) calling rates of foraging individuals increase as prey density increases (supporting the prediction of the ‘hotspot calling’ scenario in Fig. 7); (2) high calling rates in an environment increase the probability that an individual gives up foraging to transit to a distant patch; (3) individuals will emigrate from a patch being exploited as a group once quality declines below their individually determined mean intake rate (as discussed in Fig. 2); (4) larger animals will leave a patch first as quality declines since their intake rate will be more dependent on closely spaced, dense patches (Kahane-Rapport et al., 2020). If these hypotheses can be verified in future research, it will have implications for search and exploitation times of rorqual whales, their dependence on conspecifics to extend their sensory perception and their resilience to annual fluctuations in the environment.

Conclusions

The gigantic body sizes characteristic of rorqual whales not only increase the efficiency of foraging on krill (Goldbogen et al., 2019), but also appear to enable some of the foraging flexibility of species like humpback whales (Cade et al., 2020). 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, stimulating primary productivity and promoting natural aggregation areas (Slater et al., 2017). Locating and exploiting prey hotspots is essential to the foraging strategy of rorqual whales, but whale aggregations of the size and density noted here are not commonly reported. In the case of humpback whales, groups of the size and density discussed here have only been reported off South Africa seasonally and recently (Findlay et al., 2017), and have also only recently been observed during the southward migration off Australia (Pirrotta et al., 2021). However, similarly large aggregations of rorqual whales were 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, especially given that abnormally large densities of krill do not appear to be a new phenomenon (Nicol et al., 1987).

The historic reports and contemporary re-emergence of these large aggregations suggest that social cues emanating from supergroups may have played an important role as signposts to help individuals in a population more purposefully navigate patchy environments (Wilson et al., 2018), essentially improving their foraging success by extending their sensory capabilities (Hein & Martin, 2020; LaScala-Gruenewald et al., 2019). The 19th and 20th century commercial exploitation of all large cetaceans would therefore have led to massive information network disruption (Schmidt et al., 2010) as populations plummeted to numbers that were between 1% and 10% of historic abundance. However, if large populations of rorqual whales can increase their foraging efficacy by revealing the location of high-quality foraging hotspots to conspecifics, the resulting positive feedback loop may help explain why large whale populations were slow to recover from 19th and 20th century commercial exploitation, but some populations have more recently increased in abundance (Bejder et al., 2016). In contrast, some exploited, particulate-feeding species such as sperm whales, *Physeter macrocephalus*, have recovered more slowly than expected (Carroll et al., 2014; Gero & Whitehead, 2016).

Both the propensity to form large groups and the types of collective behaviour are strongly driven across taxa by the

heterogeneity, or patchiness, of resources in the environment (Gordon, 2014; Piatt & Methven, 1992). Resource dispersion hypotheses posit that heterogeneous (patchy) environments increase the degree to which living in groups is an evolutionarily stable strategy (Torney et al., 2011), but there are few systems in which these hypotheses have been explicitly tested (Johnson et al., 2002). Due to the variety of rorqual whale group sizes, as well as the newly developed ability of researchers to study these groups quantitatively in the wild (Goldbogen et al., 2013), we propose these groups are ideal systems in which to test a variety of theories related to social foraging. There is growing evidence that individual behaviour influences social foraging dynamics (Laskowski & Bell, 2014), but also that environmental variability influences individual behaviour (Araújo, Bolnick, & Layman, 2011). As large, long-lived, individually identifiable organisms, rorqual whale behaviour can be studied longitudinally, allowing the spreads of behaviours within populations to be studied quantitatively (Allen et al., 2013), and future research may be able to answer the open question of the degree to which individual rorqual whales can adjust their foraging strategies to environmental regimes that are increasingly dynamic. It may be that as a consequence of its dynamic patchiness, the marine environment encourages more cooperative dynamics generally than the terrestrial realm.

Data Availability

Code to create Fig. 7 as well as prey and tag data have been deposited at Stanford University's digital repository: <https://purl.stanford.edu/rq794kc6747>, MARS hydrophone data can be accessed at: <https://www.mbari.org/at-sea/cabled-observatory/mars-science-experiments/mars-hydrophone-data/>, surface current data (used to derive vorticity and particle accumulation) is publicly available at: <http://www.sccoos.org/data/hfrnet/>, and M1 current data is available through: <https://www.cenccos.org/data/buoys/mbari/m1/info>.

Author Contributions

D.E.C.: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Writing-original draft, Writing-review & editing; **J.A.F.:** Conceptualization, Formal analysis, Investigation, Methodology, Writing-review & editing; **W.K.O.:** Conceptualization, Formal analysis, Investigation, Methodology, Writing-review & editing; **J.R.:** Conceptualization, Data curation, Formal analysis, Investigation, Resources, Writing-review & editing; **J.C.:** Conceptualization, Data curation, Funding acquisition, Investigation, Resources, Writing-review & editing; **K.P.F.:** Conceptualization, Investigation, Project administration; **A.S.F.:** Conceptualization, Funding acquisition, Investigation, Writing-review & editing; **E.L.H.:** Conceptualization, Investigation, Methodology, Writing-review & editing; **S.M.S.:** Conceptualization, Funding acquisition, Investigation, Project administration, Writing-review & editing; **J.A.G.:** Conceptualization, Funding acquisition, Investigation, Project administration, Supervision, Writing-review & editing.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <https://doi.org/10.1016/j.anbehav.2021.09.013>.

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