

Searching for prey in a three-dimensional environment: hierarchical movements enhance foraging success in northern elephant seals

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Summary

1. Foraging theory predicts that predators adjust their movements according to the spatial distribution of prey. Since prey is often patchily distributed, area-restricted search (ARS) behaviour, characterized by sinuous search paths of predators with increased turning frequency, should be effective in foraging.

2. However, it remains unclear whether ARS behaviour actually enhances foraging success in free-ranging animals, especially in marine animals that forage in a three-dimensional (3D) environment.

3. Here, we reconstructed 3D dive paths of a highly pelagic marine predator, the northern elephant seal ($n = 3$), with multisensor data loggers that recorded depth, tri-axis acceleration, tri-axis magnetism and swim speed. We identified spatial scales of volume-restricted search (VRS, termed for 3D ARS) behaviour using spherical first-passage time analysis on 3D dive paths, accompanied with quantifying feeding rates in VRS by using mandible accelerometers that recorded feeding events.

4. Seals exhibited VRS behaviour at two spatial scales (radius of spheres): small-VRS (8–10 m) and large-VRS (17–19 m). Most feeding events occurred in VRS zones (78 and 86% for small and large-VRS, respectively), although VRS accounted for a small proportion of bottom phase of dives in distance travelled. This suggests a strong link between VRS behaviour and foraging success.

5. There was a hierarchical structure to the VRS; most small-VRS (95%) were nested within large-VRS (i.e. nested VRS). Importantly, nested VRS had significantly higher feeding rates than non-nested VRS, because nested VRS contained small- and large-VRS with higher and lower feeding rates, respectively. These results suggest that seals forage on mesopelagic prey in a hierarchical patch system where high-density patches at small scales are nested within low-density patches at larger scales.

6. We demonstrated that seals employed scale-dependent, hierarchical 3D movements and that underwater fine-scale sinuous movements (i.e. VRS) were strongly linked to higher foraging success, particularly within nested VRS zones. We suggest that seals enhanced foraging success by employing hierarchical movements that possibly reflect the hierarchical property of prey distribution. Although recent studies advocate that optimal searching behaviour would be scale-independent (e.g. Lévy walk), our study suggests that scale-dependent processes are important components of successful foraging behaviour.

Key-words: area-restricted search, bio-logging, foraging behaviour, hierarchical patch system, Lévy walk, marine predator, scale-dependent movement, three-dimensional movement

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Introduction

If predators forage optimally, they should decide where and how to feed such as to enhance foraging success and, ultimately, their fitness (Stephens & Krebs 1986). To achieve this, predators should adjust their movement paths according to the spatial distribution of prey, which is often aggregated in patches of higher prey density than the mean overall prey density of the environment (Benhamou 1992). In a patchy environment, it is expected that predators will decide to increase search effort at a smaller scale after detecting prey, because of the high probability of encountering other prey items nearby, rather than continuing to explore at a larger scale. This foraging behaviour is generally referred to as an area-restricted search (ARS; Kareiva & Odell 1987).

An ARS is a scale-dependent movement in two dimensions, characterized by a sinuous search path of a foraging animal with increased turning frequency, thus reducing travel distances (i.e. reducing net displacement within a patch) to enhance foraging success while exploring spatially heterogeneous environments (Kareiva & Odell 1987). Free-ranging animals demonstrate ARS behaviour in both terrestrial (e.g. Fryxell *et al.* 2008; Le Corre *et al.* 2008; Byrne & Chamberlain 2012) and marine environments (e.g. Fauchald & Tveraa 2003; Bailey & Thompson 2006; Weimerskirch *et al.* 2007; Bailleul *et al.* 2008). Since ARS behaviour suggests regions where animals intensely forage, ARS zones have been used for designation of important foraging zones and conservation actions (e.g. Walsh 1996; Costa, Breed & Robinson 2012; Lascelles *et al.* 2012). However, the utility of ARS as a method to infer intensive foraging areas is still debated (e.g. Pinaud & Weimerskirch 2007), because it remains unclear whether ARS actually enhances foraging success in the wild, due to the technological challenge of coupling movement paths of animals with records of feeding events (prey captures). Only a few studies have investigated the relationship between ARS and foraging success in free-ranging animals by recording both movement paths and feeding events. For example, a study addressing two-dimensional (2D) large-scale movements (varying from 5 to 90 km) of free-ranging wandering albatrosses (*Diomedea exulans*) showed that only 25% of total prey was captured in ARS zones while the rest was captured in straight-line movements (Weimerskirch *et al.* 2007), suggesting a weak link between ARS and foraging success (possibly because prey distribution follows scale-independent patterns, such as the exponential or power laws; also see Weimerskirch, Gault & Cherel (2005)). Another study found that bottlenose dolphins (*Tursiops truncatus*) exhibited foraging behaviour (i.e. fish tossing and porpoising) within small-scale ARS zones (less than a kilometre) (Bailey & Thompson 2006), but this study relied on land-based visual observations that were limited in the spatial scale observed. The paucity of fine-scale feeding event data accompanied with movement paths has hindered further understanding of the relationship between

ARS and foraging success in free-ranging animals, especially in diving animals that forage on prey in a three-dimensional (3D) underwater environment.

In the marine environment, prey is distributed in three dimensions over a range of spatial scales, often represented by a hierarchical patch structure where high-density patches at small scales are nested within low-density patches at larger scales (Fauchald, Erikstad & Skarsfjord 2000). In the hierarchical patch system, it is predicted that predators would employ scale-dependent, hierarchical movements that reflect the hierarchical properties of the prey distribution (Fauchald, Erikstad & Skarsfjord 2000). This means that predators should explore larger-scale patches by using longer travel distances with lower turning frequencies (i.e. large-scale ARS) until they find a smaller-scale patch, within which they should use shorter travel distances with higher turning frequencies (i.e. small-scale ARS) (Fauchald 1999), representing a nested ARS behaviour (see Fauchald 2009 for a review). Previous studies addressing underwater predator-prey systems supported this prediction by analysing 2D horizontal movements of diving animals (i.e. discrete positions on water surface among dives) (e.g. Hamer *et al.* 2009; Thums, Bradshaw & Hindell 2011; Benoit-Bird *et al.* 2013). However, these studies did not consider the 3D nature of foraging in diving animals (Bailleul *et al.* 2008). Fine-scale 3D dive paths and kinematics of diving animals have been reconstructed for several species to characterize foraging behaviour (e.g. Wilson & Wilson 1988; Davis *et al.* 1999; Johnson & Tyack 2003; Aoki *et al.* 2012; Goldbogen *et al.* 2015; Iwata *et al.* 2015; Williams *et al.* 2015), but such data have not been examined in the context of hierarchical movements because the analytical framework was not available to quantify the spatial scale of such 3D search behaviour (c.f. Kotliar & Wiens 1990).

Here, we deployed mandible accelerometers and 3D data loggers to record the occurrence of feeding events along a dive path, which allowed us to reconstruct fine-scale 3D foraging behaviour of a highly pelagic marine predator, the northern elephant seal (*Mirounga angustirostris*). We then employed an analytical framework using spherical first-passage time (SFPT) (Bailleul, Lesage & Hammill 2010) to quantify the spatial scale of 3D sinuous movement paths of seals under the concept of volume-restricted search (VRS), analogous to ARS for diving animals that exploit a 3D environment. Using this conceptual framework of VRS coupled with data on feeding events, we test (i) whether seals employ scale-dependent, hierarchical 3D movements and (ii) whether VRS behaviour is linked to higher foraging success, particularly within nested VRS zones.

Materials and methods

FIELD EXPERIMENTS

Fieldwork was conducted at Año Nuevo State Park, CA, USA (37°5' N, 122°16' W) on female northern elephant seals during

their breeding season to address the 2-month post-breeding foraging migration (February–April) in 2012 and 2013. Each seal was immobilized with an intramuscular injection of Telazol (Tiletamine hydrochloride and Zolazepam hydrochloride, Fort Dodge Animal Health, Fort Dodge, IA, USA) to attach the data loggers and to collect body mass and morphometric measurements (Le Boeuf *et al.* 1988, 2000). Upon return from their foraging migration, seals were immobilized to recover the data loggers and to collect post-deployment mass and other measurements.

Each seal was equipped with a 3D data logger (W1000L-3MPD3GT; see the next section), a mandible accelerometer (Kami Kami Logger; see the next section), a GPS logger (Mk10-AF; Wildlife Computers, Redmond, WA, USA), and a VHF transmitter (ATS, Isanti, MN, USA). The data loggers were wrapped in rubber splicing tape and glued to the animal's back (3D data logger and VHF transmitter), mandible (mandible accelerometer), and head (GPS logger) using 5-min epoxy with high-tension mesh netting and cable ties. In total, six animals were instrumented (three animals each in 2012 and 2013). One set of data loggers was not recovered because the seal did not return to the colony. For other two sets of data loggers, either mandible accelerometer or 3D accelerometer failed to record data (e.g. seaweed was stuck on the propeller of a 3D accelerometer, preventing us from calculating swim speed to reconstruct 3D dive paths). Therefore, we were able to collect complete sets of data from three seals to conduct further analyses.

INSTRUMENTS TO RECONSTRUCT 3D FORAGING BEHAVIOUR

The combined use of a 3D data logger and a GPS logger enabled us to reconstruct 3D dive paths, by employing a dead-reckoning method calibrated by GPS positions obtained at the water surface (e.g. Davis *et al.* 2001; Shiomi *et al.* 2010). The 3D data logger (W1000L-3MPD3GT; Little Leonardo Co., Tokyo, Japan; diameter 26 mm, length 178 mm and mass 146 g) has a depth (pressure) sensor, a tri-axis accelerometer, a tri-axis magnetometer and a speed sensor that uses an external propeller. Depth, tri-axis magnetism and swim speed (estimated from the propeller rotation; Sato *et al.* 2003) were recorded at 1 Hz. Tri-axis acceleration was recorded at 4 Hz. Raw acceleration data are considered to contain two components: (i) dynamic accelerations associated with propulsive activities (i.e. flipper strokes) and (ii) static accelerations (gravity-based acceleration) associated with the inclination of the animal's body (i.e. pitch and roll along lateral and longitudinal axes of the animals, respectively) (e.g. Sato *et al.* 2003; Shiomi *et al.* 2010). Static accelerations were obtained to reconstruct a 3D dive path (Shiomi *et al.* 2010) by applying high-pass filtering that separates the dynamic accelerations from raw accelerations with a built-in function 'FilterFIR' of IGOR Pro version 6.03 (WaveMetrics, Portland, OR, USA). This filtering process was conducted with the dominant cycle of flipper strokes, which is estimated by calculating power spectral density in each seal (Shiomi *et al.* 2010) using a built-in function 'Power Spectral Density' of IGOR Pro. Also, we applied the same filtering process (high-pass filtering with the dominant cycle of flipper strokes) to tri-axis magnetism to obtain static magnetism. Then, the 3D dive path was estimated using the freeware macro 'ThreeD_path' for IGOR Pro (distributed at http://bre.soc.i.kyoto-u.ac.jp/bls/index.php?3D_path; Shiomi *et al.* 2010) following these steps: (i) calculation of pitch and roll angles with tri-axis static acceleration, (ii) calculation of heading with pitch, roll, and tri-axis static magnetism and (iii) estimation of the 3D dive path every second with heading, swim speed and depth. Finally, the estimated 3D dive path was dead-reckoned with GPS positions at the water surface to correct errors in the horizontal positions of animals (e.g. correcting errors derived from the effect of ocean currents) (Davis

et al. 2001). The corrected 3D dive path was subsampled every 5 s to match the sampling interval of the mandible accelerometer.

The mandible accelerometer (Kami Kami Logger; Little Leonardo Co.; diameter 20.2 mm, length 73 mm, mass 48 g) has a depth (pressure) sensor to record depth every 5 s and a single-axis accelerometer (along the longitudinal body axis). The single-axis accelerometer can record the occurrence of feeding events every 5 s by using measurements of mandible acceleration at a high sampling rate (32 Hz) with an on-board data-processing algorithm, which was shown to be reliable in female northern elephant seals because feeding events do not occur during drift dives that are not related to foraging behaviour (Mitani *et al.* 2010; Naito *et al.* 2013). The on-board data-processing algorithm (i) detected a high-frequency, feeding-related jaw motion with an amplitude threshold for longitudinal acceleration of 0.3 G ($=2.94 \text{ m s}^{-2}$ in SI), (ii) separated each feeding-related jaw motion from the next one with an event duration threshold (0.5 s) and (iii) computed the occurrence of feeding-related jaw motions for every 5-s time window (Naito *et al.* 2013). Then, the mandible accelerometer stored the occurrence of feeding-related jaw motions every 5 s as binary data (i.e. 1 or 0 for the 5-s time window with at least one or no feeding-related jaw motions, respectively). Hereafter, we referred to this as 'feeding events occurred' for the 5-s time window where the binary data = 1, except for where depths were shallower than 100 m, to avoid feeding-unrelated acceleration noise recording near the surface (Naito *et al.* 2013). Finally, we put the feeding events onto the 3D dive path, thereby reconstructing the 3D foraging behaviour of ocean-migrating northern elephant seals.

DIVE ANALYSIS

Each dive was defined using a minimum depth of 10 m. Descent, bottom and ascent phases of the dive were defined following Adachi *et al.* (2014): (i) descent phase was the period from the start of a dive to the first time when the rate of depth change was negative, (ii) bottom phase was the period between the end of the descent phase and the beginning of the ascent phase and (iii) ascent phase was the period from the last time when the rate of depth change was positive to the end of the dive.

IDENTIFYING SCALE-DEPENDENT, HIERARCHICAL FORAGING BEHAVIOUR IN A 3D ENVIRONMENT

We expected that seals would demonstrate scale-dependent, hierarchical foraging behaviour because prey is often patchily and hierarchically distributed in marine environments (e.g. Fauchald 1999, 2009; Fauchald, Erikstad & Skarsfjord 2000). The spatial scales of 3D movements were identified using SFPT analysis (Bailleul, Lesage & Hammill 2010) to determine the spatial scales of VRS. SFPT was defined as the time required to cross a sphere of a given radius along the 3D dive path (Bailleul, Lesage & Hammill 2010), analogous to the time required to cross a circle of a given radius as defined for first-passage time (FPT) analysis used to identify ARS behaviour for 2D movements (Fauchald & Tveraa 2003). SFPT values should be higher, where seals show higher sinuosity along their 3D dive paths for VRS behaviour. SFPT is scale-dependent, and a plot of variance in SFPT against radii of spheres reveals the spatial scales at which the animal concentrates its search effort in VRS (see Fauchald & Tveraa (2003); Bailleul, Lesage & Hammill (2010) for details). To determine the spatial scale of VRS, we applied spheres of various radii (from 1 to 100 m) onto the 3D dive paths of each dive (Bailleul, Lesage & Hammill 2010). Then, the relative variance $S(r)$ in SFPT was calculated as $\text{Var}(\log(t(r)))$, as a function of the radius r , where $t(r)$ is the time required to cross a sphere (SFPT) of radius r along the

3D dive paths. Note that $t(r)$ was log-transformed to make $S(r)$ independent to the magnitude of the mean SFPT (Bailleul, Lesage & Hammill 2010). Finally, $S(r)$ was plotted against r to detect a peak (or peaks), identifying the dominant scales where VRS occurred (see Figs 1 and S1, Supporting information). We excluded 'drift dives' from this analysis, which accounted for only $3.6 \pm 0.3\%$ of total number of dives, because drift dives contained a highly sinuous 'drift phase' but are not related to foraging behaviour (Mitani *et al.* 2010).

To support the spatial scales of 3D movements obtained from SFPT analysis, we examined the frequency distribution of the distances between consecutive feeding events, because examining the frequency distribution of ecological events is a common practice for identifying hierarchical structures of ecological phenomena (Allen & Starr 1982), such as behavioural bouts (Sibly, Nott & Fletcher 1990). We followed Sibly, Nott & Fletcher (1990) by using a nonlinear two-process model, in which a simple Poisson random process is assumed for the ecological events (i.e. exponential distribution of the time interval between consecutive events). The nonlinear two-process model identifies the time interval to distinguish frequent behaviours from less frequent behaviours by providing an objective break point, so-called a *bout criterion* (Sibly, Nott & Fletcher 1990). The nonlinear two-process model is typically applicable to a scale-dependent process, for example, to the frequency distribution of time intervals of consecutive feeding events. This allows identification of within-bout (within-patch) feeding events (i.e. feeding events separated by short intervals smaller than bout criterion) and between-bout (between-patch) feeding events (i.e. feeding events separated by long intervals greater than bout criterion) (Johnson *et al.* 2002). Note that the frequency distribution should follow a linear model, but not a nonlinear two-process model, when feeding events occur randomly (i.e. events are generated by one random process, indicating a scale-independent process) (Sibly, Nott & Fletcher 1990; Weimerskirch *et al.* 2007). Hence, we can test whether the ecological events occur scale-dependently or scale-independently, by examining whether a non-linear two-process model or a linear model fit better to the empirical frequency distribution of ecological events (Sibly, Nott & Fletcher 1990; Johnson *et al.* 2002). In this study, we replaced 'time intervals' with 'distances' between consecutive feeding events. Then, we applied the nonlinear two-process model to the log-transformed frequency distribution of the distances (Sibly, Nott & Fletcher 1990) and also to its cumulative frequency distribution (Edwards *et al.* 2007), to test whether the frequency distribution follows a nonlinear two-process model (i.e. indicator of scale-dependent process) (Johnson *et al.* 2002) or a linear model

(i.e. indicator of scale-independent process) (Weimerskirch *et al.* 2007). In the fitting procedure of a nonlinear two-process model, a bout criterion serves as a threshold to distinguish within-bout (within-patch) from between-bout (between-patch) scales, determining the spatial scale of movements (Johnson *et al.* 2002). The fitting procedure and model selection were carried out using R version 2.15.3 (R Development Core Team 2013) to determine the bout criterion for each seal.

INVESTIGATING FEEDING RATES IN VRS ZONES

To test whether VRS behaviour is linked to higher foraging success, we calculated the number of feeding events that occurred within each VRS zone. First, SFPT was smoothed with a moving average window using five data points to remove noise (e.g. Weimerskirch *et al.* 2007). Then, each VRS zone was identified as any period where the smoothed SFPT exceeded the upper quartile (Suryan *et al.* 2006). Finally, we calculated feeding rates within each VRS zone as the number of feeding events that occurred within each VRS every 5 s (i.e. the finest time resolution of the data from mandible accelerometers).

STATISTICAL ANALYSIS

Statistical analysis was carried out using R (R Development Core Team 2013). First, to investigate the effect of VRS type (e.g. small- or large-VRS) on feeding rates, we fitted a generalized linear mixed model (GLMM) that assumes a zero-inflated Poisson distribution using the *MCMCglmm* function in the *MCMCGLMM* package (Hadfield 2010), because the count data of the number of feeding events within each VRS possessed excess zeros (Bolker *et al.* 2012; data are provided as Appendix S1). The full model included the number of feeding events within each VRS as a response variable, VRS type as a fixed effect, and the time spent within each VRS as an offset term, allowing us to investigate the effect of VRS type on feeding rate without the division process in the statistical analysis (i.e. without prior transformation to derive feeding rates by dividing the number of feeding events by time spent within each VRS). We included individual seal as a random effect. Then, we used deviance information criterion (DIC) to select the most parsimonious model among null, full, and intermediate models. Secondly, we used Akaike information criterion (AIC) to select the most parsimonious model to test whether the log-transformed frequency distribution of the distances between feeding events follows a nonlinear two-process model or a linear model. In this study, data are presented as means \pm standard deviation (SD) unless otherwise stated.

Results

The combined use of 3D data loggers, GPS loggers and mandible accelerometers allowed us to reconstruct the 3D foraging behaviour of three female northern elephant seals for 13.5 ± 3.7 days during the outbound period of the 2-month post-breeding foraging migration (covering 964.2 ± 447.8 km in a north-westward direction from the California coast; from 7.8, 4.0 and 3.9 days to 19.7, 21.5 and 14.9 days after departure, for the seals 1935, U627 and U954, respectively). A total of 880 ± 321 dives (including 724 ± 227 foraging dives that had at least one feeding event) and 9336 ± 1411 feeding events (13 ± 3 feeding events per foraging dive) were recorded for each individual. The mass and standard length (i.e. straight line between the tip of the nose and the tip of the tail) of seals

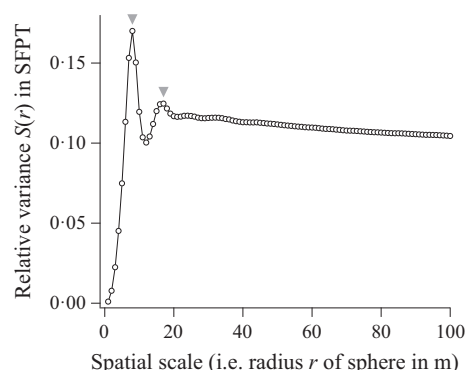


Fig. 1. Relative variance $S(r)$ in spherical first-passage time (SFPT) plotted against spatial scale (i.e. radius r of sphere) for seal 1935, showing two peaks of variance (represented as two filled grey triangles), indicating volume-restricted search (VRS) at the corresponding scales of 8 and 17 m.

were 306.3 ± 70.6 kg and 262.0 ± 25.6 cm at deployment, and 385.0 ± 50.5 kg and 261 ± 24.8 cm at recovery, respectively.

The relative variance in SFPT (i.e. $S(r)$) showed two clear peaks for all three individuals, indicating small- and large-VRS occurred at radii r of 9 ± 1 and 18 ± 1 m, with little variation among individuals (Figs 1 and S1; peaks at 8 and 17 m for seal 1935, 10 and 19 m for seal U627 and 9 and 18 m for seal U954, respectively). Most dives included at least one small- or large-VRS (79.8 ± 4.1 and $81.7 \pm 3.8\%$ of total dives included 3.3 ± 0.6 small-VRS and 4.0 ± 0.7 large-VRS, respectively). The majority of small- and large-VRS occurred within the bottom phase of dives ($88.2 \pm 3.4\%$ and $85.6 \pm 5.8\%$ for small- and large-VRS, respectively). Although the total distance travelled during VRS accounted for only a small portion of the bottom phase of dives ($15.1 \pm 2.3\%$ and $27.3 \pm 7.2\%$ for small- and large-VRS, respectively), most feeding events occurred in VRS ($78.1 \pm 4.9\%$ and $85.6 \pm 5.8\%$ for small- and large-VRS, respectively).

There was a hierarchical structure to the VRS, with most small-VRS ($94.9 \pm 4.2\%$) nested within large-VRS (i.e. nested VRS) (Fig. 2). Feeding rates of the seals were significantly higher within nested VRS, which comprised $73.7 \pm 5.3\%$ of large-VRS, than for the rest of large-VRS that occurred alone (i.e. non-nested VRS) (Fig. 3a; DIC = 28329.6 and 29986.2 in each GLMM with and without VRS type as a fixed effect, respectively). Within nested VRS, feeding rates were higher in the small-VRS portion than in the area outside of small-VRS (i.e. large-VRS portion) (Fig. 3b; DIC = 32623.0 and 35767.1 in each GLMM with and without VRS type as a fixed effect, respectively).

The frequency distribution of the distances between consecutive feeding events fitted better with a nonlinear two-

process model (i.e. indicator of scale-dependent process) than a linear model (i.e. indicator of scale-independent process) in all individuals (Table S1; Figs 4 and S2). The two processes were spatially separated by the bout criterion of 18.2 ± 2.9 m (bout criteria = 19.8, 20.0 and 14.8 for seal 1935, U627 and U954, respectively), representing less frequent feeding events connected to each other with distances longer than the bout criterion (i.e. between-patch scale) and more frequent feeding events connected to each other with distances shorter than the bout criterion (i.e. within-patch scale) (Fig. 2).

Discussion

SEALS EMPLOY SCALE-DEPENDENT, HIERARCHICAL FORAGING BEHAVIOUR IN A 3D ENVIRONMENT

We demonstrated that female northern elephant seals use scale-dependent, hierarchical movements that were composed of two steps of movements across three spatial scales: (i) movements from the between-patch scale to the within-patch scale (i.e. large-scale patches) and (ii) movements from large-scale patches to small-scale patches.

The first step of hierarchical movements (i.e. movements from the between-patch scale to the within-patch scale) was reflected in the spatial scale of large-VRS with radii of 18 ± 1 m (Fig. 1). Within-patch behaviour is identified by increased sinuosity of the movement path while between-patch behaviour should be characterized by more straight movement path (Kareiva & Odell 1987). Hence, the spatial scale of a large-VRS would indicate a boundary to distinguish between-patch from within-patch scales (e.g. Johnson *et al.* 2002). This explanation is corroborated by our observations that the distribution of the distances between feeding events represented a scale-dependent process

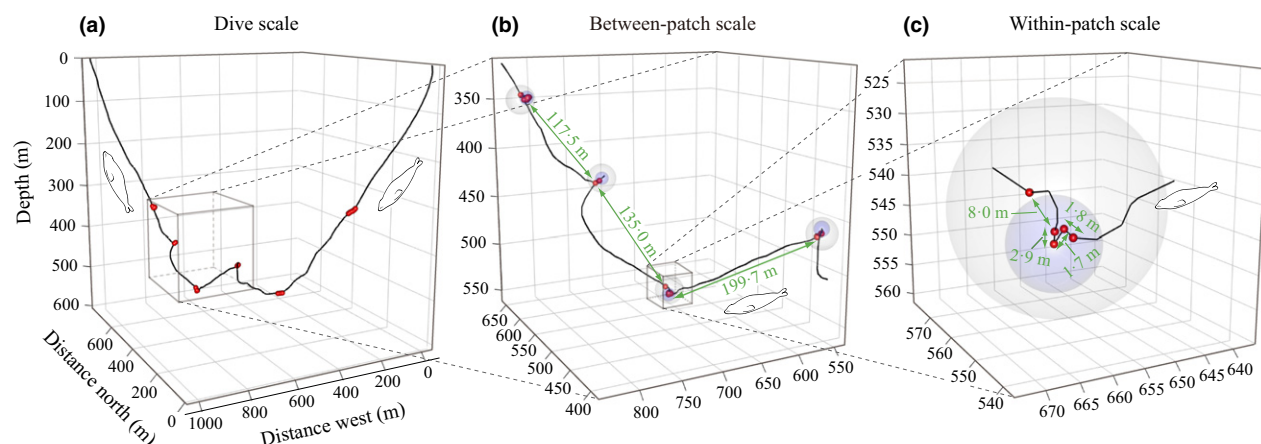


Fig. 2. Examples of 3D foraging behaviour for seal 1935 in a north-westward direction, which were separated into three panels: (a) dive scale, (b) between-patch scale and (c) within-patch scale. Open grey squares in (a) and (b) were scaled up to be shown as (b) and (c), respectively. Black lines represent the 3D dive paths of seals in all panels. Red dots represent positions where feeding events occurred, recorded using mandible accelerometers. In panels (b) and (c), transparent big grey and small blue spheres represent volume-restricted search (VRS) zones with the radius of 8 and 17 m, respectively, centred at the point with the highest values of spherical first-passage time (SFPT). Green arrows represent distances between consecutive feeding events.

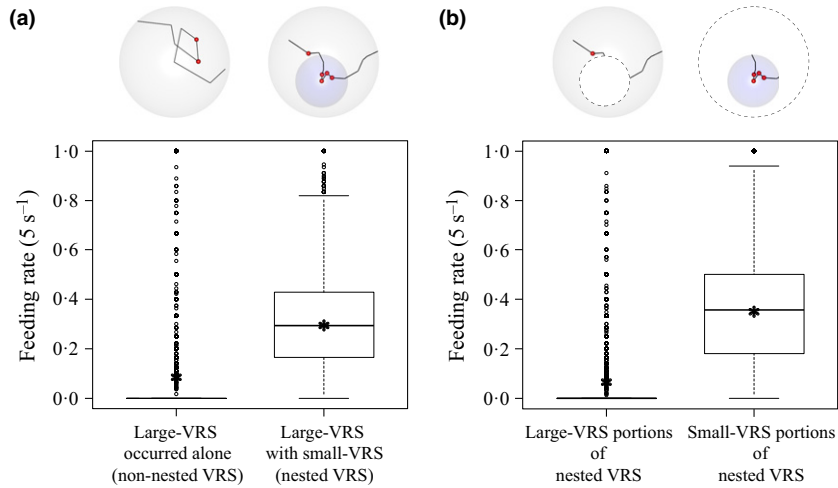


Fig. 3. Feeding rates within volume-restricted search (VRS) for all seals pooled together. In panel (a), left and right box plots represent feeding rates within non-nested and nested VRS, respectively. In panel (b), left and right box plots represent feeding rates within large-VRS and small-VRS portions in the nested VRS that is shown in the right box plot in panel (a), respectively. The mean value is indicated by an asterisk. Outliers are shown as points beyond 1.5 times the interquartile range.

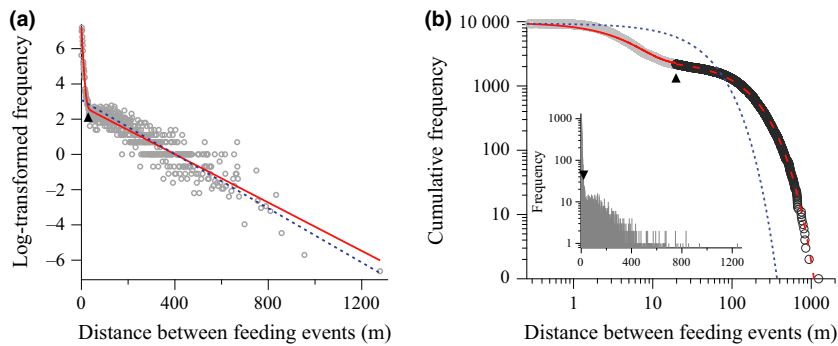


Fig. 4. Frequency distributions of the distances between consecutive feeding events for seal 1935. The panels show log-transformed (a) and cumulative frequency distribution (b) of the distance between consecutive feeding events, which were derived from the conventional frequency distribution shown as an inset in panel (b). Filled black triangles represent a bout criterion of 19.8 m. In panel (a), red solid and blue dashed lines represent a nonlinear two-process model (i.e. indicator of a scale-dependent process) and a linear model (i.e. indicator of a scale-independent process), respectively. In panel (b), grey and black circles represent values under and over the bout criterion, respectively. Two exponential distributions with exponents of 0.219 (red solid line) and 0.007 (red dotted line) were fitted for values under and over the bout criterion, respectively, to characterize a scale-dependent process. An exponential distribution with an exponent of 0.025 (blue dashed line) was fitted to all values to characterize a scale-independent process. Note that the nonlinear model (i.e. scale-dependent process) fitted better than the linear model (i.e. scale-independent process) with the frequency distributions.

(Figs 4 and S2), where the bout criterion (18.2 ± 2.9 m) matched with the spatial scale of large-VRS (18 ± 1 m) (Figs 1, 4, S1, and S2), showing a quantitative consistency between those two different measures (Sibly, Nott & Fletcher 1990; Bailleul, Lesage & Hammill 2010). Therefore, our results show that the 3D movements of seals was quantitatively characterized by the spatial scale of 18 m as a boundary of within-patch behaviour that allows seals to reduce the search area and risk moving outside of the profitable area. These results suggest that seals foraged on prey items that were connected to each other with distances shorter than 18 m and aggregated in patches, which were spatially segregated from each other over distances longer than 18 m and upwards of approximately 1200 m (Figs 2, 4 and S2).

Once seals entered a prey patch, they appeared to employ the second step of hierarchical movements (i.e. movements from large-scale patches to small-scale patches), which is supported by the two clear peaks in the variance of SFPT (Figs 1 and S1): large- and small-VRS with the scales of 18 ± 1 and 9 ± 1 m, respectively. Importantly, in our study, 95% of the small-VRS were nested within large-VRS, representing a nested VRS behaviour (Fig. 2). These results suggest that, once seals enter a large-scale patch, they use longer travel distances with lower turning frequencies (i.e. with larger net displacement within the large-scale patch) until they find a small-scale patch, within which they use shorter travel distances with higher turning frequencies (i.e. with smaller net displacement within the small-scale patch). Since higher turning frequencies likely induce higher

energetic costs (Wilson *et al.* 2013), seals are expected to employ small-scale movements only when they find more profitable small-scale patches, by following the hierarchical properties of prey distribution. Although there are potential sources of errors (especially substantial dynamic acceleration; Johnson & Tyack 2003) in the reconstruction of 3D dive paths during VRS using tri-axis accelerometer and tri-axis magnetometer, our simulation suggests that potential errors caused by substantial acceleration are likely to be less or slightly larger than 1.0 m during small- and large-VRS in distance travelled, respectively (see Text S1 and the accompanying supporting figures for more detail). Hence, the potential errors caused by substantial acceleration should not affect our results of the spatial scales of 3D movements of seals significantly.

VRS, PARTICULARLY NESTED VRS, IS LINKED TO ENHANCED FORAGING SUCCESS

If seals follow the hierarchical properties of prey distribution, we would expect that foraging success should be higher at the smaller scales of 3D movement, because prey density should be higher at the smaller scales in the hierarchical patch system (Fauchald 2009). Our expectation was supported because (i) most feeding events (approx. 80%) occurred in VRS zones although the total distance travelled during VRS accounted for only a small portion of the bottom phase of dives, (ii) nested VRS had higher feeding rates than non-nested VRS (Fig. 3a), and (iii) nested VRS were composed of small-VRS with higher feeding rates and large-VRS with lower feeding rates (Fig. 3b). These results demonstrate that seals enhanced foraging success as they searched for prey at smaller scales within a 3D environment. Our results are reasonable with respect to extra energetic costs of increased turning frequency for smaller-scale movements (Wilson *et al.* 2013), because higher foraging success at smaller scales could compensate for extra energetic costs of turning. Also, since previous theoretical and experimental studies showed good correspondence between the patterns of predators' movements and prey distribution (Fauchald 1999; Fauchald, Erikstad & Skarsfjord 2000; Benoit-Bird *et al.* 2013), our results suggest that seals forage on prey items that are distributed in hierarchical patch structures, characterized by high-density patches at small scales nested within low-density patches at larger scales (Fauchald 1999). Recent studies revealed that elephant seals primarily feed on mesopelagic fish (e.g. myctophids) (Naito *et al.* 2013; Guinet *et al.* 2014), and therefore, our results provide important implications for the distribution of mesopelagic fish, whose distribution pattern is hardly known, especially at smaller spatial scales (Irigoien *et al.* 2014). While we examined a small number of individuals, feeding rates during foraging dives of our three seals did not differ from 11 other seals that had mandible accelerometers (but not 3D data loggers) during the same post-breeding migration in 2012 and 2013 as our three seals (model selection using

AIC; see Fig. S3), suggesting that our study seals experienced the typical foraging conditions in those years.

One weakness of our study is that prey distribution and abundance are largely unknown where the northern elephant seals actually forage. Although prey distribution and abundance has been estimated in other animal systems with concurrent hydro-acoustic surveys in the coastal and shallow environments (c.f. Fauchald, Erikstad & Skarsfjord 2000; Benoit-Bird *et al.* 2013; Goldbogen *et al.* 2015), this is difficult in pelagic and deep environments where elephant seals forage. In the future, if we could observe local prey distribution patterns and changes in the patterns, we could investigate whether the scales of VRS change in response to changes in the local prey distribution. For example, we could test whether seals use different scales of VRS when foraging on solitary or schooling prey and whether the scales of VRS are flexible depending on prey distribution or fixed by innate characters.

Finally, since sensory capacity is a major factor that shapes the foraging behaviour of animals (Rice 1983), the scales of VRS should be closely related to the sensory ranges of elephant seals. In our study, all individuals exhibited peaks of SFPT values with similar scales of 9 ± 1 and 18 ± 1 m, which may imply a potential range of their sensory systems. Phocid seals seem to rely on their highly developed vibrissal system to follow hydrodynamic trails behind moving objects that have passed by at an earlier point in time (i.e. up to several tens of seconds: Hanke *et al.* 2013). Seals can also use visual cues to detect and locate prey items (Levenson & Schusterman 1997; Davis *et al.* 1999), which may specifically be important for elephant seals to forage on mesopelagic fish (e.g. myctophids) that emit bioluminescence (Vacqu  -Garcia *et al.* 2012). However, our understanding of hydrodynamic and visual perception in seals is mostly limited to laboratory experiments (Levenson & Schusterman 1997; Hanke *et al.* 2013), and little is known about how free-ranging seals actually use these sensory systems. Further investigations are needed to examine how sensory perception shapes the 3D movements and enhances the foraging success of marine animals.

In summary, we demonstrated that northern elephant seals employed scale-dependent, hierarchical 3D movements and provided the first empirical evidence that underwater fine-scale sinuous movements (i.e. VRS) are strongly linked to higher foraging success, particularly within nested VRS zones. These results suggest that seals employ hierarchical decision-making to enhance foraging success while searching for mesopelagic prey that appeared to be hierarchically structured in patches over a range of spatial scales. While we examined small number of individuals, our study is unique in quantifying the spatial scales of 3D search behaviour and foraging success in diving animals, indicating that scale-dependent processes are important components of the successful foraging behaviour although recent studies suggest that optimal searching behaviour would be scale-independent (e.g. L  vy walk) (e.g. Benhamou 2007; Sims *et al.* 2008; Humphries,

Weimerskirch & Sims 2013). We advocate the importance of reconstructing and quantifying 3D foraging behaviour to better understand the ways how marine predators make optimal decisions to enhance foraging success while exploring a 3D environment.

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Data accessibility

Data used in this study are present in the Supporting Information.

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Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Appendix S1. The data, including the number of feeding events, time spent within each VRS, VRS type and individual ID.

Fig. S1. Relative variance $S(r)$ in SFPT plotted against spatial scale for seals U627 and U954.

Fig. S2. Frequency distributions of the distances between consecutive feeding events for seals U627 and U954.

Fig. S3. Feeding rates per foraging dive for the three seals in this study in addition to 11 other seals.

Fig. S4. Frequency distributions of the deviation between two norms (i.e. Euclidean norm) of the tri-axis accelerometer vector (v_a) and gravity acceleration (g) during VRS.

Fig. S5. Illustration of spherical coordinate system.

Fig. S6. Potential errors in distance and directions travelled during small VRS.

Fig. S7. Potential errors in distance and directions travelled during large-VRS.

Table S1. Model selection table to test whether the log-transformed frequency distribution of the distances between feeding events follows a nonlinear two-process model or a linear model.

Text S1. Potential errors in the reconstruction of three-dimensional (3D) dive paths.