

## LETTERS

## Scaling laws of marine predator search behaviour

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Many free-ranging predators have to make foraging decisions with little, if any, knowledge of present resource distribution and availability<sup>1</sup>. The optimal search strategy they should use to maximize encounter rates with prey in heterogeneous natural environments remains a largely unresolved issue in ecology<sup>1–3</sup>. Lévy walks<sup>4</sup> are specialized random walks giving rise to fractal movement trajectories that may represent an optimal solution for searching complex landscapes<sup>5</sup>. However, the adaptive significance of this putative strategy in response to natural prey distributions remains untested<sup>6,7</sup>. Here we analyse over a million movement displacements recorded from animal-attached electronic tags to show that diverse marine predators—sharks, bony fishes, sea turtles and penguins—exhibit Lévy-walk-like behaviour close to a theoretical optimum<sup>2</sup>. Prey density distributions also display Lévy-like fractal patterns, suggesting response movements by predators to prey distributions. Simulations show that predators have higher encounter rates when adopting Lévy-type foraging in natural-like prey fields compared with purely random landscapes. This is consistent with the hypothesis that observed search patterns are adapted to observed statistical patterns of the landscape. This may explain why Lévy-like behaviour seems to be widespread among diverse organisms<sup>3</sup>, from microbes<sup>8</sup> to humans<sup>9</sup>, as a ‘rule’ that evolved in response to patchy resource distributions.

Predators can sometimes fine-tune their foraging by using sensory information of resource abundance and distribution at near-distance scales dominated by proximal clues<sup>10</sup>, and at very broad scales some may have awareness of seasonal and geographical prey distributions<sup>11</sup>. However, across the broad range of mesoscale boundaries (a few to hundreds of kilometres), the necessary spatial knowledge required for successful foraging will depend largely on the search strategy used. Over these scales some predators are more like probabilistic or ‘blind’ hunters than deterministic foragers. Fully aquatic marine vertebrates that feed on ephemeral resources like zooplankton and small pelagic fish typify this type of predator because they have sensory detection ranges limited by the seawater medium and experience extreme variability in food supply<sup>7,10–12</sup> over a broad range of spatio-temporal scales<sup>13–15</sup>.

Probabilistic search patterns described by a category of random-walk models known as Lévy walks<sup>4</sup> appear to describe foraging movements of some species<sup>3</sup>. These specialized random walks have super-diffusive properties comprising ‘walk clusters’ of short

move step lengths (distance moved per unit time) with longer re-orientation jumps between them. This pattern is repeated across all scales, with the resultant scale-invariant clusters creating trajectories with fractal patterns<sup>3</sup>. Lévy-walk move steps are drawn from a probability distribution with a power-law tail:  $P(l_j) \sim l_j^{-\mu}$ , with  $1 < \mu \leq 3$ , where  $l_j$  is the move-step length and  $\mu$  is the power-law (Lévy) exponent (here ‘ $\sim$ ’ means ‘distributed as’). Theoretical studies<sup>2,3,16</sup> show that Lévy walks and Lévy flights (the turning points in a Lévy walk<sup>4</sup>) across random prey distributions increase new-patch encounter probability compared with simple brownian motion, with an optimal search having an exponent  $\mu \cong 2$ . Recent studies<sup>17–19</sup> contend that Lévy walks or flights have been wrongly ascribed to some species through use of incorrect methods, while others indicate Lévy-like behaviour with optimal power-law exponents<sup>3,20,21</sup> for highest-efficiency searches, supporting the hypothesis that Lévy behaviour may represent an evolutionary optimal value of the Lévy exponent<sup>3,5,22</sup>.

We hypothesized that fully aquatic (non-aerial) marine predators should adopt a movement (search) strategy that optimises prey-patch encounter rates, thus conferring an advantage when foraging within naturally non-random prey distributions<sup>13–15</sup>. Long-term movements of large marine predators can be recorded accurately at fine temporal resolution (seconds) for long periods (months) using electronic data-logging tags<sup>23</sup>. In the largest such analysis yet attempted, we collated the vertical movements resulting from recorded diving activity within the foraging range of seven large vertebrate species that feed on patchily distributed prey (for example, zooplankton, small fish) (see Methods). Numerous investigations have tracked a predator’s horizontal movements but none have studied vertical movements for which the same considerations of ‘blind’ hunting probably hold over much shorter vertical spatial scales (tens of metres), particularly outside the well-lit near-surface zones<sup>24</sup>. We analysed a total of 1,209,088 vertical move steps for 31 individual predators from seven species and found that the large-scale structure of vertical movement was similar for the majority of species (Fig. 1). Model fits to move-step-length frequency distributions for five species across diverse taxa (shark, teleosts, sea turtle, penguin) closely resembled an inverse-square power law<sup>25</sup> with a heavy tail of increasingly longer steps intermittently distributed within the time series that is typical of ideal Lévy walks<sup>3,4</sup> (Fig. 1; Supplementary Information). Lévy exponents derived from

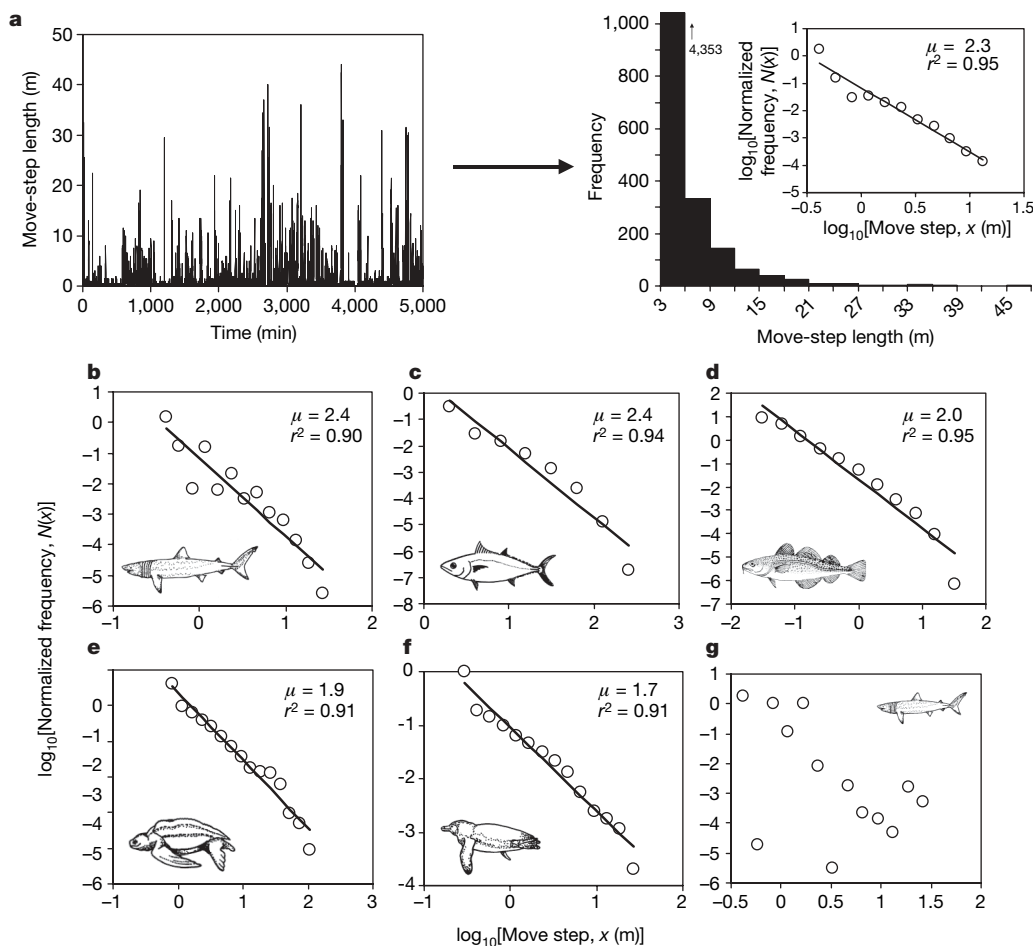
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Lévy-like move-step-length frequency distributions for the five species were maintained for individuals, and it is striking that they were close to a theoretically optimal  $\mu \approx 2$  exponent ( $\bar{\mu} \pm \text{s.d.} = 2.12 \pm 0.31$ ,  $n = 24$ ; species range:  $1.34 \leq \mu \leq 2.91$ ) (Fig. 1; Supplementary Information). Relative likelihood estimates of model fits to the move-step-length frequency distributions for all species supported only an exponential function typifying random motion for two species (catshark, elephant seal), confirming that Lévy-like processes may not predominate within vertical search strategies in all species (see Supplementary Information).

To test for the presence of long-term correlations that also characterize scale-invariant Lévy walks<sup>3</sup>, we used the root-mean-square fluctuation of the displacement,  $F(t)$ , in each time series. Uncorrelated time series arise from uncorrelated random walks for which  $\alpha = 0.5$  for the relationship  $F(t) \sim t^\alpha$  (ref. 26); in contrast, weighted means of  $\alpha$  for each species tested here were between 0.80 and 1.24 ( $\bar{\alpha} \pm \text{s.d.} = 1.08 \pm 0.17$ ,  $n = 5$ ), confirming the presence of long-range correlations in diving time series across the five species (Supplementary Information). The scaling exponent  $\beta$  of the sum of the spectra against frequency in the dive time series was 0.8 in the low-frequency regime, also consistent with long-range correlations

in scale-invariant systems<sup>26</sup> because  $\beta \approx 0$  when behaviour is temporally uncorrelated (Supplementary Information). We considered vertical foraging movements only in one dimension (depth) through time (that is, the total dimensionality is two dimensional, 2D), so we were unable to determine randomness in turning angles which would further confirm the existence of Lévy-like motion<sup>21</sup> over the full range of underwater movements; however, considering the data as 2D projections of three-dimensional (3D) movements presents no obstacle to their statistical treatment. The projection of spatially homogeneous 3D Lévy movements into 2D preserves the power-law relationship with an unchanged exponent at all length scales greater than the minimum move step of the original 3D trajectory. This invariance under projection does not hold for other move-step distributions (Supplementary Information). The Lévy-like vertical movements described here, therefore, reflect the more complex 3D movements made by a range of phylogenetically distinct marine vertebrate species, implying that Lévy-like walks may be a common strategy employed by open-ocean foragers.

Lévy-walk-like behaviour of foragers may show mechanistic links with natural prey fields if the search pattern emerges from the underlying pattern of food distribution<sup>20</sup>, or if the strategy evolved to

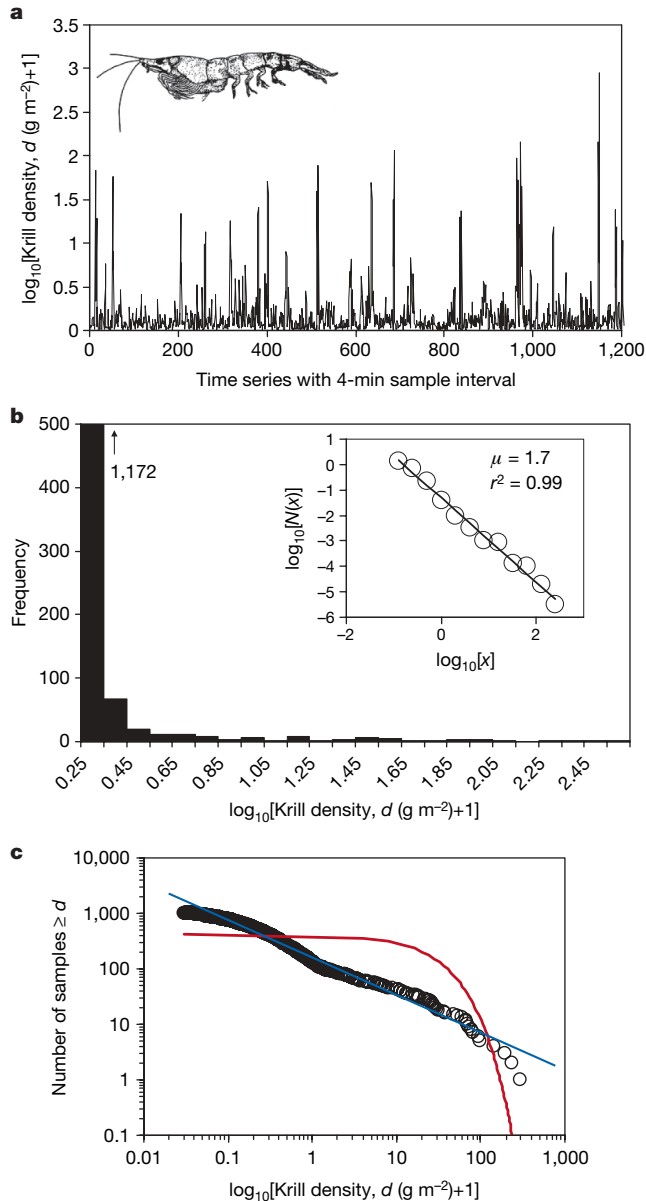


**Figure 1 | Lévy-like scaling law among diverse marine vertebrates.**

**a**, Movement time series recorded by electronic tags were analysed to determine the Lévy exponent to the heavy-tailed power-law distribution. Left, time series of vertical move (dive) steps ( $n = 5,000$ ) of an individual basking shark (*Cetorhinus maximus*) over 3.5 days, showing an intermittent structure of longer steps. Right, the move-step-length frequency distribution for the same data. Inset, the normalized log-log plot of move-step frequency versus move-step length, giving an exponent  $\mu$  within ideal Lévy limits ( $\mu = 2.3$ ). The Lévy exponent is conserved across longer temporal scales, for example, expanding the time series for this individual to 30 days ( $n = 43,200$  steps) maintains  $\mu = 2.3$  (data not shown), indicating scale-invariance in move-step distribution. **b–g**, Normalized log-log plots of the move-step

frequency distributions for: **b**, sub-adult and adult basking shark ( $n = 503,447$  move steps); **c**, bigeye tuna (*Thunnus obesus*) ( $n = 222,282$  steps); **d**, Atlantic cod (*Gadus morhua*) ( $n = 94,314$  steps); **e**, leatherback turtle (*Dermodochelys coriacea*) ( $n = 4,393$  steps); and **f**, Magellanic penguin (*Spheniscus magellanicus*) ( $n = 9,727$  steps). Lévy exponents were maintained at the individual level for 24 sub-adult and adult animals (see Supplementary Information). **g**, Normalized log-log plot of move-step-length frequency distribution for a 2.5-m-long, <1-year-old basking shark showing nonlinear form. Relative likelihood model fits to rank-frequency plots for the five species also indicated that move-step distributions were Lévy-like and not purely random (Supplementary Information).

enhance foraging success in particular prey distributions. To examine these contrasting hypotheses we analysed the structure of two different prey fields (krill, total zooplankton) consumed by some predators considered here (planktivorous shark, penguin). Krill (*Euphausia superba*) densities occurring horizontally in a current passing a moored echosounder<sup>27</sup> were measured throughout the 200m water column at consecutive, equally spaced time intervals. Krill densities showed extreme variance in amplitude through time, with an intermittent structure of large ‘jumps’ (Fig. 2a). The frequency distribution of krill density changes also closely resembled a power law



**Figure 2 | Macroscopic properties of a prey field.** **a**, Krill (*Euphausia superba*) density  $d$  (in  $\text{g m}^{-2}$ ) ( $n = 1,215$  samples) occurring horizontally and integrated vertically within the current flowing past a moored, upward-looking echosounder off South Georgia. **b**, The move-step frequency distribution of krill density follows a heavy-tailed power law reminiscent of those obtained for Lévy-walk-like predators, and as for the predators, it shows an exponent within Lévy limits and close to the optimum  $\mu \approx 2$ . **c**, Cumulative distribution or rank-frequency plot<sup>17</sup> of krill density change showing a straight-line form consistent with power-law-like and Lévy-like processes. This plot gives a Lévy exponent of 1.64. The relative likelihood model fit to the rank-frequency plot also indicated that the density-change distribution was Lévy-like and not purely random (see Supplementary Information).

with a heavy tail, giving a Lévy exponent of 1.7 (Fig. 2b, c). Root-mean-square fluctuations gave  $\alpha = 0.9$  for krill and spectral analysis revealed low-frequency changes at  $\beta = 0.3$  (Supplementary Information). Similar results were found for the zooplankton time series ( $\mu = 1.8$  and  $2.0$ ,  $\alpha = 0.9$ ; Supplementary Information). Therefore, the presence of long-range correlations and scale invariance in the spatial changes in prey density are properties in common with marine predator movements. The Lévy exponents describing the slopes of the power-law-like distributions were also similar, as were frequency spectra of predator movements and prey distribution. The similarity of Lévy exponents and frequency spectra between predator movements and prey distributions does not necessarily prove the existence of a mechanistic link between a predator’s foraging movement response and natural prey assemblages, but the close resemblance does indicate that Lévy properties (describing fractal processes) underlie both predator movements and prey distribution. Thus, for these specific ecological cases, the exponent of the searcher may represent an optimization to the heterogeneous prey fields demonstrating fractal properties.

There are, however, two competing hypotheses to explain the predator–prey interactions we propose: (1) animal search patterns are adapted stochastically to their prey field structures because their environment is so heterogeneous (predators actively search following rules of optimality), or (2) apparently ‘optimal’ search patterns may arise simply as a function of the underlying distribution of the prey field (a predator’s patterns are a by-product of the prey distribution it encounters). The results of a recent modelling study<sup>20</sup> support the latter explanation by showing that scale-free foraging patterns (Lévy walks) emerge from the interaction of animals with a particular resource distribution. Likewise, field observations of primates moving between fruiting trees fit the expected pattern probably because primates possess complex mental maps of resource location; hence, the underlying resource landscape determines the distribution of move steps<sup>20</sup>. However, this process is unlikely to account for the move-step distributions of marine species we measured because they have an incomplete knowledge of resource location. First, behavioural kineses to prey are limited to relatively small vertical distances in the ocean<sup>24</sup>, so when threshold prey densities are reached, a predator should initiate searches aimed at traversing distances exceeding the sensory detection range<sup>2,7,10</sup>. Second, strict fidelity of a marine predator to small target locations (analogous to the trees visited by primates) will be ineffective because locations of prey such as zooplankton, squid and shoaling fish often change rapidly and dynamically across a range of spatio-temporal scales<sup>7,10,14</sup>. So our empirical results favour the first explanation—predators feeding on patchy, heterogeneous prey should adapt the best probabilistic search strategy given that they are essentially ‘blind’ hunters at the spatial and temporal scales over which they typically forage. This conclusion regarding adaptation is strengthened by the vertical move-step-length frequency distribution of a 2.5-m-long, <1-year-old basking shark that we tracked for 7 months that did not conform to Lévy-like behaviour (Fig. 1g). We suggest that this striking difference in search pattern from those of mature individuals reflects ontogenetic behavioural development<sup>28</sup>, that is, juveniles learn about the underlying structure of prey distributions as they gain foraging experience.

Further support for the hypothesis that movement processes are linked to prey distributions could be inferred if there were an advantage to predators adopting Lévy walks in fractal landscapes compared to other distribution types. For a particular search strategy to evolve, it must confer an advantage in terms of higher fitness resulting from greater efficiency in energy acquisition<sup>29</sup>. To test this, we investigated the foraging success (total energy acquisition) of a Lévy searcher adapted to a natural-like, fractal prey field by simulating a Lévy-walk predator’s vertical diving movements within a virtual prey field defined by either a Lévy or random distribution. Lévy searches ( $\mu = 2.0$ ) reflecting marine predator



**Table 1 | Comparison of foraging success for simulated searchers**

Ratio	Mean foraging success (% difference)	Standard error of the mean
LL:LR	14.47	2.49
RL:RR	-0.52	0.73
RL:LL	-10.89	1.32

See text for explanation of the ratio and Supplementary Information for further details of simulation results. The mean foraging success ratio was calculated from ten replicate simulation sets, with each replicate comprising three runs of each forager type per prey field type, with each run estimating foraging success (prey encountered per distance moved) for each of 100,000 foragers. Hence, each pair of sets making up a replicate summarized searching by 600,000 foragers.

movements within Lévy (fractal)-distributed prey fields (LL, denoting a Lévy searcher in a Lévy prey field) were compared with encounter rates in ordinary, random prey fields (LR) (defined as a prey distribution resulting from a homogeneous spatial Poisson point process) (see Methods). Our expectation was that the foraging success ratio LL:LR should not deviate substantially from 1.0 (zero difference) if adapting to a fractal prey field presents no particular foraging advantage to a Lévy searcher. However, the LL:LR ratio always exceeded 1.0, and LL was 14% higher on average than LR (Table 1), which thus supports the optimality hypothesis. We next compared random with Lévy searchers in fractal fields (RL, denoting a random searcher in a Lévy prey field) and found that the RL:LL ratio, by contrast, showed a negative foraging gain (-10%), whereas comparing RL with a random forager in a random field (RR) indicated similar levels of search performance (RL:RR  $\cong$  1.0; Table 1 and Supplementary Information). These results are consistent with the hypothesis that Lévy-like searches may represent an adaptation to complex prey distributions by evolving optimal search strategies.

Our findings indicate that animals in stochastic environments necessitating probabilistic foraging may derive benefits from adapting movements described by Lévy processes. Lévy models express behavioural minimalism<sup>3</sup>, so not all movements made by marine vertebrates and other animals will be associated with optimal foraging (for example, resting, breeding and migration) and, in addition, it is unlikely that animals search with Lévy-like motion at all times, especially if, for some species, foraging decisions are predominantly deterministic within stable environments. However, evidence that Lévy-walk search patterns apply to a diverse range of taxa<sup>3,8,9,21</sup>, together with our results, suggest that foragers are adapted to optimal behaviour in complex landscapes. Hence, Lévy-like walks may be useful for developing more realistic models of how animals redistribute themselves in response to shifting resources as a consequence of climate change, fisheries extractions and other habitat modifications<sup>30</sup>. Such general and simple laws of movement as optimal Lévy walks could prove useful in robotics—for example, in an algorithm controlling the movements of autonomous robots designed to sample optimally in hostile and heterogeneous environments such as the deep sea, active volcanoes or on other planets.

## METHODS SUMMARY

**Electronic tagging.** Pressure (depth)-sensitive data-logging tags were attached to basking sharks *Cetorhinus maximus* ( $n = 6$  individuals) and small spotted catshark *Scyliorhinus canicula* ( $n = 3$ ) in the northeast Atlantic Ocean, bigeye tuna *Thunnus obesus* ( $n = 3$ ) in the North Pacific near Hawaii, Atlantic cod *Gadus morhua* ( $n = 5$ ) in the North Sea, leatherback turtles *Dermochelys coriacea* ( $n = 4$ ) in the Atlantic Ocean, Magellanic penguins *Spheniscus magellanicus* ( $n = 7$ ) off Patagonia, Argentina, and southern elephant seals *Mirounga leonina* ( $n = 3$ ) in the Pacific sector of the Southern Ocean. Full details of deployments, animal body sizes, tag types and data sources are given in Supplementary Table 1.

**Prey sampling.** Antarctic krill (*Euphausia superba*) in the top 200 m were detected at 4-min intervals within the current flowing past a moored, upward-looking data-logging echosounder at South Georgia, South Atlantic Ocean<sup>27</sup>. Logged data were processed to provide a prey-field time series of horizontal changes in krill density at a point location integrated vertically in the water

column, and scaled to account for variable current flow over time. Two zooplankton time series were also analysed (see Supplementary Information).

**Simulation program.** The purpose of simulating searches was to test the hypothesis that foraging success (biomass consumed per distance moved) by optimal Lévy walkers ( $\mu_{\text{opt}} = 2.0$ ) in fractal (natural) prey distributions exceeded prey acquisition rates within random prey fields. We developed a simulation where vertical trajectories ( $y$ , time) of Lévy foragers were routed through seascapes with heterogeneous prey patches distributed according to Lévy (describing fractal processes) or random distributions. This simulated a predator searching vertically for patchy resources.

**Full Methods** and any associated references are available in the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

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**Supplementary Information** is linked to the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

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**Author Contributions** D.W.S. conceived and planned the study, led the data analysis and wrote the manuscript. All co-authors contributed to subsequent drafts. Field data of animal movements and/or prey distributions were collected by D.W.S., E.J.S., J.D.M., G.C.H., C.J.A.B., A.S.B., M.A.H., D.M., M.K.M., D.R., V.J.W. and R.P.W. The simulation model was conceived by N.E.H. and D.W.S. with N.E.H. writing the programming code. J.W.P. and A.J. were responsible for analysis of projections of 3D Lévy movements, M.Z.A. and E.L.C.S. coded the power spectrum analysis, C.J.A.B. completed the relative likelihood modelling, and G.C.H. and M.J.W. provided additional data analysis.

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## METHODS

**Movement analysis.** For predatory fish movements (sharks, tunas, cod), the change in selected water-column depth between consecutive time intervals,  $u(t)$ , was calculated to derive a time series of vertical displacement (move) steps for each individual. For air-breathers (turtles, penguins, seals) the change in chosen maximum depth between successive dives in single foraging trips,  $u(t)$ , was used as a proxy for searching to remove the anomalous effect on the move-step-length frequency distribution caused by necessity of leaving and returning to the surface to breathe air. Time series of chosen depth changes represent short-term search decisions of predators extending across long temporal scales, enabling robust analysis of macroscopic properties<sup>3,17</sup>. Each entry in the time series  $u(t)$  is a vertical step in metres, with time measured in minutes for fish ( $t = 1, 2 \dots t_{\max}$ ) and relative elapsed time for air-breathers ( $t_1 = d_1, t_2 = d_2 \dots t_{\max} = d_x$  where  $d$  is a dive number in the series). Elapsed time was used because breathing-corrected steps traversed boundaries of fixed time intervals and was justified because animals dived continuously and variation in dive duration was relatively small within individuals. We calculated<sup>26</sup> the net displacement  $y(t)$  of each time series  $u(t)$  defined by the running sum  $y(t) \equiv \sum_{i=1}^t u(i)$  and determined the root-mean-square fluctuation of the displacement  $F(t) \equiv \sqrt{\langle (\Delta y(t))^2 \rangle - \langle \Delta y(t) \rangle^2}$  where  $\Delta y(t) \equiv y(t_0 + t) - y(t_0)$ . For power spectrum analysis<sup>31</sup> of leatherback turtle, krill and zooplankton time series, we calculated the sum of power spectra  $S(f)$  plotted against the period  $1/f$ . Histogram plots of power laws were calculated using logarithmically increasing move-step-length bins, with each bin width  $k$  (for example, 1, 2, 3...) increasing by  $2^k$  (for example, 2, 4, 8...). The frequency per logarithmic bin was normalized by dividing by total frequency  $N$  and bin width to obtain the probability density of each bin<sup>17</sup>. Relative likelihoods of models fitted to rank-frequency plots were compared using Akaike's and Bayesian Information Criterion weights (see Supplementary Information).

**Optimal foraging simulation.** A prey patch generator (see below) is used to create  $n$  unique, randomly generated variable density patches which are then 'pasted' into a 2D seascape following either a Lévy or random distribution. The initial patch is positioned using a uniform random number generator. For a random patch distribution, the relative position of the second patch ( $dx, dy$ ) is again calculated using a uniform distribution. For a Lévy patch distribution the direct distance to the second patch is calculated using a Lévy random number generator (see below) with a uniform distribution giving the angle between the two patches. Patches are thereafter positioned iteratively, with the position of the next patch based on the position of the current patch until the desired number of patches has been created. The seascape is treated as a torus; if positions exceed the preset dimensions of  $2,500 \times 5,000$  it wraps around from top to bottom and left to right. Spacing patches by distances (step lengths) drawn from a Lévy distribution yielded an underlying pattern congruent with the spatial density of patches (see Supplementary Information).

A single foraging run though the prey field starts at a random depth on one side ( $x = 0$ ) and proceeds to the other side ( $x = 5,000$ ) in a series of horizontal steps of fixed distance (in this case 1, giving 5,000 steps per foraging run). The vertical displacement at each time step is generated from either a uniform

distribution or from the Lévy random number generator. The resulting diagonal path is traversed by calculating an interpolated movement such that every cell along the path is visited by the forager. Prey biomass (density values) encountered in each grid cell are accumulated to give total biomass consumed for the foraging run.

**Prey patch generator.** The purpose of the prey patch generator is simply to generate a quasi-realistic patch rather than a square block of uniform density. A prey patch (for example, zooplankton patch) of a specified area in a 2D grid of size  $100 \times 100$  is created. The patch is created by building up a number of superimposed random walks over this grid until the specified number of grid cells has been occupied. The length of each random walk,  $L$ , is computed as the square root of the required patch area and each walk begins at the approximate centre of the grid (50, 50). This first cell is given the value  $L$ , the second  $L - 1$ , until the final cell has value 1. Grid cells reached that are already occupied are not renumbered; however, the step is still counted so that some random walks will occupy no new grid cells and cells at the edge of the growing patch will always have low density values. Random walks are repeated, building up the patch, until the required number of grid cells have been filled (that is, the required patch area has been achieved). Each completed patch is then pasted into the simulation seascape as described above.

**Lévy random number generator.** The Lévy random number generator returns an integer value between 1 and a specified maximum value, with a probability density that approximates to the power distribution  $P(n) \sim n^{-\mu}$ , where  $P$  represents the probability of the value  $n$  being returned by the random number generator and  $\mu = 2.0$  (to reflect the theoretical optimal Lévy exponent<sup>5</sup>). An integer array is generated, with each element taking a value between 1 and  $n$  (where  $n$  is the specified maximum value) such that the proportion of array elements populated by any given value is equal to the probability of that value arising from the power function. For example, if the generator has to return a maximum value of 1,000 then the array is created such that the value 1 will occupy 1,000,000 array elements, the value 2 will occupy 250,000 elements, and so on, until the value 1,000, which will occupy 1 array element:  $P(1,000) = 0.000001$ . When the generator is called to provide a uniform random number, a uniform random number generator is used to select an array element and the value of that element is returned as the Lévy random number. In the simulation, a maximum of 2,500 (the modelled depth of the sea, in metres) is used.

Theoretically, the power function should allow some rare large values to occur. Such steps are meaningless in the context of this study of vertical movements; they would take the virtual forager outside the limits of the seascape or, in the case of air breathers, beyond their physiological diving limits. When large values occur in the simulations, they are simply wrapped around (as with the prey patch generator). This method allows fast random number generation that can be done on PC platforms, but a necessary consequence is that the lack of some rare large value causes the generator to return values in a distribution nearer to  $\mu = 1.95$  than to  $\mu = 2.0$ .

31. Chatfield, C. *The Analysis of Time Series* 6th edn (Chapman & Hall, London, 1996).