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Mesoscale activity facilitates energy gain in a top predator

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How animal movement decisions interact with the distribution of resources to shape individual performance is a key question in ecology. However, links between spatial and behavioural ecology and fitness consequences are poorly understood because the outcomes of individual resource selection decisions, such as energy intake, are rarely measured. In the open ocean, mesoscale features (approx. 10–100 km) such as fronts and eddies can aggregate prey and thereby drive the distribution of foraging vertebrates through bottom-up biophysical coupling. These productive features are known to attract predators, yet their role in facilitating energy transfer to top-level consumers is opaque. We investigated the use of mesoscale features by migrating northern elephant seals and quantified the corresponding energetic gains from the seals' foraging patterns at a daily resolution. Migrating elephant seals modified their diving behaviour and selected for mesoscale features when foraging. Daily energy gain increased significantly with increasing mesoscale activity, indicating that the physical environment can influence predator fitness at fine temporal scales. Results show that areas of high mesoscale activity not only attract top predators as foraging hotspots, but also lead to increased energy transfer across trophic levels. Our study provides evidence that the physical environment is an important factor in controlling energy flow to top predators by setting the stage for variation in resource availability. Such understanding is critical for assessing how changes in the environment and resource distribution will affect individual fitness and food web dynamics.

1. Introduction

Understanding how foraging animals interact with the physical environment and thereby how spatial heterogeneity in the environment shapes individual performance and population dynamics are key goals in ecology [1–3]. Heterogeneity in the physical environment shapes ecological processes at multiple levels of organization [4], from structuring resource distribution [4] to species' abundances and distributions [5,6] to community composition [7]. The physical environment also influences trophic interactions, for example, by concentrating prey [8–10] or by enhancing predator foraging success [11]. However, knowledge on the linkages between the physical environment, behavioural ecology and individual fitness consequences is limited because the outcomes of individual movement decisions, such as energy intake, are difficult to measure in free-ranging animals [12,13].

Optimal foraging theory provides a theoretical framework for establishing these linkages, with the expectation that animals will make movement decisions and select resources that maximize their fitness gains through net energy intake [14–16]. Analysis of resource selection, i.e. the process by which animals choose to use certain resources (most commonly foods or habitats) over others, can improve understanding of how animals meet their survival

requirements [17,18]. Empirical studies typically integrate measures of individual performance in relation to movement and resource selection over broad time- and spatial scales [12], such as relating lifetime fitness to home range selection [19]. These connections are important but preclude a more mechanistic understanding of environment–performance relationships that require matching fine-scale movement decisions and selection of specific environmental features to their immediate energetic outcomes.

Assessing environment–performance relationships for wide-ranging species is particularly challenging. Such efforts require simultaneous data on animal movements via tracking technology, behavioural partitioning (e.g. foraging and transit), environmental variables at relevant spatio-temporal scales and resource acquisition and/or changes in body condition. This challenge is nowhere more apparent than in the vast and dynamic environment of the open ocean [3]. Ocean habitats may change on a scale of hours to days or weeks [20]. Here, Lagrangian coherent structures, which identify convergent mesoscale features like fronts, eddies and filaments of the order of 10–100 km, have significant biological importance as predictable foraging habitat for a wide range of trophic levels [21–23]. Such features aggregate primary producers [24,25] and consumers [8,26,27], driving vertebrate distributions through bottom-up processes [8,9,28,29]. While it has been shown that highly migratory top predators such as seabirds and marine mammals co-localize with Lagrangian coherent structures when foraging [21,23,30–32], likely deriving energetic benefits, a relationship between mesoscale features and actual energy gain in a top predator has yet to be documented.

We investigated the energetic outcomes of resource selection patterns of a migratory top predator in the open ocean. We used satellite tag data and concurrent three-dimensional dive data of northern elephant seals (*Mirounga angustirostris*) in the Pacific Ocean to identify foraging behaviour and determine potential selection of Lagrangian coherent structures. Elephant seals are a particularly appropriate species for this investigation because as capital breeders, their foraging behaviour is not constrained by the need to return to shore to feed their pups [33]. This allows them to forage over the entire northeast Pacific Ocean, following prey resources wherever they may reside [34]. As the geographical scale of inquiry can affect inference on how animals use resources, we examined selection of Lagrangian coherent structures for foraging behaviour at two hierarchical spatial scales. We followed Johnson's [18] definition of four orders of selection that species exhibit: (i) selection of a geographical range, (ii) selection of a home or subpopulation range within the geographical range, (iii) selection of habitats or regions of use within the home or subpopulation range and (iv) selection of specific sites or resources within the habitat area [18]. We specifically investigated third-order selection (i.e. selection of habitat areas with high mesoscale activity within the home or subpopulation range) and fourth-order selection (i.e. selection of Lagrangian coherent structures within a habitat area). We further investigated whether seals modulated their dive behaviour in relation to Lagrangian coherent structures. Finally, we applied a hierarchical Bayesian state-space model estimating individual fat content [35] at a daily resolution to quantify the influence of mesoscale features on net daily energy gain.

2. Material and methods

(a) Movement and body condition data

As part of a long-term monitoring effort, 213 adult female northern elephant seals were randomly selected from the population at Año Nuevo state reserve, CA, USA (37°5′ N, 122°16′ W) between 2004 and 2015 and tagged with satellite tracking units prior to their eight-month post-moulting migrations. Female elephant seals make two foraging migrations each year. A shorter February–May migration begins when females wean their pup, and ends when the female returns to the colony to moult. Upon completion of the moult, the female begins the longer post-moulting migration June–January, which ends when the female returns to the colony to give birth [34]. During these long migrations, female northern elephant seals travel thousands of kilometres to forage in productive pelagic waters in the central North Pacific Ocean, feeding on small (10–20 g) mesopelagic prey [36]. The amount of energy individual females gain over the post-moulting migration period is a strong predictor of their reproductive success [34,37]. GPS- or ARGOS-linked technologies were used to track movements, yielding hourly position estimates post-processing (electronic supplementary material, appendix S1). For ARGOS tags, which comprised the majority of tagging units, tracks were filtered for errors and smoothed using a state space model ('CRAWL' package [38] in R 3.1.1 (R Core Team 2013); see Robinson *et al.* [34] for details).

Individuals were also fitted with time–depth recorders (TDRs) to record diving behaviour. We excluded individuals with TDR failure or incomplete tracks, resulting in 142 individuals included in our analyses with 1 799 693 recorded dives. Based on dive parameters, including maximum depth, dive duration and bottom time, dives were classified into one of four dive types using a forced-choice classification programme: active-bottom (pelagic foraging in which dives are characterized by vertical prey-pursuit excursions at depth), flat-bottom (benthic foraging), drift (food-processing/rest) or v-shape (transit) [34,39]. Fifty per cent of recorded dives were classified as foraging, 31% as transit, 13% as drift and 6% as benthic. As stomach temperature records found that 74% of feeding events were associated with active-bottom foraging dives as opposed to other dive types [40], we used foraging dives as a proxy for feeding behaviour.

To link resource selection to energy gain in individual seals, we used published estimates of absolute lipid content in 29 individuals within the same dataset [35]. Daily lipid stores and lipid gain/loss were estimated from a hierarchical Bayesian state–space model that linked observations of daily drift rate (m s^{-1}) to lipid content (kg). This model has been previously described and validated by Schick *et al.* [35] and is summarized in electronic supplementary material, appendix S2. Briefly, lipid estimates were based on daily drift rates and calibrated to mass and absolute lipid measurements taken in the field before and after each migration. Changes in the rate of passive drifting during dives are used to estimate changes in at-sea body condition in northern [35,41,42] and southern elephant seals [43–45]. This is because the buoyancy of elephant seals, as measured by their drift rate, is chiefly determined by their relative amounts of lipid and lean tissue, providing a means to quantify relative fat content [43]. To account for uncertainty in both the observed drift rates and the lipid gain process, the state-space model used two re-parametrized normal distributions (see electronic supplementary material, appendix S2; [35]). The model produced daily lipid estimates for each individual with small standard errors relative to the means (mean daily lipid estimate = 137.4 ± 8.6 kg). Model results were also validated using an alternative method on a portion of the same dataset, yielding comparable results [46]. Daily lipid gain was matched with mean daily position ($N = 224 ± 5$ days per
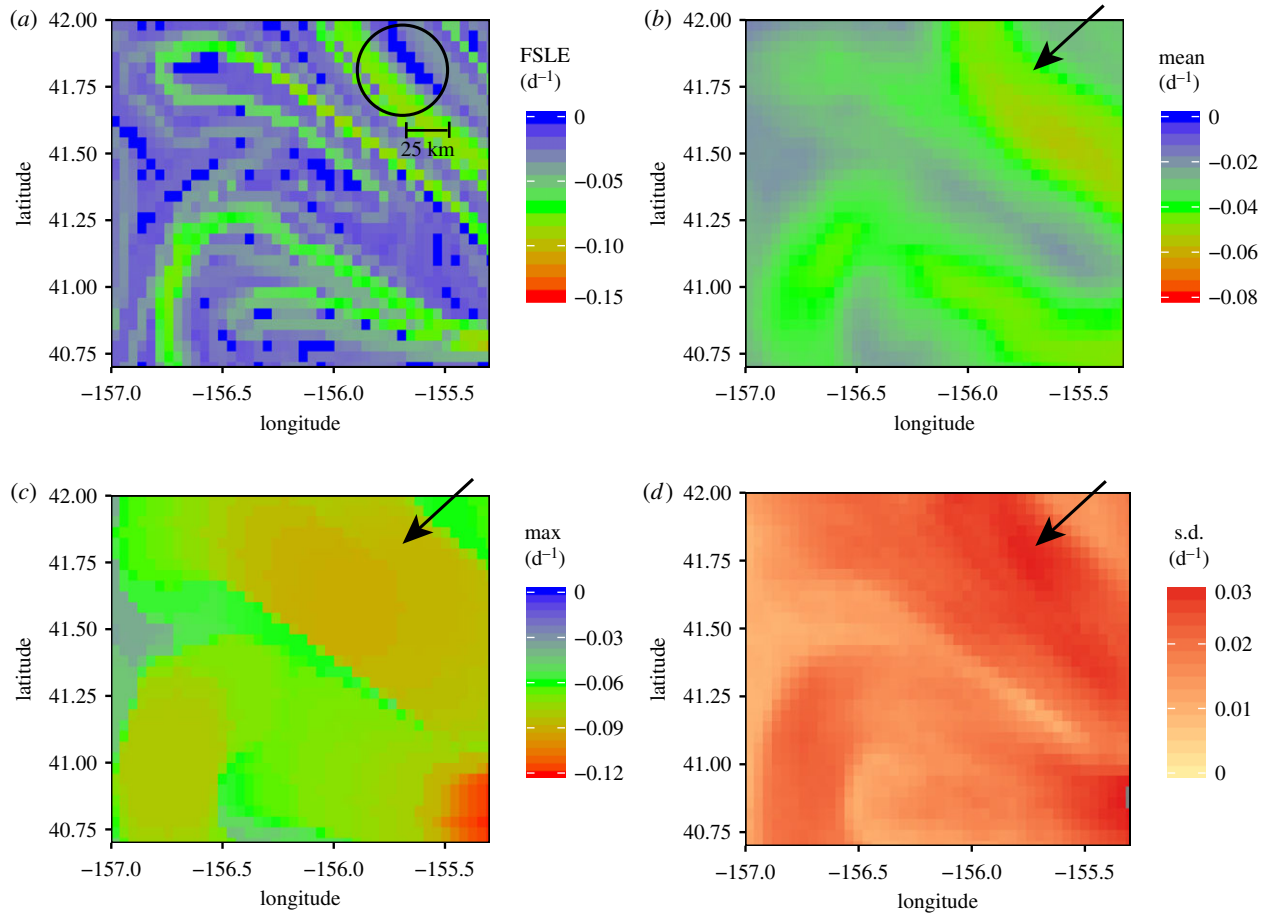
Figure 1. Lagrangian coherent structures such as mesoscale fronts, eddies and filaments are identified as linear ridges of high absolute values in FSLE fields (*a*). Relationships between point FSLE values (*a*) and spatial mean (*b*), maximum (*c*) and standard deviation (*d*) values within a 25 km (5 pixel) radius denoted by the top left circle are demonstrated in the additional panels. The centre of the circle is highlighted in the mean, maximum and standard deviation panels with arrows.

individual) in order to relate fat gain to oceanographic features [35,44]; as a second measure, we related lipid gain to the mean of environmental variables extracted for all dives per day and checked for the effects on lipid gain at a weekly timescale.

To focus analyses on the period of migration when most foraging (as opposed to directed transit) occurs, we constrained analyses in each year to the month of September. September is the midpoint of the post-moult migration period and contained the greatest number of dive events (266 561 total dives). We validated that foraging behaviour across the population is concentrated in September using three additional metrics: first passage time, rate of lipid gain and number of foraging dives per day (electronic supplementary material, appendix S3).

(b) Mesoscale features

A powerful Lagrangian technique, the finite-size Lyapunov exponent (FSLE), can identify Lagrangian coherent structures from remote sensing by measuring the rate of separation or convergence of water particles [47–49]. The FSLE is commonly used to detect fluid mixing, transport barriers and frontal activity [47–49]. Backward-in-time FSLE identifies convergent features, including density fronts and eddy-edges, whereas forward-in-time FSLE can identify regions of water mass divergence. Lagrangian coherent structures are highlighted as linear ridges of high absolute values in FSLE fields (figure 1) and are defined as absolute FSLE values of greater than 0.1 [21]. We used AVISO backward-in-time FSLE fields (www.aviso.altimetry.fr/en/data/products/value-added-products/fsle-finite-size-190lyapunov-exponents.html) [48,50]. This AVISO product, following the methodology of d'Ovidio *et al.* [48], is derived from SSALTO/Duacs global ocean absolute geostrophic velocities

(DUACS2014 DT MADT UV, 2016 version), which have a spatial resolution of 0.25° and integrate measurements from multiple altimetry sensors taken over approximately 10 days [51]. AVISO FSLE fields have a 0.04° (approx. 5 km) spatial resolution and a 4-day temporal resolution, the finest currently available over the broad spatial extent of the Pacific Basin. Because small-scale details of the velocity field are not significant for the dynamics of Lagrangian coherent structures, FSLE calculations are robust to errors and random noise in the velocity fields [23,50], and are largely insensitive to their spatio-temporal resolution, remaining valid even when the velocity field resolution is much lower than that of the derived FSLE field [52,53]. Given that Lagrangian coherent structures tend to persist over timescales of weeks to months [49,54], a 4-day temporal resolution is an appropriate timescale for mapping telemetry locations onto these structures and has been done for a number of marine predators, including elephant seals [21,55,56]. For each location, we extracted the gridded FSLE value, and the mean, maximum and standard deviation of FSLE values within a five-gridcell radius to match potential spatial error for ARGOS satellite tags (figure 1). We tested the sensitivity of our results to additional radii of three- and 10-gridcells (electronic supplementary material, appendix S4); generalized additive mixed model (GAMM) results were robust to the different radii tested, but a 5-pixel radius resulted in the lowest Akaike information criterion (AIC) scores.

(c) Statistical analyses

For all analyses, we used GAMMs to quantify nonlinear relationships between the suite of FSLE variables and (i) selection for foraging behaviour, (ii) maximum depth and bottom time
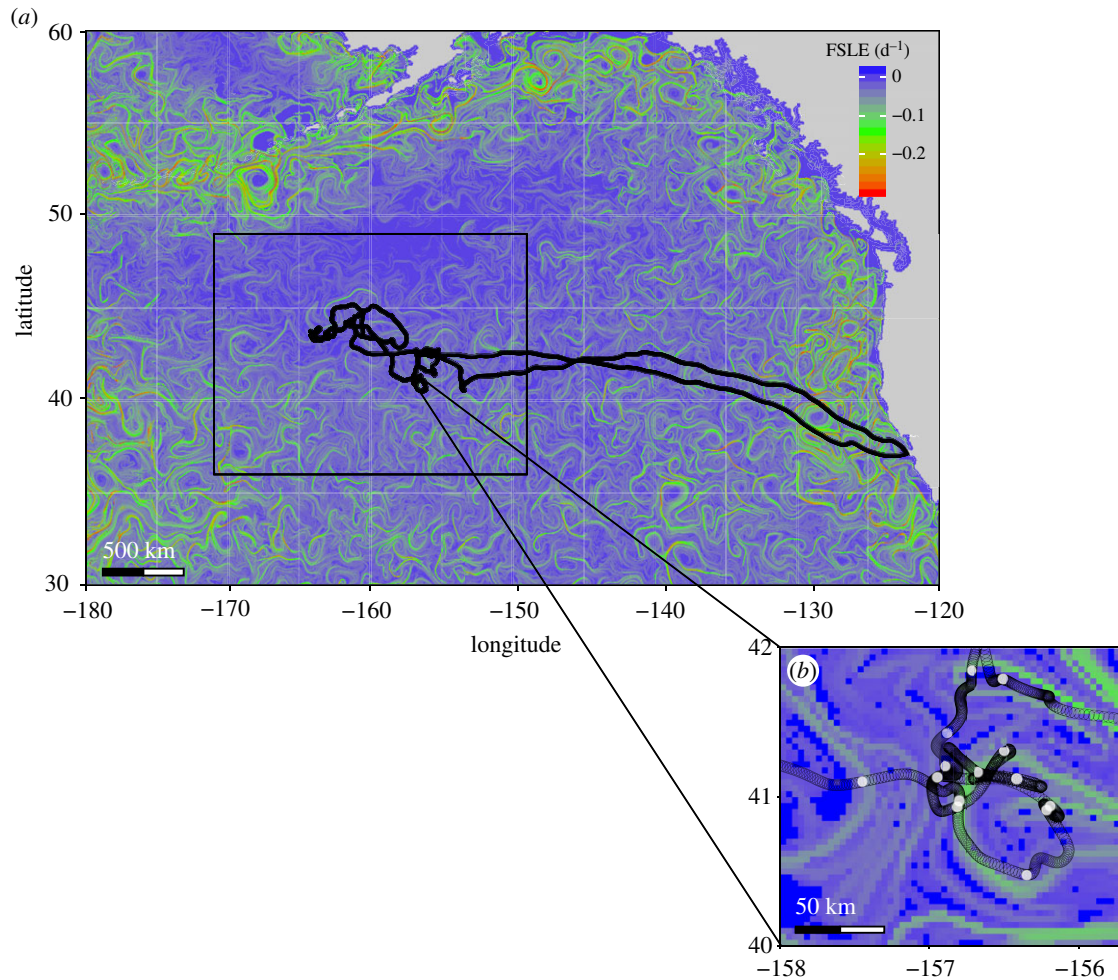
Figure 2. (a) Migration track from 2012 of an adult female northern elephant seal in relation to backward-in-time FSLEs in September 2012. The black box indicates the 95% bounding box of September telemetry locations for all individuals for measuring third-order resource selection (selection of habitat areas within a home or subpopulation range). (b) Overlap between telemetry locations (black dots) and time-matched FSLE map to explore fourth-order resource selection (selection of specific sites within a habitat area). White dots indicate foraging dive locations as captured by time-depth recorders.

(calculated as time below 95% of the maximum dive depth [40]) dive parameters and (iii) daily fat gain ('gamm4' package [57] in R 3.3.2 [58]). Individuals were nested as a random effect. We tested for spatial autocorrelation in residuals using Moran's I in the 'ape' R package [59]. Spatial autocorrelation was present in all models, so we included a term for the geographical coordinates as a fixed effect [60]. Candidate models were generated based on hypothesized combinations of FSLE variables and assessed using AIC using the 'AICcmodavg' package for R [61]. We checked that predictors included in the final models were not collinear with the *cor.test* function in the R 'stats' library [58].

Resource selection analysis relies on comparing used resources (case) to available and/or unused resources (control) [17,18]. To evaluate the selection of Lagrangian coherent structures for foraging, we therefore used a case–control design, fitting GAMMs with a binomial distribution and the canonical logistic link function. We evaluated selection for all 142 individuals in our dataset, as well as for the subset of 29 individuals for which fat gain data were available. For third-order selection (selection of habitat areas within the home or subpopulation range), we compared the characteristics of foraging dive locations with random background sampling. We sampled 10 000 points from a uniform distribution within the 95% bounding box of September telemetry locations (figure 2). Because FSLE values for a given location require time-matching, we assigned randomly generated dates drawn from a uniform distribution for each day in September between 2004 and 2015 to match the distribution of dates in our empirical dataset (electronic supplementary material,

appendix S5). To check the sensitivity of our results to the bounding box extent, we reran the analysis using a bounding box with a 50% larger extent (electronic supplementary material, appendix S5). For fourth-order selection (selection of specific sites within the habitat area), we compared the time-matched characteristics of each foraging dive location with those of 10 transit locations derived from satellite tag data [39]. To evaluate the relationship between environmental predictors, dive characteristics and fat gain, we fitted GAMMs with a Gaussian distribution.

3. Results

(a) Selection for finite-size Lypanov exponent-derived Lagrangian coherent structures

For third-order selection (selection of habitat areas within the home or subpopulation range), neither FSLE nor its spatial mean, maximum or standard deviation was associated with areas used for foraging compared to random locations. However, for fourth-order selection (selection of specific sites within a habitat area), the highest-ranking candidate model included terms for FSLE point values and its spatial standard deviation, signifying the strength and/or number of Lagrangian coherent structures in an area [62], both of which positively influenced the probability of foraging behaviour
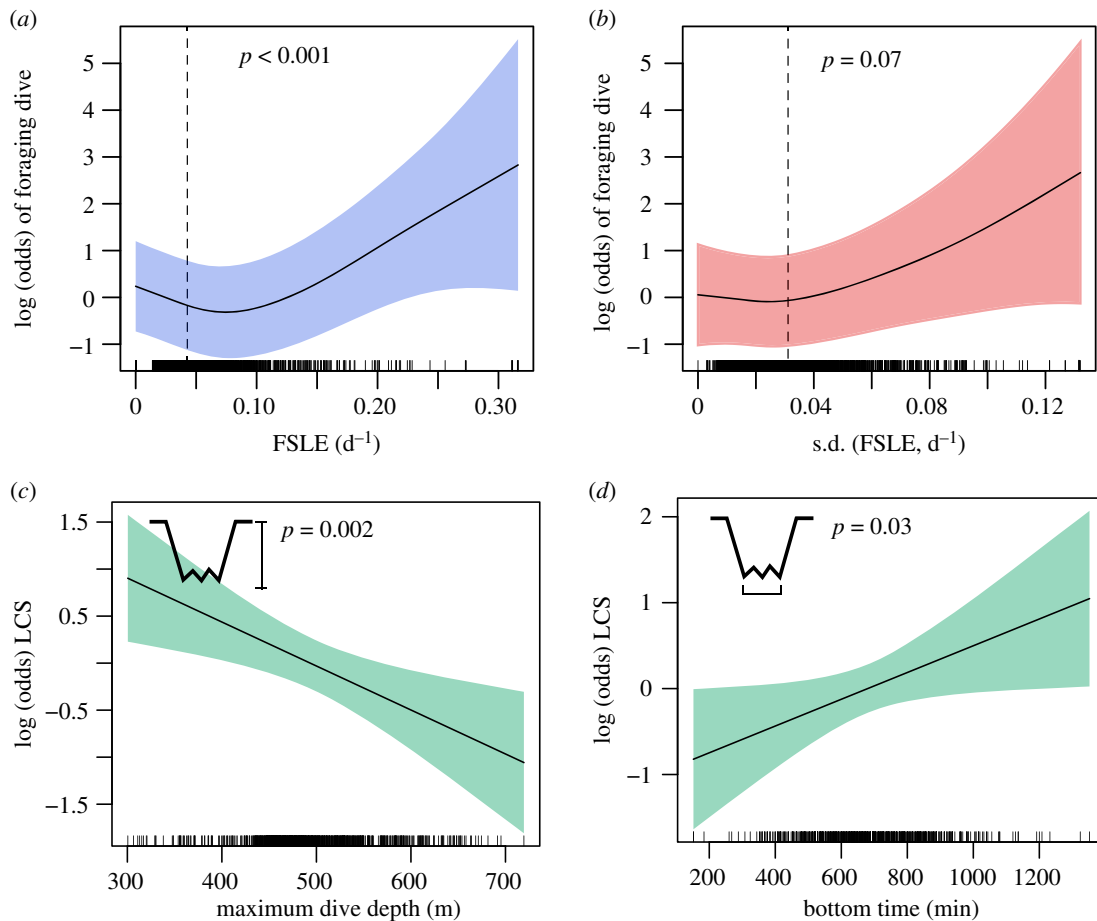
Figure 3. Response curves of GAMMs for $n = 142$ adult female northern elephant seals relating (a,b) foraging behaviour to absolute value of FSLEs and standard deviation of FSLE within a 25 km radius and (c,d) maximum dive depth and bottom time (calculated as time spent below 95% of the maximum dive depth) to the probability of a dive occurring in an FSLE-derived Lagrangian coherent structure. The vertical lines in (a) and (b) denote the average background absolute value of FSLE (0.047 d^{-1}) and FSLE spatial standard deviation (0.034 d^{-1}), respectively, within the study area. (Online version in colour.)

compared with transit ($N = 142$ individuals; FSLE: $p < 0.001$; s.d.: $p = 0.07$; figure 3a,b; electronic supplementary material, appendix S6).

(b) Modification of dive behaviour

Mean dive depth for active-bottom foraging dives was 535 ± 124 m; mean bottom time was 680 ± 162 min. The highest-ranking candidate models for predicting dive depth and bottom time included only FSLE point values. Higher absolute FSLE values were associated with shallower dive depths (edf $= 1.40$, $p = 0.03$) and longer bottom times (edf $= 1.0$, $p = 0.001$). As a second measure, shallower dive depths and longer bottom times were significant predictors of a dive occurring in a Lagrangian coherent structure ($N = 142$ individuals; $p = 0.002$ and 0.03, respectively; figure 3c,d).

(c) Influence of Lagrangian coherent structures on energy gain

The highest-ranking candidate model for predicting daily lipid gain, estimated from both mean daily telemetry location matched to FSLE variables and daily mean of FSLE variables extracted from dives, included only FSLE spatial standard deviation (electronic supplementary material, appendix S6). The spatial standard deviation had a strongly positive effect on lipid gain ($N = 29$ individuals; $p < 0.01$; figure 4a). This relationship was maintained when tested at a weekly

timescale. Fourth-order resource selection for the same subset of 29 seals mirrored this pattern, with only the standard deviation being a significant predictor of foraging behaviour (figure 4b,c).

4. Discussion

Combining satellite tracking, bio-logging, daily body fat estimates and time-matched Earth observation remote sensing revealed that areas of high mesoscale activity in the open ocean not only attract top predators as foraging hotspots, but also lead to increased energy transfer across trophic levels. We found that during post-moulting migrations, northern elephant seals selected for Lagrangian coherent structures and areas with greater mesoscale activity, measured as the spatial standard deviation in FSLE, when making fine-scale foraging decisions. Daily energy gain increased significantly with increasing spatial standard deviation in FSLE, suggesting that areas of mesoscale activity may concentrate prey fields or increase foraging efficiency, even at average depths of 500 m at which northern elephant seals forage. We show that by setting the stage for variation in resource availability, the physical environment can directly shape predator foraging behaviour and fitness via energy gain at very fine temporal scales.

We found that the spatial standard deviation of FSLE was an important component in both the resource
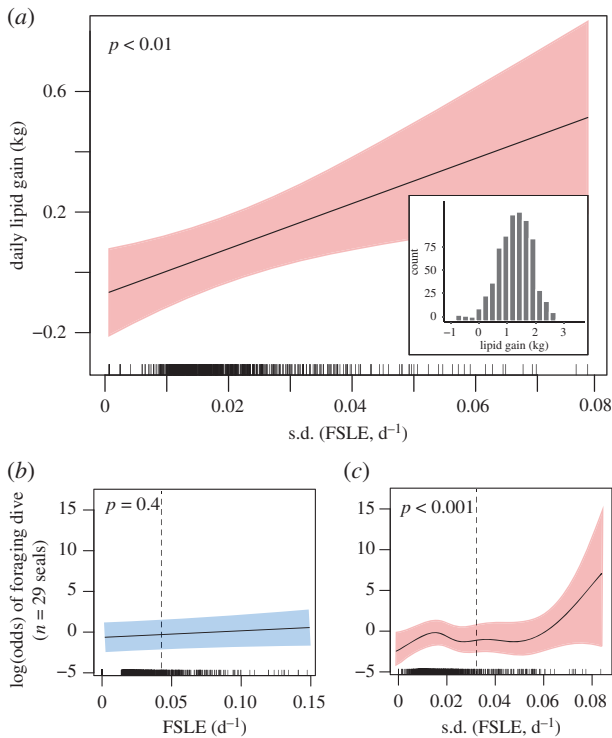
Figure 4. (Top) Response curve of GAMM relating daily fat gains to the spatial standard deviation of FSLE for $n = 29$ seals. (Bottom) A histogram shows that daily lipid gains modelled from Schick *et al.* [35] are normally distributed. Response curves of GAMM to FSLE (left) and FSLE spatial standard deviation (right) for fourth-order selection for foraging behaviour of the same 29 seals. The vertical line denotes the average background values of FSLE and its spatial standard deviation. (Online version in colour.)

selection and energy gain analyses (figures 3 and 4). Similarly, the spatial standard deviation of FSLE was found to have a significantly positive influence on residence times in fin whales [62]. The standard deviation in FSLE captures the strength and/or number of Lagrangian coherent structures in an area [62], thus representing the degree of mesoscale activity. As evident in figure 1, selection for FSLE SD may also indicate selection for the edges of Lagrangian coherent structures. Regions of high gradient in FSLE are likely where aggregations of planktonic organisms that replicate up the food chain are highest, and therefore where resource selection is greatest [8,29]. It is also possible that because the AVISO FSLE fields used cannot resolve habitat patchiness at sub-mesoscales (less than 5 km), standard deviation values were better able to capture heterogeneity at that scale than point values. Our finding that these areas facilitate energy gains in foraging elephant seals confirms the role of mesoscale activity in modulating food web dynamics [63]. While mesoscale activity is associated with increased phytoplankton and zooplankton production [63], to our knowledge ours is the first study to link mesoscale activity up the food chain to energy gain in a top predator. Quantifying prey density concurrent with FSLE dynamics is a next step in completing the puzzle.

Our results highlight the importance of assessing resource selection at multiple scales to uncover the scales at which selection processes are operating [18,64]. Female elephant seals migrate thousands of kilometres during their post-moulting migrations and likely employ different resource selection processes at different spatial scales. Indeed, our results were

sensitive to the scale at which resource selection was evaluated: we found that female northern elephant seals did not select for habitat areas in the ocean with high mesoscale activity at the regional scale (third-order; selection of habitat areas within the home or subpopulation range), but selected for Lagrangian coherent structures at a local scale (fourth-order; selection of specific sites within a habitat area) when making fine-scale foraging decisions. How elephant seals use oceanographic features and past history to drive migrations and multi-month intensive foraging periods at-sea is still an open question. At the regional (third-order) scale, larger features such as large-scale frontal systems may dictate movement patterns; in particular, northern elephant seals are known to track the highly productive Transition Zone Chlorophyll Front, a sharp surface chlorophyll gradient in the North Pacific Basin [65], during post-moulting migrations [34,66]. In addition, evidence suggests that marine predators navigate to seasonally or interannually persistent oceanographic features for foraging hotspots [29,67,68]. Given this, and the fact that elephant seals display strong interannual foraging site fidelity [69,70], FSLE persistence may be a more informative metric for assessing third-order resource selection than contemporaneous FSLE values. Fourth-order resource selection patterns also differed slightly between our global dataset and the subset of 29 individuals for which we had fat gain data, suggesting that there may be individual-level variation in resource selection patterns. Alternatively, a sample size of 29 individuals may not have been sufficiently large to capture all resource selection patterns. Our sample of 142 individuals allows better insights into population-level preferences and indicates a broad influence of FSLE on foraging behaviour, consistent with studies of other marine predators [21,23,30–32].

Relating surface oceanographic conditions to foraging activity at depth presents a challenge for inferring animal–environment relationships for deep-diving predators like elephant seals. The relationship we found between FSLE SD and energy gain indicates that a surface FSLE variable may represent subsurface processes that influence mesopelagic foraging opportunities. Aggregation at convergent mesoscale features plays an important role in food web dynamics of pelagic ecosystems and has been shown to lead to a 20- to 40-fold increase in pelagic fish production [27], which in turn attract top predators including deep-diving species [56]. In general, the shallower part of the mesopelagic zone (200–700 m depth) is known to be a biologically rich foraging habitat [71], and surface features likely induce vertical flows that impact forage availability throughout the water column. Supporting this, Della Penna *et al.* [55] found that surface geostrophic velocities were representative of horizontal velocities in the water column down to at least 500 m, and Godø and colleagues [28] observed increased concentrations of pelagic fish species within mesoscale features at depths up to 1200 m. While the relationship between dive metrics and foraging success is uncertain, shallower dives and longer bottom times at locations with Lagrangian coherent structures further suggest that elephant seals modify their foraging efforts in relation to such structures, a result consistent with Della Penna *et al.* [56] and a study relating southern elephant seal dive characteristics to mesoscale surface features [72]. However, lack of fine-scale physical–biological data in the mesopelagic zone means that linkages between surface mixing and mesopelagic trophic dynamics remain anecdotal. Thus, tightening the mechanistic links between

the physical and biological coupling in the ocean and marine vertebrate spatial ecology is a critically needed area of research [3].

This study provides insights into how animal resource selection and variation in the physical environment interact to provide energy transfer to high trophic-level consumers. While we did not specifically examine the role of Lagrangian coherent structures in affecting swimming behaviour, recent work has also shown that these convergent features can entrain elephant seals that use these areas for intensive foraging bouts [56]. Thus, the physical environment can modulate trophic interactions not only by concentrating prey, but also by facilitating predation [56]. By demonstrating that daily fat gain in elephant seals increased significantly with increasing meso-scale activity, we build upon prior work to show that the physical environment is an important factor in controlling energy flow through food webs. Moreover, because animals can select resources at relatively fine spatial scales, our findings demonstrate that individual movement decisions may have significant consequences for patterns of energy gain at similarly fine temporal scales. Such understanding is critical for assessing how changes in the environment and resource distribution will affect individual fitness and community dynamics.

References

1. Morales JM, Moorcroft PR, Matthiopoulos J, Frair JL, Kie JG, Powell RA, Merrill EH, Haydon DT. 2010 Building the bridge between animal movement and population dynamics. *Phil. Trans. R. Soc. B* **365**, 2289–2301. (doi:10.1098/rstb.2010.0082)

2. Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE. 2008 A movement ecology paradigm for unifying organismal movement research. *Proc. Natl Acad. Sci. USA* **105**, 19 052–19 059. (doi:10.1073/pnas.0800375105)

3. Hays GC et al. 2016 Key questions in marine megafauna movement ecology. *Trends Ecol. Evol.* **31**, 463–475. (doi:10.1016/j.tree.2016.02.015)

4. Ropert-Coudert Y, Kato A, Chiaradia A. 2009 Impact of small-scale environmental perturbations on local marine food resources: a case study of a predator, the little penguin. *Proc. R. Soc. B* **276**, 4105–4109. (doi:10.1098/rspb.2009.1399)

5. McGarigal K, McComb WC. 1995 Relationships between landscape structure and breeding birds in the Oregon Coast Range. *Ecol. Monogr.* **65**, 235–260. (doi:10.2307/2937059)

6. Heithaus MR, Delius BK, Wirsing AJ. 2009 Physical factors influencing the distribution of a top predator in a subtropical oligotrophic estuary. *Limnol. Oceanogr.* **54**, 472–482. (doi:10.4319/lo.2009.54.2.0472)

7. Staveley TAB, Perry D, Lindborg R, Gullström M. 2016 Seascape structure and complexity influence temperate seagrass fish assemblage composition. *Ecography* **40**, 936–946. (doi:10.1111/ecog.02745)

8. Sabarros PS, Ménard F, Lévénez JJ, Tew Kai E, Ternon JF. 2009 Mesoscale eddies influence distribution and aggregation patterns of micronekton in the Mozambique Channel. *Mar. Ecol. Prog. Ser.* **395**, 101–107. (doi:10.3354/meps08087)

9. Genin A, Jaffe JS, Reef R, Richter C, Franks P. 2005 Swimming against the flow: a mechanism of zooplankton aggregation. *Science* **308**, 860–862. (doi:10.1126/science.1107387)

10. Bost CA, Cotté C, Bailleul F, Cherel Y, Charrassin JB, Guinet C, Ainley DG, Weimerskirch H. 2009 The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *J. Mar. Sys.* **78**, 363–376. (doi:10.1016/j.jmarsys.2008.11.022)

11. Wilson AM, Lowe JC, Roskilly K, Hudson PE, Golabek KA, McNutt JW. 2013 Locomotion dynamics of hunting in wild cheetahs. *Nature* **498**, 185–189. (doi:10.1038/nature12295)

12. Gaillard JM, Hebblewhite M, Loison A, Fuller M, Powell R, Basille M, Van Moorter B. 2010 Habitat-performance relationships: finding the right metric at a given spatial scale. *Phil. Trans. R. Soc. B* **365**, 2255–2265. (doi:10.1098/rstb.2010.0085)

13. Whitlock RE, Hazen EL, Walli A, Farwell C, Bograd SJ, Foley DG, Castleton M, Block BA. 2015 Direct quantification of energy intake in an apex marine predator suggests physiology is a key driver of migrations. *Science Adv.* **1**, e1400270. (doi:10.1126/sciadv.1400270)

14. Pyke GH. 1984 Optimal foraging theory: a critical review. *Annu. Rev. Ecol. Syst.* **15**, 523–575. (doi:10.1146/annurev.es.15.110184.002515)

15. MacArthur RH, Pianka ER. 1966 On optimal use of a patchy environment. *Am. Nat.* **100**, 603–609. (doi:10.1086/282454)

16. Schoener TW. 1971 Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* **2**, 369–404. (doi:10.1146/annurev.es.02.110171.002101)

17. Manly BF. J., McDonald LL, Thomas DL, McDonald TL, Erickson WP. 2002 *Resource selection by animals: statistical design and analysis for field studies.* Boston, MA: Kluwer Academic Publishers.

18. Johnson DH. 1980 The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **61**, 65–71. (doi:10.2307/1937156)

19. McLoughlin PD, Boyce MS, Coulson T, Clutton-Brock T. 2006 Lifetime reproductive success and density-dependent, multi-variable resource selection. *Proc. R. Soc. B* **273**, 1449–1454. (doi:10.1098/rspb.2006.3486)

20. Steele JH, Henderson EW. 1994 Coupling between physical and biological scales. *Phil. Trans. R. Soc. Lond. B* **343**, 5–9. (doi:10.1098/rstb.1994.0001)

21. Tew Kai E, Rossi V, Sudre J, Weimerskirch H, Lopez C, Hernandez-Garcia E, Marsac F, Garcon V. 2009 Top marine predators track Lagrangian coherent structures. *Proc. Natl Acad. Sci. USA* **106**, 8245–8250. (doi:10.1073/pnas.0811034106)

22. Scales KL, Hazen EL, Jacox MG, Castruccio F, Maxwell SM, Lewison RL, Bograd SJ. 2018 Fisheries bycatch risk to marine megafauna is intensified in Lagrangian coherent structures. *Proc. Natl Acad. Sci. USA* **115**, 7362–7367. (doi:10.1073/pnas.1801270115)

23. Cotte C, d'Ovidio F, Chaigneau A, Lévy M, Taupier-Letage I, Mate B, Guinet C. 2011 Scale-dependent interactions of Mediterranean whales with marine

dynamics. *Limnol. Oceanogr.* **56**, 219–232. (doi:10.4319/lo.2011.56.1.0219)

24. d'Ovidio F, De Monte S, Alvain S, Dandonneau Y, Lévy M. 2010 Fluid dynamical niches of phytoplankton types. *Proc. Natl Acad. Sci. USA* **107**, 18 366–18 370. (doi:10.1073/pnas.1004620107)

25. Chelton DB, Gaube P, Schlax MG, Early JJ, Samelson RM. 2011 The influence of nonlinear mesoscale eddies on near-surface oceanic chlorophyll. *Science* **334**, 328–332. (doi:10.1126/science.1208897)

26. Labat J-P, Gasparini S, Mousseau L, Prieur L, Boutoute M, Mayzaud P. 2009 Mesoscale distribution of zooplankton biomass in the northeast Atlantic ocean determined with an optical plankton counter: relationships with environmental structures. *Deep-Sea Res. Part I* **56**, 1742–1756. (doi:10.1016/j.dsr.2009.05.013)

27. Woodson CB, Litvin SY. 2015 Ocean fronts drive marine fishery production and biogeochemical cycling. *Proc. Natl Acad. Sci. USA* **112**, 1710–1715. (doi:10.1073/pnas.1417143112)

28. Godø, O. R., Samuelsen A, Macaulay GJ, Patel R, Hjøllo SS, Horne J, Kaartvedt S, Johannessen JA. 2012 Mesoscale eddies are oases for higher trophic marine life. *PLoS ONE* **7**, e30161. (doi:10.1371/journal.pone.0030161)

29. Scales KL, Miller PI, Hawkes LA, Ingram SN, Sims DW, Votier SC. 2014 Review: on the front line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates. *J. Appl. Ecol.* **51**, 1575–1583. (doi:10.1111/1365-2664.12330)

30. Della Penna A, Koubbi P, Cotte C, Bon C, Bost C.-A, d'Ovidio F. 2017 Lagrangian analysis of multi-satellite data in support of open ocean marine protected area design. *Deep-Sea Res. Part II* **140**, 212–221. (doi:10.1016/j.dsr2.2016.12.014)

31. De Monte S, Cotté C, d'Ovidio F, Lévy M, Le Corre M, Weimerskirch H. 2012 Frigatebird behaviour at the ocean-atmosphere interface: integrating animal behaviour with multi-satellite data. *J. R. Soc. Interface* **9**, 3351–3358. (doi:10.1098/rsif.2012.0509)

32. Bon CP, Della A, d'Ovidio F, Arnould J, Poupart T, Bost C.-A. 2015 Influence of oceanographic structures on foraging strategies: macaroni penguins at Crozet Islands. *Mov. Ecol.* **3**, 32. (doi:10.1186/s40462-015-0057-2)

33. Costa DP. 1993 The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. *Symp. Zool. Soc. Lond.* **66**, 293–314.

34. Robinson PW *et al.* 2012 Foraging behavior and success of a mesopelagic predator in the northeast Pacific Ocean: insights from a data-rich species, the northern elephant seal. *PLoS ONE* **7**, e36728. (doi:10.1371/journal.pone.0036728)

35. Schick RS *et al.* 2013 Estimating resource acquisition and at-sea body condition of a marine predator. *J. Anim. Ecol.* **82**, 1300–1315. (doi:10.1111/1365-2656.12102)

36. Naito Y, Costa DP, Adachi T, Robinson PW, Fowler M, Takahashi A. 2013 Unravelling the mysteries of a mesopelagic diet: a large apex predator specializes

on small prey. *Funct. Ecol.* **27**, 710–717. (doi:10.1111/1365-2435.12083)

37. Costa DP. 1991 Reproductive and foraging energetics of high-latitude penguins, albatrosses and pinnipeds—implications for life-history patterns. *Am. Zool.* **31**, 111–130. (doi:10.1093/icb/31.1.111)

38. Johnson DS, London JM, Lea MA, Durban JW. 2008 Continuous-time correlated random walk model for animal telemetry data. *Ecology* **89**, 1208–1215. (doi:10.1890/07-1032.1)

39. Robinson PW, Simmons SE, Crocker DE, Costa DP. 2010 Measurements of foraging success in a highly pelagic marine predator, the northern elephant seal. *J. Anim. Ecol.* **79**, 1146–1156. (doi:10.1111/j.1365-2656.2010.01735.x)

40. Kuhn CE, Crocker DE, Tremblay Y, Costa DP. 2009 Time to eat: measurements of feeding behaviour in a large marine predator, the northern elephant seal *Mirounga angustirostris. J. Anim. Ecol.* **78**, 513–523. (doi:10.1111/j.1365-2656.2008.01509.x)

41. Adachi T, Maresh JL, Robinson PW, Peterson SH, Costa DP, Naito Y, Watanabe YY, Takahashi A. 2014 The foraging benefits of being fat in a highly migratory marine mammal. *Proc. R. Soc. B* **281**, 20142120. (doi:10.1098/rspb.2014.2120)

42. Webb PM, Crocker DE, Blackwell SB, Costa DP, Boeuf BJ. 1998 Effects of buoyancy on the diving behavior of northern elephant seals. *J. Exp. Biol.* **201**, 2349–2358.

43. Biuw M. 2003 Blubber and buoyancy: monitoring the body condition of free-ranging seals using simple dive characteristics. *J. Exp. Biol.* **206**, 3405–3423. (doi:10.1242/jeb.00583)

44. Biuw M *et al.* 2007 Variations in behavior and condition of a Southern Ocean top predator in relation to *in situ* oceanographic conditions. *Proc. Natl Acad. Sci. USA* **104**, 13 705–13 710. (doi:10.1073/pnas.0701121104)

45. Thums M, Bradshaw CJA, Hindell MA. 2011 *In situ* measures of foraging success and prey encounter reveal marine habitat-dependent search strategies. *Ecology* **92**, 1258–1270. (doi:10.1890/09-1299.1)

46. New LF *et al.* 2014 Using short-term measures of behaviour to estimate long-term fitness of southern elephant seals. *Mar. Ecol. Prog. Ser.* **496**, 99–108. (doi:10.3354/meps10547)

47. Prants SV. 2016 A Lagrangian study of eddies in the ocean. *Regul. Chaot. Dyn.* **21**, 335–350. (doi:10.1134/S1560354716030060)

48. d'Ovidio F, Fernández V, Hernandez-Garcia E, Lopez C. 2004 Mixing structures in the Mediterranean Sea from finite-size Lyapunov exponents. *Geophys. Res. Lett.* **31**, 1–4. (doi:10.1029/2004GL020328)

49. Beron-Vera FJ, Olascoaga MJ, Goni GJ. 2008 Oceanic mesoscale eddies as revealed by Lagrangian coherent structures. *Geophys. Res. Lett.* **35**, 1–7. (doi:10.1029/2008GL033957)

50. Haller G. 2002 Lagrangian coherent structures from approximate velocity data. *Phys. Fluids* **14**, 1851–1861. (doi:10.1063/1.1477449)

51. CNES. 2016 SSALTO/DUACS user handbook: Mozambique (M)SLA Near-Real Time Products.

See https://www.aviso.altimetry.fr/fileadmin/documents/data/tools/hdbk_duacs_moz.pdf.

52. Beron-Vera FJ, Olascoaga MJ, Goni GJ. 2010 Surface ocean mixing inferred from different multisatellite altimetry measurements. *J. Phys. Oceanogr.* **40**, 2466–2480. (doi:10.1175/2010JPO4458.1)

53. Beron-Vera FJ. 2010 Mixing by low- and high-resolution surface geostrophic currents. *J. Geophys. Res.* **115**, 373–315. (doi:10.1029/2009JC006006)

54. d'Ovidio F, De Monte S, Della Penna A, Cotté C, Guinet C. 2013 Ecological implications of eddy retention in the open ocean: a Lagrangian approach. *J. Phys. A: Math. Theor.* **46**, 254023. (doi:10.1088/1751-8113/46/25/254023)

55. Cotté C, d'Ovidio F, Dragon AC, Guinet C. 2015 Flexible preference of southern elephant seals for distinct mesoscale features within the Antarctic Circumpolar Current. *Prog. Oceanogr.* **131**, 46–58. (doi:10.1016/j.pocean.2014.11.011)

56. Della Penna A, De Monte S, Kestenare E, Guinet C, d'Ovidio F. 2015 Quasi-planktonic behavior of foraging top marine predators. *Sci. Rep.* **5**, 1–10. (doi:10.1038/srep18063)

57. Wood S. 2006 *Generalized additive models: an introduction.* Boca Raton, FL: Chapman & Hall/CRC Press.

58. R Core Team. 2017 *R: a language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing. See http://www.r-project.org.

59. Paradis E, Claude J, Strimmer K. 2004 Ape: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289–290. (doi:10.1093/bioinformatics/btg412)

60. Dormann CF *et al.* 2007 Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* **30**, 609–628. (doi:10.1111/j.2007.0906-7590.05171.x)

61. Mazerolle MJ. 2017 AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 2.1-1. See https://cran.r-project.org/package=AICcmodavg.

62. Scales KL, Schorr GS, Hazen EL, Bograd SJ, Miller PI, Andrews RD, Zerbini AN, Falcone EA. 2017 Should I stay or should I go? Modelling year-round habitat suitability and drivers of residency for fin whales in the California Current. *Divers. Distributions* **23**, 1204–1215. (doi:10.1111/ddi.12611)

63. Lévy M. 2008 The modulation of biological production by oceanic mesoscale turbulence. *Transport Mixing Geophys. Flows* **744**, 219–261. (doi:10.1007/978-3-540-75215-8)

64. Sawyer SC, Brashares JS. 2013 Applying resource selection functions at multiple scales to prioritize habitat use by the endangered Cross River gorilla. *Divers. Distributions* **19**, 943–954. (doi:10.1111/ddi.12046)

65. Polovina JJ, Howell EA, Kobayashi DR, Seki MP. 2017 The Transition Zone Chlorophyll Front updated: advances from a decade of research.

Prog. Oceanogr. **150**, 79–85. (doi:10.1016/j.pocean.2015.01.006)

66. Simmons SE, Crocker DE, Hassrick JL, Kuhn CE, Robinson PW, Tremblay Y, Costa DP. 2010 Climate-scale hydrographic features related to foraging success in a capital breeder, the northern elephant seal *Mirounga angustirostris*. *Endang. Species Res.* **10**, 233–243. (doi:10.3354/esr00254)

67. Suryan RM, Santora JA, Sydeman WJ. 2012 New approach for using remotely sensed chlorophyll a to identify seabird hotspots. *Mar. Ecol. Progr. Ser.* **451**, 213–225. (doi:10.3354/meps09597)

68. Louzao M, Delord K, García D, Boué A, Weimerskirch H. 2012 Protecting persistent dynamic oceanographic features: transboundary conservation efforts are needed for the critically endangered balearic shearwater. *PLoS ONE* **7**, e35728. (doi:10.1371/journal.pone.0035728)

69. Bradshaw CJA, Hindell MA, Sumner MD, Michael KJ. 2004 Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. *Anim. Behav.* **68**, 1349–1360. (doi:10.1016/j.anbehav.2003.12.013)

70. Costa DP, Breed GA, Robinson PW. 2012 New insights into pelagic migrations: implications for ecology and conservation. *Annu. Rev. Ecol. Evol. Syst.* **43**, 73–96. (doi:10.1146/annurev-ecolsys-102710-145045)

71. Robinson C *et al.* 2010 Mesopelagic zone ecology and biogeochemistry—a synthesis. *Deep-Sea Res. Part II* **57**, 1504–1518. (doi:10.1016/j.dsr2.2010.02.018)

72. Dragon AC, Monestiez P, Bar-Hen A, Guinet C. 2010 Linking foraging behaviour to physical oceanographic structures: southern elephant seals and mesoscale eddies east of Kerguelen Islands. *Prog. Oceanogr.* **87**, 61–71. (doi:10.1016/j.pocean.2010.09.025)

73. Abrahms B, Scales KL, Hazen EL, Bograd SJ, Schick RS, Robinson PW, Costa DP. 2018 Mesoscale activity facilitates energy gain in a top predator. Dryad Digital Repository. (https://doi.org/10.5061/dryad.2v10hs6)

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