Taking animal tracking to new depths: synthesizing horizontalvertical movement relationships for four marine predators

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Abstract. In animal ecology, a question of key interest for aquatic species is how changes in movement behavior are related in the horizontal and vertical dimensions when individuals forage. Alternative theoretical models and inconsistent empirical findings mean that this question remains unresolved. Here we tested expectations by incorporating the vertical dimension (dive information) when predicting switching between movement states ("resident" or "directed") within a state-space model. We integrated telemetry-based tracking and diving data available for four seal species (southern elephant, Weddell, antarctic fur, and crabeater) in East Antarctica. Where possible, we included dive variables derived from the relationships between (1) dive duration and depth (as a measure of effort), and (2) dive duration and the postdive surface interval (as a physiological measure of cost). Our results varied within and across species, but there was a general tendency for the probability of switching into "resident" state to be positively associated with shorter dive durations (for a given depth) and longer postdive surface intervals (for a given dive duration). Our results add to a growing body of literature suggesting that simplistic interpretations of optimal foraging theory based only on horizontal movements do not directly translate into the vertical dimension in dynamic marine environments. Analyses that incorporate at least two dimensions can test more sophisticated models of foraging behavior.

Key words: Antarctic fur seal, Arctocephalus gazella; crabeater seal, Lobodon carcinophaga; East Antarctic; foraging behavior; individual movement; marine predators; satellite tracking; southern elephant seal, Mirounga leonina; state-space model; Weddell seal, Leptonychotes weddellii.

INTRODUCTION

Understanding the mechanisms that animals use to acquire food is a pivotal problem in ecology. Foraging is a fundamental requirement of all animals and has implications for the distribution, growth, and persistence of wild populations (Kokko and Lopez-Sepulcre 2006). Foraging behavior and success at the level of the individual have consequences for that organisms' fitness (survival and reproductive success). Given that natural selection operates at the level of the individual, population and ecosystem characteristics emerge as consequences of individual strategies (behavioral, morphological, and physiological) that are sufficiently well adapted to a given ecological context (Sutherland 1996).

Optimal foraging theory (OFT) is a conceptual framework long used to examine the movement and behavioral strategies that animals use to acquire food (Stephens and Krebs 1986). Individuals are predicted to maximize their energy intake while minimizing the time spent searching for and capturing/handling food. Aquatic animals, especially diving air-breathers including birds, reptiles, and mammals, present a special case for foraging models because they must locate and capture prey distributed in a three-dimensional environment, within the constraints of oxygen availability (Kooyman 1989). Accordingly they can be considered central-place foragers, where the surface acts as the central place and the dive descent and ascent phases represent the distance or transit to food (Houston and McNamara 1985).

Explorations of how predators modify their diving behavior under this conceptual framework yield at least two countering schools of thought. The first is physiological in nature, focusing on oxygen depletion during the dive and subsequent acquisition on return to the surface. In this case, travel costs should be compensated for by energy gain: divers should maximize time spent at foraging depths, and minimize both time spent traveling between the surface and foraging depths and subsequent surface recovery time (Kramer 1988, Houston and Carbone 1992). Consequently, an increase in foraging success and energy intake (due to higher prey abundance, availability, or quality) is commonly inferred from longer dive durations, increased dive rates, and/or increased time at the dive bottom (Austin et al. 2006, Robinson et al. 2007), taking into account the greater costs associated with deeper dives (Thompson and Fedak 2001). In marine environments, this may be best

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represented by animals foraging on patchily distributed prey that are relatively even in terms of size and/or quality, e.g., great whales feeding on krill (Doniol-Valcroze et al. 2011).

The second school of thought builds on this to also incorporate ecological considerations such as prey density, quality, and distribution (Mori 1998, Thompson and Fedak 2001, Mori and Boyd 2004), because maximizing time at the foraging depth will not always provide the most efficient hunting strategy. For example, taking into account that prey patches may vary in quality, the marginal value theorem predicts that predators should leave when the marginal capture rate in the patch falls to the average rate for the habitat; thus, animals foraging in high-quality habitat (where patches are better and/or closer together) may spend relatively less time per patch (Charnov 1976). The decision to leave may be a function of prey depletion, prey evasion, or food-processing requirements (Charnov 1976, Stephens and Krebs 1986). These two schools of thought have differing predictions; to date, empirical findings do not consistently support either hypothesis, so it remains a topic of debate. It is likely that optimal solutions will vary between habitats (e.g., pelagic, benthic) and prey types (e.g., small, densely schooling prey as compared with larger, dispersed, but high-quality prey).

For mobile marine predators, telemetry provides the only practicable means of measuring foraging behavior. Most commonly, an animals' three-dimensional foraging activity is recorded via the combination of a onedimensional diving trace and a two-dimensional horizontal movement track, and these are almost always recorded at different spatiotemporal resolutions. Direct measures of feeding (e.g., via stomach temperature sensors, jaw gapes, head jerks, and other methods) are possible, yet long-term data sets are relatively rare (Bestley et al. 2010, Naito et al. 2013), so inference of feeding usually relies on ascribing the foraging components from either or both of the diving and track data. Telemetry-based studies to investigate how changes in movement behavior are related in the horizontal and vertical dimensions typically follow a three-step process: (1) filtering the horizontal locations, which can contain significant inherent error; (2) discriminating the foraging components using either process-based (e.g., hidden Markov models; Patterson et al. 2009) or more heuristic methods (e.g., first passage time; Fauchald and Tveraa 2003, Gurarie et al. 2009); (3) using statistical inference to link the vertical and horizontal dimensions; Breed et al. 2013). However, the complex individual-based time series which telemetry data comprise are driving ever more sophisticated analytical efforts that unify these steps (Jonsen et al. 2013). The true benefit of this is that the location uncertainty, which is considerable in the case of ARGOS (Costa et al. 2010) or geolocation (Winship et al. 2012) data, is carried right through to inference of foraging and associations with diving behavior or environmental influences.

Here we use an integrative state-space model (Bestley et al. 2013) to investigate how changes in marine predator behavior are related in the horizontal and vertical dimensions. A single mechanistic model of the movement process is fitted to tracking data, accounting for inherent horizontal location error (Jonsen et al. 2003, 2005), and expectations about horizontal-vertical relationships are directly tested by including diving covariates when predicting the probability of switching between movement states (nominally "resident" and "directed"). Employing a comparative approach, we use telemetry-based tracking and diving data available for four seal species in East Antarctica waters: southern elephant (Mirounga leonina), Weddell (Leptonychotes weddellii), antarctic fur (Arctocephalus gazella), and crabeater (Lobodon carcinophaga) seals, and aim to identify similarities and differences across species. Where possible, we include dive variables derived from the relationships between (1) dive duration and depth (as a measure of effort), and (2) the postdive surface interval and dive duration (as a measure of cost). This is the first multi-predator study to specifically discriminate the foraging component in the horizontal track and simultaneously quantify behavioral adjustments in the vertical dimension.

Methods

Tag data

We compiled contemporary and historical tagging data, collected between 1995 and 2011, which had simultaneous movement and diving information available. Our focus was on marine predators within the Australian East Antarctic territory, for which the most data exist in the region from Prydz Bay north toward the subantarctic Heard and Kerguelen Islands (Fig. 1).

Southern elephant (SES, n = 20 juvenile males) and Weddell (WED, n = 18 adults; 15 females, 3 males) seals were tagged during late February-March 2011 as part of the multi-annual Australian Integrated Marine Observing System (IMOS) program with Satellite-Relayed Data Loggers (SRDLs, manufactured by Sea Mammal Research Unit, University of St Andrews, Scotland, UK) at Davis station and the Vestfold Hills. These data are publicly available from IMOS (online).⁵ The antarctic fur seals (AFS, n = 5 adult males with SRDLs) were tagged during the large-scale Heard Island marine ecosystem study in January 2004 (Frydman and Gales 2007). Crabeater seals (CES, n = 13 adults; 4 females, 9 males) represent the oldest telemetry data, with satellitelinked time-depth recorders (SLTDRs, manufactured by Wildlife Computers, Redmond, Washington, USA) deployed during October-December 1995-1999 (Wall et al. 2007) under the international Antarctic Pack-Ice Seal program. CES and AFS data are publicly available from the Australian Antarctic Data Centre (online).⁶

⁵ http://www.imos.org.au/

⁶ https://data.aad.gov.au/



FIG. 1. Map of estimated positions and movement state for four East Antarctic seal species: southern elephant seals (SES, purple), Weddell seals (WED, orange), antarctic fur seals (AFS, green) and Crabeater seals (CES, red). Triangles are deployment locations. Solid circles are positions defined as "resident." Details of the Prydz Bay area indicated by the white-outlined box are shown in the inset. The Antarctic coastline is in gray and positions of the major ice shelves are in white. Bathymetric contours are at 500, 1000, 2000, and 3000 m depth (blue shading, light to dark). The dotted white line shows the climatological mean maximum ice extent during 1995–2011 for context. Note that for CES, any data during an ice-affiliated breeding period (on average three weeks) were excluded; hence some red triangles may not have tracks leading directly from them.

Although the data collection spans more than a decade, the temporal structure of the deployments and trips is not explicitly important for the purposes of this study. In cases where individual animals conducted multiple trips between East Antarctic waters and the subantarctic islands, only the first such trip was included in the analyses. For CES, only data post-breeding (i.e., once seals recommenced diving) were utilized.

Behavioral information

Location information was relayed through the global ARGOS satellite system, but the structure of the dive information varied between tag types. SRDLs relay an optimized and unbiased sample of individual dive records (Fedak et al. 2002); in all SRDL deployments (for SES, WED, and AFS), this included information on maximum dive depth (m), dive duration (s), and duration of the postdive surface interval (s). We used these data to develop two dive-based residuals, hereafter termed "dive residual" and "surface residual." The transit (ascent/descent) phase of a dive must necessarily increase with depth, so the dive residual was constructed to ascertain whether, for a dive of given depth, the duration was relatively long or short. Relatively longer dives may be indicative of relatively higher effort. For each species, we fitted a linear mixed-effect model (LMM) using a log-log relationship where depth was fitted as both a fixed and random effect; i.e., allowing both the intercept and slope of the relationship to vary among seals (Appendix A: Fig. A1). We used Pearson residuals calculated from LMMs fit via restricted maximum-likelihood estimation (REML) using the freely available R software (R Development Core Team 2013) package *nlme* (Pinheiro et al. 2013).

Similarly, we constructed a "surface residual" to determine whether, for a dive of given duration, the postdive surface interval (SI) was relatively long or short. Relatively longer SIs may be indicative of relatively higher energy expenditure. The physiological premise is that the accrued dive duration beyond which the briefest postdive SI begins to rise is a consequence of higher oxygen consumption on the preceding dive or dives, requiring longer on the surface to replace the blood and muscle oxygen stores (Kooyman 1989). For each individual, we determined minimum postdive SI (Mori and Boyd 2004, Luque et al. 2008) corresponding to the native binning of the SRDL dive duration data. For each species, we fitted a LMM to the logtransformed minimum SIs, with duration fitted as both a fixed and random effect, allowing the relationship to vary from seal to seal, as before (Fig. 2). For each individual dive, we then calculated the standardized difference between the observed and (back-transformed) predicted minimum SI such that the final "surface residual" represented log(1 + (observed SI_{k,t,d} – predicted SI_{k,d})/predicted SI_{k,d}), where k is the individual animal, t is the time stamp of the individual dive, and d is the native SRDL dive duration bin.

Nominally, SRDLs also relay a four-point summarized time–depth profile for each individual dive; however, in the 2004 AFS deployment, this information was unavailable for 73.5% of dives. Where available (i.e., for SES and WED seals), this summarized structure was used to calculate the proportion of time spent at the dive bottom, considered to include time below 80% of the maximum recorded depth for that dive (Bailleul et al. 2008). Because bottom time and dive duration varied strongly across individuals, these variables were both centered (Bestley et al. 2013) such that dive.variable_{k,t} = (dive.variable_{k,t} – mean(dive.variable_k))/SD(dive.variable_k). Maximum dive depth was log-transformed.

The SLTDR data available for CES comprised dive duration and maximum depth information summarized over 6-h periods, binned at 14 user-defined intervals (for specific details, see Wall et al. 2007). These give a relatively coarse level of information, but were used to calculate a proxy dive residual as follows. For each 6-h period, all of the maximum dive depth and duration records were assigned to the midpoint value of their bin. A total was calculated from the sum of the bin frequencies multiplied by the bin midpoints, standardized by the highest frequency if the two data streams differed. The dive residual was then calculated via the LMM procedure previously described, applied to these standardized total duration and depth values for each 6h period (in place of individual dive information). No analogous information on either postdive surface intervals or dive bottom times was available for CES.

In summary, the suite of dive variables examined in this study, where available for each species, was: (1) dive residual, (2) surface residual, (3) maximum depth, (4) bottom time, and (5) dive duration.

State-space model

To make inferences about how changes in behavior are related in the horizontal and vertical dimensions, we employed the state-space model (SSM) described in Bestley et al. (2013). In brief, animal tracking data often reveal periods of relatively directed (more linear) and resident (more sinuous) horizontal movements (putatively "traveling" and "foraging"). This behavioral process is modeled as switching between two different correlated random walks (CRW), as introduced by Jonsen et al. (2005), simultaneously dealing with inherent telemetry location error. The two CRW models, and the behavioral states that they describe at time t, differ in their values of mean turn angle and move persistence (θ_i and γ_i , respectively, where $i \in [1,2]$ is the behavioral state index such that 1 = "directed" [D] and 2 = "resident" [R]), and the probability of switching (ϕ_{ti}) from one behavioral state to the other is usually static. In the extension of Bestley et al. (2013), this switch probability varies in relation to behavioral and/or environmental covariates via a logistic function, so that movement behavior-covariate relationships can be directly quantified (through estimation of the intercept (β_i) and coefficient (m_i) parameters) within the model framework. See Bestley et al. (2013) for process model equations. Note that the covariate directly influences $Pr[D \,|\, D] = \phi_1;$ therefore $Pr[R \,|\, D] = 1 - \phi_1,$ and a positive (or negative) coefficient (m_i) indicates a reduced (or increased) switch probability from directed into resident state.

We were interested in examining the relationship between the five diving variables described previously and the probability of switching from directed into resident state, noting that there is no implicit causality, but that we are simply investigating associations. For example, an increased probability of switching from directed to resident state, in association with altered diving effort, might be a direct result of a reduced time and/or energy balance available for horizontal movement due to increased vertical activity; or it may be that the horizontal and vertical components both convey indirect evidence of (unobserved) foraging behavior. Because the primary objective was to evaluate relationships (rather than, for example, to determine the "best" of correlated predictor variables), each SSM run examined a single dive variable.

The SSM is implemented using the freely available software WinBUGS (online)⁷ and R package R2Win-BUGS (Sturtz et al. 2005). The code and a worked example are provided in the Supplement. Here, the CRW time step choice was largely driven by the availability of the dive variable data: 6 h for SES, WED, and CES, and 12 h for AFS; for all dive variable time series, the mean values for each regular time step were used in the SSM as described in Bestley et al. (2013). To fit the SSM, two Markov chain Monte Carlo (MCMC) chains of 40000 iterations were run with a burn-in of 20000. Each chain was thinned so that one in every 20 samples was retained, for a final MCMC sample size of 2000. We used a hierarchical formulation (Jonsen et al. 2006) in which parameters are estimated across multiple individual animals. However, this is computationally and memory intensive. To balance computational and time requirements, for each species we fit models to small batches of seal tracks (n = 4-6) with a mixture of relatively short and long tracks in each batch. In practice, this allowed

⁷ http://www.mrc-bsu.cam.ac.uk/software/bugs/



FIG. 2. Example showing derivation of the "surface residual" dive variable, from the relationship between dive duration and postdive surface interval. The case shown is for antarctic fur seals (data for five individual seals are represented by different colors, with fitted relationships shown for individuals (solid-colored lines) and at the population level (dashed black line)). The relationship is fitted using a mixed-effect model allowing a random effect for individuals in both the slope (here, duration) and intercept terms (see *Methods* for details). The analogous derivation of "dive residual" from the relationship between dive depth and dive duration, is shown in Appendix A, Fig. A1, for the case of Weddell seals.

SSM runs to "borrow strength" across individuals to estimate the movement parameters, so that the hierarchical formulation was more informative for less complete tracks, yet still provided some information on variability among individuals.

For Bayesian SSMs fit via MCMC, especially relatively complex ones such as those employed here,

convergence is difficult to prove, but model diagnostics are essential to reveal any major estimation flaws. We employed a number of approaches to check model convergence and fit detailed in Appendix B.

RESULTS

Within the East Antarctic region, the telemetry data available for the four seal species were largely noncontemporaneous in terms of both year and season; however, the compilation reveals distinct yet overlapping spatial habitat use (Fig. 1, Table 1). In general, Weddell seal tracks showed exclusive use of East Antarctic shelf habitats within the sea ice. In comparison, antarctic fur and crabeater seal tracks showed almost exclusive use of offshore waters, the latter predominantly within the sea ice. Use of the sea ice habitat by AFS was only illustrated by the longest individual track (17 of 144 days; 12%). These low numbers are in part due to tag loss by AFS (n = 3) and would likely also be higher for subsequent trips later in the season. Southern elephant seals tagged in Prydz Bay spent approximately half of their trip in these local shelf waters, followed by a northerly migration to either Heard or Kerguelen Islands, with two-thirds of the trip, on average, spent in sea ice. SES and AFS migrations covered the largest distance and correspondingly had the highest average daily horizontal speeds (Table 1).

The time spent in a resident as compared with a directed movement state reflected the differing nature of the tracks across species. The SSM estimated less than half of the SES (46%) and AFS (39%) positions to be in resident state, respectively, whereas the estimates for the more localized WED and CES tracks were much higher (>75%). Across species, individual animals displayed, on average, three or four residences per foraging track, each residency being around one or two weeks in duration; the exception was WED seals with a much higher number of residences per individual (nearly 10 on

TABLE 1. Trip summaries for four East Antarctic predators, where values represent mean \pm SD across individual animals.

Trip characteristics	SES	WED	AFS	CES
No. individuals	20	18	5	13
Trip duration (d)	103 ± 31	132 ± 63	63 ± 46	46 ± 14
Trip distance (km)	4512 ± 1323	2327 ± 1143	2968 ± 1822	1215 ± 588
Time on shelf (%)	55 ± 23	100 ± 2	0 ± 0	4 ± 13
Time in ice (%)	64 ± 23	99 ± 2	3 ± 5	76 ± 29
Time "resident" (%)	46 ± 10	83 ± 8	39 ± 17	76 ± 20
No. residencies	3.95 ± 1.79	9.83 ± 5.17	4 ± 3.94	2.46 ± 1.56
Duration of residencies (d)	14.77 ± 10.99	13.96 ± 14.08	6.56 ± 2.78	16.83 ± 7.82
Daily speed (km/d)				
Directed	61 ± 8	43 ± 9	64 ± 14	46 ± 9
Resident	25 ± 3	14 ± 3	29 ± 11	20 ± 4
Dive duration (s)	1183 ± 326	489 ± 122	67 ± 4	225 ± 53
Surface interval (s)	119 ± 14	181 ± 24	75 ± 5	NA
Maximum dive depth (m)				
Mean	334 + 133	119 + 38	21 + 2	54 + 27
Deepest	1468 + 392	702 + 180	154 + 53	242 + 12
Deepeer	1.00 = 572		10. = 00	12

Note: Species abbreviations are SES, southern elephant seal; WED. Weddell seal; AFS, antarctic fur seal; CES, crabeater seal; NA indicates that data are not available.

average per track). For most species, the distribution of positions defined as resident between shelf and sea ice habitats largely reflected the overall statistics given in Table 1. However, for SES, the majority of positions defined as resident actually occurred within shelf (74% \pm 34%) and/or sea ice (77% \pm 34%) habitats.

The relationships between horizontal and vertical movement patterns, as estimated within the SSM, revealed both similarities and differences across species. The full suite of posterior estimates of the covariate coefficients, across all model runs, is presented in Fig. 3 and Appendix A: Table A1. A general summary is given in Table 2.

The SSM results for the deep-diving SES and WED showed that the probability of switching from directed into resident movement state increased in association with more negative dive residuals (i.e., relatively shorter dive durations for a given depth), whereas there was no relationship for either AFS or CES (Fig. 3a, b). The switch probability increased in association with more positive surface residuals (i.e., relatively longer postdive surface intervals for a given dive duration) for all SES model runs, and in three out of four WED runs; a similar but weaker association (100% - 7.95% = 92.05%)probability that this relationship is negative) was indicated for AFS (Fig. 3c, d). The examination of maximum dive depth showed variable results within species, but there was some evidence for a negative relationship (i.e., the switch probability increasing in association with shallower dives) for SES, WED, and AFS (Fig. 3e, f). The proportion of time spent at the dive bottom could only be examined for SES and WED, and there was very little evidence (two out of eight runs) for a positive relationship with switch probability (Fig. 3g, h). Finally, there was evidence for switch probability increasing in association with shorter dive durations for SES and AFS, and more weakly so for WED, with some variability in results within species (Fig. 3i, j).

Only weak relationships were found between switch probability and any dive variable examined for CES. However, these SLTDR dive data were limited (as described in *Methods*), and diagnostics revealed evidence of issues with model fit for CES batches 1 and 2 (see model diagnostics in Appendix B). However, the results for CES batch 3 generally supported the trends we have outlined, with weaker confidence, i.e., switch probabilities increased in association with more negative dive residuals (100% - 16.9% = 83.1% probability that this relationship is negative), and shorter dive durations (100% - 18.0% = 82% probability that this relationship is negative), whereas maximum dive depth showed no real relationship (Appendix A: Table A1).

In our model, the covariates only influence switch rates directly: how dive parameters alter between the different behavioral states is a subtly different question. However, in the cases tested here, the observed patterns were actually quite consistent (Appendix A: Fig. A2). Where probabilities of switching *into* resident state were associated with more negative dive residuals, more positive surface residuals, and shallower and shorter dives, these patterns were also evident *during* resident (as compared with directed) periods.

DISCUSSION

Tracking and diving data were integrated from four antarctic seal species to test expectations regarding how predators modify their diving behavior in putative foraging areas. We used a holistic approach by incorporating traditionally separate analysis stages into a single, hierarchical state-space model, thus accounting for potentially considerable data uncertainty. In general, brief, and presumably more efficient, diving was coupled with extended surfacing intervals when animals switched into the resident state. This was clearest for the deepdiving phocid seals (SES and WED) and is in contrast with the physiological prediction from optimal foraging theory that air-breathing, diving, central-place foragers maximize time at feeding depths and minimize subsequent surface time.

The four species in this study occupied a suite of habitats from ice-free oceanic (AFS), to ice-covered oceanic (CES), and partly (SES) and heavily (WED) icecovered Antarctic shelf areas (Table 1). These species also span a great range of diving capabilities: SES (>1000 m; Hindell et al. 1991) and WED (600-800 m; Heerah et al. 2013) are known deep-divers, contrasting with the shallower niches of AFS and CES. In this study, both AFS and CES foraged in the upper water column (<250 m), but primarily focused within the near-surface waters (Table 1), although CES do dive more deeply in other regions (Burns et al. 2008). The differences in diving behavior of these species reflect resource partitioning with CES (Southwell et al. 2005), and probably also AFS in this region, which is regarded as the most krill-dependent seal species compared with the more opportunistic mixed diets reported for WED (Green and Burton 1987) and SES (Banks et al. 2014). In light of these known differences, the synergies in our results are perhaps the more striking. It is difficult to find analogues from other interspecies comparisons, which often focus solely on spatiotemporal habitat segregation or overlap (Block et al. 2011, Hindell et al. 2011) and, where possible, associated diving and/or diet differences (Kokubun et al. 2010, Waluda et al. 2010, Thiebot et al. 2012). No other multi-predator studies specifically discriminate the foraging component in the horizontal track and simultaneously quantify behavioral adjustments in the vertical dimension.

We explored a suite of commonly used behavioral indicators (maximum dive depth, dive duration, and bottom time) as well as two derived dive variables. Across species, the balance of evidence supported a switch into resident state in association with shorter dive durations and (weakly) shallower dive depths. Dive bottom time was not important, but time below 80% of the maximum dive depth may be too crude an index of



FIG. 3. Relationships between dive variables and the probability of switching into "resident" movement state. Shown are the posteriors for the coefficients (left-hand panels) and the predicted relationships (right-hand panels) for (a, b) dive residual, (c, d) surface residual, (e, f) maximum depth, (g, h) bottom time, and (i, j) dive duration. Positive or negative coefficients, respectively, indicate a reduced or increased switch probability from "directed" into "resident" state. The four predators are represented by different colors, as in Fig. 1. Repeated colors indicate multiple hierarchical SSM runs (i.e., batch runs) within a species. Posteriors (left-hand panels) from 2000 iterations of two MCMC chains are shown as smoothed kernel densities. Predicted relationships (right-hand panels) are plotted in those cases where the proportion of posterior samples falling below (or above) zero for positive (or negative) median parameter estimates is less than 5% (solid lines) or 10% (dashed lines).

TABLE 2. Summary of relationships between dive variables and the probability of switching into "resident" state for four seal species.

Species	Dive residual	Surface residual	Maximum depth	Bottom time	Dive duration
SES		+ +	_	0	
WED		+ +	_	$+\dagger$	_
AFS	0	+	_	NA	
CES	0	NA	0	NA	0

Notes: See Table 1 for species names; NA indicates that data are not available. Plus signs or minus signs, respectively, indicate a positive or negative association between the dive variable and the switch probability. Double [++, -] signs indicate strong relationships (the percentage of coefficient posterior samples straddling zero was generally less than 5%), whereas single [+, -] signs indicate weaker and/or more variable estimates across model runs. Zeros indicate that coefficient posteriors straddled zero by more than 10%. Full coefficient results are given in Appendix A: Table A1.

† In only one out of four model runs.

true foraging effort. The dive residual should actually better account for the transit/bottom components, because it indexes the amount of time spent diving after adjustment for dive depth. If so, what remains in this residual should represent actual dive bottom time; adjustment of descent/ascent times by altering speed or dive angles (Le Boeuf et al. 2000); or exploratory dive components (e.g., at the dive shoulders or interrupting the dive to seek alternate forage depths) creating more complex dive structures.

The switch into resident state was associated with relatively shorter dives for a given depth (i.e., more negative dive residuals) for SES and WED. We interpret this as indicative of higher quality forage areas, consistent with the "ecological" hypothesis outlined in the Introduction predicting that animals foraging in a habitat with a high average rate of resources acquisition should spend relatively less time per dive. The "physiological" hypothesis, in contrast, predicts that increased foraging success will be associated with longer dive durations. Thums et al. (2013) similarly reported faster descent speeds, shorter dive durations, and reduced bottom times in higher-quality habitat, as determined from long-term SES body condition indices. The lower probability of state-switching that we found in association with relatively longer dives for a given depth may also indicate that deep-diving seals actively explore the prey field in both the horizontal and vertical dimensions at these times. Because marine predators display a complex variety of adaptive diving strategies (Hindell et al. 1991), disentangling these different components requires higher-resolution data, such as those provided by accelerometers (Wilson et al. 2006).

The second derived dive variable, the surface residual, was intended as a behavioral indicator of the amount of time spent at the surface by seals after adjustment for the duration of the previous dive (or dives). Across species, the balance of evidence supported a switch into resident state in association with relatively longer surface intervals. Surface intervals are used by diving animals to perfuse their blood and muscle with oxygen, and the more depleted these stores are, whether due to many short or a few long dives, the longer it takes to reoxygenate. It seems likely that even though the dives are relatively short when switching to resident state, they might involve higher energy expenditure due to more frequent encounter and pursuit of prey (or handling of more energy-dense prey), and perhaps also increased rates of travel in the descent/ascent (Williams et al. 2004). Alternatively, successful dives may require food processing at the surface. Given that the physiology of diving will almost certainly reduce blood flow to the gut, longer surface intervals could be associated with some aspect of enhancing digestion efficiency (Sparling et al. 2007).

Despite the proliferation of modeling studies of marine predator foraging strategies, direct testing is hampered by the difficulty of obtaining empirical data on feeding activity. Those data which exist can be contradictory and lend support to both the physiological and ecological hypotheses. For example, short-term measurements of head-jerks in SES (from accelerometers; Gallon et al. 2013) and lunges in blue whales (from velocity TDRs; Doniol-Valcroze et al. 2011) suggest increased prey encounters with increased bottom durations, in agreement with the "physiological" optimal foraging hypothesis. This contrasts with the findings of this study, and those of Thums et al. (2013) based on long-term body condition in SES as described previously, which support the "ecological" hypothesis. Similar data obtained within oceanic frontal zones showed differences between shallow foraging dives (within eddyinduced upwelling) and concurrent deep foraging dives (400-900 m, targeting mesopelagic prey), associated with relatively long and short bottom times, respectively (Dragon et al. 2012). The way that predators balance their dive budgets in terms of speed of transit, bottom duration, and surface intervals is probably determined by the interaction of factors such as the quality, size, and behavior of the prey, and its vertical distribution (Thompson and Fedak 2001, Thums et al. 2013). Many species display opportunistic prey-switching and behavioral-switching strategies in response to environmental variability, so it is likely that the optimal strategy will be changeable even within species. Indeed, because economy alone is not the end-game, high-cost tactics may be used to capture high-value prey (Soto et al. 2008).

Antarctic fur seals provided an anomaly, as stateswitching was associated with shorter, shallower dives, but there was no obvious association with the dive residual. This may, in part, be a function of the relatively shallow depths exploited by these animals (predominantly in the upper 25 m), making the functional aspects of dive structure—transit to the forage patch at dive bottom and return—less distinct. With the diel vertical migration of krill into shallow surface waters, the whole of the dive might essentially be through an accessible prey field (i.e., transit is not searching), and dive signals exploring transit-bottom-recovery time may be more hidden compared with deeper diving species. Our study tended to find stronger significance in the movementdiving relationships of the deeper, more benthic-oriented divers (SES and WED), which may indicate that they have different strategies for preserving dive structures (Costa and Gales 2003). AFS also largely occupied icefree, oceanic waters during summer, potentially the lowest quality habitat in this study (Nicol et al. 2000, Thums et al. 2011). Thus, the apparent invariance in the dive residual may in part reflect patchiness or unpredictability in prey distribution, abundance, type, or quality. The most economical strategy in this case might be additional exploratory dive components, as we have discussed. For ice-affiliated species such as CES, the physical sea-ice habitat (Nicol et al. 2000) may also promote reorganization of dive structure. For example, targeting of shallowly distributed prey aggregated beneath the ice may involve shallow dives with relatively short bottom times or even an "inverted dive bottom," which is actually near the surface.

Inverted, our findings revealed a higher probability of remaining in a directed movement state in association with longer dive durations, (weakly) deeper dive depths, relatively longer dives for a given depth, and relatively shorter surface intervals between dives. Although there are likely to be multiple factors influential in transit, taken together, our findings suggest that the directed movement state is more costly for the marine predators examined here in terms of both horizontal and vertical movements. If this is considered within the context of the whole trip energy budget, there are likely to be significant differences in the consequences among species. For example, the foraging round trips undertaken by AFS are relatively short in duration, cover relatively long distances at high speed, and comprise a few relatively short resident periods on these productive forage grounds (Table 1). Taken in addition to the diving costs outlined previously, the "true" transit cost for AFS may therefore be substantially higher than for other species (such as WED and CES) that remain within a general foraging zone.

Our ecological interpretations need to be grounded within the context of the methodological approach used, the underpinning conceptual premise, and the issue of the scale of inference, so it is appropriate to address here a number of related issues. The state-space approach employed here is premised on a relatively simple twostate model underpinned by the concept of arearestricted search (Bell 1991). Although this generally applies well to central-place foragers (in the horizontal domain), it is not transferable across all species. Extensive wandering movements and continuous foraging are displayed by some marine turtles (Hays et al. 2006) and albatross (Weimerskirch et al. 2005); likewise, residential movement patterns do not always correspond to foraging, as seen in tunas (Bestley et al. 2010). Conversely, some species *only* display a residential state: the localized nature of Weddell seal movements proved challenging for some applications of the SSM (Appendix B). It is not likely that these animals truly spend much more time foraging than other species, and it may be useful to consider alternate model configurations (e.g., using speed alone) or structures (e.g., multiple states; Morales et al. 2004).

In our study, a second issue with the SSM fit arose for CES, where the information in the covariate data destabilized rather than informed runs (Appendix B). This may be related, in part, to the nature of CES movement in their post-breeding period, being perhaps closest of all the seal species examined here to a simple biased correlated random walk. However, for the most part it is likely to be a result of the coarseness of the information available from the SLTDR binned dive summary data. As the most krill-dependent species, CES might be expected to most closely conform to optimal foraging theory. While our results indicate the opposite, the limitations of the dive data mean that this remains unresolved. This gives rise naturally to a discussion of scale. Inference available from this SSM is relevant largely at the scale determined by the horizontal movement data. There are likely to be many finer-scale processes operating for each species, recorded in most detail within the observations of vertical behaviors, but not elucidated by this model structure. Examples might include diurnal patterns (including lunar influence), patch depletion effects, or specific surface behaviors. In some cases, better results may be obtained simply by including a variance structure for the time-averaged dive covariates (i.e., allowing for variability or uncertainty). However, for detailed examination of processes at the sub-patch scale, alternate model structures focused more explicitly on the diving data can be explored (Dowd and Joy 2011).

Foraging ecology is key to understanding the drivers of animal movement, elucidating the costs and benefits associated with animal decision-making and the ecological context within which these choices occur. In remote marine areas where prey distribution data are difficult to obtain, predator movements and behaviors are increasingly being used as indirect measures of ecosystem productivity (Biuw et al. 2007) and to inform understanding of hotspots of ecological significance to multiple species (Block et al. 2011, Hindell et al. 2011). Synthetic studies identifying patterns across multiple species can be pivotal for understanding ecological function and informing efforts to build whole ecosystem models. A natural extension of this work is to integrate environmental information into animal movement models to enable prediction under variable scenarios, and this will be the focus of our future directions.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A and B and the Supplement are available online: http://dx.doi.org/10.1890/14-0469.1.sm