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**Modelling the functional link between movement, feeding activity and
condition in a marine predator**

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Running header: Elephant seal movement, feeding and condition.

Abstract

The ability to quantify animals' feeding activity and the resulting changes in their body condition as they move in the environment is fundamental to our understanding of a population's ecology. We use satellite tracking data from northern elephant seals (*Mirounga angustirostris*), paired with simultaneous diving information, to develop a Bayesian state-space model that concurrently estimates an individual's location, feeding activity, and changes in condition. The model identifies important foraging areas and times, the relative amount of feeding occurring therein and thus the different behavioral strategies in which the seals engage. The fitness implications of these strategies can be assessed by looking at the resulting variation in individuals' condition, which in turn affects the condition and survival of their offspring. Therefore, our results shed light on the processes affecting an individual's decision-making as it moves and feeds in the environment. In addition, we demonstrate how the model can be used to simulate realistic patterns of disturbance at different stages of the trip, and how the predicted accumulation of lipid reserves varies as a consequence. Particularly, disturbing an animal in periods of high feeding activity or shortly after leaving the colony was predicted to have the potential to lead to starvation. In contrast, an individual could compensate even for very severe disturbance if such disturbance occurred outside the main foraging grounds. Our modelling approach is applicable to marine mammal species that perform drift dives, and can be extended to other species where an individual's buoyancy can be inferred from its diving behavior. **Keywords:** body condition; disturbance; drift dives; elephant seals; feeding ecology; satellite tracking; Bayesian state-space modelling.

Introduction

Marine predators spend most or all of their time at sea, often far from the coast and from the surface, where they cannot be easily monitored by human observers (Hays et al. 2016). Until recently, these sampling challenges meant that the mechanisms underpinning their life history characteristics remained largely unknown, and researchers were forced to infer large components of an individual's ecology from the short windows of time when the animals became accessible. Modern technologies increasingly allow these knowledge gaps to be filled (Hussey et al. 2015). It is now possible to remotely track the movement and behavior of marine predators as they roam their environment and interact with the patchy resources they encounter (Block et al. 2011). As a result, it is now feasible to investigate the functional processes that regulate animals' decision-making, and how their behavioral patterns translate into variation of their body condition (Shepard et al. 2013; Crossin et al. 2014). An individual's body condition reflects the balance between the energy it acquires via resource intake and the energy expended to support other life functions, such as growth, movement, maintenance and reproduction (Costa 2009; Kooijman 2010). In the long-term, the ability to maintain this energy balance will affect individuals' survival and reproductive success, i.e. their overall fitness, which ultimately influences the dynamics of the populations to which they belong (Kleiber 1975).

The movements of animals, as recorded by the various available tracking systems, can be grouped into functional units of behavior at multiple spatiotemporal scales (Nathan et al. 2008). At a large scale, marine predators can migrate between breeding and foraging grounds or perform seasonal trips at sea to accumulate body reserves, depending on

whether or not they need to return ashore to reproduce (Costa 1993; Boyd et al. 2014; Pirotta, Mangel, et al. 2018). Within these large scale movements, shorter bouts of activity can be identified. Typically, while moving at sea, an individual will encounter areas where resources are scarce, which it will tend to pass through relatively quickly while headed towards more profitable regions. Such transiting behavior will result in directed tracks, at relatively stable speed (Fauchald and Tveraa 2003). When reaching areas richer in food, and because of the patchy nature of resources at sea, an animal will maximize the chance of finding prey by exploring these patches with convoluted movements at variable speed, a behavior known as area restricted search (ARS) (Kareiva and Odell 1987). The distinction between these two fundamental behavioral modes has been one of the main objectives of many movement models in the past decade (Patterson et al. 2016). However, behavior can be characterized at an even finer scale when pairing telemetry devices with other tagging technologies that, for example, can record the animals' dives (Bestley et al. 2015; Joy et al. 2015). Diving patterns can provide information on the feeding activity of the animals, i.e. their ability to successfully capture food, both when they are actively foraging (in ARS mode) and, opportunistically, when transiting (Thums et al. 2011). Moreover, in some species, diving data can be used to infer changes in body condition as an animal feeds and accumulates lipids that alter its overall buoyancy (Biuw et al. 2003; Schick et al. 2013; Miller et al. 2016). These analyses are individual-based by nature of the data collection. However, the ability to characterize the functional link between an individual's behavior and the resulting energetic implications means that the variation of fitness among individuals in a population, over time and as a function of the environmental context, can be evaluated (Biuw et al. 2007; Schick et al. 2013; Crossin et al. 2014).

Being able to connect behavioral processes to population dynamics becomes critical when predicting how populations may react to increasing alterations in their habitats, following, for example, climate changes or expanding human activities in the marine environment (National Research Council 2005; New et al. 2014; National Academies 2017; Pirotta, Booth, et al. 2018). Assessing the population consequences of short-term changes in behavior is a requirement under most regulatory targets (e.g. the European Habitats Directive 92/43/EEC, or the U.S. Marine Mammal Protection Act). The disruption of an individual's activity pattern could affect its ability to feed successfully. If these disruptions are recurring, or severe enough, the ability to accumulate sufficient body reserves to survive and support reproductive efforts can be impacted. Depending on the nature of the disruption and what proportion of the population is exposed to such behavioral disturbances, these could therefore become relevant from a management perspective (New et al. 2014; King et al. 2015; Fleishman et al. 2016; Pirotta, Booth, et al. 2018).

Elephant seals (*Mirounga spp.*) represent the model species to investigate these questions, because most of the conceptual steps between individual behavior and population dynamics can be informed using empirical data (New et al. 2014). These long-lived capital-breeding phocids follow relatively homogeneous life history patterns. During a year, they spend two periods hauled out on land to molt and breed, separated by long trips at sea to feed (Le Boeuf and Laws 1994). Of particular interest is the eight-month-long post-molt foraging trip that occurs immediately prior to the breeding season. Since elephant seals are capital breeders (Costa 1993; Stephens et al. 2009), the amount of lipid mass a female manages to accumulate over such a trip is linked to the amount of energy she can transfer to her pup

during lactation and thus the pup's weaning mass. This in turn affects the pup's probability of recruitment into the population (McMahon et al. 2000; McMahon et al. 2003).

Individuals can be tracked using satellite telemetry and their diving behavior can be recorded (Le Boeuf et al. 2000). Crucially, elephant seals perform passive dives for digestion and resting, known as drift dives (Crocker et al. 1997). The drift rate, i.e. the rate at which the animal sinks or floats during a drift dive, is mainly affected by a female's buoyancy, which varies as she stores positively buoyant lipids (Biuw et al. 2003).

Therefore, the drift rate can be used to estimate the variation of an individual's lipid mass over the course of a foraging trip. This information can then potentially be paired with observed movements and behavior at sea to quantify underlying mechanistic links (Thums et al. 2008; Robinson et al. 2010; Richard et al. 2014). Several studies have described the spatiotemporal relationships between the accumulation of lipid mass and the associated characteristics of the environment in which the animals foraged (Bailleul et al. 2007; Biuw et al. 2007; Simmons et al. 2010; Robinson et al. 2012). In addition, Schick et al. (2013) and New et al. (2014) developed a state-space model to estimate daily changes in condition using information from the changes in drift rate, which New et al. (2014) used to simulate the effects of environmental changes on the corresponding populations. While successfully tracking the variation of lipid mass over the trip, the models had some fundamental limitations when used to simulate the effects of anthropogenic or environmental disturbance. Because the portion of the model describing changes in lipid mass did not fully capture the behavioral mechanisms regulating this variation, realistic simulations depended on the component of the model informed by the drift rate alone. Disturbance could therefore only be simulated as the removal of a progressively large portion of the mass

accumulated at the end of a trip (New et al. 2014). Consequently, it was not possible to assess the effects of disturbance in specific regions or sections of the trip, nor test whether the animal could compensate for disturbances that occurred early in the trip.

The aim of this study was to develop an analytical approach that concurrently estimates the location of a female elephant seal, her feeding activity over time and the resulting variation of her condition, while accounting for all sampling uncertainties. By integrating the processes governing movement, feeding activity and lipid accumulation, the model characterizes the functional mechanisms underlying the variation in behavior and body condition. This will permit the exploration of a larger set of realistic disturbance scenarios (including sporadic disturbance over a trip, or disturbance in specific foraging patches) for the evaluation of any population consequences. Moreover, the analytical approach we outline here will be applicable to other species that are known to perform drift dives, e.g. New Zealand fur seals *Arctocephalus forsteri* (Page et al. 2005), or to glide during the ascent or descent phases of their dives, e.g. deep diving cetaceans (Miller et al. 2004; Miller et al. 2016) and baleen whales (Nowacek et al. 2001), allowing the unprecedented investigation of their medium-term behavioral and energetic dynamics.

Material and methods

Study species and data

The life history of northern elephant seals (*Mirounga angustirostris*) involves two periods on land, to molt and breed, alternating with two long trips at sea to feed (Le Boeuf and

Laws 1994). In this study, we focused on the eight-month long foraging trip that follows the molt and precedes the birth of a female's pup and lactation. The timing of the post-molting trip is approximately between June and January (Le Boeuf et al. 2000).

For this study, we used data from 26 of the 29 females used by Schick et al. (2013) that were tagged at the colony of Año Nuevo (California, USA) between 2004 and 2007. Three females from the original study were excluded, because it was not possible to estimate their mass at departure and arrival following the procedure described below. While on land to molt, females were instrumented with Argos satellite transmitters (Wildlife Computers, Redmond, WA, USA or Sea Mammal Research Unit, St Andrews, UK) to track their location, and time-depth recorders (TDRs) to record their diving behavior (Wildlife Computers MK9). The satellite transmitters returned a set of latitude and longitude coordinates, as well as the Argos quality class assigned to each location (Costa et al. 2010). The TDRs recorded pressure every 8 s, from which dive information was derived as described in Robinson et al. (2010). Particularly, diving data were summarized at a daily scale to obtain median ascent rate, median descent rate, median time spent at the bottom during a dive, total number of dives per day and median dive duration (Thums et al. 2008; Robinson et al. 2010; Viviant et al. 2014; Vacquié-Garcia et al. 2015). Moreover, the daily median drift rate and total number of drift dives were estimated (Thums et al. 2008; Robinson et al. 2010). A female's weight and body morphometrics were also measured at deployment and recovery of the devices (Robinson et al. 2010), from which the lipid and non-lipid mass were estimated. Since the elliptical shape of the seals was not measured prior to 2013, estimates of lipid mass using circular truncated cones were adjusted to lipid

mass estimates using elliptical cones via a function that relates the two methods (Schwarz et al. 2015). Individual trips were assigned to one of three foraging regions (coastal, North-eastern Pacific and pelagic transition zone) based on the classification by Schick et al. (2013). More details on data collection and processing are provided in Robinson et al. (2010) and Schick et al. (2013).

Modelling approach

We developed a hierarchical state-space model to analyze location, diving and mass data from tracked female elephant seals at a daily temporal resolution. The state-space model comprised a process model, which represented the underlying functional processes governing the variation in an animal's behavior and body condition, and an observation model, which accounted for the measurement error associated with the sampling process. The process model was composed of three interlinked components:

1) The **horizontal movement component** was adapted from the discrete-time, hierarchical switching state-space model developed by Jonsen et al. (2005, 2013). Under this approach, animal movements are modelled as the sum of multiple first-difference correlated random walks. Each random walk describes the dynamics of the first difference \mathbf{d} of the locations \mathbf{x} (a vector of latitude and longitude coordinates) at time step t :

$$\mathbf{d}_t \sim \gamma \cdot \mathbf{T} \cdot \mathbf{d}_{t-1} + N_2(0, \Sigma_{\mathbf{m}}),$$

where γ indicates the degree of autocorrelation in direction and speed; \mathbf{T} is the transition matrix describing the rotational component of the walk and depends on the turning angle θ ,

i.e. $\mathbf{T}(\theta) = \begin{pmatrix} \cos \theta & -\sin \theta \\ \sin \theta & \cos \theta \end{pmatrix}$; and N_2 is a bivariate Gaussian distribution representing

process error, with covariance matrix $\Sigma_{\mathbf{m}} = \begin{pmatrix} \sigma_{\text{lon}}^2 & \rho \cdot \sigma_{\text{lon}} \cdot \sigma_{\text{lat}} \\ \rho \cdot \sigma_{\text{lon}} \cdot \sigma_{\text{lat}} & \sigma_{\text{lat}}^2 \end{pmatrix}$, characterized

by variance in longitude σ_{lon}^2 , variance in latitude σ_{lat}^2 and correlation between the two, ρ .

The switch between different correlated random walks is then regulated by a set of transition probabilities. For more details on the analytical approach the reader should refer to Jonsen et al. (2005), while the corresponding JAGS code for this component was derived from package `bsam` for R 3.3.2 (Jonsen et al. 2013; R Development Core Team 2016).

Here, the model was used to estimate the location of individual i on day t , $\mathbf{x}_{i,t}$, and its movement mode $b_{i,t}$. On each day of the trip, the individual could be in one of two movement modes (transit or area restricted search, ARS), characterized by two first-difference correlated random walks with different autocorrelation γ_b and turning angle θ_b . Specifically, transit behavior was assumed to show high autocorrelation and small turning angle, capturing directed travelling, while ARS behavior corresponded to lower autocorrelation (i.e. $\gamma_2 = \gamma_1 \cdot g$, where g is a deviate in $[0, 1]$) and large turning angle, representing encamped exploratory movements (putatively in search of food). Dummy variables, \mathbf{h} , were used to ensure turning angle values, $\boldsymbol{\theta}$, were limited to a circle (see Table S1 in Supplementary material). The movement mode of each individual in the first time step, $b_{i,1}$, was estimated using a vector of initial probabilities, $\boldsymbol{\lambda}$. For all other steps, the vector $\boldsymbol{\alpha}$ represented the transition probability from either movement mode to transiting, while the transition probabilities to ARS were defined as $1 - \alpha_b$.

2) The **feeding component** modelled the amount of feeding activity of individual i on each day t ($f_{i,t}$), expressed as a value between 0 and 1. This could be interpreted as the proportion of some maximum feeding that an individual can achieve on a day, although it remains a

relative measure, whose absolute value depends on model formulation. Feeding activity was modelled as a logistic function of movement mode ($b_{i,t}$), because feeding was expected to be higher when the animal was in ARS mode, but it also remained possible while the animal was transiting (Thums et al. 2011; Adachi et al. 2017). In the absence of more proximate measures of prey capture attempts, feeding activity was further informed by the daily average characteristics of the dive profile (see available dive metrics in section “*Study species and data*” above) (Thums et al. 2008; Gallon et al. 2013; Viviant et al. 2014; Vacquié-Garcia et al. 2015). For parsimony, and because preliminary data exploration highlighted a strong correlation among the various dive metrics, we chose to include the effect of only one of these variables. We sought to identify the dive metric that best correlated with the median daily drift rate on the following day ($r_{i,t+1}$), assuming that it would be the most representative of the individual’s success at finding food. The variable was selected using a mixed-effects model fitted using package lme4 in R (Bates et al. 2012; see Appendix S1 in Supplementary material for details). Preliminary data exploration also suggested that the relationship between the dive metrics and the drift rate varied based on the sign of the drift rate, possibly indicating different underlying behavioral processes depending on the condition (and resulting buoyancy) of the animal. Therefore, we fitted a separate feeding model depending on whether the animal was positively or negatively buoyant. As a result of this procedure, the total number of dives on a given day (when the animal was negatively buoyant; $n_{i,t}$) and ascent rate (when the animal was positively buoyant; $s_{i,t}$) were included in the final model as covariates. In alternative to this data-driven approach, we ran a different version of the model where we selected *a priori* the daily median time spent at the bottom during a dive as a mechanistic indicator of successful

feeding (Austin et al. 2006; Gallon et al. 2013; Vacqu  -Garcia et al. 2015). This also allowed us to explore the sensitivity of our results to the choice of the dive metrics that informed the feeding component (Appendix S5). In order to facilitate convergence, the dive variables were standardized. The model included an intercept term (also different depending on the sign of the drift rate) and a Gaussian distributed error term ($\varepsilon_{i,t}$) with standard deviation σ_f . Preliminary investigation supported the use of a correlated random effect by individual i on the intercept and slope term of the dive covariates (β parameters in the equation below). Therefore, for each individual i , $\beta_{i,p} \sim N_2(\mathbf{B}_p, \Sigma_p)$ and $\beta_{i,n} \sim N_2(\mathbf{B}_n, \Sigma_n)$, where the subscripts p and n stand for ‘positive’ and ‘negative’ (i.e. the sign of the drift rate $r_{i,t}$), \mathbf{B}_p and \mathbf{B}_n are the vectors of means, and Σ_p and Σ_n are the corresponding covariance matrices. Feeding activity was then obtained from the linear predictor using a logit link function. The equation for the feeding activity of individual i at time t ($f_{i,t}$) was thus:

$$\text{logit}(f_{i,t}) = I(r_{i,t}) \cdot [\beta_{1,i,p} + \beta_{2,i,p} \cdot s_{i,t} + v_p \cdot (b_{i,t} - 1)] + [1 - I(r_{i,t})] \cdot [\beta_{1,i,n} + \beta_{2,i,n} \cdot n_{i,t} + v_n \cdot (b_{i,t} - 1)] + \varepsilon_{i,t}$$

$$\varepsilon_{i,t} \sim N(0, \sigma_f^2),$$

where $b_{i,t}$ is the behavioral state (equal to 1 for transiting and 2 for ARS), v_p and v_n are the effects of being in ARS mode when positively and negatively buoyant, respectively, and $I()$ is a step function that returns a value of 0 if the argument is negative and 1 if the argument is positive.

3) The **condition component** modelled the lipid mass of individual i on each day of the trip t ($l_{i,t}$). The lipid mass depended on the lipid mass in the previous day ($l_{i,t-1}$) and varied as a function of the amount of feeding activity on that day ($f_{i,t}$), with Gaussian distributed

uncertainty $\kappa_{i,t}$ characterized by standard deviation σ_l . As for the feeding component, we included a correlated individual random effect for the intercept and slope parameters of this component (ζ_i). Therefore, for each individual i , $\zeta_i \sim N_2(\mathbf{C}, \Sigma_c)$, where \mathbf{C} was the vector of means and Σ_c was the corresponding covariance matrix. The lipid mass at departure and arrival was known with error (see below). The equation for the condition component was:

$$l_{i,t} = l_{i,t-1} + \zeta_{1,i} + \zeta_{2,i} f_{i,t} + \kappa_{i,t}$$

$$\kappa_{i,t} \sim N(0, \sigma_l^2).$$

Observation models

The observation models relate the underlying processes to the recorded data. For the horizontal movement component, an individual's location on each day $\mathbf{x}_{i,t}$ was inferred from Argos satellite fixes $\mathbf{Y}_{i,t}$ (the $Z_{i,t} \times 2$ matrix of longitude and latitude measurements on day t for individual i), each characterized by an associated location quality q (Costa et al. 2010). Following Jonsen et al. (2005), the z^{th} measured location on day t ($\mathbf{y}_{z,i,t}$) was assumed to lie on the straight line between location at t and location at $t - 1$, at j_z proportion of a day, i.e.:

$$\mathbf{y}_{z,i,t} = (1 - j_z) \cdot \mathbf{x}_{i,t} + j_z \cdot \mathbf{x}_{i,t-1} + \boldsymbol{\eta}_{z,i,t}.$$

$\boldsymbol{\eta}_{z,i,t}$ is the vector of t -distributed observation errors on the two coordinates (longitude and latitude), scaled by an individual-specific parameter ψ_i . i.e.:

$$\eta_{\text{lat},z,t,i} \sim t(0, \psi_i \cdot \tau_{\text{lat},q}, \nu_{\text{lat},q}) \text{ and } \eta_{\text{lon},z,t,i} \sim t(0, \psi_i \cdot \tau_{\text{lon},q}, \nu_{\text{lon},q}).$$

where $\tau_{\text{lat},q}$ and $\tau_{\text{lon},q}$ are the scale parameters of the t -distribution, and $\nu_{\text{lat},q}$ and $\nu_{\text{lon},q}$ represent the corresponding degrees of freedom (Jonsen et al. 2005). These parameters were derived from published data on the accuracy of each Argos location class (Costa et al. 2010) (Appendix S2 in Supplementary material).

For the observation model of the condition component, the lipid mass ($l_{i,t}$) was informed by the drift rate ($r_{i,t}$). Following Schick et al. (2013), we took:

$$r_{i,t} = \delta_0 + \delta_1 \cdot (l_{i,t}/a_{i,t}) + \omega_{i,t}$$

$$\omega_{i,t} \sim N(0, \sigma_r^2/D_{i,t})$$

where $l_{i,t}/a_{i,t}$ represents the buoyancy of individual i on day t , i.e. the ratio between the lipid and the non-lipid (hereafter lean; $a_{i,t}$) mass. Observation variance σ_r^2 was scaled by the number of drift dives on that day $D_{i,t}$ (Schick et al. 2013). While drift rate is known to be also affected by other environmental factors (e.g. salinity and temperature), previous work has shown that this relationship offers a good approximation in the absence of such information (Schick et al. 2013). The values of the lean mass at departure and arrival were known, but the model could not concurrently estimate the variation of both the lipid and the lean mass over the course of the trip. A seal's buoyancy results from the relative proportion of lipid to lean mass, and therefore changes in lean mass were not identifiable from changes in lipid mass (Schick et al. 2013). As in Schick et al. (2013), we assumed that lean mass followed a known trajectory between the measured initial and final values. We tested the use of two functional forms for the variation of lean mass over the trip: 1) linear increase of female lean mass but accounting for pup mass in the final third of the trip (New et al.

2014), 2) accumulation of the female's lean mass in the first third of the trip with no influence of pup mass (Schick et al. 2013) (Fig. S1 in Supplementary material). These forms were selected because they have been used in previous work by Schick et al. (2013) and New et al. (2014), and because preliminary investigation suggested they caused the largest differences in the final results. We present the results obtained using the first functional form, because the pup's mass is expected to have an influence on the female's density and diving behavior (Hückstädt et al. 2018). However, we also fitted the model using the second form and compared the estimated temporal patterns of feeding activity and lipid mass. The lipid mass at departure ($t = 1$) and arrival ($t = T_i$) were estimated with uncertainty as described in section “*Study species and data*” above. We assumed these had a Gaussian distribution: $l_{i,1} \sim N(m_{i,1}, \phi_{i,1})$ and $l_{i,T_i} \sim N(m_{i,T_i}, \phi_{i,T_i})$, where \mathbf{m}_i and $\boldsymbol{\phi}_i$ are the vectors of empirical mean and standard deviation estimates at the start and end of the trip.

Prior distributions and model fitting

We defined prior distributions and constraints for the model parameters to incorporate existing knowledge and optimize sampling from the posterior distribution. For the horizontal movement component, we used the same priors as in the R package *bsam* (Jonsen et al. 2013). Where there were missing values in the total number of dives per day, truncated Gaussian priors were provided, centered on the median value of the variable for the corresponding individual, with standard deviation 1 and truncation at the extremes of the observed range for that variable. All other priors and constraints are summarized in Table S1 in Supplementary material.

The model was fitted in a Bayesian framework using JAGS run from R (library runjags) (Denwood 2016). Markov Chain Monte Carlo (MCMC) algorithms were first optimized during 5,000 adaptation iterations, and then iterated until convergence of the parameters. We ran three parallel chains, starting at different initial values. Convergence was assessed by visually inspecting trace and density plots, in order to identify an appropriate size of the burn-in, which was then set to 50,000 iterations. Convergence was also confirmed by checking that the Brooks-Gelman-Rubin diagnostic fell below 1.1, and that the Monte Carlo error was less than 5% of the sample standard deviation. There was substantial autocorrelation in the posterior samples for some of the parameters (e.g. δ) despite several attempts at re-parameterizing the model, which required us to run each chain for 900,000 iterations in order to obtain a large enough effective sample size (≥ 400) to approximate the posterior distribution (Lunn et al. 2013). For ease of computation and storage, we thinned the chains. We retained one in every 150 iterations, since preliminary investigation suggested this would make the posterior samples independent. The joint likelihood (as in McClintock et al. (2013)) and the JAGS code for the model are provided in Appendices S3 and S4 in Supplementary material.

Using the feeding component to simulate the effects of disturbance

Understanding the fine scale temporal dynamics of an individual's feeding activity and changes in condition is critical when simulating the effects of disturbance. In particular, disturbance can be quantified in terms of the lost feeding opportunities a female experiences and their effect on her condition when she returns to shore to pup (New et al. 2014). In order to use the model presented here to this purpose, it is first necessary to verify

that the feeding component (i.e. the estimates of feeding activity over a trip) can reasonably predict the changes in lipid reserves in the absence of the information provided by the drift rate in the observation model. Therefore, we computed the lipid mass at each time step using the posterior estimate of feeding activity in that day and the individual-specific parameters, starting from the estimated value of lipid mass at departure. We then compared these projected estimates with the posterior estimates of lipid mass obtained using the full (process and observation) model. We sampled 10,000 random values of feeding activity, lipid mass at departure and model parameters from the posterior distribution to account for the observed uncertainty in these quantities.

To demonstrate the ability of the model to predict the consequences of disturbance, we chose one individual with a typical lipid gain trajectory and for which estimated and projected lipid mass matched well (individual 10, ID 2005027). We then simulated five scenarios of increasing disturbance, i.e. corresponding to 10, 30, 50, 70, 100 lost feeding days. On these days, the feeding activity was set to the minimum observed for that individual. We then used the same procedure described above to calculate the time series of lipid mass based on feeding activity and the estimates of the model parameters. We distributed disturbed days over the course of a foraging trip in five different ways: randomly, in the first part of the trip (starting on day 1, forward), in the last part of the trip (starting on the last day, backward), removing the days when feeding activity was lowest, or removing the days when feeding activity was highest.

Results

The 26 tracks of female northern elephant seals corresponded to 21,733 satellite fixes. All model parameters showed satisfactory convergence (Table S2 in Supplementary material). The horizontal movement component of the model returned the animals' corrected and regularized locations, resulting in 5,827 daily positions (Fig. 1). Moreover, it identified periods where individuals engaged in transit and ARS behavior (Fig. 1). Behavioral state at each location was extracted from the posterior estimates, following the criteria suggested by Jonsen et al. (2007) to reflect uncertain classifications (i.e. whenever the posterior mean was ≥ 1.25 and ≤ 1.75). As a result, the behavioral state was uncertain in 12% of all locations. The seals spent 27% of the remaining time, on average, in ARS behavior, with large individual variability (Table S3 in Supplementary material).

The feeding component of the model characterized the variation in feeding activity over the duration of a trip (Fig. 2). Most individuals were found to increase their feeding activity in the central part of the trip, but there was a large degree of heterogeneity in fine-scale individual strategies (Fig. 2). As expected, being in ARS mode had a positive effect on feeding activity and 40% (SD = 18) of the total feeding activity occurred while in this mode, but animals were also estimated to be feeding in transit, particularly while returning to the colony. On average, the total number of dives had a negative relationship with feeding activity when an animal was negatively buoyant, while ascent rate had a positive effect when the animal was positively buoyant. However, the individual random effect on the $\beta_{i,p}$ parameters suggested substantial individual differences in both the mean feeding activity (as represented by the model intercept) and the effects of the covariates. The results

of the alternative version of the model that used bottom time to inform this component highlighted some fine-scale differences in the relative amount of feeding activity on any given day, although the overall pattern across the trip remained comparable (Appendix S5 and Fig. S6).

The condition component of the model estimated the variation in lipid mass over the duration of the trip (Fig. 3). Model intercept was negative, reflecting the decrease in lipid mass from one day to the next as the result of energy expenditure, while feeding activity led to an increase in lipid mass. As highlighted in Schick et al. (2013), lipid mass initially declined as a seal left the colony, rapidly increased during the main foraging phase of the trip and then decreased slightly while the individual was returning to the colony. The relative magnitude of the decrease in lipid mass during the outward and return phase of the trip is affected by the shape of the functional form for the lean mass (here, a linear increase of female lean mass, accounting for pup mass in the final third of the trip). Individual 11 (ID 2005028) and 22 (ID 2006057) were exceptions to this overall trend, showing an initial short burst of lipid accumulation (corresponding to a burst in feeding activity) but returning from the trip with less than average lipid mass. Individual 11 also showed a different spatial use of the range, engaging in a shorter trip in the coastal area close to the colony, during which it appeared to feed at a high rate (Fig. 4). In contrast, individuals foraging in the pelagic transition zone performed longer trips, with lower but highly variable mean daily feeding activity, leading to a larger but variable accumulation of lipids (Fig. 4). Finally, the trips of individuals foraging in the North-eastern Pacific showed intermediate features (Fig. 4). Estimates from the three model components were combined to visualize the spatial

variation in feeding activity and lipid mass over the course of the foraging trip (Fig. S2 in Supplementary material).

The posterior estimates of the lipid mass across the trip showed a satisfactory match with the projected estimates calculated using the posterior estimates of feeding activity (Fig. S3 in Supplementary material). The mean difference between the lipid mass measured at the end of the trip and the final lipid mass estimated using the time series of feeding activity was 3.4 kg (SD = 3.5), corresponding to 4% of the mean total lipid gain over a trip. The choice of functional form for the variation in lean mass over the trip had an effect on both the lipid mass and the feeding activity estimates (Fig. S4 in Supplementary material). While the overall trend remained similar, the relative difference in lean mass in different portions of the trip affected buoyancy and the resulting estimate of lipid mass. As a result, the corresponding feeding activity required to support the changes in lipid mass also shifted. Under the second functional form (accumulation of the female's lean mass in the first third of the trip with no influence of pup mass (Schick et al. 2013)), lean mass was assumed to be higher earlier in the trip (Fig. S1 in Supplementary material). Therefore, individuals were estimated to accumulate more lipid mass in this phase, to ensure sufficient buoyancy to justify the observed drift rate. Similarly, their decrease in lipid mass in the return phase of the trip was more marked.

When simulating the effects of disturbance for a sample individual, the severity of the effect increased with the number of lost feeding days, during which feeding activity was minimized (Fig. 5). However, the way in which lipid mass was affected was highly dependent on when disturbance occurred (Fig. 5). The disturbed female was found to be

able to compensate better overall when disturbance occurred in the first phase of the trip, leading to a reduction of the final lipid mass ranging between 3% (for a 10-day disturbance) and 82% (for a 100-day disturbance) compared to the lipid mass in the baseline scenario. However, severe disturbance (≥ 50 days) at the start of the trip was predicted to cause the lipid mass to approach or even fall below 0, which would correspond, in reality, to the individual dying of starvation. This outcome resulted from the animal not having sufficient reserves shortly after leaving the colony to buffer the lack of feeding activity. In contrast, disturbance concentrated in the last phase of the trip or randomly over the trip led to a higher reduction in the final lipid mass (6-88% and 7-87%, respectively), although lipid mass followed a different temporal pattern. In both scenarios, the animal was not at risk of starvation, except under the most extreme disturbance (100 days). If the disturbance occurred on days when feeding activity was lower, a large number of disturbed days had a relatively smaller effect (ranging between 1% for a 10-day disturbance and 52% for a 100-day disturbance). Conversely, removing days with high feeding activity had a strong impact on the accumulation of reserves (corresponding to a 12-100% reduction in lipid mass at the end of the trip), even when the number of disturbed days was comparatively low (e.g. 30 days; Fig. 5). In this scenario, more than 70 disturbed days were predicted to lead to starvation.

When we assumed females accumulated all lean mass during the first third of the foraging trip, the effects of disturbance were generally predicted to be smaller (Fig. S5 in Supplementary material). Specifically, the lipid mass at the end of the trip was, on average, 6% (SD = 6), 8% (SD = 10) and 4% (SD = 2) greater than under the first functional form

for the scenarios with disturbed days distributed randomly, when feeding activity was lower and when feeding activity was higher, respectively. Because individuals were predicted to accumulate a larger lipid mass in the first phase of the trip, the difference was even more pronounced when disturbance was concentrated at the end, with a 16% (SD = 11) larger final lipid mass under the second functional form. For the same reason, the difference was less pronounced when disturbance concentrated in the first part of the trip. In this scenario, the final lipid mass was greater (2.6%; SD = 2.4) using the first functional form, but the larger buffer under the second form kept the animal further away from starvation during the disturbed period. The results of simulated disturbance were also partly affected by the choice of dive metrics for the feeding component: using bottom time resulted in the lipid mass at the end of the trip being larger across scenarios (Appendix S5 and Fig. S7).

Discussion

We developed a spatially-explicit behavioral model to monitor how a marine predator's condition varies as it moves through the environment encountering prey resources. The approach has the advantage of including an explicit model for feeding activity, which represents the intermediate step between movement and condition. It explores the reciprocal influences of movement on feeding activity and of feeding activity on condition and, as a result, captures the underlying functional processes that regulate an individual's ecology and decisions while it uses its habitat.

The model can therefore be used to answer fundamental questions on the feeding ecology of the target species. Particularly, it allows the identification of the areas and times that are most important for foraging, as well as the relative amount of feeding activity occurring at these locations. Moreover, our results shed light on how movements are paired with feeding. Seals were found to exploit localized feeding grounds, but also feed opportunistically while travelling if the opportunity arose (Thums et al. 2011), especially during the return trip to the colony. Importantly, the fitness implications of these behavioral strategies can be assessed by looking at the resulting variation in condition, which in turn affects the condition and survival of their offspring (McMahon et al. 2000; McMahon et al. 2003). In the case of the elephant seals analyzed here, individuals in the pelagic transition zone showed larger variability in feeding and condition compared to animals in the North-eastern Pacific, suggesting that feeding in the latter region could be more reliable. However, some individuals in the pelagic transition zone could achieve higher feeding activity and lipid deposition than animals in the North-eastern Pacific, as indicated by higher maximum values in Fig. 4. The single animal that remained along the coast travelled a shorter distance and was estimated to feed more per day, but was able to accumulate smaller lipid reserves compared to animals in the two other regions, a finding that matches the results for coastal animals in Schick et al. (2013). However, a larger sample is needed to draw robust conclusions regarding this strategy. Some of these patterns could also emerge from the animals losing lean mass (resulting in a buoyancy gain), a process that cannot be detected by the model. The hierarchical structure of the model explicitly quantifies individual differences in behavioral strategies, which have been shown to interact with environmental variability to affect individual fitness (Abrahms et al. 2018).

Our modelling approach is directly applicable to the marine mammal species that are known to perform drift dives (Lesage et al. 1999; Page et al. 2005). Many other species of diving animals swim by alternating stroking and gliding during the ascent or descent phases of their dives (Williams et al. 2000). The gliding rate, which is also affected by an individual's buoyancy, could therefore be used to track the variation of condition over time (Nowacek et al. 2001; Miller et al. 2004; Miller et al. 2016), although this would require the appropriate modification of the observation model. In addition, gliding periods can only be characterized using high-resolution tags, which currently have short deployment durations in cetaceans. New analytical techniques for more efficient onboard processing and data transmission will help overcome some of these limitations (Cox et al. 2018).

Because the main objective of this study was to develop an approach to model movement, feeding and condition within the same analytical framework, we chose to inform the feeding component by parsimoniously selecting the dive metrics that best correlated with drift rate, under the assumption that successful feeding would lead to higher accumulation of lipid mass and thus higher buoyancy. Therefore, these metrics acted as data-driven proxies of feeding activity, in line with other studies that found features of the diving behavior (here the number of dives per day and the median ascent rate) and of the horizontal movement (comparable to the use of transit rate in previous studies) to correlate well with feeding activity (Thums et al. 2008; Robinson et al. 2010; Gallon et al. 2013; Viviant et al. 2014; Vacquié-Garcia et al. 2015). However, dive metrics could be partly confounded with the effects of buoyancy on animals' diving abilities. Future work could re-parameterize the feeding component using data from accelerometer sensors, which lead to a

more direct identification of successful prey capture events (Naito et al. 2013; Guinet et al. 2014), allowing feeding activity to be interpreted in absolute, functional terms and translated to an explicit measure of energy intake. Moreover, when we tested the sensitivity of our results to the dive metrics selected (Appendix S5), we found that, while the overall pattern was retained, differences in the estimated feeding activity could substantially affect the predicted effects of disturbance. Therefore, when using the model to predict the effects of disturbance, more proximate measures of feeding success should be used, or the use of multiple dive metrics could be explored (Robinson et al. 2010). Our analysis also suggests that what constitutes a suitable proxy may change over the course of the trip, particularly as the condition and buoyancy of the animal (and thus its diving performance) changes (Adachi et al. 2014), and that the relationship of these proxies with feeding may vary among individuals (Robinson et al. 2010). Future work should also explore whether the selected metrics are consistent proxies of feeding activity at different temporal scales (Viviant et al. 2014; Vacquié-Garcia et al. 2015) and across the range of habitats used by the animals, as this may affect the estimation of feeding activity in space and time.

Characterizing these links is critical to developing predictive tools for assessing the effects of human activities and environmental changes on species that are exposed to an increasing variety of stressors (Crain et al. 2008; National Academies 2017). Anthropogenic disturbances are known to interfere with the natural activity patterns of animals (Frid and Dill 2002), particularly by interrupting their feeding activity (e.g. DeRuiter et al. 2016). Therefore, the ability to simulate reduced feeding activity during a trip allows explicit modelling of the processes mediating the effects of disturbance. Similarly, changes in

climate will affect prey availability and distribution, which might also impact feeding activity (Crocker et al. 2006; Hazen et al. 2013). A strength of our approach is that disturbance can be simulated at any point during a foraging trip, with variable pattern and duration. Therefore, the animals' vulnerability during different phases of a trip or in different regions and their ability to compensate for missed feeding opportunities can be explicitly explored. As an example, we used the time series of feeding activity from one female to simulate different patterns of disturbance. We found large variability in the predicted effect of disturbance on the final lipid mass depending on when it occurred during a trip. The female was predicted to compensate more efficiently for disturbance occurring early on in the trip, when feeding activity was also lower, but during this phase she was found to be at a higher risk of starvation due to the limited buffer reserves available at departure from the colony. In contrast, disrupting the individual's feeding activity in important foraging patches (as exemplified in the scenario where disturbance concentrated on days of high feeding activity) was shown to potentially lead to dramatic consequences. Female elephant seals have been shown to decrease their residence times in prey patches as a result of environmental disturbance from El Niño Southern Oscillation (Crocker et al. 2006). Simulating the effects of disturbance by reducing an individual's feeding activity on given days is therefore appropriate to model behavioral responses to anthropogenic and environmental stressors. However, an exhaustive simulation across all individuals should be carried out before drawing any general conclusion on the predicted consequences of disturbance. Such simulation should also consider the ability of individuals to compensate for disrupted foraging by increasing the duration of their foraging trip (Crocker et al. 2006).

The functional form assumed for the variation in lean mass over the trip was found to have a substantial influence on model results. A mechanistic understanding of the patterns of female and fetus growth over the trip will be required to clarify this uncertainty, but, in the absence of such information, multiple functional forms can be used to provide a range of severity of the predicted effects of disturbance.

Tracking animals' condition and how it varies as the result of their behavior and the environment they encounter is one of the key challenges for marine organisms (Crossin et al. 2014). From a theoretical perspective, it allows us to understand the functional processes that regulate an individual's decision-making and resulting fitness. From an applied perspective, quantifying these functional links forms the basis for predicting the effects of the environmental and anthropogenic stressors on their populations (Halpern et al. 2008). Here, we presented an analytical approach that tackles this challenge and can be extended and adapted to multiple species and contexts.

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Data accessibility statement

Analyses reported in this article can be reproduced using the data provided by Pirotta, Schwarz, et al. (2018).

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Figure legends

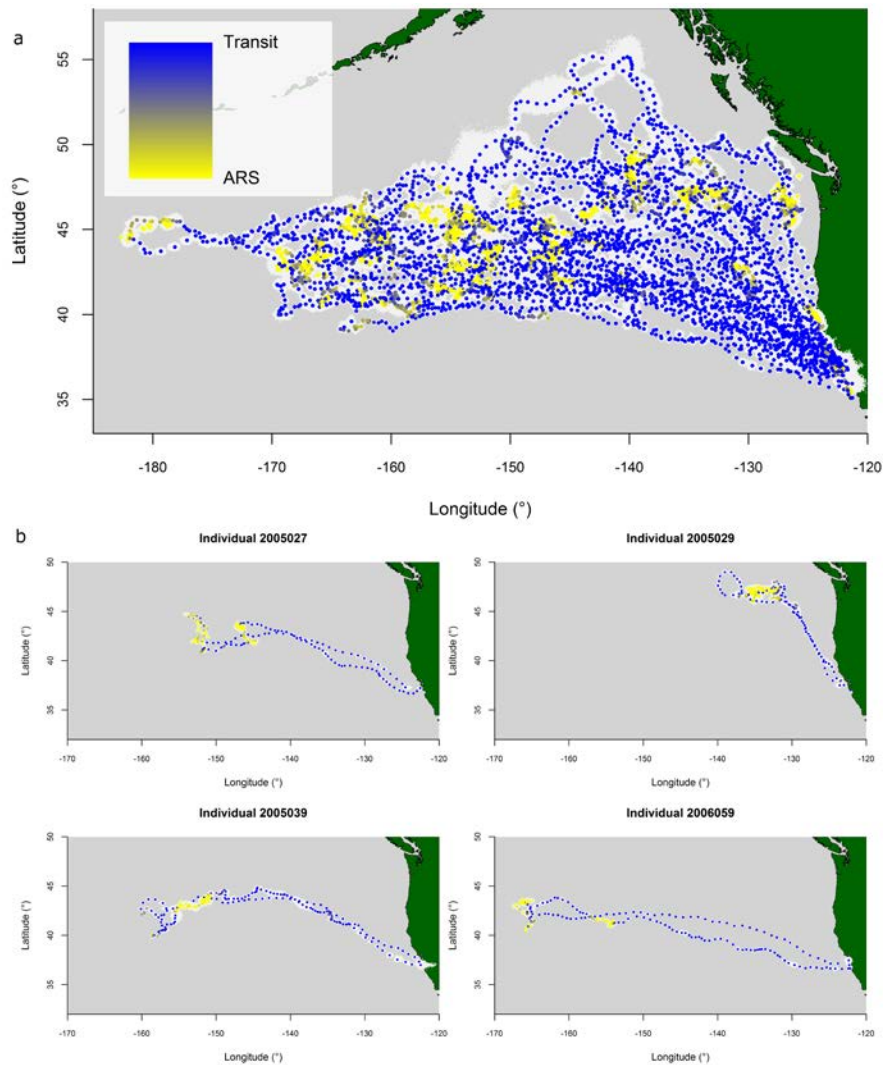


Figure 1. Results of the horizontal movement component of the model. Locations are colored based on the posterior estimate of the categorical behavioral mode. The gradation of colour between the extremes (blue for state = 1, transit, and yellow for state = 2, area restricted search [ARS]) indicates the ability of the model to assign a univocal state to each location (Jonsen et al. 2007). The uncertainty around the estimated locations is shown in white. a) All tracks; b) separate tracks of four animals, as an example.

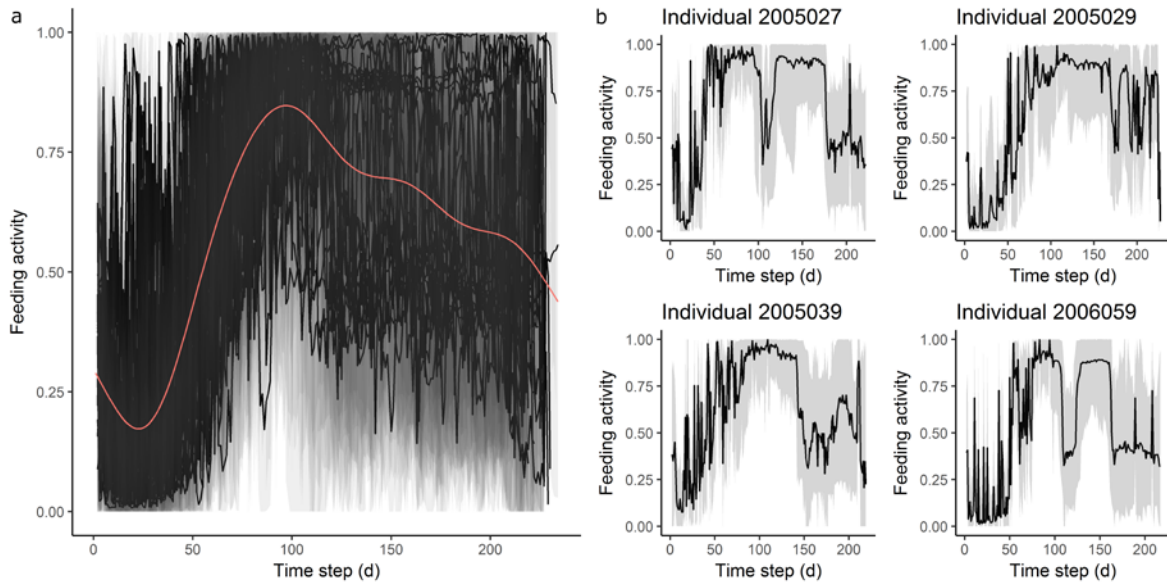


Figure 2. Results of the feeding component of the model. Feeding activity varies between 0 and 1, and can be interpreted as the proportion of some maximum feeding that an individual can achieve on a day. a) Results for all tracked seals, with the black line representing median feeding activity, and the grey region the uncertainty around these estimates. In red, the overall trend estimated as a thin-plate regression spline fitted using function `gamm` in package `mgcv`, with a random effect by individual (Wood 2006). b) Variation of feeding activity for four individuals, as an example.

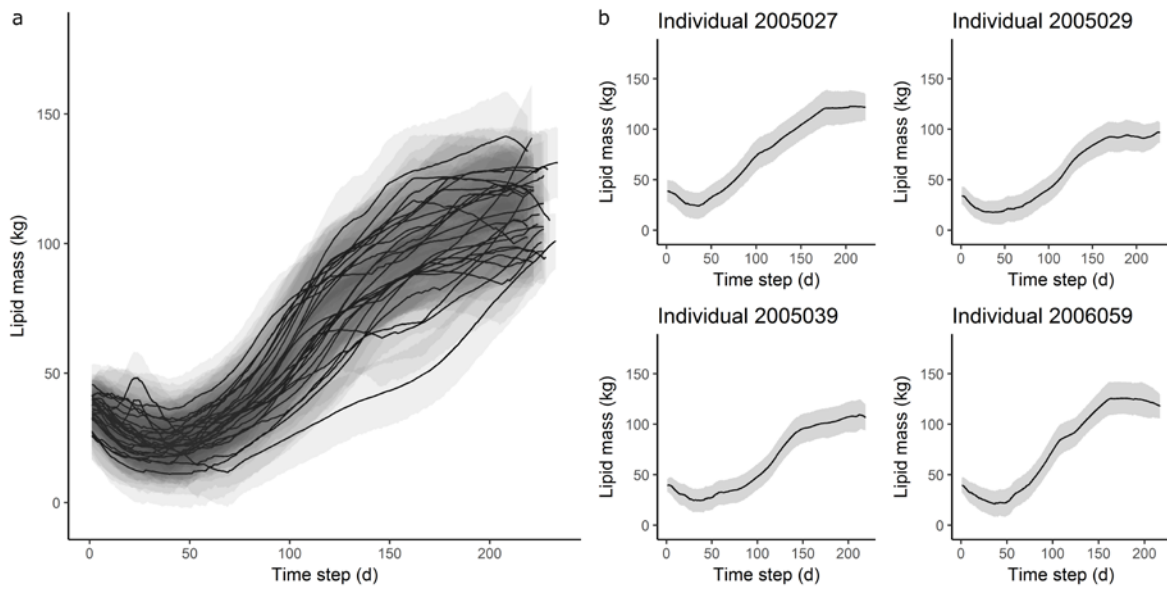


Figure 3. Results of the condition component of the model. a) Variation in lipid mass for each individual as the trip progresses, with the black line representing the median individuals' lipid mass (kg), and the grey region the uncertainty around these estimates. b) Variation in lipid mass of four individuals, as an example.

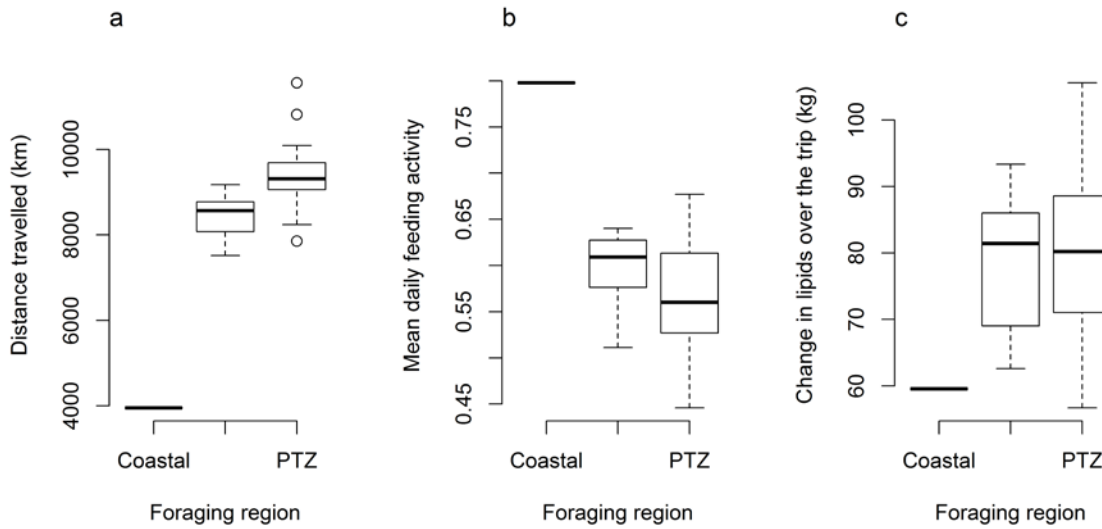


Figure 4. Characteristics of the foraging trips by region where most of the foraging occurred. a) Total distance travelled; b) mean daily feeding activity; c) total change in lipids over the trip. The foraging region was classified as either coastal (1 individual), North-eastern Pacific (NEP; 7 individuals) or pelagic transition zone (PTZ; 18 individuals). The distribution of the response variables was summarized using box plots, where the box represents the inter-quartile range, the whiskers extend to 1.5 times the inter-quartile range from the box, and the black line is the median.

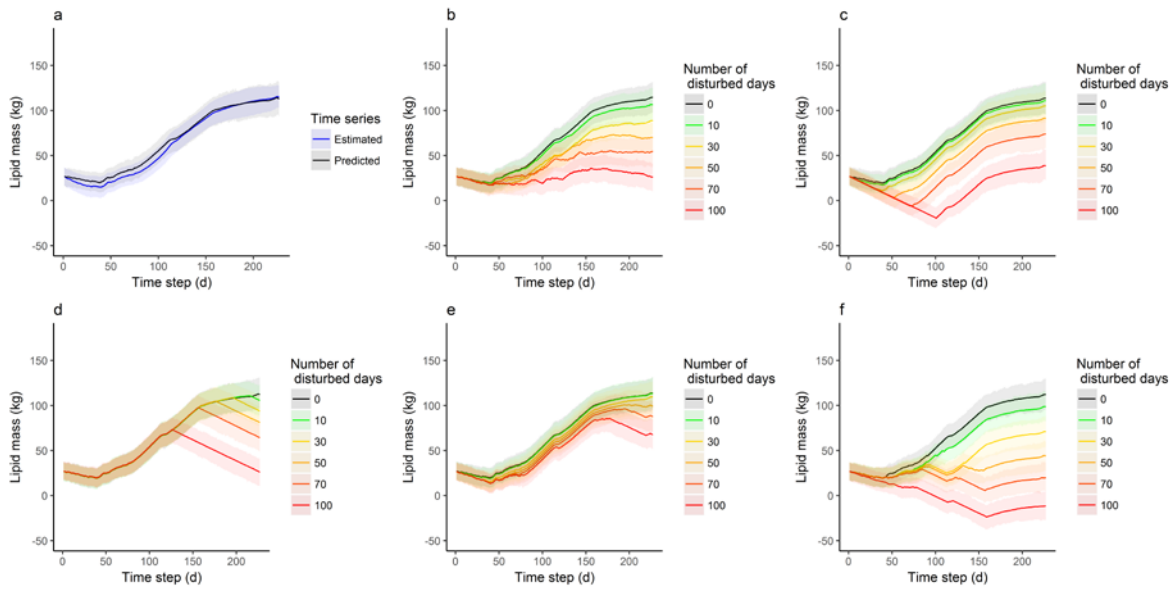


Figure 5. Simulated effects of an increased number of disturbed days on the lipid mass of individual 2005027. a) Posterior estimates of the lipid mass overlaid with the time series of lipid masses obtained using the estimated feeding activity on each day. In b)-f) disturbed days are distributed randomly, at the start of the trip, at the end of the trip, on days of low feeding activity and on days of high feeding activity, respectively. The shaded areas represent the uncertainty around the lipid mass predicted for each scenario. The horizontal dashed line represents a lipid mass of 0 kg.