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Drivers of behavioural transition in foraging adult female southern elephant seals (*Mirounga leonina*) tracked from Bouvetøya

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*Cover: Southern elephant seal (Mirounga leonina), captured at Bouvetøya 2015
Photo: Chris Oosthuizen*

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ABSTRACT

Southern elephant seals are abundant top trophic predators with a circumpolar distribution in the Southern Ocean. They spend up to 80% of their life at sea on long-ranging migrations to remote foraging grounds. During breeding and moulting they haulout on subantarctic islands. During these migrations they dive continuously to great depth, encountering various environmental conditions. They are further known to target frontal areas and mesoscale eddies. Due to ecosystems changing, with high latitude areas being especially sensitive, it is of major importance to understand behavioural drivers in order to predict how they will react.

They display site fidelity (breeding), allowing for retrieval of telemetry tags collecting high resolution data. In this study, data from five adult female southern elephant seals tracked from Bouvetøya in 2015 were analysed. This data covered their post-moult foraging migration. By identifying changes in move persistence values along the tracks, behavioural transitions periods were extracted to study the post-moult foraging behaviour of female southern elephant seals. More specifically, the dive and feeding efficiency during transition zones, defined as significant changes horizontal movement persistence, was analysed as a function of depth and physical features such as the mixed layer depth, top of circumpolar deep water as well as subsurface maximum.

Keywords: southern elephant seal, foraging behaviour, move persistence, animal telemetry

ABBREVIATIONS

Abbreviation	Definition
ACC	Antarctic Circumpolar Current
ARS	Area-restricted search
CROPS	Changepoints for a range of penalties
CTD-SRDLs	Conductivity-temperature-depth satellite relay data loggers
DD	Dive depth
DE	Dive efficiency
FE	Foraging efficiency
LME	Liner mixed effects model
MLD	Mixed layer depth
PELT	Pruned Exact Linear Time
PF	Polar Front
SAF	Subantarctic Front
STF	Subtropical Front
subMAX	Subsurface temperature maximum
topCDW	Top of circumpolar deep water

1 INTRODUCTION

The Southern Ocean, generally defined as the global ocean South of 35° S latitude, is characterised by the Antarctic Circumpolar Current (ACC) and its frontal structures (Chapman et al., 2020; Sokolov & Rintoul, 2009). Flowing in a clockwise direction around the Antarctic continent, the current plays a key function in global ocean circulation and productivity by controlling the mixing of the upper and deep waters of the world (Frölicher et al., 2015; Murphy et al., 2013). As a result, the ACC majorly impacts the climate and biogeochemical cycles at a global scale by regulating the oceans capacity to both store and transport carbon dioxide and heat (Rintoul, 2018). The fronts concentrated within the ACC can be considered as oceanographic boundaries between water masses with differing properties, such as salinity and temperature (Orsi et al., 1995; Sokolov & Rintoul, 2009). As a consequence, these act as a barrier for north-south exchange of water, resulting in the Southern Ocean being highly biogeographically isolated (Clarke et al., 2005). Three major fronts are recognized: The Subtropical Front (STF), the Subantarctic Front (SAF) and the Polar Front (PF) (Belkin & Gordon, 1996). The northern boundary of the ACC is distinguished by the STF, where the surface water properties are differentiated from the warmer and saltier waters of lower latitudes. Below this front, the ACC flows around the globe undisrupted, uniquely connecting ocean basins (Orsi et al., 1995). Further south, the SAF separates the Subantarctic zone in the north from the Polar frontal zone in the south, whereas the PF is identified as the area where cold Antarctic surface water sink below the Subantarctic water (Orsi et al., 1995). Fronts and other mesoscale features such as eddies are known to serve as favourable foraging grounds for top predators such as seabirds and marine mammals (Bailleul et al., 2010; Bakun, 2007; Dragon et al., 2010). This is mainly a result of locally enhanced primary production, which further attracts prey species to the area. Increase in prey abundance has also been suggested to be caused by convergence processes, transporting marine organisms to the frontal zones (Murphy, 1995).

Animal movement is driven by the need of an individual to fulfill its life history requirements, such as energy acquirement, mating, avoiding predators as well as staying within its physiological optima (Shaw, 2016). In marine predators, the spatial distribution and density of prey is a fundamental predictor of its movement patterns (Goldbogen et al., 2015; Womble et al., 2014). Vast ranging migrations are often costly due the high energetic need of locomotion,

but this behaviour persist as the overall fitness of the animal is increased (Dingle, 2014). This is also predicted by the optimal foraging theory, which states that an animal will adjust its movement behaviour to maximize net energy gain (MacArthur & Pianka, 1966; Pyke, 1984). As a prey aggregation is encountered, the predator will respond by altering its horizontal and vertical movement patterns in order to intensify foraging within the patch (Charnov, 1976; Thums et al., 2011). For several species, this is exhibited as a behaviour termed area-restricted search (ARS) (Kareiva & Odel, 1987) and can be observed as a decrease in swimming speed and increase in turning rates (Jonsen et al., 2005). As the prey aggregation becomes depleted, the animal is expected to alternate its prey species to transit to another prey patch (Van Baalen et al., 2001). The transitioning should occur in a way that minimizes time spent between foraging areas (Jonsen et al., 2005), and is characterised by lower turning rates and an increase in displacement speed (Fauchald and Torkild, 2003). As a result, changes in horizontal movement patterns have been used by several studies as proxies for identifying foraging behaviour in marine predators (Bailleul et al., 2008). However, this does not capture the four-dimensional structure of the marine environment (time, depth, and space) and the way air-breathing mammals utilize the vertical aspect of the ocean (Dragon et al., 2012). Vertical structuring of the ocean is of major importance for creating areas of high productivity due to its physical gradients, and the concentration of prey species is often targeted by predators (Dragon et al., 2012). These gradients, already touched upon earlier, are especially strong in polar areas due to the high seasonality (Nicholls et al., 2008).

Quantifying spatiotemporal distribution and foraging effort of marine predators allows us to gain a greater understanding of ecological patterns and processes in marine environments such as resource availability (Melbourne-Thomas et al., 2013). Data collection in remote regions has previously been limited by logistical challenges. However, advances in animal-borne data loggers and satellite tracking technologies have transformed our ability to collect data in otherwise inaccessible areas (Aarts et al., 2008). As *in situ* oceanographic parameters, such as salinity, conductivity and temperature, are recorded simultaneously with diving and movement behaviour, we gain a better understanding of the effect of environmental variability on movement patterns exhibited (Costa et al., 2010). Equipping seals with environmental collectors is of great importance for studying the spatio-temporal dynamic ocean physics in remote and inaccessible regions such as many Southern Ocean areas (Fedak, 2004). These under-sampled areas are often the ones of high interest due to their physical and biological aspects, as well as role in regulating global climate (Pauthenet et al., 2018). Although animals

act as so called “adaptive samplers” and collect data in an irregular way, they often target areas of importance, such dynamic ocean structures where resource availability is high (Guinet et al., 2001). Data gained from animal tracking has majorly improved our knowledge on seasonal distribution, movement ranges as well as allowing more reliable population estimates to be calculated for several species (Hays et al., 2019). This, together with a better knowledge of important foraging ground as well as resource distribution, is of high value for conservation policy and allows for designation of area protective boundaries and management programmes (Hays et al., 2019).

Colony-based marine mammals that haul out for breeding and moulting are considered as central place foragers (CPF) during breeding (Olsson & Bolin, 2014). CPF are animals with a home range and are often associated with migrations to distant foraging grounds. A suggested cause for this behaviour is related to density dependence, resulting in prey depletion in proximity of the colony (Ashmole, 1963) or more profitable foraging areas being spatially separated (Oppel et al., 2015). For this reason, central place foragers are ideal subjects for telemetry studies, as retrieved tags allows for a much greater resolution of data collected compared to data transmitted via satellite (Hays et al., 2016). Case in point being the southern elephant seal (*Mirounga leonina*), the largest of the pinniped species (Le Boeuf & Laws 1994). These vast ranging predators haul-out on sub-Antarctic islands for breeding (early September to mid-November) and moulting (December to March), but spend up to 80% of their life at sea on long-ranging migrations to remote foraging grounds (Hindell et al., 1991; McIntyre et al., 2010). In their pursuit of prey, consisting mainly of myctophid fish and cephalopods (Cherel et al., 2008) they perform some of the most impressive dives conducted by any mammalian species. They often reach depths of more than 1000 meters (McIntyre et al., 2010), and may remain submerged up to two hours (Le Boeuf & Laws 1994). In fact, most of their life is spent at depths of 300-400 meters, only to be punctuated by short two to three minute surface intervals (Hindell, Slip, et al., 1991). During their extensive dives and long migrations southern elephant seals encounter a wide range of differing environmental conditions and several studies has associated them with ocean features such as mesoscale eddies and fronts (Bailleul et al., 2010; Campagna et al., 2006; Massie et al., 2016). Divergence in foraging strategies has also been noted between the sexes, as males seemingly target the Antarctic continental shelf and ice zone habitats more often, whereas females exhibit a more pelagic foraging behaviour (Authier et al., 2012; Biuw et al., 2007; Biuw et al., 2010; Hindell et al., 1991; Labrousse et al., 2015).

Further, they display high sexual dimorphism, with males being up to ten times larger than females (Le Boeuf & Laws 1994).

This abundant top-trophic predator has a circumpolar distribution in the Southern Ocean (Le Boeuf & Laws 1994). Currently, four genetically distinct populations are acknowledged: the Kerguelen population in south Indian Ocean, the Macquire population in the south Pacific Ocean, Peninsula Valdés population in Argentina and the South Georgia population in the south Atlantic Ocean (McMahon et al., 2005). Out of these, the South Georgia population is the largest, hosting more than half of the global population (Boyd et al., 1996). These populations experienced major declines between 1950s to 1990s, and a decrease is still to be observed in the Macquire population and some Kerguelen subpopulations (McMahon et al., 2005). Observing changes in population size may be an indication of major changes within ecosystem function or structure (Barbraud & Welmerskirch, 2001). Currently, the Southern Ocean is experiencing a more rapid warming than the global average (Turner et al., 2014) with consequent increase in winds over the past decades (Meredith & Hogg 2006). It has been speculated that this could result in an increase in eddy activity and overall changes in frontal structures (Le Quere et al., 2007). As these features are known to be attractive foraging areas for southern elephant seal, it is important to gain an understanding of behavioural drivers, in order to predict how they will behave when facing differing environments.

The main objective of this thesis is to study the post-moult foraging behaviour of female southern elephant seals. More specifically, the dive and feeding efficiency during transition zones, defined as significant changes horizontal movement persistence, was analysed as a function of depth and physical features such as the mixed layer depth, top of circumpolar deep water as well as subsurface maximum.

2 MATERIAL AND METHODS

2.1 Study area and tag deployment

In this thesis the at-sea movements of seals from a small South Georgian subpopulation, namely the colony at Bouvetøya (54°25'S, 03°20'E). will be studied. The island is located at the Mid-Atlantic Ridge, south of the PF, with 1600 km to the Antarctic continent and 2600 km to Southern Africa. This colony has only been subject to a handful of previous studies (e.g. Biuw et al., 2010), therefore it is of great interest to gain a better understanding of the at sea movement patterns of these seals. In 2015, eight adult female southern elephant seals were tagged post-moult with conductivity-temperature-depth satellite relay data loggers (CTD-SRDLs, Sea Mammal Research Unit, St Andrews, UK) with GPS at Nyrøysa/Westwindstranda. This area is recognized as the island's largest suitable haulout area. The seals were immobilized and handled as described in (Baker et al., 1988; Field et al., 2002; McMahon et al, 2000) and animal handling occurred in accordance with the Regulation of Animal Experimentation of the Norwegian Animal Research Authority. The deployed instruments collect GPS and CTD data at very high resolution, but due to limited satellite bandwidth only a subset of the data was transmitted. Five tags were retrieved allowing the full dataset of GPS and CTD to be recovered and used for further analysis.

2.2 Data analysis

The collected data spans from the end of January to November and is covering their post-moult foraging migration. Locations on land and short post-breeding segments were removed. All analyses were performed using R Statistical Software (v4.1.1; R Core Team 2022).

2.2.1 Move persistence analysis

Horizontal changes in movement patterns were identified by estimating time-varying move persistence along the tracks using the *fit_mpm* function in the *foieGras* R package (Jonsen & Patterson, 2019). This model calculates the autocorrelation in speed and direction over successive locations, resulting in a continuum of move persistence values ranging from 0 (low persistence) to 1 (high persistence) across trajectories (Jonsen et al., 2019). Low move

persistence values are related to ARS behaviour, whereas high persistence values are indicative of travelling. This method represents the natural continuum of animal movements most accurately, as opposed to dividing transects into discrete behavioural states (Breed et al., 2012; Michelot et al., 2017)

To achieve regular location estimates along the tracks, a continuous-time correlated random walk state-space model was fitted to the data by using the *fit_ssm* function in the *foieGras* R package (Jonsen et al., 2019). Although the recovered GPS data is high in resolution, regular location estimates were considered more applicable for further analysis. As the above-mentioned autocorrelation between successive locations is influenced by the time steps used, comparisons were made of predicted move persistence over different time intervals (1h, 2h, 3h and 6h). As the mean time difference of recovered GPS locations was below one hour for each seal, a 1h time step was considered most suitable.

2.2.2 Changepoint analysis

To detect change in the seals migratory behaviour, changepoint analysis was applied to the derived move persistence values along the tracks. Changepoints are points where a change in statistical properties of a sequence of data can be observed and may therefore indicate transitions between different states (R. Killick et al., 2012). To identify multiple changepoints, the cost function was minimised over the possible number of changepoints and the locations of these (Eq. 1).

$$\sum_{i=1}^{m+1} [C(y_{(\tau_{i-1}+1):\tau_i})] + \beta f(m) \quad \text{Eq. 1}$$

C is the cost function of a segment, in which y is the signal and the τ_i is the number of splits. $\beta f(m)$ is a penalty to guard against overfitting the data, as adding changepoints always reduces overall cost. For this project Pruned Exact Linear Time (PELT) (Killick et al., 2012) algorithm was chosen as changepoint search method. Due to the pruning step involved, PELT is computationally efficient without reduction in accuracy of resulting segmentation and was therefore used for this project. The PELT search algorithm requires a penalty constant to avoid under- or over-fitting the data. This constant is user defined and not always straight forward to determine. To reduce subjectivity when deciding penalty value, changepoints over a range of

penalties (CROPS) developed Haynes (Haynes et al., 2017a) was used. This method results in optimal segmentations across a continuous range of penalty values and further allows evaluation of suitable penalty choices by creating a diagnostic plot of number of changepoints against the change in test statistic. Lavielle (2005) suggests choosing the segmentation where the most significant decrease in cost due to the addition of changepoints occur. As the penalty value is initially increased, true changes can be detected and the cost decreases rapidly. Eventually false positives (changepoints due to noise) are added and the change in cost will be small. As the cost noticeably changes it can be seen as an “elbow” on the plot and these points can then be considered the plausible range of segmentations. By inspecting the elbow plots, a penalty value of 0.6 was decided upon to obtain an optimal number of changepoints (Appendix A). A minimum segment length (Minseglen) of 72h was assigned as it was found to most accurately identify transition periods of interest (for details on Minseglen function within PELT, see Qiu et al., 2021). Above mentioned algorithms are all integrated into the changepoint R package (Killick & Eckley, 2014), and for this study, the identification of changes of mean was used.

2.3.3 Extraction of behavioural transition periods

For extracting behavioural transition periods along the animal’s movement trajectory, a time buffer was added before and after each identified changepoint. To discard data noise, a spline was fitted to the move persistence values using the function *smooth.spline* in R and further by calculating the difference of consecutive smoothed values. The beginning and end of a transition zone were determined as where the differential crosses zero. On some occasions, visual inspection showed that the behavioural transition continued past the first zero crossing and here the time buffer was extended. Further, the segments were labelled as IN or OUT, depending on whether the seal was entering or leaving low move persistence behaviour.

2.3.4 Diving parameters

Depth was recorded continuously at a temporal resolution of 4 seconds throughout the track. Individual dives with associated dive summaries were obtained using the *diveMove* R package by Luque (2007) These summaries include information on maximum depth attained, start time of each dive, end of descent and start of ascent, duration of each of these phases as well as the time spent at bottom and post dive duration (surface interval). *DiveMove* identifies dive phases by fitting a cubic spline model to each dive, and in this study the default unimodal regression

model was used. End of descent is then considered to occur at the location of first minimum derivative, whereas the beginning of ascent is detected by the reversed sign of comparison. Further, it provides a measuring of vertical distance covered during descent, ascent, and the bottom phase of a dive. The latter is a measure of up and down movement or “wiggling”, a movement that has been linked to foraging or search for prey (Hindell et al., 1991). We considered bottom distance as a proxy for foraging efficiency, while acknowledging that irregularities during the bottom phase of a dive is not always related to feeding.

Diving efficiency (DE) was calculated in accordance to Ydenberg & Clark (1989):

$$DE = \frac{\textit{bottom duration}}{(\textit{dive duration} + \textit{post_dive duration})} \quad \text{Eq. 2}$$

2.3.5 Environmental parameters

Four to twelve CTD profiles were generated daily, with data being collected every second during the ascent phase of dives. To examine how the elephant seals interact with or dive in relation to different water masses, the position of the mixed layer (MLD), the top of circumpolar deep water (topCDW) and the depth of subsurface maximum (subMAX) was inferred from water temperature readings. MLD and topCDW were identified using a derivative method. This approach requires a smoothing of the temperature profile, as results differentiating from a noisy profile can be hard to interpret (Kelley, 2018). Therefore, a smoothing spline using the *smooth.spline* function in R was fitted to the data and resulting maximum and minimum differentiated values were used to locate MLD and topCDW, permanent thermocline. For dives without CTD profiles, values for MLD, topCDW and subMAX were linearly interpolated using the *approx* function in R.

Coordinates for each dive were estimated by fitting a correlated random walk as a continuous-time model by the use of the *fit_ssm* function in R and by adjusting the *time.step* to the timing of each dive. As the coordinates were assigned, sun angle was assigned by the use of *solarpos* function in the *maptools* R package (APPENDIX B).

2.3.6 Modelling approach

Linear mixed effects models (LME) was used to test whether dive depth (DP) during a transition, diving and foraging efficiency (DE and FE), was influenced by MLD depth topCDW, subMAX as well as time of day ($day/night$). The general form of the fixed effect part of the model is:

$$g(\mu) = \eta = \alpha + \beta_1MLDdepth + \beta_2topCDW + \beta_3subMAX + \beta_4day/night + \beta_5IN/OUT + \beta_5IN/OUT:diveNO + \varepsilon \quad \text{Eq. 3}$$

Where $g(\cdot)$ is the link function, which transforms the expectation of the response variable to the linear predictor, μ is the expected value of the response (DP , DE and FE) and ε is the residuals that are assumed to be independent and identically distributed $N(0, \sigma^2)$. Individual was added as random effect. The models were fitted using the *lmer* function in the *lme4* R package. Model residuals were extracted and checked to approximate normal distribution (APPENDIX C). To investigate whether dive parameters change along a transit (rather than simply between IN and OUT transitions) we run a second model with diveNO as a continuous variable interacting with IN/OUT:

$$g(\mu) = \eta = \alpha + \beta_1MLDdepth + \beta_2topCDW + \beta_3subMAX + \beta_4day/night + \beta_5IN/OUT + \beta_5IN/OUT:diveNO + \varepsilon \quad \text{Eq. 4}$$

To see whether MLD, topMAX and subMAX as well as time of day were important predictors for both IN and OUT transitions, as well as only IN segments. This was done by adding number of dive within each segment to the equation.

3 RESULTS

3.1 Tracking

Summary of tag duration and mean frequency can be seen in Table 1. Mean tag longevity was 261 days with a range of 216 to 277 days, and a total of 41627 locations were recorded (mean 8184.2 ± 535.3 locations). As tracks were trimmed to only cover post-moult migrations, these spanned on average 226 days (range 203 to 236). Overall mean GPS location frequency for these was 41.4 ± 29.4 min. High individuality was to be observed in the seals movement patterns as can be seen in Figure 1. Two of the seals migrated over to South Georgia to breed, arriving at the island only 5 days apart in beginning of October. Breeding at Bouvet was observed by one individual in the end of September. The tracks of the two remaining seals did not cover the breeding haulout. However, one of them stopped by Bouvet for a couple of days in May, to then continue its foraging trip.

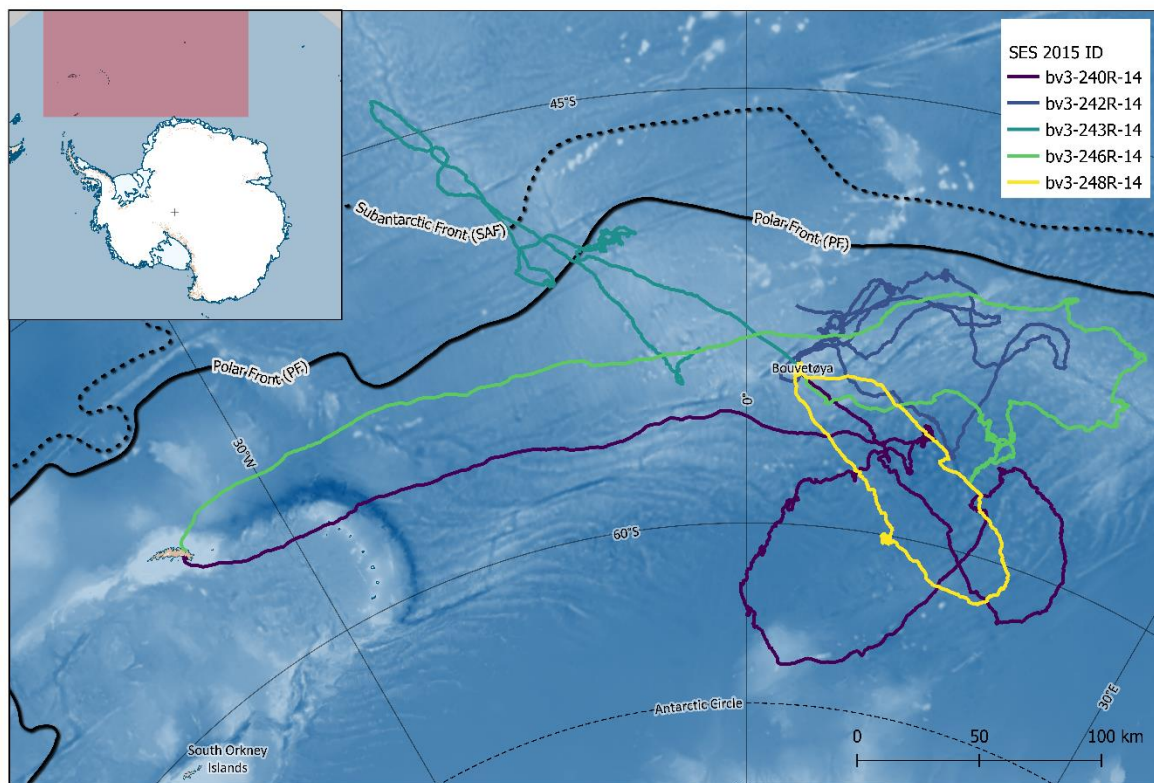


Figure 1 Map showing individual post-moult foraging tracks, colour coded for each animal. Polar front and Subantarctic front indicated by a black solid and dashed line, respectively. Map produced in Quantarctica (Matsuoka et al., 2018).

Table 1 Tag longevity and duration of trimmed tracks used for further analysis within the study (only covering post-moult migration), as well as mean frequency of trimmed GPS locations recorded.

ID	Tag longevity start - end	Trimmed start - end	Mean GPS location frequency (trimmed)	Breeding and other haulout
bv3-240R-14	2015-01-27 2015-10-30	2015-02-14 2015-10-01	37.61 ± 16.76 min	South Georgia
bv3-242R-14	2015-01-27 2015-09-01	2015-02-10 2015-09-01	47.22 ± 28.01 min	Breeding not covered, at Bouvet end of May
bv3-243R-14	2015-01-23 2015-09-15	2015-01-23 2015-09-15	47.43 ± 47.33 min	Breeding not covered, at Bouvet end of April
bv3-246R-14	2015-01-27 2015-11-24	2015-02-10 2015-10-06	41.43 ± 19.01 min	South Georgia
bv3-248R-14	2015-01-27 2015-10-31	2015-02-07 2015-09-30	40.29 ± 26.96 min	Bouvet

3.2 Movement characteristics

Move persistence along the seals movement trajectories can be seen in Figures 2a-e.

Seal bv3-240R-14 (Figure 2a) began its foraging migration on the 14th of February in a south-eastern direction, and first low move persistence movement occurred approximately seven days after leaving Bouvetøya on the 2nd of February. This was followed by several periods of moving in and out of high persistence, and in the end of August the movement changed to be highly directional during its migration to South Georgia, arriving there on the 1st of September.

Seal bv3-242R-14 (Figure 2c) left Bouvetøya 10th of February. Heading in an eastern direction, first lower move persistence was encountered on the 14th of February. This seal did a loop in north-eastern direction and returned to Bouvet for a couple of days in end of May. This was followed by another round trip in north-eastern direction, crossing its previous movement trajectory. The track ended on the 1st of September before haulout could be recorded, and the seal did not change its heading towards Bouvet at that point.

Seal bv3-243R-14 (Figure 2d) left Bouvetøya on the 23rd of January, moving with high persistence in a north-western direction. Lower move persistence behaviour was first exhibited mid-February, and it remained within this area until the middle of May. It then continued its migration to the north-east, doing a U-turn in beginning of May and moving in a directional manner back towards Bouvetøya with lower move persistence values noted at the end of the track. The collected data did not cover breeding haulout and ended on the 15th of September.

Seal bv3-246R-14 (Figure 2b) began its foraging migration on the 10th of February and first behaviour of lower mover persistence was to be observed approximately four days later. The migration was headed in an eastward direction with several periods of moving in and out of lower move persistence. Around the 8th of August it began its highly directional migration over to South Georgia in the west, reaching the island on the 6th of October.

Seal bv3-248-14 (Figure 2e) left Bouvetøya on the 7th of February, headed in a south-eastern direction. First lower move persistence was exhibited on the 16th of February. It changed its heading towards north in end of March, reaching Bouvet on the 23rd of April and remaining there for a couple of days. This was followed by five months of lower move persistence spent south-west in proximity of Bouvetøya. The seal hauled out to breed to breed on the 30th of September.

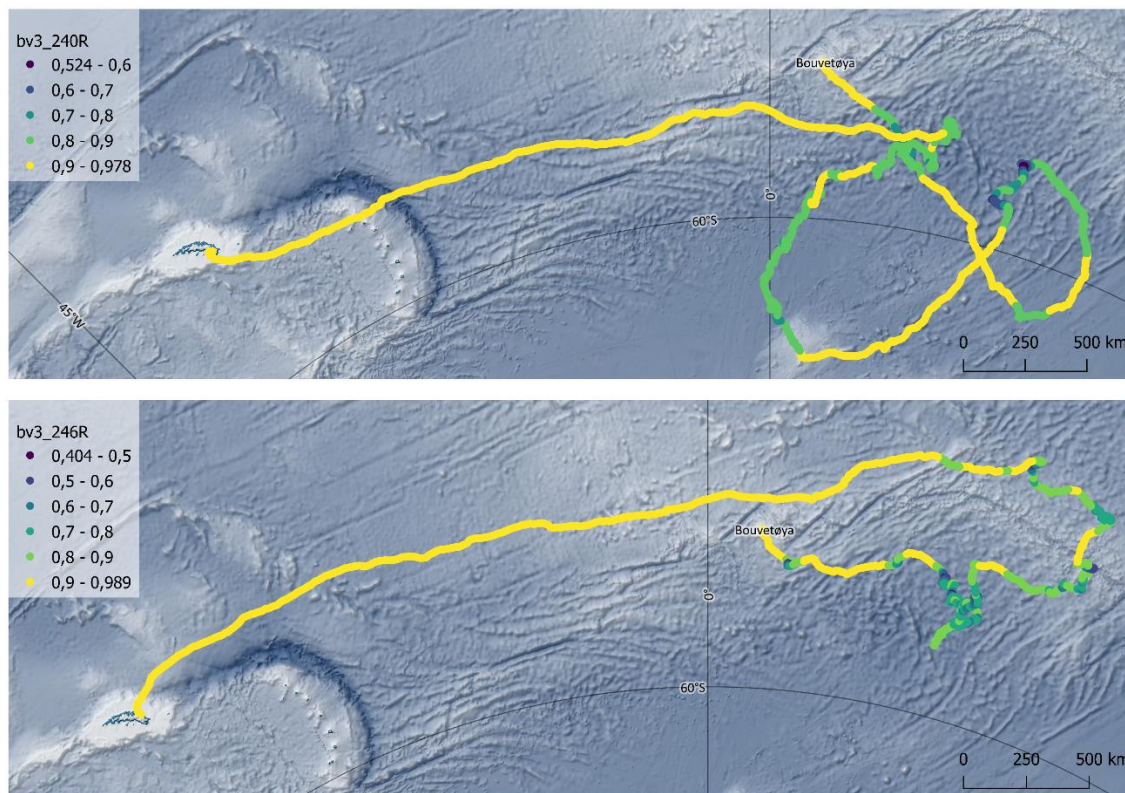


Figure 2a-b Post-moult migration of individual bv3-240R-14 & bv3-246R-14. High move persistence values (travelling) indicated by yellow, whereas low move persistence values are indicated by green-blue colour. Map produced in Quantarctica (Matsuoka et al., 2018).

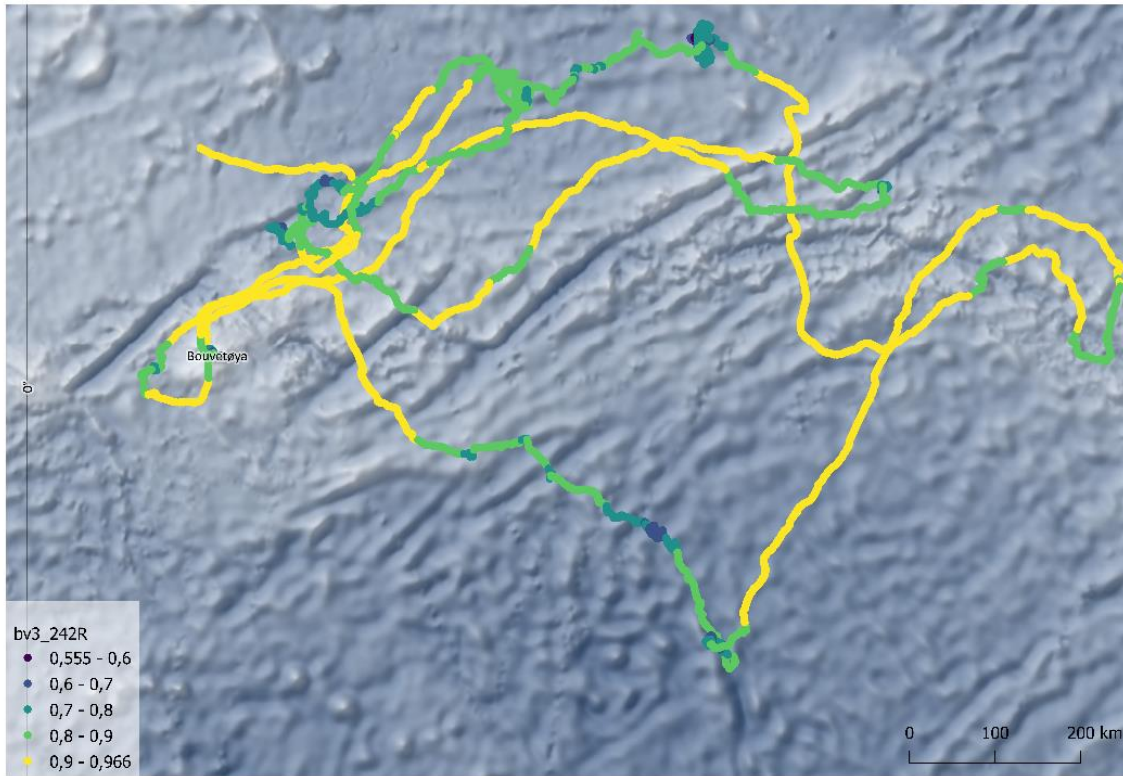


Figure 2c Post-moult migration of individual bv3-242R-14. High move persistence values (travelling) indicated by yellow, whereas low move persistence values are indicated by green-blue colour. Map produced in Quantarctica (Matsuoka et al., 2018).

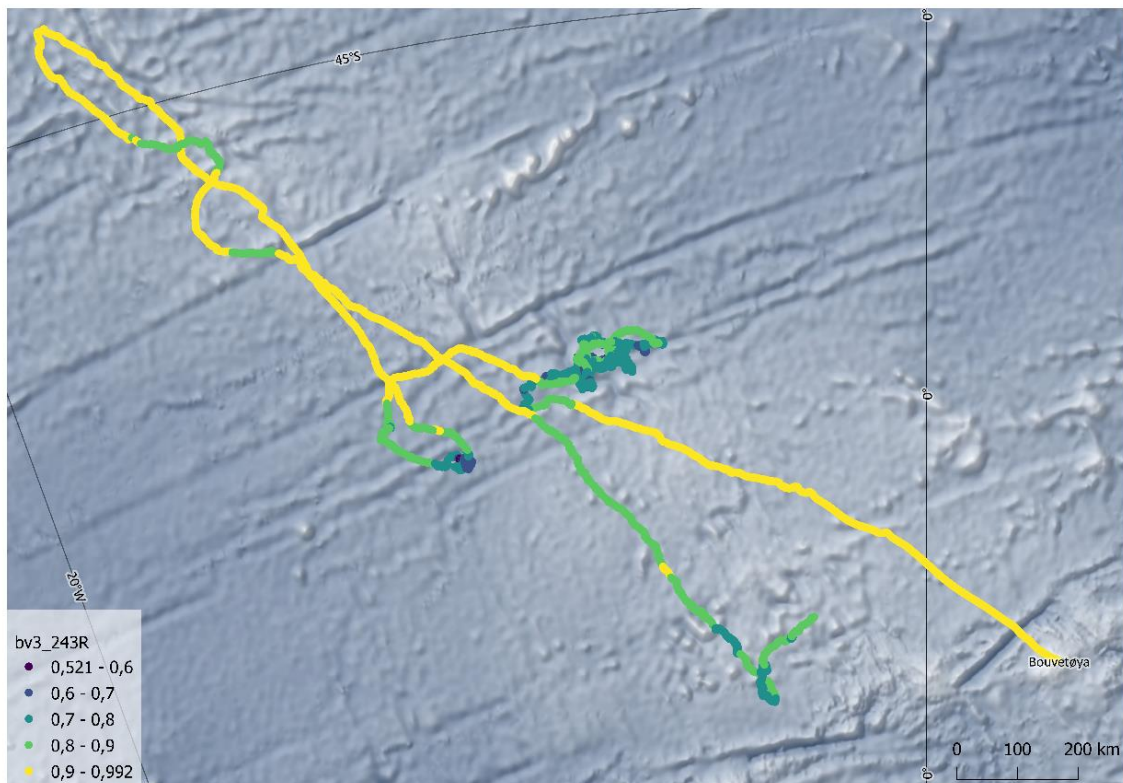


Figure 2d Post-moult migration of individual bv3-243R-14. High move persistence values (travelling) indicated by yellow, whereas low move persistence values are indicated by green-blue. Map produced in Quantarctica (Matsuoka et al., 2018).

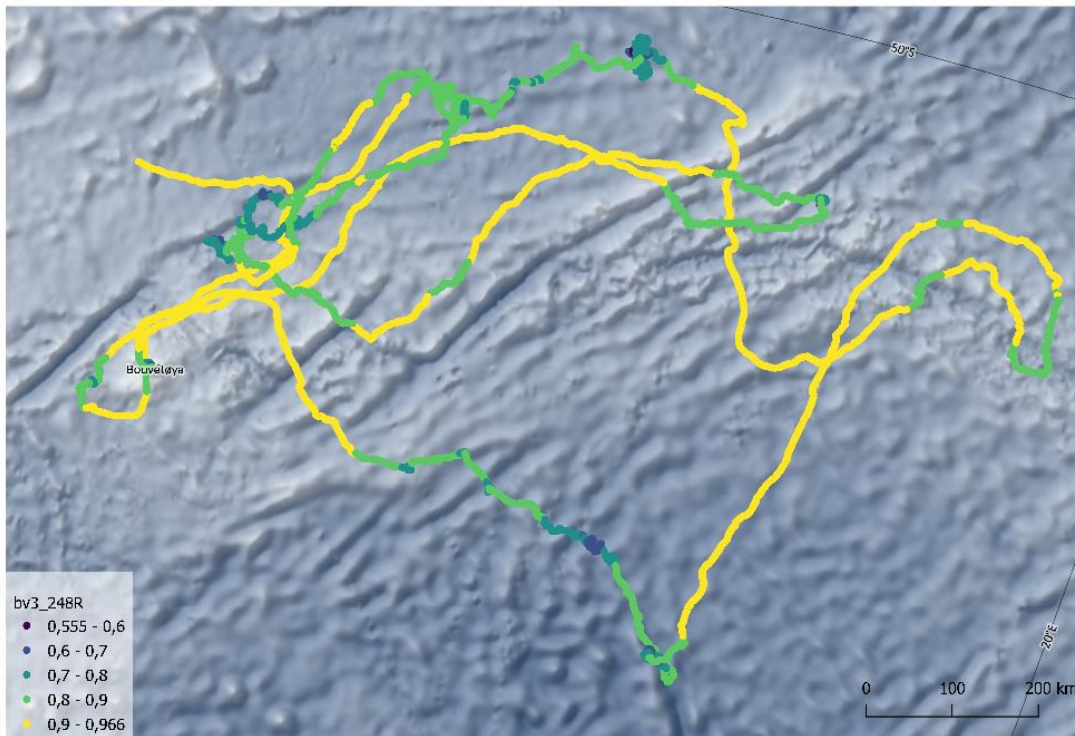


Figure 2e Post-moult migration of individual bv3-242R-14. High move persistence values (travelling) indicated by yellow, whereas low move persistence values are indicated by green-blue colour Map produced in Quantarctica (Matsuoka et al., 2018).

3.3 Changepoint analysis & extraction of transition zones

Changepoint detection was applied for identifying where a change in movement patterns occurred. The PELT algorithm identified a total of 67 changepoints, ranging from 9 to 21 between individuals. Further, a time buffer was added before and after each changepoint and the generated transition zones had a mean duration of 5.53 ± 3.02 days (see table 2 for transition summaries). Due to lack of CTD and TDR data in two of transition zones for seal bv3-243-14, these were removed from further analysis. The first excluded transition occurred in the beginning of the track, and the other at the end the due to irregular TDR and CTD recordings, likely because of the tag reaching the end of its battery life. Out of the 65 remaining transitions, 35 were labelled IN, and 30 were labelled OUT. The mean duration for the IN segments (4.91 ± 2.23 days) were shorter than the OUT ones (6.74 ± 3.79 days). Location of identified changepoints together with associated changepoints are summaries in figure 3a-e.

Table 2 Mean and standard deviation of duration of behavioural transition zones expressed in days, together with total amount of transitions

	Total duration IN & OUT	No of transitions	Duration IN	No of transition IN	Duration OUT	No of transition OUT
Bv3-240R-14	7.90 ± 4.26	9	6.93 ± 2.58	5	9.12 ± 6.00	4
Bv3-242R-14	5.14 ± 2.69	15	5.32 ± 3.12	8	4.94 ± 2.31	7
Bv3-243R-14	7.32 ± 3.07	8	5.55 ± 0.96	5	10.25 ± 3.25	3
Bv3-246R-14	4.56 ± 2.53	21	3.25 ± 0.92	11	6.00 ± 3.00	10
Bv3-248R-14	4.75 ± 1.86	12	5.19 ± 2.19	6	4.31 ± 1.53	6
Total	5.53 ± 3.02	65	4.91 ± 2.23	35	6.74 ± 3.79	30

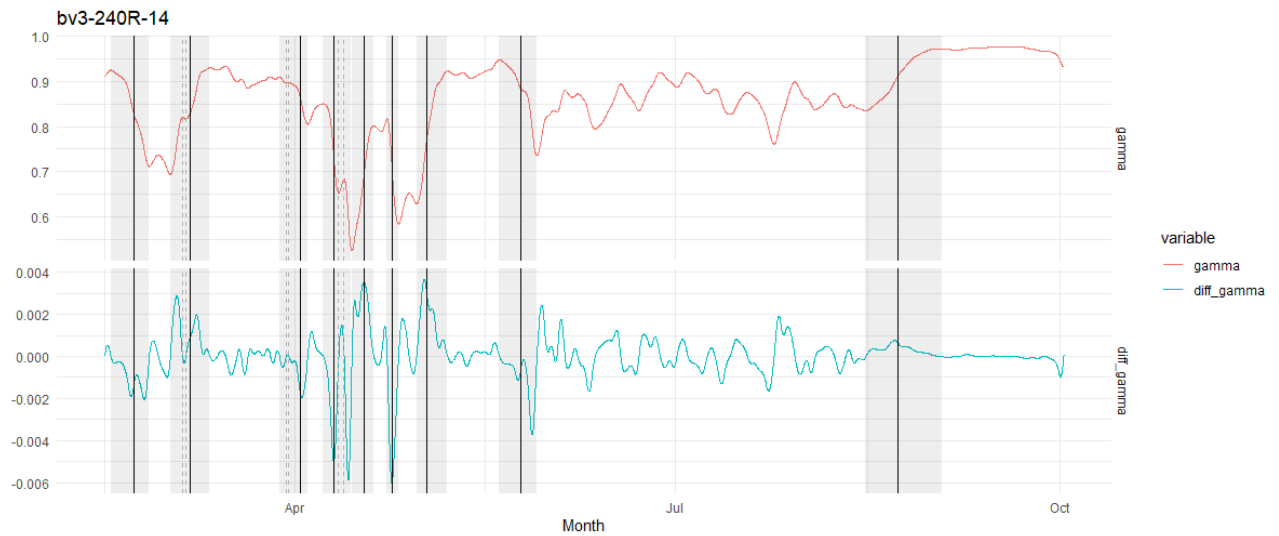


Figure 3a Horizontal move persistence with identified changepoints along transect for seal bv3-240R-14. Changepoints are indicated as black vertical lines with shaded area representing behavioural transition zones. Move persistence is shown as a red line, whereas the difference of consecutive move persistence values are shown as a green line. Dashed vertical lines represent zero differentials that were ignored to cover whole transition zones.

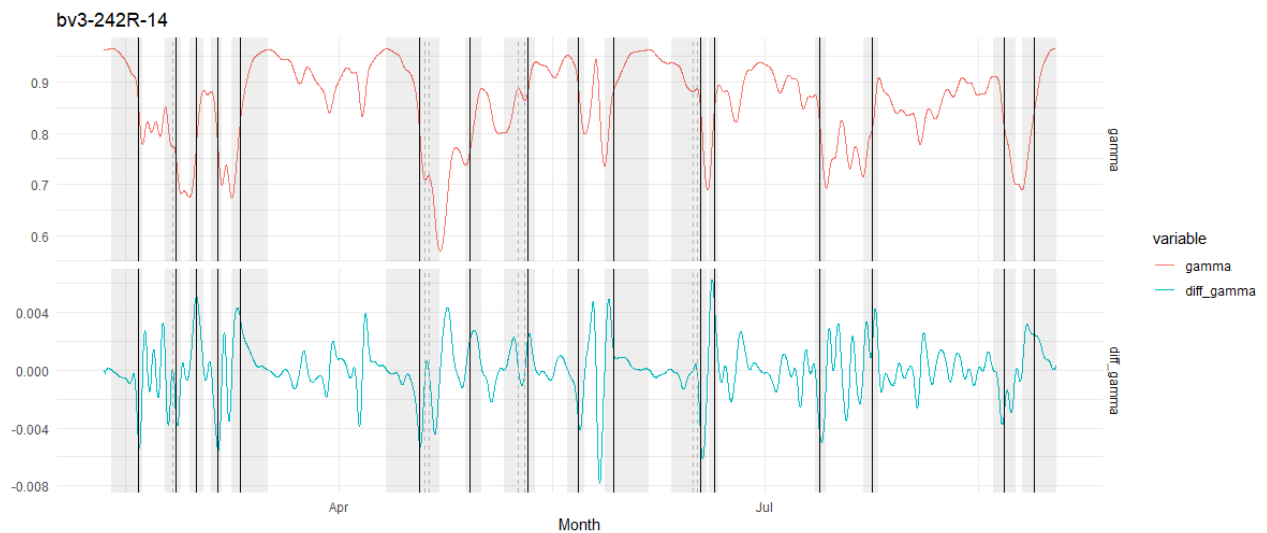


Figure 3b Horizontal move persistence with identified changepoints along transect for seal bv3-242R-14. Changepoints are indicated as black vertical lines with shaded area representing behavioural transition zones. Move persistence is shown as a red line, whereas the difference of consecutive move persistence values are shown as a green line. Dashed vertical lines represent zero differentials that were ignored to cover whole transition zones.

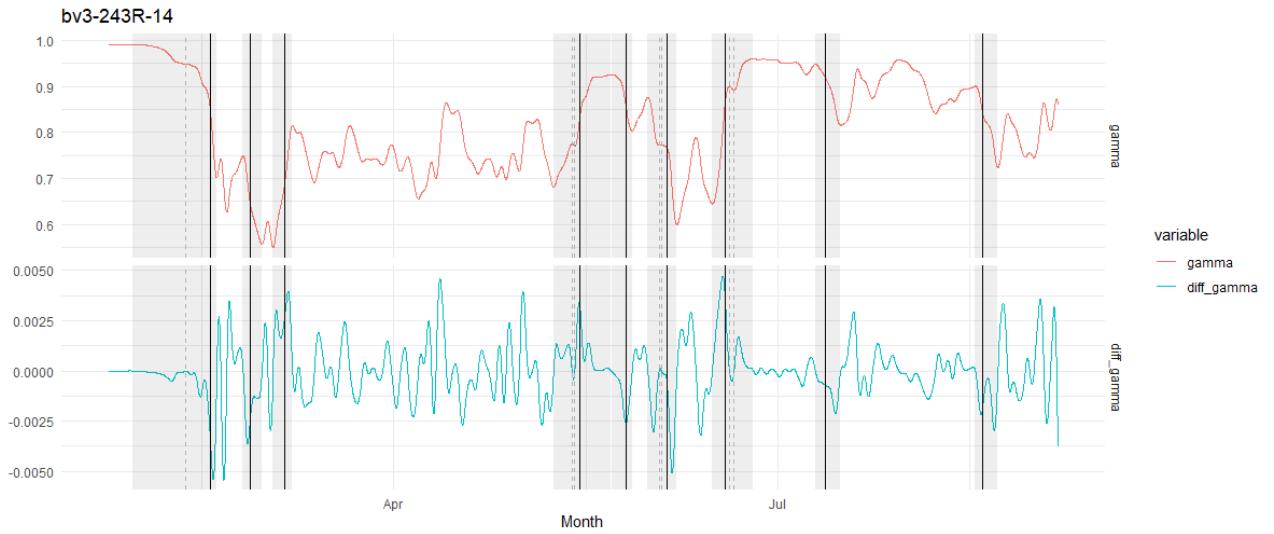


Figure 3c Horizontal move persistence with identified changepoints along transect for seal bv3-243R-14. Changepoints are indicated as black vertical lines with shaded area representing behavioural transition zones. Move persistence is shown as a red line, whereas the difference of consecutive move persistence values are shown as a green line. Dashed vertical lines represent zero differentials that were ignored to cover whole transition zones.

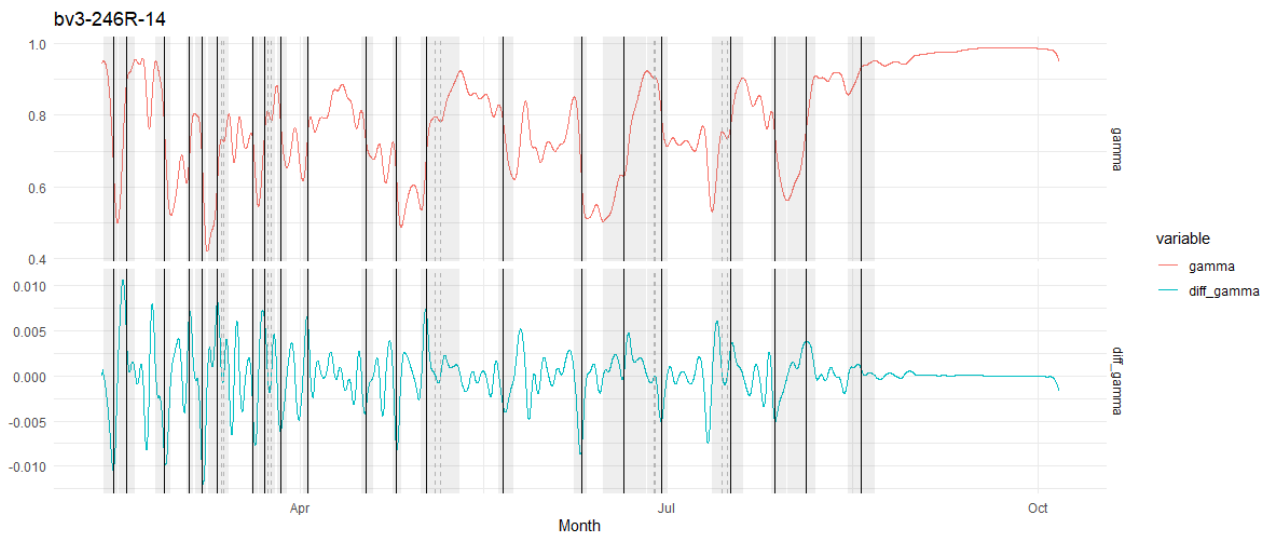


Figure 3d Horizontal move persistence with identified changepoints along transect for seal bv3-246R-14. Changepoints are indicated as black vertical lines with shaded area representing behavioural transition zones. Move persistence is shown as a red line, whereas the difference of consecutive move persistence values is shown as a green line. Dashed vertical lines represent zero differentials that were ignored to cover whole transition zones.

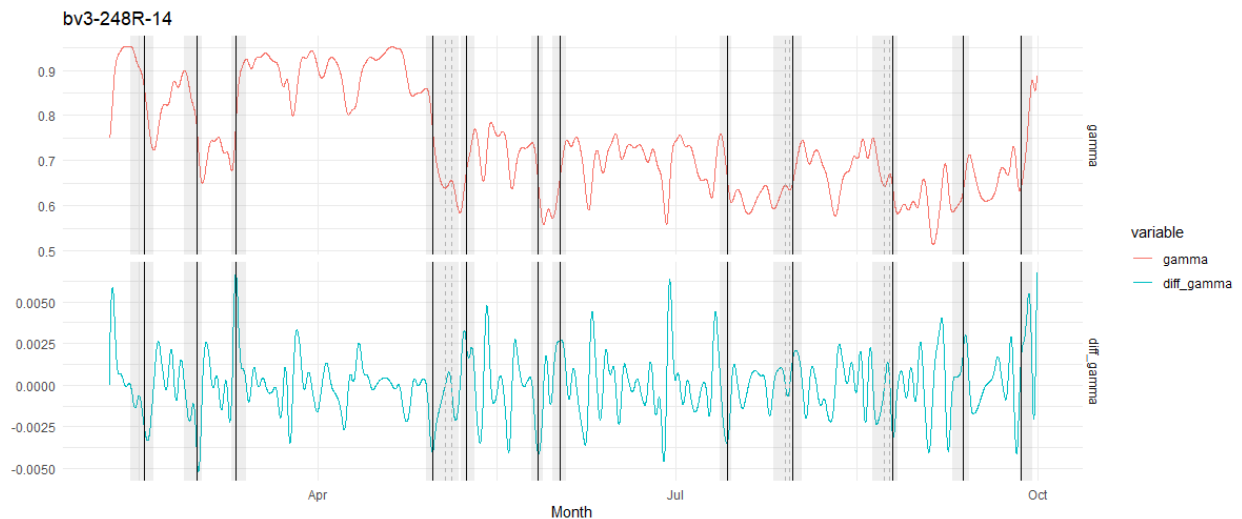


Figure 3e Horizontal move persistence with identified changepoints along transect for seal bv3-248R-14. Changepoints are indicated as black vertical lines with shaded area representing behavioural transition zones. Move persistence is shown as a red line, whereas the difference of consecutive move persistence values is shown as a green line. Dashed vertical lines represent zero differentials that were ignored to cover whole transition zones.

3.4 Dive & environmental parameters

Overall, 49086 dives were recorded (9817.2 ± 1379.2). The deepest dive of every seals measured more than 1000 m, with deepest dive recorded being 1388.2 m performed by seal bv3-246R-14. Average maximum depth attained was 455.2 ± 181.9 m, whereas most time was spent at depths of 404.4 ± 165.8 m. The longest dive recorded lasted for 125.5 minutes (seal bv3-242R-14), and mean duration of dives were 31.2 ± 12.3 min. Mean duration of post-dive surface intervals was 2.1 ± 1.2 min. In total 15478 dives were covered by the extracted transition zones and used for further analysis. A total of 2127 CTD profiles were generated for the behavioural transition zones.

3.7 Modelling results

Summary of LME results can be seen in Table 3.

Table 3 Summary of LME results to test whether mean dive depth (DP) during a transition was influenced by depth of MLD, topCDW and subMAX. Individual added as random effect.

Predictors	Effects on Mean Dive Depth			Diving Efficiency			Vertical Bottom distance		
	Estim.	CI	p	Estim.	CI	p	Estim.	CI	p
(Intercept)	326.61	285.21 – 368.01	<0.001	0.26	0.22 – 0.29	<0.001	138.65	112.97 – 164.33	<0.001
topCDW	-0.05	-0.12 – 0.03	0.214	0.00	-0.00 – 0.00	0.107	0.38	0.26 – 0.50	<0.001
MLD	0.53	0.41 – 0.64	<0.001	0.00	0.00 – 0.00	<0.001	0.93	0.74 – 1.12	<0.001
subMAX	0.24	0.20 – 0.31	<0.001	0.00	-0.00 – 0.00	0.305	0.12	0.03 – 0.20	0.007
Day/Night	-106.21	-111.03 – -101.38	<0.001	-0.02	-0.03 – -0.01	<0.001	-50.89	-58.75 – -43.04	<0.001
IN/OUT	16.21	11.07 – 21.01	<0.001	0.01	0.00 – 0.01	0.016	20.74	12.67 – 28.81	<0.001

Effects on Mean Dive Depth

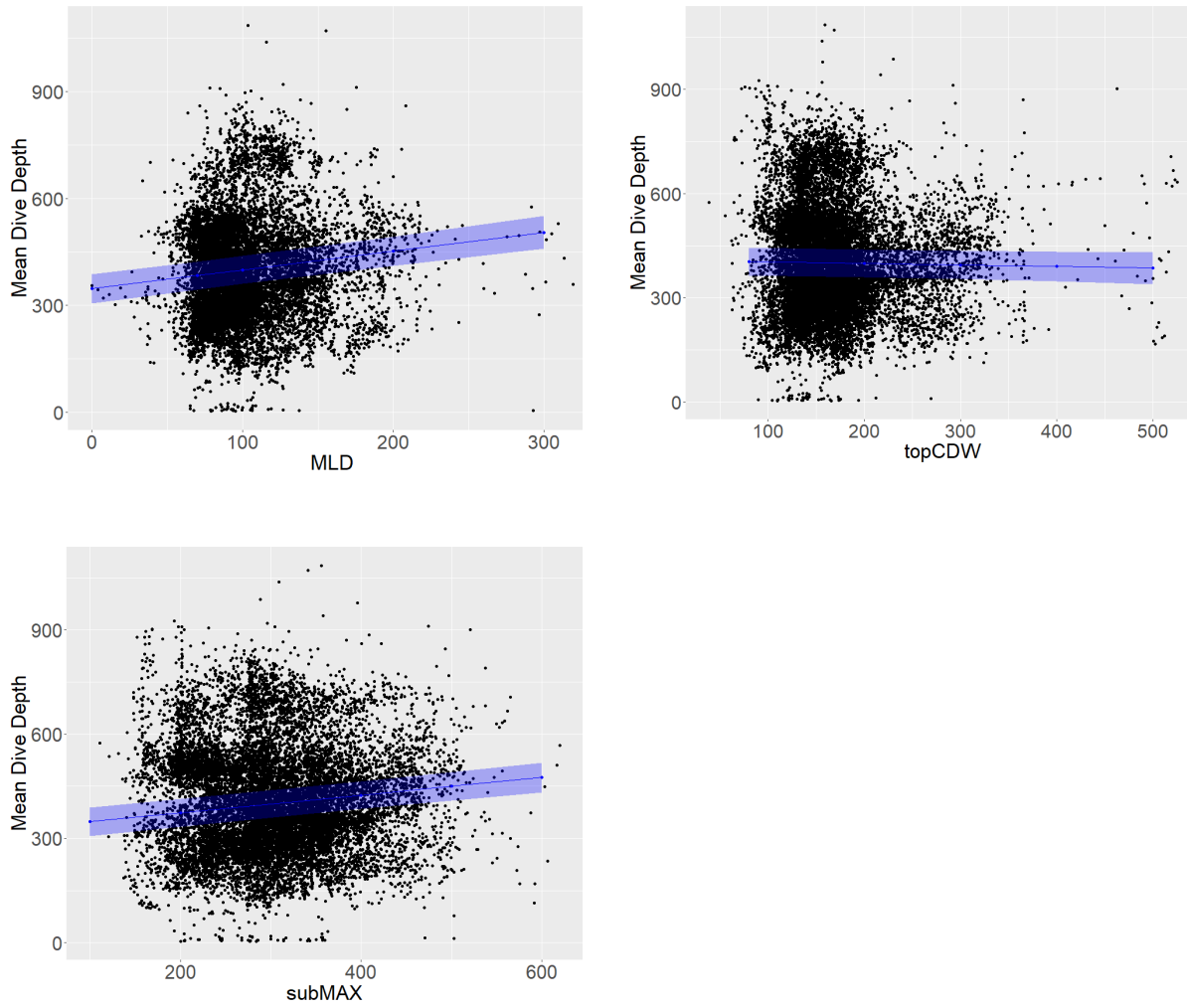
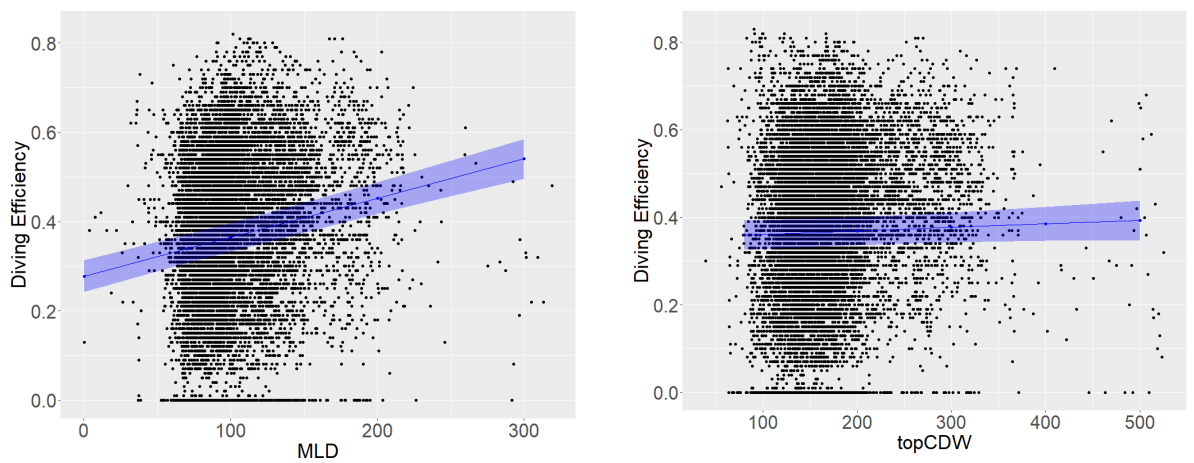


Figure 4a-c Result of LME to test whether mean dive depth (DP) during a transition was influenced by depth of MLD, topCDW and subMAX. Individual added as random effect.

Effects on diving efficiency



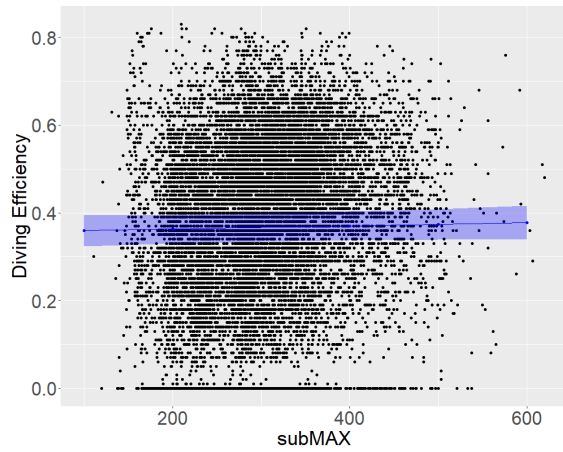


Figure 5a-c Result of LME to test whether diving efficiency (*DE*) during a transition was influenced by depth of MLD, topCDW and subMAX. Individual added as random effect.

Effects on Vertical Bottom distance

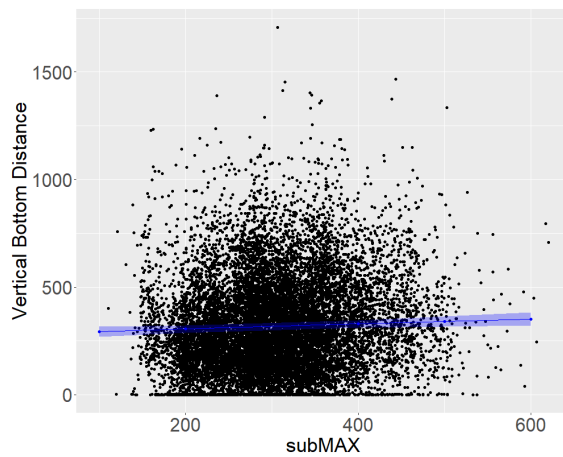
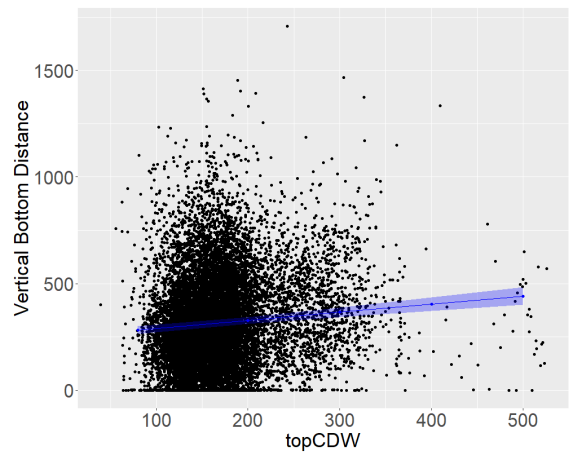
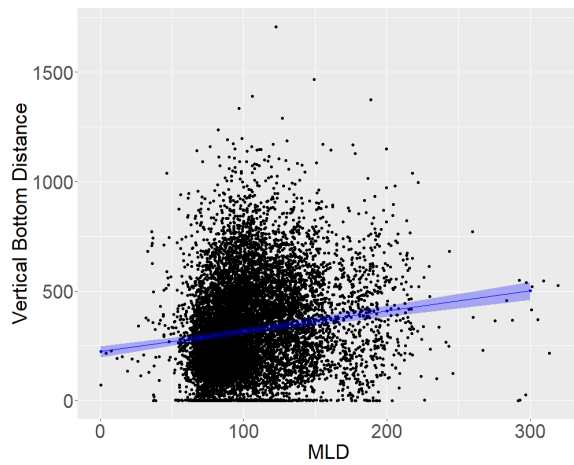


Figure 5a-c Result of LME to test whether vertical bottom distance (here as FE) during a transition was influenced by depth of MLD, topCDW and subMAX. Individual added as random effect.

Table 4 Model of interaction – testing whether MLD is important for both IN and OUT transitions, or only IN.

<i>Predictors</i>	Effects on Mean Dive Depth - INTERACTION		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	324.37	281.64 – 367.10	< 0.001
topCDW	-0.05	-0.12 – 0.03	0.214
MLD	0.55	0.39 – 0.71	< 0.001
subMAX	0.25	0.20 – 0.31	< 0.001
Day/Night	-106.20	-111.03 – -101.38	< 0.001
IN/OUT	19.87	1.60 – 38.14	0.033
MLD:in_out	-0.04	-0.21 – 0.13	0.670

Table 5 Model of interaction – testing whether trend is different for IN and OUT segments

<i>Predictors</i>	Effects on Mean Dive Depth - TREND		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	334.94	292.56 – 377.32	< 0.001
topCDW	-0.03	-0.10 – 0.05	0.482
MLD	0.51	0.39 – 0.63	< 0.001
subMAX	0.24	0.19 – 0.30	< 0.001
dayNightnight	-106.35	-111.17 – -101.53	< 0.001
in_outOUT	23.15	14.89 – 31.40	< 0.001
diveNo_transit	-0.04	-0.07 – -0.02	0.001
in_outOUT:diveNo_transit	-0.05	-0.09 – -0.01	0.023

4 DISCUSSION

4.1 Movement characteristics

This study sheds light on the movement patterns and transitioning behaviour of southern elephant seals belonging to a seal colony subject to only a few previous studies. High individuality of movement patterns was to be observed as previously has been acknowledged by Biuw et al., 2010. As two seals migrated over to Bouvet,

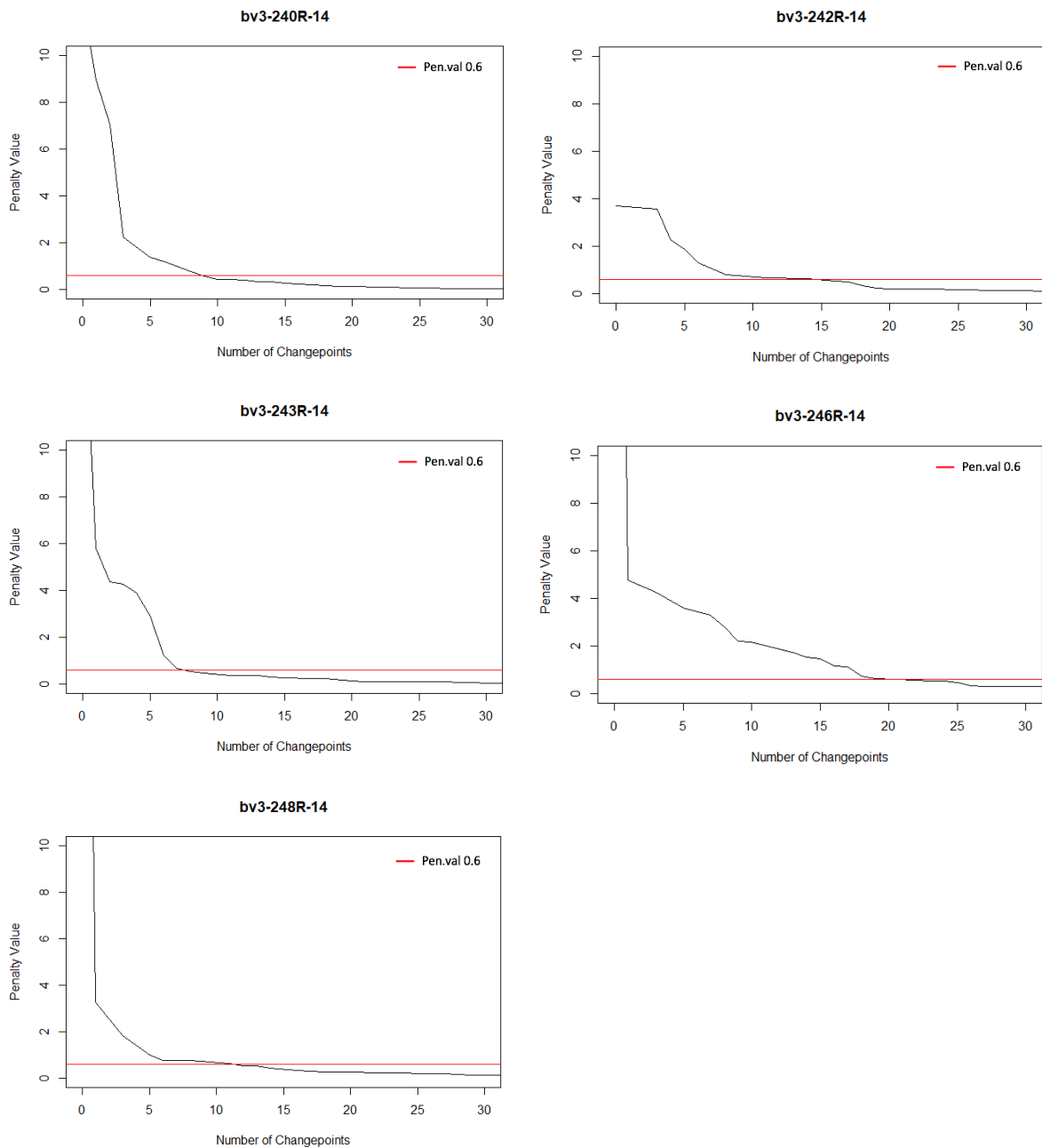
Several multiple changepoint search methods have been proposed for minimising Equation 1, such as the approximate but computationally fast binary segmentation method (Scott & Knott, 1974) the exact but computationally costly segment neighbourhood algorithm (SN) (Auger & Lawrence, 1989) and Pruned Exact Linear Time (PELT) (R. Killick et al., 2012). PELT is based on the optimal partitioning algorithm proposed by (Jackson et al., 2005) and is similar to SN as it is an exact method. Due to the pruning step involved, PELT is computationally efficient without reduction in accuracy of resulting segmentation and was therefore chosen for to identify changepoints in the move persistence values along the seals movement paths. The PELT search algorithm requires a penalty constant to avoid under- or over-fitting the data. This constant is user defined and not always straight forward to determine. To reduce subjectivity when deciding penalty value, changepoints over a range of penalties (CROPS) developed Haynes et al., (2017) was used. This method results in optimal segmentations across a continuous range of penalty values and further allows evaluation of suitable penalty choices by creating a diagnostic plot of number of changepoints against the change in test statistic. Lavielle (2005) suggests choosing the segmentation where the most significant decrease in cost due to the addition of changepoints occur. As the penalty value is initially increased, true changes can be detected and the cost decreases rapidly. Eventually false positives (changepoints due to noise) are added and the change in cost will be small. As the cost noticeably changes it can be seen as an “elbow” on the plot and these points can then be considered the plausible range of segmentations. Due to individual differences in movement behaviour these plots look different for each seal, and some level of subjectivity is unavoidable in case of choosing individual penalty values. Therefore, it was decided that a set penalty value together with a minimum segment of would be used for all seals. By trying out different penalty values corresponding to the elbow of the plots, together with different segment lengths, the most plausible values were determined.

APPENDIX

APPENDIX A: Changepoints over a range of penalties (CROPS)

Diagnostic elbow plot generated by the CROPS function in the changepoint R package. Chosen penalty value of 0.6 is indicated by red line.

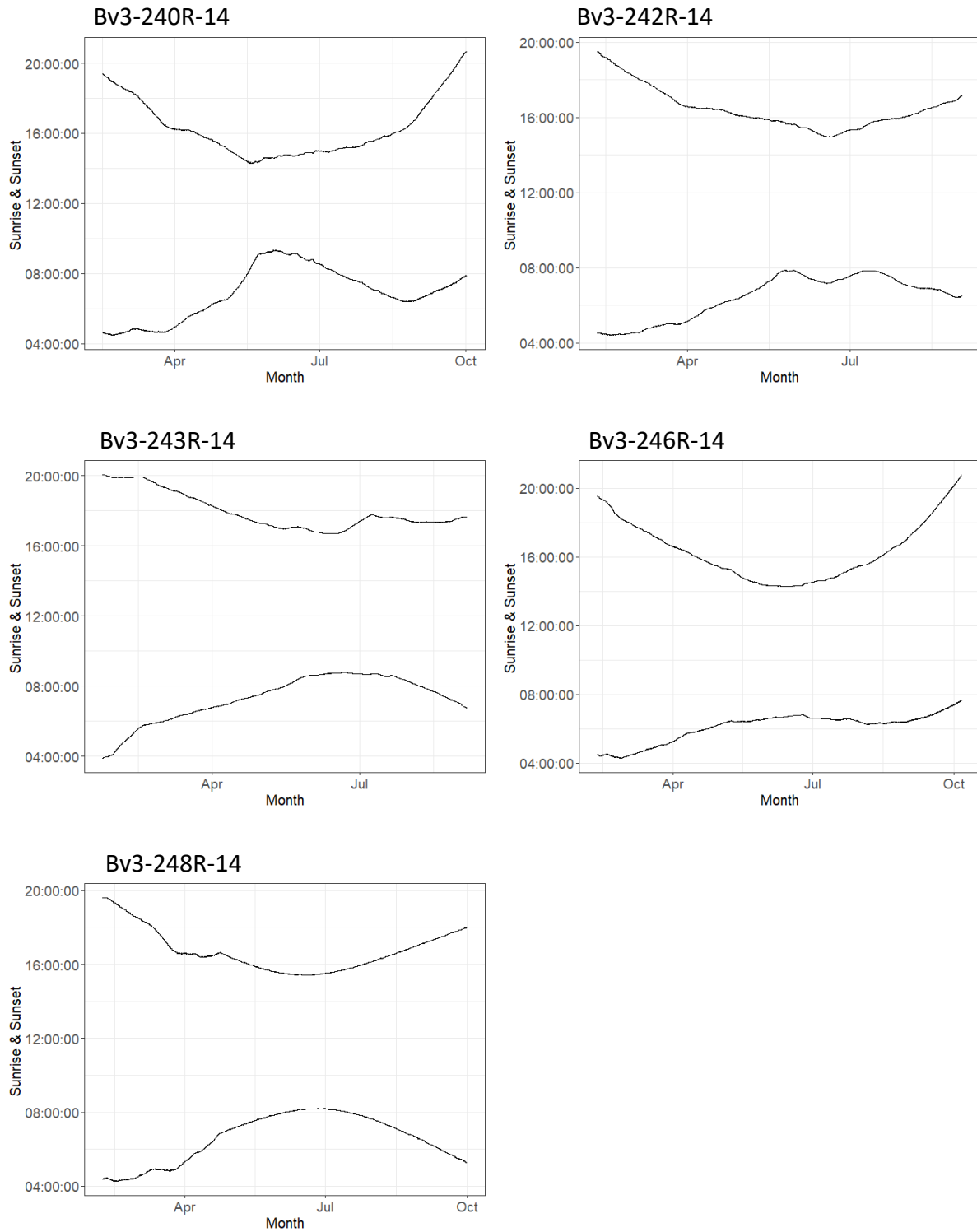
CROPS elbow plot



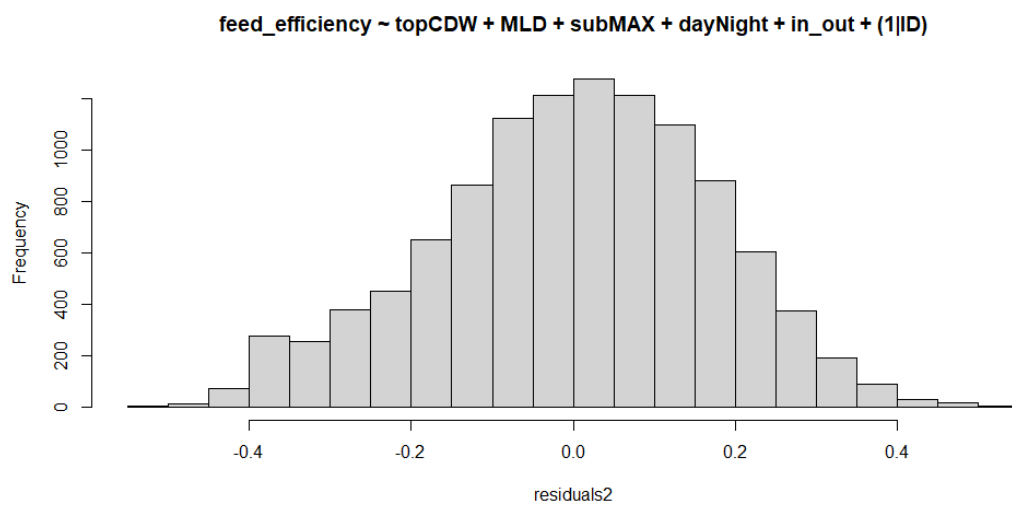
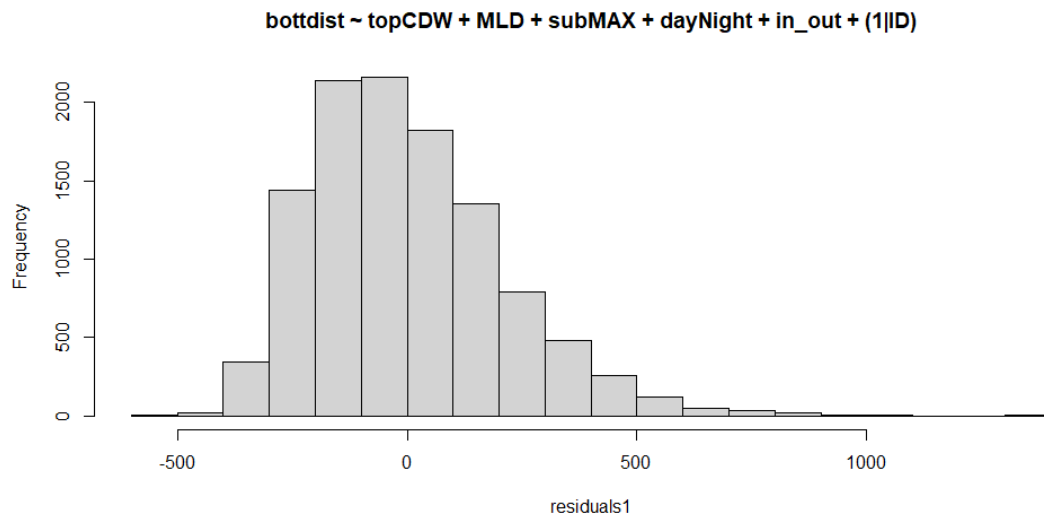
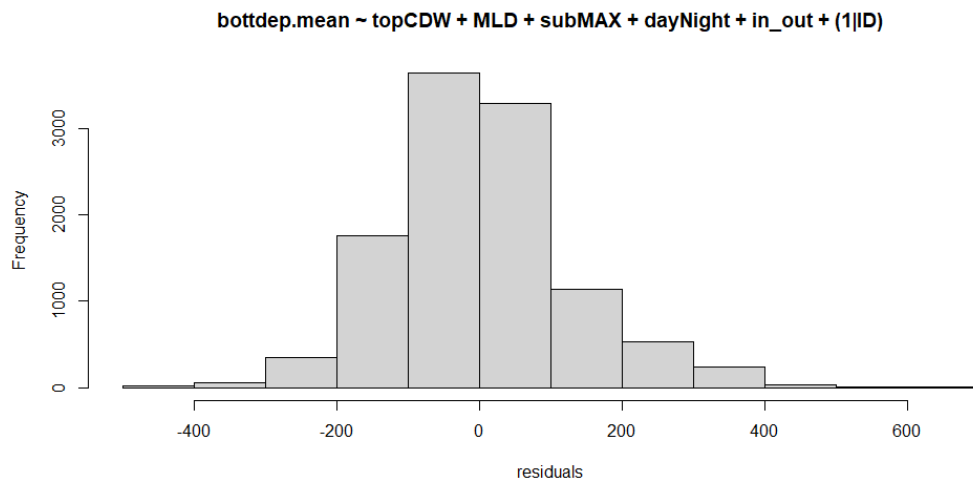
APPENDIX B:

Sun angle was assigned to each dive by the use *solarpos* function in the *maptools* R package.

Timing of sunrise and sunset



APPENDIX C: Residuals (measure of error) for linear mixed models



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