ANGLIA RUSKIN UNVERSITY

FACULTY OF SCIENCES AND TECHNOLOGY

CHINSTRAP PENGUIN (*PYGOSCELIS ANTARCTICUS*) FORAGING HABITAT MODEL FOR THE SOUTH ORKNEY ISLANDS

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A thesis in partial fulfilment of the requirements of Anglia Ruskin University for the degree of Doctor of Philosophy (PhD)

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This work is dedicated to Gian,
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ABSTRACT

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The Southern Ocean is under several threats due to global human activities but also to local resource exploitation. The chinstrap penguin (*Pygoscelis antarcticus*) is a key species in the Antarctica marine food web. Along with other predators, it has been impacted, albeit mostly indirectly, by harvesting in the past. The recent overlap and competition with krill fisheries necessitates constant attention and a better understanding of how this species utilises its environment; this can be achieved partly by developing a model of their foraging habitat.

In this context, birds from two different colonies in the South Orkney Islands have been tracked with GPS devices and TDR loggers during the breeding season. The resulting dataset allowed me to create a three dimensional representation of their foraging trips. The different methodological approaches I designed allowed me to assess how the birds use their environment across space and time. By studying changes in movements, I was able to detect when the birds were foraging. Linking these foraging locations with explanatory environmental variables, I was then able to develop a foraging habitat model for this species around the South Orkney Islands.

The model went through a series of performance measurements and validation processes. The final resulting map offers a picture of where chinstrap penguins forage from their colonies. The range of foraging, the density of birds, the hotspot areas, the depths of foraging and how these parameters change with time can be used to support policies and management targets. I believe these results can also be useful for further studies.

Key words: *Pygoscelis antarcticus*, foraging habitat modelling, tracking data, GIS, machine learning

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Chapter I INTRODUCTION

I.1 The context of the study: the Southern Ocean

The Southern Ocean is the largest marine ecosystem in the world. Biological productivity, food web interactions and all the organisms living in this environment are influenced by the climate, bathymetry and prevailing oceanographic currents. Human activities, mainly greenhouse gas emissions, historical harvesting of marine mammals and fish and modern day fisheries, also have an impact on the dynamic and equilibrium of the Southern Ocean ecological network.

a. Abiotic factors

Climate

The climate around the Antarctic continent is mainly driven by strong westerly circumpolar winds with maximum intensity around the Antarctic Circumpolar Current (ACC). The air temperature over the ACC are between 4° and 8°C during the summer. Surface water temperature during the same period of the year and along the same latitude are between 1° and 2°C. The sea ice cover varies extensively between the summer and the winter with a minimal extent in February-March and maximum extent in September-October (Knox, 2001b).

Polar Regions are where the highest recent increases in ocean temperatures have been recorded; for example, the ACC has warmed faster than the global ocean as a whole (Gille, 2002) whilst Polar seasonal sea ice has diminished in many locations (Murphy et al., 1995; de la Mare, 1997; Stammerjohn et al., 2012). The West Antarctic Peninsula is one of the regions with the highest temperature warming rates on Earth (Ducklow et al., 2007). Observed wind increase in the Southern Ocean, which might be due to climate change, can influence temperature through heat transport (Meredith and Hogg, 2006).

Bathymetry

The Southern Ocean is divided by three deep-water basins between 4,000 and 6,000 m deep: the Atlantic-Indian Basin, the Indian-Antarctic Basin and the Pacific-Antarctic Basin. In the Atlantic-Indian Basin, the Scotia ridge divides the Argentine Basin in the north and the Weddell Basin in the south. Shelf breaks in the Southern Ocean are usually deeper than in other parts of the world (Knox, 2001b). The definition of the shelf break used in this study corresponds to the 500 m bathymetric contour line (Wienecke et al., 2000).

Currents and fronts

Around the Antarctic continent, water circulation is complex with important spatial and temporal variability, especially due to the dynamic of sea ice cover. The other main force driving currents and fronts is the westerly wind inducing an eastward relatively slow but consistent

current. In the Scotia Sea, the ACC compromises several fronts, from north to south: the Sub-Antarctic Front, the Polar Front and the Southern ACC Front. Another important water movement in the context of this study is the Weddell Gyre, extending east of the Antarctic Peninsula to 20°W and from the continent to the Scotia ridge. This deep water sea flow is strongly influenced by the El Niño Southern Oscillation (Flores et al., 2012a). Figure I-1 represents these main water currents across the Scotia Sea.

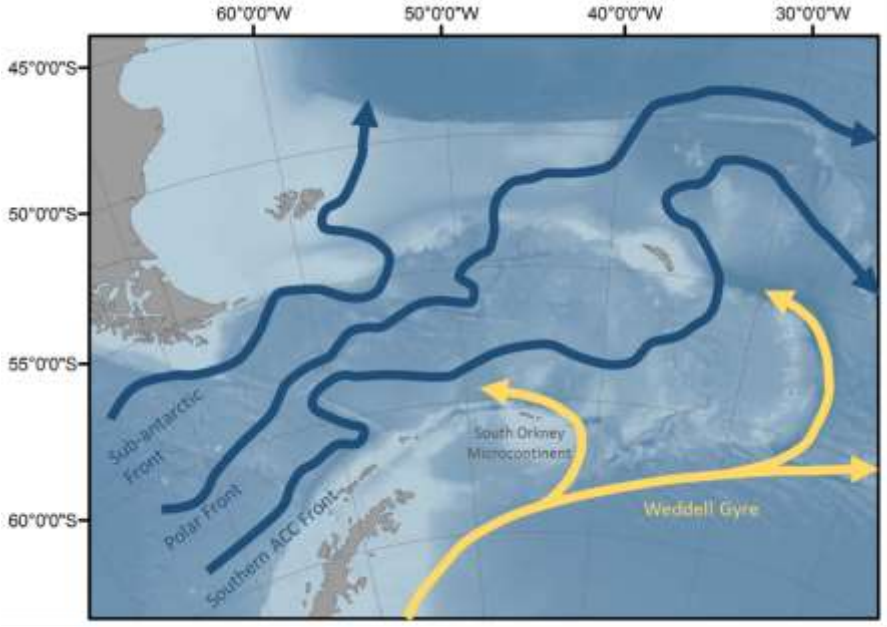

Figure I-1: Representation of the three eastward fronts and the Weddell Gyre across the Scotia Sea.

Water circulation will transfer heat and energy across different regions, contributing to the melting of the Polar ice sheets. Convergence of water with different temperature will create vertical movement which can bring up nutrient (upwelling) into the euphotic zone where phytoplankton can bloom. In the south Atlantic, water currents are also responsible for transporting krill from the west Antarctic Peninsula or the Weddell Sea across the Scotia Sea (Hofmann et al., 1998; Fach, Hofmann and Murphy, 2006). Any change in water movement patterns will have an impact on local productivity with repercussions for the whole food webs (Venables et al., 2012).

b. Biotic factors

The biological systems of the Southern Oceans are strongly impacted through variability and changes in the physical environment (Mcbride et al., 2014). However, other changes in the Polar Regions are also happening, including the recovery of marine mammal populations following decades of poorly managed harvesting (Laws, 1977; Ballance et al., 2006; Mori and Butterworth, 2006; Trathan, Ratcliffe and Masden, 2012). The "krill surplus" hypothesis (Laws, 1977) relates to the exploitation and removal of large quantities of krill predators in the 19th and early 20th centuries and the response of the ecosystem to these

changes. These large scale drivers of change are complex and the consequences are potentially difficult to disentangle from those associated with climate change (Trathan and Reid, 2009).

Antarctic krill

In the Southern Ocean, Antarctic krill (*Euphausia superba*) occupies a predominant role in marine food webs and is therefore a key prey item for numerous higher trophic level species. It is absent from most Sub-Antarctic regions but is very abundant in the southwest Atlantic sector, including across the Scotia Sea and at Sub-Antarctic South Georgia (Atkinson et al., 2008). Despite being considered as a planktonic species, later larval stages and adults have some degree of mobility and can therefore migrate to favourable habitat or escape from predators (Knox, 2001a). Another important characteristic of this species is its ability to aggregate at various spatial and temporal scales (Miller and Hampton, 1989; Murphy et al., 1998; Knox, 2001a; Zhou and Dorland, 2004).

There are many factors that influence the spatial distribution of krill: e.g. front and gyres (Amos, 1984), sea ice (Knox, 2001a; Flores et al., 2012b), and shelf edges (Siegel, 2005). Despite the fact that krill is capable of active movements, water circulations are important factor in driving krill swarms distribution (Nicol, 2006). Melting sea-ice water release important algal biomass. These sea-ice communities are essential for grazers like krill; therefore the sea-ice edge (or marginal ice zone) is an key habitat for krill (Loeb et al., 1997; Ballard et al., 2001; Brierley et al., 2002). These bottom-up explanations are complemented by top-down approaches where krill predators will influence the populations and distribution of krill (Zhou and Dorland, 2004; Atkinson et al., 2008).

As well as variation in the horizontal distribution of krill, there are also important vertical distribution patterns. During its life cycle, all the different stages (eggs, larvae and adults) will occupy different parts of the water column. In addition, adults are known to vertically migrate towards the water surface during the night (Zhou and Dorland, 2004; Everson, 2008; Cresswell et al., 2009). This basic behaviour of balancing near surface foraging where the resources are and protection from predators in deeper water is completed by more complex movements. Vertical migration by individual krill can also be driven by food availability in the water column, individual level of satiety and social interactions (Gaten et al., 2008).

Changes in the population of krill have been recorded and linked with changes in climate (Atkinson et al., 2004; Santora et al., 2009; Flores et al., 2012a). Krill habitat future projections based on an increase in sea temperature and a decrease in sea ice predict potential important failure of successful spawning (Piñones and Fedorov, 2016).

Being such a central species in the Southern Ocean ecosystem, Antarctic krill requires particular attention, especially as it is also the target of a developing international fishery. Indeed, krill is one of the few under-developed sources of marine protein (Grant et al., 2012) so will require careful management by the responsible management authority, the

Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR).

Penguins as krill predators

There are numerous species of predator that directly or indirectly depend on krill. Some are purely marine species and other rely on land for part of their life cycles. The effects of the recovery of krill predator populations after the ban on commercial whaling are not fully understood and partially entangled with climate change (Trathan and Reid, 2009).

Some penguin species are thought to have switched to krill as their main dietary item only recently (Emslie and Patterson, 2007). This could be a consequence of the krill surplus hypothesis or because of the depletion of alternative prey due to fisheries (Ainley et al., 2007).

In the Scotia Sea, chinstrap penguins (*Pygoscelis antarcticus*) have been used by CCAMLR as an ecosystem monitoring species for management. Understanding how chinstrap populations respond to change is therefore critical for CCAMLR's management approach. Chinstrap populations have shown considerable fluctuation during the past century (Trivelpiece et al., 2011; Lynch et al., 2012). It has been postulated that changes in numbers, including recent decreasing trends, can be explained by variations in Antarctic krill abundance and population dynamics (Volkman, Presler and Trivelpiece, 1980; Lishman and Croxall, 1983; Forcada et al., 2006; Hinke et al., 2007; Flores et al., 2012a), with possible links to climate change and direct habitat modifications (Ducklow et al., 2007). Large scale climatic events like El Niño–Southern Oscillation (ENSO) and the Southern Annual Mode (SAM) will impact climatic and environmental conditions like air and sea temperatures, katabatic winds and sea-ice extend. These fluctuations will cascade on krill distribution and abundance and with therefore have significant effects on penguin foraging behaviour and breeding success (Forcada and Trathan, 2009; Bost et al., 2015).

The combination of these population responses, the position of chinstrap penguins in the southern ocean food chain and therefore their potential sensibility to increasing krill fisheries make Pygoscelis species good candidates as key indicator species (Zamon et al., 1996; Alonzo, Switzer and Mangel, 2003a). However, to be reliable indicators, a much better understanding about their ecology is still needed, especially about how they utilize available food sources through both time and space.

c. Krill fisheries

Krill fisheries started in the early 1960s and then gradually increased to a peak in 1982 with 528,201 tonnes. Harvesting then declined in the early 1990s due to a combination of economic and political factors and stayed stable around 100,000 tonnes (Nicol and Endo, 1997). In recent years, they have again increased to between 200,000 and 300,000 tonnes per annum.

The geographical distribution of the catches shifted focus from the Indian to Atlantic oceans in the early 1990s. From being circumpolar, the fisheries are now concentrated around the Antarctic Peninsula, the South Orkney Islands and South Georgia. In addition, the fishing vessels moved from pelagic to coastal areas, moving closer to the breeding colonies (Murphy et al., 1997; Hill et al., 2006; Nicol, Foster and Kawaguchi, 2012; Silk et al., 2016).

In the context of an observed and predicted krill decline due to reduction in sea-ice (Atkinson et al., 2004) and ocean acidification (Kawaguchi et al., 2013), the increasing spatial overlap between fisheries and natural predators can have serious negative ecosystem consequences. The amount of krill caught, the length of the fishing season and the capacity for harvest can have a huge impact on penguin's reproductive success and parental survival (Mangel and Switzer, 1998; Reid et al., 2004). CCAMLR's precautionary approach with small-scale management units, local allocated catch limits and trigger levels (Hewitt et al., 2004) is therefore welcome especially as the use of new fishing techniques, despite being labelled as "eco-friendly", is too recent to show any evidence on potential ecosystem effects (Nicol, Foster and Kawaguchi, 2012)

I.2 Introduction to the research

a. The study area

This study focuses on the South Orkney Islands located in the southern Scotia Sea. The archipelago lies on the north edge of the South Orkney Microcontinent (Busetti, Zanolla and Marchetti, 2001), at the convergence between the ACC in the north and the Weddell Sea gyre in the south (see Figure I-1). This geographical situation, coupled with bathymetric features offering conditions for high productivity (vertical upwelling currents along the continental slope, marine canyons retaining nutrients and prey) and the availability of nesting sites make this archipelago an ideal location for breeding populations of Pygoscelis penguins, especially chinstrap penguins, and therefore for developing a foraging habitat model.

Signy Island benefits from a long term penguin populations monitoring programme (e.g. Trathan, Croxall and Murphy, 1996; Dunn et al., 2016); also birds have been tracked from this location previously (Lynnes et al., 2002). The area to the northwest of Signy is also an area of extensive krill harvesting (CCAMLR, 2016), allowing me to provide potential evidences to support fisheries management propositions.

The penguin tracking data used in this study have been collected from two colonies located at the Gourlay Peninsula (Signy Island) and Cape Geddes (Laurie Island), see Figure I-2. The first colony is facing south while the second one faces in a northward direction. The differences between these two sites will be discussed in details in Chapter III, but the contrasting conditions at both colonies enable me to build a model

that can be representative of the entire environment for all the penguin colonies around the archipelago.

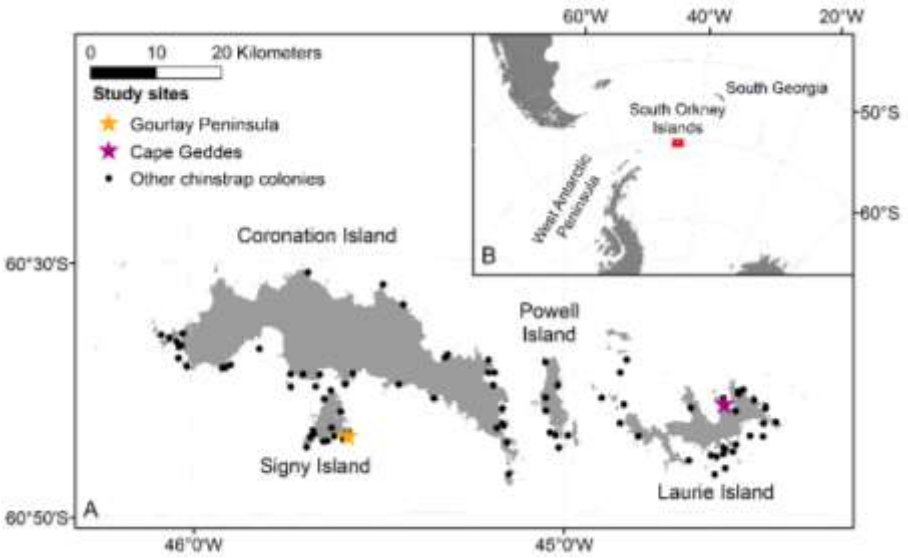

Figure I-2: Location of the South Orkney Islands and the two colonies where tracking data were collected for this study. (A) in relation to the Scotia Sea (B).

b. The focal species

Distribution

Chinstrap penguins have a circumpolar distribution with colonies in the Antarctic Peninsula, South Shetland Islands, South Orkney Islands, South Sandwich Islands, South Georgia, Bouvet Island and Balleny Islands. This species occupies the middle of the combined geographic range of species from the same genera: Adélie penguin (*P. adeliae*) reaches higher latitudes and Gentoo penguin (*P. papua*) reaches lower latitudes. Although chinstrap penguins are classified as of least concern (LC, BirdLife International 2016), some subpopulations are in decline (Forcada et al., 2006; Barbosa et al., 2012). The species is considered as an ecosystem indicator species whose population can indicate broad scale issues in the functioning of marine ecosystems (Lynnes, Reid and Croxall, 2004; Boersma et al., 2009). As important consumers in the marine ecosystem, they rely on relatively stable, oceanographic, climatic and sea ice conditions that will determine their prey availability. These environmental variables will also influence the suitability of their breeding and moulting habitats, which are easy to monitor (Forcada and Trathan, 2009). As such, it is included in CCAMLR's Ecosystem Monitoring Programme (CEMP, Agnew 1997).

In the South Orkney Islands, chinstrap penguins represent the dominant avian species. They often share the same breeding sites with Adélies, but both species show a different breeding chronology, Adélies starting their breeding cycle earlier (Trivelpiece, Trivelpiece and Volkman, 1987). Within the archipelago, long-term population trends show a decline in chinstrap population at Signy (Dunn et al., 2016) and Laurie Islands (Coria et al., 2011).

Breeding cycle

Chinstrap penguins arrive at the colony after Adélie penguins early November (Signy data). The nest is a circular platform of small stones. Two weeks after arrival, two eggs are laid (91% of the time in Signy). The first incubation shift is carried by the female. The incubation period lasts approximatively 36 days. The guard period lasts 3 to 4 weeks when both parent will alternately attend the chick(s). The crèche period will then last until fledging when the chicks are approximately 50 days old. The adult will moult in the colony or elsewhere late February-early March. The mould lasts 13 days and the adults will depart the colony in March-April.

c. Tracking and bio-logging

Due to the size of the early prototypes, most bio-logging (or biotelemetry) devices were first used on marine mammals and turtles (Kooyman, 2004). The non-exhaustive review presented here focuses on the use of bio-logging on penguins.

Early studies concerning penguin foraging had to rely on measuring trip durations from timing departures and arrivals at the colony. At-sea observations allowed researchers to estimate bird swimming speeds. The combination of both speed and trip duration gave estimates of foraging trip ranges (Williams and Siegfried, 1980). The development of speed measuring devices allowed improvement of these estimates (Wilson, Nagy and Obst, 1989; Wilson et al., 1996).

The use of time-depth recorders (TDR) gave information about how penguins used the vertical component of their habitat over time enabling researchers to draw dive profiles (Lishman and Croxall, 1983; Naito, Asaga and Ohyama, 1990; Croll, Osmek and Bengtson, 1991; Williams et al., 1992).

Apart from at-sea observations (Trathan et al., 1998), the use of radio-tracking devices allowed researchers to measure an individual bird's habitat spatial use (Trivelpiece et al., 1986; Croll, Osmek and Bengtson, 1991). The spatial and temporal resolution of these studies were greatly improved by the deployment of platforms terminal transmitters (PTT, Wilson et al. 1997). In the 2000s, the attachment of Global Positioning Systems (GPS) based devices started to become more common (Ryan et al., 2004). The miniaturization of GPS receivers allowed to accurately measure the foraging range for a number of marine species, providing crucial information about how these species were using their habitat (Lynnes et al., 2002). Spatial resolution then increased, especially in the context of diving animals that spend little amount of time at the surface, with the development of GPS Fastloc techniques (Dujon, Lindstrom and Hays, 2014).

The joint deployment of GPS based devices and TDR loggers allowed researchers to combine horizontal and vertical dimensions providing a three-dimensional model of movement (Kuhn et al., 2010; Bestley et al., 2014). Parallel deployment of additional devices (accelerometer,

ingestion detector) allowed researchers to detect fine-scale underwater changes of direction and record prey ingestion events (Naito, 2004). The increased level of detail of the recorded information allowed researcher to gather information across the complete range of ecological scales, from punctual feeding events to macro-scale movements (Rutz and Hays, 2009). Some of the hypotheses that have been tested thank to the advance of bio-logging include hunting tactics, aerobic diving limits, central place foraging and oceanographic associations (Kooyman, 2004). See Wilmers et al. (2015) for a review on how ecologists used bio-logging devices.

d. Foraging theories and concepts

The data collection devices described in the previous section allowed ecologists to gain fine scale information about an animal's movements and physiology. One of the aims of the movement ecology discipline is to relate datasets collected by tracking device to bird's activities, especially foraging behaviours.

Early foraging models suggested that animal have full knowledge about the distribution of their prey and therefore use decision rules to optimize their foraging (Macarthur and Pianka, 1966; Schoener, 1971). These theoretical models were unsuitable for marine air breathing predators due to the patchiness characteristics of their prey, the difficulty to predict their location and the fact that they are often out of the predator's perceptual range (Ford et al., 2014). Therefore, imperfect information and random and unpredictable resource locations were included in foraging models (Chimienti et al., 2014). Foraging energetics also had to be taken into account, especially when prey are difficult to locate (Chappell et al., 1993)

There are several existing foraging theoretical models such as "optimal foraging theory" (Perry and Pianka, 1997) and even an "optimal diving theory" (Vacquié-Garcia et al., 2015). These provide conceptual frameworks and an array of hypotheses that can be tested through experimentation and data collection. Some of these hypotheses relate to the time spent in prey patches in relation to the quality of the patches (Watanabe, Ito and Takahashi, 2014) or the optimal diving depth (Mori, 1998). The inclusion of foraging energetics (Chappell et al., 1993), body condition and sex (Mori, 1998) were integrated into those models. The methods developed allowed researchers to apply these theoretical concepts to data collected during tracking studies (Masello et al., 2010; Gallon et al., 2013; Watanabe, Ito and Takahashi, 2014).

Penguins are considered as central-place foragers as their foraging range is constrained by the amount of time (and therefore distance) they can spend away from the nest. But, as air breathing divers, they are also restricted in the vertical dimension of the foraging. The surface acts as a central point to which they have to come return within a limited amount of time (Doniol-Valcroze et al., 2011). They can therefore be considered as central place foragers in both the horizontal and vertical dimensions (Ford et al., 2014).

I.3 Aims, challenges and approaches

a. Aims of the study

The over-arching aim of this study is to develop a foraging habitat model for chinstrap penguins in the South Orkney Islands that can represent how the entire population uses their available habitat and how it changes over time. The model will be based on the data collected from tracking devices and TDR loggers that will be combined with a range of environmental explanatory variables from various sources. Due to operational reasons, my data were limited to two phases of breeding, incubation and brood, and to two sites, Signy and Laurie Island.

The secondary questions related to this main objective are:

1. What changes occur during the breeding season? Is a single habitat foraging model sufficient for the whole breeding season?
2. Is it possible to identify the foraging parts of the trip and reliably distinguish these from resting and commuting periods?
3. Where are foraging hotspots located that are used by the tracked birds?
4. Which are the main explanatory variables driving the foraging habitat model?
5. Is it possible to evaluate and validate the foraging habitat model and transfer it to other colony sites in the South Orkney Islands?
6. What are the characteristics of the vertical use of the habitat?
7. What are the differences between two colony locations?
8. What are the temporal and spatial scales relevant to characterise chinstrap penguin foraging?

Questions 4 and 5 will be specifically covered by Chapter VII; contributions to the other questions will come from several chapters.

b. Challenges and approaches

Collecting ecologically relevant information from tracking devices and TDR loggers tends to generate a large amount of data, especially if the frequency of recording is high. Manipulating, managing and analysing these large datasets can be challenging. The amount of noise in the data can be significant. The data generally cover several dimensions (through space and time), often with autocorrelation and colinearity. The biological processes behind these datasets are complex, confounded and patterns are generally difficult to extract. The data used for the habitat modelling part have different spatial and temporal scales. Moreover, there are no standard agreed methods to process multidimensional tracking datasets (Gurarie, Andrews and Laidre, 2009; Womble et al., 2013).

For this study, I will develop my own methodology based on flexible tools and algorithms necessitating minimal parameterisation. The choice

of technique will not be tied to rigid mathematical models but will still enable me to take into account the complexity of the data. The results will be validated using different techniques to ensure that the signals and trends detected are confirmed where possible. I believe this approach will produce interesting results with some novel analytical methods.

I.4 Overview of the study

a. Changes at the scales of the trips and the breeding season (Chapter IV)

This first analytical chapter will consider several metrics at the scale of the foraging trips. I will consider the changes in multidimensional metrics (time and space in three dimensions) over the course of the breeding season to detect any major differences between the incubation and brood stages. The influence of additional factors, such as the colony site, the sex of birds or individual bird characteristics will also be considered.

The results suggest that foraging strategies significantly changed after hatching. It will therefore be necessary to develop two stage-specific habitat use models, one for incubation and one for brood. There is also some site-specific effects on foraging trip characteristics that can be explained by differences in the abiotic environment. I will therefore carefully assess how the habitat models developed in Chapter VII incorporate site-specific characteristics.

b. Detection of the behaviour modes at the scale of the foraging trips (Chapter V)

In this chapter, the fine scale details of bird activity, including surface and dive metrics, will be considered. I will use a segmentation process to divide foraging trips into homogeneous sections. Several behavioural modes will then be inferred to these segments using two different methods. I will then compare the different time allocations for each behaviour by phenological stage, colony and sex.

The results confirm the changes occurring through time and differences between sites observed previously at the scale of the foraging trips. Moreover, this important step allows me to differentiate between foraging and non-foraging parts of the trip and therefore define the input data for the habitat model (Chapter VII).

c. Spatial distribution of the foraging at different scales (Chapter VI)

The previously determined foraging locations will be mapped for each period of breeding, incubation and brood, and for each study site. The spatial points will then be aggregated at different scales corresponding to the resolutions of the different environmental variables used in the foraging model to test the spatial scale effect. I will also perform some point density calculations to identify foraging hot spots for each colony and breeding stage.

Comparing the spatial aggregation of different point inputs (from raw GPS data to inferred foraging behaviour) will enable me to assess whether different data sources with different level of details (historical datasets for example) can be used and compared. The identification of foraging hotpots and their location in relation to both colony sites will confirm and support results from previous chapters.

d. Foraging habitat modelling (Chapter VII)

Finally, foraging habitat models will be developed using the different levels of data defined earlier in relation to a series of environmental variables aggregated at different temporal resolutions. I will create one model for each breeding stage (incubation and brood). The models will be evaluated and validated using both information about the prey field and a site cross-validation process. The contribution of each environmental variable will be discussed and the possibility of extrapolate the resulting model to the whole archipelago will be reviewed.

My analyses show that the best foraging habitat model resulted from the use of a random forest algorithm with dynamic environmental variables aggregated at a weekly temporal scale. The evaluation of its performance and the validation process confirm the robustness of the model. The high quality habitat locations indicated by the model are realistic.

Chapter II METHODOLOGY FOR THE DATA COLLECTION, FILTERING AND PROCESSING

This chapter describes the collection of the primary data including the bird sampling, the devices set up and deployment, the raw data pre-processing and filtering and the calculation of the different derived metrics. All the collected and derived variables are summarised in section II.4b, page II-35.

II.1 Data collection

The methods described in this chapter focus on the 2013-14 dataset from Gourlay Point (Signy) which correspond to the data collected by the author. The procedures are considered to be the same for the other datasets (other seasons and/or locations); however, inevitably there were small differences, as the methods were implemented by different field operatives. After discussion with other field operatives, these differences were judged not to be of ecological significance; for example, differences included the period and duration of work, and the amount of tape, glue and handling time for instrumenting each bird.

a. Colonies description and calendar

Gourlay Point

On the south-east tip of Signy Island, the Gourlay Peninsula (approximate position Lat. 60° 44′ S, Long. 45° 36′ W) is composed of 3 finger-like capes with cliffs and smoother slopes over a predominantly rocky shore. Numerous studies have been carried out in the area, to the extent that there are two small huts that are used as shelter and as working space.

The Peninsula is colonised by chinstrap and Adélie penguins in numerous small colonies or sub-colonies. Some of the locations are occupied by a mix of both species while others are occupied by just a single species. On the whole Signy island, chinstrap and Adélie population sizes were estimated at 19,530 and 18,333 pairs respectively (Dunn et al., 2016). The colonies where the sampling was undertaken were relatively small sub-colonies occupied by both species. The sub-colonies mainly faced east lying along the top of a slope above a rocky bay (Figure II-1). The choice of the sub-colony was dictated by convenience (the colony is visible from the huts) and in order to minimise interference with other colonies where long term population dynamic studies take place. Birds were sampled from different parts of the colony in order to provide a representative cross section of nest sites and therefore probable age and experience of the parents (Ainley, LeResche and Sladen, 1983; Barbosa et al., 1997).

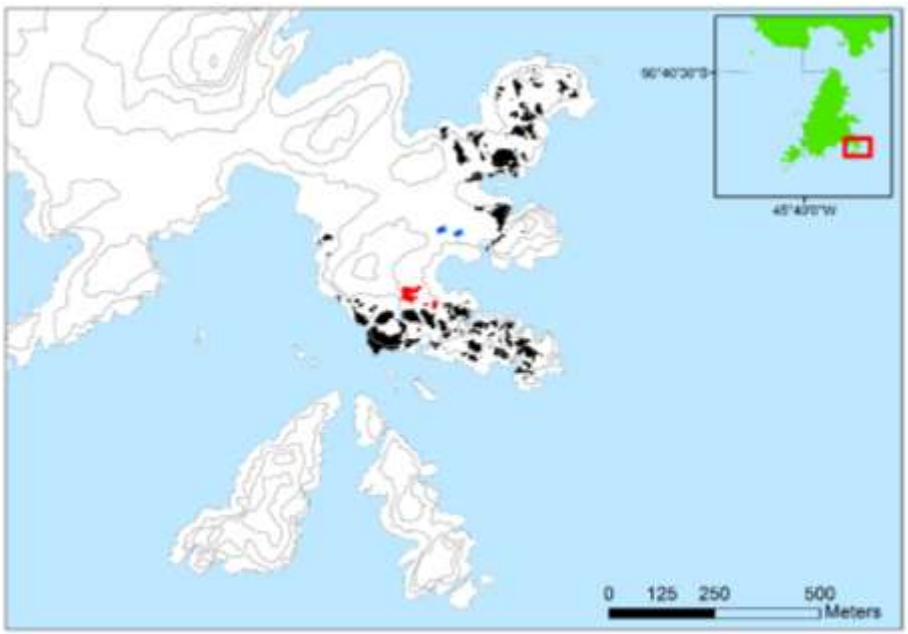

Figure II-1: The Gourlay Peninsula pygoscelid colonies shown in black with the targeted sub-colonies used for this study shown in red; the huts are shown in blue; adapted from Waluda et al. 2014.

Cape Geddes

Cape Geddes (approximate position Lat. 60° 41′ S, Long. 44° 34′ W) is located at the eastern entrance of Browns Bay at the northern end of the Ferguslie Peninsula on Laurie Island in the South Orkney Islands.

The location is colonised by chinstrap penguins in numerous small colonies or sub-colonies with approximately 7000 pairs. The location mainly faces north-west lying in a rocky bowl overlooking a rocky bay (see Figure II-2). Birds were sampled from different parts of the largest sub-colony in order to provide a representative cross section of nest sites and therefore probable age and experience of parents (Ainley, LeResche and Sladen, 1983).

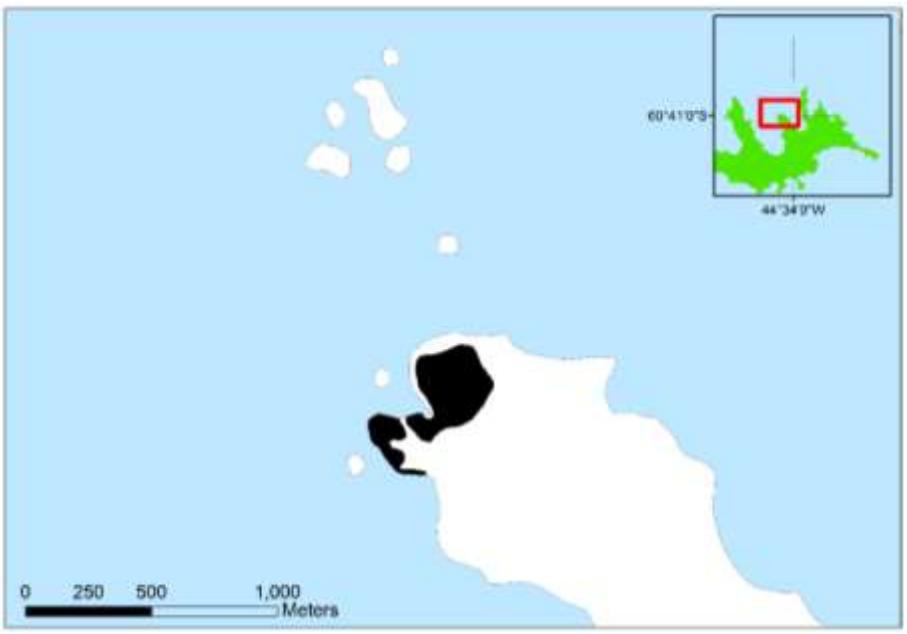

Figure II-2: Cape Geddes and the studied chinstrap colony (adapted from Coria et al. 1996).

Calendar constraints

Due to the remoteness of the field locations and the logistic constraints (ship calls), the timing of the data collection was not optimal in relation to the breeding calendar. It varied between colonies and seasons. Although the study endeavoured to cover the incubation and the brood stages of the breeding stages, there were some differences in the coverage of these stages (early, middle or late). The sampling calendar is presented in section III.2 page III-43.

b. Devices description and setting

GPS

The Global Positioning System (GPS) devices used for this study were Fastloc F2 from Sirtrack©. This technology has demonstrated an increase in location accuracy, especially for marine animals when the surface time for positioning acquisition is very short (Dujon, Lindstrom and Hays, 2014). Devices weighed 39 g in air and were hydrodynamically shaped by the manufacturer to decrease drag in water.

The GPS devices were equipped with a wet switch and could be set to record a location every 4 minutes when wet; on land (dry) the device would save battery power by recording a location every 30 minutes only. Devices were switched on in the morning leaving the research station, enabling the GPS to stabilize reception of signals from the GPS satellite constellation and therefore ensuring that the accuracy would be optimal once deployed.

To gain an estimation of the accuracy of the GPS data, the distances between the points collected while the birds were at the colony and a reference point (the centroid of all the points in the colony) were calculated (see II.2a page II-22 for a description on how GPS data were

split between “at the colony” and “foraging” points). During brood, these “static” locations were not optimal as the birds were standing and therefore the device’s antenna was not getting a full view of the sky. During incubation, birds were laying on the nests, providing a better position for the reception of GPS signals. In addition, they were not moving (Ryan et al., 2004) or were moving relatively slowly and they were not intermittently submerged; for example, birds might change their orientation depending upon wind direction. During these periods, 65% of the points were recorded within 100 m to the reference point (95% within 243.1 m). These estimated inaccuracies were higher than those measures by Hazel (2009) who found that 95% of the distances were within 101 m. This might be due to the differences in the method (Fastloc device models and configuration) as well as distinct local atmospheric conditions. It is also plausible that local topography can influence how well devices ‘see’ the GPS satellite constellation, especially near the horizon.

Overall, 95% of the points recorded at the Geddes colony were within 289 m to the reference point (4.8% within 100 m). For Gourlay, 95% of the points were within 214 m and 78.1% of the points were within 100 m to the central point. The difference in accuracy between both sites could be due to local topographical conditions that can impact the reception of GPS signals; at Cape Geddes, there is a steep hillside immediately behind the colony that potentially might obscure a proportion of the GPS satellite constellation. When comparing the data for each site and season, the different sampling sizes might also impact the spread of values (Figure II-3). This seems to indicate an operator effect as each seasonal deployment from each site was made by a different person.

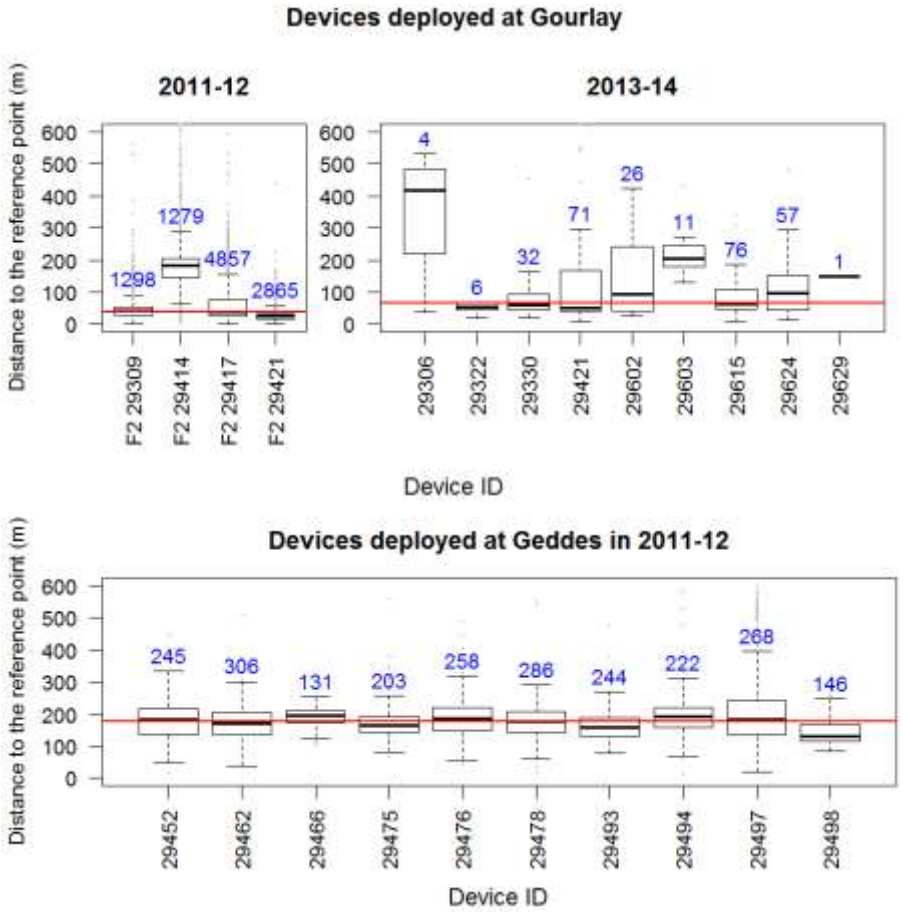

Figure II-3: Distribution of the distances between the points recorded at both colonies and a central reference point for each deployed GPS devices. The blue values are the number of points and the red lines represent the median distance for each colony and season.

As observed by Hazel (2009), the number of acquired satellites had an important impact on the device accuracy (see Figure II-4). An accuracy estimate based on colony static tests is conservative as the satellite acquisition was better at sea (78.5% of GPS points with more than 5 satellites versus 75.4% of points with a similar number of satellites on land), confirming the potential impact of topography on GPS accuracy on land. An estimated precision of 250 m would fit more than 95% of the captured locations in the colonies (95% of the locations with more than 5 satellites are within 219 m versus 397 for less than 5 satellites). This precision matched the minimal temporal resolution of inferred behaviours (see V.2b, page V-82) and the resolution of the most accurate environmental variable used in the habitat model (see VI.2b, page VI-118).

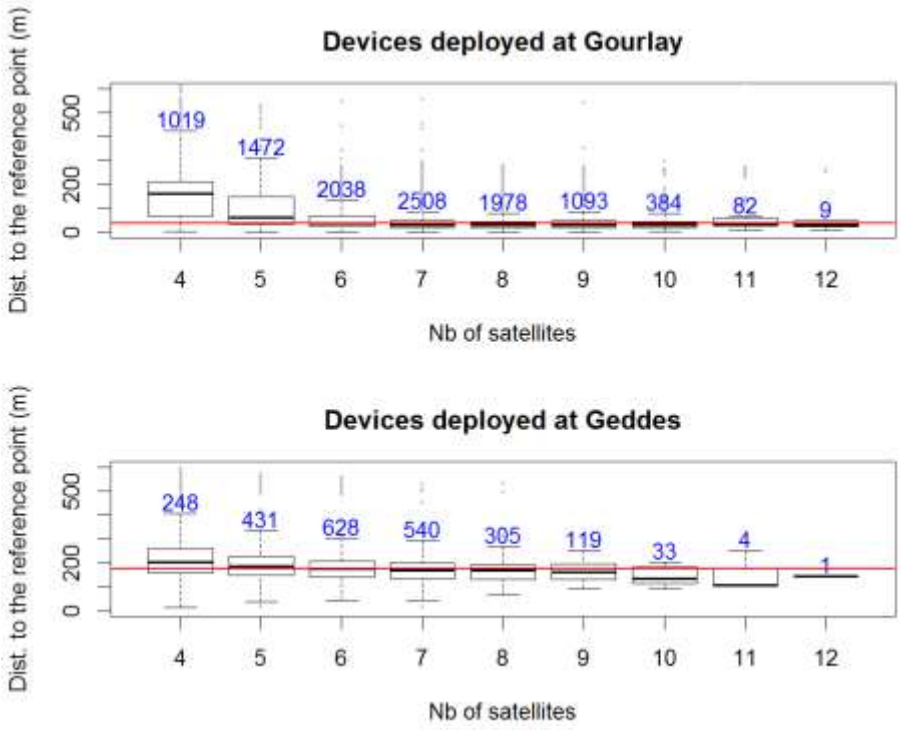

Figure II-4: Influence of the number of satellite in the accuracy of the location for both sites. Blue values represent the number of points and the red lines are the median values per site.

TDR

The time-depth recorder (TDR) models used in this study were Lotek© LAT 1810 and Cefas© G5 (CEFAS Technology Ltd, Lowestoft, UK). The Lotek© devices were used on all the Geddes 2011-12 deployments and three of the Gourlay 2013-14 deployments. The instruments weighed 2.7g and 6.3g for the G5 (Hays et al., 2007) and Lotek respectively.

The TDR were set to record one pressure and temperature measurement every second during the 2011-12 deployments (Geddes and Gourlay) and every two seconds during the 2013-14 deployments (Gourlay only). Recording only occurred when the devices were in the water based on their wet switch.

Timing

Just before deployment, all devices times were synchronised with an online atomic clock using Greenwich Mean Time (GMT). The local solar time at the South Orkney was GMT+3. All times considered in this study were GMT.

c. Bird sampling and devices deployment

Choice of study individuals

At each device deployment, a different area of the colony was targeted, to minimise potential impact and disturbance to surrounding nest sites. During incubation and early brood, the birds standing on the nests were

marked with blue stock marker dye (Figure II-5); the dye used is temporary and is regularly used for marking animals on farms, it washes out of the feathers after birds have been at sea for a number of days. This allowed for monitoring of when both parents were at the nest and were about to exchange parental duties. The marked birds that were not sitting on the nest anymore could be captured and equipped with the devices. This method ensured that the deployment was optimized as the selected birds would be ready to go foraging, minimizing unnecessary drains on device battery and memory use at the colony.

Figure II-5: Bird marking to detect incubation role swapping. Marked standing birds are ready to leave the colony to forage and are therefore good candidates for device deployment. © F. Manco.

During later brood, when the chicks were not on the nest anymore and parents were not on guard duties, the birds that were observed feeding the chicks were identified as breeding birds and therefore as candidates for study. They were captured and equipped after completing chick feeding.

Capture

The targeted individuals were caught with a net, transferred into an opaque bag and brought to the working hut for devices deployment and biometrics measurements (see II.1e, page II-20).

Device attachment

The GPS and TDR devices were attached together using superglue and a cable tie before attaching to the study animal. These device packages were attached to the plumage along the centreline of the back using methods adapted from Wilson et al. (1997). They were glued to the back central feathers with 2-parts Epoxy glue and secured with waterproof Tesa ® tape (Figure II-6). At Signy, when deploying some of the larger TDR instruments, both devices were attached separately along the centre of the back.

Figure II-6: GPS and TDR on a bird. © F. Manco.

Capture and deployment generally took less than 10 minutes for an experienced field operative. During most of the manipulation, the bird was retained in the bag in order to keep it from any unnecessary visual disturbance, thus reducing potential stress levels. The equipped individual was then released in the proximity of the nest and monitored to record any abnormal behaviour.

d. Devices recovery

Timing

During incubation, as soon as an equipped bird was observed back on the nest, the devices would be immediately recovered, as the GPS battery life was only sufficient to collect data from a single long incubation trip. During brood, the loggers were left on the penguins for approximately 5 days, enabling them to collect data from several shorter foraging trips.

Re-capture and device detachment

If the bird was on the nest, a bag was put on its head to ensure minimal disturbance while the Tesa ® tape was cut and the devices recovered. This manipulation was generally less than 5 minutes. During the later brood stages, when the chicks and adults were not on the nests location anymore, the procedure was slightly more complex, as the bird had to be captured with a net and placed in a bag in order to recover the device. During incubation and early guard, the nest was covered to ensure the offspring remained warm and were not vulnerable to Sub-Antarctic skua (*Catharacta antarctica*; synonym *Stercorarius antarcticus*) or snowy sheathbills (*Chionis alba*).

Data download

Once recovered, the devices were transported to the Signy research station where the data were processed. The data from the Fasloc GPS had to be post-processed to generate the positions. This procedure was undertaken using the Sirtrack software and required access to the almanac of the GPS satellite constellation. Each deployment would generate a position file. The GPS device's memory was cleared and the battery was recharged overnight. At Geddes where no internet access was available, the almanacs were downloaded directly from the GPS satellites using a custom built receiver.

The download of the TDR data was straightforward, without any additional step. It generated a pressure/temperature file. The filenames contained the identifier of the device and the date and time of the download.

The links to both device files were stored in the deployment database.

e. Potential effects of the devices

Previous studies showed some detrimental effects from attached instruments: slower swimming speeds, excessive preening and pecking, increase in energetics expenditure and overall a decrease in nesting success as reported by Ballard et al. (2001). It is worth noting that these potential effects are difficult to measure: Ballard et al. (2001) mentioned that the trip duration, which is a relatively easy variable to observe on birds without devices, is not optimal to measure instrument effect. The equipped birds might stay in the same groups as other unequipped birds but might alter their diving behaviour as reported by Kooyman et al. (1992) and Ropert-Coudert et al. (2000). Watanuki, Mori and Naito (1992) detected a significant instrument effect using feeding efficiency and chick survival.

Ballard et al. (2001) measured no differences in nest success between equipped and unequipped birds. Recent devices, like the ones used during this study, are lighter (<2% of the weight of the birds) and more streamlined with a smaller cross section than those used in the past. Although no additional data has been collected to measure any potential instrument effect, the very low nest failure rate (1 out of 89 deployments) allowed me to conclude that there was no important instrument effect on the bird's reproductive success.

f. Biometrics and other variables

The birds were weighed before deployment using a Pesola © spring balance and at Geddes (2011-12), the tracked individuals were also weighed at the end of the deployment while recovering the devices. The phenology (incubation or brood) was also recorded. At Geddes (2011-12), the number of eggs and chicks and any changes in the offspring at the end of the deployment was noted.

The bill lengths (culmen) and depths were measured for each study bird to the nearest tenth of a millimetre using a Vernier calliper (Figure II-7).

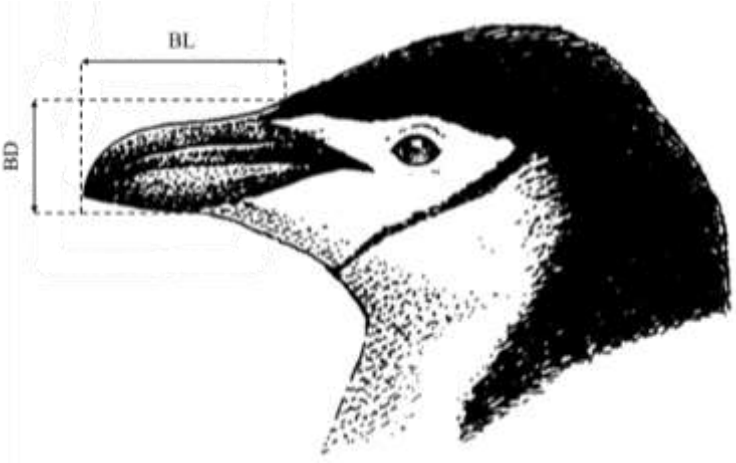

Figure II-7: Bill measurements: length (BL) and depth (BD); adapted from Amat et al. (1993).

g. Sex from bill measurements

Chinstrap penguins show very little sexual dimorphism and are therefore very difficult to sex. Apart from dissection, molecular techniques and behaviour cues (reproduction position and first individual to incubate) methods which are either invasive or difficult to apply, there is some slight morphological dimorphism that can be used to determine the sex of individuals (see Amat, Vinuela, & Ferrer, 1993 and Polito et al. 2012). In this study, the discriminant functions defined by both two studies were used (see Figure II-8). The functions agreed on 81.2% of the birds; all the remaining birds were classified as female by the expression defined by Amat et al. (1993).

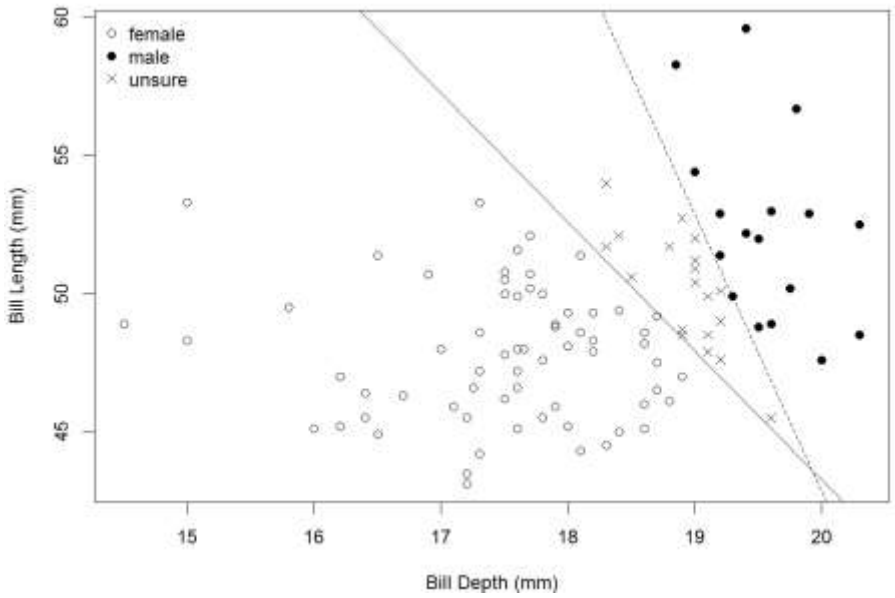

Figure II-8: Distribution of the bill measurements and the discriminant functions separating males and females. The dashed line is derived from Amat et al. (1993) *and the solid one from* Polito et al. (2012).

II.2 Data description and processing

a. Global Positioning System (GPS)

Deployment data upload and mapping

From the deployment database, each position file for each deployment was opened and merged into a series of spatial locations with a time stamp and a deployment identifier. The default coordinates were latitude and longitude (WGS 1984). The locations were re-projected using an Universal Transverse Mercator projection centred on zone 23 south (EPSG 32723) leading to a set of coordinates x and y in metres. This projection was the default reference system used for this study. It facilitated minimisation of local distortion and therefore imprecision when calculating distances and angles. A first filter was applied by removing the locations with null coordinates (12% of the locations, see Table II-1, page II-26).

Identification of trip start and finish points

The position files contained some points that were not part of the foraging trips (acquired on the way from the research station to the colony and/or when the bird was at the colony). In order to filter out these locations, each deployment data points was plotted using GIS software (ArcGIS, ESRI). The points were considered as a temporal sequence and the last point in the colony was classified as the trip starting point. The first point back in the colony was classified as the trip ending point (Figure II-9). There was no need to use a distance threshold to determine which points were in or out of the colony as the very linear shape of the early and late sections of the trips made it very easy to distinguish what was part of the trip or not. Foraging trips were therefore

made of a single start point in the colony followed by a series of points at sea and a single end point back in the colony.

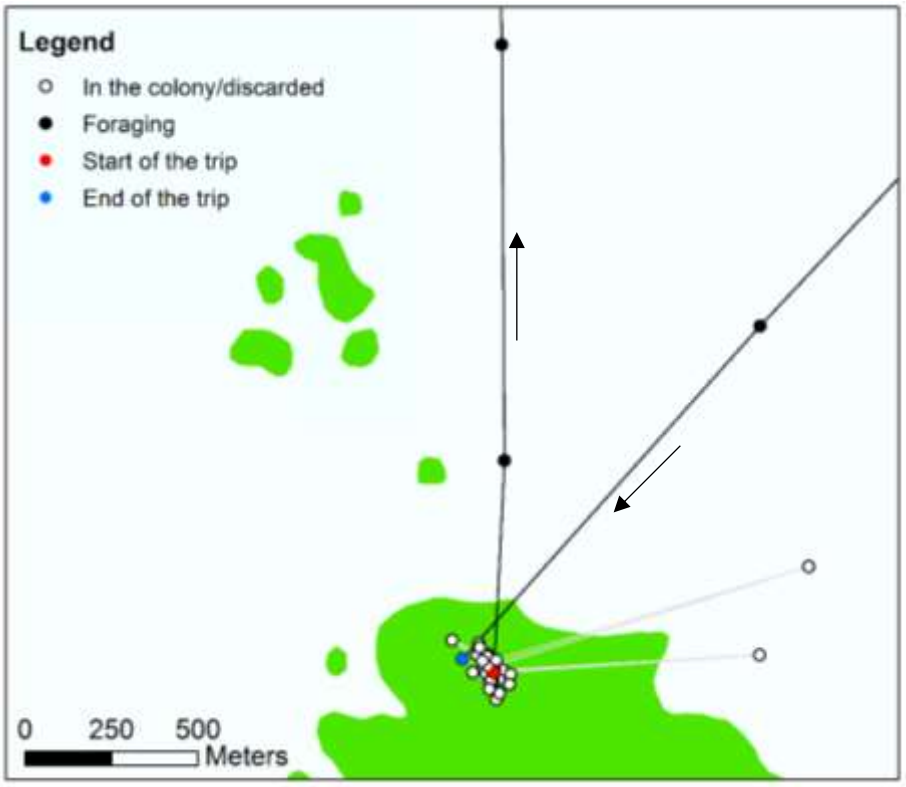

Figure II-9: example of the visual distinction between the foraging trip points and the locations at the colony enabling identification of the start (red) and end (blue) trip points. The black lines represent the foraging trip and the grey lines represent the sequence of points not part of the trip (in the colony).

For four trips (two from each colony), it was not possible to define a start or end point as the data acquisition from the GPS device started or ended outside of the colony (see Figure II-10). In order to complete these trips, the first point in the colony was duplicated (in case the missing point was the end point; otherwise the last point in the colony was duplicated). The time stamps of these duplicated locations were changed based on the time and distance with the last or previous at sea point and an average commuting speed of 2 m s^{-1} (Davis and Darby, 2012). The fact that the reconstructed last section of the trip crossed land on Figure II-10, which is possible but unlikely, illustrates some of the limitations of this method.

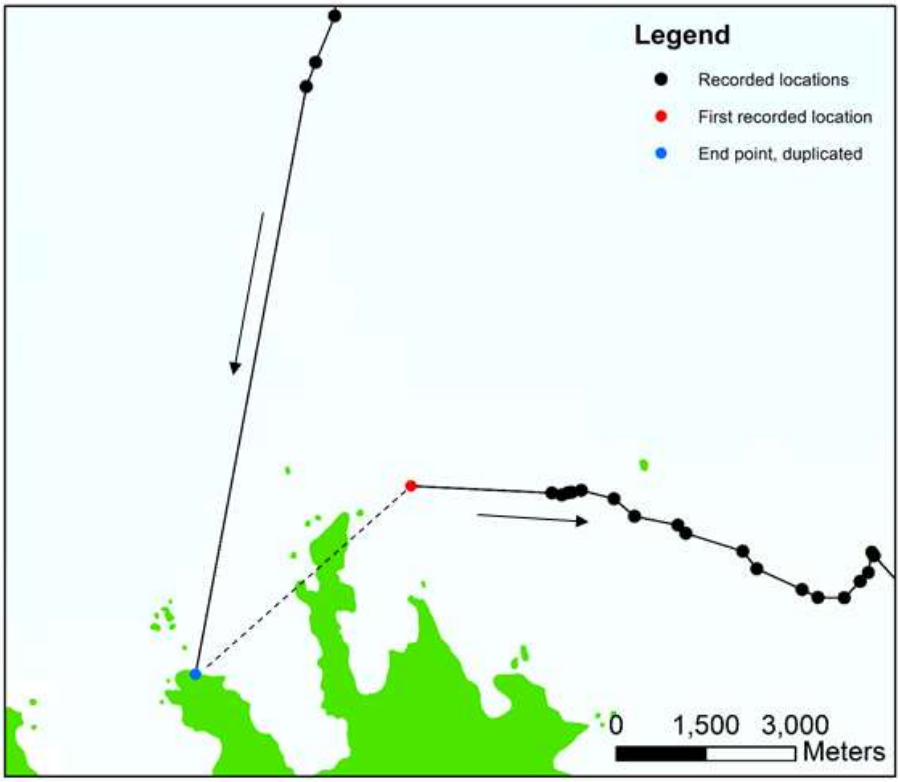

Figure II-10: Example of an incomplete trip where the first recorded location was outside the colony (red point). To complete the trip, the end point of the trip (blue point) was duplicated and its time stamp was changed based on the time and the distance to the first recorded location (red point) and an average commuting speed of 2 m s^{-1}.

Removing the locations that were not part of the foraging trips allowed me to discard an additional 22% of the recorded points (see Table II-1, page II-26). The trip nomenclature used in my database of foraging trip descriptors combined the deployment identification number and a unique trip identifier: for example, trips 34_59 and 34_60 are from the same bird indicated by its deployment number (34).

Calculation of the surface metrics

The R package 'adehabitatlr' (Calenge, 2006) was used to calculate a series of surface metrics from the filtered positions. For each position i (defined by coordinates x_i and y_i and time t_i), the time difference in seconds $\Delta(t_i, t_{i+1})$ and the distance in metres to the next position ($Dist_{i \to i+1}$) were calculated. From these two variables, the speed to the next location was derived in m s^{-1} (Figure II-11 and Equation i).

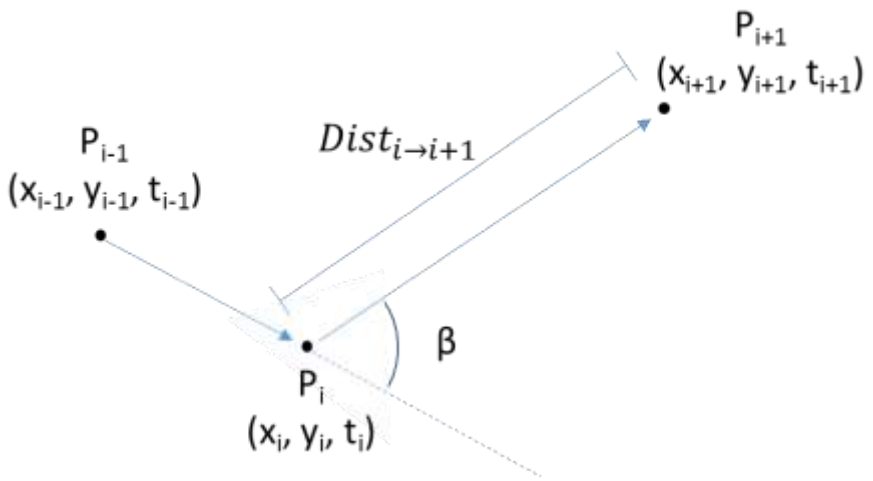

Figure II-11: For each P_i position, the distance to the next point P_{i+1} ($Dist_{i \to i+1}$) is calculated along with the relative angle (β) which is the angle between the segment from the previous point (P_{i-1}) and the segment to the next point (P_{i+1}). A relative angle of 0 means that the three points are perfectly aligned. A positive relative angle means that the bird turned in the anticlockwise direction.

$$Speed\ at\ P_i = \frac{Dist_{i \to i+1}}{\Delta(t_i, t_{i+1})}$$

Equation i: Calculation of the speed at a location based on its distance ($Dist_{i \to i+1}$ in metres) and time difference ($\Delta(t_i, t_{i+1})$ in seconds) to the next location.

The same package ('adehabitatlr') also estimated for each location the angle between the segment from the previous point and the segment to the next point (relative angle, β, see Figure II-11). These angles were expressed in radians ranging from 0 to $+\pi$ (anticlockwise) and 0 to $-\pi$ (clockwise). The absolute value of the relative angle was retained as an indication of the sinuosity of the track (0 to $+\pi$).

Locations validation

In addition to the removal of null coordinates, the positions were validated through visual control of locations with a calculated speed above 4 m s^{-1}. Although some very high and unrealistic speed measurements (the maximum value was 1.5 km s^{-1}) were produced from the automated process, all speeds close to the threshold were visually inspected. Moreover as the speed was derived from the distance and time difference between two successive locations, the point with an abnormal speed might not be the one that had to be discarded (Figure II-12).

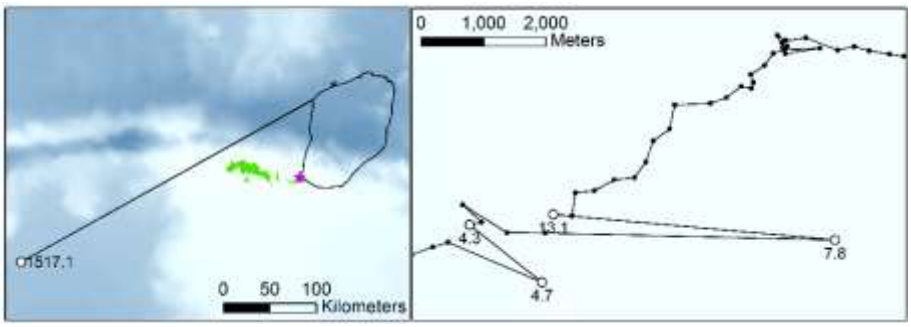

Figure II-12: Examples of location check combining speed and visual check. The left trip has a very obvious location error with a speed of more than 1.5 km s^{-1}. The right trip shows a mixture of locations with realistic and unrealistic speeds. In the case where two successive points have high speed values, only a visual check of the trajectory can help to decide which point have to be discarded.

Once the locations were validated (304 points were discarded from the entire dataset), the surface metrics (speed and angles) could be re-calculated on the filtered positions only. Table II-1 summarize the number of positions from the raw GPS data to the final filtered locations with a break down by seasons, colonies and breeding stages.

Table II-1: Number of locations recorded for this study from the raw data including points in the colony and erroneous locations eventually discarded by filtering positions.

			Geddes (2011-12)		Gourlay (2011-12)		Gourlay (2013-14)	
	No locations	% from raw data	Incubation	Brood	Incubation	Brood	Incubation	Brood
Raw data	73,031	100%	31%	14%	11%	12%	30%	2%
Filter 1 (non-zero coordinates)	64,330	88%	33%	14%	8%	13%	30%	2%
Trip allocation	48,370	66%	40%	14%	1%	4%	39%	2%
Missing start/end	48,374	66%	40%	14%	1%	4%	39%	2%
Filter 2 (speed and visual checks)	48,070	66%	40%	14%	1%	4%	39%	2%

b. Time-Depth Recorder (TDR)

Deployment data upload and validation

From the deployment database, each TDR data file was loaded and the depths plotted against time (dive profiles) to help highlight any measurement issue. The foraging trip coordinates, defined by the GPS data (II.2a, page II-22) were merged with the dive profiles to check whether both datasets were temporally matching and if they were any anomalies in the data (Figure II-13).

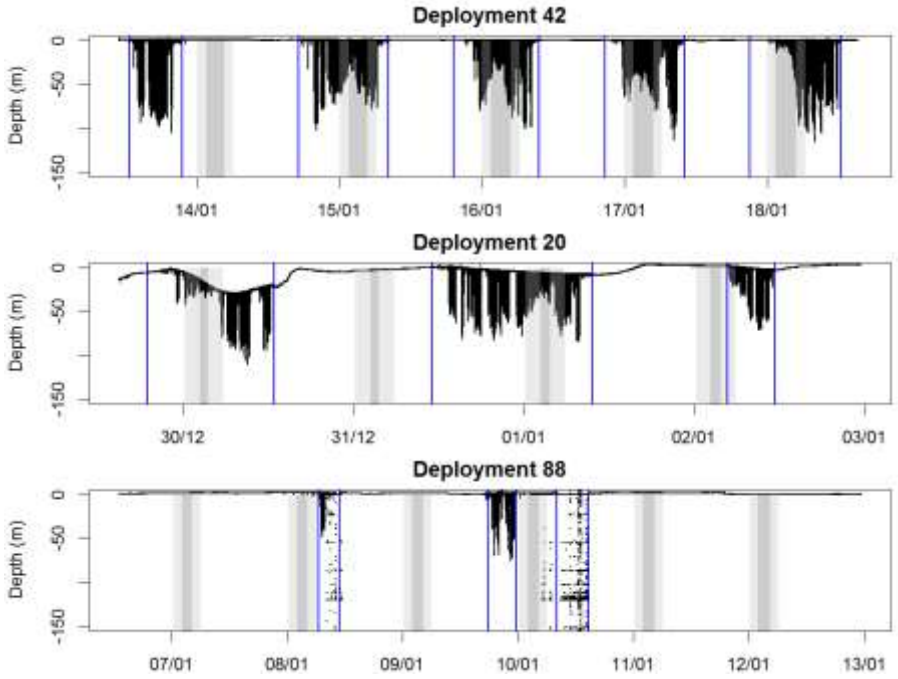

Figure II-13: Examples of using the dive profiles as visual checks between the TDR data and the trip timing from the GPS data (the vertical blue lines represents GPS-derived trip temporal boundaries). The grey areas represent the different night periods (light grey: twilight, dark grey: night, see II.2d). Deployment 42 (top) shows a good match for its five foraging trips. Deployment 20 (middle) shows a drift in the TDR measurement that has to be corrected; surface offset correction is sometimes required for TDR data. Deployment 88 (bottom) shows erratic measurements; with the exception of the second foraging trip, the other data has to be discarded.

Two deployments (9 and 20, the latter is presented on Figure II-13) showed important drift in the pressure measurement. This was corrected by splitting the measures into portions with an approximate constant drift slope. Each measure was then adjusted based on a linear drift between the start and the end of the portion. During three deployments (65, 70 and 82), the TDR expired before the end of the trip; the incomplete dive data for these datasets were discarded. For three deployments (89, 107, 108), the timing did not match the trips defined by the GPS data; some trips could be retained but others had to be discarded. Several TDR devices (6) showed erratic measures and had to be discarded (for deployment 88, one trip could be retained, see Figure II-13).

Dive identification

The R 'diveMove' package (Luque, 2007) was used to process the TDR data and identify individual dives. The depth threshold value was set to 5 m to avoid near-surface noise in the data and minimise the effect of measurement drift (Bengtson, Croll and Goebel, 1993). Although Takahashi et al. (2003) used a lower threshold (1m). It might be possible that shallow foraging dives (<5m) might have been lost during this study, but changing the threshold for a sample of trips (N=10) to 1m mainly increased the number of dives without detectable bottom phase, which truly represent travelling dives. A series of metrics for each dive was calculated: the dive timing (beginning and end of the dive and total

dive duration), the maximum depth and the time interval to the next dive (post-dive interval).

Dive phases

The 'diveMove' package also derived additional metrics based on identifying the different phases for each dive: a descent, a bottom and an ascent phase. Unfortunately, the package was not always successful in detecting the bottom phase (more specifically, the end of the bottom phase, see Figure II-14, dive 30). An alternative method applied a nonparametric change point detection on the derivative of the dive depth over time to find the three dive phases ('ecp' R package, James & Matteson 2014). Figure II-14 compares the different dive phase identification for both methods.

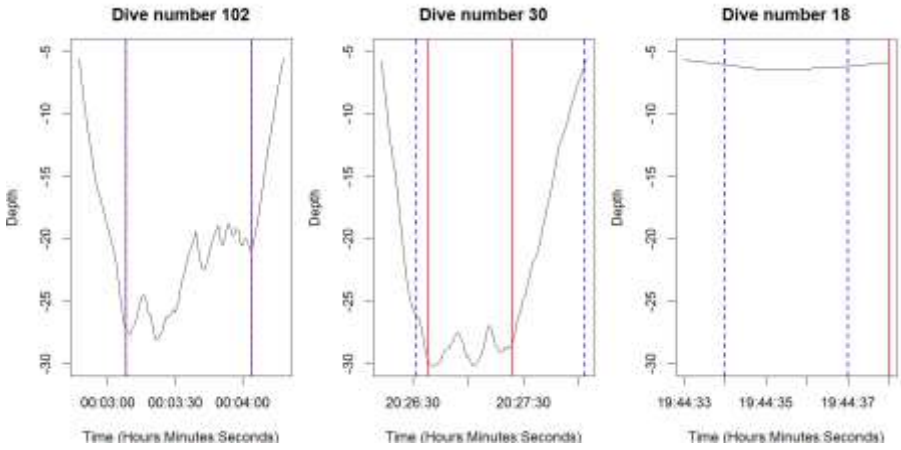

Figure II-14: Examples of bottom phase identification comparing the 'diveMove' algorithm (blue dashed lines) and the change point detection algorithm used in this study (solid red lines). Dive 102 (left) shows a perfect match between both algorithms. Dive 30 (middle) illustrates the issue for the 'diveMove' algorithm in identifying the end of the bottom phase. Dive 18 (right) is considered as a dive as it goes below the 5 m threshold but doesn't have a clear bottom phase.

For a series of dives, the change point detection algorithm couldn't identify a proper bottom phase (although 'diveMove' did, see dive 18 Figure II-14). The majority of these dives were short shallow dives (duration was less than 20 s and 98.8% were less than 10 m deep) and might be considered as porpoising or travelling dives. They were therefore discarded. Table II-2 summarizes the number of TDR measurements and dives identified with a break down by seasons, colonies and breeding phases.

Table II-2: Total number of raw pressure measurements before and after trip allocation. Number of dives detected by 'diveMove' and result after filtering out the dives without bottom phase.

			Geddes (2011-12)		Gourlay (2011-12)		Gourlay (2013-14)	
		% from total	Incubation	Brood	Incubation	Brood	Incubation	Brood
Pressure measurements	36,682,598	100%	43%	29%	1%	4%	18%	5%
Trip allocation	18,297,012	50%	41%	26%	<1%	3%	29%	1%
Dives	78,820	100%	47%	23%	<1%	1%	26%	2%
Dives with bottom phase	71,216	90%	48%	23%	<1%	1%	25%	2%

Once the different phases were defined, the timing (start, end and duration in minutes) and the vertical movements for each phase could be calculated (in metres). From the timing and vertical distances for the descent and ascent phases, the speed of descent and ascent could be derived (m s^{-1}).

Broadness index and dive efficiency

The broadness index was calculated as the ratio between the time spent at the bottom and the total dive time (Scheffer, Bost and Trathan, 2012). The dive efficiency was defined and calculated as the ratio between the time spent at the bottom of the dive and the sum of the total dive time and post-dive duration (Kuhn et al. 2010; Cook et al. 2012, Equation ii).

$$dive\ efficiency = \frac{time\ at\ the\ bottom}{total\ dive\ time + post\ dive\ duration}$$

Equation ii: Calculation of the dive efficiency for each dive.

c. Merging the GPS and TDR datasets

Position interpolation

Because of the different temporal resolutions between the GPS dataset (one data point every 4 minutes at best as locations could not be generated during dives) and the TDR dataset (one data point every 1 or 2 seconds), an interpolation technique was used to estimate intervening horizontal positions during the 4 minutes recording interval and while diving, thus providing temporally matching datasets. Having temporally regular tracks with no gaps in the sequences of data improves the fine scale analyses of foraging trips (see Gurarie et al. 2009 and Chapter V).

Although the simplest and most often used approach is a linear interpolation, which assumes that animal moved in a straight line (Lonergan, Fedak and McConnell, 2009), Tremblay et al. (2006) and Dean et al. (2012) recommended using a curvilinear interpolation technique to increase the temporal resolution of the GPS dataset. This type of interpolation will also generate smoother surface metrics changes, which will improve the segmentation process during the fine scale analysis of foraging trips (see V.2b, page V-82). There are several curvilinear interpolation techniques available, the Bezier curve being

one of them. Unfortunately, the resulting interpolated tracks with this technique avoid the known original locations, where the lowest uncertainty is. In this study, I therefore used the cubic hermite interpolation algorithm (Hintzen et al. 2010). Figure II-15 represents examples of these different interpolation techniques.

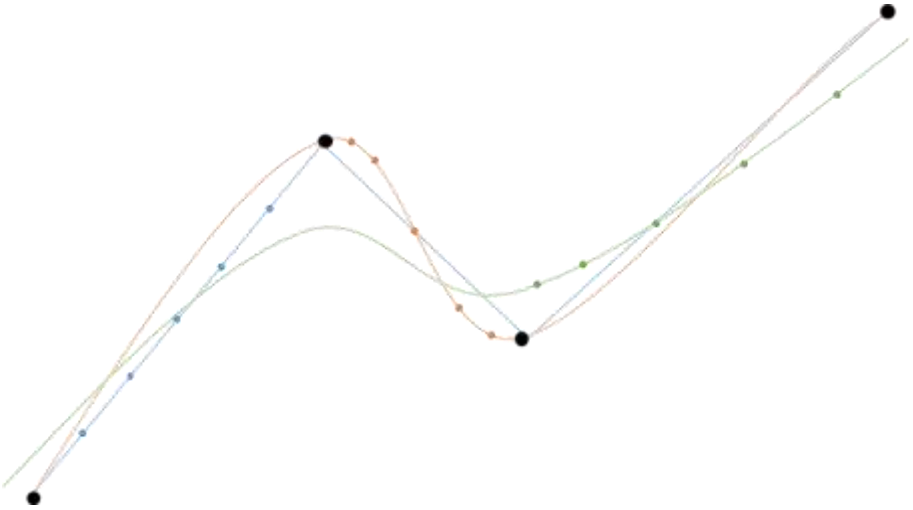

Figure II-15: GPS locations (black dots) with different interpolation techniques: the blue line is a linear interpolation, the green curve is based on a Bezier technique and the red curve represents the method used in this study (cubic hermite interpolation). The small dots represent the one minute interpolated locations with a clear view on how their distribution along the line or curves varies with the interpolation technique.

For each position, the geographic heading to the next point was calculated and used together with the speed as inputs for the spline interpolation algorithm. This technique was applied to build a one-minute resolution track which provided a useful compromise between resolution, accuracy and computing time. It is also in line with the dive time resolution as the recorded mean dive time was 63 seconds.

To relate the added spatial uncertainties resulting from the interpolation process with the uncertainties from the original GPS dataset, buffer areas were plotted around each GPS location. For each point, a buffer was created based on measured errors during the static tests corresponding to the number of acquired satellites during the acquisition of the location (see Figure II-16). In average, 94.1% of the interpolated positions fall within the median error estimated error range (standard deviation of 4.9%). This confirmed that the interpolation process didn't add more uncertainty in relation to the original GPS locations, as observed by Tremblay et al. (2006).

Surface metrics on the interpolated positions

The surface metrics (speed and relative angles) were calculated on each interpolated positions using the same method described in II.2a. A final check on each interpolated position, with a focus on locations with speeds close to 4 m s^{-1} forced me to discard another 49 locations. The interpolation process had to be re-run on the filtered positions and the surface metrics were re-calculated on the final interpolated positions (see Table II-3).

Distances to colony and part of the trip

The Euclidean distance to the colony was measured in kilometres for each interpolated location. The point with the greatest distance from the colony (trip maximum range) was classified as the maximum point of the trip. All previous points were attributed to the outward part of the trip and all successive points were considered as being part of the return section of the trip.

Merging the dives with the interpolated positions

For each trip, the beginning of each dive was matched to the closest one minute interpolation location. In cases where there were several dives per minute (641 dives from the complete database), all such dives were retained and linked to the same location. Table II-3 presents the number of locations from the filtered GPS data (see Table II-2), the number of interpolated locations and the total interpolated position merged with the dives (with an increase in the number of location due to dives occurring during the same one minute interval). See Figure II-16 for an example of merged interpolated positions with dives.

Table II-3: Number of points from the filtered GPS positions, the 1 minute interpolated locations and the merging results with dive data. The increased number of locations after the merge indicates that some 1 minute locations were matched with several dives.

	No locations	Geddes (2011-12)		Gourlay (2011-12)		Gourlay (2013-14)	
		Incubation	Brood	Incubation	Brood	Incubation	Brood
Filtered GPS position	48,070	40%	14%	1%	4%	39%	2%
Position interpolation	417,926	30%	19%	1%	2%	46%	2%
Interpolated positions trip with dives	418,567	30%	19%	1%	2%	46%	2%

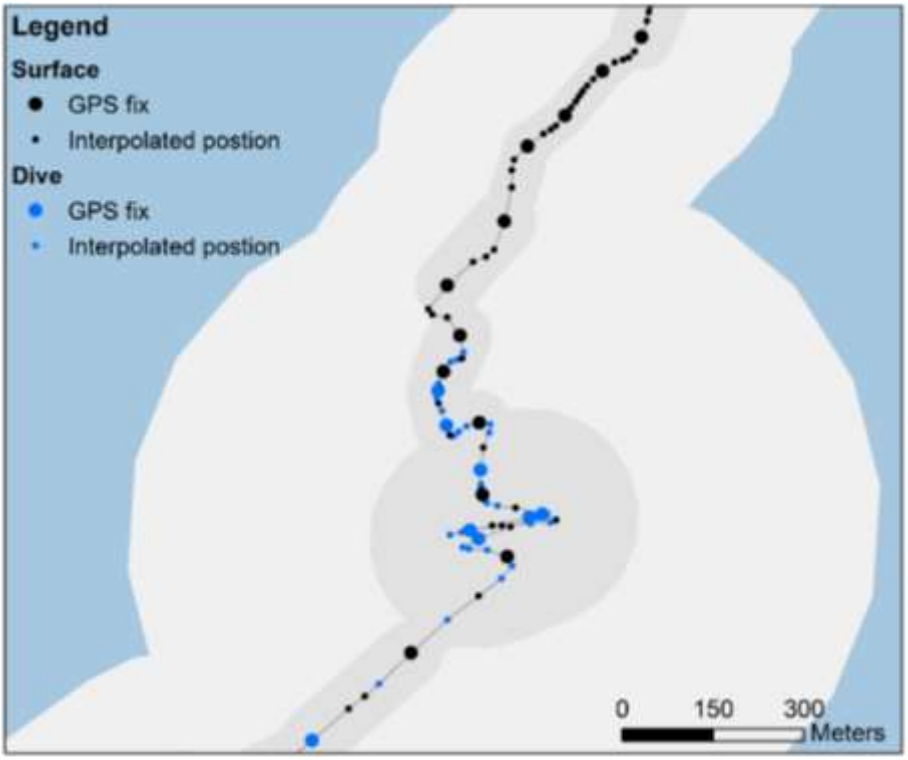

Figure II-16: Portion of a foraging trip with the original GPS fixes and the 1 minute interpolated positions (size of the point) and an indication of whether a dive is associated with the point (colour). The grey areas represent estimated GPS uncertainties based on the in colony static tests and the number of acquired satellites for each GPS location (see II.1b, page II-14, dark grey is the median location error and light grey is the 95% quartile error).

d. Period of the day and moon phase

Time and especially the period of the day has an important impact on predators foraging for krill as a result of changes in luminosity and the vertical migration of their prey (Zhou and Dorland, 2004; Everson, 2008; Cresswell et al., 2009). To incorporate this parameter, the solar elevation angle was calculated on each interpolated position based on its geographic coordinates and its date and time using the Analysis of Oceanographic data 'oce' R package (Kelley and Richards, 2016).

The civil twilight threshold (-6º below horizon) was applied on the solar elevation angle to attribute the period of the day (day: > 0º above the horizon, twilight: between 0 and -6º below horizon and night: <-6º below the horizon) for each location.

The same 'oce' package was also used to calculate the percentage of moon illumination for each interpolated position.

II.3 Trip metrics

A series of variables could be measured and derived for each foraging trip. Some were based on the surface data only (the trip maximum range for example); others were combining the horizontal surface dataset with the vertical dive data in order to consider the foraging as the exploitation of a volume (Zamon et al., 1996; Wilson and Peters, 1999; Wilson, 2010).

a. From the surface data only

The trip duration was calculated from the time difference between the first and last points of the trip identified from the GPS data as previously described (see II.2a on page II-22). The post-trip duration (time spent at the colony between two successive trips) was also calculated for the deployments including several trips (54 trips out of 221).

The trip direction (clockwise or anti-clockwise) was estimated visually. For very direct trips with nearly overlapping commuting section and a single limited foraging area or trips where the outward and return section were crossing each other several times, the trip direction couldn't be clearly attributed (27 trips out of 221).

The total surface trip length was the sum of all the distances between the points (see II.2a). The maximum trip range was defined as the maximum distance to the colony measured from each location (see II.2c). The Foraging Zone Coefficient (FZC) was calculated as the ratio between the total trip surface length and the maximum range, indicating the circularity of the foraging trip; low values indicating a more direct linear trip (see Scheffer et al. 2012).

For each trip, the number of points classified as being part of the outward portion of the trip (II.2c) divided by the total number of points from the trip allowed to calculate the percentage of trip time the outward portion represented.

Similarly, the number of points attributed to the twilight or night periods of the day (II.2d) divided by the total number of points from the trip estimated the percentage of night activity.

b. From the dive data only

For the trips that included complete TDR data, the total dive duration (II.2b) was divided by the trip duration to estimate the percentage of dive time. The number of dives occurring during the twilight or night periods of the day divided by the total number of dives indicated the percentage of night dive for each trip.

c. From the merged GPS+TDR dataset

To be able to consider the utilized foraging habitat as a volume, the 3-D length of the trips with TDR data was measured by summing the distances between each interpolated positions in a three dimensions volume (x, y and maximum depth). This length was then divided by the trip duration to approximate habitat volume exploration speed, as a potential indicator of resource use.

To incorporate the diving vertical elements of the trips, the sum of the vertical distances (dive descent and ascent distances and vertical distances at the bottom of the dives, II.2b) was divided by the surface trip length to estimate a ratio of vertical versus horizontal habitat exploration per voyage.

II.4 Summary of the collected data

a. The process

The workflow from the deployment data, raw GPS and TDR data to the final 1 minute interpolated locations merged with the diving data is presented in Figure II-17.

The GPS data allowed me to identify the start and end of the foraging trips. The surface metrics derived from the projected GPS data were used to filter out any abnormal locations. This validation process (visual check of each trip with the aid of directly calculated speeds) was iterated several times in order to fully validate the remaining positions.

From the filtered positions and their surface metrics, a spline interpolation process was applied to generate a regular temporal succession of locations (1 minute interval). The surface metrics were calculated on the interpolated positions and an additional visual and speed check was performed.

The trip timing from the GPS data was used to link the TDR data to individual foraging trips. The TDR data were then processed to identify individual dives and recognize the different dive phases. The timings and vertical metrics for each dive phase were derived.

The different dives were then merged with the temporally matching interpolated positions to recreate a three-dimensional model of the foraging trips.

Finally, from both the surface and dive metrics, a series of trip characteristics could be calculated.

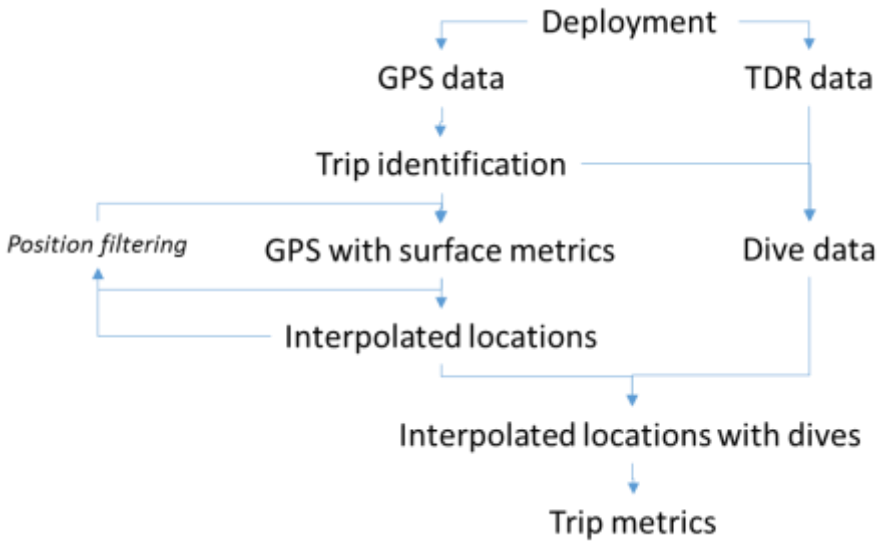

Figure II-17: Summary of the data collection and processing. From the deployment database through the workflow on the data collected by both devices leading to the 1 minute interpolated locations linked with the dive data. Finally several trip metrics were derived.

b. The complete dataset

In total, the devices were deployed on 109 different birds. At Geddes in 2011-12, 35 incubating birds and 25 brood birds were tagged. At Gourlay, 7 incubating and 9 brood birds were equipped in 2011-12 and an additional 27 incubating and 6 brood birds in 2013-14.

Out of these 109 deployments, 5 birds didn't have a GPS, 7 birds didn't go to sea, 1 never came back and 7 had some GPS device malfunction. Therefore 89 deployments had usable tracking data. In 2013-14, one bird did a very long and atypical incubation trip (almost 20 days, see Figure IV-6, page IV-60), resulting in the failure of the nest). The data from this bird (one trip: 75_173) was therefore discarded after being confirmed as an outlier (see IV.2a, page IV-48).

From the remaining 88 deployments, 8 showed unusable TDR measurements and 4 had incomplete dive data (the TDR devices expired during the trip). For an additional 4 deployments, only a subset of their trips had complete dive data. The GPS and TDR data were complete and matching for 77 deployments totalled 192 foraging trips (see Table II-4). One incubation deployment from Gourlay in 2013-14 (65_166) had a very poor location frequency (median time interval of 34 minutes). The GPS device was not re-deployed afterwards. Despite this, the trip was kept for subsequent analyses,

Table II-4: Total number of deployments and subsets with complete GPS and TDR data with the resulting number of foraging trips in total and per colony, season and breeding stage.

	No deployments	No trips	Geddes (2011-12)		Gourlay (2011-12)		Gourlay (2013-14)	
			Incubation	Brood	Incubation	Brood	Incubation	Brood
All deployments	109							
Complete GPS data	89	221	65	100	9	19	16	12
Complete GPS and successful breeding	88	220	65	100	9	19	15	12
Complete GPS+TDR data	76	192	65	97	2	13	7	8

c. The variables

The deployment database (Table II-5) contained information about the deployment: location (colony), timing (season, device deployment and recovery, breeding stage) and different biometrics (bill measurements and birds weight). The putative sex of the bird was derived from the bill measurements. At Geddes (2011-12), the birds were also weighed at the end of the deployment and more detailed information about the offspring were collected.

Table II-5: Deployment data included some temporal (green) and spatial (blue) variables. It also inclued some direct and derived biometric variables (yellow).

Variables	Derived variables	Comments	
Deployment ID			
Season		2011-12 or 2013-14	
Colony		Geddes or Gourlay	
Deployment timing		Date and time of deployment and recovery	II.1c and II.1d
Breeding stage (incubation/brood)	Bird offspring	Number of eggs/chicks at device deployment and recovery – Geddes (2011-12) only	II.1e
Bill measurement (mm)	Sex	Based on Amat et al. 1993 and Polito et al. 2012	II.1g
Bird weight (kg)		Deployments from Geddes (2011-12) also included weight after device recovery	II.1e

The data from the GPS contained temporal (date and time) and spatial information (coordinates). The combination of both allowed me to determine the start and end of each trip. From their coordinates, the distances and the relative angles between points were derived. The distances and time between points allowed to calculate the speed of the bird.

The interpolated positions dataset contained the same variables but at a higher frequency (1 min^{-1}). The distance from each location to the colony was measured and the points were categorised as being on the outward or return part of the trip. From the temporal information, the points were classified as being part of the day, twilight or night (Table II-6).

Table II-6: GPS and interpolated locations based temporal (green), spatial (blue) and combined spatio-temporal (red) variables.

Variables	Derived variables	Comments	
GPS DATA			
Deployment and trip ID			
Date and time	Trip start and finish		II.2a
Coordinates (Longitude/Latitude)	Coordinates (x/y)	Using a UTM zone 23 south projection system	
	Distances between points (m)		
	Relative angles (rad, absolute value)	The calculated relative angle varied from $-\pi$ to $+\pi$; it was converted to positive angles (absolute value) as an indication of the sinuosity of the track	
	Speed (m s^{-1})	From the distance and time difference to the next point	
INTERPOLATED DATA			
Deployment and trip ID			
Date and time	Period of the day (day/twilight/night)	Based on the sun elevation and civil twilight threshold (<-6°: Night; -6° to 0: Twilight and >0: Day)	II.2d
	Moon illumination (%)	From the date, time and spatial coordinates	
Coordinates (x/y)	Distances between points (m)		II.2a
	Relative angles (rad, absolute value)	See the comment in the GPS DATA section above	
	Distance to the colony (km)		II.2c
	Part of the trip (outward or return)	All points before the furthest point to the colony are considered outward.	
	Speed (m s^{-1})		II.2a

The data from the TDR contained the time and depth measurements. The derived dive data incorporated some temporal information for each dive (dive start, finish and duration) and the timing of the dive phases (descent, bottom and ascent). It also included a one dimension spatial information (maximum depth and vertical distances for each dive phase). From the descent and ascent times and distances, the descent and ascent speeds were derived. The broadness index and dive efficiency were calculated as measures of the amount of time spent at the bottom of the dive (Table II-7).

Table II-7: Raw TDR and derived dive variables. The measures and processes lead to a series of temporal (green), one dimension spatial (blue) and combined spatio-temporal (red) variables.

Variables	Derived variables	Comments	
TDR DATA			
Deployment and Trip ID		From the trip timing defined by the GPS data	II.2b
Date and time			
Depth (m)			
DIVE DATA			
Deployment and Trip ID			
Dive ID		Calculated by diveMove (Luque, 2007)	II.2b
Dive timing (start, end)	Total dive time		
	Post-dive duration		
	Maximum depth (m)		
Descent time (s)	Descent speed (m s^{-1})	Calculated using change point detection on depth derivative	
Descent vertical distance (m)			
Bottom time (s)			
Bottom vertical distances (m)			
Ascent time (s)	Ascent speed (m s^{-1})		
Ascent vertical distance (m)			
	Broadness index	Bottom time divided by the total dive time, Scheffer et al. (2012)	
	Dive efficiency	Bottom time divided by the sum of the total dive time and the post-dive duration, Kuhn et al. (2010)	

Finally, a series of trip aggregated metrics were defined from either the surface data, the dive data or the combined surface and dive dataset. Similarly for other datasets, the trip metrics contained a mixture of temporal and spatial based variables (see Table II-8).

From the surface data, the trip start and end times allowed to derive the trip duration and post-trip duration. The other time-based variables were the percentage of outward part of the trip and the percentage of night activity. The spatial variables were the trip direction, surface length, maximum range and the derived foraging zone coefficient.

From the dive data, two temporal variables were derived: the percentage of dive time and the percentage of night dives.

Finally, from the merged surface and dive data, the ratio between the vertical movements during the dives and the trip surface length was calculated. As a spatio-temporal variable, the trip exploration speed was estimated as the 3 dimensional length of the trip (sum of the surface length and maximum depths) divided by the trip duration.

Table II-8: Trip variables derived from the GPS data, the dive data and the merged GPS+dive data leading to a series of temporal (green), spatial (blue) and spatio-temporal (red) variables.

Variable	Derived variables	Comments	
Trip ID			
From the surface data			
Trip start and end	Trip duration (hours)		II.2a
	Post-trip duration (hours)		II.3a
Trip direction		Clockwise or anti-clockwise	
Trip surface length (km)	Foraging Zone coefficient	Sum of all the distances between points (trip surface length) divided by the maximum distance to the colony (trip maximum range); Scheffer et al. (2012)	II.3a
Trip maximum range (km)			
Percentage of outward time		Percentage of time spent on the outward part of the trip (before the point of maximum distance)	
Percentage of night activity		Percentage of trip during the twilight or night parts of the day	
From the dive data			
Percentage of dive time		The total dive time for the trip divided by the trip duration – trips with dives only	II.3b
Percentage of night dives		Percentage of dives during the twilight or night parts of the day – trips with dives only	
From the merged surface and dive data			
Exploration speed (m min^{-1})		Three dimensions length of the trips (surface and dive) divided by the trip duration – trips with dives only	II.3c
Vertical/horizontal distances		Ratio between the sum of the vertical components of the dives and the trip surface length	

Each deployment and trip is described in Appendix II.

d. Spatial and temporal resolutions

The spatial resolution of the GPS data were estimated to be 250 m based on the pseudo static tests while the birds were at the colony (see page II-16).

The final GPS temporal resolution (mean time difference between GPS points of 8.7 minutes with a regular 1 second TDR measurement intervals), following interpolation and merging gave a regular 1 minute temporal resolution dataset.

These spatio-temporal resolutions will be compared with temporal resolution of the inferred behaviour modes (Chapter V) and the environmental data inputs for the habitat model in Chapter VI and Chapter VII.

Chapter III COLONIES AND YEARS COMPARISONS

This chapter will describe some of the main abiotic and biotic differences between the two colony sites. The sample sizes, the temporal scale of the sampling and some results about the foraging trips timings will be presented for both sampling seasons. Finally, differences in parental weights and reproductive effort will be reported.

III.1 Main colony differences

a. Abiotic

Differences between environmental conditions available to birds from both colony sites will be presented and discussed in more details in Chapter VII. Here the main dissimilarities in bathymetry, surface currents and sea ice cover will be briefly described.

Figure III-1 presents a general view of part of the Gourlay Peninsula chinstrap colony where deployments were made. The site is located on a raised flat area overlooking a small bay. The top of the colony (foreground) is occupied by Adélies and the bottom and edges are occupied by chinstraps, as the latter established their nests later in the season (Carlini et al., 2005).

Figure III-1: General view of the Gourlay Peninsula colony fragment with Adélie penguins in the foreground. © F. Manco.

Figure III-2 and Figure III-3 present some views of the Cape Geddes chinstrap colony.

Figure III-2: General view of the old FID hut at Cape Geddes with a small part of the chinstrap penguin colony. © P. Trathan.

Figure III-3: Typical nesting habitat at the Cape Geddes chinstrap penguin breeding colony. © P. Trathan.

The underwater landscape is an important feature potentially allowing marine predators to navigate. The hydrography has also a crucial role in driving horizontal and vertical currents. As the latter transport nutrients and plankton, productivity can be concentrated around some oceanographic features such as shelf breaks, canyons, seamounts, etc… The effect of bathymetry on fledging success has been reported by Chiaradia et al. (2007) for little penguins and several studies highlighted how predators use continental slope areas (Ichii et al. 1998; Trathan et al. 2003; Trathan et al. 2006; Atkinson et al. 2008; Siegel et al. 2013).

Figure III-4 shows the bathymetry profiles available from both sites and which part of the depth range is covered by typical incubation and brood

trips. It is clear that although long incubation trips from the Gourlay Peninsula can reach the continental slope, the shorter brood trips have to remain over the shelf area. From Cape Geddes, birds are able to reach the shelf slope during the whole breeding season due to its proximity.

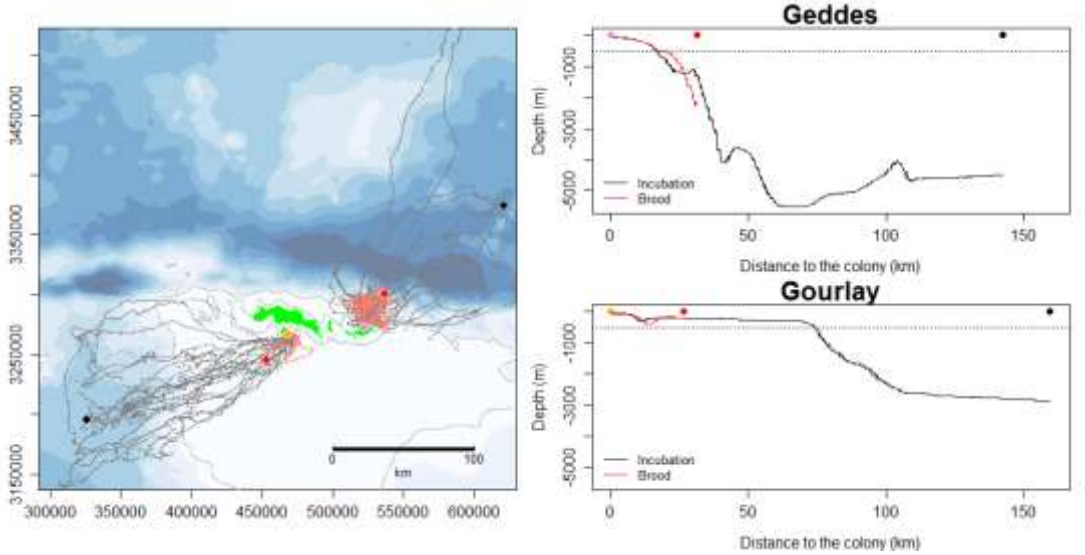

Figure III-4: Bathymetry and foraging trips recorded from both colonies (left; black lines represent incubation trips and red lines represent brood trips). The right graphs represent a bathymetry profile between the colony and the most distant point from a typical incubation (black dot) and brood (red dot) trips.The horizontal dotted lines represent the locations of the 500 m isobath.

Current regimes are also very different along both sides of the archipelago. On the north side, weak westerly currents are present close to the shore and they flow to the opposite direction and are stronger offshore. On the south side of the archipelago, currents are weaker and more variable in direction.

Another important difference due to the orientation of the coast relates to the presence or absence of sea ice. On the south side of the archipelago, pack ice pushed by winds from the Weddell Sea or Antarctic Peninsula is more likely to accumulate (as seen on Figure III-1). The sea ice can have an impact on local conditions (sea temperature) and will influence Adélie and chinstrap penguins differently, the latter usually preferring open waters (Lynnes et al., 2002). It is usually absent later in the breeding season.

b. Biotic

The main biotic differences between both sites relate to inter and intra-specific competition. As mentioned earlier, the Gourlay Peninsula colony contains an assemblage of sympatric Adélie and chinstrap penguins. In contrast, the Cape Geddes colony only hosts chinstraps. Figure III-5 maps the different chinstrap and Adélie penguin colonies on the South Orkney Islands. Adélies colonies are mainly distributed along the southern coasts of the islands (with one exception on the north coast of Laurie Island).

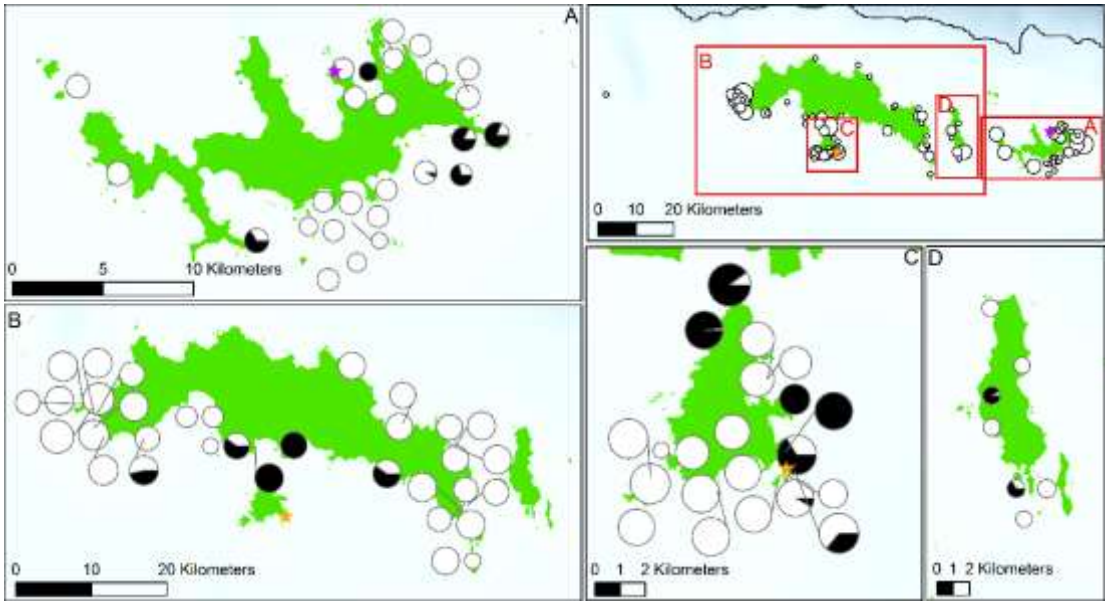

Figure III-5: Colony sizes and distribution on the main South Orkney archipelago islands. The size of the circles is proportionate to the total chinstrap and Adélie population and is represented with a logarithmic scale. When both species are present at the same site, the black areas represent the ratio of Adélie penguins. The largest population estimate for each island are: 75,200 on Laurie Island (A), 300,000 on Coronation Island (B), 72,126 on Signy Island (C) and 21,320 on Powell Island (D). Estimates are from Trahan and Lynch, 2008, unpublished.

Despite having asynchronous life cycles, it is likely that both species have foraging areas that might overlap as they share the same habitat and resources. In years of poor krill availability, Lynnes et al. (2002) reported that Adélie penguins had to forage further offshore. The same authors mentioned that this probably competitive exclusion didn't have any effect on Adélie reproductive success. In addition, chinstrap penguins are known for being able to dive in lower light conditions (Wilson and Peters, 1999).

In terms of intraspecific competition, the chinstrap populations at the Gourlay Peninsula and around Signy Island are much larger than at Cape Geddes. Resulting competition between congeners is therefore probably more intense around the Gourlay Peninsula.

III.2 Sample sizes and timing

The distribution of the number of trips recorded from each colony site during both 2011-12 and 2013-14 seasons through time is presented in Figure III-6. A more intensive deployment campaign was carried out from Cape Geddes leading to a larger amount of recorded trips. But the site was only sampled during the 2011-12 season. The data sample from the Gourlay Peninsula in 2011-12, included some early incubation and later brood trips. In 2013-14 from the same location, the sampling had to stop shortly after hatching due to logistical reasons.

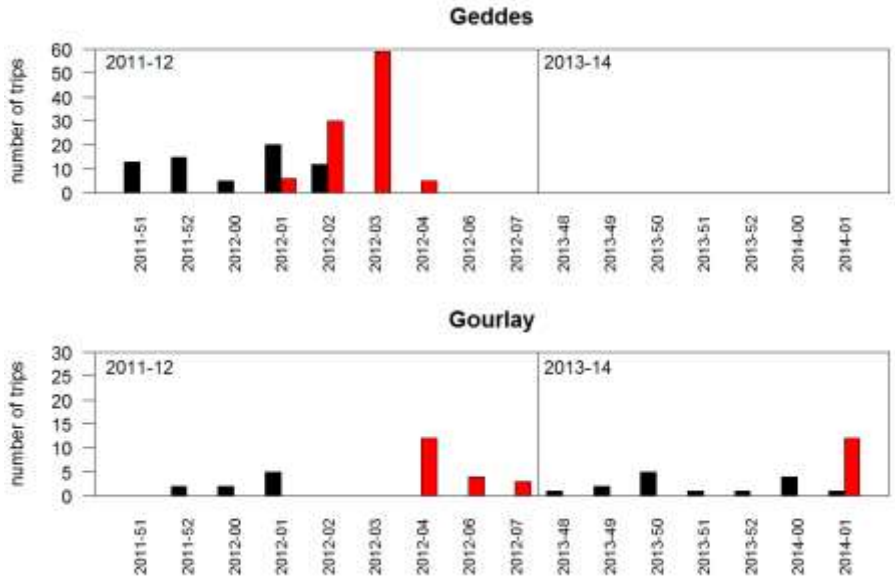

Figure III-6: Sampling calendar: number of trips recorded per week from both colony sites during seasons 2011-12 and 2013-14. Black bars represent incubation trips and red bars brood trips.

This distribution of the sampling across sites and through time is not ideal. Unless specified, both seasonal data will be merged for the analyses.

Figure III-7 shows the distribution of the departure and arrival times across sites and seasons. It clearly confirms that birds rarely initiated or terminated trips at night (Jansen, Boveng and Bengtson, 1998). It doesn't show particular peak departure or arrival hours during the day contrasting with what Wilson & Peters (1999) observed with mainly early morning or late afternoon departures. The moon cycle does not seem to influence trip timings, although to properly include this factor in the analysis it would be necessary to take into account moon rising times and cloud cover. The main visible trend is probably an increase in late afternoon departures from Cape Geddes towards the end of the brood phase. The peak hatching date (6th of January), represented on the same figure by a vertical red line, was calculated as the average mid-trip day for the trips when hatching happened. It was the same across colonies and seasons.

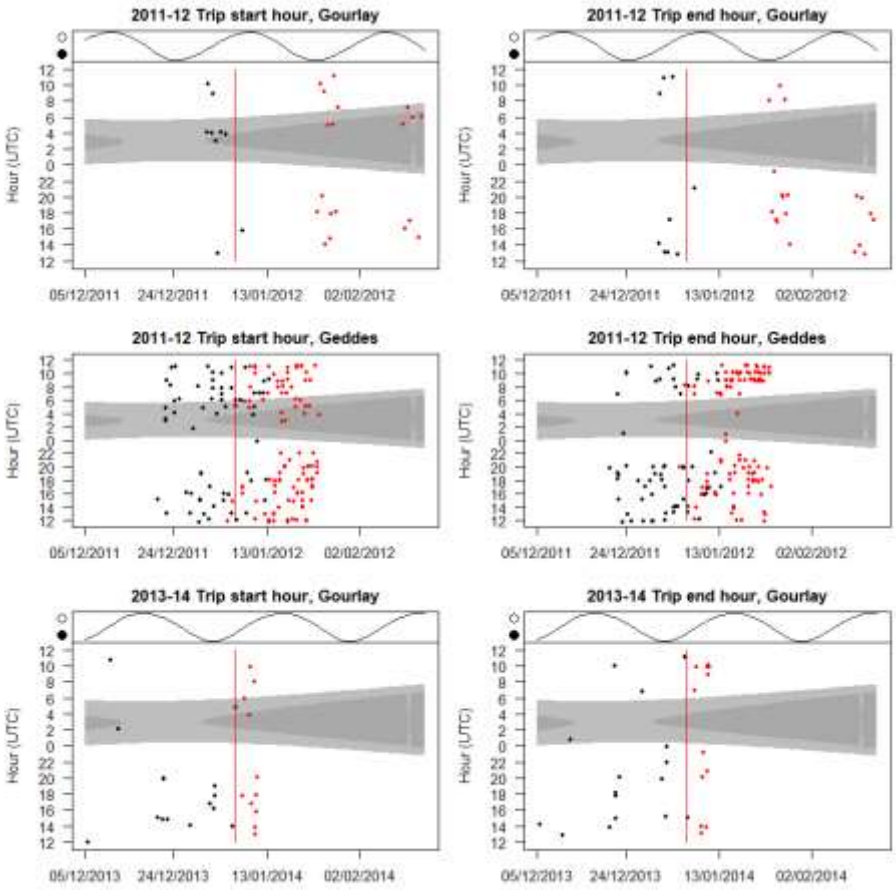

Figure III-7: Foraging trip start and end times at the two locations during the two sampling years in relation to the moon phases (○ and ●) and night and twilight periods of the day (shaded areas, the lighter shade represents the twilight period). Black dots are incubation trips and red dots are brood trips. The vertical red line represents the peak hatching date (6th of January).

III.3 Parents weights and productivity

There was a significant difference in parental weights between the different combination of breeding stages, seasons and colony locations (Kruskal-Wallis chi-squared = 21.4, df = 5, p-value < 0.01, Figure III-8), but this was mainly due to the lighter birds from Cape Geddes during brood. If this colony and stage were omitted, the weight distributions were not significantly different (Kruskal-Wallis chi-squared = 4.5, df = 4, p-value = 0.348). Only the data from Cape Geddes showed birds tend to gain mass during incubation and lose mass during brood as observed by Hart, Mann, et al. (2010) for macaroni penguins.

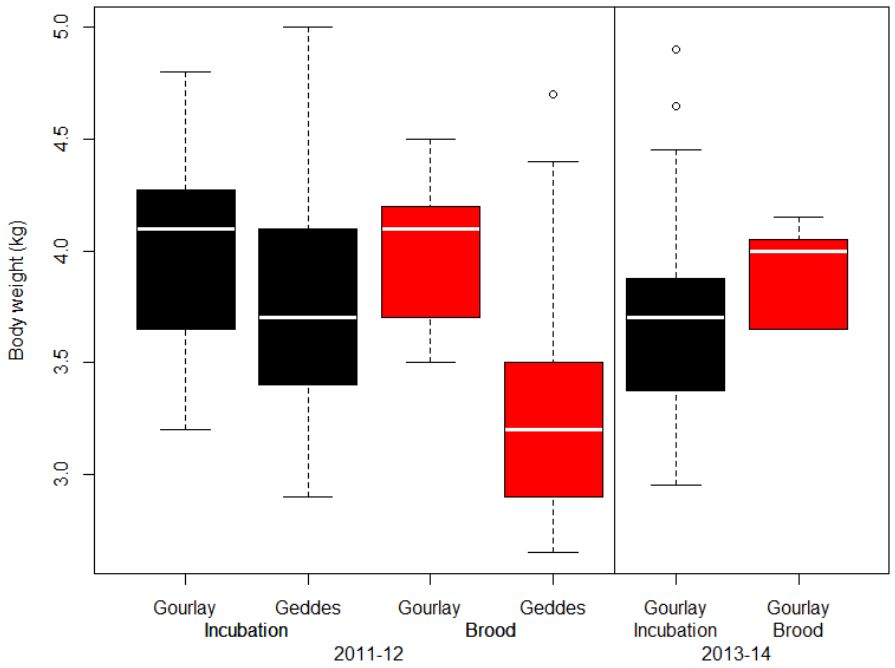

Figure III-8: Parental weight distribution for the different colony sites, breeding stages and seasons.

The distribution of the number of offspring per nest is presented in Table III-1. This is not a measure of reproductive success as the later relates to the number of fledging chicks per nest at the end of the breeding season. In this study, we only have the number of offspring (eggs or chicks) at the moment of device deployment, which corresponds to an indication of reproductive effort.

Table III-1: Reproductive effort as the number of offspring (eggs or chicks) per nest during deployment. Note: this data is absent for Gourlay 2011-12.

Season	Stage	Colony	Tracked birds	Offspring 1	Offspring 2	% 2	Off./nest
2011-2012	Incubation	Gourlay	7	-	-	-	-
		Geddes	35	2	33	94%	1.94
	Brood	Gourlay	9	-	-	-	-
		Geddes	25	5	20	80%	1.80
2013-2014	Incubation	Gourlay	27	21	6	22%	1.22
	Brood	Gourlay	6	1	5	83%	1.83

At Cape Geddes, the number of offspring decreased during the breeding season, which is expected due to chick mortality through predation or other causes. During brood, a similar ratio of one or two chicks were recorded at both sites. But during incubation the lower ratio recorded in Gourlay is difficult to explain. Either the incubation or the brood count is not representative. Because of these differing results, probably due to a low sample size, I am cautious when using these data as an indication of reproductive effort.

III.4 Summary of the differences between two sites

In terms of oceanographic conditions, the Gourley colony is further away from the continental shelf break than the Geddes. Only trips during incubation, when birds do not have the constraint of feeding their chick, can potentially reach the slope areas. From Geddes, birds can easily access these areas during the entirety of the breeding season. Currents are stronger on the North side of the archipelago and are more consistent in direction (westerly currents close to the shore and easterly currents further offshore). In the waters around the Gourlay Peninsula, the currents are weaker and more variable in direction. The amount of sea-ice is another important difference: during incubation, there can still be some sea-ice along the coast of Signy as the north coast of Laurie is usually free throughout the breeding season.

On Signy, both Adélie and chinstrap penguins are present within mixed species colonies. The colonies around Cape Geddes mainly contain chinstrap. In addition, penguin populations are larger around the Gourlay peninsula than around Cape Geddes. Both the intra and inter-specific competitions are potentially greater for the birds in the Signy colonies. Bird's fitness, indicated by their weight, is not different across sites and season, with the exception of the Geddes birds during brood that showed lighter weights. The average number of offspring per nest observed at the moment of the deployment was higher in Geddes than in Gourlay.

These observations suggest that the habitat might be more favourable on the north side of the archipelago thanks to the accessibility of the continental shelf break and stronger currents potentially bringing more preys. There is also less competition for resources and the birds seem to produce more chicks.

Chapter IV CHANGES AT THE SCALES OF THE FORAGING TRIPS AND THE BREEDING SEASON

This chapter assesses changes in trip foraging metrics that take place over the breeding season at small and medium spatial and temporal scales and whether the colony, the sex of the bird or individual preferences have an impact on trip foraging characteristics.

IV.1 Introduction and aim

The reduction in foraging trip duration between incubation and brood is well documented for breeding seabirds in general (Weimerskirch et al., 1993) and for penguins in particular (Williams and Siegfried, 1980; Charrassin et al., 1998). The distinct phases of breeding have different constraints which determine how long individuals can be absent from the nest. When the clutch is complete one parent remains ashore to incubate the eggs while the other goes to sea to forage for a number of days. When the foraging individual returns, the parental roles swap. During the incubation period, long pelagic trips allow birds to build up reserves and recover from fasting (Croxall, 1984). On hatching, the brood phase starts with a guard period when the chicks are mostly brooded by one parent whilst the other is at sea foraging. Again, both parents alternate roles. When the chicks are thermally independent and can protect themselves from raptorial seabirds, both parents leave their chicks in crèches and forage to meet their own needs and the increasing demands of their growing offspring (Williams, 1995). During chick rearing, foraging trips are usually short and access to prey is restricted, primarily because foraging locations need to be in close proximity to the nest site.

In this chapter, the changes in the foraging trip metrics are considered over the course of the breeding season, not only in the horizontal dimension (range and shape), but also in relation to vertical exploitation of the environment; that is considering the available habitat as a volume (Zamon et al., 1996). I will also consider the differences between day and night, as well as the influence of the colony location, the sex of the bird, individual preferences, as well as any variation throughout the breeding season.

I predict that variation in trip metrics through time will reflect the reduction in the available habitat along with an increase in the pressure to forage and meet the growing requirements of the offspring (Meyer et al., 1997; Charrassin et al., 1998; Jansen, Russell and Meyer, 2002).

IV.2 Method

a. Data exploration and pre-processing

The different trip metrics considered in this chapter were described in section II.3, page II-32 and summarized in Table II-8. Two metrics relate to the spatial horizontal exploitation of the habitat: the trip maximum

range and the foraging zone coefficient. Three variables related to the trip timing: the *trip duration*, the *percentage of outward time* and the *percentage of night activity*. Three other metrics containing the vertical component of foraging were included: the *percentage of dive time*; the *percentage of night dive*; and the *vertical/horizontal distance ratios*. Finally one metric linking the exploited habitat volume (horizontal and vertical dimensions) and the trip timing, the *exploration speed*, was used.

These metrics were chosen as they represented a single value for each trip, which was more indicative than using average values from multiple dives (e.g. dive depth or bottom time). They also integrated all the dimensions of use of the habitat (horizontal, vertical and time).

Variable correlations

Some of the trip metrics showed highly significant correlations. The trip duration and trip maximum range had a Pearson coefficient of 0.94 ($p<0.01$). The percentage of night activity and the percentage of night dives had a Pearson coefficient of 0.86 ($p<0.01$). Finally, the percentage of dive time and the vertical/horizontal distance ratio had a Pearson coefficient of 0.69 ($p<0.01$). Weaker but significant correlations were also found between several other trip metrics (Figure IV-1). However, as some of the metrics followed a long-tailed distribution (such as the trip duration, maximum range and vertical/horizontal distances ratio) caution is required when considering correlation coefficients.

The percentage of outward time was the only metric that did not show any significant correlation with any other metric. Despite these significant correlations, colinearity was not considered in the analysis, as every trip metric was modelled separately during the main analysis (IV.2b, page IV-52).

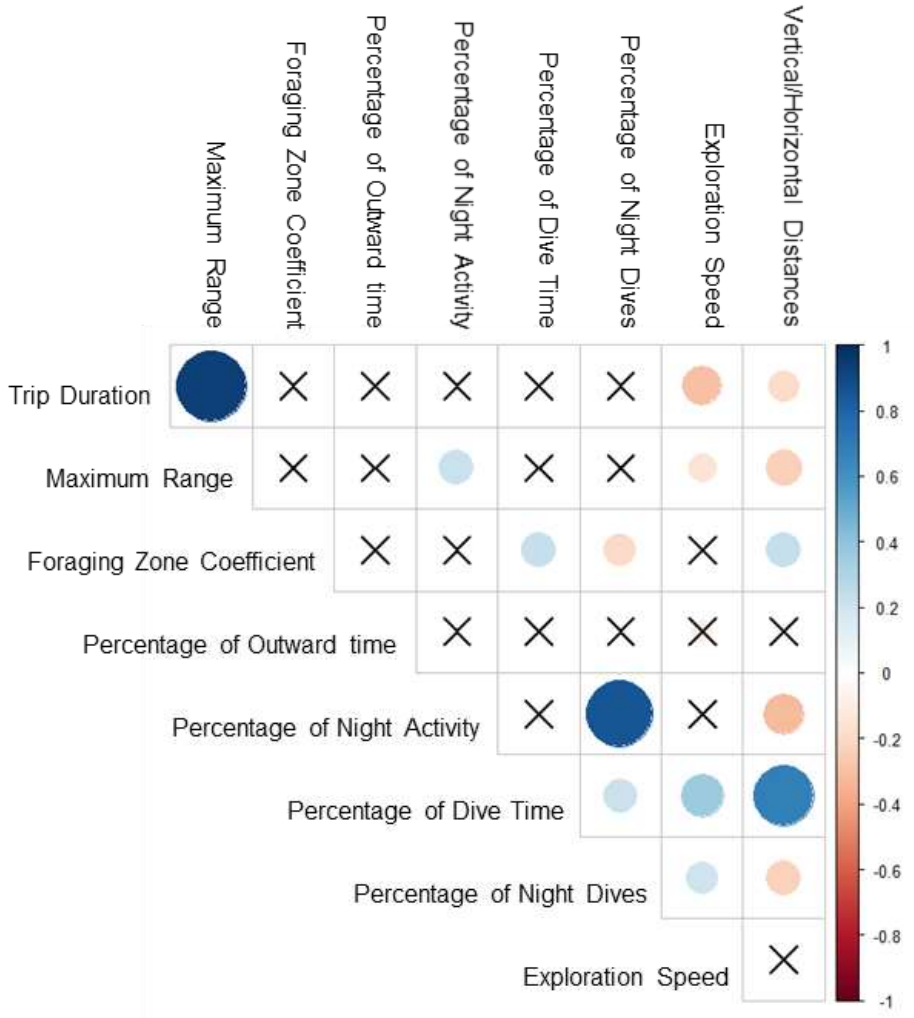

Figure IV-1: Significant positive (blue) and negative (red) correlations between the different trip metrics at a 0.01 significance level; crosses "×" indicate non-significant correlations.

Data imputation

This process is defined as the replacement of missing values. 12.7% of the foraging trips did not have any valid TDR data (see II.4b, page II-35). Three strategies were used in order to manage the missing values (the percentage of dive time, the percentage of night dive, the exploration speed and the vertical/horizontal distances ratio) of the dive dependent trip variables:

- discarding the trips with missing data
- replacing the missing data with mean values by stages (incubation or brood)
- missing data prediction

The first option is straightforward but required discarding of incomplete datasets.

For the second option, the replacement mean values per breeding stages for each dive derived trip metrics are presented in Table IV-1.

Table IV-1: Mean values per breeding stage for the four dive derived metrics used to replace the missing data.

	Incubation	Brood
Percentage of dive time	23.9%	26.6%
Percentage of night dive	19.8%	25.2%
Exploration speed (m s^{-1})	57.8	66.6
Vertical/horizontal distances	27.9	38.8

For the third option (missing data prediction), the missing values were predicted after a random forest modelling algorithm was trained on the complete dataset (see IV.2b for a description of the technique). For each dive dependent trip metric, the model used a combination of the other trip measures along with the colony and the temporal variable (days to hatching) to predict the value. Table IV-2 presents the performance of the modelling (percentage of variance explained) for each variable and the relative contribution to the model from each co-variable (as a percentage of the total increase in node purity).

Table IV-2: Results of the random forest modelling of the four dive derived metrics. The percentage of variance explained indicates how well the model performed. The percentage of the increase in node purity is a measure of the relative contribution from each co-variable to the model. Higher values mean that variables can be used to split the data into more homogenous groups ("purer" groups) and therefore has a higher importance for producing a more accurate model. The values have been transformed to a percentage to allow comparison between models.

		% of the increase in node purity						
	Variance explained	Trip duration	Trip maximum range	Foraging Zone Coefficient	Percentage of outward time	Percentage of night activity	Time (days to hatching)	Colony
Percentage of dive time	25.4%	18%	21%	19%	12%	10%	18%	4%
Percentage of night dive	79.8%	22%	23%	6%	4%	36%	5%	3%
Exploration speed (m s^{-1})	34.7%	18%	21%	15%	12%	11%	20%	3%
Vertical/horizontal distances	50.6%	20%	29%	11%	10%	8%	18%	3%

The model with the highest performance was predicting the percentage of night dives, mainly from the associated percentage of night activity metrics. This is logical, as higher night foraging time means a higher chance of night dives (also indicated by the high correlation between these variables). The second best model was trying to predict the vertical/horizontal distances ratio. For this metric, the most contributing variables were the trip maximum range (which was strongly linked with the horizontal distances), the trip duration and the time of day. Finally, the percentage of dive time and the exploration speed were both derived from the same set of co-variables: the trip maximum range, the time of day, the trip duration and to some extent, the foraging zone coefficient.

The influence of these three different data imputation techniques on the prediction accuracy of the models was evaluated (see IV.3a, page IV-57).

Outliers

Outliers can have a strong influence on some data analysis methods such as a principal component analysis (PCA) or generalized regression modelling. A density based local outlier detection algorithm (LOF, Torgo 2010) was therefore used to detect which trips could be considered as outliers. Local outlier factors for each trip were calculated for the three different datasets resulting from the data imputation techniques.

The very long incubation trip 75_173 was consistently ranked with the highest outlier factor. This trip lasted almost 20 days and resulted in the failure of the nest after the partner abandoned it (see Figure IV-6). This confirmed that this trip was a "true outlier" and should be discarded (see II.4b, page II-35).

Another trip (48_117) had consistently high outlier scores (ranked twice second and once fourth), mainly due to its very fast exploration speed (92.2 m min^{-1} against an average of 62.8 m min^{-1}). Finally, 12_16 appeared twice in the top five highest scores, but its metrics didn't show any extreme values.

Apart from 75_173, no other trips had apparently valid biological or methodological reasons to be excluded from the analyses.

Temporal predictive variable (days to hatching)

Although hatching is a single specific event in time, birds are known to change their foraging behaviour gradually towards the end of the incubation (Weimerskirch, Stahl and Jouventin, 1992). After hatching, the offspring demands are increasing with their development. The trip metrics were therefore modelled using time as a continuous predictor variable instead of considering the breeding stages as discrete categories.

From the peak hatching date, determined for each season and colony (see III.2), the temporal difference between the start of each trip and the peak hatching date were calculated in days. This number of "days to hatching" was used as the temporal predicting variable.

b. Analytical approaches

Principal Component Analysis (PCA)

For the Principal Component Analysis, the failed trip 75_173 was discarded and the missing derived TDR values were replaced by random forest model imputed data. The variables were then scaled and centred (R Core Team, 2015).

The trips and the metrics were projected in the first four dimensions of reduced space. The trip points were labelled according to the breeding stage and the colony to assess whether they were any relationship between these factors and the point distribution.

Linear mixed models (LMM)

A mixed model regression allowed me to include random effects, therefore taking into account clusters or blocks of observations (Bolker et al., 2009). In the case of this study, this would be the effect of the colony location or the sex of the individuals or the individual itself in the cases where several foraging trips were recorded from the same individual (pseudo replicates).

Ideally, a generalized mixed model (GMM) method would be used with non-normally distributed metrics (with a specific family fitting the distribution of the variable). Unfortunately, the interpretation of the results and specifically the interactions between the fixed and random effects can be very challenging for GMM. Therefore the chosen approach was to transform some of the variables, ensuring that the fitted residuals of the variable had a regular distribution. A linear mixed model (LMM) was then applied on the transformed variable; the trip duration and the maximum trip range had to be log transformed. The vertical/horizontal distance ratio was also log-transformed after adding the value of 1 to avoid negative transformed values. The outlier trip 75_173 was discarded and the missing derived TDR values were replaced by random forest modelled ones. Diurnal trips only where discarded for the modelling of the percentage of night activity and the percentage of night dive variables.

Each foraging trip metric was modelled using time as a predicting variable (days to hatching) and the colony as a random effect. The fixed and random effects were tested through a backward elimination of all effects (Kuznetsova, Bruun Brockhoff and Haubo Bojesen Christensen, 2016).

Random Forest (RF)

Random forest is an ensemble of decision trees classifying the data into subsets and predicting the outcome either as a class mode (classification) or as a mean prediction (regression). Each tree is built by not only subsampling the data, but by randomly discarding some of the co-variables. This “bagging” process allows for testing the prediction of each decision tree and also for assessing the contribution from each co-variable. The trees with the best performance are kept for the next iterations in this machine learning process (Breiman, 2001).

This algorithm required no variable transformation (Olden, Lawler and Poff, 2008). Similarly to the linear mixed model, the outlier trip 75_173 was discarded, the missing derived TDR values were replaced by random forest modelled ones and the diurnal trips only where discarded for the modelling of the percentage of night activity and the percentage of night dive variables. Each trip metric was modelled against the time predictive variable (days to hatching) along with the colony. An additional randomly generated variable was added as a co-variable, enabling me to have a baseline while comparing the ranking of each co-variable based on their relative importance in the model. Each model

was tested for overfitting and validated according to Murphy et al. (2010) and Evans et al. (2010).

Prediction of the accuracy of the models

To compare each method's prediction accuracy, the linear regression between the observed and the predicted values for each metric was calculated according to Piñeiro et al. (2008). This also allowed me to measure the influence of the different missing data imputation techniques on the performance of the models.

For the linear mixed model method, in order to avoid using the same dataset to train and test the model, a ten fold cross-validation process was applied. A stratified random method was used to create the folds, ensuring that the sampling was balanced across breeding stages (linked to the temporal predictive variable) and between colonies (random effect). The model was trained on 9 folds and the predicted metric values calculated from the unused remaining fold.

In the case of the random forest method, the predicted values for each metric were automatically calculated on the trips that were not included in the training of the model during the bagging process, see Liaw & Wiener (2002).

Workflow summary

Table IV-3 summarizes the different analytical approaches with their advantages and disadvantages and Figure IV-2 presents the workflow from the data pre-processing leading to the different analytical methods and accuracy prediction.

Table IV-3: Comparison of the three analytical methods used in this chapter.

	Pros	Cons
Principal Component Analysis (PCA)	• Easy to interpret and plot • Stable	• Variables might have to be transformed • No significance levels • No mathematical model • Only numerical variables
Linear Mixed Models (LMM)	• Relatively easy to interpret (linear model) • Stable • Significance levels are provided • Include random effect variables	• Variables might have to be transformed • Relies on a chosen mathematical model • Training and test sets are necessary to measure prediction
Random Forest (RF)	• No variable transformation are necessary • Can include non-numerical variables • Usually higher prediction scores • Prediction can be measured on the "out of the bag" dataset	• No significance levels • Some level of stochasticity • No mathematical model • The prediction of a continuous value (RF as "regression") is not as performant as the prediction of a class (RF as "classification")

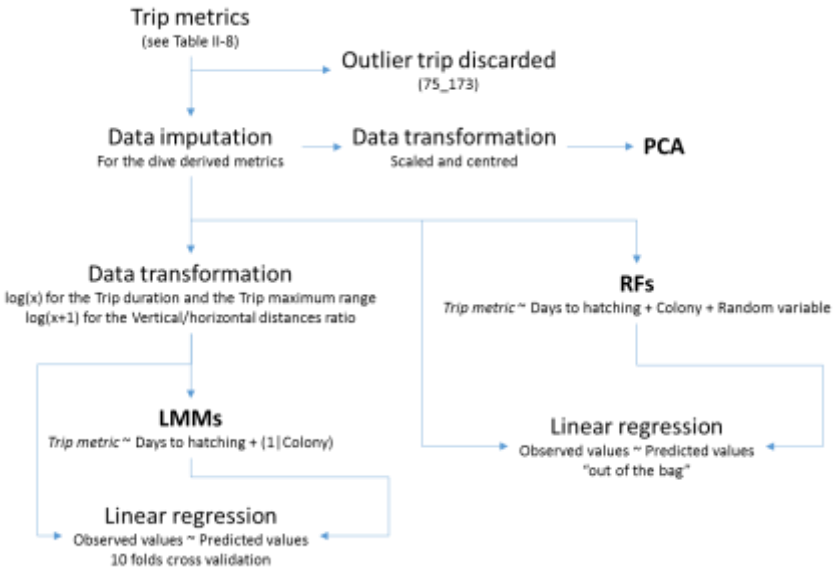

Figure IV-2: Workflow summary from the trip metrics calculated in Chapter II to the three analytical methods: principal component analysis (PCA), linear mixed models (LMM) and random forest (RF). Linear regressions were used to assess the prediction accuracy of the models. The modelling formula annotation is compatible with the R syntax (R Core Team, 2015) *with the dependent variable on the left and the independent co-variables on the right of the "~" symbol. The co-variables are combined using the "+" symbol. The* "(1|)" *annotation refers to random effects for the LMM.*

c. Effects of sex or individuals

To test the effect of sex as a random effect, the linear mixed model method was repeated but this time with the putative sex of the bird (see II.1g, page II-21) included as a random effect.

To estimate the effect of individual birds (pseudo-replicates), the data available were restricted to the deployments including several trips. These were mainly brood trips and the temporal extent of the available data was limited (up to 30 hours). It was therefore not relevant to try to predict the change of the metrics over time. As an alternative method, the Euclidean distances between trips in the multi-dimensional space defined by all the trip metrics (scaled and centred as for the PCA) were calculated. Intra-individual distances (distances between trips from the same individuals) were compared with inter-individual distances (distances between trips from different individuals) to assess whether trips from the same individuals were more similar.

IV.3 Results

a. Data input

The different data inputs generated by the three data imputation techniques (see IV.2a, page IV-48) were evaluated through the prediction accuracy of the linear mixed model and the random forest model.

Figure IV-3 shows that replacing missing dive data due to the failure of the TDR devices during some deployments usually gave better results than discarding the trips. As a lot of these deployments related to late brood when the amount of data was already scarce, I decided to keep these trips and complement the dataset with estimated values. Using a random forest model to guess missing values gave higher prediction scores for most variables (except the exploration speed). The results presented in the following sections were therefore generated using this imputation technique.

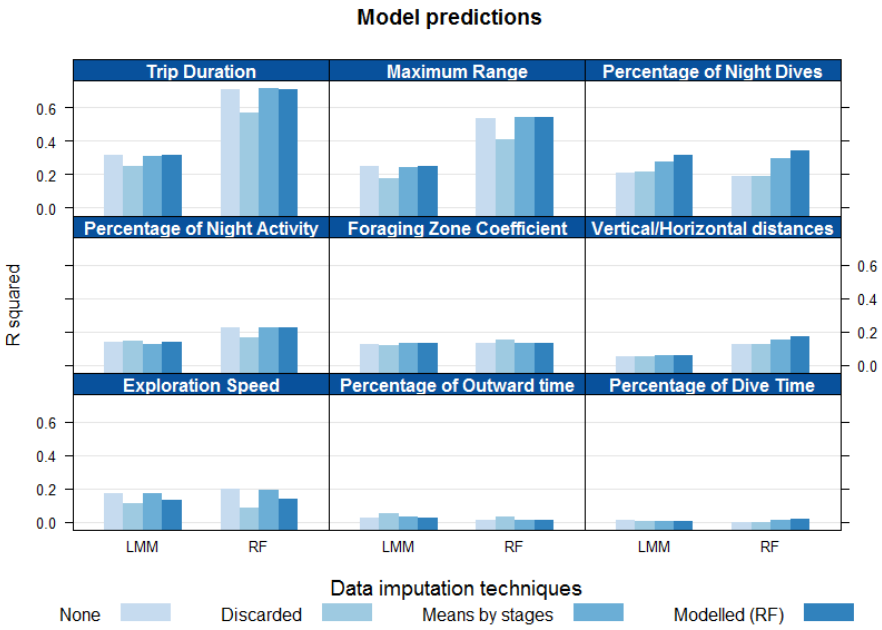

Figure IV-3: Effects of the different missing data imputation strategies on the prediction accuracy for the different modelling approaches and modelled variables (linear mixed model, LMM and random forest, RF).

b. Trip metrics description

The density plots for every trip metric by breeding stage (incubation versus brood) are presented in Figure IV-4. Figure IV-5 shows the breakdown of these metrics by colony (Cape Geddes or Gourlay Peninsula).

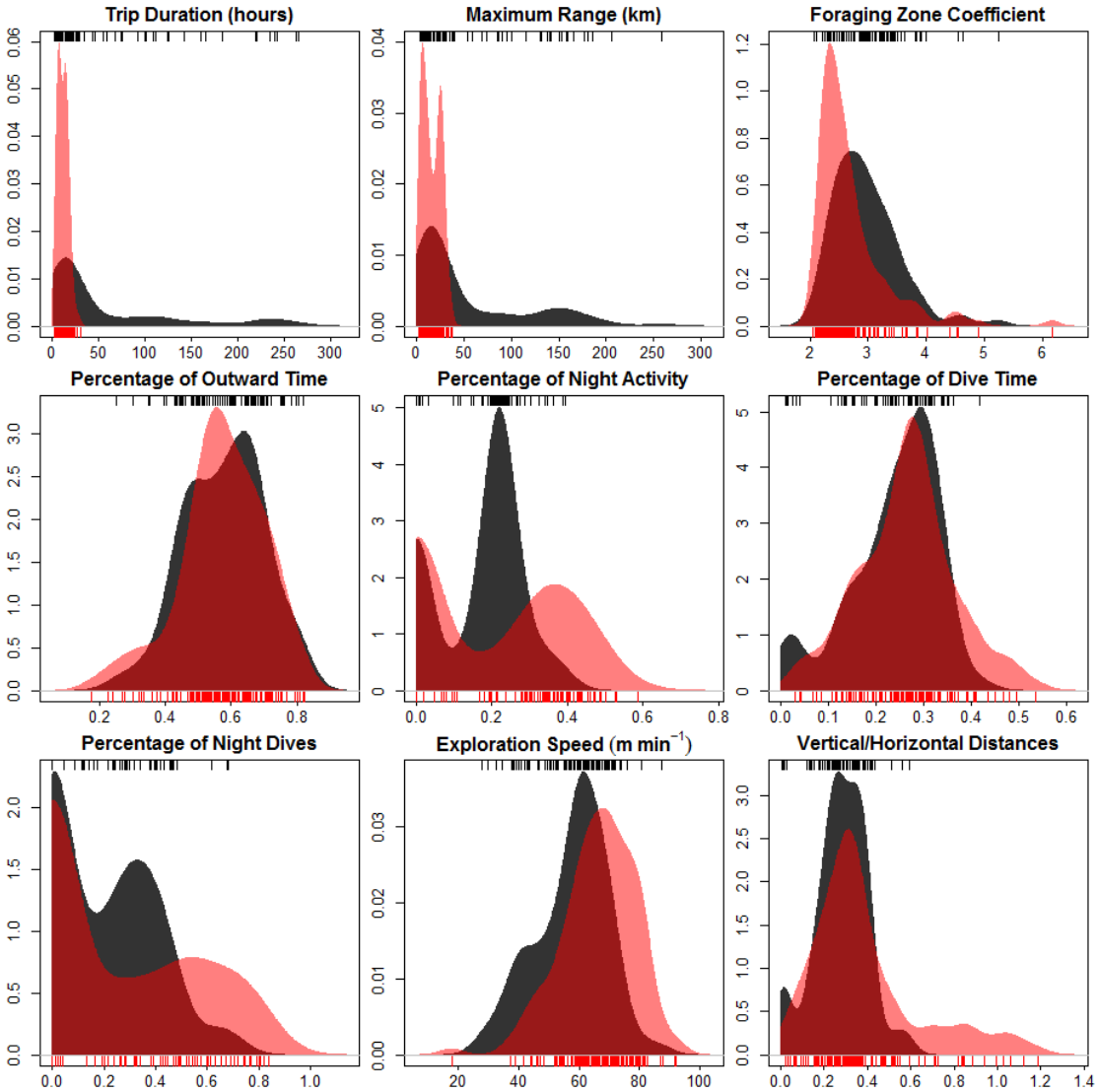

Figure IV-4: Density distribution of the different trip metrics according to the different breeding stages (black for incubation and red for brood).

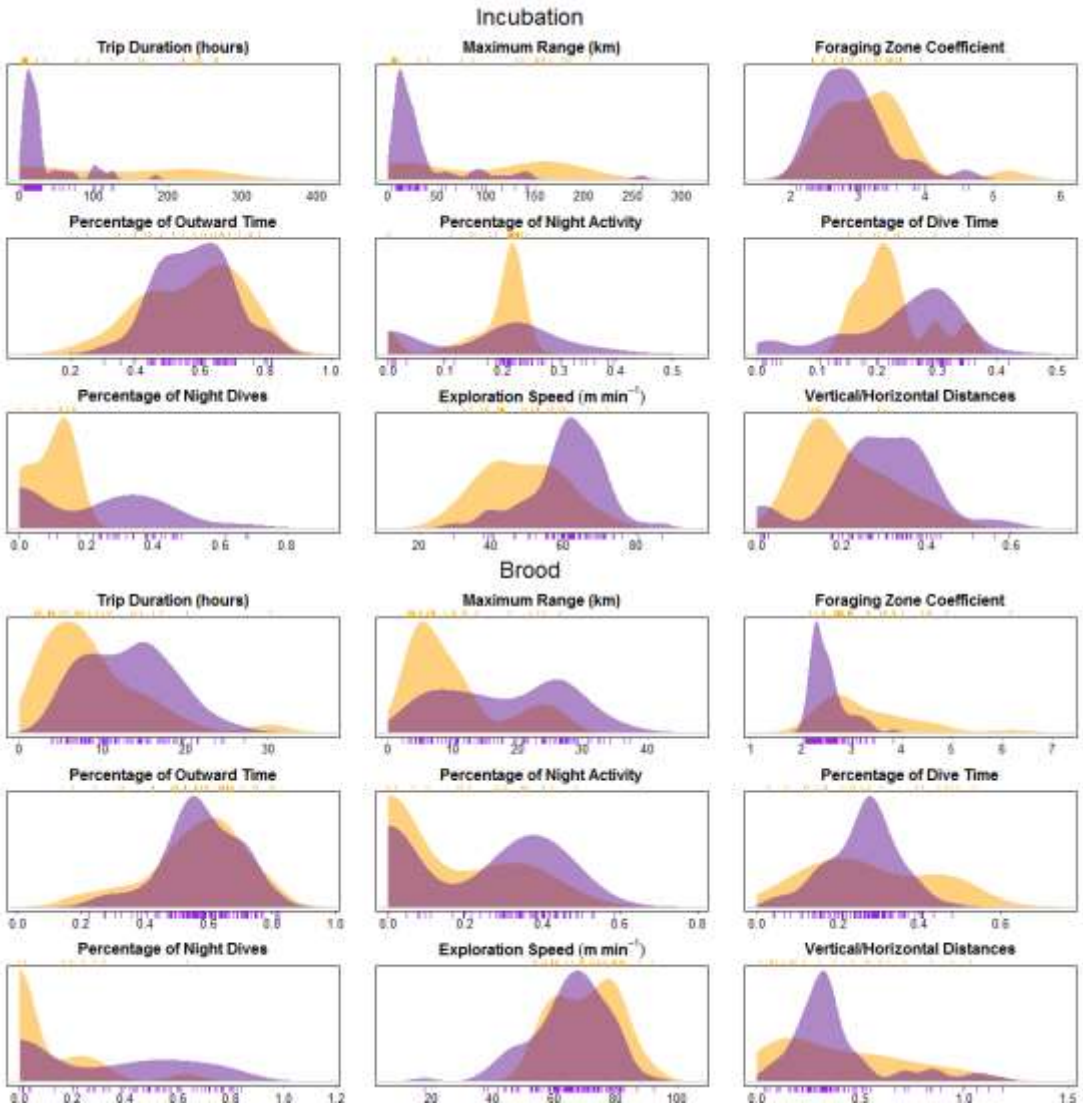

Figure IV-5: Density distribution of the different trip metrics according to the different breeding stages and colony locations (Cape Geddes in purple and Gourlay Peninsula in orange).

Trip range, duration and direction

Historically, before tracking devices were small enough to be carried by penguins, the main estimate of trip length was the trip duration. Direct observations at the colony enabled field operators to record when the birds were leaving or returning to their nests and therefore the duration of foraging. At sea observations allowed observers to estimate bird's travelling speed; other experiments using swim tanks provided additional estimates of swim speed (Clark and Bemis, 1979). From the trip duration and an average speed, the estimated trip range could be derived (Williams and Siegfried, 1980). Pre-GPS bio-logging devices and telemetry techniques allowed researchers to estimate more precisely the distance travelled and foraging trip ranges (Wilson, Nagy and Obst, 1989; Trivelpiece et al., 1986). In addition to calculating the trip duration without having to continuously monitor the colony (see II.2a, page II-22), the devices used in this study allowed me to very accurately estimate travel speed and trip total ranges.

Trip duration and trip range showed similar patterns, which was confirmed by their high correlation coefficient (Pearson coefficient of 0.92). Although there was a large overlap between trip duration and range for both breeding stages (plenty of short incubation trips were observed mainly from Cape Geddes), the incubation trip values distribution were characterised by a long tail towards long far ranging trips (up to 258 km and 19 days). In contrast, the brood trips were limited in their length (37 km) and duration (30 hours). Incubation trips from Gourlay appeared to be longer while Geddes trips appeared longer during brood.

When comparing both metrics, the trip range metric indicates additional information not directly visible in the trip duration values. Its density distribution for the brood stage showed a bimodal shape from both colonies. This could suggest separate foraging locations at different distances (see Figure IV-6 and see also VI.3e, page VI-126) but with similar trip duration.

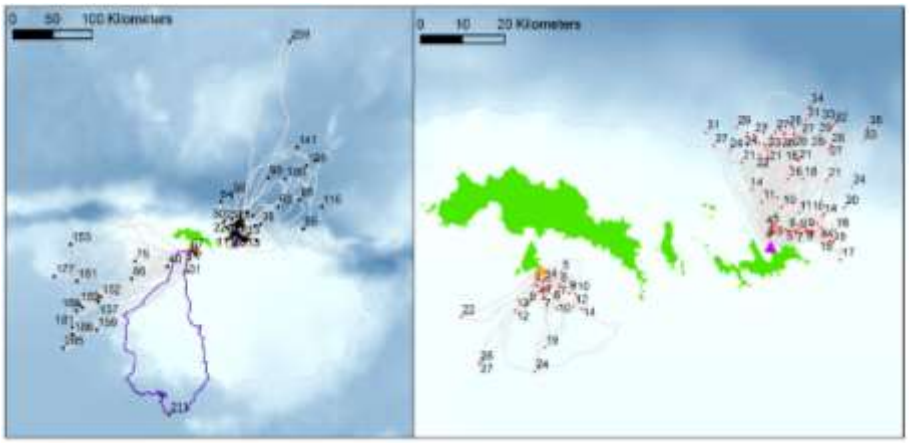

Figure IV-6: Trip maximum ranges for incubation trips (left) and brood trips (right). The very long south orientated incubation trip 75_173 from Gourlay (blue) was discarded as it resulted in the failure of the nest. The dashed line represents the 1000 m isobath.

When several trips per bird were recorded, most of them didn't clearly alternate between short chick provisioning and longer parental recovery trips as observed for other species (Clarke, 2001; Saraux et al., 2011). Figure IV-7 suggests that the main driver for long or short trips was the day period covered by the trip (diurnal or nocturnal).

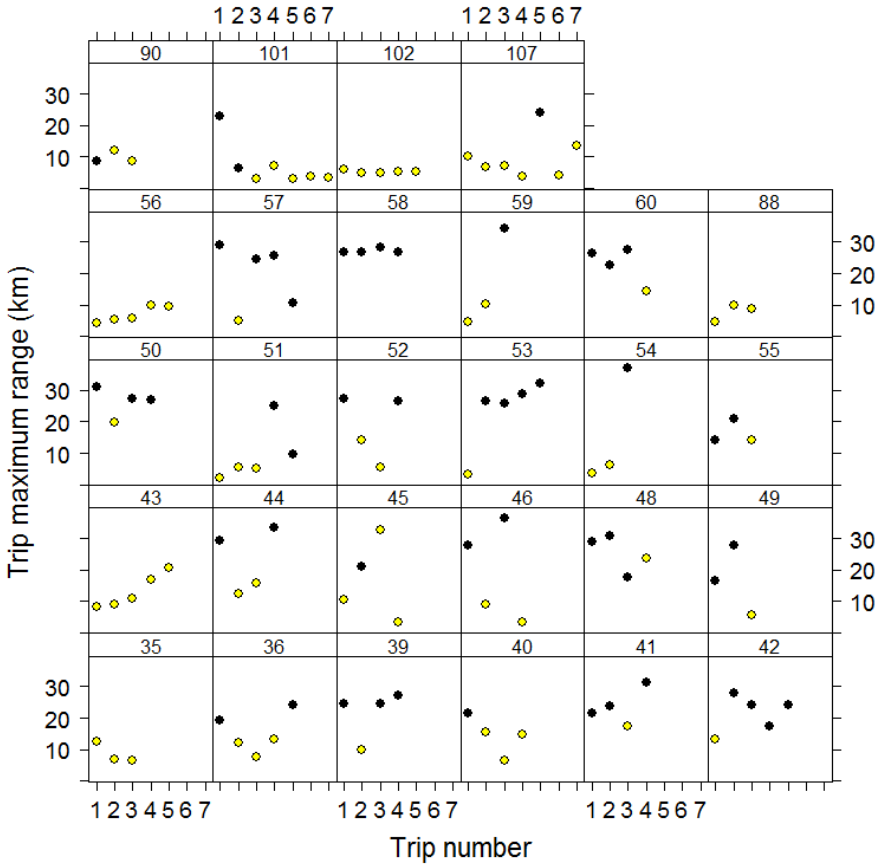

Figure IV-7: Succession of trip maximum ranges when more than 2 trips per bird were recorded. The plot number from 35 to 107 is the deployment ID. Points are coloured according to the night activity (yellow for diurnal trips and black for nocturnal trips).

The foraging trip directions showed a significant difference between sites (Table IV-4); birds tended to travel mainly in an anti-clockwise direction from Cape Geddes and mainly in a clockwise direction from the Gourlay Peninsula (χ^2=6.987, N=190, p=0.008). There were no significant differences in the travel direction between the incubation and brood stages at Geddes (χ^2=0.292, N=151, p=0.589) and Gourlay (χ^2=3.732, N=42, p=0.053).

Table IV-4: Trip directions per breeding stage and colony.

		Geddes		Gourlay	
	No trips	Incubation	Brood	Incubation	Brood
Clockwise	97	30	38	16	13
Anti-clockwise	96	33	50	3	10
Undetermined	27	2	12	5	8

Foraging Zone coefficient

The foraging zone coefficient varied from 2.04 (very direct trip, the minimal possible value being 2) to 6.17 (trips with more complex

shapes). Figure IV-8 shows the shape of trips with extreme FZC in comparison with a trip with a FZC close to the average value (2.82). The coefficient is positively correlated with the trip duration but not with the trip maximum range. The change in the distribution of the values over time suggested that the brood trips were more direct than the incubation trips (reduction in the FZC). The colony specific distributions appeared to indicate more direct foraging trips from Cape Geddes.

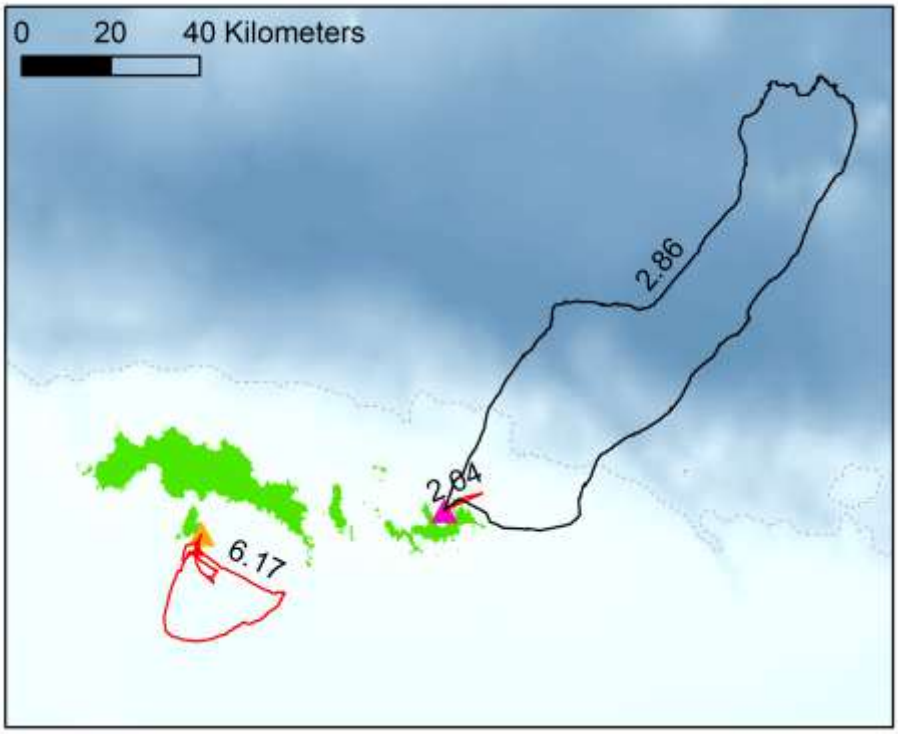

Figure IV-8: Examples of two brood trips with extreme foraging zone coefficient values (one very direct trip from Geddes, FZC of 2.04 and one very irregular shaped trip from Gourlay, FZC of 6.17). The incubation trip from Geddes (black) represents a trip with a FZC value close to the average value.

Percentage of outward time

The outward section of the trips represented between 17.5 and 82.2% of the total trip duration with an average of 57.7% ±12.6%, indicating that the birds tended to spend less time on the way back with a more direct and faster return section of the trip. This suggests a slightly more direct trip back to the colony with some opportunistic feeding as reported by Wilson & Peters (1999). The distribution of the value did not suggest any patterns or differences between colonies and stages.

Night activity

In addition to the trips with 0% of night activity (N=74), trips starting or ending during the night but with mainly daylight time (N=32) were included as diurnal only trip. There was no significant difference in the number of diurnal only trips between colonies ($\mathcal{X}^2$=1.55, N=220, p=0.213). But there was a significant difference between stages with more diurnal only trips during brood: 54.2% versus 39.3% for incubation ($\mathcal{X}^2$=4.12, N=220, p=0.042).

When several trips were recorded from the same bird, 75.9% of the birds didn't display any clear preferences between overnight or diurnal only trips. However, 7.4% of the birds showed an exclusive preference in overnight trips and 16.7% did diurnal trips only (Table IV-5).

Table IV-5: Occurrences of overnight or diurnal only trips (or mix of both strategies) for birds with several foraging trips.

		Geddes		Gourlay	
	No birds	Incubation	Brood	Incubation	Brood
Mixed	41	14	21	1	5
Only overnight trips	9	3	3	1	2
Only diurnal trips	4	3	1	0	0

The percentage of night activity was positively correlated with the trip maximum range, suggesting that far incubation and brood trips had more overnight time. It was also negatively correlated with the vertical/horizontal distances ratio, which indicated that a high ratio of night activity was linked with shallower diving.

This variable showed a clear bimodal distribution. Both incubation and brood stages had a first peak just above 0% of night activity corresponding to the diurnal trips. The incubation trips then showed a second peak around 20%. This value was equal to the average night time ratio at the South Orkney Islands during that season. It was logical that incubation trips, most of which included overnight time, indicated a peak of night activity matching the night time ratio. Brood trips showed a second peak at around 40% of night activity indicating over-night foraging trips, but this could also be linked with the fact that nights were longer during brood.

Percentage of dive time

The time spent diving was strongly positively correlated with the vertical/horizontal distances ratio, which confirmed that these two metrics indicated a higher vertical exploitation of the habitat. It also showed weaker positive correlations with the foraging zone coefficient, the percentage of night dive and the exploration speed.

This metric didn't display any strong pattern or clear differences between stages and colonies, except that the brood trips included higher dive time values, while some incubation trips (mainly from Geddes) had very low dive ratios. Only one incubation trip had a percentage of dive time higher than 40% versus 12 brood trips (see Table IV-6).

Table IV-6: Trip distribution according to their percentage of dive time and phenological stages.

% dive time	Incubation	Brood
< 10%	6	6
10 – 40%	82	113
> 40%	1	12

Percentage of night dives

The percentage of night dives was highly positively correlated with the percentage of night activity and therefore showed similar patterns: a peak just above 0% for diurnal trips, a peak around 20% for incubation trips and a peak around higher values for brood trips. For this metric, the values measured on the Geddes trips appeared higher than the ones from the Gourlay data.

Table IV-7: Trip distribution according to their percentage of night dives by colony and phenological stage.

	Incubation			Brood		
% night dives	Geddes	Gourlay	Total	Geddes	Gourlay	Total
< 15%	2	13	15	7	9	16
15 – 50%	34	9	43	23	7	30
> 50%	3	0	3	29	1	30

Exploration speed

The exploration speed was negatively correlated with the trip duration and maximum range and positively correlated with the percentage of dive time and night dives. This appeared to indicate that an increase in the vertical exploration of the habitat was linked with an increase in the exploration speed. Although the metric did not show any correlation with the vertical/horizontal distances ratio.

The exploration speed in both horizontal and vertical planes showed an increase from incubation to brood, especially for the trips recorded from Gourlay (see Table IV-8).

Table IV-8: Trip distribution according to their exploration speed by colony and phenological stage.

Exploration	Incubation			Brood		
speed	Geddes	Gourlay	Total	Geddes	Gourlay	Total
< 50 m min^{-1}	8	3	11	11	0	11
50 – 70 m min^{-1}	47	20	67	50	14	64
> 70 m min^{-1}	10	1	11	39	17	56

Vertical and horizontal distance ratio

The ratio between the vertical and the horizontal components of the foraging trips was weakly positively correlated with the foraging zone coefficient and strongly correlated with the percentage of dive time. It was negatively correlated with the trip maximum range, the percentage of night time and the percentage of night dives. The trip maximum range and the night activity and dives were linked with a more horizontal exploitation of the habitat and therefore a lower ratio. In contrast, the

percentage of dive time logically indicated a more vertical exploitation of the habitat and a higher ratio.

This variable indicated that the brood trips tended to have a more vertical habitat use (with 5 foraging trips from 3 birds showing more vertical distances covered than horizontal distances with a ratio higher than 1, see Table IV-9).

Table IV-9: Trip distribution according to their vertical and horizontal distance ratio by colony and phenological stage.

Vert./Hor.	Incubation			Brood		
Distances	Geddes	Gourlay	Total	Geddes	Gourlay	Total
< 0.2	10	5	15	14	9	23
0.2 – 0.5	52	19	71	66	14	80
0.5 - 1	3	0	3	16	7	23
> 1	0	0	0	4	1	5

c. Changes in the metrics over the season: pre and post-hatching differences

Principal Component Analysis (PCA)

The first two axes of the PCA (see Figure IV-9 top plots) explaining 49.4% of the data variability showed that the data in this reduced dimension space was grouped into three clusters. A first group of points on the top-left corner of the plane (negatively correlated with both axes 1 and 2) concentrated the long, far ranging trips which mainly occurred during incubation at Gourlay Peninsula (except one trip from Cape Geddes). This group had a low vertical/horizontal distance ratio and low exploration speed.

A second group of points towards the bottom of the plane (negatively correlated with axis 2) represented the trips with a high percentage of night activity and night dives and low foraging zone coefficient and vertical/horizontal distances. These were mainly brood trips recorded from Cape Geddes.

Finally, the last group of points were positively correlated with the first axis and strongly positively linked with the vertical to horizontal distances ratio. These were mainly diurnal, short brood trips and were not specific to any colony.

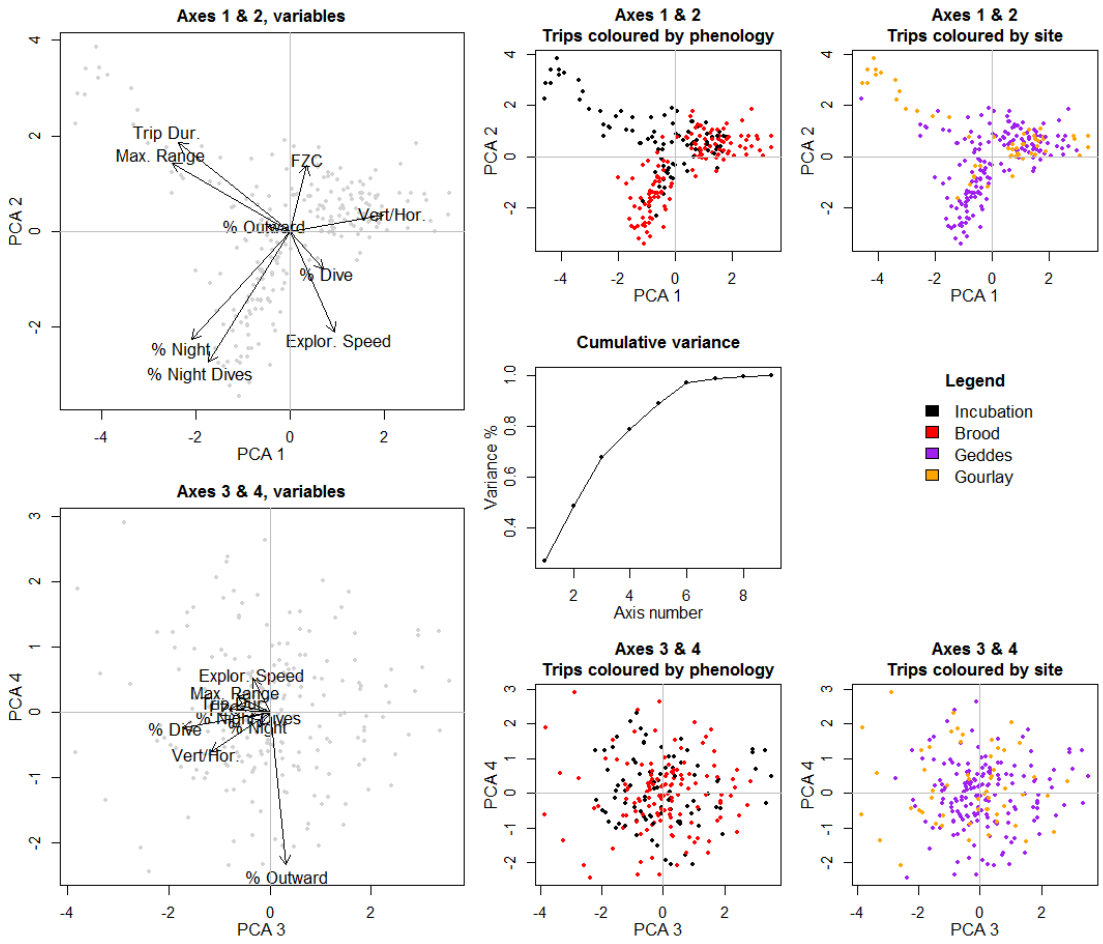

Figure IV-9: First four axes of the PCA. Axes 1 and 2 (top plots, respectively 27.1 and 22.3% of the variance). Axes 3 and 4 (bottom plots, respectively 18.8 and 11.1 % of the data variability). With labelling of the points based on the breeding stages (black : incubation and red : brood) and the colonies (purple: Geddes and orange: Gourlay).

Axis 3 (18.8% of the data variability, Figure IV-9 bottom plots) was negatively correlated with the vertical exploitation of the habitat (with the percentage of dives and vertical/horizontal distances ratio metrics). At the extreme positions along this axis were brood trips from Gourlay (negative values) and incubation trips from Geddes (positive values). The rest of the variables or points did not show any clear pattern. The fourth axis (11.1% of the data variability) was mainly negatively correlated with the percentage of outward time, without any visible arrangement between stages or colonies.

Linear mixed models (LMM)

The scatter plots between each response variable and the fixed effect (days to hatching) are presented on Figure IV-10. The shaded areas represent the 80% confidence interval of the model prediction for each random effect (colony). The model's parameters and probability values are presented in Table IV-10.

All the models, except the ones applied to the foraging zone coefficient, the percentage of outward time and the percentage of night dives showed a significant contribution from the fixed effect. The trip duration and trip maximum ranges decreased as the breeding season progressed. The

percentage of night activity, the percentage of dive time, the exploration speed and the vertical/horizontal distances ratio all increased during the breeding season.

Only two metrics showed a significant contribution from the random effect: the foraging zone coefficient and the percentage of night dives. The first one indicated that the Geddes trips were more direct than the Gourlay trips. The second one suggested that the Geddes trips had higher night dive ratios than the Gourlay trips.

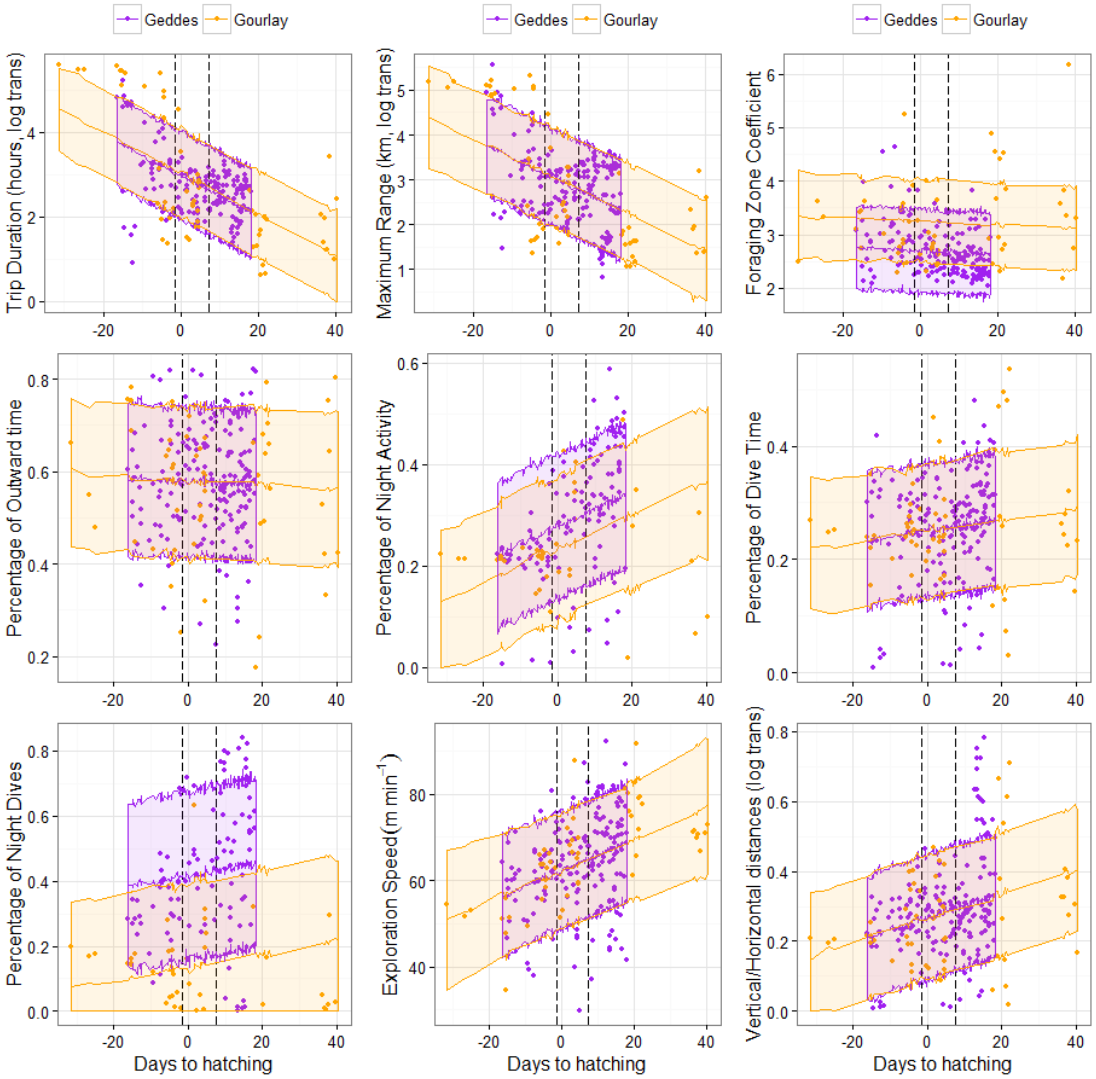

Figure IV-10: Response variables plotted along time with the prediction and the 80% confidence interval of the linear mixed models for each random effect (colony). The left and right vertical dashed lines respectively represent the start of the first brood trip and the end of the last incubation trip.

Table IV-10: Parameters of the LMM and significance value for the fixed and random effects for each response variable.

		Fixed effect			Random effect	
Response variable	Transformation	Intercept	Coefficient	P value	Chi. square	P value
Trip duration (h)	Log(x)	3.00	-0.048	< 0.01	0.14	0.708
Trip maximum range (km)	Log(x)	3.09	-0.042	< 0.01	0.00	1.000
Foraging Zone Coefficient		2.97	-0.003	0.287	32.7	< 0.01
Percentage of outward time		0.58	-0.0004	0.569	0.00	1.000
Percentage of night activity		0.26	0.003	< 0.01	3.25	0.071
Percentage of dive time		0.25	0.001	0.057	0.00	1.000
Percentage of night dive		0.28	0.002	0.106	47.5	< 0.01
Exploration speed (m min^{-1})		62.4	0.359	< 0.01	0.00	1.000
Vertical/horizontal distances	Log(x+1)	0.27	0.003	< 0.01	0.00	1.000

Random Forest (RF)

Figure IV-11 shows the same trip metrics dispersion including the 80% predicted confidence interval for each colony for the random forest models.

Table IV-11 summarizes the different numerical outputs for each model with the percentage of variance explained by each model, the contribution of each covariate to the model (in relative increase in node purity) and the p value for the significance test for each model.

Similarly to the linear mixed models, the decreasing trip duration and the trip maximum range values over time was well modelled (high percentage of variance explained and high contribution from the temporal predictor). The modelling of the foraging zone coefficient showed a high contribution from the colony factor, as previously revealed by the LMM algorithm. The model based on the percentage of outward time was not significant with a very low portion of the variance explained. The percentage of night activity, the exploration speed and the vertical/horizontal distances ratio showed similar explained variance and a high contribution from the days to hatching response variable. The model based on the percentage of dive time, although significant, showed low explained variance and similar contributions between the temporal predictor and the colony effect.

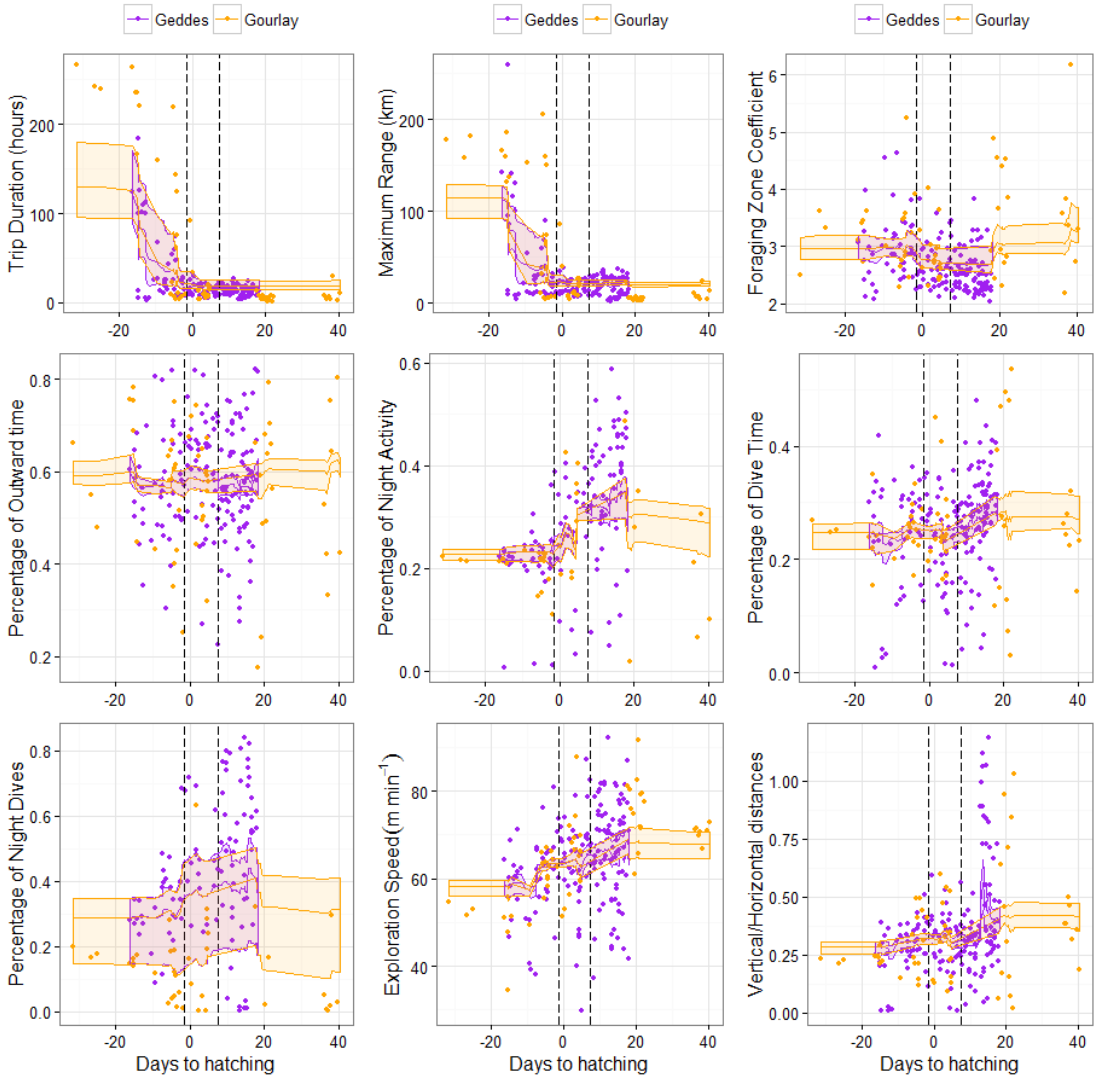

Figure IV-11: Response variables plotted along time with the prediction and 80% confidence intervals of the random forest models for each colony. The left and right vertical dashed lines respectively represent the start of the first brood trip and the end of the last incubation trip.

Table IV-11: Parameters from the RF models with the percentage of variance explained, the relative increase in node purity for each co-variable and the p value for the model significance test.

Response variable	% variance explained	Rel. increase in node purity: Days to hatching	Rel. increase in node purity: Colony	Rel. increase in node purity: Random variable	P value
Trip duration (h)	63.53	74%	14%	12%	0.002
Trip maximum range (km)	50.43	77%	15%	8%	0.002
Foraging Zone Coefficient	12.64	50%	29%	22%	0.002
Percentage of outward time	<0.01	48%	47%	5%	0.572
Percentage of night activity	22.30	63%	28%	9%	0.002
Percentage of dive time	0.58	49%	46%	5%	0.030
Percentage of night dive	33.92	36%	27%	37%	0.002
Exploration speed (m min^{-1})	13.61	62%	34%	4%	0.002
Vertical/horizontal distances	16.38	61%	35%	4%	0.002

d. Between sex differences

When undertaking similar linear mixed models (each trip metric against days to hatching as the predictive temporal) but with the putative sex of the bird as the random effect, none of the models showed a significant effect of the sex on the differing trip metrics. This result was consistent, whether the sex was determined using one or other of the discriminant functions (see II.1g, page II-21).

This was consistent with Lynnes et al. (2002) and Miller et al. (2010) who found no differences in travelled distances or time spent at the shelf break between sexes for chinstrap penguins. Similarly, de León et al. (1998) found no difference in meal size between sexes for the same species. In contrast for macaroni penguins, Barlow & Croxall (2002) found differences between male and female foraging ranges during chick rearing. Similarly, Watanuki et al. (2010) recorded shorter trips during brood for male Adélie Penguins. But Angelier et al. (2008) did not find any difference in foraging effort between sexes for the same species.

e. Inter-individual differences

The differences (distances) between trips from the same individuals (intra-individual distances) were significantly smaller than the differences between trips from different individuals (inter-individual distances, see Figure IV-12, t=-6.9154, df=202.06, p<0.01). This result suggested that there is a strong individual effect on the foraging trip characteristics (pseudo-replicates).

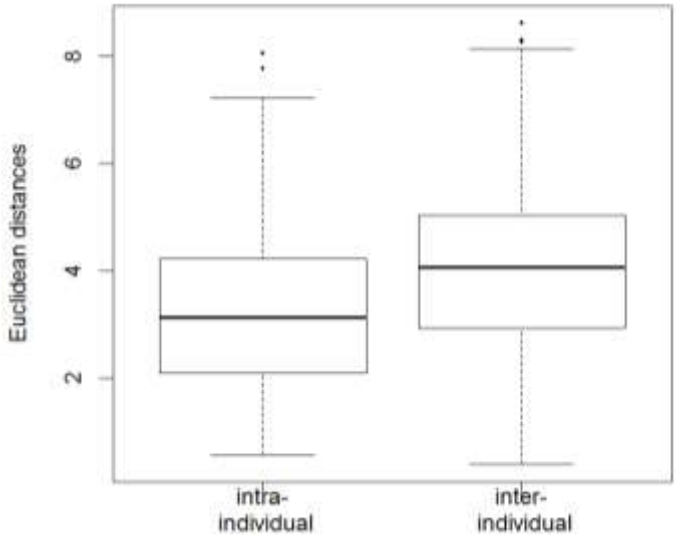

Figure IV-12: Distribution of the distances between the trips from the same individuals (intra-individual) and the distances between the trips from different individuals (inter-individual).

IV.4 Discussion of the results, implications, limitations and summary

The different methodological approaches allowed me to draw similar trends and patterns, although with some differences in data processing and accuracy. The changes in the different trip metrics over the breeding season and the influence of the colony location will now be discussed. The limitations and uncertainties about these results and their implications for the next chapters will also be described.

a. Changes in the foraging trips characteristics over time

Trip distances, durations and exploration speeds

Unsurprisingly, the well-known reduction in foraging trip duration and range was clearly represented on the PCA and confirmed in both models. The necessity to feed the chicks after hatching restricted the amount of time each parent could allocate to foraging. This reduction meant that the birds might not be able to extent their foraging beyond a certain distance (Chappell et al., 1993; Charrassin et al., 1998). A gradual reduction in foraging duration and range towards the end of the incubation was consistent with the characteristic for this species (Williams, 1995) and was confirmed mainly from data collected from Cape Geddes. The greater contrast between incubation and brood trips from Gourley can be explained by the fact that birds could only reach the continental shelf break during incubation. During brood, they did not have enough time to travel that far and return to feed their chicks, so they stayed in the vicinity of the colony. Lishman (1985) measured ranges of 132 km and 66 km for incubation and brood respectively from Signy, similar to the ones measured during this study (205 and 26 km). This reduction in foraging time and therefore distance lead to an intensification of the foraging and therefore an increase in the exploration speed metric, indicated by the PCA and confirmed by both the LMM and RF models.

Night and day activities

In addition to the trip duration and range, the second most important change was linked with the timing of the foraging trips. Two different confounding trends were observed: an increase in diurnal foraging trips and an increase in the frequency of night dives when the trip included some night time.

The first observation confirmed the predilection for daylight foraging during brood reported by Jansen et al. (1998) and Jansen et al. (2002), and the first study reported annual variations in diurnal versus nocturnal preferences. This might be explained for visual predators such as penguins as they may experience difficulty in locating and capturing prey in darkness (Williams, 1995).

In addition, the contradictory increase in night foraging, especially for the foraging trips recorded from Cape Geddes, might be explained by diel krill migration (Zhou and Dorland, 2004; Everson, 2008; Cresswell et al., 2009). This is supported by the observed shallower dives during the night (see V.3b, page V-91) which has been previously reported by several studies (Bengtson, Croll and Goebel, 1993; Wilson and Peters, 1999; Takahashi et al., 2003; Croll et al., 2006; Miller and Trivelpiece, 2008), indicating shallow easier access to prey during the night. However, though krill swarms may be shallower at night, their density might be lower (Everson, 1982). In some cases, bioluminescence could help predators to find their prey (Grinnell et al., 1988; Bengtson, Croll and Goebel, 1993; Miller and Trivelpiece, 2008). Jansen et al. (1998) also reported a shift in prey species during night foraging where bird might forage more on myctophid fishes rather than krill. The absence of stomach content or guano content analysis unfortunately did not allow to test this hypothesis.

During brood, overnight trips tended to be significantly further off shore than diurnal trips only (average of 21.4 and 8.6 km respectively) confirming what Miller et al. (2010) observed for this species. This might indicate two distinct foraging locations according to the timing of the trip (see VI.3e, page VI-126).

Vertical exploitation of the habitat

In parallel with the horizontal reduction of the available foraging habitat, two trip metrics were linked with the vertical exploitation of environment: the percentage of dive and the vertical/horizontal distances, both being highly correlated. On the PCA, these two metrics seemed to be negatively related to long incubation trips and to trips with high percentages of night activity or night dives.

The modelling approaches both showed a significant but weak increase in the vertical exploitation of the habitat during the breeding season (the LMM coefficients for the percentage of dive time and the vertical/horizontal distances was respectively 0.001 and 0.003; the RF explained variance was respectively 0.56% and 16.4%). As mentioned earlier, dive depth was strongly linked with the period of the day and as

the percentage of night activity increased after hatching, shallow night dives effect might partially mask the deeper exploitation of the habitat.

When modelling the vertical/horizontal distances ratio using a random forest algorithm including not only the temporal predictor variable (days to hatching) but also the percentage of night activity, the model performed better (33.1% of variance explained, the R-squared between the observed and the predicted values doubled to reach 0.364). The days to hatching scored 44% of the relative increase in node purity, the percentage of night activity was second with 30% and the random variable scored 23%. A bi-variable dependency plot (Figure IV-13) confirms a very strong increase in the vertical/horizontal distance ratio during the breeding season especially for trips with low night time activity.

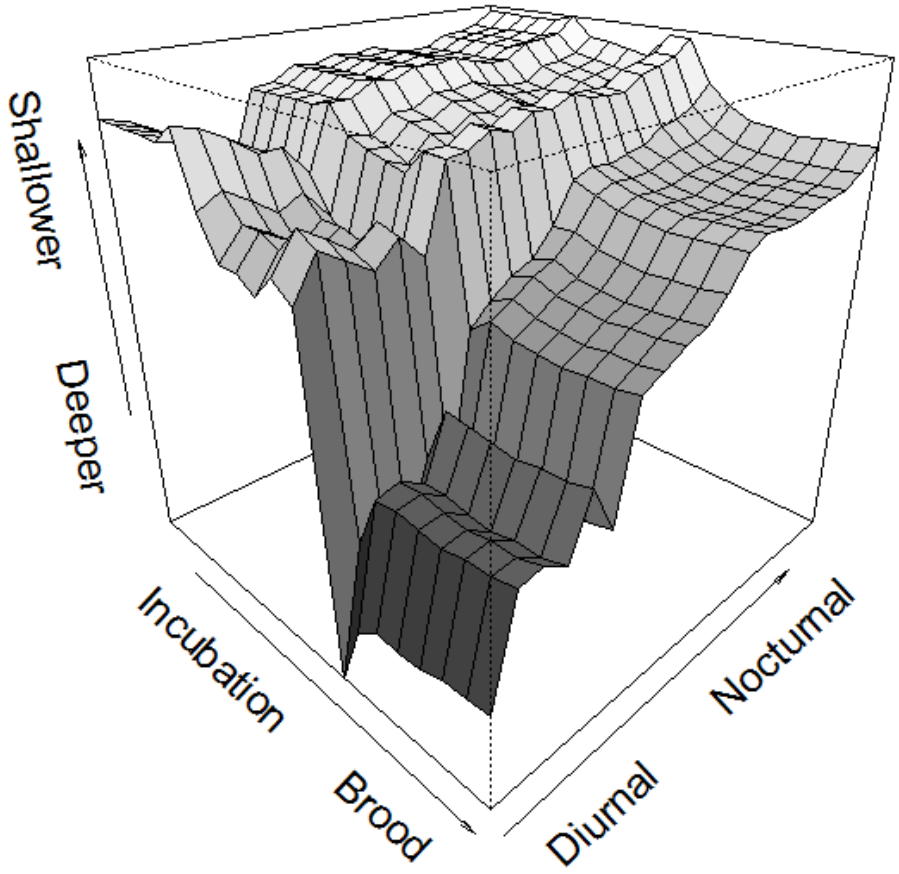

Figure IV-13: Predicted vertical/horizontal distance ratio in relation to the breeding season and the period of the day.

This increase of dive depth during brood hasn't been described previously for chinstrap penguins. Charrassin et al. (1998) reported similar observations for king penguin, while Hart, Coulson, et al. (2010) recorded shallower dives during incubation for macaroni penguins.

Deeper brood dives could be explained by a number of factors. These include the constraints imposed by a reduction in foraging range: the birds may need to better exploit the available ocean volume given the increase in intra-specific competition as other individuals from the same colony must also forage within waters close to their nest sites. The

combination of more birds coupled with the growing needs of the chicks could drive birds to dive deeper to increase their energy intake. When comparing several krill predators, Veit et al. (1993) suggested that deep divers can increase their foraging efficiency by staying closer to the colony. Prey depletion in the proximity of the colony, as measured for Adélie penguins by Ainley et al. (2004), can also be the reason for this increase of dive depth through intra-specific competition. It is also possible that change in dive depth was driven by a change in prey distribution along the water column. Temporal shifts in krill stages along the Antarctic Peninsula had been observed (Siegel, 1988) and it is possible that juvenile present earlier in the season exploited a different depth range than adults present later in the breeding season.

b. Colony differences

Both linear mixed models and random forest modelling methods did not indicate a clear difference in the trip foraging timing, ranges and exploration speeds between the two colonies. But the observed maximum ranges of the foraging trips from Gourlay Peninsula were further than the ones from Cape Geddes (although the longest trip was recorded from Geddes). During incubation, frequent shorter trips were recorded from Geddes, as these were quite unusual from Gourlay.

The proximity of the shelf break was an important difference between the two colonies (see III.1, page III-40). This oceanographic feature is considered to be an important krill habitat (Ichii et al., 1998; Atkinson et al., 2008; Santora et al., 2012) and therefore potential predator foraging area (Trathan et al., 2006; Miller et al., 2010). Gourlay incubating birds confirmed this by reaching the shelf break on almost every trip, without displaying typical shorter trips as hatching approached. This is similar to what Lynnes et al. (2002) reported from the same location.

The foraging zone coefficient indicated more direct trips from Cape Geddes. This can be explained during brood by the fact that the birds tried to reach the shelf break. By targeting this location, the shape of the foraging trips are less circular. Contrastingly, during brood the birds from Gourlay could not reach the shelf break due to its distance to the colony, which was incompatible with their chick rearing constraints. There were no important oceanographic feature to orientate their foraging. This might have driven them to explore a larger area and therefore to do more circular trips, increasing the chances of encountering prey swarms when no particular cue was available.

Both the linear mixed model and the random forest methods indicated that the percentage of night dives was influenced by the site with trips from Cape Geddes having more night dives than the ones from Gourlay Peninsula. This can again be explained by the bathymetric differences between both colonies. Deeper waters around Geddes meant that during the day, a substantial amount of potential prey migrate to deeper depths, beyond the dive limits of the birds. To mitigate that, birds might be driven to better exploit the night time vertical migration of their prey. At

Gourlay, over the continental shelf, the prey vertical escape space was more limited, meaning that perhaps there was less incentive for birds to forage at night.

An additional difference between foraging trips from both locations was the observed trip directions (mainly anticlockwise from Geddes and clockwise from Gourlay). This might be linked with local differences in currents and will be investigated in chapter VII.3a.

Despite several differences between the oceanographic features available from the two colonies, the models did not reveal an important "colony effect". Which seems contradictory with Bengtson et al. (1993) and Miller et al. (2010) stating that local conditions have a strong influence on penguin foraging. These two researches were based in the South Shetland Islands and it might be possible that local conditions were even more contrasted in this archipelago than in the South Orkney Islands.

c. Prediction accuracy

Comparing both methods

Both modelling methods showed similar trends although these were non-linear for the random forest models and applied to the un-transformed variables. But the direction of the trends were matching and both methods agreed on the strong colony effect for the percentage of night dives and the foraging zone coefficient.

When comparing the prediction accuracy in trying to guess each trip metrics from the fixed and random effects (LMM) or co-variables (RF), the top three modelled variables were the trip duration, the trip maximum range and the percentage of night dives for both methods. Although the random forest algorithm tended to underestimate the predicted values (see intercept values on Table IV-12), it outranked the linear mixed model technique for these best predicted metrics (higher coefficients of determination, see Table IV-12).

Table IV-12: Linear regression parameters between the observed and the predicted trip metrics from both modelling with a graphical representation of the relationship between the observed (y axis) and predicted (x axis) values for incubation (black) and brood (red) trips. The variables are ordered by decreasing model predictions averaged between the linear mixed model (LMM) and the random forest (RF)

		LMM		RF	
Trip duration (h) (transformed for LMM)	Intercept	0.123		-13.560	
	Slope	0.955		1.493	
	R squared	0.314		0.713	
Trip maximum range (km) (transformed for LMM)	Intercept	0.105		-11.268	
	Slope	0.964		1.375	
	R squared	0.247		0.545	
Percentage of night dive	Intercept	0.008		-0.016	
	Slope	0.975		1.041	
	R squared	0.313		0.340	
Percentage of night activity	Intercept	0.026		-0.017	
	Slope	0.906		1.062	
	R squared	0.135		0.224	
Exploration speed (m s^{-1})	Intercept	4.214		-12.652	
	Slope	0.934		1.197	
	R squared	0.134		0.140	
Foraging Zone Coefficient	Intercept	0.229		0.515	
	Slope	0.919		0.817	
	R squared	0.129		0.133	
Vertical/horizontal distances (transformed for LMM)	Intercept	0.047		-0.071	
	Slope	0.834		1.209	
	R squared	0.061		0.169	
Percentage of outward time	Intercept	2.416		0.949	
	Slope	-3.189		-0.646	
	R squared	0.023		0.010	
Percentage of dive time	Intercept	0.134		0.114	
	Slope	0.477		0.556	
	R squared	0.004		0.016	

In summary, LMM provided an effective way to test the influence of random effects (colony). The RF algorithm was able to handle raw data and non-linear relations while still estimating the effect of the colony. The accuracy of RF method was generally better, although the predicted values tended to be lower than the observed ones.

d. Limitations and uncertainties

The main limitation of these analyses was related to the data: its noise and distribution had a potential large impact on the analyses. Matching learning methods such as random forests proved more robust to deal with data that show distributions with long tails or non-linearity (De'ath 2007).

Sample sizes and the unbalanced distribution of the sampling (see III.2, page III-43) limited the abilities of the analyses to explore random effects. In this study, 75% of the foraging trips were recorded from Cape Geddes. There were chances that this colony was strongly driving the results of the analyses. Similarly, the difference in sampling at Gourlay

Peninsula during both 2011-12 and 2013-14 seasons, not only in terms of sample size, but also in terms of timing (87.8% of the trips from this colony were recorded in 2011-12 and these were mainly late brood trips), made the comparison of both seasons very difficult.

Across the Scotia Sea, krill recruitment, abundance and size distribution shows important inter-annual variability (Atkinson et al., 2001). Although these annual changes in the prey field might have an impact on the food chain (Charrassin et al., 1998), Croll et al. (2006) and Lynnes et al. (2002) suggested that chinstrap penguins don't increase foraging effort in response to low prey abundance.

In order to explain some of the observed chinstrap foraging trip characteristics and changes through the season, additional information from the other actors of the Southern Ocean food chain is required. A fine scale knowledge of the prey distribution and temporal changes over the breeding season is necessary to validate some of our observations. Interspecific competition and niche partitioning with sympatric Adélie penguins (Lishman, 1985; Lynnes et al., 2002; Lynnes, Reid and Croxall, 2004; Miller et al., 2010) can be very intense during brood and will have an impact on the distribution of the foraging realised niche. Similarly, predation of penguins is an important factor that should ideally be included in the models (Veit, Silverman and Everson, 1993; Ainley and Ballard, 2012).

e. Summary

This chapter assessed the main changes in the foraging trip metrics during the breeding season. The results showed clearly that there is an increase in foraging effort after hatching. It is hypothesised that more intense foraging during brood across all dimensions is mainly driven by more food demand from the offspring. It is also possible that changes in prey availability could also influence changes in foraging effort although the lack of data about prey field do not allow me to test this hypothesis. The constraints before and after hatching are very different. In the context of developing a habitat model, it is necessary to separate both breeding stages and develop one model for each.

In addition to the temporal scale of the breeding season (weeks), there are important changes occurring at higher temporal resolutions. This chapter emphasized the influence of the prey vertical migration between the day and the night on predator vertical exploitation of the habitat. This temporal factor (hours) has to be incorporated in the foraging model.

The sex of the birds was not detected as an important confounding variable, but the individual itself appears to have an impact on the trip characteristics. This pseudo-replicate effect is a crucial limitation for this study.

Finally, despite the important biotic and abiotic differences between both colonies (see Chapter III), the main trip metrics and their most significant changes were very similar. This is a very encouraging result in the context of the development of an interpolated global habitat model

for the South Orkney Islands based on the data available from these two colonies.

Chapter V DETECTION OF THE BEHAVIOUR MODES AT THE SCALE OF THE FORAGING TRIPS

This chapter considers the changes within chinstrap penguin foraging trips and tries to infer the bird's behaviour while at sea. Changes during the season as well as the influence of the colony or sex of the bird on the different behaviours are assessed. The distinction between different behaviours is an important input for habitat modelling (Chapter VI and Chapter VII).

V.1 Introduction and aims: detecting foraging and other behaviours

Since high resolution GPS tracking devices have become available, the study of fine scale animal movement has become a central question for avian ecologists, linking foraging behaviour with community ecology. This topic is especially crucial for marine species whose behaviour is very difficult to observe directly at sea. Tracking marine species, and seabirds in particular, can provide a useful insight on their at-sea foraging. Understanding their movement patterns can help identify and locate different behaviours, a key step for the development of a foraging habitat model (Hart and Hyrenbach, 2009; Kuhn et al., 2010). For example, Humphries et al. (2010) linked changes in foraging strategies for several marine species that could be detected through the characteristics of their movement in response to their environment.

Breeding penguins are central place foragers in both the horizontal and vertical dimensions. Their foraging range is restricted by the location of the colony and the necessity of either relieving their partner at the nest during the incubation phase or feeding the chicks during the brood and crèche phases (Williams and Siegfried, 1980). The vertical dimension is also limited as air breathing divers, like penguins, are physiologically limited in their foraging depth and therefore access to prey (Kooyman and Ponganis, 1998). As demonstrated in the previous chapter, time is an important factor at different scales: energy requirements change during the course of the breeding season and the animals respond to their prey's diel migration by adapting their foraging timing and depth. In addition, chinstrap penguins are slow moving (non-flying) birds that exploit prey that is generally patchy, difficult to predict and locate from the surface and whose distribution varies in time. All these factors make penguins a difficult model to test various optimal foraging theories (Ford et al., 2014).

There are challenges and limitations on the choice of analytical tools available, due to the nature of the data: the dataset is large, has multidimensionality (in space and time), has non-independent sequential data points (high autocorrelation) and strong stochasticity. At the moment, there are no standard agreed method with which to process such datasets and define behavioural units (Gurarie, Andrews and Laidre, 2009; Womble et al., 2013).

In this chapter, I will infer the bird's at sea behaviour modes during their foraging trips based on fine-scale changes in the surface and dive metrics

for each trip. I propose and compare two methods: one based on a semi-automatic unsupervised classification of behaviour modes and another based on a trained model with some *a priori* expert knowledge about the behaviour (supervised classification).

I predict that in addition to the trivial distinction between foraging and commuting, this method will allow me to detect additional behaviours, such as exploratory diving or surface resting. The influence of the site, the stage in the breeding season and the sex on the time allocation for the different behaviour modes will be considered and discussed.

V.2 Method

a. Past approaches and method used in this study

Previous studies using similar datasets have used different techniques to assess animal behavioural changes across space and time from tracking based data acquisition. These ranged from simple thresholds in the movement metrics (Naito, Asaga and Ohyama, 1990; Halsey, Bost and Handrich, 2007) to more complex first passage time and area restricted search analyses (Fauchald and Tveraa, 2003; Per and Torkild, 2003; Sommerfeld et al., 2013), space-state models (Patterson et al., 2008; Bestley et al., 2014), hidden Markov models (Hart et al., 2010; Agarwala, Chiel and Thomas, 2012; Dean et al., 2012), or fractal methods (Macintosh et al., 2013). Few of them integrated the vertical dimension with the horizontal dimension in their analysis of behavioural change (Bestley et al., 2014). Some authors identified dive bouts along the foraging trips, which are indicative of feeding locations and allows to detect foraging success (Watanuki et al., 2002; Bost et al., 2015). But this approach requires the definition of various threshold (maximal surface time, minimum number of dives, see Watanabe, Ito and Takahashi, 2014 for example), which is not compatible with the general approach of this study.

The methodological approach used in this study is based on change point detection of time series (Madon and Hingrat, 2014). This process, considered as an important step in movement analysis (Shamoun-Baranes et al., 2012), allowed me to take into account the non-independent sequencing of the data (Gurarie, Andrews and Laidre, 2009; Benson, 2016). The tools and packages chosen for this study were in accord with the heuristic approach of this research which tries to minimize parameterization during the data processing.

Using both surface and dive metrics that were interpolated at a regular and relatively high temporal frequency (see II.2c, page II-29) allowed me to integrate multiple dimensions in the change detection. Combining these three dimensions enabled me to capture complex interactions between metrics and therefore detect more detailed behaviour than a simple commuting/foraging distinction (Carter et al., 2016).

b. Foraging trips segmentation

This section describes the method used on the complete (GPS + TDR) data (74 incubation and 118 brood foraging trips) after the failed very long incubation trip 75_173 was removed.

Data preparation

The time series segmentation process required intense computing time; it was therefore decided to reduce the number of dimensions (variables) of the data series to four. Two surface metrics (speed and relative angle, see II.2a, page II-22) and two dive metrics (maximum depth and dive efficiency, see II.2b, page II-26) were retained as being independent and plausible *a priori* indicators of the different behaviour modes (Per and Torkild, 2003; Patterson et al., 2008; Ford et al., 2014; Hays et al., 2016).

The interpolated positions that were not linked to any dives had missing data for dive related metrics. These missing data were replaced by zeros to ensure that these points were included in the segmentation process.

Because of the different ranges of values between all the variables, they were transformed (centred and scaled) to ensure an equal contribution to the segmentation process from each metric (see Figure V-1).

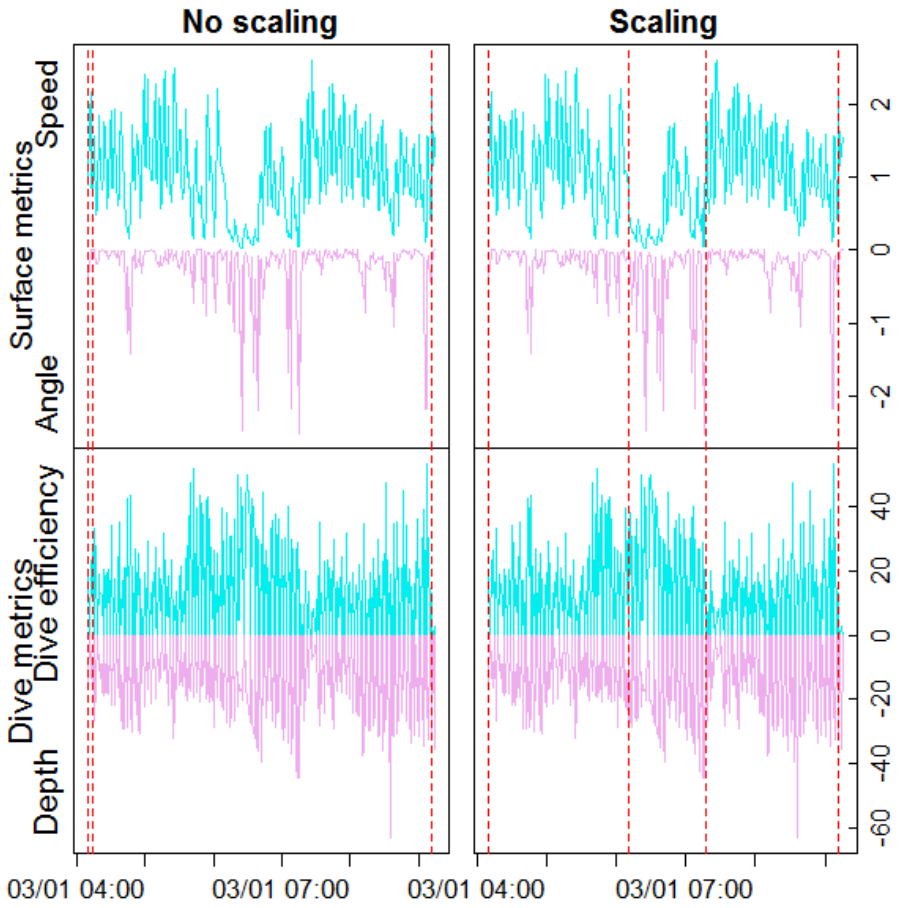

Figure V-1: Effect of the variable transformation on the segmentation result (red lines). This portion of a trip had very homogenous dive metrics (bottom plots) with some variations in the surface metrics (top plots). Without any variable transformation (left), the changes in the surface metrics are not taken into account by the segmentation process. On the right plot, the surface and dive metrics have been transformed (centred and scaled, although the values presented here are the raw data) leading to an additional segment with low speed and high sinuosity.

Time-series segmentation

The algorithm used for the segmentation process was the "divisive hierarchical estimation for multiple change point analysis" from the 'ecp' R package (James and Matteson, 2014). This method allowed for multivariable datasets and required only few parameters. Each foraging trip was processed separately.

The parameters required by the segmentation algorithm were the maximum number of random permutation for the permutation validity tests of each segment (R, Gandy 2009), the moment index which determined the distance between and within segments (α) and the minimum number of observations between change points (k, minimum segment size). A sensibility analysis was carried on a small number of trips (4) to measure the impact of different parameter values on the segmentation process and the resulting number of segments (see Appendix I). The R parameter had very little impact on the segmentation results, but a higher number of permutations lead to an important increase in processing time. It was therefore set to 60. The moment index had an impact on the number of segments; lower values lead to an increase in the number of segments. In order to avoid a too detailed

segmentation, the default value of 1 was retained. Finally, the minimal number of points per segment had very little effect on the result of the segmentation. The retained value of 5 (which meant that segments could not be shorter than 5 minutes) was consistent with the spatial resolution of the data: using the observed median speed of 0.72 m s^{-1}, a bird could travel the distance of 214.8 m in 5 minutes; which is similar to the measured resolution of the GPS during the static test where 95% of the locations were within 243.1 m (see II.1b, page II-14).

When the number of segments was less than 3, the process was repeated with the constraint of having 3 segments which would force the routine to split the trip into at least an outbound, a middle and a return to the colony segments.

c. Behaviour modes

Two different approaches were used to infer the behaviour of birds during each segment. A first semi-automatic unsupervised method (segment clustering) enabled minimal operator influence to group the segments into different clusters which could then be attributed to different behaviours. The second approach was based on an expert classification of each segment within a sample of all the foraging trips (approximately 30%). A machine learning algorithm was trained on this dataset to predict and infer the behaviour modes for the rest of the dataset (supervised classification).

Segment data aggregation

The different surface (speed and relative angle) and dive (maximum depth and dive efficiency) metrics were aggregated for each segment using the median value. The percentage of dives for each segment was also calculated and the day period for the segment was estimated using the mode of the day period. Twilight and night classes were aggregated into a single night class. Table V-1 presents the different segment metrics used for the clustering process.

Table V-1: Using the 1 minute interpolated GPS position data merged with the TDR dive data to identify aggregated segment metrics for the cluster analysis (method 1, top part of the table) and the additional variables used for the second method (expert based classification, bottom part of the table). The measures and processes lead to a series of temporal (green), one dimension spatial (blue) and combined spatio-temporal (red) variables

INTERPOLATED GPS MERGED WITH DIVE DATA Table II-6 and Table II-7	DATA AGGREGATED BY SEGMENT	
VARIABLES USED IN THE FIRST METHOD		
Speed (m s^{-1})	Median Speed (m s^{-1})	II.2a
Relative angles (rad, absolute value)	Median Relative angles (rad, absolute value)	
Maximum depth (m)	Median Maximum depth (m)	II.2b
Dive efficiency	Median Dive efficiency	
Period of the day (day/twilight/night)	Mode of the period of the day per segment, simplified to have two classes (day/night)	II.2d
	Percentage of dive time (number of 1 min interpolated positions linked with a dive / total number of interpolated positions in the segment)	V.2c
ADDITIONAL VARIABLES FOR THE SECOND METHOD		
	Segment duration as a percentage of the total trip duration	
	Mean moon illumination (%)	II.2d
	Random variable	

Method 1: Semi-automatic segment clustering

The dataset was separated according to the breeding stage (incubation or brood), as bird activity and recorded metrics can be different depending upon the time within the breeding season, as observed in Chapter IV.

The dissimilarity measure between all the segments for each stage during the clustering process was the Gower's distance from the 'cluster' R package (Gower, 1971; Maechler et al., 2016). This coefficient allowed a mixture of scalar variables (surface and dive metrics and the percentage of dive) and categorical variables (the simplified period of the day) to be included. The variables were standardized during the process.

From the resulting dissimilarity matrix, a dendrogram was drawn using a Ward's minimum variance clustering criterion (Murtagh and Legendre, 2014). The number of clusters was sequentially increased until it was not possible to infer a reasonable behaviour for each cluster from the values of the different metrics.

For the incubation segments (Figure V-2), the first cut-off point enabled me to separate the day and night segments. The next cut point separated the day segments into a cluster with high speed, low relative angles, few shallow dives (4%), and low dive efficiencies. This could be interpreted as the commuting parts of the trips. The other cluster had low speed, high relative angles, frequent (41%) and deeper dives with high efficiency values. This could indicate the foraging parts of the trips (Kareiva and Odell, 1987; Per and Torkild, 2003; Patterson et al., 2008; Carter et al., 2016; Hays et al., 2016). Adding a cluster cut the night segments into two groups: they both had similar speed, but one had high relative angle, more frequent (55%) deeper dives with higher efficiencies. This was

classified as night-foraging; the other with opposite characteristics, only 12% of dives and a slightly higher speed was classified as being night-commuting or night-resting. The next cut-off point distinguished the mainly surface commuting segment into commuting and resting, the latter having slower speeds, higher sinuosity and very low dive frequency (1%). An additional cluster distinguished foraging with another group of segments with higher travelling speed, lower turning angles, a high frequency (42%) of shallower dives with lower dive efficiencies. It was therefore considered as containing exploration dives. Williams et al. (1992) classified gentoo penguin shallow dives as searching/exploratory dives. The little amount of time spent at the bottom of the dive resulting in the lower dive efficiency measures for this cluster (see II.2b, page II-26) could indicate V-shaped dives which are typical of non-foraging, exploratory dives (Wilson et al., 1996; Wilson and Peters, 1999; Charrassin et al., 2001; Ford et al., 2014). Finally, the last cutting point separated the foraging segments with a group of segments with similar surface metrics but less frequent (34%) deeper dives with lower efficiencies.

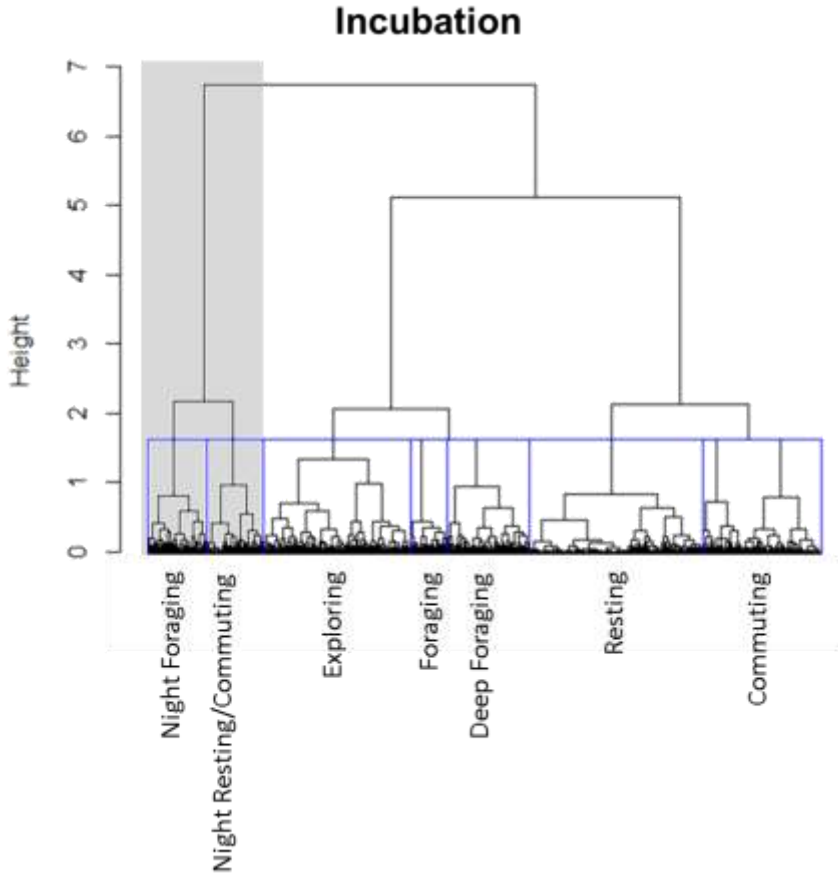

Figure V-2: Dendrogram for the incubation segments with the cut-off point and the resulting seven clusters and their inferred behaviour modes. The shaded area presents the night segments.

The clustering of the brood segments generated the same number of behaviour modes, but in a slightly different order (see Figure V-3). The split between shallower and deeper foraging clusters happened at the

fourth step. The exploring dives were separated from the deep foraging dives at the last step.

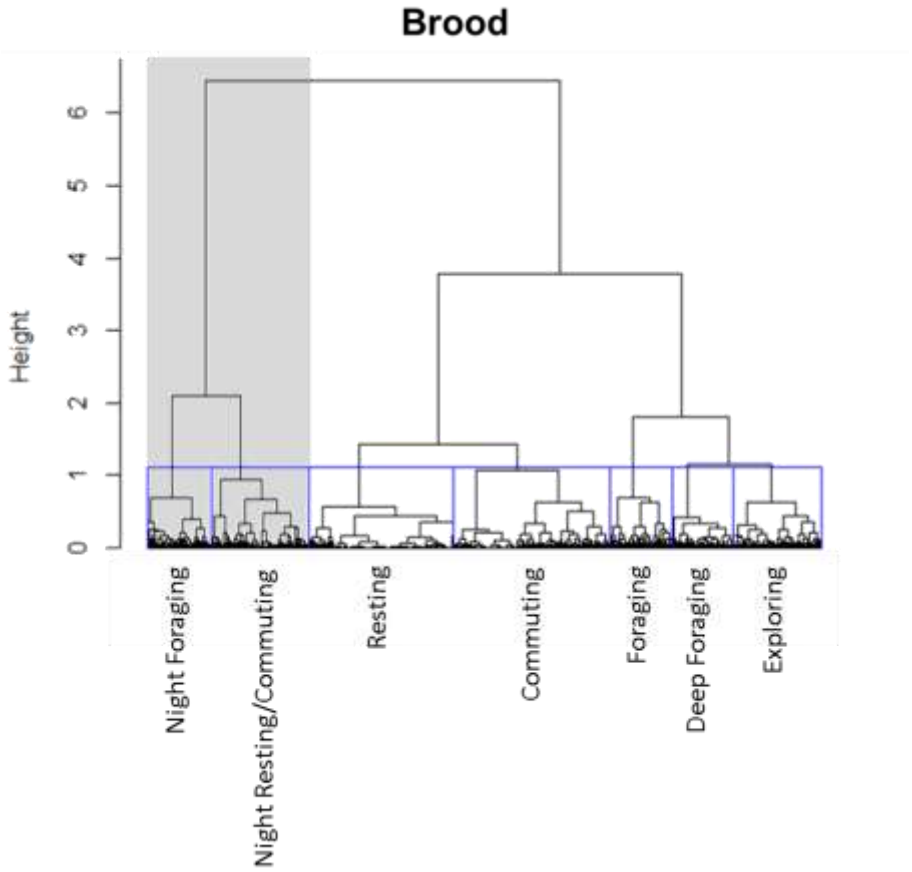

Figure V-3: Dendrogram for the brood segments with the cut-off point and the resulting seven clusters and their inferred behaviour modes. The shaded area presents the night segments.

Method 2: Expert-based behaviour mode classification

As an alternative method, a subset including approximately a third of the trips was visually inspected and the segments classified into different behaviour modes. This random sample including 22 incubation trips (29.7%) and 35 brood trips (respectively 24.7 and 26.7% of the total trips) was used as a training dataset. For each of the 887 resulting segments, the behaviour mode was determined based on the time of the day and a visual inspection of the different surface (speed and angle) and dive (maximum depth and dive efficiency) metrics. The horizontal shape of the foraging trip was also considered in the evaluation. The same foraging modes resulting from the previous semi-automatic method were identified; Table V-2 shows the number of segments that had been attributed for each behaviour modes on the training subset.

Table V-2: Behaviour attribution for the training dataset to model the behaviour modes.

	Behaviour mode	Incubation 22 trips	Brood 35 trips
Day	Commuting	113	137
	Exploring	115	64
	Foraging	112	85
	Resting	88	16
Night	Foraging	46	52
	Commuting	27	32

From this training set, a random forest was developed to try to predict the behaviour mode for each segment based on the same variables as used in the segmentation process (the surface and dive metrics, the period of the day and the percentage of dive time for the segment) along with the segment duration as a percentage of the total trip duration, the mean moon illumination, the phenological stage and a randomly generated variable (see Table V-1).

The trained model was then applied to the remaining segments to predict their behaviour modes.

Incomplete dataset (GPS only)

For the 28 trips where TDR data were missing, I investigated whether behaviour modes could be predicted without the dive metrics. A random forest model was developed on the complete dataset (GPS and TDR) to predict the inferred behaviour modes from the previous methods for each interpolated position.

The variables used in the model combined the surface metrics (speed and relative angles), positions along the trip as a percentage of the total trip length, the part of the trip (outward or return), the distance to the colony, the phenology, the period of the day (day, twilight or night), the percentage of moon illumination and the phenology (Table V-3). The putative sex and the colony site were not included, as they were not improving the performance of the models.

Table V-3: Variables used to predict the behaviour modes for each 1 minute interpolation location without using dive metrics. Temporal only variables are in green, spatial only variables are in blue and spatio-temporal variables are in red.

INTERPOLATED GPS MERGED WITH DIVE DATA Table II-6 and Table II-7	
Breeding stage (Incubation/Brood)	II.1e
Speed (m s^{-1})	II.2a
Relative angles (rad, absolute value)	
Part of the trip (Outward, Return)	II.2c
Distance to the colony	II.2c
Period of the day (day/twilight/night)	II.2d
Moon illumination	II.2d
Position along the trip as a percentage of the total trip duration	
Random variable	

d. Summary of the process

Figure V-4 summarizes the workflow for this chapter from the interpolated one minute location merged with dives to the attribution of the behaviour modes using trip segmentation and two different methods for behaviour mode classification. The estimation of the behaviour modes for the trips without TDR data is also included.

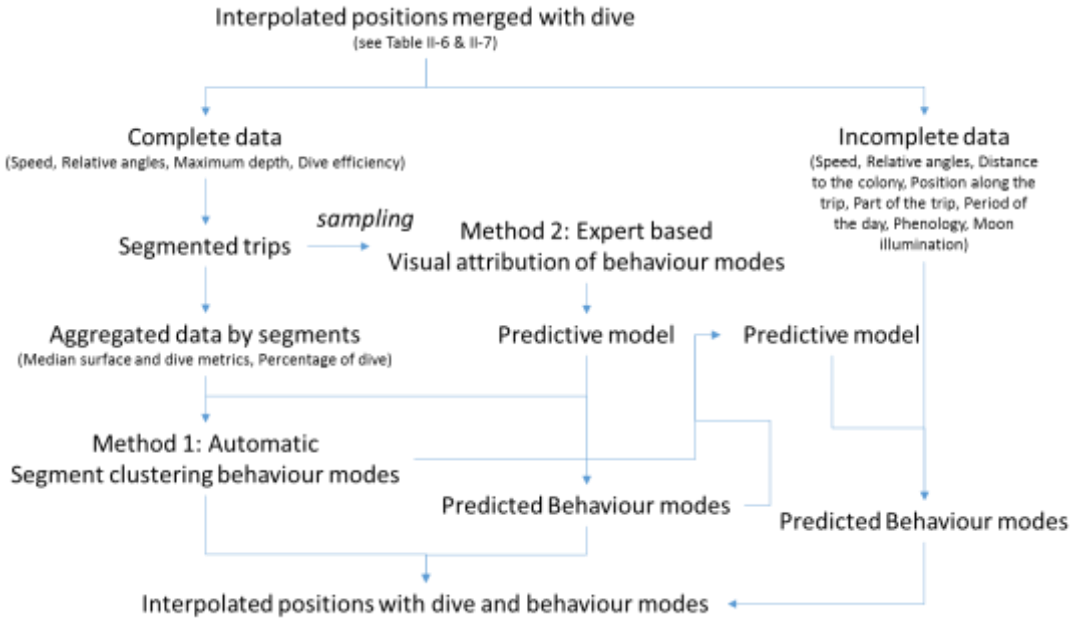

Figure V-4: Workflow summary from the one minute interpolated positions merged with the dive data to the trip segmentation and the two methods for behaviour mode attribution: the first method was a semi-automatic cluster analysis of the segments; the second was an expert-based modelling of a sample of all the trips which was then applied to the remaining trips.

V.3 Results

a. Results of the segmentation process

The segmentation process on the complete dataset (GPS+TDR, 192 trips, 267,762 one minute interpolated positions) found 3,161 segments with averages of 25.2 and 10.9 segments per incubation and brood trips respectively. The number of segments was strongly correlated with the trip duration (Pearson coefficient of 0.894, $p<0.01$). Segments lasted between 5 minutes and 14.3 hours with a median duration just above an hour (63 minutes). Segment lengths ranged between 71 m to 93.9 km and less than 1% of the segments (29) were shorter than the estimated spatial resolution of the GPS locations (250 m, see II.1b, page II-14).

The distribution of the number of segments per trip for the different parts of the breeding season and by site (Figure V-5) confirmed what have been observed previously about trip duration and ranges. Incubation trips have more segments than brood trips especially from Gourlay. Geddes brood trips showed a bimodal distribution with trips with few segments (less than 10) and longer trips with more segments, confirming the potential existence of two main foraging locations from this colony as discussed in the previous chapter.

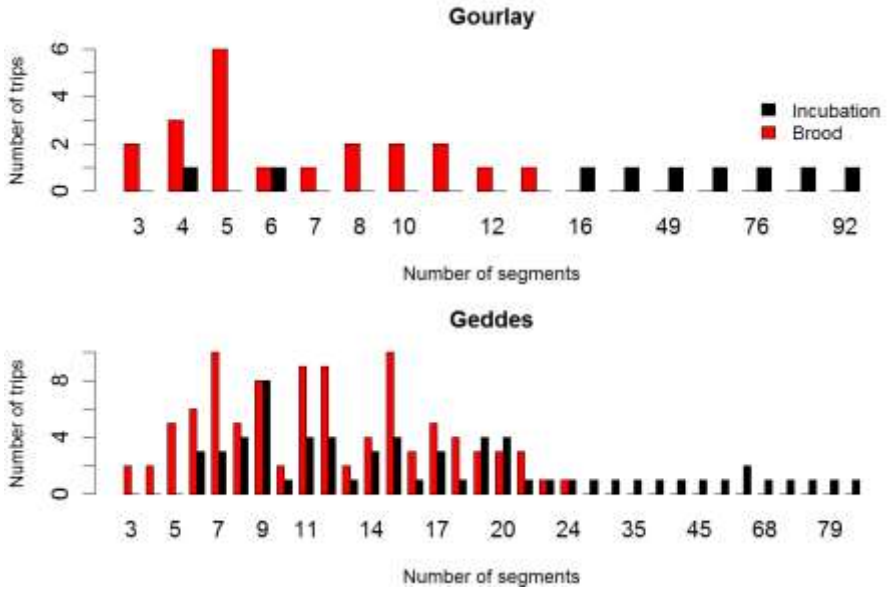

Figure V-5: Distribution of the number of segments per trip by site and breeding stage.

For trips with some nocturnal activity, a large number of change points occurred at, or near to, the day period change (sunset or sunrise, see II.2d, page II-32) as seen on Figure V-6. The median time difference between a segment change point and sunset was 30 minutes (interquartile range of 44.8 min) and 27.5 minutes for the sunrise (interquartile range of 37.3 min). This confirmed that 1) certain important changes took place at these key moments; 2) the chosen metrics were reasonable proxies for these changes and 3) the segmentation process was able to detect these changes.

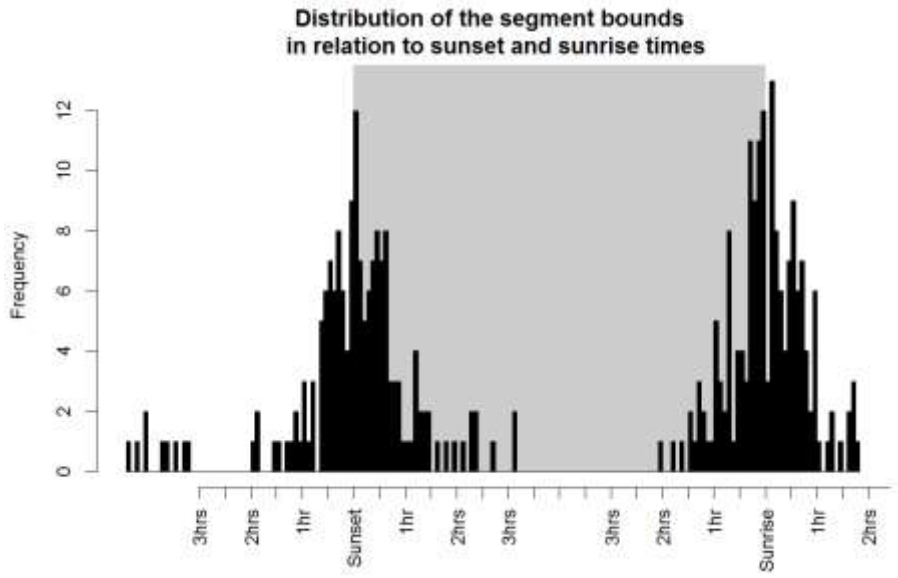

Figure V-6: Temporal distribution of the closest segment boundaries to the sunset (left) and sunrise (right) times.

b. Behaviour modes

Method 1: Semi-automatic segment clustering

The cluster analysis separated the day and night (twilight and night) activities. Then, diving activities allowed me to distinguish foraging and non-foraging parts of the trips. In addition to this basic distinction for both day and night periods, the clustering process allowed me to detect some additional behaviour modes. Day segments without dives were divided between commuting and resting based on the surface speed and sinuosity. And diurnal segments with dives were divided into foraging and exploring based on the dive depth and dive efficiency. For both phenological stages, the day foraging activities were split based on the maximum depth: a shallower and a deeper foraging. This was clearly visible on the bimodal distribution of the maximum depth during the day (see Figure V-7A for brood). When plotting the frequency distribution of the three foraging behaviour modes (foraging, deep foraging and night foraging) along the hour of the day (Figure V-7B), it was clear that these differences in depth reflected the diel migration of the krill (see IV.4a, page IV-72). The deep foraging modes happened mainly around midday and replaced shallower foraging that occurred in the early or late hours of the day. For simplification, both foraging modes were therefore merged.

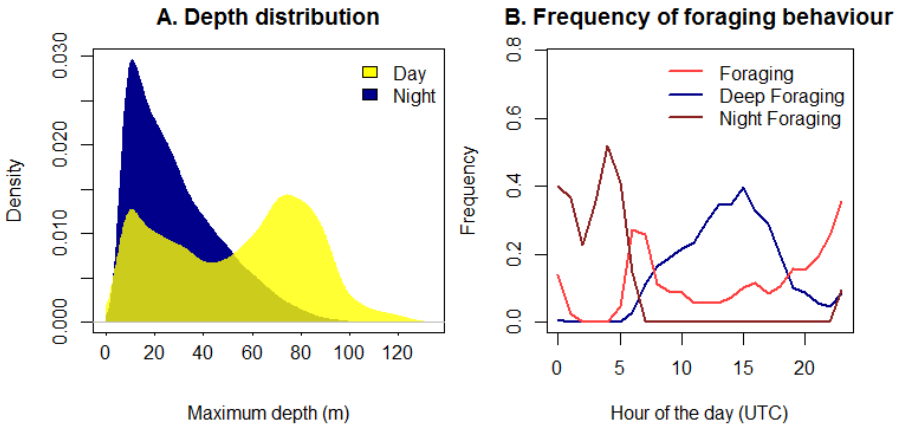

Figure V-7: A. Density distribution of the recorded maximum depth during the day and night time periods showing a bimodal shape for the daylight dives. B. Frequency distribution of the different foraging activities along the day.

The time allocations for each behaviour mode by phenological stages are presented in Table V-4. As expected, foraging was the most represented behaviour (22%), followed by exploring (21%). Resting was the third activity with the highest allocation (18%). Commuting (16%), night foraging (10%) and other night activities (13%) accounted for the rest of the time allocation.

Table V-4: Percentage of time at sea spent on each activity detected by the cluster analysis for both phenological stages.

		Semi-automatic method	
	Behaviour mode	Incubation	Brood
Day	Commuting	13%	19%
	Exploring	27%	14%
	Foraging	18%	26%
	Resting	21%	15%
Night	Foraging	10%	11%
	Resting/Commuting	10%	16%

During incubation, the birds spent more than a quarter of the time exploring. They spent more time resting than foraging and commuting. The nights were equally split between foraging and non-foraging activities. During brood, slightly more than a quarter of the time was spent foraging, followed by commuting, resting and exploring. During night, the birds allocated more time to non-foraging activities.

While investigating the unexpected very high time allocation in resting activities, I realised that the majority of the trips (67.2%) started with a resting segment and more than a quarter (26.6%) also ended with the same behaviour. This was an effect of the interpolation process (see II.2c, page II-29), as the starting and ending point had speeds of 0. As the birds were moving quite fast away and back to the colony, the number of GPS locations was low and therefore the point interpolation process created a series of artificial locations with regular speed variations (Figure V-8). The cluster analysis used the resulting low

median speed and absence of dives for these segments to classify them as resting.

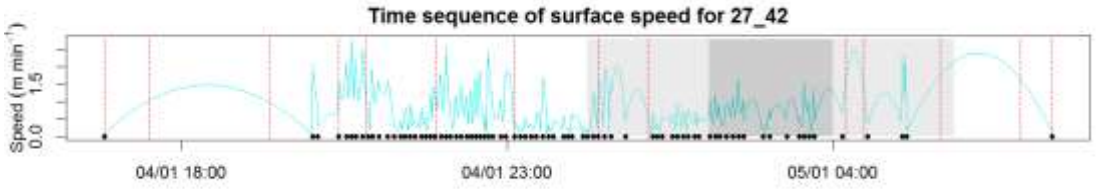

Figure V-8: Example of the influence of the interpolation process on the speed surface metric at the start and end of a foraging trip. The black dots represent the true GPS locations in the time series. The red dashed lines represent the result of the segmentation process. The light and dark grey areas represent respectively the twilight and night periods of the day

Figure V-9 presents the distribution of the different surface and dive metrics for all the 268,909 interpolated locations by behaviour mode and breeding stage. These values confirmed some of the changes along the season observed at the scale of the foraging trips in Chapter IV. The dive depths tended to be deeper during brood for most of the dive related behaviour modes. Day commuting had the highest speed and lowest changes in direction while resting had the lowest velocities. Foraging (day and night) showed the highest relative angles and dive efficiencies. Exploring behaviour was characterised by relatively fast and straight tracks, medium to deep (especially during brood) dives and lower dive efficiencies than during foraging.

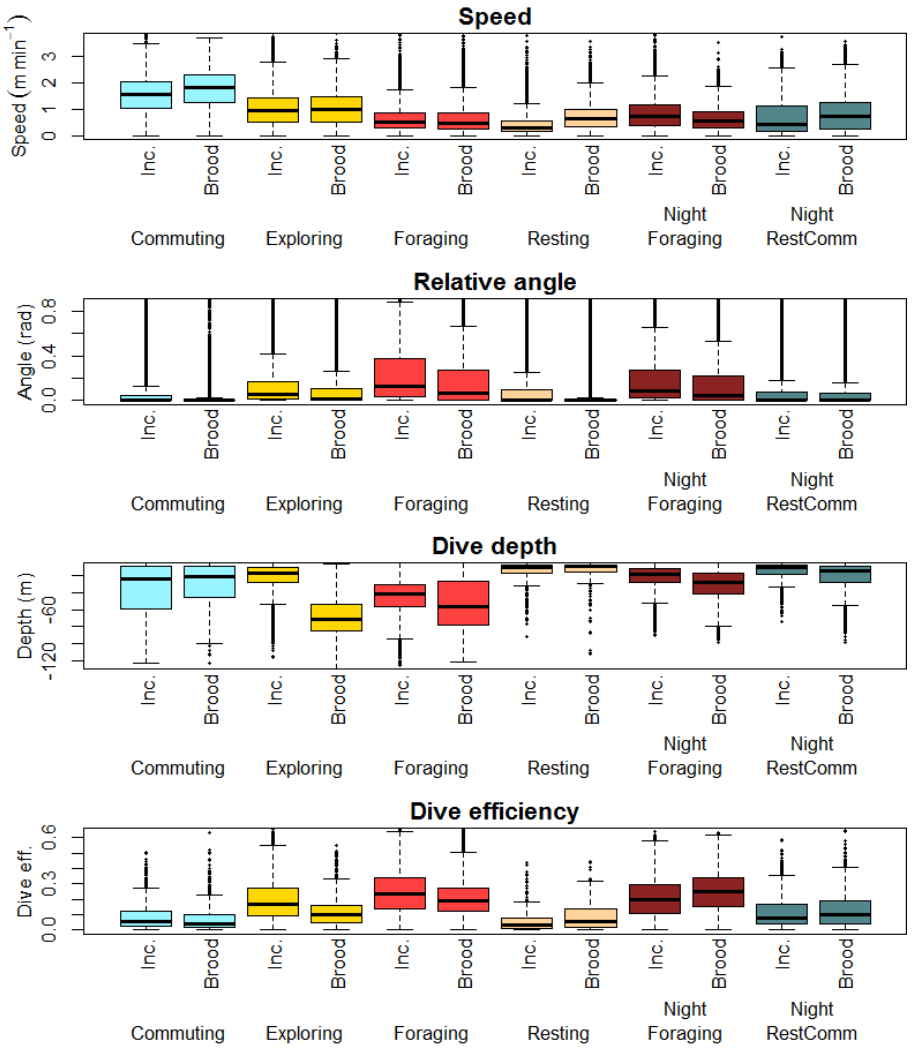

Figure V-9: Distribution of the different surface and dive metrics for the behaviour modes generated by the segment clustering.

An example of a Geddes incubation trip segmentation is presented in Figure V-10, showing both surface and dive metrics as time series, the result of the behaviour classification and a spatial representation of the trip with the location of the different behaviour modes. The first (not visible) and last segments were classified as resting, illustrating the issue with segments with a high number of interpolated positions. This trip included some overnight time and the depth curve clearly shows the regular shift in dive depth as the bird followed the vertical migration of its prey during the dark hours.

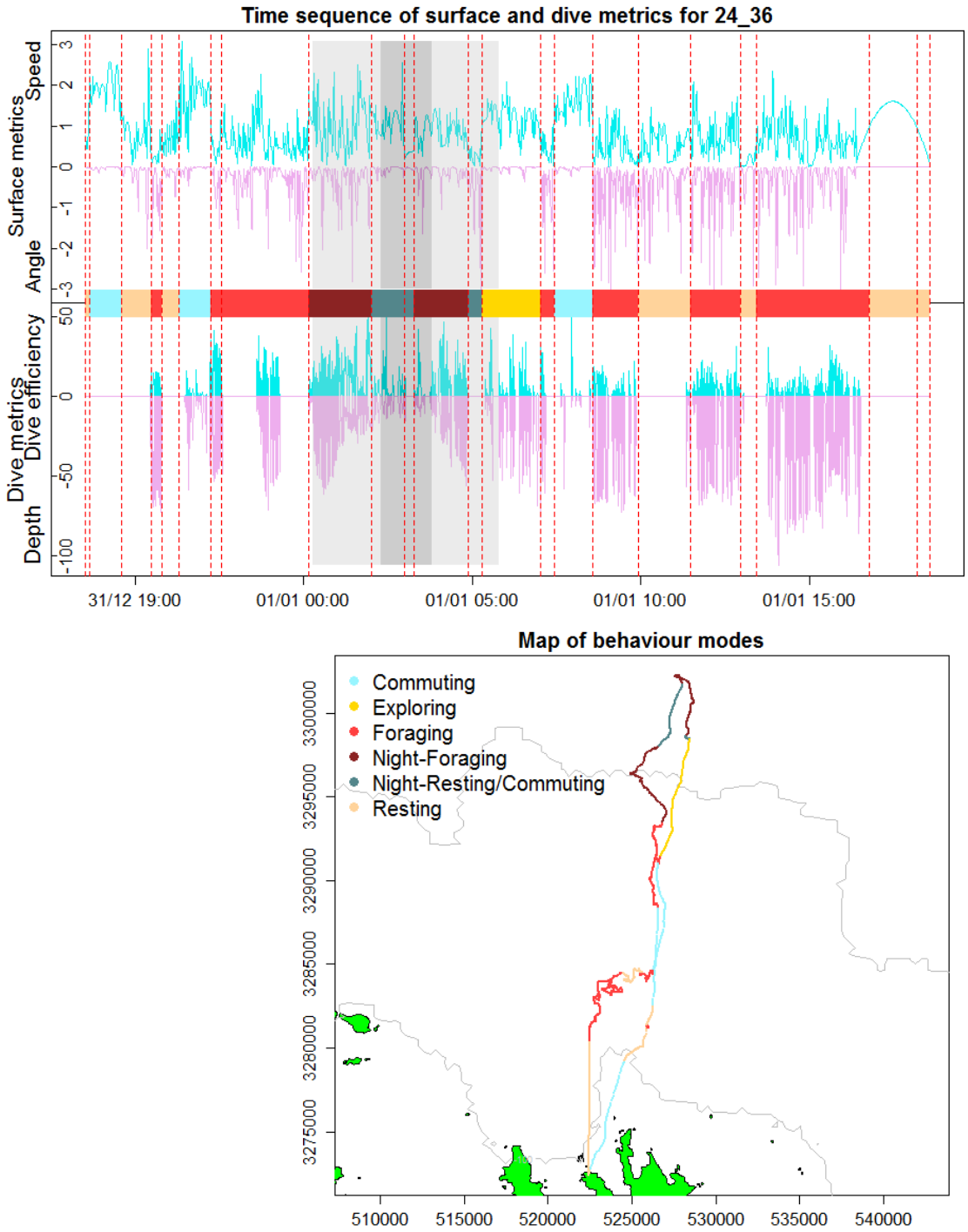

Figure V-10: Example of a trip segmentation with the result of the semi-automated behaviour classification from the segments clustering. The graph on the top show the surface and dive metrics. The red vertical dashed lines represent the segments limits and the shaded areas indicate the twilight and night periods. The regular bell-shaped curve for the speed at the end of the foraging trip (classified here as resting) is an artefact due to the interpolation process (see .Figure V-8). The bottom map shows the spatial distribution of the different segments and behaviour modes along the foraging trips.

Method 2: Expert-based behaviour mode classification

While training the models, the 'out-of-the-bag' (this is a method of measuring the prediction error of random forests, boosted decision trees, and other machine learning models utilizing bootstrap aggregating to sub-sample data into training and test sets) error rate was 18.02%,

indicating a reasonable modelling accuracy. Table V-5 reports the break-down of the classification error by behaviour mode. Foraging and commuting behaviour (for day and night) had the lowest error rates. Resting behaviour had a slightly higher error rate and the behaviour with the highest misclassification rate was exploring, confirming the difficulty to distinguish this behaviour from foraging and commuting.

Table V-5: Classification error when training the random forest on the incubation and brood trip samples.

	Behaviour mode	Classification error
Day	Commuting	15%
	Exploring	34%
	Foraging	13%
	Resting	19%
Night	Foraging	7%
	Resting/Commuting	16%

The ranking of the most contributing variables to the model is presented in Figure V-11. All the variables but one had higher importance scores than the random variable. The period of the day showed high scores, which is reasonable, as it easily allowed to identify a third of the classes (2 out of 6). The percentage of dives was similarly ranked, as it allowed to distinguish between surface (commuting and resting) and dive related behaviours (foraging and exploring). The dive metrics were ranked between the speed and the relative angle, all having comparable contribution to the model. Finally, the position along the trip (as a percentage) had a contribution just above the baseline from the random variable. The moon illumination and the breeding stage had similar or lower contribution to the random variable. This result for the last variable confirmed that the choice of a a single model for both incubation and brood stages was correct.

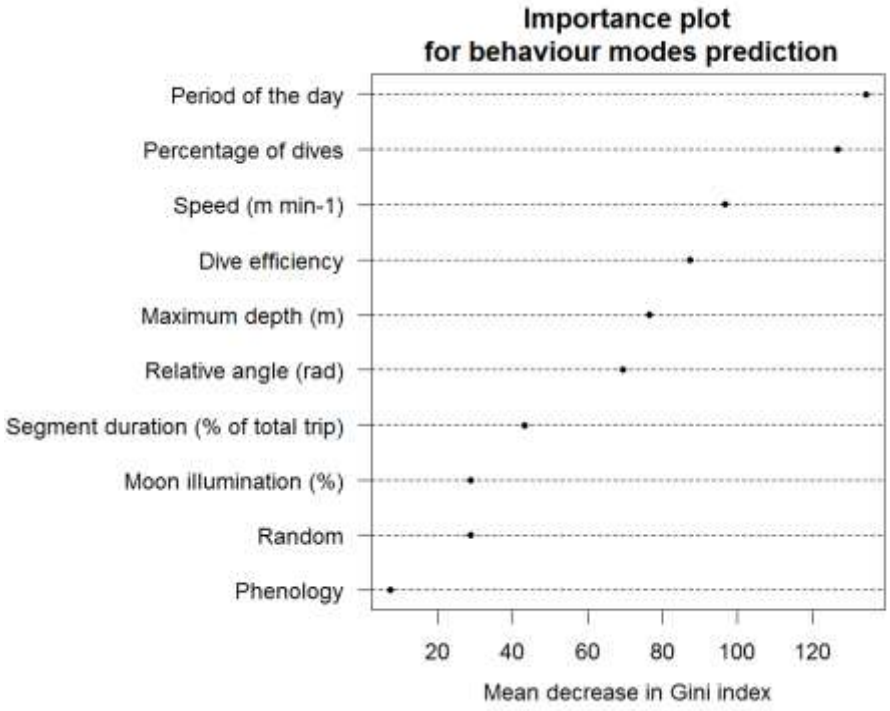

Figure V-11: Importance plots for the variables involved in predicting the segment behaviour modes through the random forest algorithms. The Gini index indicates changes in node purity when the variable is discarded when building each individual tree. Variables with high decrease in this index are important contributor to the model.

The percentage of time at sea spent on each behaviour mode is presented in Table V-6. Similarly to the behaviour modes estimated with the cluster analysis, the two behaviours with the highest time allocations were foraging (27%) and exploring (22%). By decreasing importance, the next activities were commuting (19%), night foraging (14%), resting (9%) and other night activities (9%). The differences between both methods are developed later, but a lower attribution to resting behaviour for this method indicated that it was more performant in distinguishing between resting and commuting. Only 3.1% of the trips had their first or last segments classified as resting which is more realistic.

Table V-6: Percentage of time at sea spent on each activity predicted by the model based on expert behaviour mode classification for each phenological stage.

		Expert based	
	Behaviour mode	Incubation	Brood
Day	Commuting	11%	26%
	Exploring	27%	17%
	Foraging	26%	29%
	Resting	15%	2%
Night	Foraging	13%	16%
	Resting/Commuting	8%	11%

Figure V-12 presents the same trip example as Figure V-10, but with the expert based behaviour mode classification (the results for each trip are presented in Appendix II). The first and last segments were correctly classified as commuting. It also appeared that only segments with very

intense diving activity were classified as foraging (approximatively more than 25 dives per hour).

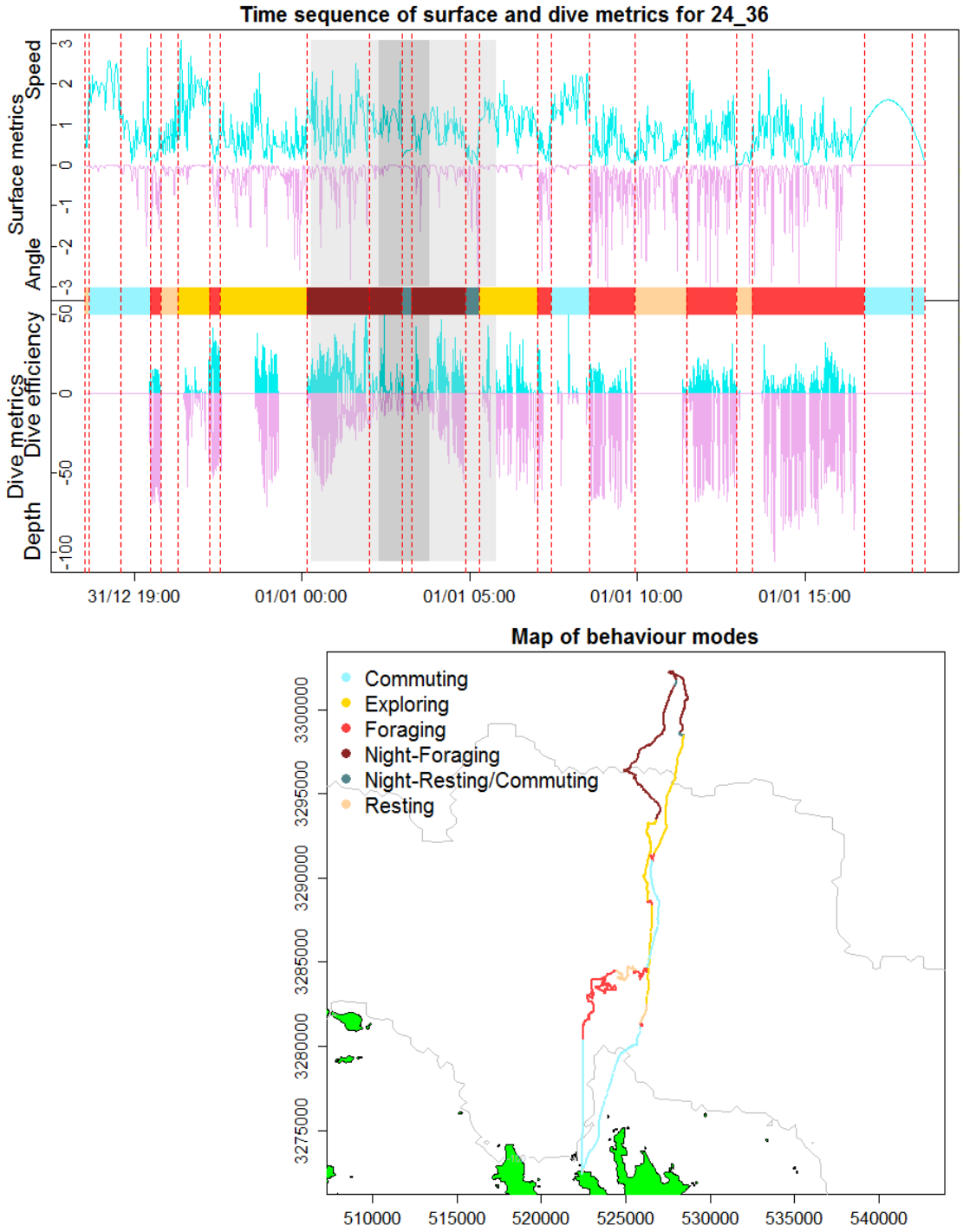

Figure V-12: Example of a trip segmentation with the result of the expert-based behaviour classification. The graph on the top show the surface and dive metrics. The red vertical dashed lines represent the segments limits and the shaded areas indicate the twilight and night periods. The bottom map shows the spatial distribution of the different segments and behaviour modes along the foraging trips.

Comparing both methods

When comparing the behaviour modes for each segment between both methods, there was a global matching rate of 66% of the segments (Table V-7). The behaviour modes with highest matching scores were night and

day foraging. The night non-foraging and day commuting activities were close to the global matching score of 66%. Finally, the exploring and resting modes had the lower match with approximately half of the segments misclassified as commuting or foraging.

Table V-7: Confusion matrix between the behaviour modes from the semi-automatic cluster analysis (rows) and the expert based modelling (columns).

		Expert based						
		Commuting	Exploring	Foraging	Resting	Night Foraging	Night Resting/Commuting	% of matching classification
Automatic	Commuting	**401**	213	12	3	0	0	64%
	Exploring	34	**320**	205	19	0	0	55%
	Foraging	1	57	**509**	0	0	0	90%
	Resting	391	48	3	**315**	0	0	42%
	Night Foraging	0	0	0	0	**285**	2	99%
	Night resting/Commuting	0	0	0	0	95	**248**	72%
% of matching classification		48%	50%	70%	93%	75%	99%	**66%**

When comparing the percentage of activity per trip inferred from both methods (Figure V-13), the night activities showed the highest correlation scores (R^2 of 0.875 for foraging and 0.81 for non-foraging behaviours). Day foraging activities also showed a good match for both methods (46.9% of the trips had the same foraging activity budget); although for 11 trips, the expert based method was able to detect some foraging activity that were not perceived by the first method. On the resting scatterplot, the misclassification of the starting and ending segments of the trips by the first method are clearly visible (48.4% of the trips had some resting activity detected by the first method and none detected by the second method). There was no apparent differences between incubation and brood trips.

In summary, both methods agreed on the classification of the key foraging (day and night) behaviours. The expert based classification was more subjective (although the choice of the number of clusters and their attribution for the first method was also strongly influenced by the operator) but seemed to lead to a more accurate classification of resting and in some cases of foraging behaviours.

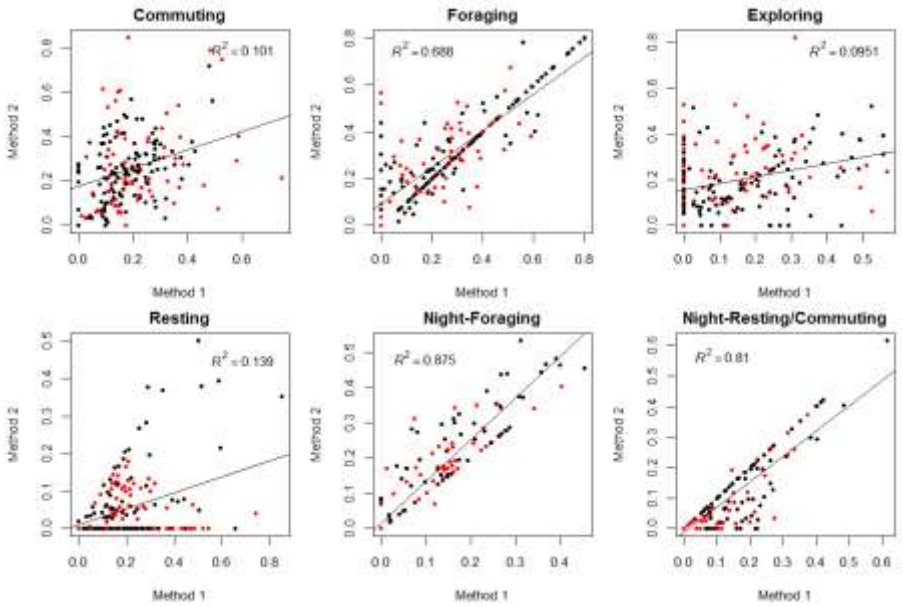

Figure V-13: Relationships between the percentage of time allocated for each behaviour modes detected using both methods. Method 1 is the semi-cutomatic cluster classification of segments as method 2 is the expert-based segments classification. The points are coloured according to the stage of the birds at the start of the trip (black: incubation trips, red: brood trips).

Incomplete dataset (GPS only)

When training individual interpolated position behaviour based on GPS only data, the model inferred from the results of the cluster analysis performed slightly better than the model based on the second method (out of the bag error rate of 3.37% versus 3.58%). The misclassification scores per behaviour were very similar except when predicting the day resting behaviour based on the expert classification method (Table V-8).

Table V-8: Missclassification scores for each behaviour while training the model to predict behavior modes using GPS based data only. Method 1 refers to the activities inferred from the cluster analysis of the different segments. Method 2 is based on the expert classification of a subsample of segments.

	% classification error in prediction	
Observed	Method 1	Method 2
Commuting	4%	3%
Exploring	3%	4%
Foraging	3%	4%
Resting	4%	6%
Night Foraging	3%	2%
Night resting/Commuting	2%	2%

The ranking of the contribution of the variables to the models based on the behaviour modes inferred from both methods were very similar (Figure V-14). Two thirds of the variables showed higher scores than the random variable. The part of the trip and the phenology had similar or lower contribution to the random variable. The absence of influence of the breeding stage on the inferred behaviour based on surface only data is consistent with the modelling of the expert based method (Figure V-11, page V-97). The surface metrics were ranked in the same order (speed was slightly more important than relative angle). The period of the day showed different rankings as it was the most contributing

variable with the percentage of dives for the second method. On the surface only data, it was ranked similarly to the speed. The most surprising difference was the contribution of the moon illumination, ranked as the second strongest variable. In contrast, during the expert based classification, it showed a very weak contribution.

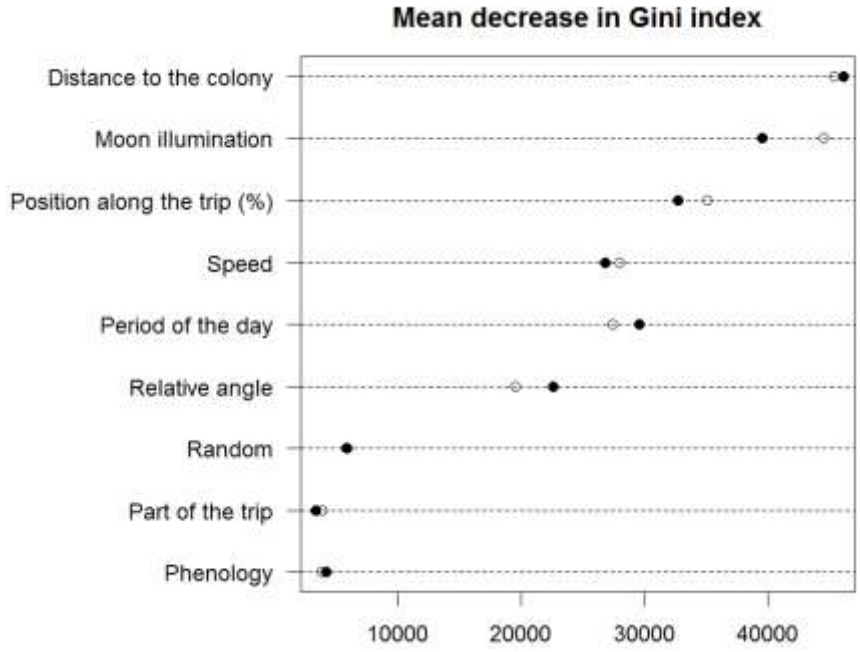

Figure V-14: Importance plot for the variables involved in predicting the behaviour modes for each interpolation locations for the trips without TDR data through the random forest algorithm. The hollowed dots represent the model trained with the behaviour modes from the first method; the solid dots represent the model trained using the results from the second method.

The partial dependency plots on Figure V-15 (the curves presented here are based on the inferred behaviours from the second method) show the likelihood curves for the different behaviour modes in response to the six most contributing variables. With increasing distances to the colony, especially from 30 km, the probability of classification of both day and night foraging augmented as the probability of commuting decreased. Day resting and night non-foraging activities showed a similar pattern with a drop close to the colonies and then an increase to reach a plateau just before 100 km to the nests. Exploring behaviours didn't show any strong variations with this variable.

The moon illumination didn't affect most of the day behaviours (foraging, exploring or resting), which was logical. Just after the new moon phase, the probability of classification of night non foraging behaviours increased until the first quarter when it slowly declined. The night foraging activity showed a reverse trend. Day commuting showed higher probabilities at new moon, half and full moon.

Along the trips, the probability of night behaviour modes was high at the beginning of the trips, which was consistent with the 12% of the trips that started at night or twilight periods (III.2, page III-43). The night foraging probability was high at the start of the trips and then was gradually replaced by non-foraging activities with a peak between 20

and 40% of the trips duration. The final steep likelihood increase in night non-foraging activities reflected the small amount of trips (2%) that ended with a night commute. Day foraging and exploring showed similar patterns with a peak around mid-trip. The commuting curve showed an inverse trend. The trends for these three daylight behaviour modes fitted the pattern of short brood foraging trips with some intense foraging preceded and followed by the commute from and to the colony.

Along the speed gradient, the likelihood of commuting and exploring behaviour showed similar trends with an increase until the velocity of the birds was higher than 2 m s^{-1}. Day and night foraging had also similar pattern with an increase in likelihood from very low speeds to around 1 m s^{-1} for day foraging and 2 m s^{-1} for night foraging. Then the classification probability for these behaviour modes decreased. The likelihood of resting behaviour decreased with increasing speed to then reach a plateau above 2 m s^{-1}. The night non-foraging activity likelihood curve showed high scores in both low and high speeds, indicating a mixture of resting and commuting behaviours.

As expected, the day light period excluded night activities and showed high likelihood of day foraging and exploring modes. As the twilight and night periods of the day seemed to mostly reject commuting and resting activities.

The likelihood curves along the surface relative angles showed most of the variations for very low values, with a strong dichotomy for straight (angle of 0) and non-straight (angle > 0) portions of the trips. The former indicated a high change of commuting and night non foraging activities. And the latter were linked with day and night foraging, resting and exploring behaviours.

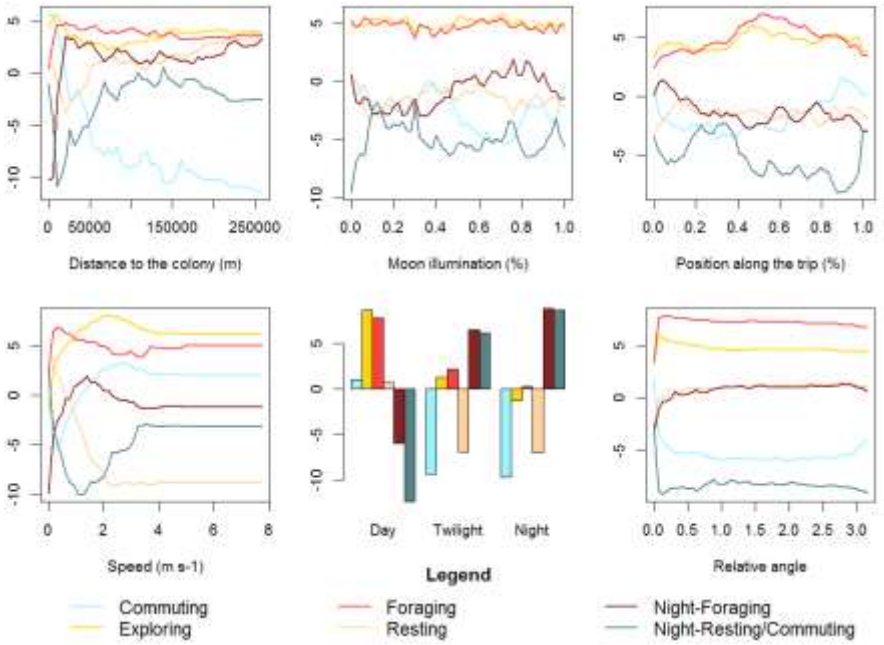

Figure V-15: Partial dependency plots showing the marginal effect of the 6 most contributing variables included in the random forest model to the probability of each behaviour mode (based on the expert based classification). The Y axes represent the logit contribution of each variable to the probablity of the behaviour mode.

Table V-9 compares the global distribution of the percentage of time spent on the different inferred activities on the complete and incomplete dataset. The results from the surface only based model tended to underestimate commuting and day and night foraging activities and overestimate exploring, resting and night non foraging classes.

Table V-9: Comparison of the time allocated to the different behaviour modes between the complete dataset (GPS+TDR, both methods) and the predicted modes on the incomplete dataset (GPS only) using the results from both classfication methods while training the model.

	Complete dataset		Incomplete dataset (surface only) based on	
Activity	Method 1	Method 2	Method 1	Method 2
Commuting	15%	16%	7%	7%
Exploring	23%	24%	36%	32%
Foraging	21%	27%	12%	19%
Resting	19%	11%	24%	20%
Night Foraging	10%	14%	7%	9%
Night resting/Commuting	12%	9%	14%	13%

c. Changes in the behaviour modes over the season and comparison between sites and putative sexes

The summary data presented here only cover the trips with complete dataset (GPS and TDR), as the inferred behaviour modes from surface only metrics should be considered with caution. Figure V-16 shows the percentage of time the birds spent doing each behaviour activity with a

break down by phenological stages and sites. It also compares the results from both methods.

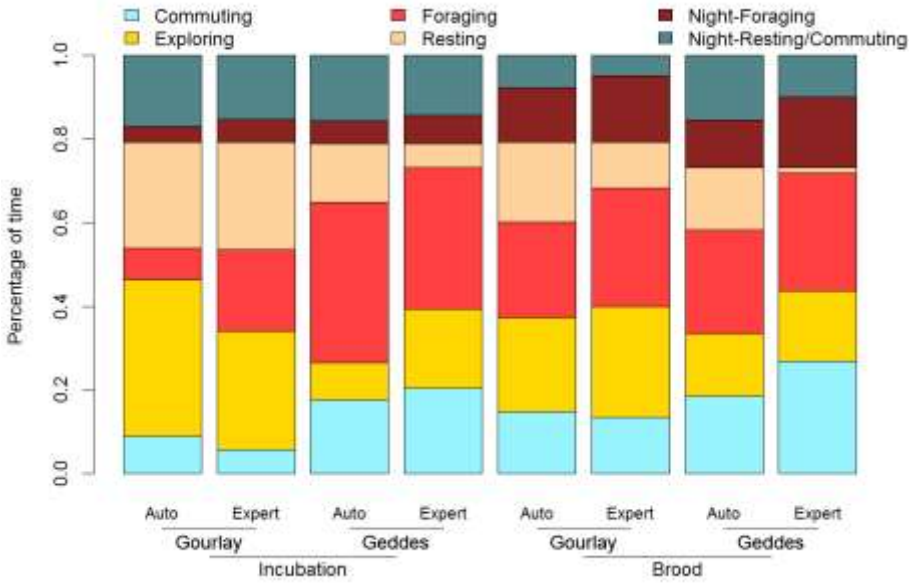

Figure V-16: Percentage of time spent for each behaviour modes with a comparison between breeding stages, sites and between the results from both methods (automatic clustering versus expert-based classification).

Figure V-17 maps the different inferred behaviour modes from the expert based classification method along incubation and brood trips. Changes along the season and differences between sites are discussed below. The spatial distribution of foraging is studied in Chapter VI.

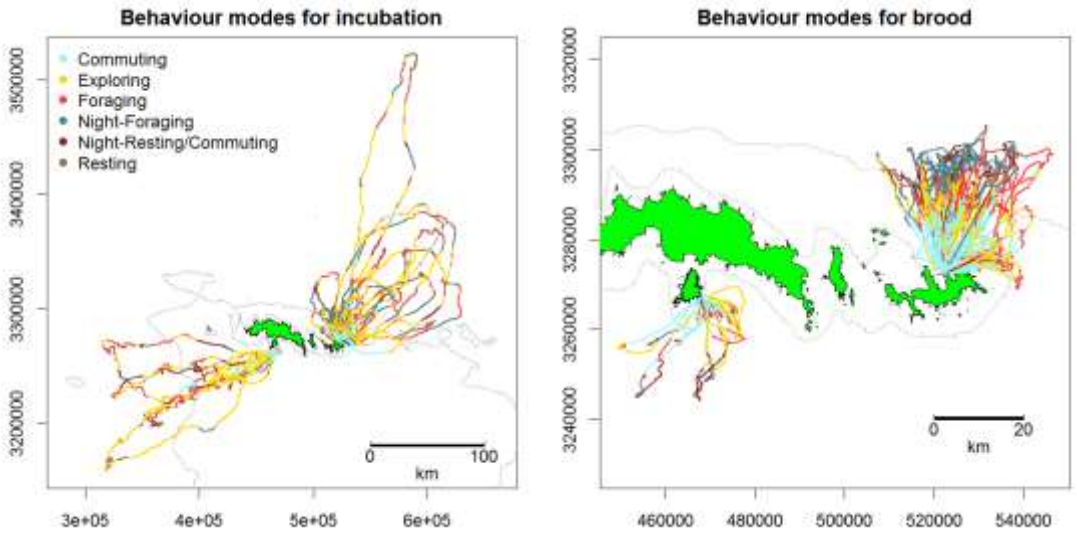

Figure V-17: Maps showing the spatial distribution of the different behaviour modes (expert based method only) for incubation (left) and brood (right) trips.

Comparison between stages including the site effect

The changes in time spent on each behaviour mode along the breeding season were tested through a linear mixed effect model. The colony site was incorporated as a random effect. Table V-10 summarises the coefficients and probability values for the fixed (phenology) and random

(site) effects for the results from both methods. Figure V-18 graphically represents the changes of the inferred activities from the expert based classification only between incubation and brood with the modelled trend per colony site.

The amount of commuting activity did not change significantly along the season with no significant site effect. The amount of time spent exploring decreased from incubation to brood, although this trend was not significant for the first method. The amount of foraging activity significantly increased during brood similarly across both sites. Resting activity significantly decreased during brood, especially for trips from the Gourlay Peninsula for the second method classification. All night activities significantly increased after hatching. The intensification of night foraging was more pronounced on the trips from Cape Geddes. And the increase of non-foraging night activities was more important for the trips from the Gourlay Peninsula.

Table V-10: Coefficients and p values for the linear mixed models assessing the changes between incubation and brood (fixed term) by colony sites (random term) for the different behaviour modes results from both classification methods.

		Method 1 (cluster)			Method 2 (expert based)		
		Fixed term		Random term	Fixed term		Random term
	Behaviour mode	Coefficient	p value	p value	Coefficient	p value	p value
Day	Commuting	-0.034	0.060	1.000	0.033	0.154	0.401
	Exploring	-0.008	0.734	1.000	-0.077	<0.001	1.000
	Foraging	0.076	0.009	1.000	0.056	0.039	1.000
	Resting	-0.084	<0.001	1.000	-0.066	<0.001	<0.001
Night	Foraging	0.038	0.056	-	0.066	0.002	<0.001
	Resting/Commuting	0.105	<0.001	0.024	0.077	0.001	0.012

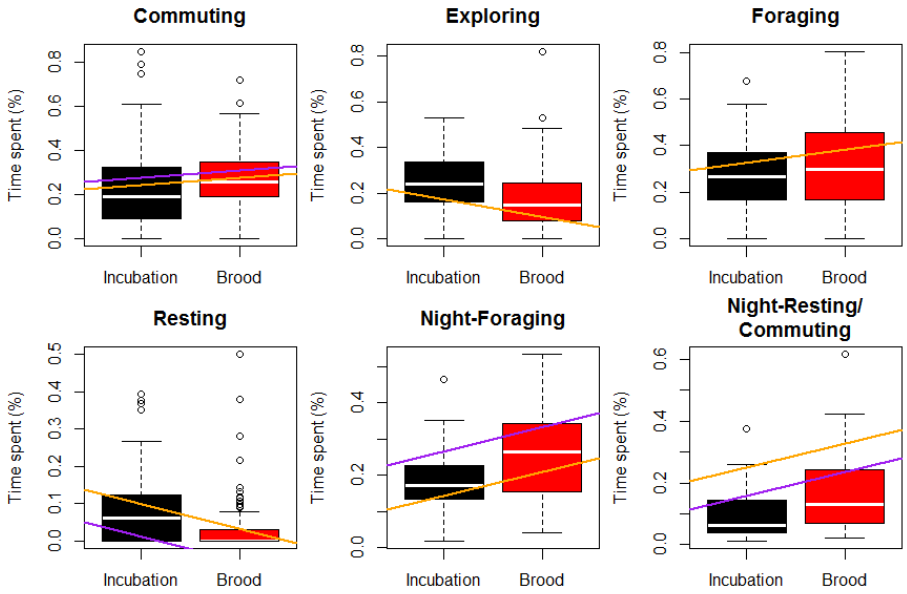

Figure V-18: Distribution of the time allocation for the different behaviour modes between incubation (black) and brood (red) with the trend by colony site (orange: Gourlay, violet: Geddes) estimated by the linear mixed model.

Comparison between putative sexes

When using a similar method to assess any differences in behaviour modes allocation between males and females, none of the activities showed any significant differences between putative sexes inferred from both methods used in this research (II.1g, page II-21).

V.4 Discussion of the results, limitations and implications for the habitat modelling

The results of the segmentation process and both behaviour mode classifications will be discussed, compared and assessed through other results from other similar studies. Temporal changes and differences between sites and putative sexes in the different activities budgets will be commented and compared with the results from Chapter IV. Finally, I will describe the difficulty in validating the results from this chapter and what are the implications for the next chapters leading to the final foraging habitat model.

a. Segmentation and behaviour modes

Methodological choice

Numerous studies tried to detect changes in behaviour based on data acquired through bio-logging devices, especially for diving marine predators. Differences in the metrics recorded by the devices (surface only, dive only or a combination of both), the complexity of the dataset and the various experiences of the practitioners lead to different approaches. This absence of consensus on a methodological framework resulted in the use of a variety of tools and techniques focusing either on spatial metrics, temporal changes or mechanistic models (Gurarie et al., 2016).

When using methods only focusing on surface trajectories, like the area restricted search, it is difficult to discern resting and foraging behaviours because of their horizontal characteristics (low speed and high sinuosity, as mentioned by Sommerfeld et al., 2013, for Masked Boobies, *Sula dactylatra*; see also Carter et al., 2016). Mechanistic models are more complex and necessitate high parameterisation, assumptions or additional devices to actively detect feeding. Ultimately, Gurarie et al. (2016) stressed that the choice of the method should be driven by the research question(s). In this chapter, I intended to detect changes in behaviours along the foraging trips, in order to identify foraging activities whose locations will be used in the final habitat model (Chapter VII).

The method chosen in this study was a time series data segmentation which is recognised as an important step in animal movement analysis (Shamoun-Baranes et al., 2012). One of the main advantage of this method was to explicitly include autocorrelation, which is a key issue for modern high resolution tracking data (Gurarie et al., 2016). Furthermore, this technique allowed me to integrate both horizontal (surface metrics) and vertical (dive metrics) dimensions to detect changes in behaviour (Dragon et al., 2012). Vacquié-Garcia et al. (2015) demonstrated that in elephant seals, dive parameters are 4 times more performant in predicting prey capture than surface parameters only.

Parameterisation and validation

The parameters required by the time-series segmentation process were validated through a sensitivity analysis of the different options required by the method. The results were visually checked and the fact that the segments matched diel changes which are key biological moments (changes in prey distribution and therefore foraging patterns, see Wilson, 1993; Jansen et al., 1998 and Watanuki et al., 2010) was very encouraging. Furthermore, the cluster analysis (method 1) allowed to split the multimodal distribution of dive depths. In addition to the night dives, shallow dives during the early or late parts of the day were differentiated from deep midday dives; although they were all associated with foraging activities. The identification of the different foraging depths matching the hourly variations in prey vertical distribution represented an important validation of the process. It also confirmed that changes in small temporal scales which are biologically relevant were detected.

Using two different methodologies to identify behaviour modes (an unsupervised cluster analysis and a supervised expert based classification) allowed to cross validate the inferred behaviours. The cluster analysis was performed separately for incubation and brood trip segments, as Chapter IV underlined important changes after hatching. But the convergence in the behaviour modes detected for both breeding stages (5 daylight and 2 night activities) confirmed similar patterns in the clustering of surface and dive metrics. The high matching scores, especially when distinguishing foraging and non-foraging behaviours (88% of segments matched between both methods) which will represent

a crucial input for the habitat models (Chapter VI and Chapter VII), allowed to validate the process.

Behaviour modes

Apart from the classical foraging/commuting distinction, my method allowed to identify additional behaviour modes (day exploring and resting). Surface resting segments can have very similar track metrics to foraging bouts (low speed and relatively high sinuosity) but incorporating dive data allowed me to separate these two modes. The distinction between exploratory dives and proper feeding dives was more difficult. Several studies on different diving predators used dive shapes (V shape versus U shape, Williams et al. 1992; Wilson 1993; Wilson et al. 1996; Takahashi et al. 2003; Watanuki et al. 2010; Mattern 2001; Ainley & Ballard 2012; Cook et al. 2012; Gallon et al. 2013; Sommerfeld et al. 2013; Ford et al. 2014; Carter et al. 2016). In this study, exploratory modes were detected through a combination of surface (higher speed and lower angles than foraging) and dive (shallower dives and lower dive efficiencies) metrics. For Southern Seals, Dragon et al. (2012) characterised exploratory dives by having lower descent speeds. From my results, both the descent and ascent median speeds from foraging dives were approximately twice as fast as from exploratory dives (1.58 m s^{-1} versus 0.85 m s^{-1} for descent speeds and 1.36 m s^{-1} versus 0.66 m s^{-1} for ascent speeds, both from the expert based classification).

There are very few studies trying to quantify different activities at sea for penguins. Using radiotelemetry to study at sea daylight foraging behaviour of chick rearing chinstrap penguins, Trivelpiece et al. (1986) found that the birds spent 38% of the foraging trip travelling (porpoising and underwater travelling), which is very similar to my findings (35%). They classified 14% of the trips as “horizontal diving”, which combined long and short dives with important travel distances. This mode was hypothesised as a prey searching mode and had slightly lower time allocation than my exploring mode (23%). The feeding dives accounted for 45% of the foraging trips, slightly higher than the 37% measured in this study. And finally, the surface resting represented 3% of the trip duration for both studies (all activity ratio reported here were extracted from the expert mode classification and diurnal only trips). Despite a very different method based on data acquired through different technologies, the time budget allocation were surprisingly similar. On King George Island, Wilson & Peters (1999) recorded 18% of V shaped dives, which is slightly lower than the 26% and 33% of dives within exploratory segments classified by this study for methods 1 and 2 respectively. But the same authors didn’t find any difference in depths or vertical and horizontal speeds between V and U shaped dives.

Although both behaviour classification methods showed similar results (except the over-estimation of resting behaviour for the clustering classification) and some metrics and allocation budgets corresponded to the results from previous studies, there were unfortunately no solution

to “ground truth” this behaviour mode classification and fully validate the results from one or the other method (see V.4d below).

b. Temporal changes of the foraging

The increase of the day and night foraging activities and decrease of surface resting behaviour after hatching confirmed the results from Chapter IV showing an intensification of foraging both during the day and during the night to feed the chicks.

The absence of a clear change in commuting allocation between incubation and brood was counter-intuitive, as birds had to cover larger areas during the long incubation trips. It is possible that incubation exploring mode could be a mixture between commuting and some opportunistic feeding. This could indicate a more or less continuous foraging as observed by Ford et al. (2014) for Adélie penguins in the Ross Sea. This loose continuous foraging, which is different than the intense diving activities classified as foraging mode, showed a significant decrease after hatching. It confirms that brood foraging is more intense and during that period, the birds probably try to locate and feed on dense krill swarms.

c. Differences between sites

There were no significant site effects in the time allocation of the commuting, exploring and foraging between incubation and brood. Geddes showed a higher night foraging activity baseline, which was similar to the results from Chapter IV discussed previously (see IV.4b, page IV-75). The higher non-foraging activity baseline in Gourlay is just the reverse of the previous statement.

More surface resting activity in Gourlay during incubation could be due to the higher probability of having important sea ice-cover south of the archipelago at that time of the year. Adélie penguins showed differences in foraging behaviour between colonies in relation to sea-ice cover (Watanuki et al., 1997). Although chinstrap penguins tend to avoid sea-ice (Lynnes, Reid and Croxall, 2004), icebergs and growlers can represent a good place to rest and a refuge from predators as observed for Emperor penguins (Watanabe, Sato and Ponganis, 2012).

The absence of a clear difference on foraging effort between sites again confirmed the results from Chapter IV and represented an encouraging step towards the interpolation of the habitat model from these two sites to the whole South Orkney archipelago.

d. Limitations and uncertainties

Scales

The segmentation process was in line with the spatial and temporal uncertainties of the location data (see V.2b, page V-82). The median segment duration was just above an hour with a long tail in the distribution of the values towards few very long segments (up to 14.3

hours). Apart from some extremely long segments, this temporal scale was compatible with changes along the day, especially in regards to the vertical distribution of the prey as discussed earlier.

The spatial scale of inferred behaviour will be discussed in the next chapter, but was significantly higher than the location uncertainties (99% of the segments were above the 250 m threshold). This will allow an accurate positioning of the foraging behaviour (Bestley et al., 2014).

Missing TDR

Trying to infer behaviour modes for the trips with surface only data added a layer of uncertainties (Benson, 2016; Carter et al., 2016). The predictive models showed good performances and most of the contribution from the variables were meaningful and compatible with previous results. The surprising important contribution from the moon illumination conditions (second most contributing variable), with more night foraging likelihood from half-moon, indicated that penguins as visual predators rely on some light levels to locate preys (Cannell and Cullen, 1998; Bost et al., 2002). However, as this variable was not contributing to the expert-based classification of the complete GPS+TDR dataset, this result and interpretation should be considered with caution.

When comparing the time allocation for all behaviours between the complete trips and the GPS only trips; the behaviour based on the first method showed no significant differences for all day activities as the modes based on the second method showed differences in exploring and both day and night foraging. This could be due to the imbalance between phenological stages between both datasets: they were more incubation trips with missing TDR (16.8% versus 9.9% of the brood trips) as the training model included more brood trips (61.5% versus 38.5% of incubation trips).

As there are no solutions to validate the behaviour modes for the incomplete dataset, the use of the resulting identified foraging locations for the habitat model will tested separately in Chapter VII.

Behaviour modes validation

Inferring behaviour modes and foraging activities in particular without additional proof of prey handling and/or capture didn't allow me to assess the performances of the different methods and to properly validate my findings (Viviant, Monestiez and Guinet, 2014; Wilmers et al., 2015; Carter et al., 2016). Several studies used various additional "ground truthing" devices to detect prey capture as accelerometers (Yoda et al., 1999; Kokubun et al., 2011; Gallon et al., 2013; Viviant, Monestiez and Guinet, 2014) sometimes in combination with video cameras (Watanabe and Takahashi, 2013; Watanabe, Ito and Takahashi, 2014) or ingestion sensors (Wilson and Peters, 1999; Ropert-Coudert et al., 2000; Charrassin et al., 2001; Bost et al., 2007; Hanuise et al., 2010) or devices recording beak openings (Takahashi et al., 2004). For Charrassin et al. (2001), changes in oesophageal temperature confirmed that dives with

little time at the bottom as being non feeding dives (see also Gallon et al. 2013). Takahashi et al. (2004) reported similar trends using beak opening rates. My results showed that bottom times were marginally shorter during dives from exploring segments against dives from foraging segments. Hanuise et al. (2010) found a good correlation between wiggles at the bottom of the dives and prey ingestion, but stated that vertical undulations only were not a good enough proxy. The vertical distances at the bottom of the dives were slightly higher for dives included in the foraging segments than dives included in the exploratory segments.

Although the absence of a validation process did not allow me to confirm the behaviour modes classification or to compare to performance of both methods, some observed trends were similar to the findings of previous studies about diving predators. Even if some uncertainties remain in the attribution of behaviour modes, especially for the exploring segments, I feel confident about using the locations of the foraging modes detected by both methods as inputs for the spatial analyses (Chapter VI) and habitat models (Chapter VII).

e. Summary

The segmentation process allowed me to use a combination of surface and dive metrics to detect change points along the foraging trips. Two classification methods were used to infer different foraging and non-foraging activities both during the day and night segments. Although the first method only required minimal operator inputs, which is in line with the heuristic approach for this study, the second method based on a manual classification of a sample of foraging segments seemed to perform better.

The inferred behaviour for the 192 foraging trips with complete (GPS and TDR) data were used to train a model to predict the behaviour changes for the 28 foraging trips with no TDR data based on surface metrics only.

While the results from this chapter were in agreement with previous chapters and results from other similar studies, there were unfortunately no additional data collected to validate the results. Therefore, four different sets of results (method 1 and 2, with or without incomplete trips) will be used in the following two chapters leading respectively to a spatial analysis of the foraging location and the final habitat model.

Chapter VI SPATIAL DISTRIBUTION OF THE FORAGING AT DIFFERENT SCALES

This chapter maps the different data input generated from the previous chapters in order to identify the main locations targeted by the birds. Changes through the course of the breeding season and differences between both colonies are considered. The vertical dimension is also included. Identifying the spatial distribution and temporal changes of foraging hot spots provides important information as a preparation for the final habitat modelling (Chapter VII).

VI.1 Introduction and aims

In the previous chapters, the raw data were processed to generate several types of potential input for the final chapter on foraging habitat models (Chapter VII). In Chapter II, the raw GPS data were filtered to remove probable position errors. In the same chapter, the foraging trips were temporally and spatially interpolated to build 1 minute resolution tracks allowing me to link and therefore locate the dive events recorded by the TDR devices. In Chapter V, two methods were used to infer the bird's behaviour and separate foraging and none-foraging dives and their locations. All these different data inputs are characterised by varying spatial and temporal resolutions.

Several changes over the course of the breeding season were reported in Chapter IV; some of them (trip duration and range) will have a direct impact on the spatial location of foraging. Chapter IV and Chapter V also identified fluctuations in diving behaviour and changes between day and night.

This chapter will now study how these variations across different time scales (breeding season and day/night) might impact the spatial distribution of foraging and habitat use. As with the previous chapters, any temporal and spatial changes in foraging will be compared between colony sites to estimate how trends might be site specific (Miller et al., 2010), or transposable to other colonies.

Several methods exist to process location data and aggregate them to identify core foraging areas. Each method has its limitations, strengths and weaknesses. In this chapter, I will use a range of methods to 1) compare different data inputs and their aggregation at different scales, 2) calculate the time spent per area, 3) locate and measure the core foraging areas, and finally 4) include dive depths to consider the foraging zones as volumes.

Aggregation at different spatial scales

Marine predator foraging is influenced by spatial and temporal scales (Hunt et al., 1999; Wakefield, Phillips and Matthiopoulos, 2009). Macro scales (> 100 km) can be relevant during incubation when birds try to reach fronts (Bost et al., 2009; Scheffer, Bost and Trathan, 2012) but are less relevant during brood when they are constrained by the proximity

to their nest (Ichii et al., 2007; Blanchet et al., 2013). Meso-scales (10 to 100 km) are important as the birds will use oceanographic features (shelf slopes, canyons or seamounts) and variations in environmental variables to determine areas where prey availability can be predicted (Davoren, Montevecchi and Anderson, 2003; Pinaud and Weimerskirch, 2005; Trathan et al., 2008; Kokubun et al., 2015). At these scales, currents, fronts and eddies will concentrate nutrients and/or prey, enhancing productivity (Hunt et al., 1999). At finer scales (< 10 km) changes in foraging patterns can reflect encounters with patchy prey swarms whose locations are more difficult to predict at small scales (Becker and Beissinger, 2003; Wakefield, Phillips and Matthiopoulos, 2009; Dragon et al., 2012; Ford et al., 2014). The average Antarctic krill swarm sizes recorded by Macaulay et al. (1984) are within this fine spatial scale.

The spatial distribution of the different levels of data will be compared and aggregated at different spatial scales. This will allow me to estimate how comparable the resulting estimated areas from different datasets might be. As technologies develop (additional devices collecting more variables or dimensions, higher resolution), it is important to evaluate whether comparison with historical data with coarser resolutions and/or incomplete data is possible (Ratcliffe and Trathan, 2012; Warwick-Evans et al., 2015). It will also allow me to assess how varying spatial resolutions impact the representation of foraging areas which will provide important insights for the final habitat modelling as environmental variables have different spatial resolutions.

Time in areas

The time spent in fixed areas of one square kilometre is an easy to calculate metric (Page et al., 2006; Soanes et al., 2013) and provides useful information about habitat use and how it varies between incubation and brood for each colony site. Although in marine environment, angular units are usually used (e.g. Lynnes et al. 2002 used 0.1º x 0.1º grids), I am using projected metric units to make sure the grid square have equal areas over the whole study site. One square kilometre is a convenient measure and the size of the grid is not that crucial, as I am more interested in relative values rather than absolute values to compare breeding stages and colony sites.

Foraging areas

Identifying core foraging areas or “hot spots” where resources and predators are aggregated is a key issue for conservation in general and marine spatial planning in particular (Nur et al., 2011; Tancell et al., 2013; Boyd et al., 2015). From the different data input, I will use two methods (minimal convex polygons and kernel analysis) to delineate the core areas used by birds from both colonies. The size and shape of these areas will be described and compared across sites and between incubation and brood.

Foraging volumes

Finally, incorporating dive depths will allow me to consider foraging habitat as a volume. Considering how predators exploit their habitats through the vertical dimension is very important, especially for diving species (Lescroël et al., 2010; Wilson, 2010; Carter et al., 2016). The previous chapters (Chapter IV and Chapter V) highlighted some differences in the way that tracked individuals exploited the water column through various temporal scales (differences between day and night and between incubation and brood) and also between colonies. A model will be developed to assess how dive depths vary with different variables including the horizontal use of the habitat and the distance to the colony.

I predict that the spatial distribution of the different data inputs will reveal some pattern in the way birds exploit their potential habitats. These results will confirm some findings from the previous chapters and prepare inputs for an extrapolated foraging habitat model for the whole archipelago.

VI.2 Method

a. Different levels of input

GPS points (1)

The filtered GPS locations (see II.2a) represent the common starting point for most similar studies based on tracking devices. This dataset was therefore considered as the reference data input. It contained 45,780 points from 192 trips with complete datasets (GPS+TDR) and 28 trips with only GPS data. Figure VI-1 maps all the GPS locations from both sites during incubation and brood with an indication of the locations recorded at night (18.2% of points for incubation and 26.9% for brood).

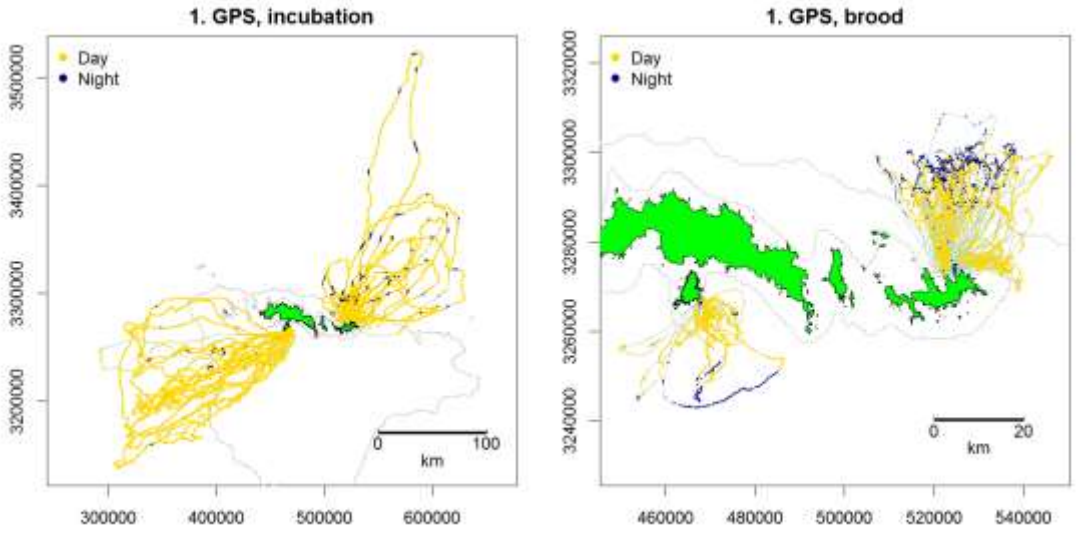

Figure VI-1: Spatial distribution of the GPS location (data input 1) recorded from the Gourlay Peninsula and Cape Geddes during incubation (left) and brood (right) with an indication of the period of the day.

Dives locations (2)

The TDR data available for 192 trips were temporally matched with the one minute interpolated foraging tracks (see II.2c) allowed me to locate dive events (with dives deeper than 5 m, see II.2b). Figure VI-2 maps the 66,045 dives from the complete foraging trips from both sites during incubation and brood with a distinction between diurnal and nocturnal dives (24.8% of all dives for incubation and 38.9% for brood were nocturnal).

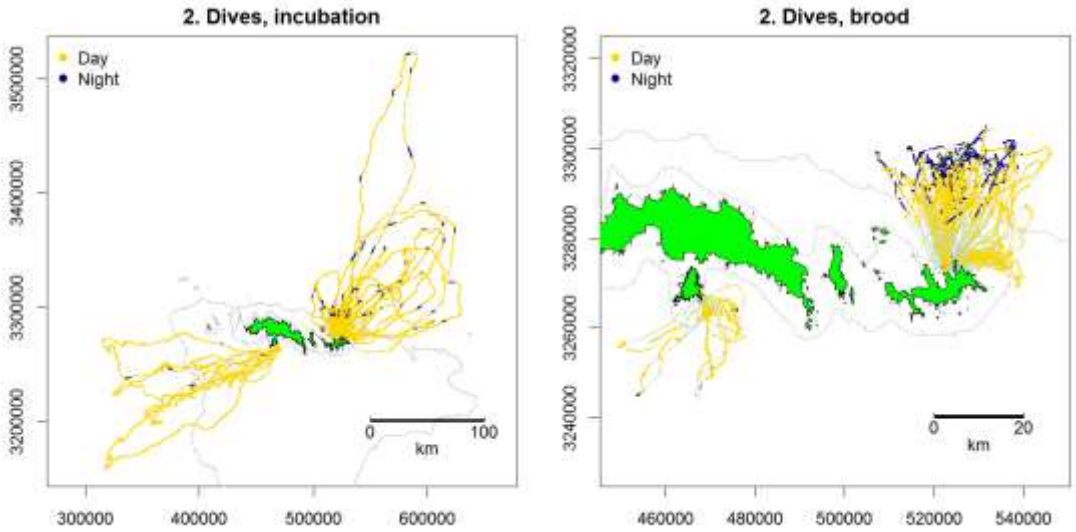

Figure VI-2: Spatial distribution of the dives deeper than 5 m (data input 2) recorded from the Gourlay Peninsula and Cape Geddes during incubation (left) and brood (right) with an indication of the period of the day.

Foraging modes: method 1, only complete data (3a)

The segmentation process and the different subsequent behavioural mode classifications used in Chapter V allowed me to identify the potential foraging parts of the trips. Figure VI-3 maps the 83,740 1 minute interpolation locations that were classified as foraging using the

semi-automatic clustering (Method 1, see V.2c, page V-84) for the 192 complete trips (GPS+TDR) from both sites during incubation and brood with a distinction between diurnal and nocturnal locations (32.5% of all points for incubation and 30.5% for brood).

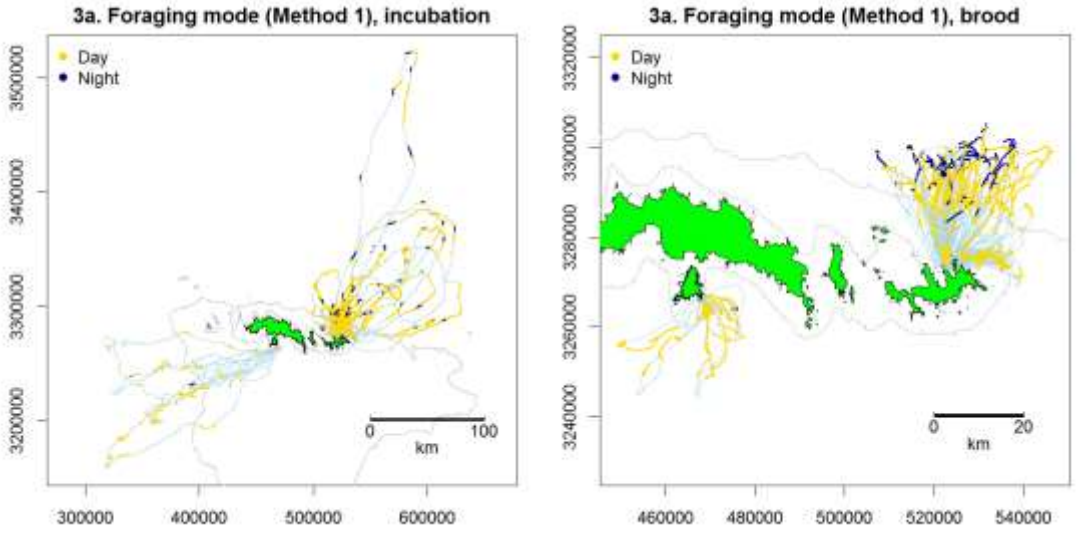

Figure VI-3: Spatial distribution of the inferred foraging modes based on the semi-automatic clustering (Method 1) from complete trips only (data input 3a) acquired from the Gourlay Peninsula and Cape Geddes during incubation (left) and brood (right) with an indication of the period of the day.

Foraging modes: Method 1, including trips with missing TDR (3b)

Figure VI-4 maps the same data input as the previous section (3a) but including the 28 trips without TDR data. The behavioural modes for these trips were inferred from a mix of surface only variables and different temporal variables (see V.2c) using the behaviour modes from the semi-automatic clustering (Method 1) as a training set. The 106,976 inferred foraging locations from both sites during incubation and brood are mapped with a distinction between diurnal and nocturnal locations (34.2% of all points for incubation and 29.2% for brood).

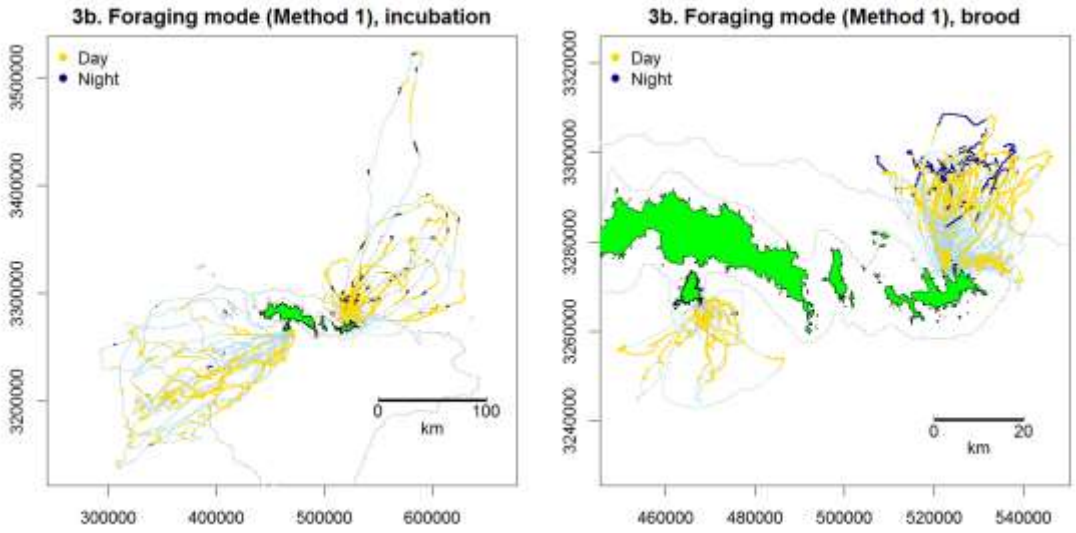

Figure VI-4 Spatial distribution of the inferred foraging modes based on the semi-automatic clustering (Method 1) from complete and trips with missing TDR data (data input 3b) acquired from the Gourlay Peninsula and Cape Geddes during incubation (left) and brood (right) with an indication of the period of the day.

Foraging modes: Method 2, only complete data (4a)

Figure VI-5 maps the 1 minute interpolated locations that were part of segments classified as foraging by the expert based classification technique (Method 2) for the 192 trips with complete dataset (GPS+TDR). The 108,102 inferred foraging locations from both sites during incubation and brood are mapped with a distinction between diurnal and nocturnal locations (31.0% of all points for incubation and 36.0% for brood).

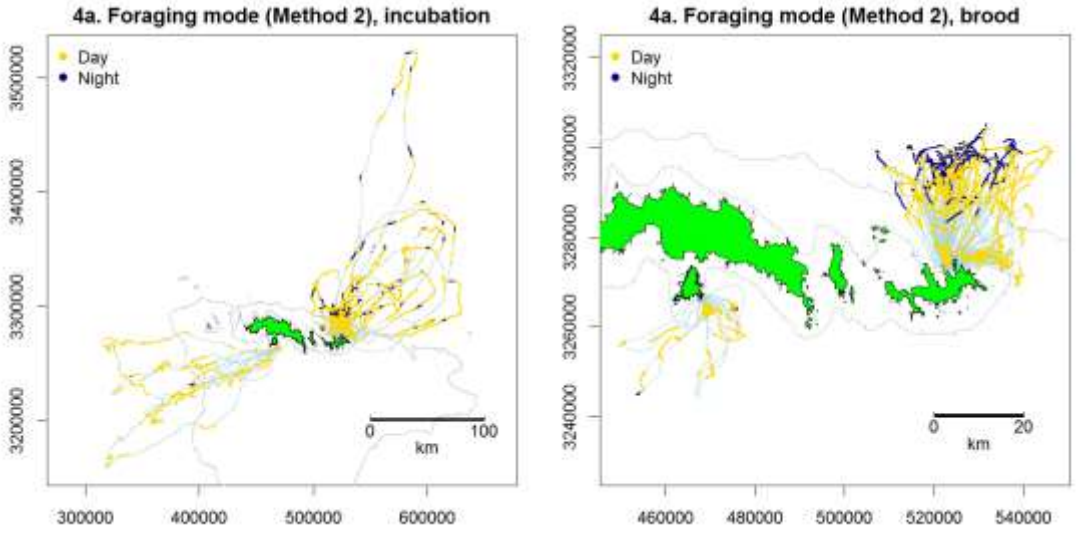

Figure VI-5 Spatial distribution of the inferred foraging modes based on the expert based classification (Method 2) from complete trips only (data input 4a) acquired from the Gourlay Peninsula and Cape Geddes during incubation (left) and brood (right) with an indication of the period of the day.

Foraging modes: Method 2, including trips with missing TDR (4b)

Finally, Figure VI-6 represents the same locations as the previous data inputs (Method 2 to identify foraging segments for the 192 trips with complete data). In addition, this dataset also includes the 28 incomplete

foraging trips (missing TDR) where the foraging behaviour modes where inferred based on various surface and temporal variables using the behaviour modes identified from Method 2 as a training set. The 142,727 inferred foraging locations from both sites during incubation and brood are mapped with a distinction between diurnal and nocturnal locations (31.3% of all points for incubation and 35.9% for brood).

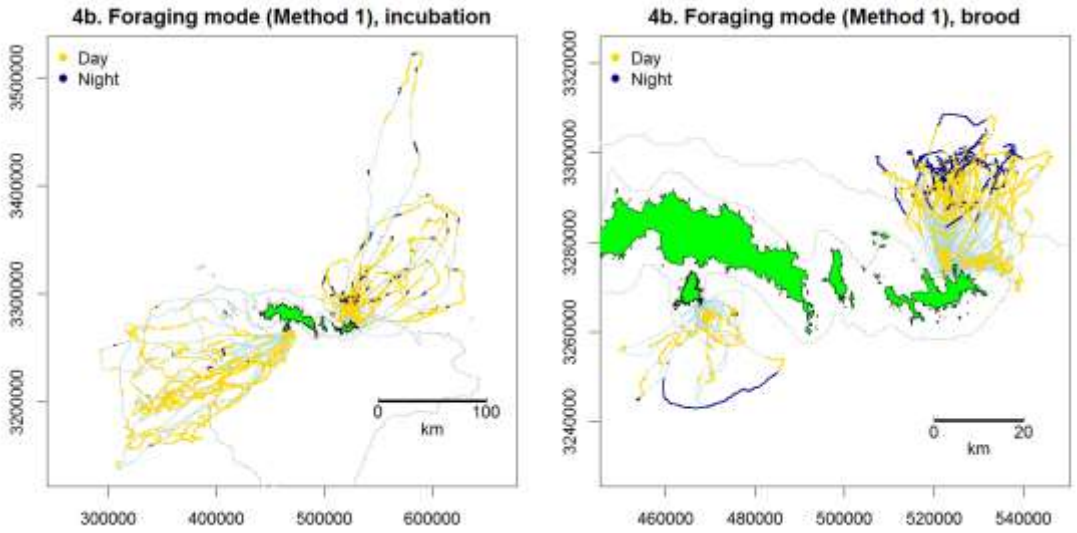

Figure VI-6 Spatial distribution of the inferred foraging modes based on the expert based classification (Method 2) from complete and trips with missing TDR data (data input 3b) acquired from the Gourlay Peninsula and Cape Geddes during incubation (left) and brood (right) with an indication of the period of the day.

Table VI-1 contains the sample sizes in the different data inputs with a breakdown by phenological stages and colony sites.

Table VI-1: Number of locations in the different input levels with an indication whether the dataset contains trips with missing TDR data.

		Incubation		Brood	
Input	Include missing TDR	Gourlay	Geddes	Gourlay	Geddes
1. GPS locations	Yes	16988	19221	2722	6849
2. Dives	No	12839	34306	2373	16527
3a. Foraging modes (Method 1)	No	6079	45374	4599	27688
3b. Foraging modes (Method 1)	Yes	26329	45374	6365	28908
4a. Foraging modes (Method 2)	No	13337	55978	4268	34519
4b. Foraging modes (Method 2)	Yes	45111	55978	5915	35723

b. Grid aggregation at various spatial resolutions

The six data inputs described in the previous section were aggregated using different spatial resolutions. These were based on the cell sizes of the different environmental variables that will be used for the habitat modelling in Chapter VII (see Table VI-2 and section VII.2a, page VII-143, for a complete description of these variables). The conservative spatial resolution of the GPS data (250 m, see II.1b, page II-14) and cell sizes of 600 m (brood only), 1000 m and 2000 m were also included. For brood data, as trips during this stage covered a much smaller areas, the

highest aggregation scale was limited to the resolution of the Net Primary Productivity (NPP, 8260 m).

Table VI-2: Spatial resolution (cell sizes) used for the different spatial locations aggregations for incubation and brood data. The different environmental variables included in the foraging habitat model are described in VII.2a, page VII-143.

Cell size (m)	Description	Used for Incubation (I) and/or Brood (B)
250	Conservative GPS accuracy	I+B
344	Bathymetry	I+B
600	-	B
1000	Resolution of the time-in-area (VI.2c)	I+B
2000	-	I+B
4130	Sea Surface Temperature (SST)	I+B
8260	Net Primary Productivity (NPP)	I+B
12400	Mean Sea Level Anomalies (MSLA)	I
17700	Sea Ice Cover	I
19150	Surface Currents (Longitude)	I
34645	Surface Currents (Latitude)	I

The point datasets were transformed into grids with increasing cell sizes (decreasing resolution). The number of points for each cell was totalled. The correlation between the number of points per grid square for the reference data set (1, GPS, as this input represents a common feature from most tracking studies, Warwick-Evans et al., 2015) and the other data input for each spatial resolution was calculated using Pearson's correlation coefficient.

c. Time-in-area changes during the breeding season

In order to measure spatio-temporal activity or time-in-area (Soanes et al., 2015), the total number of 1 minute interpolated positions (see II.2c, page II-29) was summed for each cell of a one kilometre square grid.

The resulting amount of time was divided by the number of tracked birds (deployments) for each site and breeding phase to avoid sampling bias and then multiplied by each colony population estimates (for Gourlay, the total Signy population estimate was used: 19530, Dunn et al., 2016, and 7116 for Geddes, Coria et al. 2011). The change in distribution of this weighted time-in-area between incubation and brood was assessed using a generalized linear mixed-effects model with a poisson distribution ('lme4' R package, Bates et al. 2015) including the colony site as a random effect.

d. Potential foraging areas

As a first approximate estimation of the foraging areas, I used the minimum convex polygon (MCP) method to delineate simple potential foraging areas from the GPS locations (data input 1). These zones (one per colony site and phenological stage) included all the recorded GPS locations and were therefore within range from the nesting sites.

Although this techniques has been used in many studies to define species spatial distribution ranges, it is known to be strongly biased by outlier locations (Burgman and Fox, 2003; Nilsen, Pedersen and Linnell, 2008).

e. Utilisation distribution

The simple grid aggregation described in sections b and c is a straightforward method to estimate spatial aggregation with the advantage of an optimal control of the aggregation scale. The control of the grid size is very convenient in the context of Marine Spatial Planning (Warwick-Evans et al., 2015). Unfortunately, the results from this method can be biased as the positioning of the grid will influence whether a point might fall in a given cell or not and therefore the results. A more robust method to estimate spatial utilisation from a series of points based on a kernel density estimator was therefore used (Seaman and Powell, 1996; Keating and Cherry, 2009; Benoit-Bird et al., 2013; Tancell et al., 2013; Kokubun et al., 2015).

This method used the different data inputs to generate kernel density estimators along the horizontal plane (R package 'adehabitatHR', Calenge 2006). The smoothing parameter or search radius was calculated from the "ad hoc" reference method (Worton, 1995). From these density estimators, the percentage volume contour (Silverman, 1986) was used to delineate the zones where the highest density estimators were located defining the utilisation distribution (Hazel, 2009; Soanes et al., 2015). The areas, perimeters and area-perimeter ratios as a measure of compactness of these zones ($Area/Perimeter^2$, Bogaert et al. 2000) and distances from the centroids of the resulting polygons to the colony were calculated. The overlap between the different data inputs, between incubation and brood and between diurnal and nocturnal locations were also computed.

f. Foraging volumes

As an exploratory tool, a three-dimensional kernel density estimator was calculated for the 1 minute interpolated tracks merged with the dive data (data input 2). In addition to the two horizontal coordinates (X and Y), dive depth was entered as the vertical coordinate (Z). The 3 dimensions density estimator was calculated and plotted using R 'sm' package (Bowman and Azzalini, 2014).

To analyse the vertical use of the foraging areas in relation to the potential intensity of use of these areas, a model was created to predict the mean dive depth in each one kilometre square cell from proxies of foraging intensities. The later were the distance to the colony for each cell (closer areas will be more intensively used) and the total observed time spent in each cell. Other measure of central tendency was tested (median) but the mean depth contributed to the best predictive model. To limit the bias due to the temporal migration of the preys, only the diurnal dives were used and the shallower night dives were discarded.

Different data inputs were considered for the model (all dives, foraging dives inferred from method 1 and foraging dives inferred from method 2). The colony site and the phenological stage were added as covariates. A random noise variable was also added into the model. A random forest analysis was ran to predict the mean dive depth for each one kilometre square grid.

g. Summary of the process

The processes from the previous chapters leading to the different data inputs are illustrated in Figure VI-7. The different methodological approaches for this chapter are also indicated.

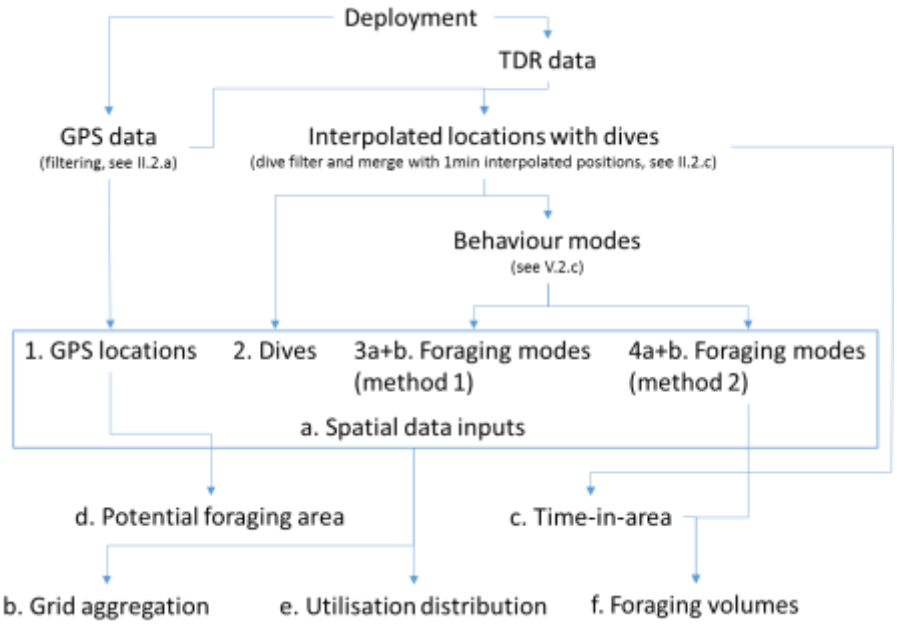

Figure VI-7: Workflow summary from the filtered GPS locations and interpolated locations merged with dives (Chapter II) and the locations of the inferred foraging modes (Chapter V) to the different ways of measuring total spatial use.

VI.3 Results

a. Spatial and temporal scales of the data inputs

Table VI-3 summarizes the spatial and temporal resolutions of the data inputs. For the GPS and the dive locations (1 and 2), the time resolution was the average time difference between two successive locations and the space resolution was the mean distance between the two points. For the foraging modes data inputs (3a, 3b, 4a and 4b), the temporal resolution represented the average foraging segment duration and the spatial value was based on the average segment surface length.

Table VI-3: Spatial and temporal resolutions of the different data inputs. See the main text for a description of the different values. The variability is represented by the half interquartile range.

Input	Include missing TDR	Time	Space
1. GPS locations	Yes	5±1 min	234±153 m
2. Dives	No	2±1 min	85±53 m
3a. Foraging modes (Method 1)	No	76±85 min	5.46±3.55 km
3b. Foraging modes (Method 1)	Yes	4±17 min	0.45±1.24 km
4a. Foraging modes (Method 2)	No	76±41 min	5.28±3.27 km
4b. Foraging modes (Method 2)	Yes	3±8.5 min	0.19±0.73 km

The important resolution differences between the foraging modes based only on complete data (GPS+TDR: 3a and 4a) and the foraging modes including missing TDR (3b and 4b) was a consequence of the prediction of the behaviour mode. For trips without a TDR, the bird activity was inferred for each individual 1 minute interpolated position (see V.2c, page V-84) instead of having the interpolated positions aggregated by segments and having one single behaviour mode for the whole segment for the complete trips.

b. Grid aggregation at various spatial resolutions

The gridded maps for the different data inputs across all resolutions are presented in Appendix III; Figure VI-8 shows an example for the GPS points collected during brood. It is quite clear that at small cell sizes (high resolution), most grids only contained few points (58.3% of the GPS locations aggregated on 250 m grid cells contained one single point). On the opposite end of the range, at large cell size (low resolution), the area was covered by only a few cells and fine details were lost. At intermediate resolutions (cell size of 2000 m on Figure VI-8), there was a better contrast between zones with a low number of points and zones with higher activity, allowing me to identify different foraging hotspots. The distribution of the counts per cell at the 2000 m scale shows the best separation between cells with low counts and cells with high counts. This bimodal distribution is less clear for other scales.

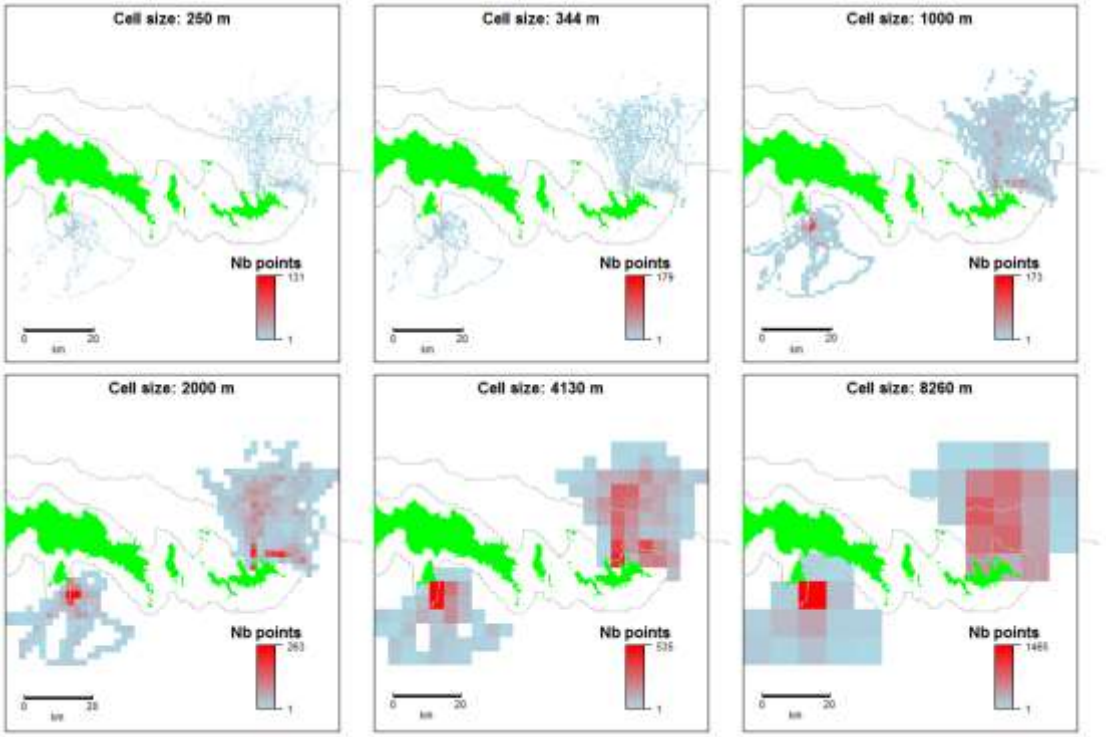

Figure VI-8: Example of location counts aggregated at different grid cell sizes (GPS, data input 1, during brood). Note that the 600 m resolution is not included in this figure.

Comparison between the different levels of input with the reference (GPS points) across different resolutions

When correlating the point counts per cell between the GPS points and the other data inputs across varying cell sizes, Spearman's coefficients were high (Figure VI-9). They varied from a minimum value of 0.71 (dives during brood at a cell size of 1000 m) to a maximum value of 0.97 (incubation foraging identified through method 2 including missing TDR data at the coarser resolution).

At high resolution (small cell sizes), all data inputs, except the dive locations had similar correlation coefficients with the GPS locations. The coefficients tended to increase with cell sizes as lower resolution (large cell sizes) led to higher point aggregation which attenuated spatial differences between the data inputs.

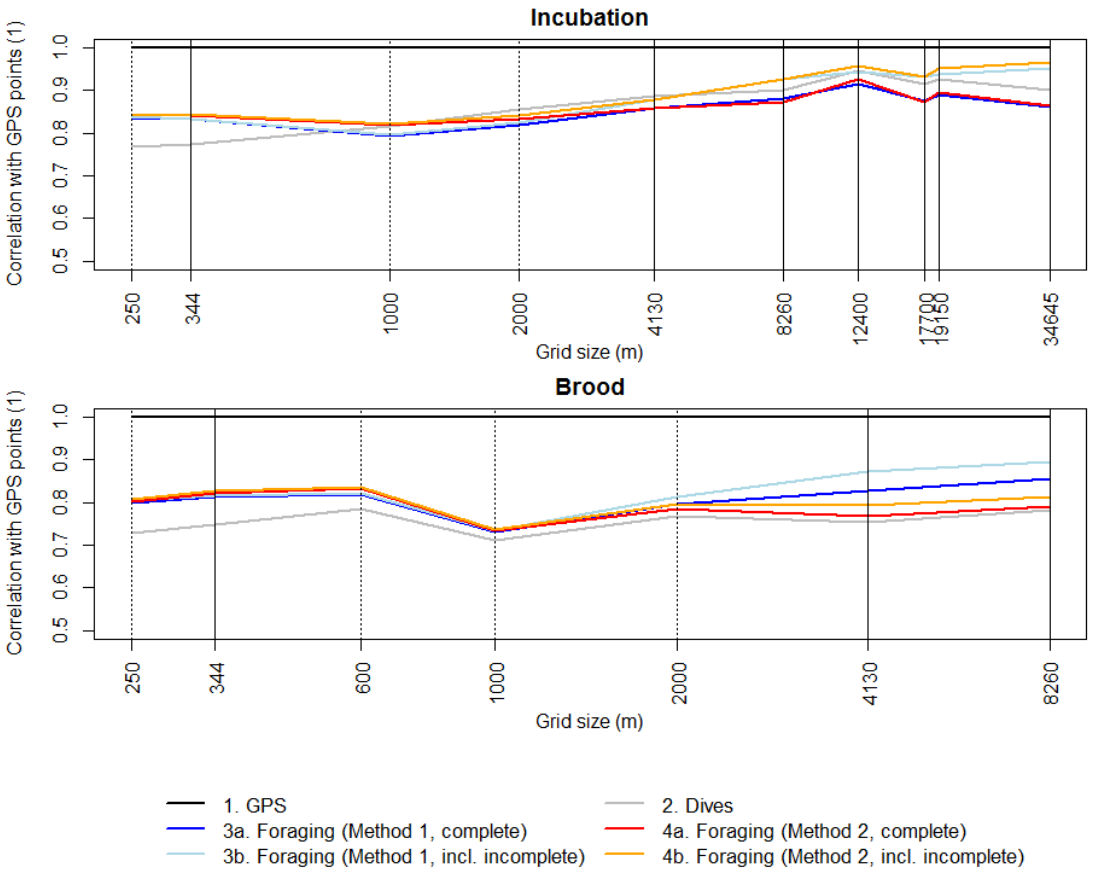

Figure VI-9: Spearman correlation coefficients between the GPS location counts and the other data inputs aggregated on different spatial resolutions.

The grid sizes with the lowest coefficient variation between data inputs were 4130 m (resolution of the Sea Surface Temperature variable) for incubation and 1000 m for brood. The latter being also the resolution with the lowest correlation with the GPS location counts.

c. Time-in-area changes during the breeding season

The distributions of the time spent per square kilometre weighted by the colonies population sizes along the breeding season are presented in Figure VI-10 (values are log transformed for better visibility).

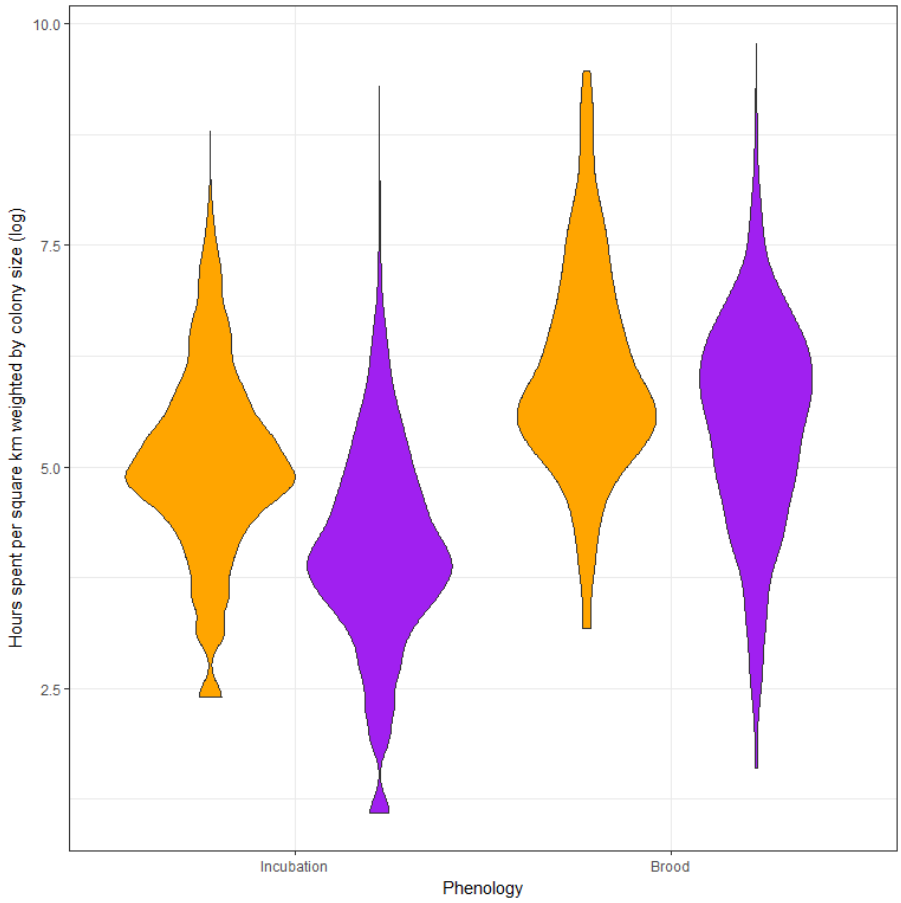

Figure VI-10: Distributions of the number of hours spent per square kilometre number weighted by the population size for each colony (Geddes in purple and Gourlay in orange) and evolution during the breeding season.

The distribution of the amount of time spent significantly increased after hatching (z value=832.5, p<0.01) with a steeper slope from the Geddes colony (1.42 versus 1.24 for Gourlay; the model with the random effect based on a random slope was better than without random effect or with a fixed slope: Chi Square=3007.5, df=2, p<0.01). This indicated an intensification of habitat use after hatching, especially for the Cape Geddes colony.

d. Potential foraging areas

The potential foraging areas defined using minimal convex polygons based on the GPS locations are presented on Figure VI-11. Although the result included large areas that were not used by studied birds, these areas could potentially be reached by other non-tracked individuals as they laid within observed ranges and directions. These extended towards the north-north-east from Cape Geddes and towards the west-south-west from the Gourlay Peninsula. Saturation curves show that for most colony and breeding stage, the number of trips is sufficient to reach a plateau for the potential foraging areas, even for the incubation trips from Gourlay where the sampling is quite low. For the brood trips from the

same location, the plateau on the saturation curve is not as clear as for the other site and breeding stages.

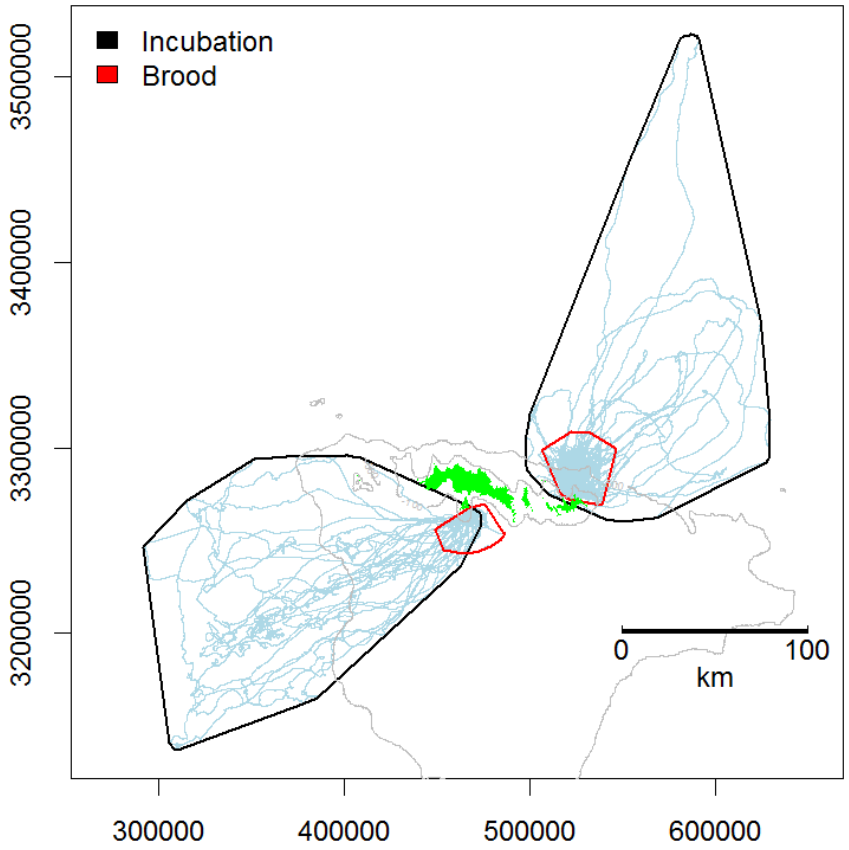

Figure VI-11: Potential foraging areas from both colony sites during incubation and brood estimated as minimal convex polygon drawn from the GPS locations.

The areas of the different potential foraging polygons are reported in Table VI-4. When divided by the sample size (number of tracked birds), the resulting weighted areas measured from Cape Geddes were approximately half of the ones from the Gourlay Peninsula. This ratio was similar for both phenological stages.

Table VI-4: Minimal Convex Polygons (MCP) areas from both colony sites and across phenological stages with the ratio of area per measured tracked bird.

Stage	Site	MCP Area (km^2)	No birds	Area per bird (km^2)
Incubation	Gourlay	18493	20	924.6
	Geddes	20637	35	589.6
Brood	Gourlay	645	9	71.6
	Geddes	1097	25	43.9

e. Utilisation distribution

Localisation and bandwidths

The kernel densities for all the data inputs are stacked in Figure VI-12 using transparency. It shows that during incubation although birds from Cape Geddes had long-range trips, most of the activity was concentrated near the colony. In contrast, the birds from the Gourlay Peninsula

covered a larger area with high concentration of locations well beyond the continental slope. During brood, two foraging zones off Laurie Island are clearly visible (towards the east over the shelf or the north off the shelf)

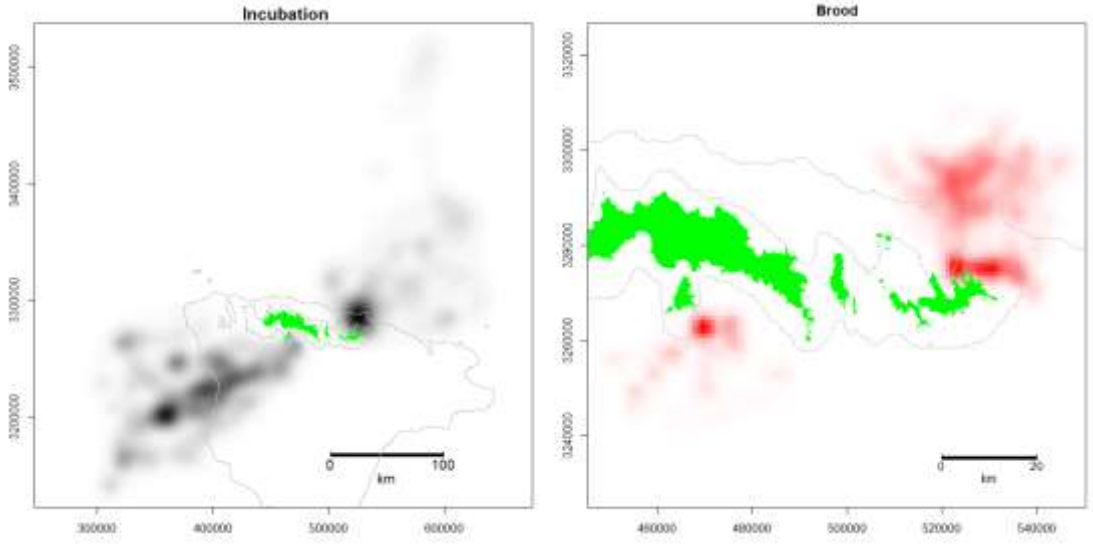

Figure VI-12: Kernel density estimators overlapping for all data inputs during incubation and brood. The darker areas combine higher density estimators and high consistency between the different data inputs.

The calculated kernel bandwidth smoothing parameters for the kernel density estimators for each site, phenology and data input are presented in Table VI-5. The bandwidths or search radius were larger for the incubation data than for the brood data as the area covered by the points was larger. There was no significant difference between sites for incubation (t = 0.67618, df = 9.9916, p-value = 0.514) or for brood (t = 1.4093, df = 9.9762, p-value = 0.189).

Table VI-5: Calculated kernel bandwidth smoothing parameters for the different data input per phenology and colony.

		Incubation (m)		Brood (m)	
Input	Include missing TDR	Gourlay	Geddes	Gourlay	Geddes
1. GPS locations	Yes	7983.1	8550.2	1515.6	1791.1
2. Dives	No	7300.1	7610.0	1594.5	1543.7
3a. Foraging modes (Method 1)	No	7265.2	6807.6	1305.9	1471.9
3b. Foraging modes (Method 1)	Yes	6802.8	6807.6	1284.1	1484.0
4a. Foraging modes (Method 2)	No	6735.6	6948.9	1314.3	1423.2
4b. Foraging modes (Method 2)	Yes	5990.5	6948.9	1478.6	1433.9
AVERAGE		7012.9	7278.9	1415.5	1524.6

Delineation

Figure VI-13 presents the percentage volume contours with different thresholds extracted from the kernel density estimators on the GPS dataset (1) for incubation and brood. As expected, the areas increased with the density probability. For the area overlap calculations, the chosen threshold for the density contour was 75% to focus on the core areas and

discard areas that might be only visited by a single outlier trip. This threshold also allowed me to mitigate the known overestimation of home ranges through the kernel density estimator (Seaman and Powell, 1996).

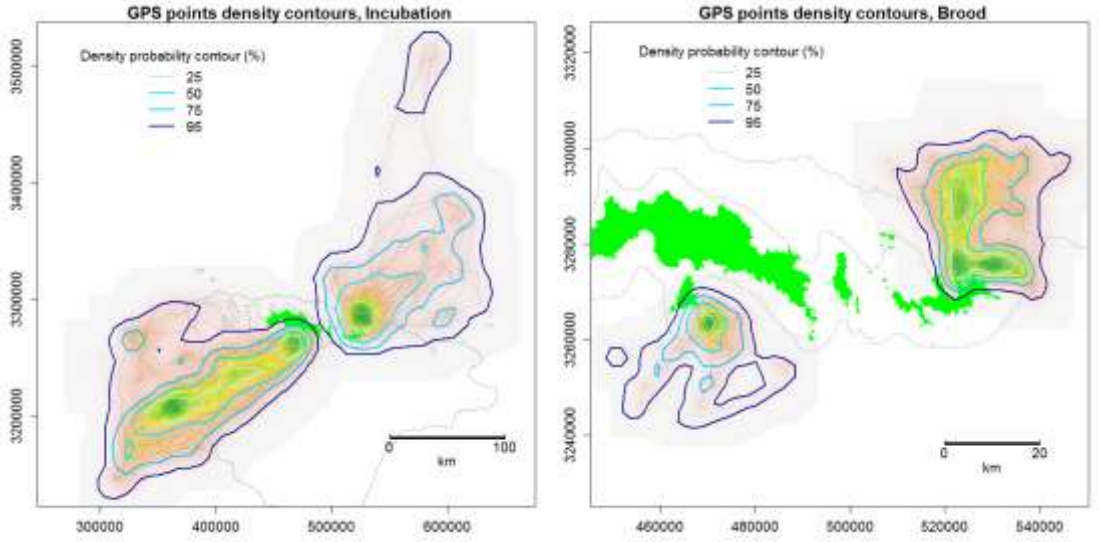

Figure VI-13: GPS locations (data input 1) overlaid with the kernel density estimators (colour scale from grey – low to green – high) and the delineation using different percentage contour thresholds.

Areas, localisation and shape

The metrics for the 75% utilisation distribution areas are presented in Table VI-6. The weighted areas calculated from Gourlay showed important variation between the different data inputs due to the large number of trips with missing TDR data from that colony (15 during incubation and 10 during brood).

Table VI-6: Metrics for the 75% probability contour of the kernel estimators per data inputs, sites and breeding stages.

	Weighted areas (km^2 per trip)				Area-perimeter ratio (10^{-8})				Centroid dist. to colony (km)			
	Incubation		Brood		Incubation		Brood		Incubation		Brood	
Input	Gourlay	Geddes	Gourlay	Geddes	Gourlay	Geddes	Gourlay	Geddes	Gourlay	Geddes	Gourlay	Geddes
1	494.2	233.2	19.2	18.5	3.3	3.2	3.5	3.6	102.7	79.7	9.2	14.3
2	807.5	240.5	23.4	18.5	1.9	3.2	1.9	3.2	104.4	80.4	10.1	14.6
3a	520.9	168.4	14.8	18.0	2.3	1.9	1.8	2.7	114.9	64.7	10.4	14.7
3b	377.1	168.4	16.8	17.7	2.5	1.9	3.1	2.8	107.8	64.7	9.6	15.4
4a	628.6	199.8	12.1	18.2	1.5	1.9	2.6	2.5	101.2	78.4	8.8	14.6
4b	393.4	199.8	20.6	18.0	1.6	1.9	2.7	2.6	104.5	78.4	10.7	15.2
AVERAGE	537.0	201.7	17.8	18.1	2.2	2.3	2.6	2.9	105.9	74.4	9.8	14.8
± SD	±161	±30.7	±4.1	±0.3	±0.6	±0.6	±0.6	±0.4	±4.9	±7.6	±0.7	±0.4

Similar to the potential foraging areas defined by the MCP, the average surface covered per bird from Gourlay was much higher than the one covered by birds from Geddes during incubation. After hatching, both weighted areas from the two colonies were very similar.

The area-perimeter ratios, as a measure of compactness, indicated that brood utilisation distribution had slightly higher ratios (more circular)

than during incubation, although the difference was not significant (W = 106, p-value = 0.053). The shape of the areas was not significantly different between the sites (W = 86, p-value = 0.436).

The centroid of the 75% utilisation distribution areas was more distant from the Gourlay Peninsula than Cape Geddes during incubation; whilst after hatching, it was the reverse.

Overlap

Figure VI-14 maps the 75% contours of the kernel density estimators for the different data inputs. The overlap ratios are presented in Table VI-7. The perfect overlap between the foraging behaviour inputs with and without the trips with missing TDR (3a and 3b; 4a and 4b) for incubation trips from Geddes was probably due to the fact that all the trips recorded from that location before hatching were complete datasets (GPS+TDR). Similarly, the very high overlap between the same data inputs (3a and 3b; 4a and 4b) for brood foraging locations from Geddes was also due to the very low number of trips with missing TDR (only 3 trips).

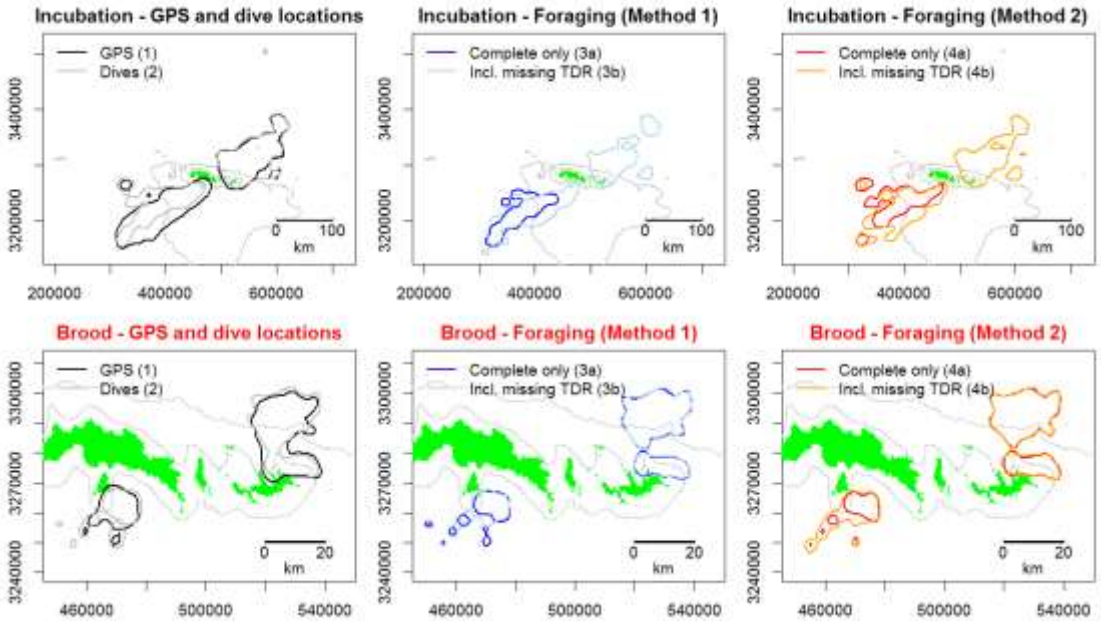

Figure VI-14: Overlap of the 75% probability contours from the kernel density estimators for the different data inputs, sites and phenological stages.

The 75% utilisation distribution based on dive locations showed a high overlap with the one based on GPS locations, especially for Geddes. The weaker overlap from the Gourlay data could be explained again by the high number of trips with missing TDR data but also by more resting behaviour during trips recorded from this colony (see V.3c page V-103). Indeed, resting behaviours were associated with a high rate of GPS locations but very few dives.

The foraging modes inferred from the two different methods generally showed some of the highest overlaps: 80% for both 3a-4a and 3b-4b for incubation trips from Geddes; 91% for both 3a-4a and 3b-4b for brood trips from the same location; only 52% for 3a-4a for incubation trips from Gourlay but 71% for 3b-4b from the same colony and breeding

period; and finally 79% and 76% for respectively 3a-4a and 3b-4b for brood trips from Gourlay.

The overlap ratios were generally better from Cape Geddes (average of 81%) than from the Gourlay Peninsula (average of 57%). This was still true when excluding the incomplete dataset (3 trips from Geddes and 25 trips from Gourlay) which raised the average of overlap from Gourlay Peninsula to 62%.

Table VI-7: Overlap between the different areas defined by the 75% kernel density estimator for the different data input, colony sites and phenological stages (incubation in black and brood in red).

Data Inputs	1. GPS locations	2. Dives	3a. Foraging modes (Meth. 1)	3b. Foraging modes (Meth. 1)	4a. Foraging modes (Meth. 2)	4b. Foraging modes (Meth. 2)
Geddes						
1. GPS locations		85%	65%	65%	77%	77%
2. Dives	75%		63%	63%	75%	75%
3a. Foraging modes (Meth. 1)	75%	87%		100%	80%	80%
3b. Foraging modes (Meth. 1)	77%	87%	94%		80%	80%
4a. Foraging modes (Meth. 2)	74%	87%	91%	90%		100%
4b. Foraging modes (Meth. 2)	76%	87%	89%	91%	94%	
Gourlay						
1. GPS locations		49%	40%	68%	37%	69%
2. Dives	60%		54%	45%	74%	50%
3a. Foraging modes (Meth. 1)	55%	62%		46%	52%	47%
3b. Foraging modes (Meth. 1)	69%	63%	61%		37%	71%
4a. Foraging modes (Meth. 2)	49%	51%	79%	55%		47%
4b. Foraging modes (Meth. 2)	61%	61%	56%	76%	51%	

Comparison between pre and post-hatching

Figure VI-15 represents the overlap of the utilisation distributions based on the different data inputs shown on a single map per phenological stage. The average overlap between the different datasets was higher during brood then during incubation from both colonies (Geddes brood: 85%, Geddes incubation: 78%, Gourlay brood: 61%, Gourlay incubation: 53%).

From Geddes, the totality of the brood foraging area defined by the 75% utilisation distribution was included in the incubation foraging area. By contrast, in Gourlay only 62% of the brood foraging area overlapped with the area targeted before hatching.

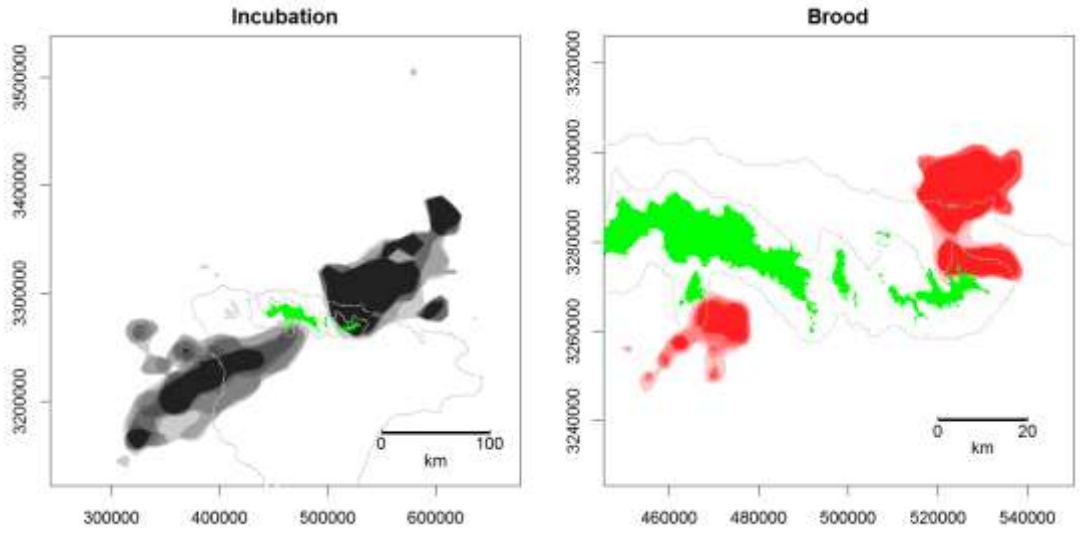

Figure VI-15: Spatial overlap of the 75% kernel density estimator for the different data inputs for incubation and brood.

Comparison between day and night foraging areas

When computing the intersection of the 75% utilisation distribution for day and night (twilight + night) periods, the percentage of overlap was greater during incubation (48 and 59%) than during brood (17 and 18% for Gourlay and Geddes respectively). This was due to the fact that most incubation trips included overnight time, while during brood, trips were either diurnal or nocturnal (see IV.4a, page IV-72). Figure VI-16 presents the day and night areas overlaps for all the data inputs.

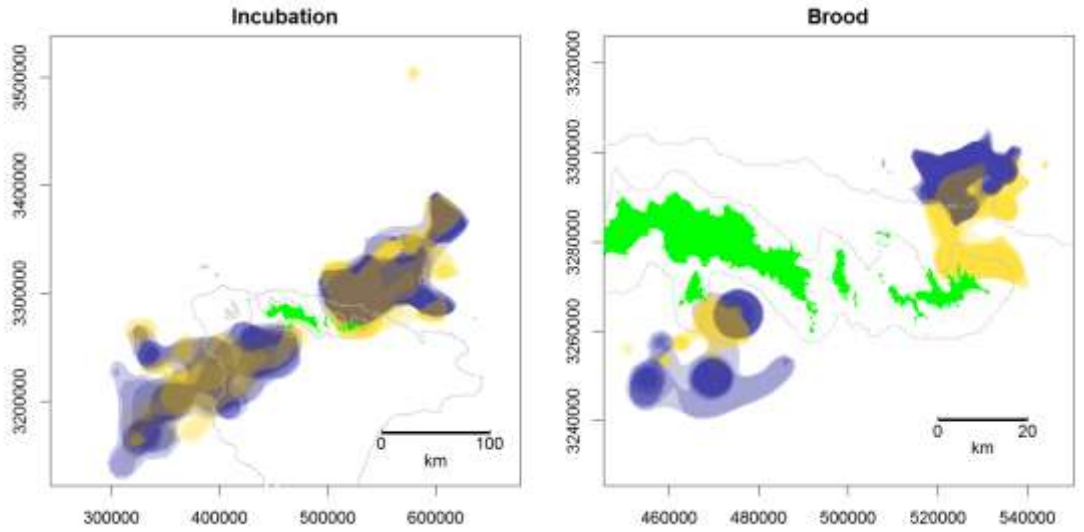

Figure VI-16: Spatial overlap of the 75% kernel density estimator for the different data inputs between day and night (night and twilight) periods. Day data are represented in yellow and night data (night and twilight) are represented in blue.

The figure suggests that the two different foraging zones for chick rearing birds from Geddes presented earlier (over the shelf and off the shelf) were linked with diurnal and nocturnal activities. From that location, 52 trips went north reaching the oceanographic slope and 48 trips went east and stayed over the shelf. There was a clear distinction

between diurnal and nocturnal trips: 93.8% of the diurnal only trips stayed over the shelf and 94.2% of the trips with some night activity reached the oceanographic slope (Figure VI-17a).

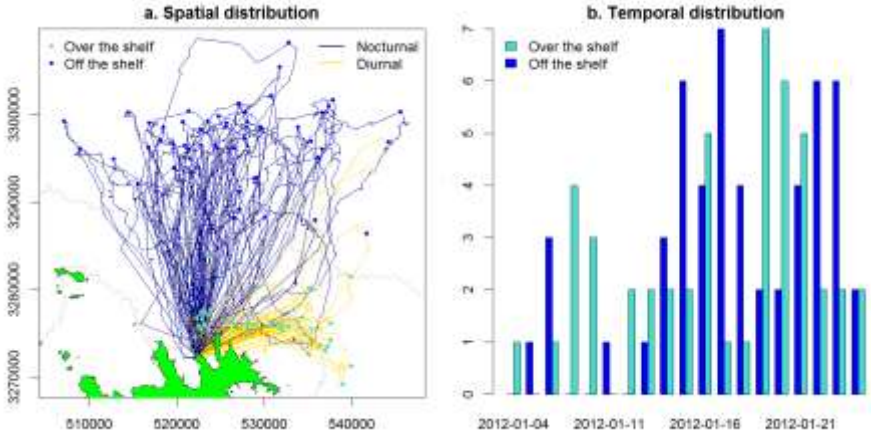

Figure VI-17: Spatial (a) and temporal (b) distribution of the exploitation of the two foraging zones for brood trips from Geddes: over the shelf or off the shelf. On the map (a), the points represent the maximum distance from the colony for each trip. In addition, the trip lines are colour coded based on the period of the day (diurnal or nocturnal trips).

The temporal distribution of the exploitation of these two different foraging areas showed that these areas were stable through time and therefore did not result from a temporary krill swarm with opportunistic feeding (Figure VI-17b).

The birds did not show any individual preferences. Out of the 25 brooding birds tracked from Geddes, 2 stayed exclusively over the shelf and 2 only went off the shelf; 6 had the same number of trips to both zones, whilst 7 had more trips over the shelf and 8 showed a preference for nocturnal off the shelf trips. The temporal sequence between diurnal and nocturnal trips did not show any specific pattern among birds (individuals alternating between short diurnal and long nocturnal trips for example, see also Figure IV-7 page IV-61). Birds targeting the off shelf area were leaving the colony later in the afternoon than the birds that stayed over the shelf, illustrating how birds foraging north really aimed for overnight trips.

From Gourlay during brood, nocturnal foraging seemed to be more distant from the colony, suggesting a similar pattern but without the close presence of the oceanographic slope. Unfortunately, due to the small sample size (31 trips from 9 birds), it was not possible to get a clear picture from that colony.

f. Foraging volumes

Kernel density estimator volumes are represented in Figure VI-18 where deeper dives closer to the colonies are clearly visible except from the Gourlay colony during incubation.

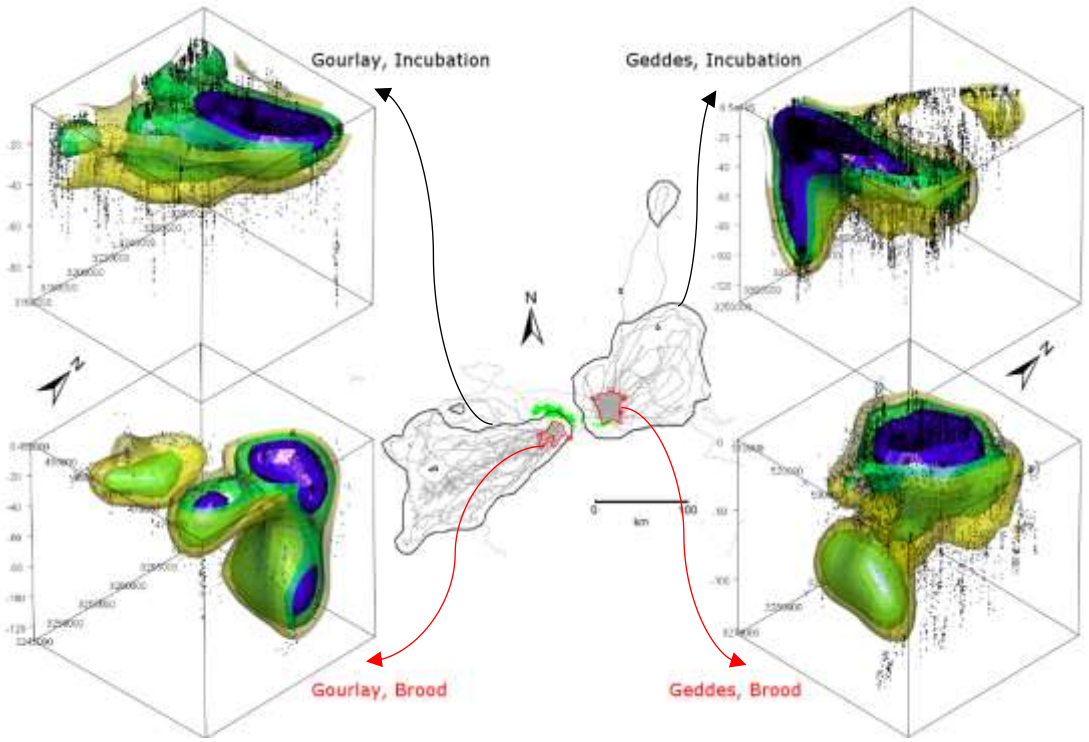

Figure VI-18: kernel density estimator volumes per colony and phenological stage.

The best model predicting the mean depth per square kilometre in relation to distance to the colony and time-in-area was based on foraging dives only inferred from the method 2 (expert-based). It managed to explain 33.3% of the variability of the response variable. The predicted out-of-the-bag dive depths showed a weak but significant correlation with the observed mean depths (R^2 of 0.348, $F_{1,2185}$, $p<0.01$). The average performances of the model suggested that other aspects in addition to the ones included in the model might influence dive depths. Nevertheless, when looking at the variable importance ranking (Table VI-8), the main contributor to the model was the distance to the colony. The time-in-area showed a weaker contribution, just above the phenological stage. The site location variable importance was just above the one for the random noise variable suggesting no important differences between colonies.

Table VI-8: Variables importance when modelling the average dive depth per square kilometre.

Variable	Increase in node purity
Distance to the colony	158268
Time-in-area	66648
Phenological stage	49341
Site	35740
Random noise	30809

Figure VI-19 shows the predicted mean dive depth by the model in relation to the distance to the colony, the time-in-area, the colony site and the phenological stage. Dives were deeper closer to the colony except in areas with low temporal use. The longer time spent in areas close to the colony where deeper dives occurred could be linked with birds recovering at the surface after deeper dives. The model "slope" was

steeper during incubation, but this was due to the range of distances been much wider during that stage. The predicted dive depths started to plateau after a similar approximate threshold of 25 kilometres from the colony across both sites and during both temporal stages. Mean dive depths were deeper after hatching.

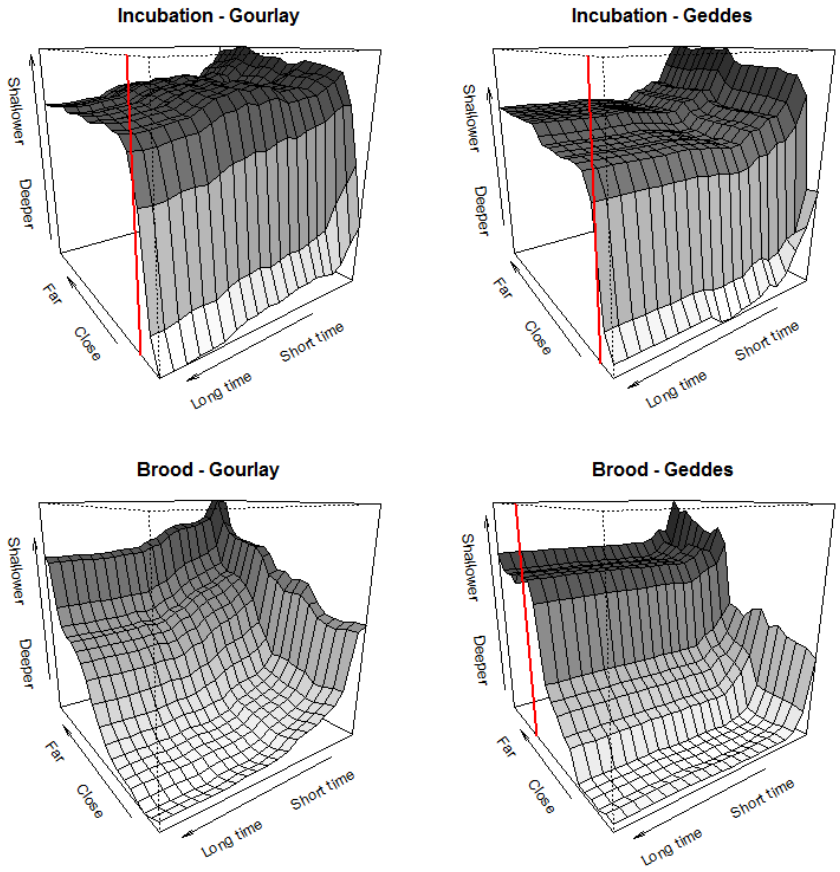

Figure VI-19: Predicted mean dive depth (vertical axis) in relation to the distance to the colony and the time-in-area for each colony site and phenological stage. The vertical red line represents the 25 km distance from the colony where most of the predicted shallower dives started (outside the plot for Brood - Gourlay).

VI.4 Discussion of the results, limitations and implications

In this section, the main results from the various approaches to the spatial distribution of the different data inputs will be summarized and discussed in relation to the results from previous chapters and other studies. The limitations due to the quantity and quality of the available data and the methodology will also be discussed. Finally the implications of the main findings on the final habitat modelling (Chapter VII) will be considered.

a. Comparing the different data inputs

During the spatial aggregation process, the different data inputs showed strong correlations with the baseline GPS data across increasing resolutions (average of 0.875 and 0.795 for incubation and brood respectively). This confirmed that GPS was a good indicator of foraging.

In fact, during commuting, accuracy and point acquisition were usually limited (Ryan et al., 2004), as demonstrated by the fact that the segments classified as day or night foraging had the highest rate of GPS locations (day and night foraging had between 12 and 19% of GPS locations contrasting with ratios between 3 and 10% for commuting modes, see Table VI-9).

Table VI-9: Percentage of true GPS locations in the segments attributed to different behaviour modes depending on the method used and the phenological stage (see V.2c, page V-84).

		Semi-automatic clustering (Method 1)		Expert-based classification (Method 2)	
	Behaviour mode	Incubation	Brood	Incubation	Brood
Day	Commuting	10%	5%	5%	3%
	Exploring	17%	10%	16%	10%
	Foraging	19%	15%	19%	15%
	Resting	9%	5%	10%	12%
Night	Foraging	18%	13%	18%	12%
	Resting/Commuting	9%	8%	7%	6%

The convergence between the different data inputs was optimal at medium scale (4130 m for incubation and 1000 m for brood) where small differences in the details were lost and foraging hotspots patterns could be identified.

The overlap of the 75% utilisation distribution between the different data inputs was higher from Geddes and during brood from both sites. This could be due to the lower number of trips with missing TDR recorded from that location (less discarded points between the different data inputs). Birds from this colony also foraged in a smaller area (including during incubation), decreasing the chances of point dispersion (see also time-in-area below). In general, the average overlap was strongly correlated with the sample size (Figure VI-20); the higher overlap of utilisation distribution areas could therefore also be explained by the higher sample size from Geddes.

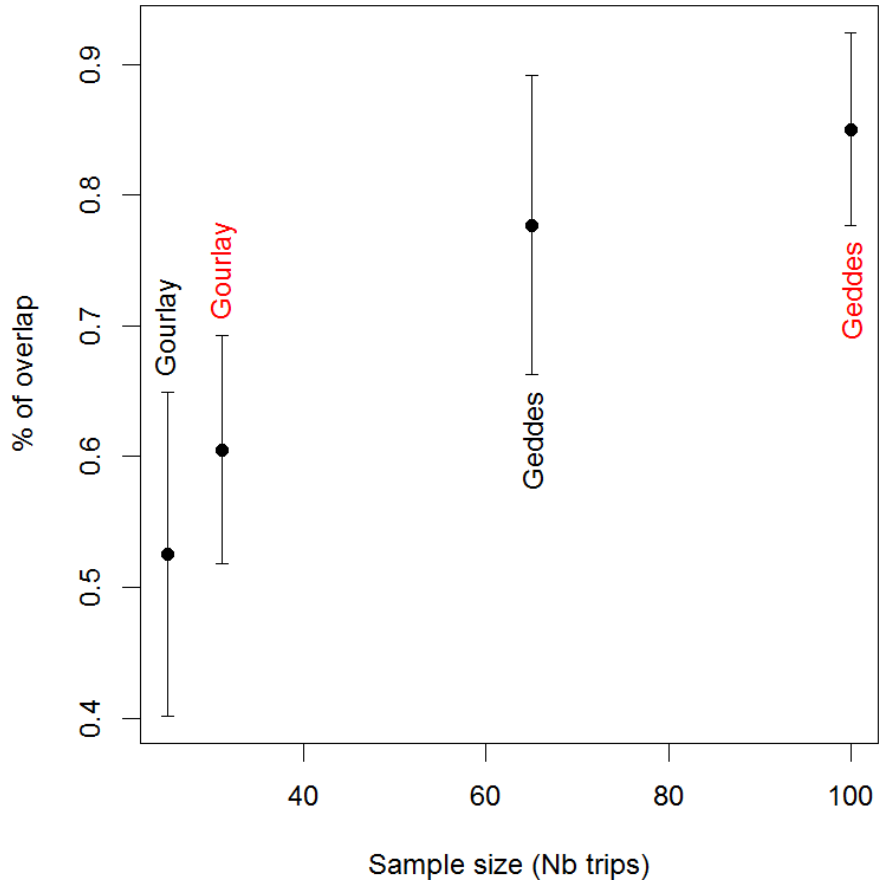

Figure VI-20: Relationship between the percentage of overlap of the different utilisation distribution areas and the sample size for the different colonies and phenological stages (black for incubation and red for brood). The points represent the mean values from the different data input overlaps and the error bars are based on the standard deviations.

b. Time-in-areas

The reduction in the available foraging habitat space after hatching led to an increase in point density as measured by the weighted time-in-area. From lower values during incubation, the rise in time per square kilometre from Cape Geddes was steeper. Higher time-in-area during incubation from Gourlay Peninsula could be explained by the fact that the birds used a narrower "commuting corridor" to reach the oceanographic slope. The angles between the colonies and the most extreme trip maximum points (see II.2c, page II-29) along the latitude for Gourlay and longitude for Geddes were 39.0 degrees and 91.9 degrees for Gourlay and Geddes respectively. The steeper increase in time-in-areas for Geddes can be explained by a smaller potential foraging area measured by the minimum convex polygon method, although the areas defined by the utilisation distribution were similar for both sites. Another explanation could be a linked with prey availability. The continental slope is usually a favourable habitat (Ichii et al. 1998; Trathan et al. 2003; Trathan et al. 2006; Atkinson et al. 2008; Siegel et al. 2013; although Hunt et al., 1992 reported that macaroni penguins didn't target shelf break areas in South Georgia) which could lead to a more intense exploitation of a limited area.

c. Foraging areas

The minimal convex polygon and the delineation of the utilisation distribution unsurprisingly indicated similar directions for the foraging areas. Birds were travelling towards the north from Cape Geddes and the west-south-west and south for incubation and brood respectively from Gourlay Point. The finer approach using the utilisation distribution highlighted that although some very long foraging trips were recorded during incubation from Cape Geddes, most of the activity was concentrated very close to the colony. The kernel density approach also allowed me to differentiate two foraging destinations from Cape Geddes during brood: one towards the north off the shelf and one towards the west over the shelf.

The weighted sizes of the foraging areas were consistently larger for Gourlay Peninsula during incubation for both methods, although the minimal convex polygon method gave larger estimates as mentioned in the methods (VI.2d, page VI-119). During brood, the weighted areas covered from both colonies were similar using the utilisation distribution method, as the minimum convex polygon method indicated a larger foraging zone for Gourlay.

The centroids of the 75% utilisation distribution areas confirmed that during incubation, birds tended to stay closer to the shore from Cape Geddes. This was in line with the presence of short incubation trips from this colony described previously (see IV.3b, page IV-57). This could be explained by the shorter distance to the shelf break but also by less competition due to Geddes being a smaller colony, as foraging ranges can be related to colony size (Ainley et al., 2004). From the Gourlay Peninsula, the areas close to land appeared as an obligatory commuting corridor in and out of the colony. This could be explained by greater resource depletion (or slower replenishment above the shelf) or by inter-specific competition with chick-rearing Adélies from Gourlay (Lynnes et al., 2002; Wilson, 2010). During brood, the areas from Geddes were further off shore, especially when the birds decided to opt for overnight trips reaching the continental shelf slope. These more distant foraging grounds could be associated with high productivity areas, which are worth the travel effort. Similar patterns have been observed by Boersma et al. (2009) in Magellanic penguins foraging along the Argentinian coast and reaching offshore mixing fronts.

The shape of the areas defined by the 75% utilisation distribution supported these results: more compact and circular zones from Cape Geddes where areas were closer to the shore and larger and more elongated zones from Gourlay Peninsula where birds had to travel further to reach off shelf waters during incubation and therefore have less time for a circular path (especially for the dive and foraging data defined by method 2). The measured circularity of the foraging zones indicating a narrowed path from Gourlay does not match the recorded shapes of the foraging trips as the Foraging Zone Coefficient indicated more direct trips from Geddes (see IV.3b, page IV-57). This suggests

that trip-based descriptions might differ from results based on pooled data.

d. Foraging volumes

The modelling of the diurnal dive depths revealed deeper dives in the vicinity of the colonies, especially where time-in-areas was important. This particularly impacted chick-rearing birds, as foraging range decreased and point density increased. This finding also confirms the results of Chapter IV showing an increase of the vertical/horizontal distances ratio. Lescroël et al. (2010) also measured an increase in dive depth for Adélie penguins as the season was progressing. They also demonstrated that better breeders were able to perform deeper dives towards the end of the season. Staniland and Boyd (2003) observed differences in depths between shelf, oceanic and far oceanic with more shallower dives offshore in Antarctic fur seals (*Arctocephalus gazella*).

The necessity to dive deeper when closer to the shore could be due to different krill swarms characteristics over the shelf (krill maturity: Ichii et al., 1998 and Atkinson et al., 2008; swarm sizes: Cox et al., 2010; or swarm densities: Cresswell et al., 2009) which might drive penguins to dive deeper to find more rewarding prey patches. This is particularly important as deeper dives represent higher energy expenditure (Wilson, 1993; Blanchet et al., 2013) and imply reduced bottom time (Wilson et al., 1996) and increased post-dive durations for recovery (Lescroël et al., 2010; Bestley et al., 2014). Another possible explanation for deeper dives closer to shore relates to prey depletion due to higher predator densities (Birt et al., 1987; Murphy, 1995) affecting primarily shallower water. Finally, a third factor could be krill predator avoidance behaviour. Zhou & Dorland (2004) reported that krill responded to the presence of predators by forming denser swarms and staying at deeper depths.

e. Spatial and temporal scales

Different techniques used to represent spatial resolution of foraging

The various techniques used in this chapter have different advantages. From the easy and straightforward minimal convex polygon to represent potential foraging areas to the more complex and informative kernel density to represent utilisation distribution, all these techniques have limitations. The first one is not very accurate and might include areas not targeted by birds. The second one requires choices to define the smoothing parameters and the delineation threshold. The grid aggregation technique stands between those two extremes, providing a good representation of the distribution of foraging but it is strongly influenced by the choice of a grid size.

Despite its more complex use, the kernel density area is probably the most accurate technique as it allows to incorporate all the points while smoothing outliers. Combined with a delineation threshold, it is able to define and quantify areas of high foraging concentration.

Spatial resolution

The different data inputs showed varying spatial resolutions from less than a hundred of metres (dive locations) to a few kilometres (foraging modes from method 2). During the spatial aggregation of the different data inputs, convergence with the reference GPS locations happened at scales of a few kilometres. It means that at these scales, the different data inputs showed roughly the same information than the GPS data.

These scales of a few kilometres were comparable to the estimated bandwidth for the kernel density estimators (around 7000 m for incubation and 1500 m for brood). At these scales, the fine noise of the location data was lost and the smoothened hot spot foraging areas were revealed. These spatial resolutions corresponded to fine scale oceanographic biophysical phenomena (Becker and Beissinger, 2003).

Between day and night

During brood, birds from Cape Geddes targeted two distinct locations with either diurnal or overnight trips. According to Ichii et al. (2007), these two areas potentially provide different prey characteristics: the shelf area exploited during diurnal trips has more abundant immature krill but with lower energy content. In addition, in these locations, according to the same authors, krill do important diurnal migrations as they stay nearer to the surface over the slope. Shallower dives, as the ones occurring over the shelf-break, indicate higher prey encounter rates and are therefore linked with better foraging habitats (Bestley et al., 2014). Although chinstrap penguins are considered to be time-minimizers and therefore prefer areas closer to their nests (Blanchet et al., 2013) this study shows that they tended to alternate between both energy-maximizer (longer foraging trips to target better quality prey patches) and time-minimizer strategies. There were no individual preferences with some birds consistently foraging in the same areas but the majority of the individuals alternated between the two locations. This contrasts what Boersma et al. (2009) observed for Magellanic penguins where the majority of the tracked individuals repeatedly targeted the same area. It is worth noting that the birds targeting different areas did not show any significant differences in body weights or mass gains after deployment. It might be possible that birds try to maximise their chances to find prey patches by varying locations and not relying on a single good potential area. Some habitat are predictable and birds will return consistently to these coarse-scale often associated with shelf-edges (Weimerskirch, 2007). It could also be a consequences of the timing required to reach both areas: after an afternoon start and a long overnight trip to the shelf break area, a bird might decide to do a shorter trip over the shelf in the morning. Another explanation could be just the opportunity for a bird to join a group of congeners aiming for a certain location without any real choice of the direction of travel.

The small sample size from Gourlay Peninsula does not allow me to determine whether birds from that colony follow the same pattern. Takahashi et al. (2003) observed shorter diurnal trips and longer

overnight trips from that location, suggesting that this might be the case. However, the longer distance to the shelf-break reduces options for birds from this colony; long overnight trips might simply enable birds to avoid depleted areas or areas with more intense competition and might not offer a different quality of prey field, as I hypothesize for Cape Geddes.

Between incubation and brood

At the scale of the breeding season, the main driver of change is the constraint of feeding the chicks after hatching. The subsequent reduction in foraging range has a cascade effect on the accessibility of the foraging areas: smaller fishing grounds will have to be shared by more birds. This higher bird density leads to an increase in predatory pressure and competition, resulting to deeper dives.

The prey patches might be depleted, especially in the shallower strata of the water column or might react and dive deeper to avoid predators. They might also use oceanographic features like continental shelf-break to escape predators. Birds might then target shallower areas where the prey cannot escape: see Takahashi et al. (2003) who observed benthic feeding in chinstrap penguins from Signy Island.

The combination of increased food demand from the offspring, higher intra-specific competition due to a reduction of available habitat and potential prey depletion or avoidance creates an increase in foraging pressure for breeding birds after hatching. Additional human-related impacts on the birds, their ability to forage or their prey distribution and abundance can have important negative effects on their breeding success.

f. Limitations and implications for the habitat modelling

Limitations

Due to the different sample sizes between colonies and phenological stages, it is difficult to gain a comprehensive comparison between sites across the breeding season. The number of recorded trips showed a strong influence on the convergence of the spatial distribution of the data and therefore on the delineation of the foraging hot spots.

In terms of data quality, the mix of spatio-temporal scales from the different data input, especially the ones that are influenced by trips with missing TDR data (foraging modes), increases the difficulty in getting a clear picture of the spatial distribution. Comparison of the different data inputs is also more difficult. As a lot of the trips with missing TDR were recorded from Gourlay Point, it contributes to the difficulty in comparing both sites.

The key spatial and temporal scales for the distribution of the bird locations are too coarse in comparison with the scales driving prey swarms distribution (hundreds of metres horizontally, tens of metres vertically and few hours in terms of temporal scales, Macaulay et al., 1984). Pooling foraging tracks by breeding stages allows me to increase sampling size and cover higher areas, but this reduces the spatio-

temporal resolution of the data, masking fine-scale phenomena that might alias or match krill swarms dynamics.

Implications

Although the previous chapters did not show strong differences between both colonies in terms of trip characteristics (Chapter IV) and inferred behaviour modes (Chapter V), the spatial distribution of the core foraging areas identified by this chapter showed some important local effect. The oceanographic features influencing prey distribution and the available habitat are quite different from both colonies. This limitation will have to be considered carefully during my habitat modelling chapter, especially with respect to considerations of scale during the evaluation of whether a single model is transferable to different colonies.

The previous chapters generated several data inputs which showed some degree of convergence, but also some differences. At this point, it is not possible to assess their contribution and validate one or another as being a more accurate representation of the foraging. All these data inputs will therefore be used in my habitat modelling (Chapter VII).

Some results from this chapter confirmed the importance of integrating the vertical dimension of foraging as well as different finer temporal scales (diurnal versus nocturnal). Keating & Cherry (2009) suggest it is necessary to develop utilisation distribution models based on four dimensions (3 spatial dimensions and time) to include more detailed spatio-temporal interactions. This has the potential to detect changes and hot spots at a finer scale.

Finally, information about the prey field increasingly stand out as the missing piece of the puzzle. Any fine scale temporal and/or spatial changes are potentially linked with prey distribution and variation. Without any evidence from the distribution of krill and its spatio-temporal variability, it is difficult to validate any finding or conclusion about predator distribution and dynamics.

Chapter VII FORAGING HABITAT MODELLING

This chapter will combine the different data inputs from the previous chapters with environmental covariables to derive foraging habitat predictions for the whole South Orkney archipelago. The different models will be compared, evaluated and validated to select the strongest final habitat model.

VII.1 Introduction and aims

In conservation, marine spatial planning and fisheries management, knowing how key species use their environment is a crucial aspect of objective, evidence-based evaluation. It can support the definition and delineation of protected areas or other important areas (Key Biodiversity Areas, Important Bird Areas), it can also drive policies or mitigation procedures (Pichegru et al., 2012). Data generated by tracking studies can help defining the most used areas (Tancell et al., 2013; Soanes et al., 2015).

The concept of habitat has been used by many authors and has different definitions and underlying aims depending upon context. It is organism-specific and contributes to the definition of their ecological niche, different species will use different habitats which fluctuates with time and space over different scales (Hall et al., 1997). For chinstrap penguins, their habitat will change between the austral winter and summer seasons. During the breeding period, there is the reproductive land-based habitat and, centred on the colony, their at-sea foraging habitat. In the previous chapters, several changes in their foraging behaviour have been highlighted within the breeding season before and after hatching. And in Chapter V, some behavioural changes at the scale of the foraging trip have been described. The standard definition of habitat proposed by Hall et al. (1997) includes "the resources and conditions present in an area that produce occupancy".

For marine predators, obtaining information about the spatial distribution of their food resources is difficult as it is patchy, invisible from the surface and varies with time. Therefore the identification of their foraging habitat has to rely on the "conditions" where the animals are as an indication of the availability of their food resources. To define and model these foraging habitats and their variability through time, I will use the location data identified in the previous chapters indicating probable foraging behaviour. I will also use maps of oceanographic features that can indicate krill hot spots (Santora et al., 2012) and covariables from remote sensing as proxies for prey distribution (Boyd et al., 2015).

The relationship between the location data from both study sites and the different variables will be processed by several different algorithms to produce predictions of foraging habitat interpolated for all the chinstrap colonies of the South Orkney Islands. Different methods will be used to evaluate and validate the models and identify the method, data input and variables providing the best foraging habitat model. This model should

integrate habitat preference, accessibility and competition (Wakefield, Phillips and Matthiopoulos, 2009).

VII.2 Method

The habitat models were developed from the various data inputs generated in the previous chapters. Four different modelling algorithms were used to contrast the environmental conditions between locations where the birds were considered to be foraging and locations where they were not. Two different modelling rounds were computed to compare the influence of the temporal resolution at which environmental variables were averaged.

a. Environmental variables

The environmental variables (also called explanatory variables) used for the habitat modelling were either static in time (constant at the temporal scale of this study: bathymetry and derived variables, benthic morphology and geometric variables) or dynamic (sea surface temperature, net primary productivity, mean sea level anomalies, sea ice cover and surface currents).

Bathymetry and benthic geomorphic classes

The shape and depth of the seabed have an influence on vertical water movement and structure and therefore productivity. They can also be used as landmarks by diving predators (Mattern et al., 2007). Some studies have found evidence of benthic feeding in chinstrap penguins which is obviously dependent on bathymetry (Takahashi et al., 2003; Kokubun et al., 2010).

A high resolution bathymetry model for the South Orkney Islands was obtained from Dickens et al. (2014). The slope and aspect (orientation of the sea floor) maps were derived from the bathymetry data using the R "raster" package (Hijmans, 2016). A geomorphic classification of the benthic zone was also provided by Dickens et al. (2014, supplementary materials). All these variables had a resolution of approximately 300 m.

Geometric variables

A series of "geometric variables" were used to incorporate the constraints related to the colony locations for central-placed foragers such as chinstrap penguins. They also included an estimation of bird at-sea densities to integrate intraspecific competition. Finally this group of variables also incorporated the distances to the continental slope which is agreed to be a favourable habitat (Ichii et al. 1998; Trathan et al. 2003; Trathan et al. 2006; Atkinson et al. 2008; Siegel et al. 2013).

To map the distance to the closest chinstrap colony, a cost distance analysis was performed using the "gdistance" R package (van Etten, 2015). This allowed me to incorporate the land as a barrier in the calculation of the distances by attributing a very high friction value to the land pixels (999999) in contrast to a low value for the sea pixels (1).

A similar process was performed but with the 500 m isobaths lines as starting points to generate the distance to the 500 m isobaths map.

The bird at-sea density map was generated as a function of distances to the closest colony and population size at the colony. For all chinstrap known nesting site on the South Orkney Islands, a density estimate was calculated for each pixel of the study area using Equation iii (Wakefield et al., 2011):

$$Dens_c = \frac{Pop_c}{Dist_c{}^2}$$

Equation iii: Calculation of the at sea bird density raster for a focal colony c as a function of the population of the colony (Pop_c) and cost distance ($Dist_c$) from each pixel to the focal colony.

The resulting density maps for each focal colony were then summed to obtain the final bird density raster. The resolution of these geometric variables matched the grid size of the bathymetry variable (approximately 300 m).

Dynamic environmental variables

A series of physical and oceanographic dynamic variables recorded from various remote sensing sources were included to map local changes in the environment. These variables might indicate upwelling and high productivity and therefore prey availability (Becker and Beissinger, 2003; Pinaud and Weimerskirch, 2005; Bost et al., 2011).

Sea surface temperature (SST) is one of the main driver of nutrient availability and therefore biological processes (Lima, Olson and Doney, 2002). This was measured from the MODIS instrument (Werdell et al., 2013; Ocean Biology Processing Group, 2015) at a spatial resolution of approximately 4 km and aggregated over the phenological stage (round 1) or over 7 days (round 2).

Net primary productivity (NPP) was used as an indication of local marine productivity (Kokubun et al., 2015). It was derived from chlorophyll and temperature data measured by MODIS using the Vertically Generalized Production Model (Behrenfeld and Falkowski, 1997; Ocean Productivity, 2015). The resolution of this dataset was approximately 8 km. The original daily data were averaged to generate a weekly temporal resolution dataset.

Sea level anomaly was derived from altimeter satellites provided by COPERNICUS, the European Earth Observation Programme (Copernicus - Marine environment monitoring service, 2015). The spatial resolution was approximately 12 km. As the original data were available at the daily resolution (sea level anomaly, SLA), its values were averaged over 7 days to produce the mean sea level anomaly (MSLA).

Sea ice concentration was measured using several passive microwave instruments and was processed using the algorithm developed by the NASA team (Cavalieri et al., 1992, 2015). The spatial resolution was approximately 18 km and the original daily data were averaged over 7

days to produce weekly sea ice concentration. The presence of fast ice (sea ice that is attached to land) can have a positive effect on phytoplankton communities with a positive cascade on higher trophic levels, but also a negative impact on ice-avoiding species like chinstrap penguins (Fraser et al., 1992). Long trend series of fast-ice extend in the South Orkney Islands showed a decline in fast-ice and important annual variation, which can be linked with larger scale atmospheric events like El Niño–Southern Oscillation (Murphy et al., 1995). Despite being a potentially key environmental variable, it is difficult to use remote sensing technologies to distinguish fast-ice with sea-ice that has been pushed along coastal regions.

Finally, surface currents play an important role in the distribution of nutrients and prey transport and replenishment (Murphy et al., 1998; Hunt Jr et al., 2016). Current data used in this study were generated by the Earth & Space Research (ESR, 2009) from multiple sensors and satellites (Bonjean and Lagerloef, 2002). From the surface current vectors, the speeds and directions were extracted. The temporal resolution was 5 days and the spatial resolution was approximately 19 km along parallels and 34 km along meridians.

All the spatial and temporal resolutions for these variables are summarized in Table VII-1.

Variable processing and resolutions

The environmental variables were cropped based on the maximum range measured by incubation trips, rounded at the nearest 100 km (300 km). The resulting extent of the studied area was between latitude 63.5° S and 57.9° S and longitude 52.1° W and 39.0° W. All the environmental variables were re-projected using the coordinate reference system used for this project (Universal Transverse Mercator projection centred on zone 23 south, EPSG 32723).

Figure VII-1 presents the resolutions of the different environmental variables in relation to the spatial extent of the brood foraging trip; from the very high resolution bathymetry (343m) to the coarse current data resolution (34.6 km along lines of latitude). For modelling, all the environmental variables were resampled to match the resolution of the finest spatial grid (bathymetry). The gridded values for the new environmental rasters with higher spatial resolution were generated using a bilinear interpolation method (Hijmans, 2016).

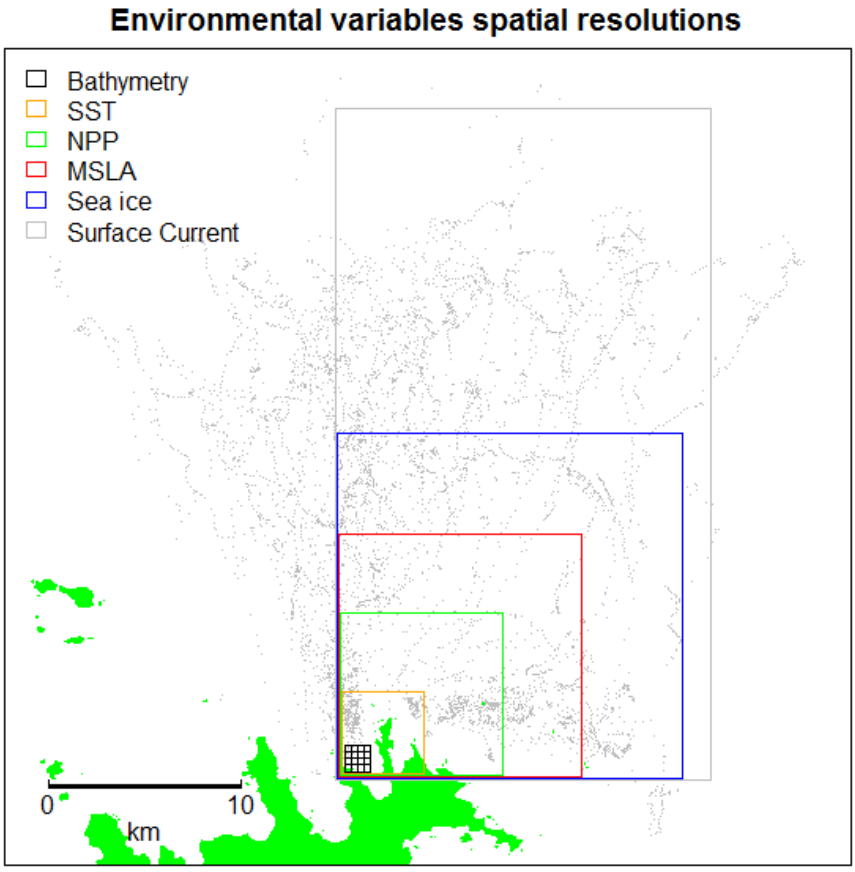

Figure VII-1: Original grid sizes of the different environmental variables in relation to the extent of the brood foraging from Cape Geddes.

In terms of temporal resolutions, the varying environmental variables were averaged at the scale of the breeding season for modelling round 1 (see VII.2c). For round 2, a weekly resolution (or 5 days for the currents, see Table VII-1) was used.

Table VII-1: Spatial and temporal resolutions for the different environmental variables.

Description	Spatial (km)	Temporal
Bathymetry	0.344	-
Slope	0.344	-
Aspect	0.344	-
Geomorphic classes	0.344	-
Distance to colonies	0.344	-
Distance to 500m isobaths	0.344	-
Bird at sea density	0.344	-
Sea Surface Temperature (SST)	4.130	7 days
Net Primary Productivity (NPP)	8.260	7 days
Mean Sea Level Anomalies (MSLA)	12.400	7 days
Sea Ice Cover	17.700	7 days
Surface Currents	19.150 (Long.) 34.645 (Lat.)	5 days 5 days

b. Foraging versus non-foraging

All the different modelling approaches contrasted the environmental variables for the locations that could be considered as foraging (presence) with non-foraging locations (pseudo-absences, Aarts et al. 2008). These foraging and non-foraging locations had different definitions for each data inputs.

For each GPS point (data input 1), one pseudo absence location within the corresponding minimal convex polygon for the colony and breeding stage (see VI.2d, page VI-119) was randomly generated. For the dive locations data input (2), each one-minute interpolated location associated with a dive deeper than 5 m was attributed as a foraging location (true presence). Locations without dives (or dives shallower than 5 m) were considered as pseudo-absences. For the inferred foraging modes (data inputs 3a, 3b, 4a and 4b), each one-minute interpolated location within an inferred day or night foraging segment was considered as foraging (true presence). The locations from segments attributed to other inferred behaviours (resting, commuting and exploring) were classified as pseudo-absences. See Table VII-2 for a summary of the classification of the different data input as presence or pseudo-absence points.

For each data input true presence (foraging) or pseudo-absence (non-foraging) location, the explanatory variables were extracted according to both modelling temporal resolutions (breeding stage or week) and the time stamp of the location.

Table VII-2: Methods for the classification of the different data input as presences or pseudo-absences for the modelling

Input		Include missing TDR	Presence	Pseudo-absence
1	GPS locations	Yes	GPS filtered location	Random location within MCP
2	Dives	No	1 minute interpolated location with dive >5 m	1 minute interpolated location without dive or < 5 m
3a	Foraging modes (Method 1)	No	1 minute interpolated location within an inferred day or night foraging segment	1 minute interpolated location outside an inferred day or night foraging segment
3b	Foraging modes (Method 1)	Yes		
4a	Foraging modes (Method 2)	No		
4b	Foraging modes (Method 2)	Yes		

Out-of-range points.

In order to account for accessibility and to force the model to discard areas that were beyond the maximum recorded foraging distance from the colonies, random out-of-range points were generated. For incubation, 1000 random points were produced outside a 205.5 km buffer zone from land. For brood, 1700 random points were generated

outside a 37.2 km buffer zone from land to have a similar random point density for both breeding stages. Figure VII-2 shows the distribution of these random out-of-range points for incubation and brood.

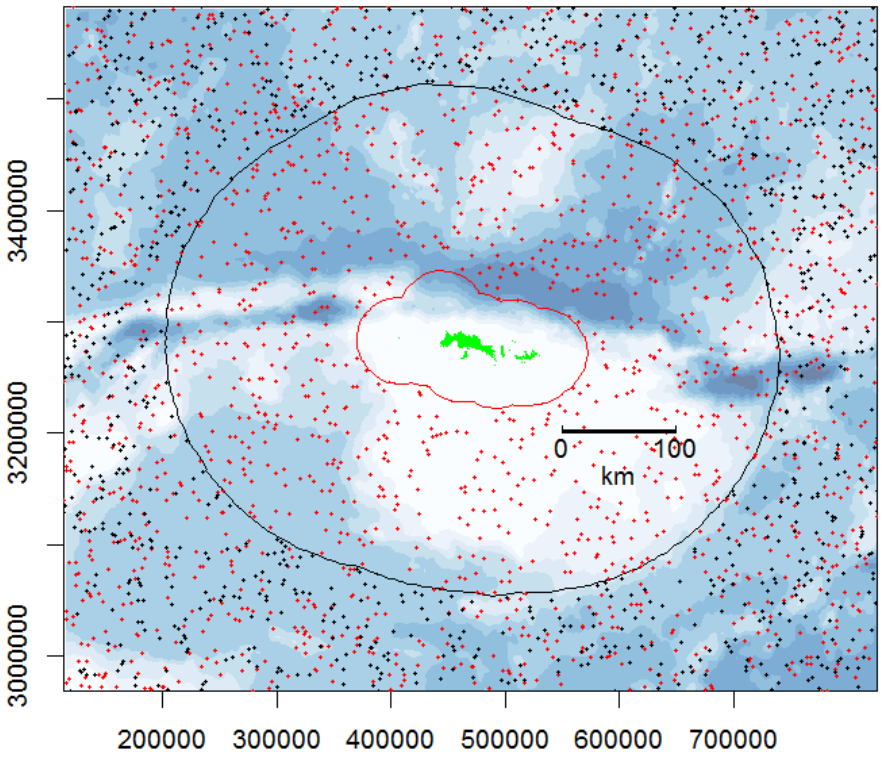

Figure VII-2: Out of range random locations for incubation (black dots) and brood (red dots). The black and red lines represent buffer areas of respectively 205.5 and 37.2 km from land.

Because these out-of-range random locations didn't have a time stamp, the associated dynamic explanatory variables were extracted from the averaged values by breeding stage for both modelling rounds (see VII.2c).

c. Modelling approaches

The modelling techniques used in this study included the maximum entropy approach (MaxEnt, Phillips et al. 2004), the Generalised Boosting Models (GBM also called boosting regression trees, BRT, Friedman 2001), the Generalised Additive Models (GAM, Hastie & Tibshirani 1990) and the random forest (RF, Breiman 2001). Incubation and brood data were modelled separately to generate one foraging habitat model for each breeding stage.

Two rounds of modelling were run in order to compare the influence of the temporal resolution while aggregating environmental variables that varied in time. The first round was based on the temporal resolution of each breeding season stage (incubation and brood). The explanatory variables were extracted to each data input according to the whether they would belong to an incubation or a brood trip. For the second round, the environmental variables were aggregated on a weekly temporal scale. The values for each data input were extracted based on the time stamp of the data location (year and week number). The second round approach

allowed to include a seasonality effect, as the locations along trips recorded in 2013-14 would match the conditions of that year instead of an average between both 2011-12 and 2013-14 seasons.

d. Model evaluations and validations

In order to compare the different modelling techniques, temporal resolutions and data inputs, the model performances were evaluated. In addition, the outcomes of each model (habitat probability map) were validated using two different techniques.

Model evaluation

To assess the model's performances, the receiver-operating characteristics (ROC) and the derived areas under the curves (AUC) were calculated using the "pROC" R package (Robin et al., 2011). This method was suitable for "presence/absence" binary data and was comparable across the difference modelling techniques.

Validation using krill survey

A key validation process in foraging modelling is to try to integrate the distribution of prey (Boyd et al., 2015). In this chapter, I will use the data obtained from a ship-based krill survey carried out in 2011-12 around the South Orkney Islands. Due to instrument calibration issues, the data from this survey could not be used as absolute values to generate individual krill abundance. Nevertheless, I believe the data are still useful as relative values, allowing me to compare areas with relatively high and low krill abundances.

For each ship location, the krill backscatter signal was summed throughout the water column. Then the locations were aggregated by hour for the validation of the incubation models and by 30 minutes for the validation of the brood models. The median was used to aggregate the krill values. By comparing these values with the habitat modelling, I was able to evaluate the correlation between the relative krill values and the probability of foraging from the models.

Site cross-validation

Another way of validating the model which also helped to assess how the model results might be suitable for the other surveyed colonies in the archipelago was to use a site cross-validation process. A separate model was run for each colony data. The correlation between both results was computed using a pixel by pixel comparison (Levine et al., 2009). It was also possible to compare the predicted probability of foraging generated by one of the colonies model with the observed activity of birds from the other colony. This enabled me to generate another set of area under the curves values (AUC).

Final foraging habitat

By ranking the scores evaluating the different modelling approaches (model performance, krill validation and site cross-validation), it was

possible to determine which modelling technique, which temporal resolution and which data input was providing the best model for chinstrap penguins foraging habitat around the South Orkney Islands.

Seasonality

To assess the effect of the season, independent models based on the 2011-12 and 2013-14 data were created with the dynamic variables matching the season. Predications were then modelled with the observed seasonal conditions and compared using a similar pixel-by-pixel comparison as used during the site cross-validation.

e. Summary of the process

Figure VII-3 summarizes the process from the different data location inputs, the matching static and dynamic environmental variables and the two modelling rounds with the different algorithms. From the habitat prediction modelling outputs, the validation step allowed me to identify the best combination of data input, modelling technique and temporal scale to generate the final habitat foraging model.

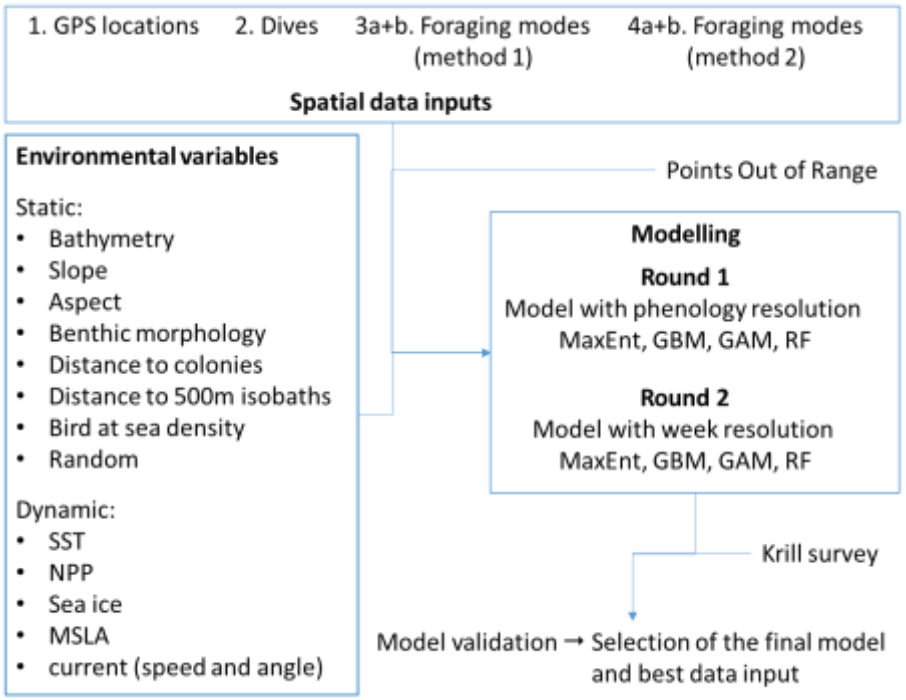

Figure VII-3: Worflow summary showing the different data inputs, environmental variables, modelling round and the final validation process.

VII.3 Results

a. Environmental maps and envelopes

In this section, the different environmental variables included in the habitat model are summarized on maps and figures. The later show the distributions of the values within the potential foraging zones (minimum convex polygons based on the GPS locations, see VI.2d, page VI-119) and at the different data input locations. The average values within the

potential foraging zones per phenological stage and for each colony are presented in Table VII-3. The values for the dynamic environmental variables presented here were aggregated by phenological stage and therefore used during modelling round 1.

*Table VII-3: Average values for each environmental variable within the minimal convex polygon associated with each colony and each breeding site; *: for these categorical variables, the reported value is the mode.*

	Incubation		Brood	
Variable	Gourlay	Geddes	Gourlay	Geddes
Bathymetry (m)	-1577	-3585	-237	-1015
Slope (%)	3.22	7.23	1.89	11.96
Aspect *	SW	SE	SW	N
Geomorphic classes *	Shallow flat ocean	Shallow flat ocean	Cross shelf valley	Steep shelf slope
Distance to colonies (km)	80.9	111.8	13.1	18.8
Distance to 500m isobaths (km)	39.0	89.2	48.6	8.3
Bird at sea density	0.0004	0.0002	0.0017	0.0013
Sea Surface Temperature (SST, °C)	-1.16	-0.66	-0.34	-0.41
Net Primary Productivity (NPP, mg C m^{-2} day^{-1})	269.9	257.4	487.5	229.7
Mean Sea Level Anomalies (MSLA, m)	0.057	0.055	0.053	0.044
Sea Ice Cover (%)	5.2	1.3	0.0	0.0
Current speed (m s^{-1})	0.048	0.101	0.053	0.061
Current direction *	E	E	SE	W

Benthos variables

The bathymetry, its derived variables (slope and aspect) and the benthic morphology maps are presented in Figure VII-4 with the minimal convex polygons. Figure VII-5 presents the proportion of the different values available within the minimal convex polygons and "used" by the birds (values extracted from the locations of the different data input).

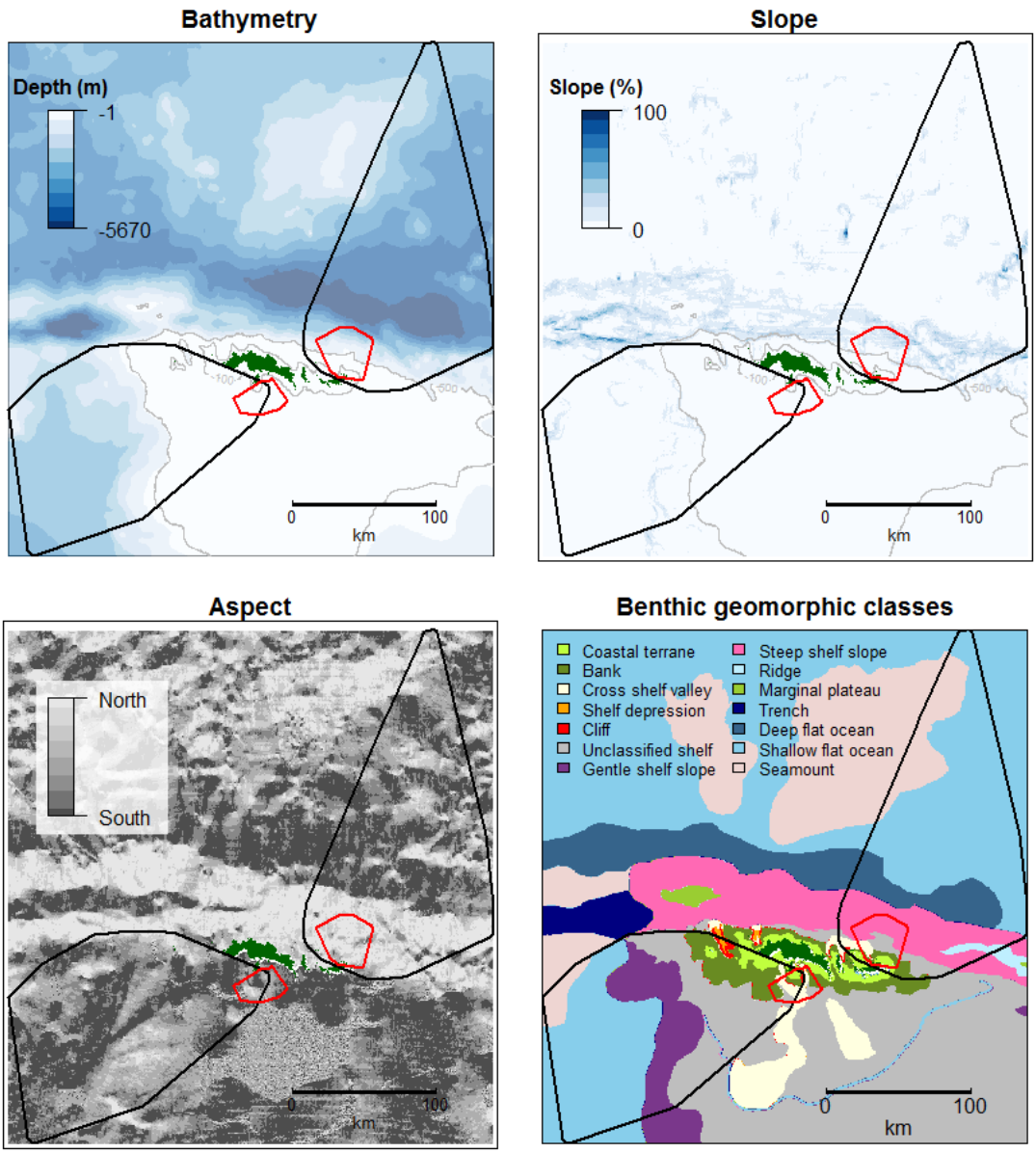

Figure VII-4: Maps showing the spatial variation of the bathymetry and derived metrics (slope and aspect) and the diversity of benthic geomorphic categories. The polygons represent the potential foraging areas during incubation (black) and brood (red) defined using the minimal convex polygon method from the GPS dataset.

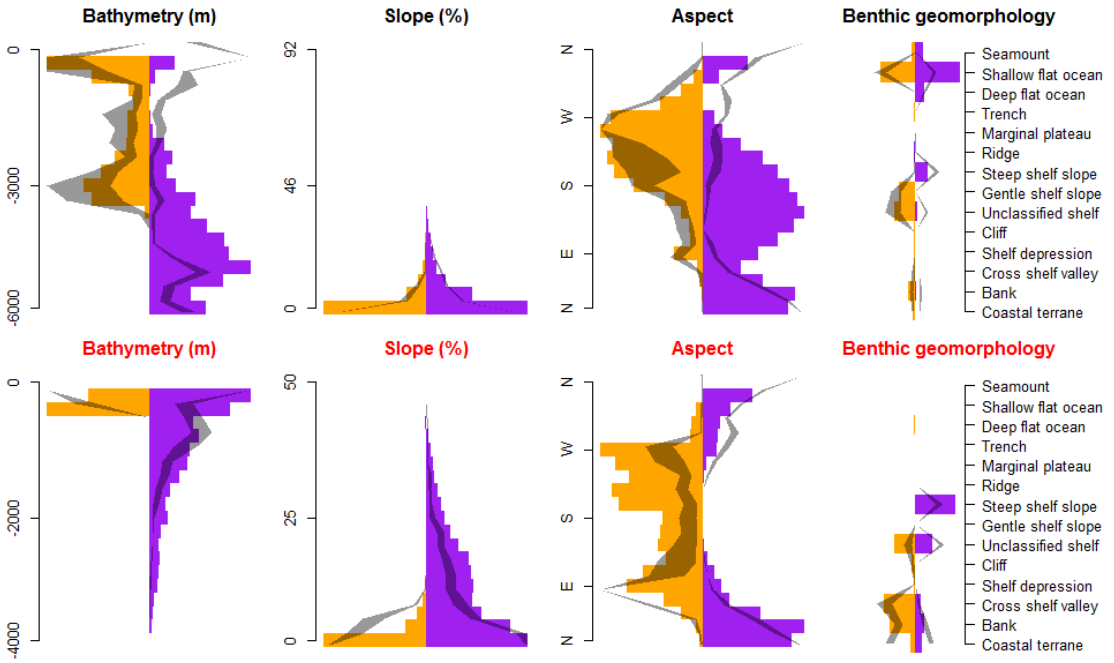

Figure VII-5: Proportion of the different bathymetry and derived variables and benthos categories within the potential foraging areas from Gourlay Peninsula (orange) and Cape Geddes (violet) during incubation (top graphs) and brood (bottom graphs). The grey shading represents the variability of the values extracted at the foraging locations corresponding to the different data inputs.

The birds from Cape Geddes had access to deeper waters during the whole breeding season (see also the availability of the "Deep flat ocean" benthic category). But during incubation, they mostly stayed in shallower waters, which confirmed the shorter incubation trips previously mentioned for this colony. The slopes available were also steeper from Cape Geddes and the "Steep shelf slope" benthic category was available before and after hatching. In terms of aspect, the birds from Geddes stayed mainly over north facing slopes during both stages, although they had access to a wider range of orientation bathymetry during incubation. Birds from the Gourlay Peninsula mainly used all the range of available conditions, except for the aspect: they mainly stayed over south-west facing slopes during incubation and east facing slopes during brood.

Geometry variables

The maps on Figure VII-6 show the spatial distribution of the different geometric variables in relation to the potential foraging areas indicated by the minimal convex polygon for each colony and breeding stage. Figure VII-7 reports the proportion of the different geometric variables available to and used by the birds for each colony and breeding stage.

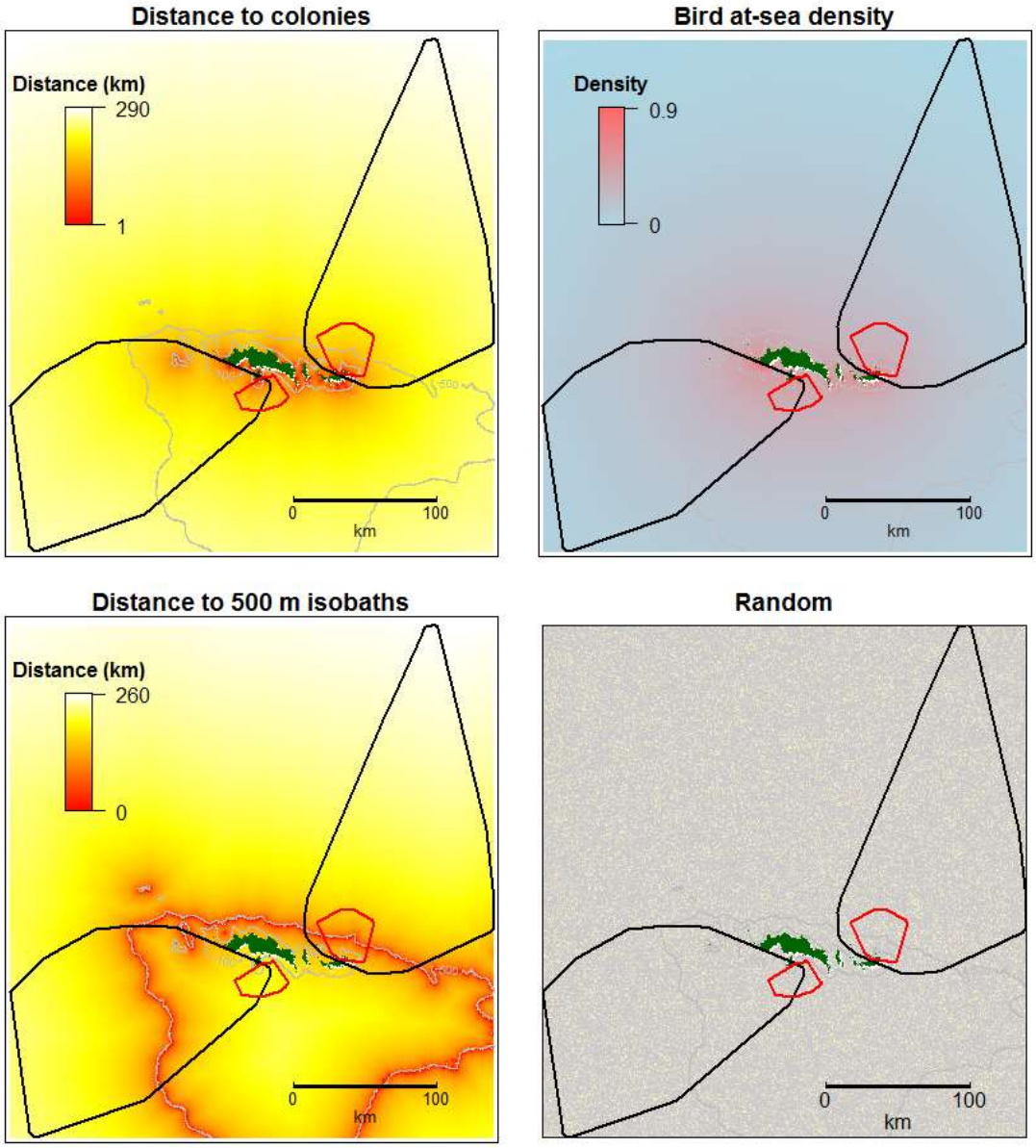

Figure VII-6: Maps showing the spatial variation of the geometry variables (distances to the colonies, distances to the 500 m isobaths and bird at-sea density). The random noise variable is also reported. The polygons represent the potential foraging areas during incubation (black) and brood (red) defined using the minimal convex polygon method from the GPS dataset.

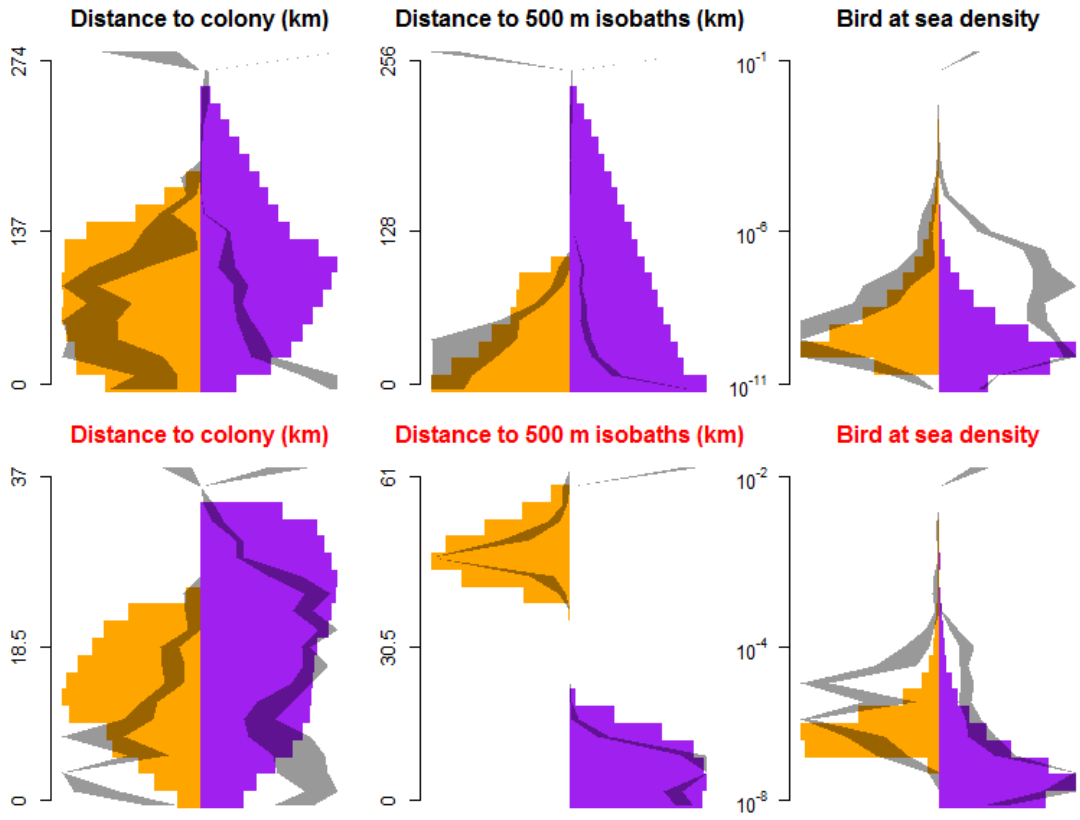

Figure VII-7: Proportion of the different geometry variables within the potential foraging areas from Gourlay Peninsula (orange) and Cape Geddes (violet) during incubation (top graphs) and brood (bottom graphs). The grey shading represents the variability of the values extracted at the foraging locations corresponding to the different data inputs.

Although the potential foraging areas from Cape Geddes covered a wider range of distances from the colony, the birds spent most of their time closer to their nests, especially during incubation. During brood, the bimodal shape of the distances from Geddes corresponded to the two distinct foraging areas discussed in the previous chapter (over the shelf and off the shelf, see VI.3e, page VI-126). From the Gourlay Peninsula, the brooding birds seemed to stay closer to the colony.

The access to the shelf break, illustrated by the distance to the 500 m isobaths, was one of the most distinctive features between both colonies, especially during brood when the birds from the Gourlay Peninsula did not access the oceanographic slope. During incubation, although the potential foraging area from Cape Geddes expended beyond the shelf break, most of the birds stayed in the vicinity of the slope.

The bird at-sea density within the potential foraging areas was slightly higher from the Gourlay Peninsula than from Cape Geddes. The distribution of the data points in relation to the density did not demonstrate a clear avoidance of the most used areas. On the contrary, the birds seemed to prefer to forage in areas of higher densities (especially birds from Cape Geddes during incubation and to a lesser extent, birds from the Gourlay Peninsula during brood). The general increase in density after hatching described in the previous chapter was also visible in Figure VII-7.

Environmental variables

Figure VII-8 maps the sea surface temperature and the net primary productivity in relation to the potential foraging areas for each colony and breeding stage. On Figure VII-9, the spatial distribution of the mean sea level anomalies and the sea ice concentration are mapped. And Figure VII-11 maps the surface current vector fields aggregated by breeding stages. Figure VII-10 and Figure VII-12 represent the proportion of the values from these environmental variables available and used by the birds.

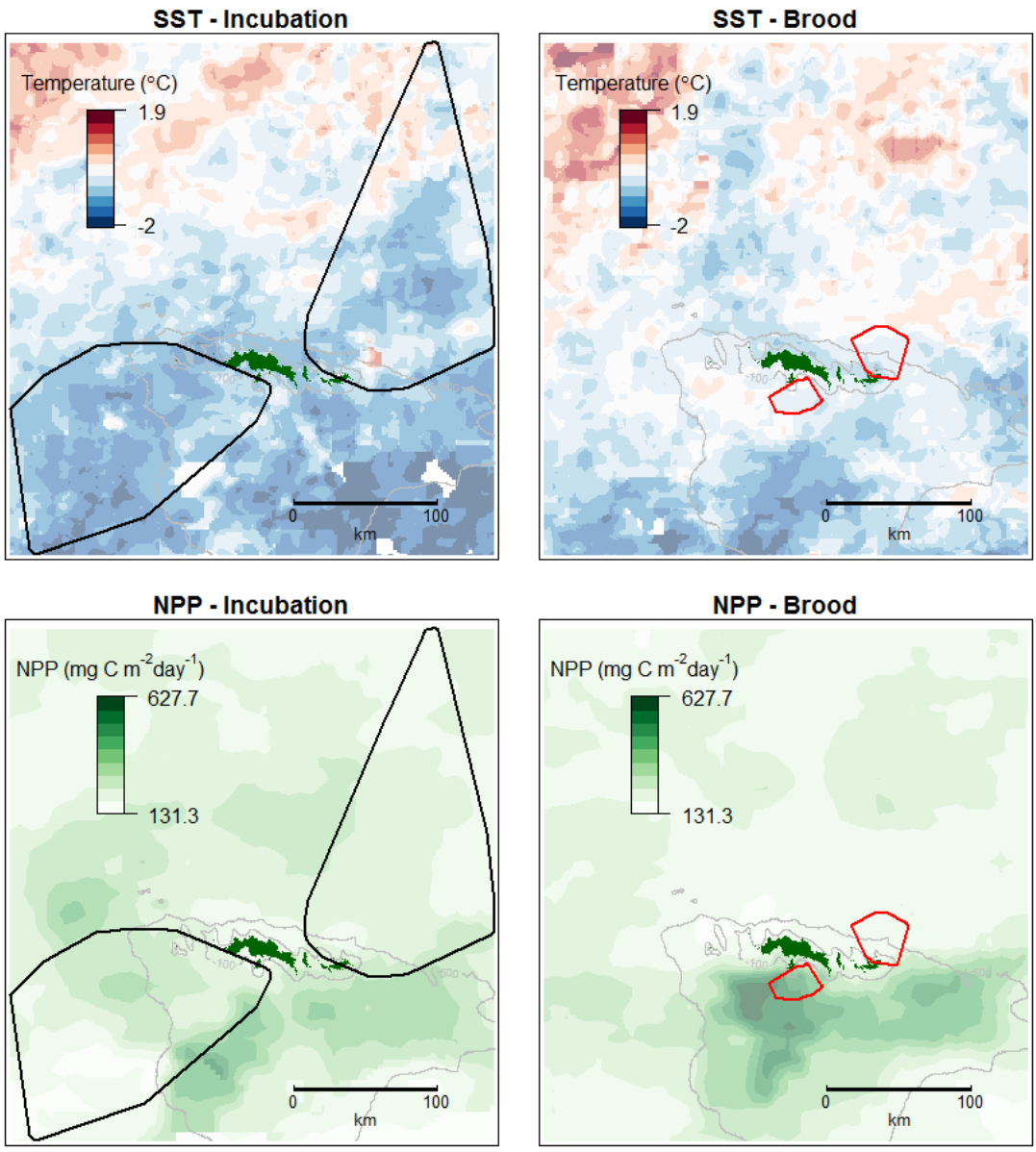

Figure VII-8: Maps showing the spatial variations of the sea surface temperature (SST) and net primary productivity (NPP) averaged by phenological stage (incubation to the left and brood to the right). The polygons represent the potential foraging areas during incubation (black) and brood (red) defined using the minimal convex polygon method from the GPS dataset.

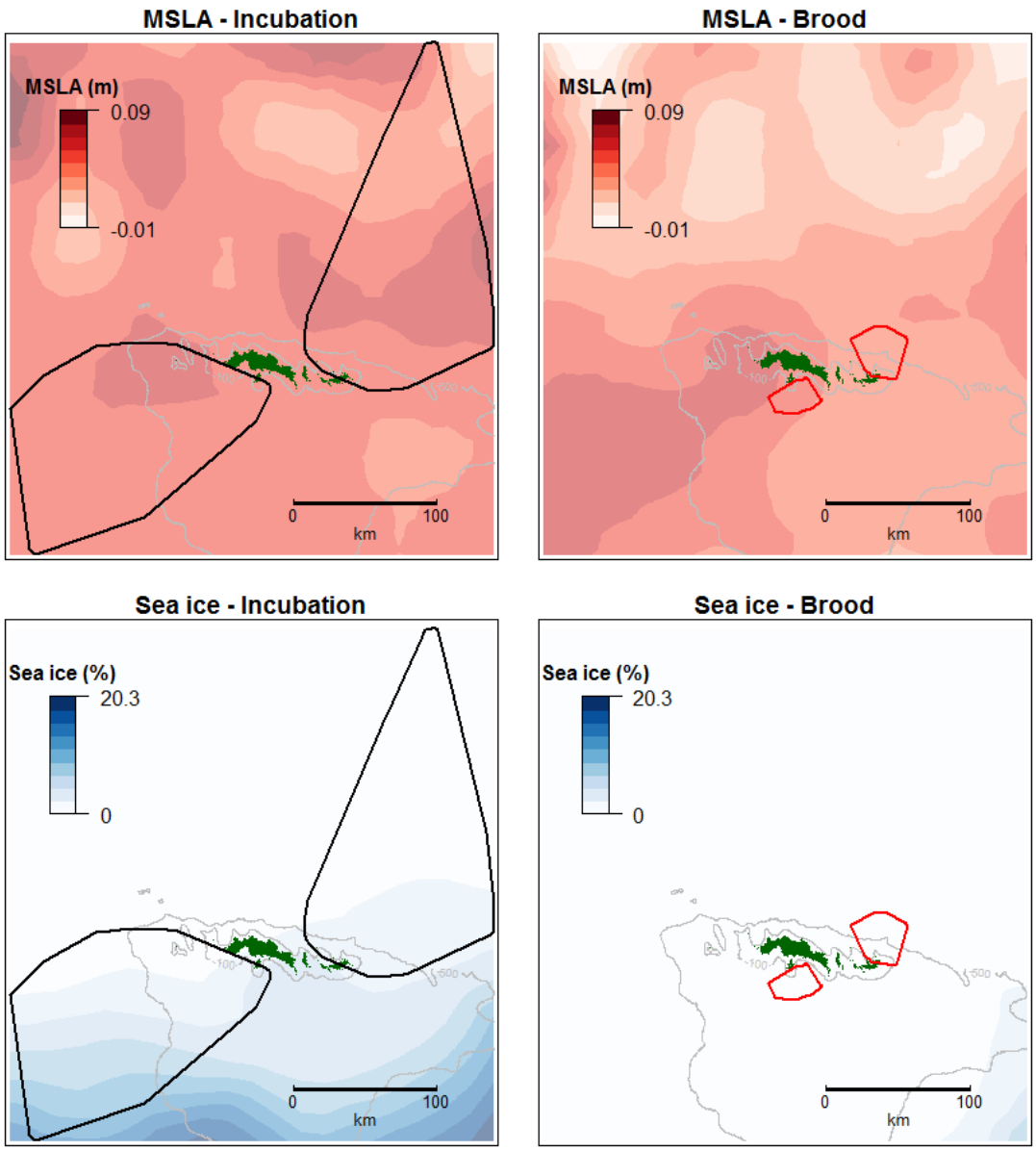

Figure VII-9: Maps showing the spatial variations of the mean sea level anomalies (MSLA) and sea ice cover averaged by phenological stage (incubation to the left and brood to the right). The polygons represent the potential foraging areas during incubation (black) and brood (red) defined using the minimal convex polygon method from the GPS dataset.

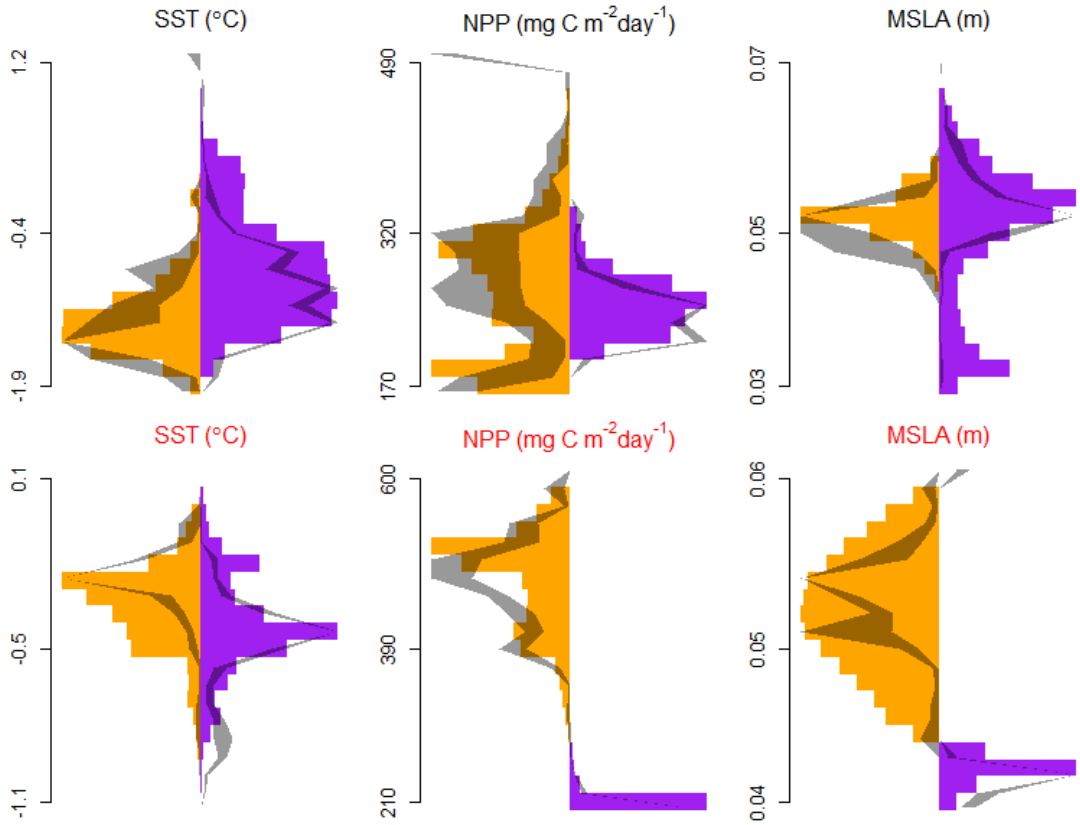

Figure VII-10: Proportion of the sea surface temperature (SST), net primary productivity (NPP) and mean sea level anomaly (MSLA) averaged within the potential foraging areas from Gourlay Peninsula (orange) and Cape Geddes (violet) during incubation (top graphs) and brood (bottom graphs). The grey shading represents the variability of the values extracted at the foraging locations corresponding to the different data inputs.

The average sea surface temperature within the potential foraging areas increased during the austral summer as expected. The temperatures were colder around the Gourlay Peninsula during incubation (average of -1.16°C versus -0.66°C from Cape Geddes) due to the presence of sea ice south of the archipelago. During brood, the difference was reversed and the waters around the Gourlay Peninsula were slightly warmer (average of -0.34°C versus -0.41°C for Cape Geddes). This could be due to shallower water, weaker currents and a weaker influence from vertical currents due to the distance from the closest bathymetric slopes. These factors potentially reduced water mixing and increased warming. The bird utilisation matched the range of available temperatures, except during brood when birds from the Gourlay Peninsula tended to stay in warmer waters as the birds from Cape Geddes showed a secondary peak in colder water. This could match the over the shelf foraging hot spot, as temperature appeared to be colder in that specific area (see Figure VII-8).

The range of values for the net primary productivity within the potential foraging areas from the Gourlay Peninsula was wider than within the area from Cape Geddes. Productivity was also much higher during brood along the south coast of the archipelago and this was particularly true during the 2013-14 season (see Figure VII-13). This could be explained by higher sea-ice concentrations earlier in the year that might have increased the algal bloom after melting (see Appendix IV). The birds

exploited the available range of productivity values and did not show any clear preference towards areas with high productivity.

The distribution of the mean sea level anomaly values was very similar for both colonies, although the potential foraging areas from Cape Geddes included a secondary peak with lower values. Interestingly, these lower values were not targeted by the birds. During brood, the range of available values was very different between both sites, with a reduction of measured anomalies in the vicinity of Cape Geddes.

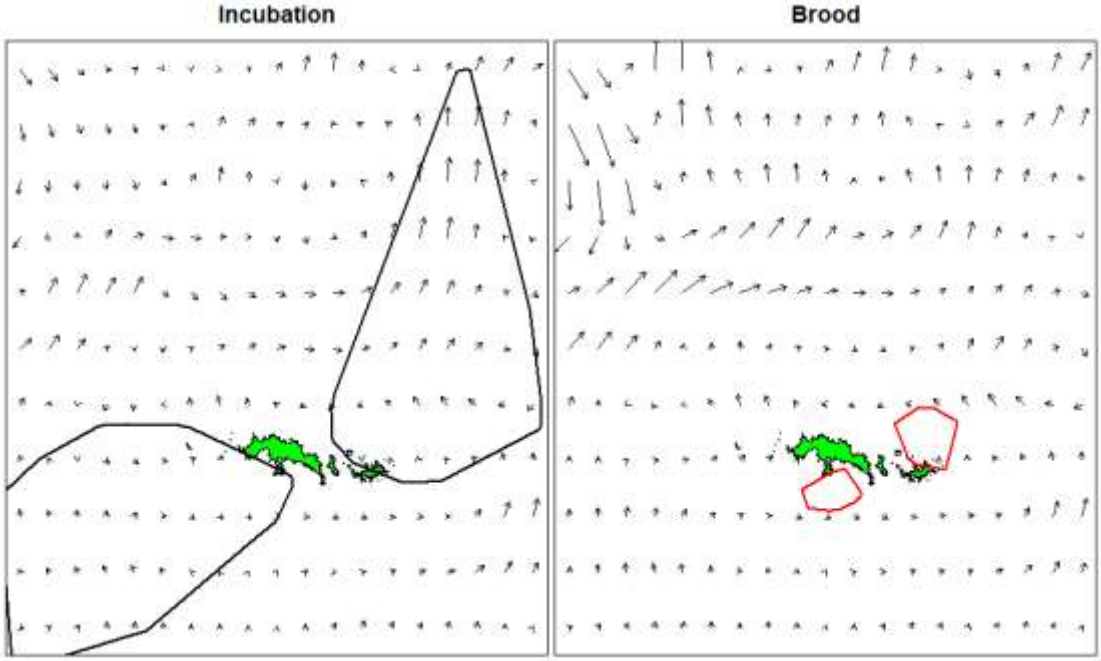

Figure VII-11: Maps showing the current fields averaged by phenological stage (incubation to the left and brood to the right). The polygons represent the potential foraging areas during incubation (black) and brood (red) defined using the minimal convex polygon method from the GPS dataset.

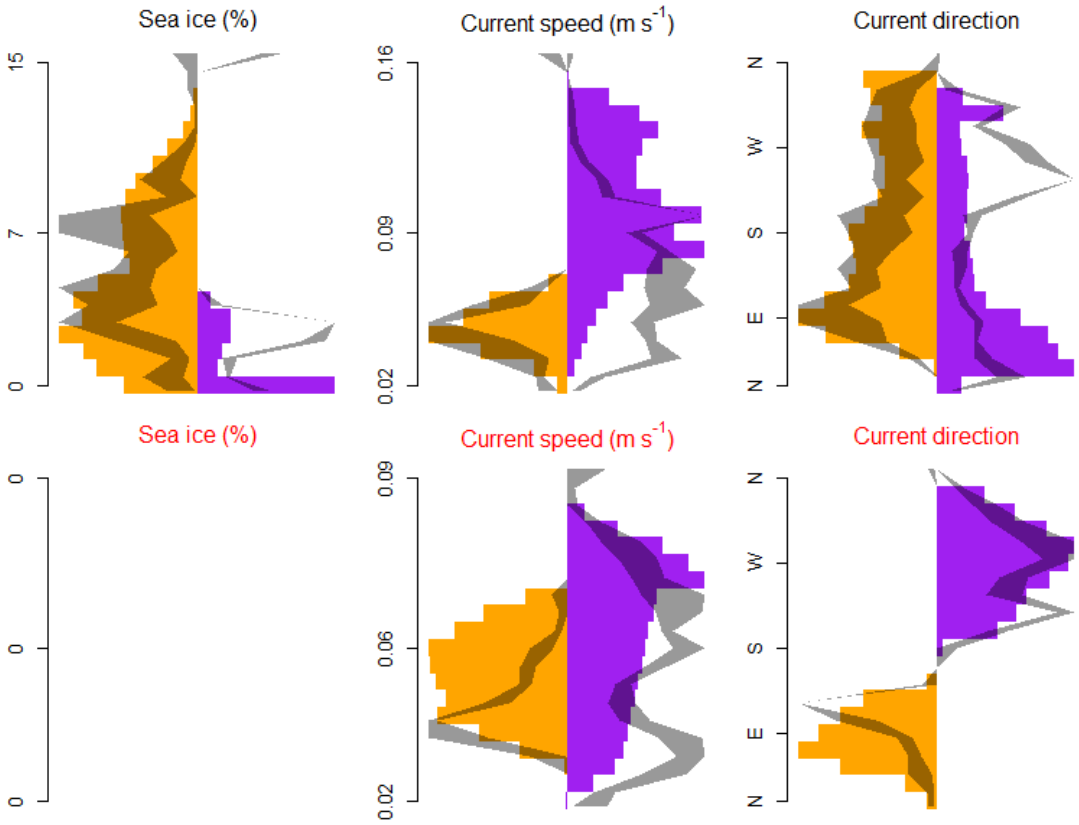

Figure VII-12: Proportion of the sea ice cover, current speed and current direction averaged within the potential foraging areas from Gourlay Peninsula (orange) and Cape Geddes (violet) during incubation (top graphs) and brood (bottom graphs). The grey shading represents the variability of the values extracted at the foraging locations corresponding to the different data inputs.

During incubation, sea ice cover was more important within the potential foraging areas for Gourlay Peninsula as discussed previously (III.1a, page III-40). After hatching, the sea ice disappeared from the waters surrounding the archipelago. It is worth noting that the presence and amount of ice was very different between seasons 2011-12 and 2013-14 (see Appendix IV).

The currents were stronger within the potential foraging areas for Cape Geddes, especially off shore in the zones that could be reached by longer incubation trips. During that stage, most of the birds stayed closer to the shore where the currents were weaker. During brood, the birds from Gourlay Peninsula avoided the stronger currents. From Cape Geddes, the bimodal distribution of the current speed corresponded to the two foraging hot spots: over the shelf in weaker currents and off the shelf in stronger currents. During incubation, the birds from Gourlay Peninsula exploited the wide range of current directions, as from Cape Geddes, the birds that stayed in the vicinity of the colony were mainly in westerly currents and the birds that travelled further off shore were in north-easterly currents. During brood, the main current directions from both colonies were opposite and the birds didn't seem to target any specific direction.

The weekly variations for the different environmental variables are presented in Appendix IV; Figure VII-13 shows the example of the NPP,

stressing the importance of seasonality in the range of available conditions.

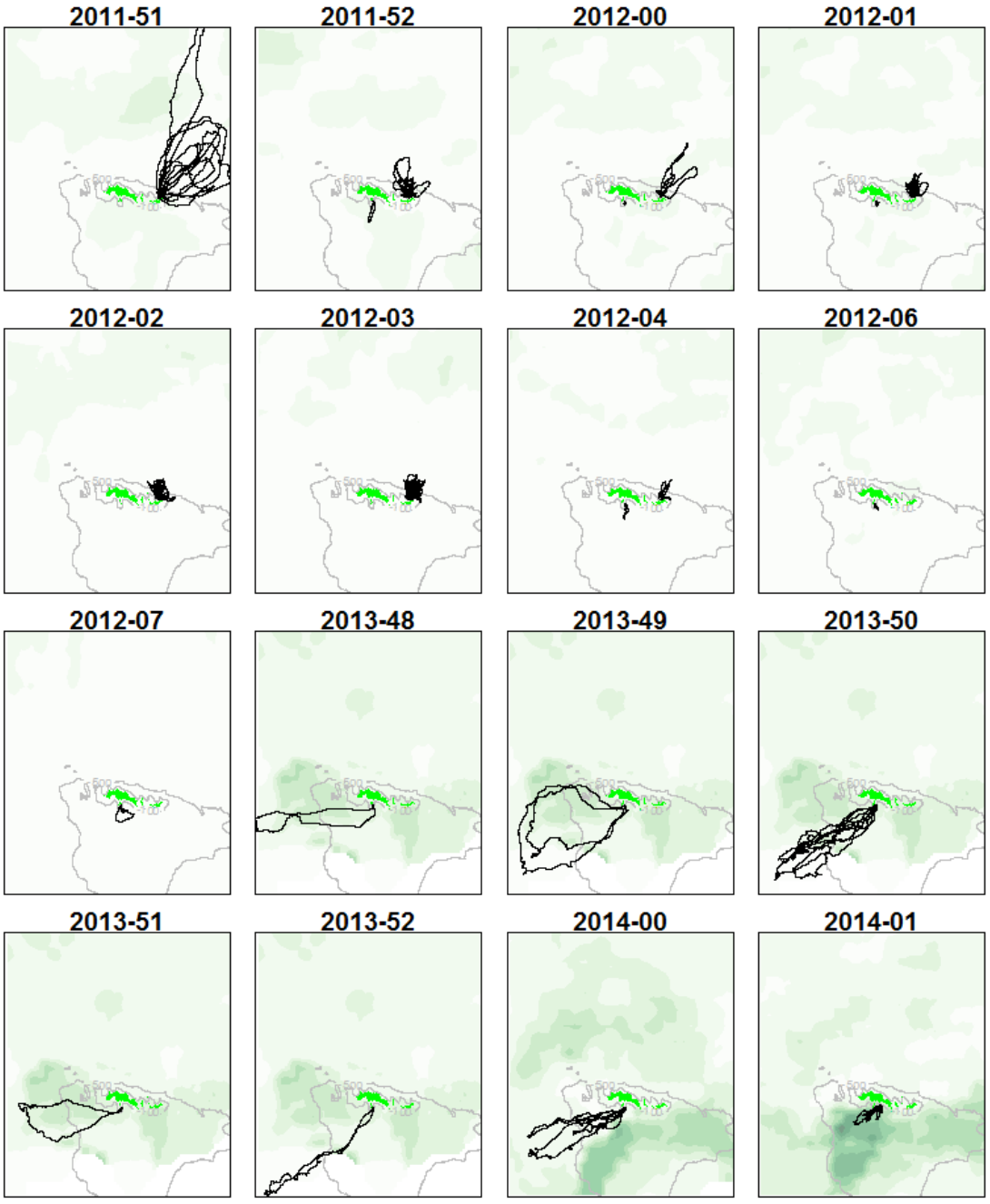

Figure VII-13: Weekly variability of the NPP variable with the matching sampled trips from both colonies during seasons 2011-12 and 2013-14. The other variables are presented in Appendix IV.

b. Model evaluations

All the model prediction output maps are presented in Appendix V. Figure VII-14 shows the distribution of the area under the curves values for the different modelling rounds, breeding stages and modelling techniques. Most of the AUC values were in the "useful application" threshold (0.7-0.9) defined by Swets (1988). MaxEnt, GBM and GAM

algorithms showed similar accuracies, but the random forest method provided much higher performances (above 0.9).

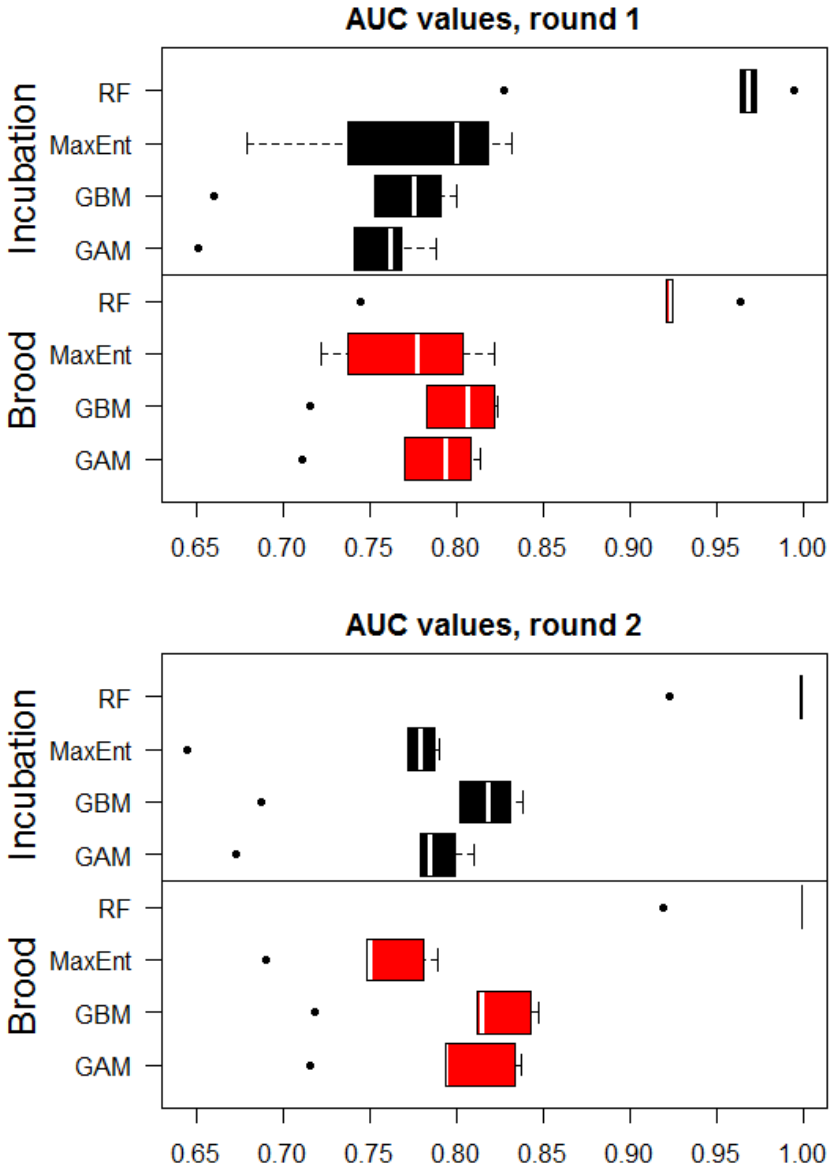

Figure VII-14: Distribution of the area under the curves (AUC) values for both modelling rounds, phenological stages and modelling algorithms.

In terms of temporal resolution, the second round of modelling with the dynamic variables aggregated on a weekly scale mostly showed an increase in performance, especially for the random forest algorithm. Despite relatively good performances during the first modelling round, the output foraging probability maps for the random forest algorithm showed some signs of over-fitting (Figure VII-15 for an example based on data input 4b).

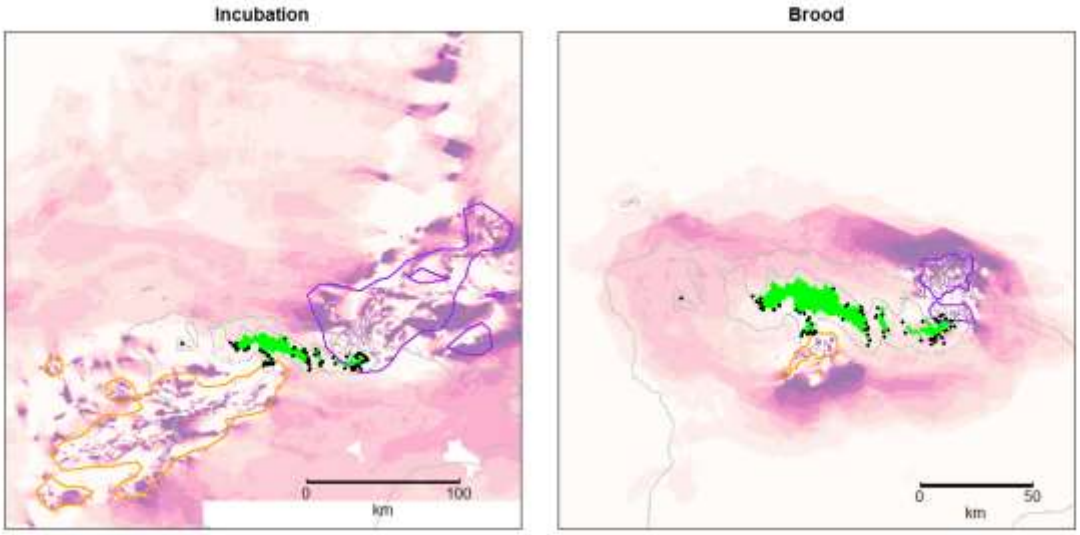

Figure VII-15: Foraging habitat probability maps built from data input 4b with the dynamic variables aggregated by phenological stage (round 1) and a random forest algorithm. The orange and violet polygons represent the 75% utilisation distribution of the data input for Gourlay and Geddes locations respectively.

c. Model validations

Krill survey

Figure VII-16 shows the krill relative measures aggregated every 30 minutes overlaying the foraging model for incubation (model produced by round 2, data input 4b and random forest algorithm).

The Pearson correlation coefficients between the measured krill values and the habitat modelling probabilities were very low. For incubation, only 18% of the correlation were statistically significant, but most of them showed a positive correlation. For brood, 85% of the correlation were statistically significant and all of them were positive. The best score for incubation was attributed to data input 1a (GPS points) based on the GBM algorithm and the dynamic variables aggregated by phenological stages (round 1), but it indicated a negative correlation. For brood, the highest score was given by data input 4a (behaviour mode inferred by method 2 without missing TDR data) based on the GBM algorithm and the dynamic environmental variables aggregated by weeks (round 2).

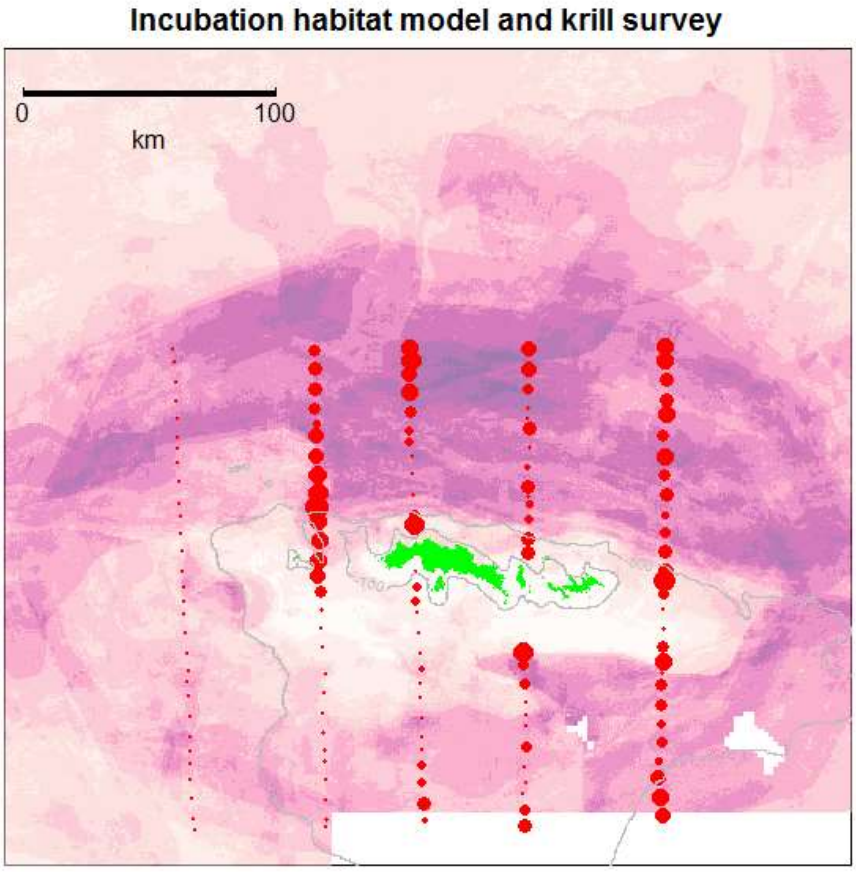

Figure VII-16: Krill transects and relative measures aggregated every 30 minutes overlaying the foraging habitat model for incubation. Model generated by round 2, data input 4b and random forest algorithm.

Site cross-validation

Figure VII-17 shows an example of the overlap between habitat model predictions based on Geddes only and Gourlay only data (model issued by round 2, data input 4b and random forest algorithm). The map indicates that the model generated by the Gourlay Peninsula data was able to identify most areas with high probability of foraging generated from the Cape Geddes data. The reverse did not seem to be true, as the model created from the Cape Geddes colony failed to identify foraging areas south of the archipelago.

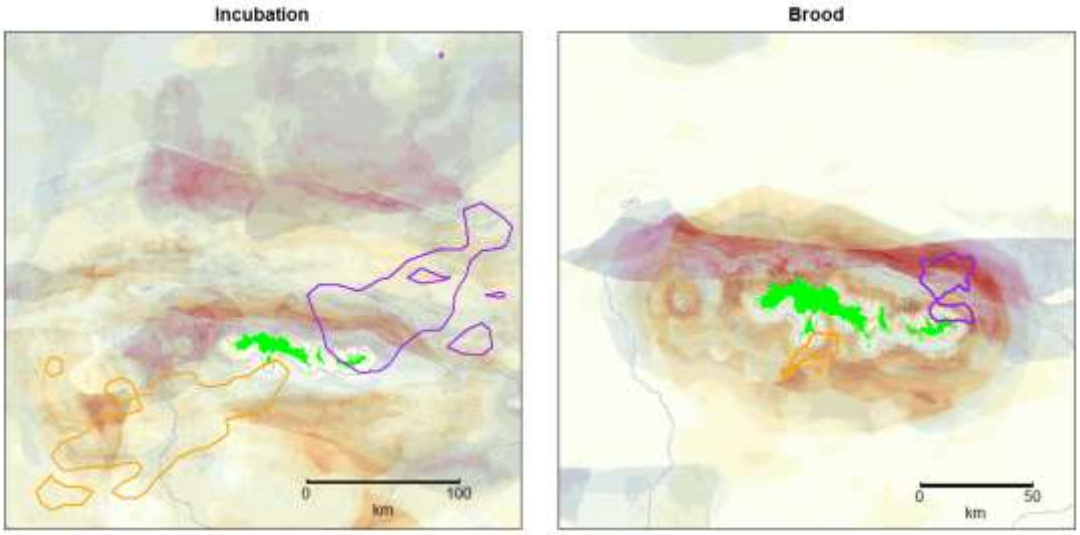

Figure VII-17: Site cross-validation of the habitat model. The orange shading represents predictions identified using the Gourlay Peninsula dataset while the violet shading is inferred from the Cape Geddes dataset. Model generated by round 2, data input 4b and random forest algorithm. The orange and violet polygons represent the 75% utilisation distribution of the data input from Gourlay and Geddes locations respectively.

The AUC values from the cross-validation process were in the low accuracy range (Swets, 1988): between 0.49 and 0.66 for incubation and 0.45 and 0.79 for brood. The highest scores for both phenological stages were given by the GPS dataset (1a) and the random forest algorithm during the first round of modelling (dynamic variable aggregated at the scale of the breeding stages). The pixel-by-pixel correlations were all significant and two-thirds of them were positive, although the Pearson coefficient were quite low (ranging from -0.57 and 0.62 for incubation and -0.30 and 0.81 for brood). The highest scores were obtained for data input 3a (foraging behaviour inferred from method 1 without missing TDR) and data input 1a (GPS points) for incubation and brood respectively. Both generated using the random forest algorithm and using the dynamic variables aggregated by phenological stages (round 1).

d. Final foraging habitats

Input selection

All the different model combinations (except the MaxEnt results, as these were excluded from the cross-validation process due to poor model performance) were ranked based on the AUC score, the correlation coefficient with the krill data, the AUC score and the correlation coefficient from the cross-validation process. All the ranks were summed to provide a final rank score. Table VII-4 presents the 10 best models for both phenological stages; all the results are reported in Appendix VI.

Table VII-4: The 10 best ranking models defined by the model performance (AUC), the validation with the krill data (Spearman correlation coefficient), the site cross-validation performance (AUC) and spearman correlation coefficient. "+" and "-" indicate positive and negative correlation. Greyed coefficient are statistically non-significant. Bold rows indicate the final best model[1].

Round-Input-Model	Model performance AUC	Rank	Krill validation Correlation	Rank	Site cross-validation AUC	Rank	Correlation	Rank	Final Rank
INCUBATION									
2-4a- RF	0.9996	2	0.27 +	4	0.6241	2	0.30 +	9	17
2-4b-RF	**0.9989**	**4**	**0.29 +**	**2**	**0.5701**	**7**	**0.22 +**	**10**	**23**
1-1a-RF	0.9949	5	0.11 -	19	0.6647	1	0.53 +	4	29
2-2b-RF	0.9227	10	0.21 +	9	0.5571	16	0.45 +	8	43
2-3b-RF	0.9991	3	0.27 +	3	0.5261	28	0.20 +	11	45
2-4b-GBM	0.8020	16	0.19 +	11	0.5855	4	0.11 +	16	47
1-1a-GBM	0.7910	19	0.30 -	1	0.5661	9	0.02 +	20	49
2-3a-RF	0.9997	1	0.21 +	10	0.5276	27	0.12 +	14	52
2-4a-GBM	0.8180	14	0.22 +	7	0.5528	20	0.17 +	12	53
1-3a-RF	0.9716	7	0.02 +	28	0.5536	18	0.62 +	1	54
BROOD									
2-4b-RF	**0.9996**	**3**	**0.36 +**	**3**	**0.6425**	**3**	**0.60 +**	**2**	**11**
2-3a-RF	0.9997	2	0.31 +	7	0.6470	2	0.42 +	9	20
1-1a-RF	0.9639	5	0.28 +	17	0.7914	1	0.81 +	1	24
2-4a-RF	0.9997	1	0.34 +	4	0.6197	8	0.36 +	12	25
2-3b-RF	0.9994	4	0.31 +	9	0.6162	9	0.46 +	7	29
2-2b-RF	0.9190	10	0.32 +	6	0.6017	11	0.51 +	4	31
2-4b-GBM	0.8430	12	0.36 +	2	0.6141	10	0.01 +	21	45
1-4a-RF	0.9244	7	0.27 +	18	0.5891	16	0.48 +	5	46
2-4a-GBM	0.8470	11	0.36 +	1	0.5760	20	0.14 +	17	49
1-2b-RF	0.7444	29	0.29 +	14	0.6216	7	0.48 +	6	56

The random forest algorithm generated 70% and 80% of the 10 best overall scores for incubation and brood respectively. The models based on the weekly aggregation of the dynamic variables (round 2) represented 70% of the 10 best overall scores for both incubation and brood.

In terms of data input, data 4a (behaviour modes inferred from method 2 without missing TDR data) had the highest overall score for incubation and data 4b (behaviour modes inferred from method 2 with missing TDR data) had the highest score for brood.

The later data input (4b) had the best combined overall score and was therefore chosen as the final habitat model.

Habitat map

The final habitat prediction map based on data input 4b using the random forest algorithm and the dynamic variables aggregated on a weekly basis is shown in Figure VII-18. The black and red insets detail a trough along the northern shelf break which is believed to be an important krill retention area (PN Trathan pers. comm.). The blue inset on the brood

[1] The round corresponds to the temporal aggregation of dynamic environmental variables (1: scale of the phenological stages, 2: weekly scale). The data inputs are: 1 GPS locations, 2 dive locations, 3 foraging modes inferred from method 1, 4 foraging modes inferred from method 2, a indicate the use of complete trips only, b corresponds the whole data set with and without missing TDR measurements. The models are: GBM Generalised Boosting Models, GAM Generalised Additive Models, RF random forest.

foraging prediction shows how the eastward foraging zone used by the birds during diurnal only trips was integrated in the prediction.

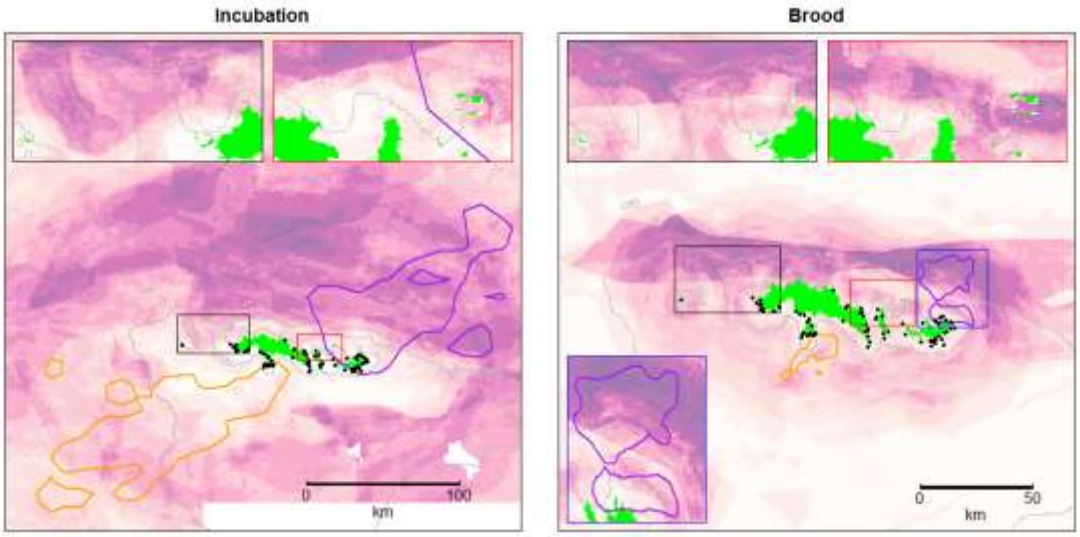

Figure VII-18 : Final habitat map for incubation (left) and brood (right). The orange and violet polygons represent the 75% utilisation distribution of the data input for Gourlay and Geddes locations respectively. The black dots show the location of the known chinstrap colonies. The balck inset represents the Monroe and Coronation troughs, the red inset represents the Powell trough. The blue inset details the brood foraging habitat from Cape Geddes with both over the shelf and off the shelf foraging zones.

Variable importance plots

The variable importance scores for modelling round 2 and the random forest algorithm are presented in Figure VII-19. Most of the variables, except the sea ice, were above the random variable. The main driving variable for both phenological stages was the distance to the colonies, which was expected for a central place forager. The bird at-sea density came second for both stages. The ranking of the variables was very similar for both stages, the main differences being a higher importance for the mean sea level anomalies before hatching and a higher importance for current direction after hatching.

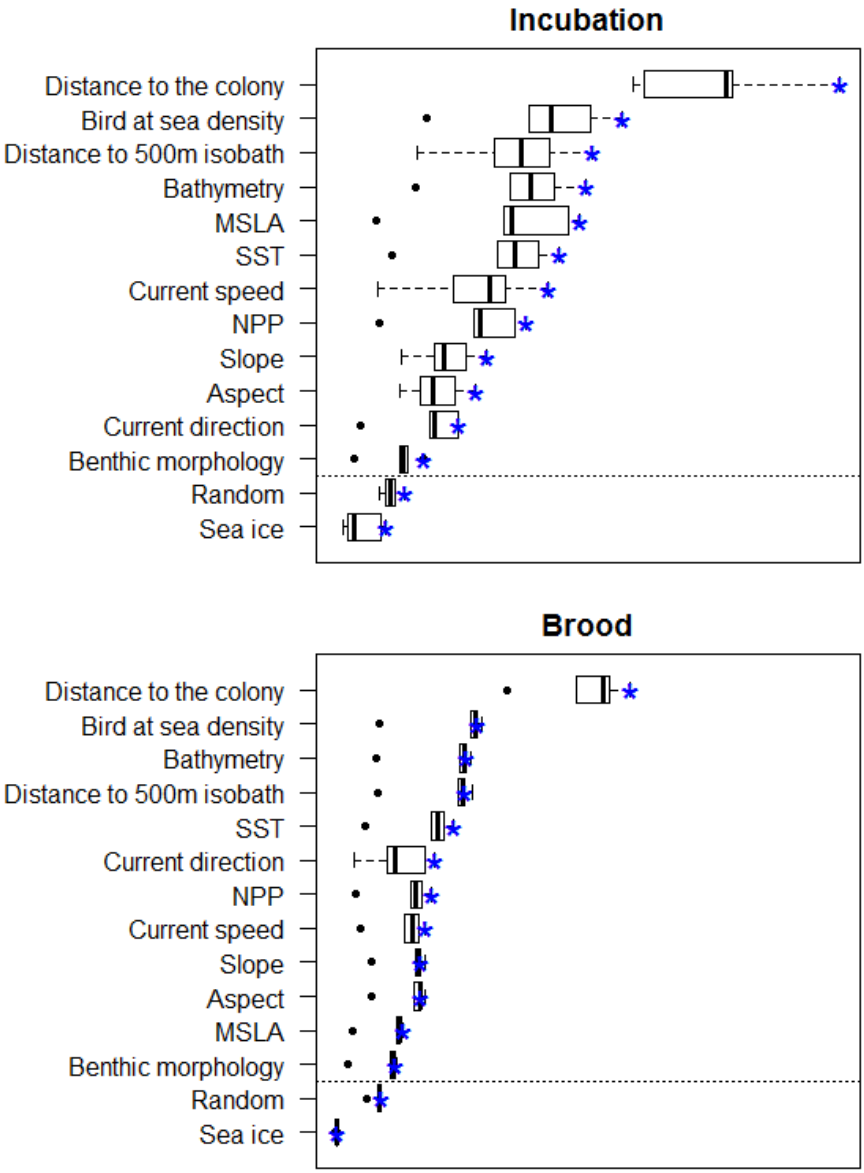

Figure VII-19: Variable importance plots for incubation and brood for round 2 models with the random forest algorithm. The blue stars represent the scores for data input 4b.

Partial dependence plots

The partial dependence plots for the eight most contributing variables for the models are presented on Figure VII-20 for the incubation model and Figure VII-21 for the brood model.

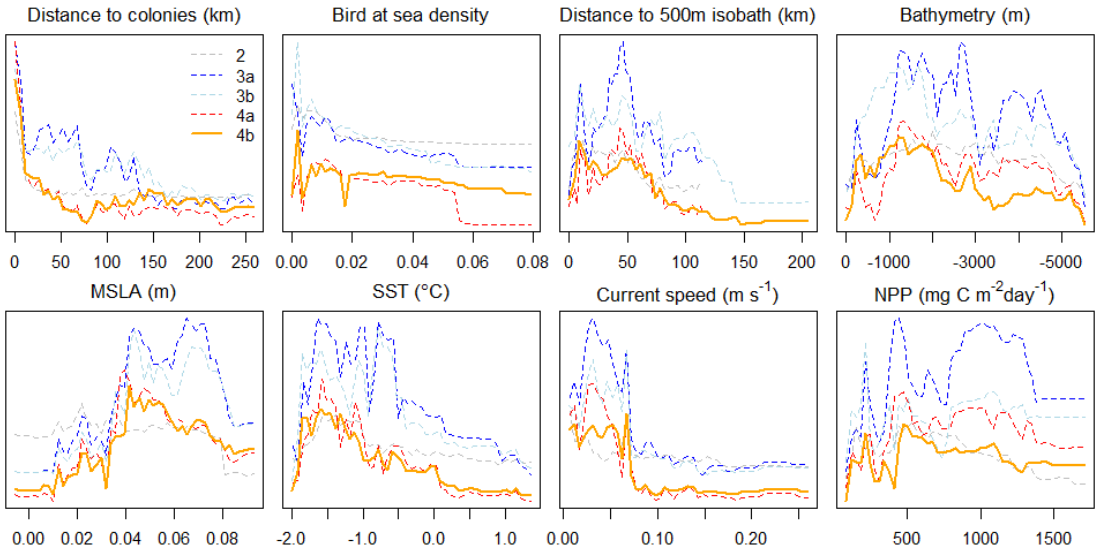

Figure VII-20: Partial dependence plots for the eight most contributing variables for incubation for the different data inputs. Higher values reflect higher foraging probabilities.

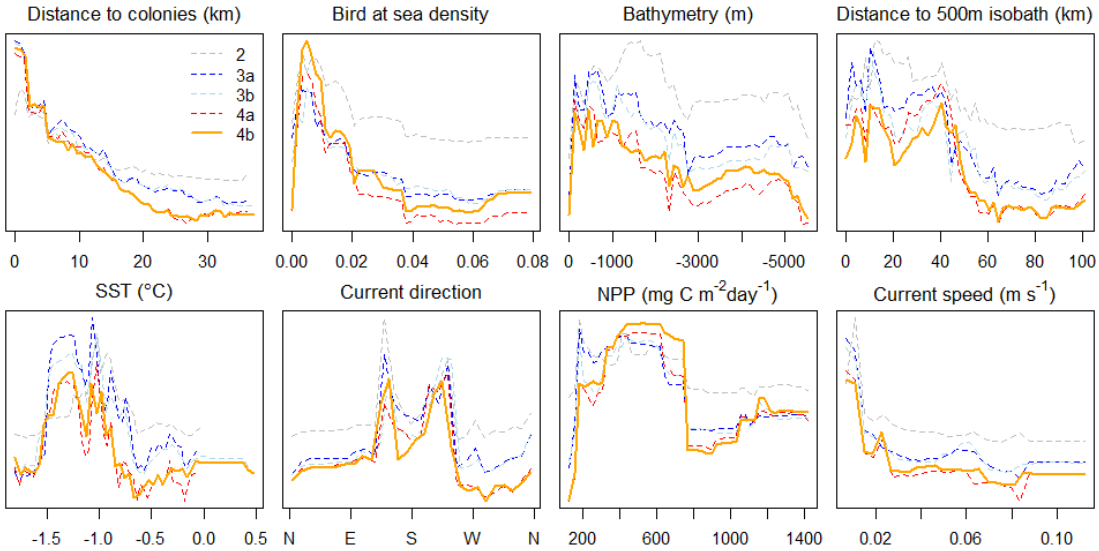

Figure VII-21: Partial dependence plots for the eight most contributing variables for brood for the different data inputs. Higher values reflect higher foraging probabilities.

These partial dependency plots show that favourable foraging habitat was in the vicinity of the colonies (less than 50 km during incubation and less than 15 km during brood). The model also predicted that good foraging habitat was also in areas with lower bird at-sea densities, especially during brood, which is contradictory with the environmental envelopes showing no clear avoidance of high bird at sea densities by the tracked individuals (see VII.3a). Although areas with very low densities were also unfavourable; which could indicate areas too far from the colonies and inaccessible by birds. Favourable foraging habitats were also in the vicinity of the 500 m isobaths (less than 75 km during incubation and less than 50 km during brood). Very shallow waters and waters deeper than approximately 1500 m were slightly less favourable. During incubation, high mean sea level anomalies were indicating favourable habitat. Cold waters were indicating better habitats but not under -1.8°C and -1.5°C for incubation and brood respectively. Water

with strong surface currents were unsuitable habitats, especially during brood. After hatching, south-east and south-west currents indicated better habitats, but these might just reflect the local condition encountered by the birds at both sites. Finally, the net primary productivity didn't show a clear pattern for the incubation habitat model (habitat seemed more favourable in higher productivity areas). During brood, better habitat seemed to have lower net primary productivity (less than 700 mg C m^{-2} day^{-1}) but still above 200 mg C m^{-2} day^{-1}.

Weekly foraging habitats

Finally, Figure VII-22 illustrate how the final foraging habitat model generated weekly foraging habitat maps from the corresponding weekly values of the dynamic environmental variables. The time series showed that although some areas were quite stable and offered some predictability, other patches of predicted favourable habitat seemed to vary in location and size.

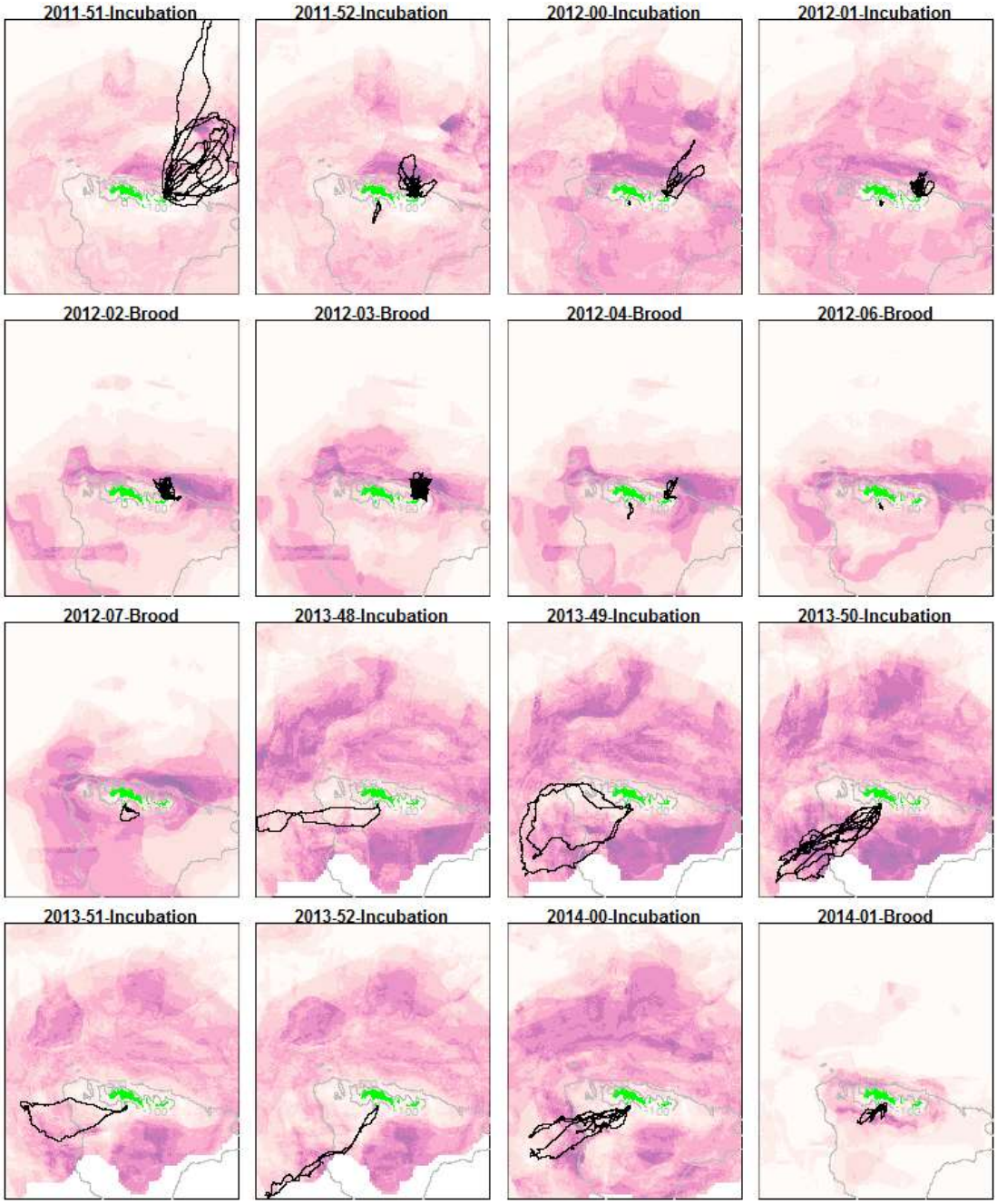

Figure VII-22: Weekly foraging habitat model predictions covering incubation and brood for the seasons 2011-12 and 2013-14. The foraging trips sampled during each week are also represented.

The Pearson correlation coefficients between paired incubation and brood weekly predictions are presented in Table VII-5. The coefficients averaged 0.80 for incubation and 0.75 for brood. The weeks belonging to the same surveyed season had higher correlations than cross-season comparisons (0.87 versus 0.74 for incubation and 0.86 versus 0.54 for brood). This was particularly true for brood, but season 2013-14 had only one week (12 recorded foraging trips during that week).

Table VII-5: Pairwise correlations between weekly foraging habitat predictions. The top-right part of the table contains Pearson correlations for incubation and the bottom-left part of the table contains the coefficients for brood. Cells shaded in green indicate comparisons between weeks from the same season as red shaded cells are cross-season comparisons.

		2011	2012		2013				2014		Year
		52	00	01	48	49	50	51	52	00	Week	
		0.9	0.78	0.77	0.75	0.74	0.74	0.74	0.73	0.73	51	2011
			0.84	0.79	0.74	0.73	0.74	0.72	0.72	0.72	52	
				0.87	0.73	0.72	0.76	0.72	0.71	0.74	00	2012
					0.74	0.73	0.77	0.75	0.73	0.75	01	
	03	0.89				0.94	0.89	0.89	0.89	0.84	48	
2012	04	0.89	0.88				0.9	0.89	0.87	0.81	49	
	06	0.83	0.8	0.87				0.94	0.91	0.84	50	2013
	07	0.82	0.84	0.86	0.88				0.98	0.87	51	
2014	01	0.53	0.53	0.55	0.54	0.56				0.88	52	
	Week	02	03	04	06	07						
Year				2012								

Seasonality

The seasonal model predictions are presented in Figure VII-23. The pixel by pixel correlations were weak for incubation (Pearson coefficient of 0.38) and very weak for brood (0.13). But the figure also shows the bias due to the sampling effort. Only a few trips were recorded from the Gourlay Peninsula in 2011-12 (9 short incubation trips and 19 brood trips) and no deployments were carried out in 2013-14 from Cape Geddes.

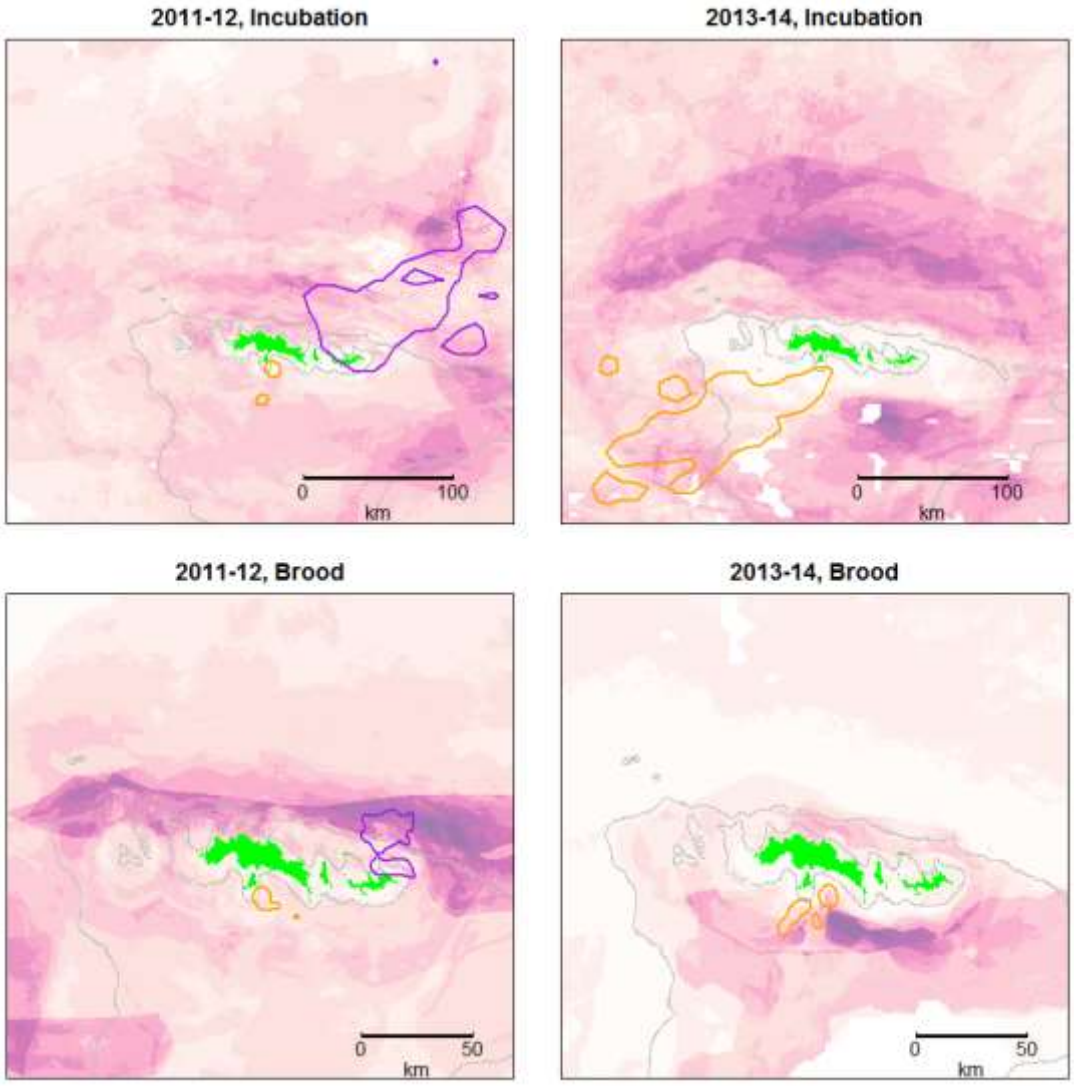

Figure VII-23: Seasonal foraging habitat prediction with the 75% utilisation distribution of the data input for Gourlay (orange polygons) and Geddes (violet polygons) locations.

VII.4 Discussion of the results, summary and limitations

The results from the modelling and the validation process will be summarized and discussed in this section. The limitations due to the data available and the methodology will be highlighted as will the other confounding variables not included in the models. This is important as these limitations contribute to the interpretation of the final foraging habitat model.

a. Results from the models

Model selection

In most of the scoring, the models generated from the random forest algorithm outranked the ones generated by all other algorithms. This confirms the popularity of this technique for generating foraging habitat models for seabirds (Bost et al., 2011; Oppel et al., 2012; Scales et al., 2016).

There was a clear increase in model performance when using the dynamic environmental variables at a higher temporal resolution (round 2). This suggests the importance of matching as closely as possible the observations with the environment. This approach also allowed me to incorporate seasonal differences in environmental conditions into the model.

Incubation and brood models showed similar performance. During the validation process, the incubation models showed higher correlation coefficients with krill data. This could be due to a better match between the spatial extent of the krill survey and the larger foraging ranges before hatching. During the site cross-validation process, the brood AUC values were higher as well as the correlations between the predicted habitats from both colonies. It is probable that during brood, the main constraint of staying in the proximity of the colony to feed the chicks might reduce opportunities and attenuate local differences in conditions and therefore create similar predictions between sites.

Finally, the validation process allowed me to compare the different level of data inputs. The type of data with the highest ranking was the inferred foraging behaviour based on the expert method including missing TDR data. The inputs generated simply using GPS or dive locations did not produce the best models. The former could not be used in the round 2 due to the random nature of the pseudo-absences and the difficulty of attributing dynamic environmental variables to random locations without time stamps. In addition, the round 1 predictions generated by the GPS locations, despite being ranked 3rd during the validation process, were clearly over fitted (see Appendix V). The dive locations were ranked 5th overall in the validation process and their predicted habitat had correlation coefficients of 0.69 and 0.88 with the best model for incubation and brood respectively. The data input based on the other inferred foraging behaviour modes (method 1, with or without missing TDR data – 3b and 3a) showed lower ranking (6th and 4th) but higher correlation coefficients with the best model (0.71 and 0.91 for 3b and 0.60 and 0.92 for 3a for incubation and brood respectively). When the trips with missing TDR were discarded (4a), the overall model ranking was 2nd and it prediction maps were strongly correlated with the reference final prediction (0.88 and 0.97 for incubation and brood). This suggests that although the model evaluation scores and the predicted habitat maps were quite similar, the process of detecting foraging behaviour is an important step and provides more information than inputs based on just GPS locations or combined GPS and dive data.

Habitat prediction

The main driver for both the incubation and brood habitat predictions was the distance to the colony which is expected from central place foragers. The prediction habitat maps show less favourable foraging grounds in close proximity to colonies, which can be explained by prey depletion. This Ashmole effect is also illustrated by the strong influence of the bird at-sea density on the models. When foraging, the birds have to balance the necessity of reducing the energy consuming commuting

part of the trip with trying to avoid competition with their congeners and other krill predators. The models seemed to capture the trade-off and the lower habitat quality near the shore, which is wider during incubation when birds have less time constraints and can forage further off shore. However, it is difficult to distinguish between intraspecific competition and attraction which can be an important factor to help prey detection in social foragers (Boyd et al., 2015).

The oceanic features and the important contribution of the oceanic slope to favourable foraging habitats in particular (Ichii et al. 1998; Trathan et al. 2003; Trathan et al. 2006; Atkinson et al. 2008; Siegel et al. 2013). were also captured by the model. The most important foraging zones on the prediction maps were located along the 500 m isobaths, especially on the north side of the archipelago where it is easily accessible from the penguin colonies. In contrast, its influence seems less important on the south side of the South Orkney Islands. On the south side the oceanic slope is further offshore and less accessible, especially during brood. The prediction model shows that birds tended to avoid very shallow areas. This suggests that tracked penguins during this study were not relying on benthic feeding as observed by Takahashi et al. (2003) and Kokubun et al. (2010).

Chlorophyll and primary productivity are usually considered as good predictors of favourable foraging habitat (Boersma et al., 2009; Jaud et al., 2012). Sea surface temperature (Trathan et al., 2008; Scheffer, Bost and Trathan, 2012) and surface currents (Cotté et al., 2007) are also acknowledged to be good proxies for high quality habitat models. Regrettably these variables only provide limited contributions to the model and/or the direction of influence were in contradiction to results from some previous studies. Grémillet et al. (2008) and Boyd et al. (2015) suggest that environmental variables from remote sensing sources might not always be adequate to predict prey distribution and therefore foraging habitat. The former authors showed some mismatch between chlorophyll a distribution recorded via remote sensing and some trophic levels. This can be explained by the impossibility to detect chlorophyll in deeper layers of water and by the temporal lag between the development of phytoplankton and the appearance of grazer. The second authors reported that SST is not a good predictor of prey distribution and that mechanical models should be used instead. Similarly Santora et al. (2012) suggest that chlorophyll might not be suitable to predict krill habitat. It is also possible that these variables are not useful to support predictions at the very fine scale considered in this study (both spatial and temporal dimensions). The spatial resolution of these variables is very coarse in regards to the resolution of the data input and behaviour modes classification. There is a significant negative correlation between the spatial resolution and the variable importance in the round 2 random forest model (r^2=0.258, $F_{1,118}$=41.06, $p<0.01$). Similarly, the temporal scale (one week) is also very coarse, but better than the aggregation at the scale of the foraging stages as suggested by the better performances during modelling round 2.

When comparing the foraging prediction with the actual observations (Figure VII-18), the habitat model matches the foraging locations recorded from Cape Geddes. However, at the Gourlay Peninsula, it seems that the birds did not target the most favourable habitats. Instead of heading south-west toward the oceanic slope, they could reach a zone predicted as good habitat south of Powel and Laurie islands. They could also swim around the west tip of Coronation Island to reach more favourable predicted habitats. One explanation for this sub-optimal exploitation of the habitat could be the competition with other penguins from colonies located south of Laurie or on Monroe islands. This is confirmed by Trathan et al. (2006) and Masello et al. (2010) who observed spatial segregation between adjacent colonies.

At very local scales, the model seemed to predict the a priori favourable habitats provided by canyons located along the north side of the continental shelf. The prediction maps showed some unrealistic abrupt linear changes (see for example the brood prediction on Figure VII-18). This could be due to a combination of model artefacts and/or coarse resolution of the environmental variables.

b. Limitations

Sample size and variables resolutions

One of the main limitations of this foraging habitat model is linked with the sample size (Aarts et al., 2008; Carter et al., 2016). This study only included two colonies and the number of tracked birds is unbalanced between both sites. Furthermore, the sampling covered two breeding seasons from the Gourlay Peninsula and only one from Cape Geddes. The oceanographic conditions in the vicinity of both colonies were very different and the dynamic variables changed between both breeding seasons, as probably did prey availability (Murphy et al., 1998; Saunders et al., 2007; Rombolá, Marschoff and Coria, 2009). Although Jansen et al. (2002) didn't observe annual changes in krill abundance and Santora et al. (2012) suggests that years with lower krill recruitment are buffered by the longevity of krill and its reproduction over several years. Despite these limitations, the different validation procedures allowed me to check the utility of the models. The cross-validation in particular showed how good a model from one colony is to predict foraging habitat in the vicinity of the other colony. That step showed that the model based on the Gourlay data was better at predicting the habitat along the north coast of the archipelago than the reverse. The performance of the cross-validation was quite average. Using the weekly temporal resolution also allowed me to make sure that seasonal variations were included in the models.

The other main limitation is related to the spatial and temporal resolution of the dynamic environmental variables. The important difference between the accuracy and frequency of the birds' locations and the grid size and temporal scale of the predictor variables creates a mismatch between the real conditions and the values included in the model (Aarts et al., 2008). Remote sensing data are also prone to different biases

(cloud cover and sea ice preventing the collection of data) that would generate missing data and/or inaccurate measurements. To alleviate these issues, some ground truthing procedures would allow me to estimate the inaccuracies and discrepancies for the different variables.

Methodology

Limitations when modelling habitats from tracking data are related to the positive spatial and temporal autocorrelation of the data points and colinearity between explanatory variables (Aarts et al., 2008; Dormann et al., 2013). For example, the bird at-sea density was built in relation to the distance to the colonies. Net primary productivity is also partially dependent on sea surface temperature. The random forest algorithm partially mitigates these issues through sub sampling of the data and the variables during the building of trees (Breiman, 2001).

A methodological issue is related to the different random locations generated for the models (pseudo absences for the GPS dataset and points out-of range for all models). Because these random locations do not have a timestamp, they can't have accurate associated dynamic environmental variables. There are no ways to mitigate this, except by attributing a random date and time to these locations, which might increase uncertainties.

In the previous chapters, I reported how important the vertical exploitation of the habitat is. Birds closer to land had deeper dives and the dive depth also varied with the period of the day. This vertical component is absent from the modelling. It would be quite difficult to integrate it, mainly because the environmental variables acquired from remote sensing only relate to the superficial surface layer of water. The actual model only considers surface conditions, but it is known that the prey distribution and therefore the foraging habitat is influenced by changes throughout the water column that cannot be measured remotely (Santora et al., 2012).

Model validation

Most of the model validation and evaluations were based on the area under the curve (AUC) metric, which compares the rates of true positive (the model prediction matches a positive presence) and the rates of false positive (the model misclassified a presence or an absence). But this measure is not completely bias-free. Indeed, the AUC is strongly influenced by large number of absences and is not reliable in predicting rare events (Manel, Williams and Ormerod, 2001).. It is also influenced by the spatial extend to which the models are carried (Lobo, Jiménez-valverde and Real, 2008). Other ways of validating the models should be explored.

Finally, the models were partially validated using some information describing the prey field. In addition to being sure that the instruments used are correctly calibrated and that the measures are useful, the temporally reduced overlap between the tracking of birds and the prey survey introduces other limitation in this important validation process.

In addition, it is known that birds might not forage where their prey is most abundant (Boyd et al., 2015). It could be because the location of high prey density are out of reach. Or maybe because of competition with other krill predators (Hunt, Heinemann and Everson, 1992). It has also been suggested that penguins might not target the most dense krill swarms and prefer lower krill densities (Cox et al., 2010).

c. Conclusion

Despite the numerous limitations linked with the data quality (accuracy, resolution, sample size, etc…) and those in relation to the validation process, the various predictions showed some convergence and the predicted foraging habitat maps seemed to generate a realistic picture of chinstrap foraging hotspots around the South Orkney Islands. The models fulfilled the aims of integrating habitat preferences and accessibility. In order to evaluate how the competition (intra- and interspecific) is covered by the foraging habitat model, more tracking data from adjacent colonies and/or other sympatric species is required.

The method highlighted the importance in identifying the inferred foraging parts of the tracking data. It also emphasized the importance of temporal variations (over the course of the breeding season, between years) and the necessity of matching as closely as possible the observations with real local and dynamic conditions. As the accuracy, frequency and resolution of tracking devices increase, it will be possible to identify fine scale foraging patterns. To match this level of details, it is now important to obtain finer and more accurate covariables that can be used for the models. Matching information about the prey distribution in terms of spatial and temporal resolution is also important for validating marine predator foraging habitats.

Chapter VIII GENERAL DISCUSSION

In this final part, the results from the previous chapters will be summarized. The use of the habitat model by individual birds will be related to their fitness and reproductive effort. The main limitations of the whole study will also be discussed. Finally, the potential overlap between fisheries and foraging habitat will be commented upon and some proposal for management will be made.

VIII.1 Summary of the different results

Chapter IV compares characteristics at the scale of the foraging trips between colonies and how the different metrics varied over time. Most of the trip metrics changed during the breeding season, indicating an increase in foraging pressure with a reduction of available habitat after hatching. This intensification of foraging activity was illustrated by an increase in exploration speed, deeper dives and more nocturnal activity. These trends were comparable between both colony sites, providing encouraging evidence to support a model that could be extrapolated to other colonies. This chapter also highlighted the importance of temporal scales, not only over the breeding season, but also between day and night activities.

In Chapter V, two different methodologies were developed to infer changes in behaviour throughout foraging trips. The trips were segmented based on the temporal variations in surface metrics (speed and changes in direction) and dive metrics (depth and dive efficiency). The allocation of a behaviour mode for each segment was based on two different approaches: a semi-automatic (data clustering and manual behaviour mode identification for each cluster) and an expert-based method (behavioural allocation through visual inspection of a data subset followed by a supervised classification of the whole dataset). Two-thirds of the segments had matching modes from both methods, reaching 84% for the foraging modes. Behavioural modes were also attributed to incomplete trips (trips without dive data) using a supervised classification process.

The investment in foraging activities showed a significant increase after hatching and was consistent for both colonies (although the increase in night foraging activity was more important for birds from Cape Geddes). Despite the facts that these behaviour modes cannot be validated by other observation data, the results from this chapter are confirmed by previous findings from this study and other related investigations.

The next chapter (Chapter VI) used different techniques to spatially represent the range of potential data inputs for the final foraging habitat modelling. Indeed, the previous chapters generated six possible data inputs: the basic filtered GPS locations, the interpolated 1 minute resolution locations merged with dive data (Chapter II) and the two sets of foraging modes inferred from the two methods used in Chapter V), each with or without trips with missing TDR data. The effect of spatial scales, matching the resolutions of the environmental variables used in

the final modelling chapter was also assessed through a grid aggregation process. The other two techniques, minimum convex polygon defining potential foraging areas and kernel density estimator delineating utilisation distributions, allowed the identification, measurement and spatial representation of feeding "hotspots".

The different data inputs showed good overlap and similarities between sites and breeding seasons. When assessing the influence of the spatial resolution, optimal convergence was reached at medium scales (between 1 and 10 km). The main factor limiting the overlap between the utilisation distributions defined by the different data inputs was related to the sample size. The Geddes colony showed less variation between the different utilisation distributions due to the higher number of foraging trips recorded from that location. After hatching, the reduction in available habitat lead to an increase in the time spent per unit area. The later was also related to the depths of the dive, providing a potential explanation for deeper dives during brood and suggesting a vertical resource depletion near the colonies.

This chapter (Chapter VI) contrasted with the previous ones as the spatial distribution of foraging showed some differences between sites, which might be explained by bathymetric and oceanographic features. Birds stayed closer to the Cape Geddes colony during incubation, as the continental shelf slope was easily accessible. During brood, the birds from the same colony showed two different strategies: either a longer nocturnal trip northward reaching the continental slope or a shorter diurnal trip eastward over the shelf. The birds from the Gourlay Peninsula did not show the same patterns during brood; they tended to stay closer to the colony, probably due to the inaccessibility of the shelf slope.

The last chapter (Chapter VII) used several modelling techniques to contrast geometric and environmental variables between foraging and non-foraging locations from the different data inputs to generate habitat models. The same 6 data inputs used in the previous chapter were compared. The explanatory variables combined bathymetry and derived variables including benthic geomorphic classes, geometric variables representing constraints related to the colony locations and remotely-sensed physical and oceanographic parameters. Due to the dynamic nature of the later set of variables, they were temporally aggregated along two scales (breeding stages and weeks) during two modelling rounds. In each round, four algorithms (MaxEnt, GAM, GBM and random forest) were used on the 6 different data inputs. Each model was evaluated based on a measure of their performance. They were also validated using information about prey distribution and through a cross-site corroboration process.

By combining the evaluation and validation phases, it was possible to identify the best modelling technique, data input and temporal scale aggregation for the dynamic variables. The random forest algorithm generated the best models. The weekly temporal scale for the variables created better models than the aggregation by breeding stages, the later

showing signs of over-fitting. Finally, the inferred foraging modes based on the second method of behaviour mode inference (Chapter V) with the inclusion of data from incomplete trips provided the best input for the modelling.

The final habitat model was mainly driven by geometric variables (distance to the colony and bird at-sea density) and bathymetry-derived variables (mainly the distance to the continental shelf slope). The other environmental variables, despite showing weaker contributions to the model, were also important as emphasized by the importance of having a good temporal match between the data collection and the measured conditions. The derived foraging habitat probability map showed good local predictions for zones known for high prey aggregations. It also included accessibility and how it varied between breeding stages. Finally, areas of low habitat quality identified in the vicinity of the colonies indicate that the model accounted for competition and prey depletion.

a. Answers to the secondary questions

The answers to the secondary research questions listed in I.3a (page I-9) are presented in Table VIII-1.

Table VIII-1: Answers to the secondary questions from each chapter.

		Chapter IV	Chapter V	Chapter VI	Chapter VII
1	What changes occur during the breeding season? Is a single habitat foraging model sufficient for the whole breeding season?	Reduction in foraging range after hatching. Trip metrics indicate an increase in pressure after hatching.	Increase in foraging activities after hatching.	Reduction in foraging range after hatching. Higher time spent in area unit during brood.	Two different foraging habitat models due to the different ranges.
2	Is it possible to identify the foraging parts of the trip and reliably distinguish these from resting and commuting periods?		Yes, but they cannot be validated (although both methods offer some similarities).		In the foraging habitat model, the inferred behavioural modes based on method 2 showed better performance.
3	Where are foraging hotspots located that are used by the tracked birds?			During brood, Geddes birds target two different areas depending of the period of the day.	The model showed prey depletion near the coast. North side of the continental shelf.
4	Which are the main explanatory variables driving the foraging habitat model?				Distance to the colony, bird at-sea density, distance to the oceanographic slope,
5	Is it possible to evaluate and validate the foraging habitat model and transfer it to other colony sites in the South Orkney Islands?				The cross-validation process show that the data from Gourlay was more skilful.
6	What are the characteristics of the vertical use of the habitat?	Increase in foraging depth after hatching, especially during day trips.	Different dive depths for exploratory and foraging dives. Shallower dives during night foraging.	Deeper dives in the vicinity of the colony, especially in areas with high utilisation time	The 25 km threshold where dives are deeper (Chapter VI) cover most of the favourable brood habitat (see Figure VIII-4, page VIII-196)

7	What are the differences between two colony locations?	Differences in night activity. Longer ranges from Gourlay. Geddes trips were less circular.	Differences in night activity.	Better convergence from different data inputs at Geddes due to sample size. Higher time per area unit in Gourlay during incubation and Geddes during brood. In Geddes birds stayed closer to shore.	Foraging habitat from the model seems more favourable from the Geddes colony.
8	What are the temporal and spatial scales relevant to characterise chinstrap foraging?	Differences between incubation and brood and day/night activities.	Differences between incubation and brood and day/night activities. Resolution of behaviour mode is one hour.	Different data inputs converged between 1 and 10 km. During brood, Geddes birds targeted two different areas during the day and night.	Week resolution for explanatory variables increased the model performance.

VIII.2 Foraging habitat effect on bird fitness and population sizes

a. Bird fitness and reproductive effort

This section will relate the foraging habitat generated in the previous chapter with data collected at the individual bird level. This will enable me to relate bird fitness and reproductive effort with the results from the habitat model. The bird's weight measured during the attachment of the device will be considered as an indication of body condition (Watanuki, Takahashi and Sato, 2010) and therefore fitness.

In order to a link birds' individual measurements to their ability or need to use good quality foraging habitat, as defined by the result of the foraging habitat model generated in the previous chapter: a good quality habitat is represented by cells with a high probability of foraging generation by the model. The values extracted from the habitat model for each 1 minute interpolated location along each foraging trip were summed and divided by the trip duration. This trip weighted habitat use was then averaged for each deployment (results by trip are included in the trip summary data presented in Appendix II) and a random forest model was built to predict values from the bird's trips characteristics (trip range, see II.3 and percentage of behavioural modes, see V.3c) and biometrics (weight, mass gain/loss and reproductive effort – number of eggs or chicks, see II.1e). The inferred sex, site, season and a randomly generated variable were also added to the model. The model was run 10 times with a different subset of training and testing sample for cross-validation.

The 10 models explained on average 60.3% of the variability of the data. The predicted weighted habitat use was significantly correlated with the observed values (R^2 of 0.65, $F_{1,68}$=124.6, p value<0.01). The maximum trip range, percentage of foraging activity, both the weight and mass gain/loss and the phenology had a higher contribution to the model than the random variable (Figure VIII-1 A). The inferred sex, the colony site, the season and the number of offspring had very weak contributions to the model. The partial dependency plots (Figure VIII-1 B to F) show that longer trips allowed the birds to reach more favourable habitats as observed in Procellariiform parents by Chaurand & Weimerskirch (1994) and Weimerskirch et al. (1997). A high percentage of time spent in inferred foraging behaviour was also linked with a higher habitat quality, which was expected as foraging locations were used to generate the foraging model. Lighter birds are known to undertake longer trips (Clarke, 2001; Watanuki et al., 2002) and my results show that they targeted locations with better habitats as observed by Saraux et al. (2011). Brood trips targeted better quality habitats, despite the foraging trips being shorter and therefore contradicting the effect of foraging range. This again emphasizes the increased constraints after hatching and the necessity to improve foraging efficiency as the size of the available habitat decreases. Finally, birds that increased their body mass at the end of the deployment also targeted higher habitat quality

locations. Dragon et al. (2012) correlated mass gains with forging intensity in southern elephant seal.

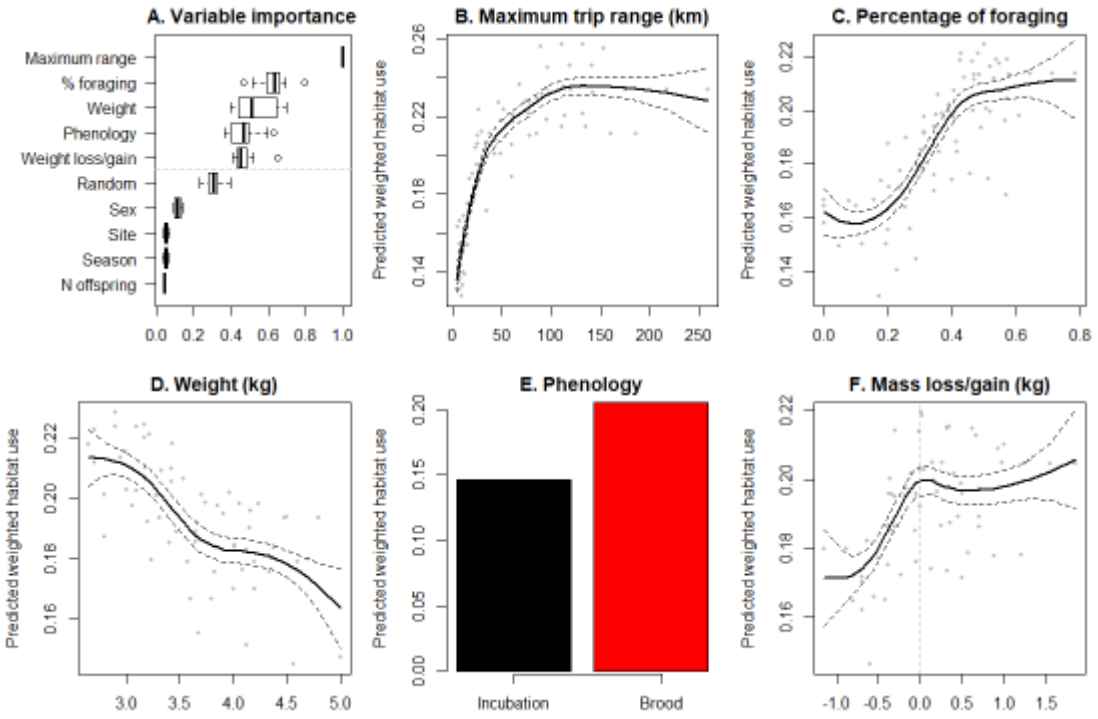

Figure VIII-1: Results from modelling the weighted habitat use from aggregated trip metrics and biometrics. A: variable importance plot, B to F: partial dependency plots for each variable with a higher contribution to a random variable.

The inferred sex (sexes from both discriminant functions, see II.1g page II-21 showed similar results) did not strongly contribute to the model. This confirms the results from Chapter IV (see page IV-71) showing that foraging trips and strategy does not differ between sexes. Saraux et al. (2011) found no differences in little penguin foraging between sexes. In contrast, Barlow & Croxall (2002) and Hart, Mann, et al. (2010) found differences in foraging between males and females for macaroni penguins. Angelier et al. (2008) reported no differences in body conditions between male and female Adélies penguins. Due to the absence of a strong sexual dimorphism, it is usually assumed that there are little differences in foraging bejaviour between sexes. Some studies recorded small but significant differences that sometimes only happen at a particular stage of the breeding cycle (Clarke et al., 1998). Foraging differences between sexes can be due to different energetic investment in the reproduction (Chappell et al., 1993). They can also reduce inter-specific competition for resources. This might only be visible in year of poor resource availability, which might increase segregation in foraging between sexes. Maybe the amount of resources in the years covered by this study and others that did not allow to clearly show any difference between sexes.

Despite Cape Geddes birds having access to a potentially better foraging habitat, the colony location did not contribute to the model. Birds from the Gourlay Peninsula were slightly heavier than the birds from Cape Geddes (3.8 versus 3.6 kg) but the difference was not significant (t=1.99,

df=29.6, p=0.06). The difference in sample size and the fact that some variables were missing from some Gourlay deployments (mass loss/gain, number of offspring) mean that the model was probably mainly driven by the data from Cape Geddes and therefore did not enable me to accurately identify any site differences.

The model did not show any seasonality effect despite the fact that the environmental conditions fluctuated between years and the seasonal foraging habitat models were different (see VII.3d, page VII-166). Also prey abundance and distribution probably differed between seasons (Murphy et al., 1998). For the final habitat model, both seasons were merged and this might explain the absence of seasonal differences. It could also be due to sampling differences (no deployments in 2013-14 from Cape Geddes), therefore this result has to be taken with caution.

Croll et al. (2006) reported that chinstrap penguins don't vary their foraging efforts with prey seasonal fluctuations, which would confirm the low representation of year as factor in the model. The same authors suggested that the reproductive success of the breeding pairs would vary with prey availability. Lescroël et al. (2010) linked Adélie foraging efficiency with breeding success and Jansen et al. (2002) highlighted the higher demand and therefore more frequent and longer foraging trips for chinstraps rearing two chicks. The tracked birds from Cape Geddes had more offspring per nest than the birds from the Gourlay Peninsula which might confirm the higher habitat quality available from the Laurie Island colony (although the offspring counts from the Gourlay Peninsula have to be considered with caution, see III.3, page III-45). But the low contribution from the number of offspring in the prediction of the weighted habitat use didn't confirm that parents with more offspring targeted higher foraging habitat areas. For Adélie penguins, Chappell et al. (1993) suggested that reproductive effort is not linked with increased foraging effort.

Despite the limitations due to the data sampling, the links between trip characteristics, bird biometrics as indicators of bird's fitness and the values extracted from the foraging habitat model provide an additional important validation of the final habitat model results.

b. Colony population sizes

To assess whether the quality of the foraging habitat has an influence on the colony population sizes, the relationship between the number of breeding birds and the probability of good foraging habitat in the vicinity of each site was assessed. The latter was defined for each phenological stage as the average habitat probability within a 90° sector perpendicular to the shore reaching the average maximum range recorded for the stage (incubation and brood). The results showed no significant relationship between the estimated colony population size and the average probability of the foraging habitat model available from each colony (R^2 of 0.029, $F_{1,90}$=2.66, p value=0.11 for incubation and R^2 of 0.014, $F_{1,90}$=1.29, p value=0.26). However, this approach is limited by the sector definition of the area available from each colony. Although the

birds from Cape Geddes followed that rule by foraging towards the north, the birds from the Gourlay Peninsula travelled towards the South West during incubation. Chinstrap penguins tracked from the southern tip of Powell Island, swum northward to reach the northern continental shelf break (PN Trathan pers. comm.).

Despite having access to less favourable habitat, the birds from the different colonies at Signy have larger population sizes than the colony from Cape Geddes. Maybe the land topography allows better nesting sites or snow cover and sea ice at the start of the breeding season might affect access to the site. Other krill predators (Adélie penguins and seals) can also influence the colony size through competition for resources; unfortunately, inter-specific competition was not included in the models.

Another explanation is linked with the nature of the foraging habitat model: as it includes competition through the bird at-sea density variable, it might give higher scores to locations that are nearer smaller colonies. Finally, the population estimates might not be reliable for all the colonies as some are more accessible and might have more frequent and up-to-date censuses.

VIII.3 Limitations and confounding factors

a. Sample size, annual variations and interspecific competition

Sample size

The main limitation for this study relates to the number of tracked individuals and, more specifically to the unbalanced sampling between both colony sites and both seasons. In total, tracking data were obtained from 109 birds, 60 birds from Cape Geddes, 16 birds from the Gourlay Peninsula in 2011-12 and 33 birds from the same location in 2013-14. This sample size accounted for less than 0.0001% of the total chinstrap penguins population for the South Orkney Islands estimated at 600,000 pairs (Poncet and Poncet, 1985). This limited sample size in most tracking studies has been discussed by Aarts et al. (2008) and Carter et al. (2016). Moreover, the sampling only included breeding individuals. Non-breeders are often discarded in population estimates and tracking studies as they often have different foraging patterns and don’t necessarily act as central-place foragers (Davoren, Montevecchi and Anderson, 2003). As unconstrained birds, they tend to expand their foraging range and therefore potentially do not compete with breeders for resources (Page et al., 2006; Bost et al., 2015). The discarded bird from Gourlay showed a very different foraging track (see Figure IV-6, page IV-60): heading South instead of South-West and very long. Although it reached areas not targeted by other tracked birds, it could still be potentially competing with other birds, as it was feeding on the way to this foraging ground. It might have fed upstream and therefore affected the downstream prey field used by other breeding birds. The effect of these non-breeders are very difficult to integrate in the models and the absence of reliable estimate of non-breeders with the different colonies did not allow me to try to quantify their impact.

Although having two colonies with contrasting local conditions allowed me to build a stronger, transferable habitat model, data from more colony sites would be preferable. Including east and/or west facing colonies and locations where birds can choose between different directions (as on Powell Island) would complement this model based on a north and a south-facing colony.

Annual variations

My foraging habitat modelling suggests some potential annual fluctuations in the intensity and spatial location of the high quality foraging hotspots. Climate variations, either gradual as climate change or cyclic as the El Niño-Southern Oscillation, have an effect on krill reproduction and transport across the Scotia Sea inducing seasonal variability in prey availability (Murphy et al., 1998; Saunders et al., 2007; Forcada and Trathan, 2009; Rombolá, Marschoff and Coria, 2009; Fielding et al., 2014).

Several studies measured annual variations in penguin foraging (Jansen, Boveng and Bengtson, 1998; Jansen, Russell and Meyer, 2002; Miller and Trivelpiece, 2008), although it is not always possible to relate those changes to prey availability, as they can be driven by other factors (Jansen, Russell and Meyer, 2002). According to these authors, the main factor is internal as foraging effort is strongly driven by the number of offspring. The spatial distribution of krill in relation to the coast will vary and influence foraging effort. The adult body conditions, which could be a consequence of over-wintering conditions, will have an impact on chick provisioning. According to Croll et al. (2006), chinstrap penguins might adjust reproductive success instead of foraging effort in response to prey availability.

In order to develop a model with an optimal integration of spatial (colonies) and temporal (seasons) variations, it is important to have a balanced sampling regime between sites and years. This would allow a similar contribution from each sampling population and the ability to independently test both seasonality and colony location factors.

Interspecific competition

Including intraspecific competition in a model when individuals have to compete for resources but may also engage in some level of social foraging (Ford et al., 2014; Boyd et al., 2015) can be challenging. My habitat model appeared to include at least the competition aspect as demonstrated by the Ashmole prey depletion effect. It would have been interesting to include data from neighbouring colonies to assess how much competition exists between colonies. The direction of travel from the Gourlay Peninsula seems to suggest that they were excluded from more favourable habitats by birds from other colonies as an example of spatial segregation reported by Trathan et al. (2006) and Masello et al. (2010). From the same authors, birds will predominantly feed in locations that will allow them to avoid competition from other land-based predators based in nearby colonies. The fact that there is little niche partitioning between chinstrap and Adélie penguins will increase

intra-specific competition between these species. Finally, as colonies are closer than the average foraging range, a large overlap is expected.

Interspecific competition, especially with sympatric Adélie penguins and Gentoo penguins, was not included in the model, as only chinstrap tracking data were involved. Although competition between all Pygoscelid species is mitigated to some extent by a shift in phenology (Black, 2016), in cases of low krill availability, competition can increase segregation in foraging areas (Lynnes et al., 2002). The same authors reported that chinstraps appear to outcompete Adélies. Wilson & Peters (1999) reported a similar competitive exclusion but in the vertical dimension where chinstrap were able to dive deeper and exploit lower levels of luminosity.

Penguin predators can also have an important role in habitat use as they can contribute to spatial segregation (Masello et al., 2010). Including tracking data from several species, including other krill predators (seals, cetaceans…), enables the development of models that can take into account multispecies interactions to predict movements and habitat use (Benson, 2016; Hays et al., 2016).

b. Methodological uncertainties

Data complexity and analytical approaches

The development of tracking devices lead to the development of a new discipline with its own paradigms: movement ecology (Ran, 2008; Benson, 2016; Hays et al., 2016). The complexity of high resolution data generated from these studies can create difficult methodological issues. The analytical tools have to take into account the high level of temporal and spatial autocorrelations typical of these datasets. They also have to deal with non-linear relationships and multiple explanatory variables (Redfern et al., 2006). In addition, some authors suggest that data-centred disciplines such as movement ecology might replace traditional hypothesis-testing approaches with pattern-identification (Benson, 2016). The same author recommend moving tracking studies towards real-scale experimentation studies.

In this research, I have tried to use analytical approaches that are not restricted to rigid mathematical models tied with prerequisites and limitations. Machine learning methods bring several advantages, as they are very flexible and can deal with complex problems with interacting parameters (Olden, Lawler and Poff, 2008). The downside is that the results can be more difficult to interpret and the absence of significance levels make them appear suspicious to the eyes of numerous traditional ecologists. It was therefore important to compare the predictions of these techniques with more traditional methods and to use validation processes when possible.

The tools and the models used in this research can certainly be improved and optimized, but I think the main trends and results have been identified and validated by a range of available complimentary data.

Locations uncertainties (GPS and interpolated locations)

Most of this study relies on a single source of data: the GPS coordinates provided by the tracking devices. The uncertainties linked with this source had to be estimated (see II.1b, page II-14), especially in the case of marine animal (Ryan et al., 2004). The different filtering methods were useful to discard abnormal GPS fixes. The issue related to missing points (long periods with no fixes) is more difficult to solve. Thankfully, it only happened for one foraging trip 74-172, see Appendix II).

Linking the GPS and TDR datasets was done by artificially increasing the resolution of the tracking locations through positions interpolating on a one minute resolution. Generating such a large amount of artificial locations can increase uncertainty, but thanks to the already high resolution of the original GPS dataset (one point every 4 minutes) and the meticulous filtering of irregular locations, the interpolated track stayed within the range of uncertainties of the GPS dataset.

Inferred behaviour modes

Combining surface and dive metrics to infer behaviour modes proved to be a key step towards an appropriate level of information for the final habitat model. Additional variables can be added in the time series segmentation process, if enough computing power is available. Some studies have suggested that the incorporation of environmental variables in the detection of foraging behaviour (Carter et al. 2016), can be important. This is particularly relevant in the case of surface currents, as an individual might appear stationary and therefore resting while it is swimming against the current or can appear to be commuting while it is actually resting at the surface drifting with the flow.

The main limitation in the behavioural mode identification process was due to the absence of any information to validate my results. Additional devices such as cameras, accelerometers or ingestion detection devices can be very useful in reducing uncertainties in the identification of foraging activities (Watanabe and Takahashi, 2013). In the case of this study, the behaviour modes inferred from the two different techniques could not be differentiated until the validation phase for the derived foraging habitat model.

In complement to more bio-logging, diet data either through stomach flushing or stable isotopes analysis would have provided more evidence about potential differences in prey choices between individuals, locations, seasons, etc. Hunting techniques may vary for different prey, which could be detected through fine scale changes in movement data. In addition, targeted prey can be an important niche segregation parameter and should be included in any foraging habitat model.

Spatial and temporal scales

A major difficulty I had to overcome whilst using different sources of data was related to varying spatio-temporal scales. Figure VIII-2 summarizes the extent in time and space for the different datasets used in this study: from the data input, foraging trips and explanatory

variables for the habitat model. The ranges corresponding to different prey aggregations are also represented.

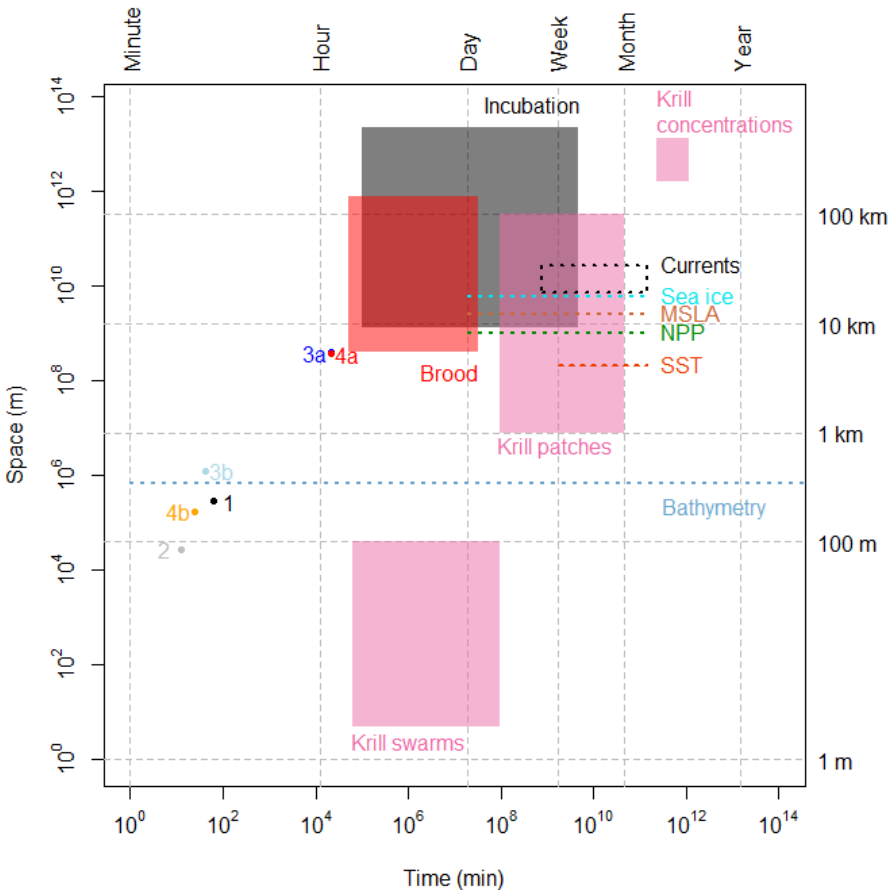

Figure VIII-2: Spatio-temporal scales of the different dataset used in this study. The points represent the different data locations[2]*. The black and red boxes represent the data aggregated by incubation and brood foraging trips. The coloured dotted lines show the different explanatory variables used in the habitat model*[3]*. Finally, the pink boxes delineate different krill aggregation states(as described by* Murphy et al. 1998*).*

It is quite obvious that there is very little overlap between the different dataset. The high resolution bathymetry data and to some extent, the sea surface temperature (SST) have spatial resolutions matching those of the data inputs. Although most of the dynamic environmental variables could be available at a daily temporal resolution, they were averaged over a week (5 days for the currents) due to missing data, which is probably too coarse for this kind of study. An improvement for a similar study would be to use higher resolution data from remote sensing when available, in both time and space.

The different data input where generally within the spatial ranges of the smallest krill aggregation structure (swarms). Direct feeding

[2] Data location inputs: 1: GPS, 2: 1 minute interpolated position with dive deeper than 5 m, 3a, 3b, 4a and 4b: interpolated locations within foraging segments based on two methods – 3 and 4 – and with or without missing TDR data – b and a.
[3] Explanatory variables acronyms: sea surface temperature (SST), net primary productivity (NPP), mean sea level anomaly (MSLA).

observations though camera devices could help demonstrate which prey aggregation scales are important for penguins.

In addition to the temporal mismatch between data input and the explanatory variables, acquired data from remote sensing only relate to the superficial layers of the ocean. They don't match the depth of prey distribution (Santora et al., 2012). Unfortunately, getting synchronous data and measurement throughout the water column is expensive as it requires a vessel and dedicated complex measuring tools. An additional temporal mismatch can happen along the trophic chain where high chlorophyll a concentrations can indicate areas of high productivity but low concentrations can also indicate high zooplankton grazing.

c. Prey distribution

As previously discussed, assessing the strength of inferred behaviour modes and foraging habitat model would require information about prey distribution and dynamics. The influence of prey abundance and availability on predators have been reported by several studies (Hunt, Heinemann and Everson, 1992; Boyd and Murray, 2001; Alonzo, Switzer and Mangel, 2003b; Croll et al., 2006; Benoit-Bird et al., 2013; Boyd et al., 2015). Krill abundance changes are subject to annual patterns in productivity and recruitment (Loeb et al., 1997) and transport through large oceanic scales (Siegel, 1991). Local scale spatial distribution will be more important than global abundance, especially for central-place foragers (Croll et al., 2006). Many studies inferring foraging behaviours based on tracking data lack direct information on prey distribution (Dragon et al., 2012), and some authors, such as Boyd et al. (2015), recommend contemporaneous recording between prey and predators.

Despite not having optimal accurate and synchronous information about prey distribution, the foraging habitat modelled in this study managed to include shelf break areas where krill is mostly expected (Silk et al., 2016). Some information on krill distribution were included in the model validation process and contributed to assessment of the strength of the results. It is also worth noting that using prey distribution information to support foraging habitat models is not always adequate as predators might not target areas where preys are the most abundant (Hunt, Heinemann and Everson, 1992; Zamon et al., 1996; Cox et al., 2010; Boyd et al., 2015).

The development of unmanned surface vehicles that could follow a tracked animal would allow me to get synchronous information about prey field and provide supporting data to validate foraging behavioural modes. It might also allow for the collection of additional explanatory variables at very high spatio-temporal resolution, providing ground-truthing information for remote sensed data. This would lead to a more robust foraging habitat model.

d. Interpolation for the whole archipelago

The cross-site validation process I followed is the only option that allowed me to assess whether the model could be extrapolated to other colonies. It demonstrated that the model based on the Gourlay Peninsula dataset was more skilful in predicting foraging areas from Cape Geddes than the reverse. This emphasises the importance of including data from locations with contrasting conditions to cover a large extent of the range of local variation. It would be optimal to collect data from other colonies to further validate this model. Nevertheless, as it has been built with data from two very different colonies, I predict that the final habitat model has a good chance of representing foraging from other colonies around the South Orkney Islands archipelago.

e. Suitability in other predator studies

Despite the numerous limitations mentioned in the previous sections, the method used in this study, from tracking data to a foraging habitat model, appears to suit the focus species and seems to be transposable to other colonies across the South Orkney Islands archipelago. In order to progress towards multispecies modelling and include other krill (or higher trophic level) predators, I would like to assess how suitable this method might be for other air breathing predators (Murphy et al., 2012).

Energetic expenses whilst foraging, dive depths and durations can be very different between penguins, flying seabirds and pinnipeds. The way these taxonomic groups deliver resources to their offspring is also very different (regurgitation versus maternal milk) and will influence their foraging strategies and timing. Species also fall on the continuum of income and capital breeder. Travelling speed and dive duration will have an impact on the tracking sampling frequency. As a result the tracking interpolation technique will need to be adapted to the different species, leading to potentially different temporal and spatial resolutions for each taxonomic group. Variation in surface movement linked with differences in diving physiologies also mean that the behaviour modes inference method will have to be adapted for each species in order to incorporate how they use their three-dimensional habitat at a fine scale.

The last part of the method, the habitat modelling, can probably be transposable to other species if they have similar constraints related to prey distribution (Benoit-Bird et al., 2013; Hays et al., 2016) as long as they classify as central-place foragers.

VIII.4 Proposition for fisheries management

Prey exploitation either by natural predators or by fisheries is not homogeneous; it is concentrated in space and time where the prey are predictable (Santora et al., 2012). In the Scotia Sea, krill fishing moved from pelagic areas to shelf breaks and submarine valleys (Murphy et al., 1997; Trathan et al., 1998; Hill et al., 2006; Silk et al., 2016). Reid et al. (2004) reported an important spatial overlap between krill fisheries and natural predators. Krill fisheries can have an impact on krill availability

to predators even in the absence of spatial overlap. Indeed, fishing upstream can affect prey replenishment in areas of intense foraging such as in the vicinity of colonies. Ainley et al. (2007) has previously reported krill depletion due to fisheries.

The direct mortality due to by-catch of seabirds is low in krill fisheries (9 birds in 2016 in subareas 48, CCAMLR 2016). The impact of krill fisheries on penguin populations is more difficult to assess but Mangel & Switzer (1998) reported a reduction in Adélie penguins reproductive success and parental survival due to krill fisheries. This is mainly linked with the length of the harvesting season and the amount of krill caught. Alonzo et al. (2003a) mentioned changes in foraging behaviour for the same penguin species due to harvesting. The diminution of sea-ice cover enables fisheries to shift their operation towards the south and in coastal waters which can significantly increase their overlap with natural krill predators. The impact of krill fisheries could potentially be important, especially during key parts of the breeding cycle when birds are under huge pressure to feed their chicks and compete with congeners and other predators. During seasons when conditions are not optimal, any increased pressure from krill harvesting can have huge impact on reproductive success.

The reported annual catch of krill in Subarea 48.2 is presented in Figure VIII-3 (CCAMLR 2016). CCAMLR set a precautionary trigger level of 279,000 tonnes for this subarea which represents 45% of the total krill catch limit. The catch stayed well below this level between 2005 and 2015 (ranging from 21.3 to 69.1% of the trigger level with an average of 33.4%). Nevertheless, the potential expansion of krill fisheries in the future could increase catches and impacts (Hill et al., 2006). An increase in fisheries in addition to the negative impacts of climate change on krill recruitment (Flores et al., 2012a) would have a potentially significant impact on krill predator populations, especially if the exploitation is concentrated near breeding sites. The catch data indicate that fisheries mainly operate on the western part of the South Orkney Islands, more specifically along the northern shelf break (PN Trathan, pers. comm.) which is an area highlighted by the foraging habitat model (Figure VIII-4).

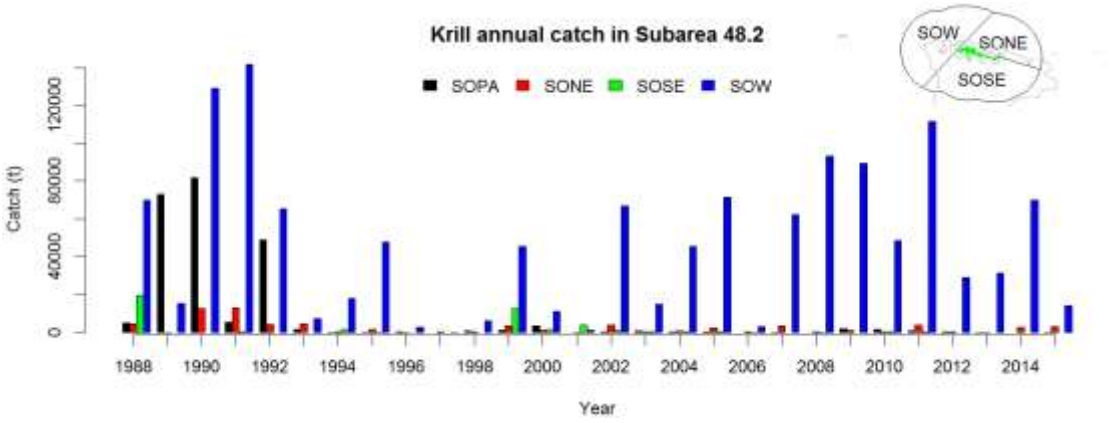

Figure VIII-3: Reported krill annual catch from small-scale management units (SSMUs) in Subarea 48.2: Pelagic area (SOPA), Northeast (SONE), Southeast (SOSE), West (SOW). Source of data: CCAMLR Statistical Bulletin V29.

Penguin species are potentially impacted by many cumulative human or human-induced activities. It is therefore justifiable to establish marine-protected areas (MPAs) to protect these species, especially in coastal breeding areas (Trathan et al., 2015). Incorporating scientific evidence to demonstrate and evaluate the size of the required protected area is difficult. Pichegru et al. (2012) assessed the impact of a 20 km no-take zone around the world's largest African penguin colony and determined that it was too small to mitigate population decline.

Figure VIII-4 presents how a 25 km area from the coast would mostly cover the favourable foraging habitat during brood, which is a critical period of the breeding cycle. During incubation, constrains are not as strong as birds can forage further offshore and escape highly depleted areas near the coast as indicated by the model. As mentioned earlier, it is important to take into account upstream fishing activity to ensure sufficient krill replenishment in the coastal zones.

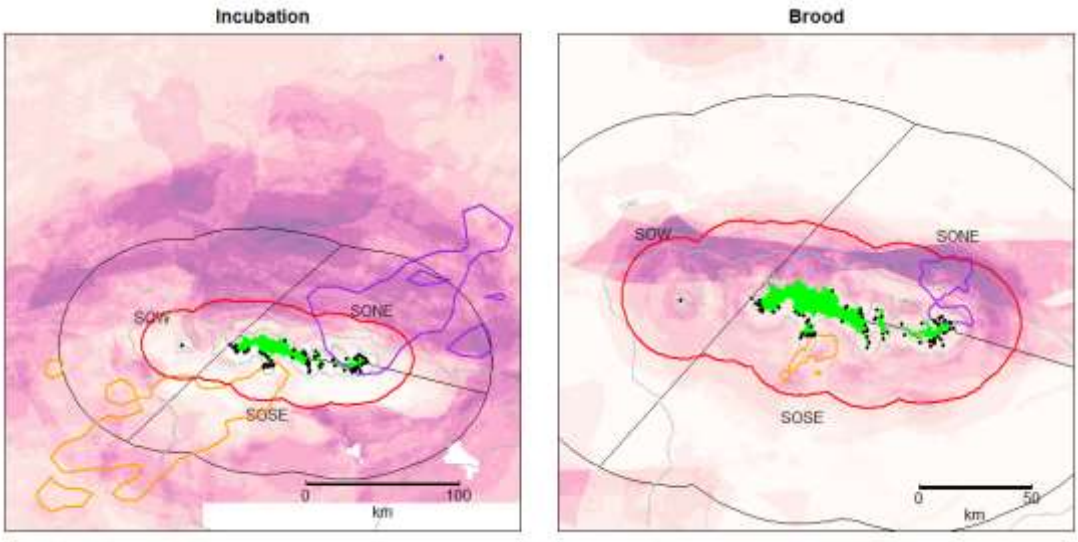

Figure VIII-4: Foraging habitat map for incubation (left) and brood (right) with the 75% utilisation distribution from both colonies (Gourlay in orange, Geddes in violet). The black areas represent CCAMLR small-scale management units (SSMUs). The red area delineates a proposed restricted area 25 km from the coast.

This distance of 25 km also corresponds to the threshold indicating where modelled dive depths change (see IV.3e, page IV-71). Deeper

dive within this 25 km limit indicate intense foraging activities with higher risks of prey depletion. I therefore believe that this proposed area gives a good indication of a three-dimensional foraging hotspot where constraints on bird foraging are high (competition, high energy expenditure due to deep dives) and therefore human activities and fisheries in particular should be restricted.

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APPENDIX I

This first table presents the difference due to the scaling process on the segmentation results for a sample of 4 foraging trips.

Trip ID	Scaling	Trip duration (h)	Random permutation R	Moment index (α)	Processing time (min)	Resulting number of segments
14_20	FALSE	59.6	60	0.1	5.52	38
14_20	TRUE	59.6	60	0.1	8.52	76
24_36	FALSE	25.1	60	0.1	0.72	19
24_36	TRUE	25.1	60	0.1	0.97	35
33_56	FALSE	10.4	60	0.1	0.09	14
33_56	TRUE	10.4	60	0.1	0.12	27
39_76	FALSE	19.9	60	0.1	0.34	18
39_76	TRUE	19.9	60	0.1	0.56	41

The next table indicates the effect of the number of random permutation (R) and the moment index (α) on the number of segments for the same sample of trips.

Trip ID	Trip duration (h)	Random permutation R	Moment index (α)	Processing time (min)	Resulting number of segments
14_20	59.6	30	1	3.74	40
14_20	59.6	60	1	8.72	42
14_20	59.6	120	1	18.03	42
14_20	59.6	30	0.7	4.10	50
14_20	59.6	60	0.7	7.90	50
14_20	59.6	120	0.7	15.48	50
14_20	59.6	30	0.3	5.02	58
14_20	59.6	60	0.3	10.57	59
14_20	59.6	120	0.3	18.12	68
24_36	25.1	30	1	0.43	12
24_36	25.1	30	0.7	0.56	23
24_36	25.1	60	1	1.09	23
24_36	25.1	120	1	2.70	23
24_36	25.1	120	0.7	2.21	25
24_36	25.1	60	0.7	1.16	26
24_36	25.1	30	0.3	0.63	31

24_36	25.1	60	0.3	1.56	34
24_36	25.1	120	0.3	2.70	36
33_56	10.4	30	1	0.04	7
33_56	10.4	30	0.7	0.05	11
33_56	10.4	60	1	0.10	12
33_56	10.4	120	1	0.25	12
33_56	10.4	60	0.7	0.11	13
33_56	10.4	120	0.7	0.23	15
33_56	10.4	30	0.3	0.07	17
33_56	10.4	60	0.3	0.17	20
33_56	10.4	120	0.3	0.29	21
39_76	19.9	30	1	0.24	21
39_76	19.9	60	0.7	0.53	23
39_76	19.9	60	1	0.52	23
39_76	19.9	120	1	1.25	23
39_76	19.9	30	0.7	0.28	24
39_76	19.9	120	0.7	1.06	24
39_76	19.9	30	0.3	0.35	28
39_76	19.9	60	0.3	0.77	30
39_76	19.9	120	0.3	1.39	34

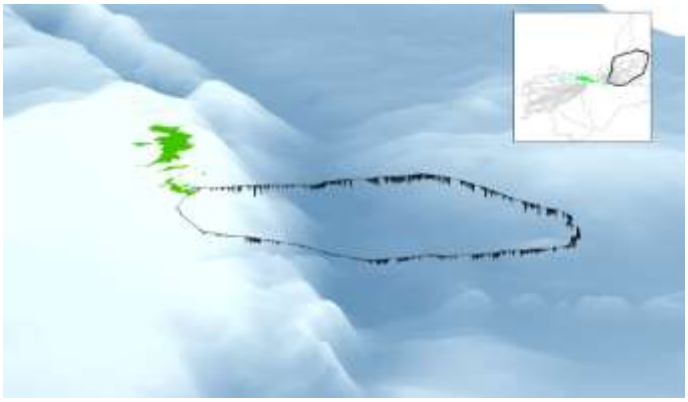
Finally, the last table presents the effect of the minimal segment size on the segmentation results for the same sample of trips.

Trip ID	Trip duration (h)	Random permutation R	Moment index (α)	Minimal segment size (min)	Processing time (min)	Resulting number of segments
14_20	59.6	60	1	2	6.31	41
14_20	59.6	60	1	5	6.20	40
14_20	59.6	60	1	10	6.14	39
24_36	25.1	60	1	2	0.83	23
24_36	25.1	60	1	5	0.82	23
24_36	25.1	60	1	10	0.82	22
33_56	10.4	60	1	2	0.06	11
33_56	10.4	60	1	5	0.05	7
33_56	10.4	60	1	10	0.07	12

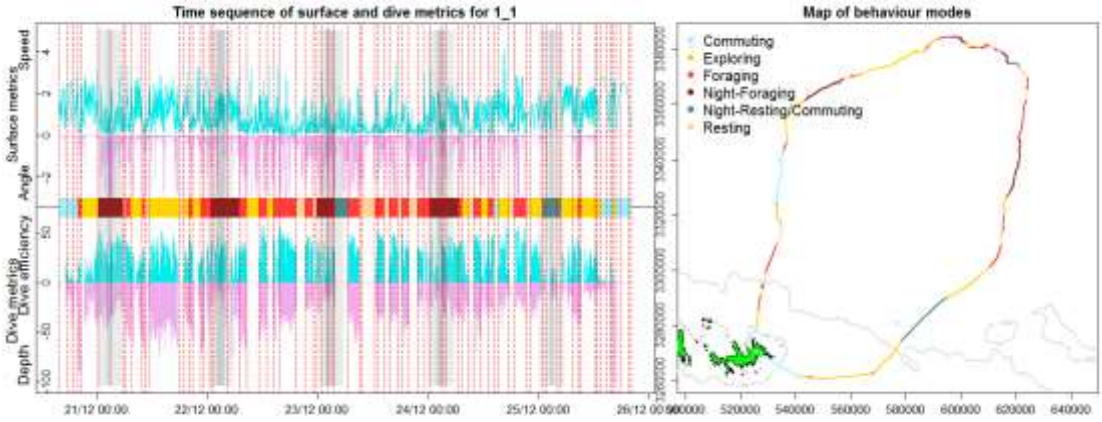
39_76	19.9	60	1	2	0.40	23
39_76	19.9	60	1	5	0.42	23
39_76	19.9	60	1	10	0.39	23

APPENDIX II

Deployment	**1**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	45.2x16.2
Sex	female
Weight (kg)	3.1 (0.7)
Offspring	2

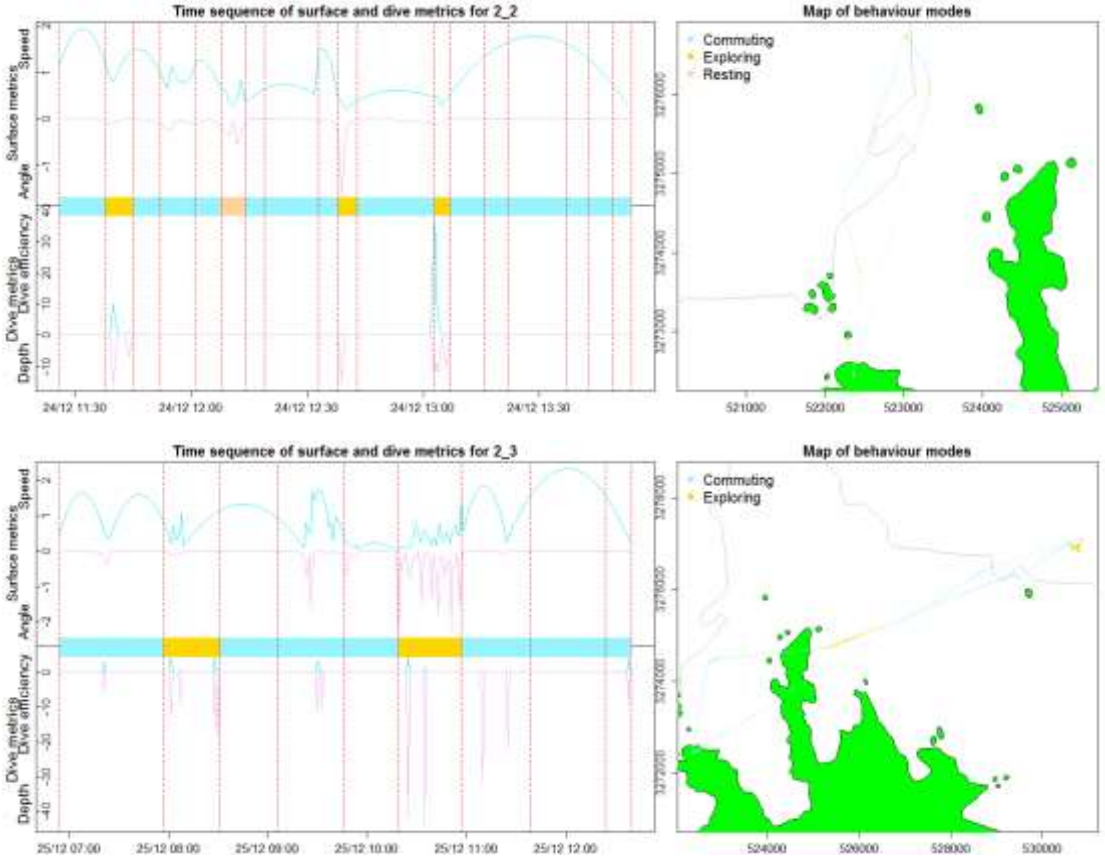


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
1_1	20-12 (15)	25-12 (20)	124.4	NA	C	142.0	22%	28%	0.25	44%	0.29

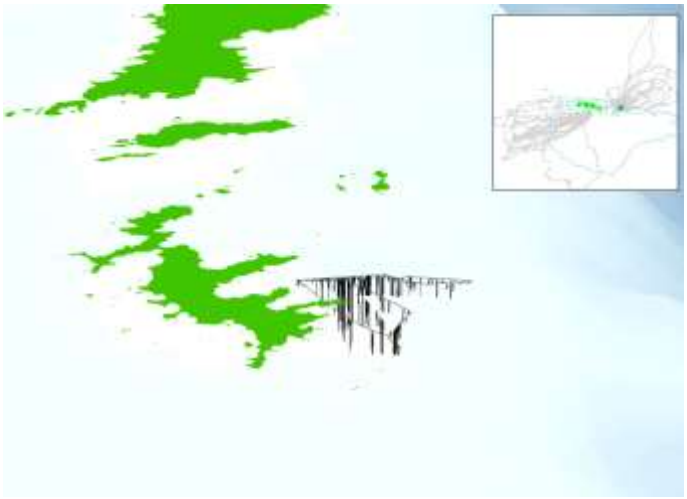


Deployment	**2**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	45.2x18
Sex	female
Weight (kg)	3.3 (-0.7)
Offspring	2

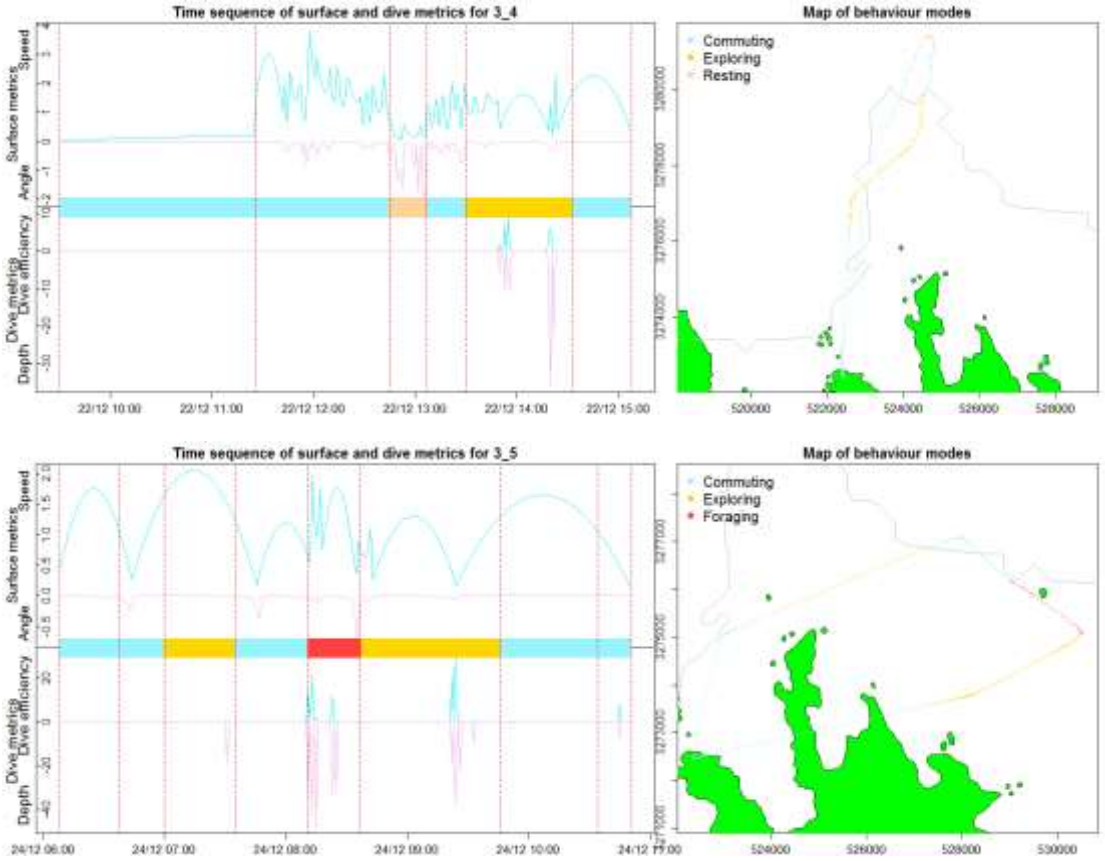
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
2_2	24-12 (11)	24-12 (13)	2.5	17.0	C	4.4	0%	0%	0.01	0%	0.02
2_3	25-12 (06)	25-12 (12)	5.8	NA	C	9.7	0%	0%	0.02	0%	0.04



Deployment	**3**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	47x16.2
Sex	female
Weight (kg)	3.4 (-0.8)
Offspring	2

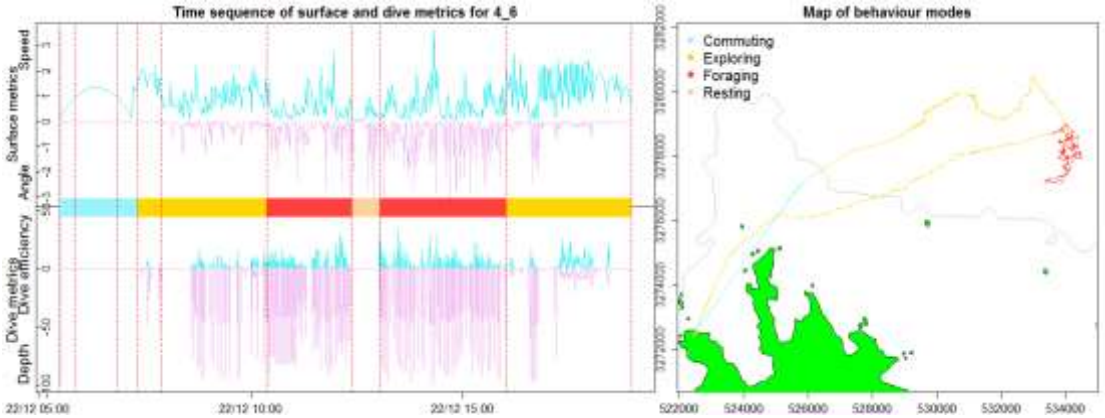


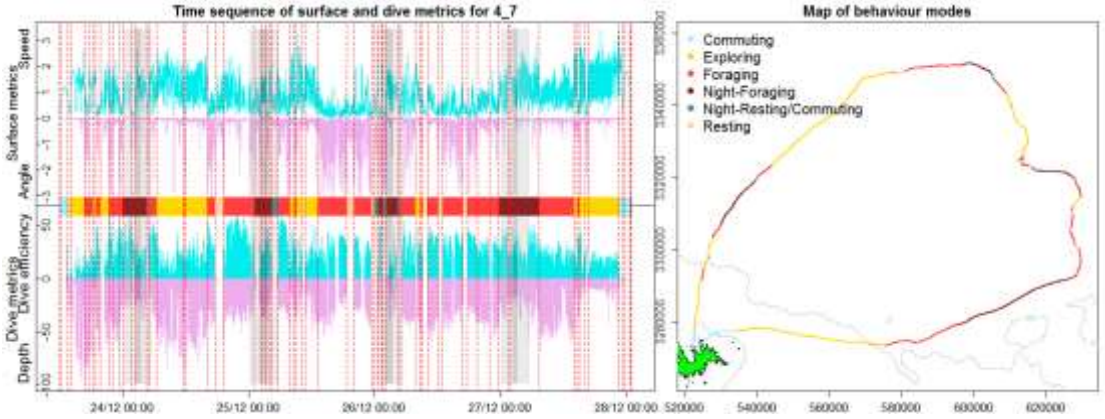
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
3_4	22-12 (09)	22-12 (15)	5.6	39.0	C	9.2	0%	0%	0.01	0%	0.05
3_5	24-12 (06)	24-12 (10)	4.7	NA	C	8.6	0%	0%	0.03	9%	0.03



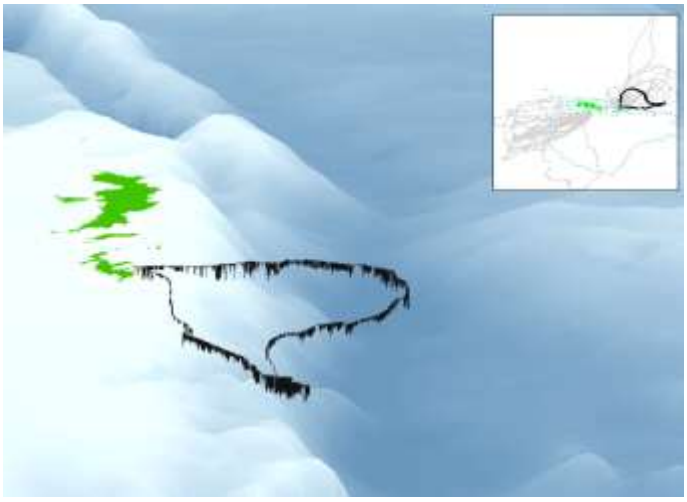
Deployment	**4**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	50.2x19.75
Sex	male
Weight (kg)	3.75 (0)
Offspring	2

Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
4_6	22-12 (05)	22-12 (18)	13.5	16.9	C	13.5	1%	0%	0.39	37%	0.10
4_7	23-12 (11)	28-12 (01)	109.2	NA	C	115.8	21%	23%	0.33	61%	0.32

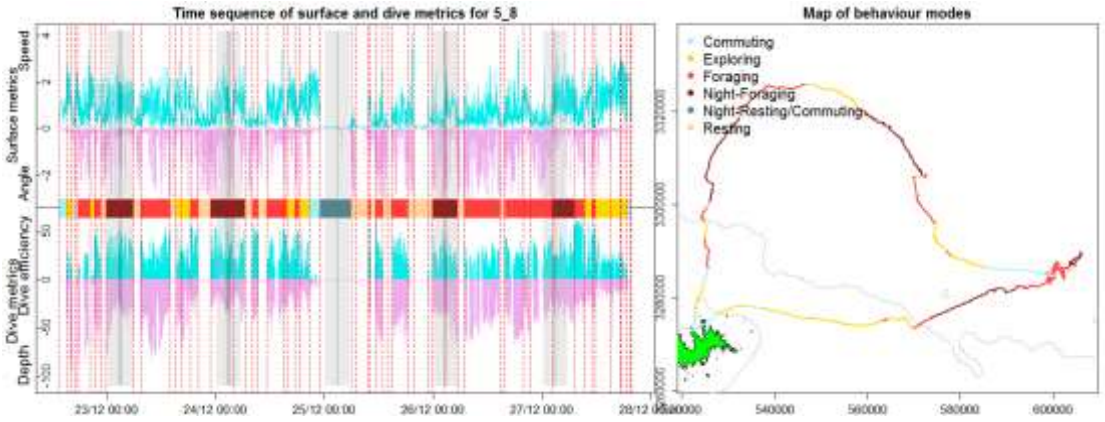




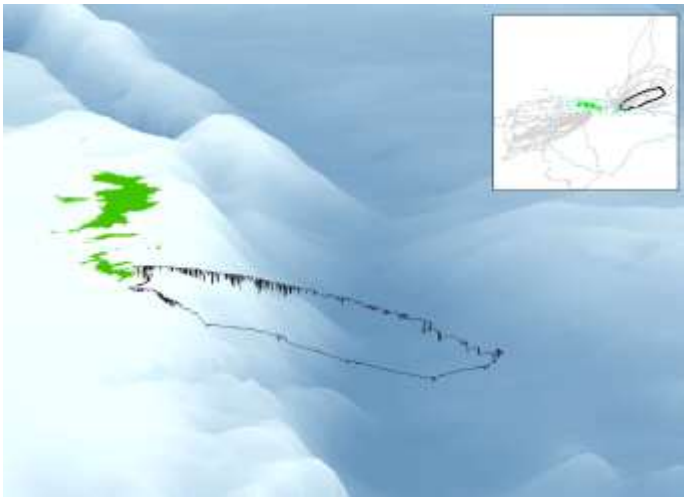
Deployment	**5**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	51.2x19
Sex	unsure
Weight (kg)	3.9 (0.2)
Offspring	2



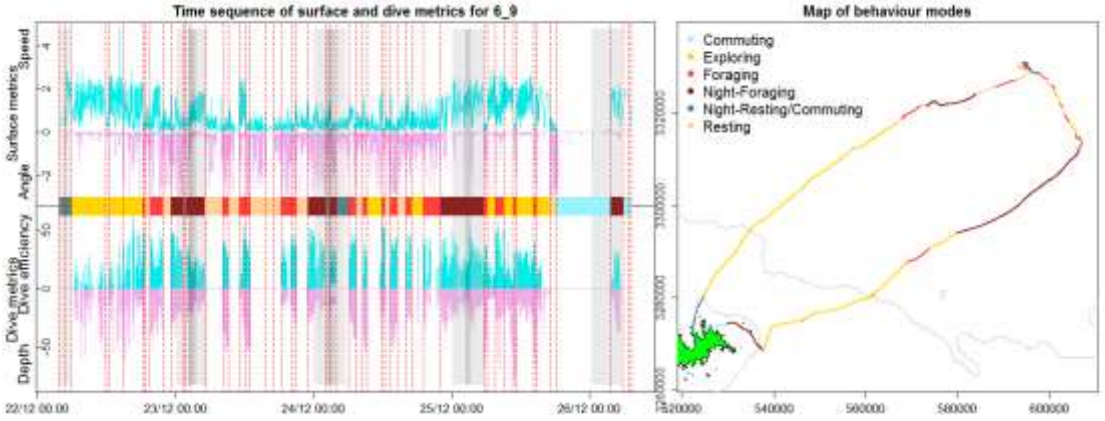
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
5_8	22-12 (13)	27-12 (19)	126.3	NA	C	85.4	21%	28%	0.30	56%	0.37



Deployment	**6**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	48x17.6
Sex	female
Weight (kg)	3.4 (0)
Offspring	2

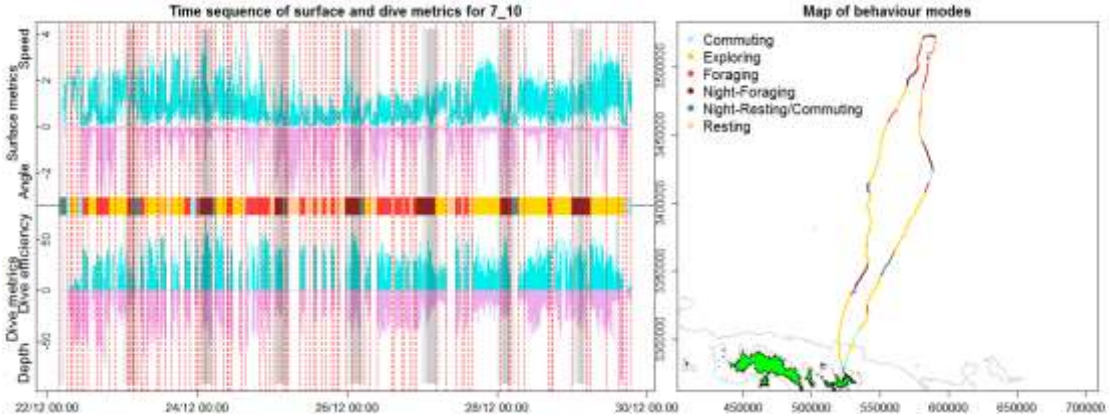


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
6_9	22-12 (03)	26-12 (07)	99.6	NA	C	95.1	24%	34%	0.20	39%	0.29

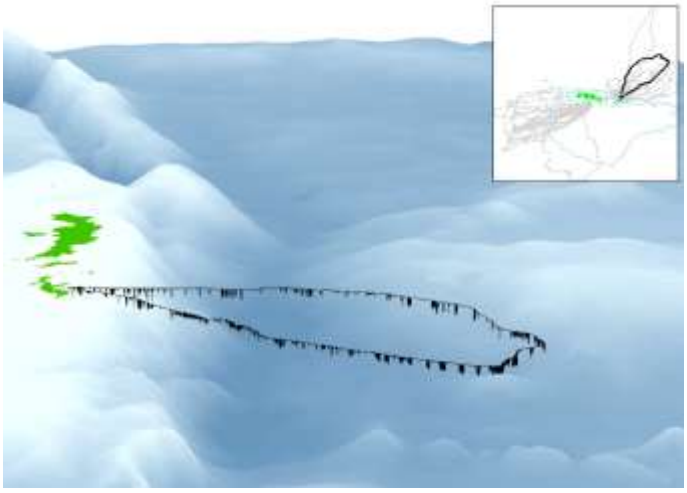


Deployment	**7**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	45.1x16
Sex	female
Weight (kg)	3.3 (1.1)
Offspring	2

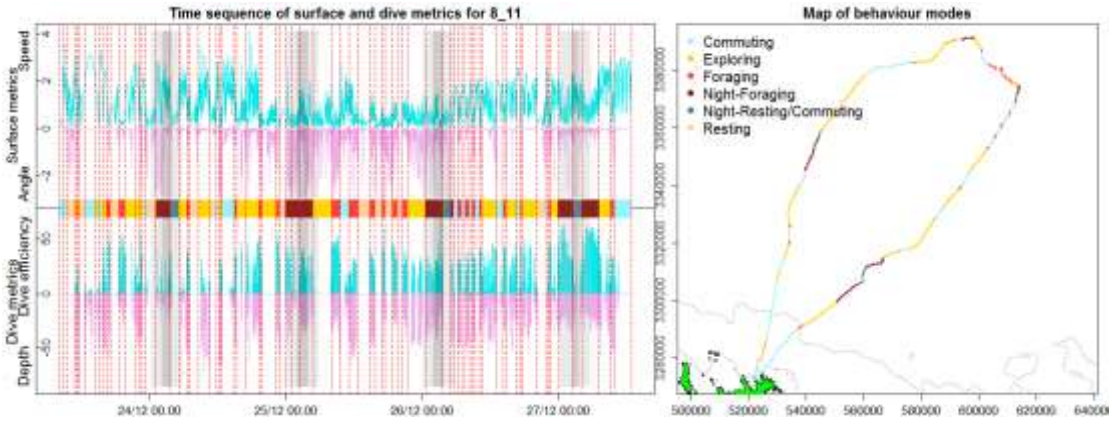
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
7_10	22-12 (03)	29-12 (19)	183.4	NA	AC	258.7	23%	27%	0.22	36%	0.24



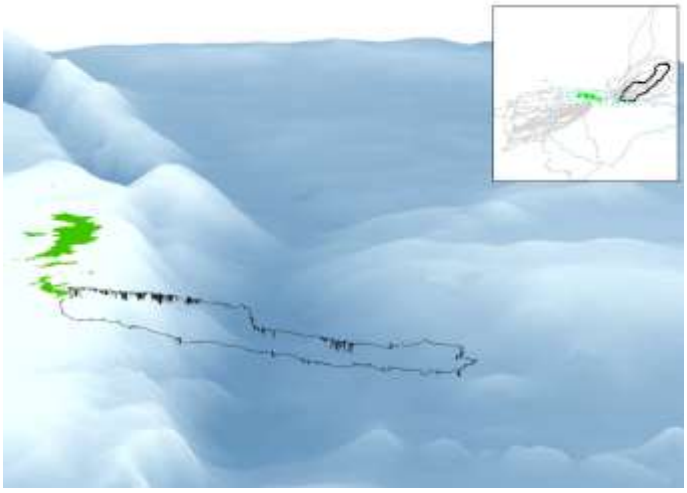
Deployment	**8**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	49.4x18.4
Sex	female
Weight (kg)	3.8 (0.2)
Offspring	2



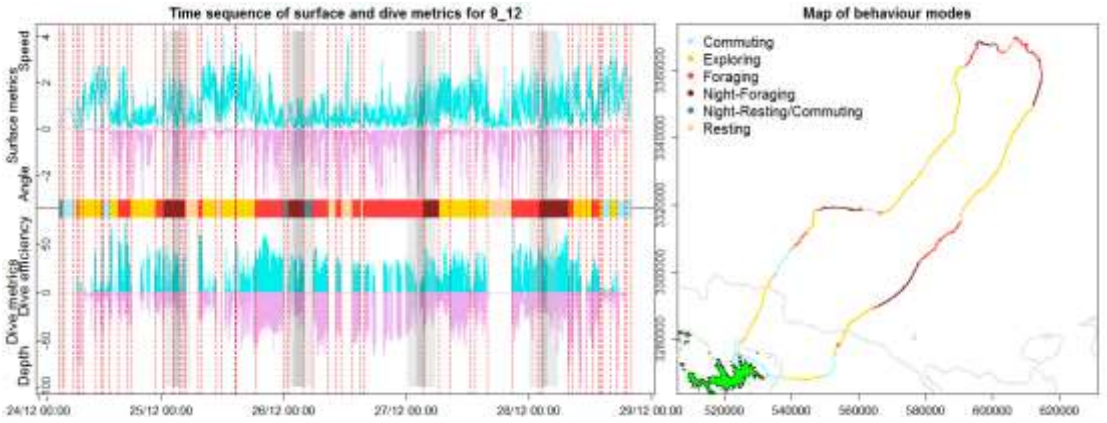
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
8_11	23-12 (08)	27-12 (12)	100.8	NA	C	140.9	22%	34%	0.20	31%	0.30



Deployment	**9**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	47.9x18.2
Sex	female
Weight (kg)	3.4 (0.7)
Offspring	2

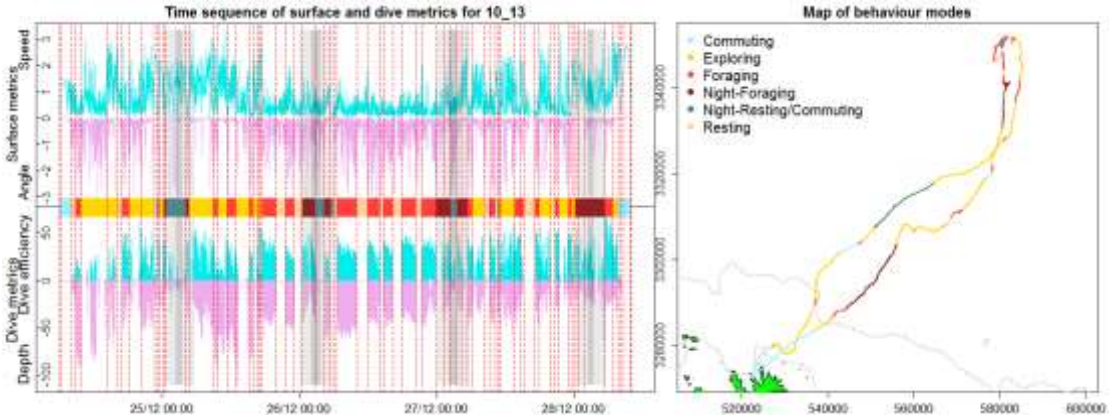


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
9_12	24-12 (04)	28-12 (20)	112.1	NA	C	129.8	21%	29%	0.26	47%	0.31



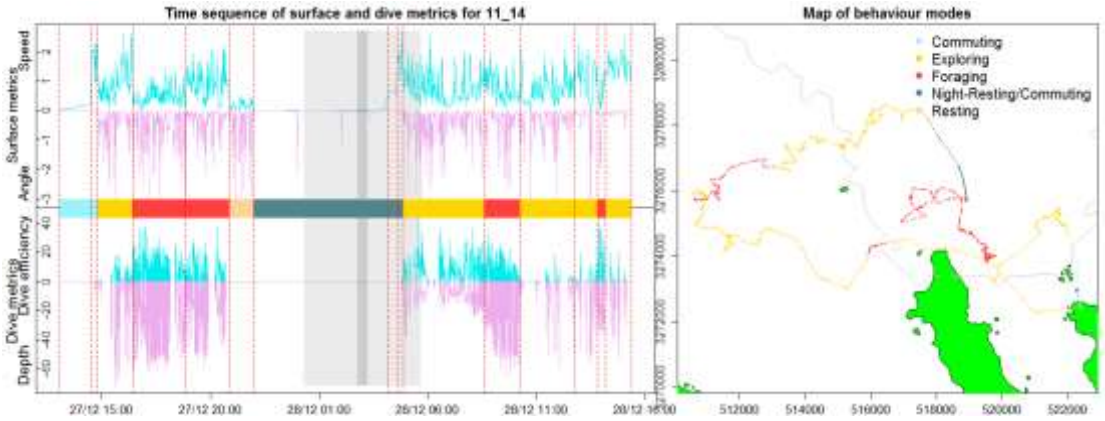
Deployment	**10**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	50x17.5
Sex	female
Weight (kg)	3.6 (0.6)
Offspring	2

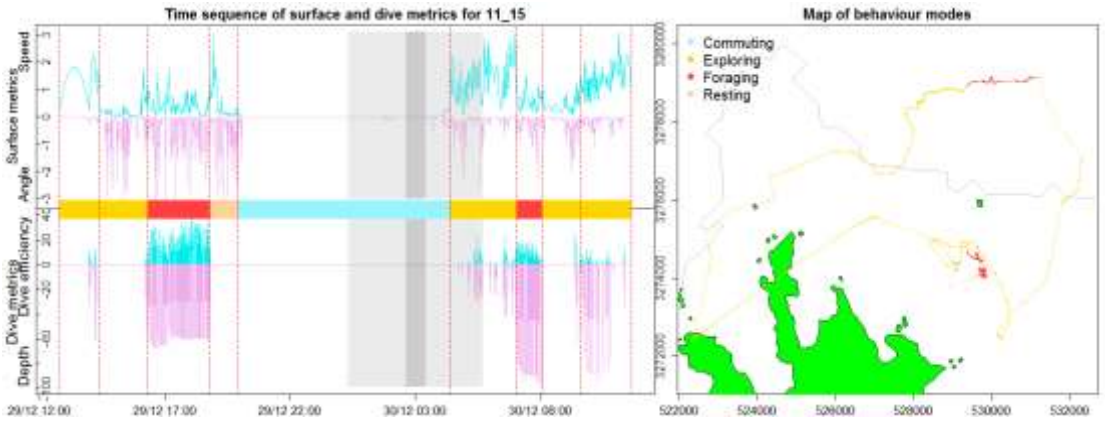
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
10_13	24-12 (06)	28-12 (10)	100.1	NA		99.8	22%	27%	0.36	43%	0.30



Deployment	**11**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	45.9x17.9
Sex	female
Weight (kg)	3.2 (1)
Offspring	2

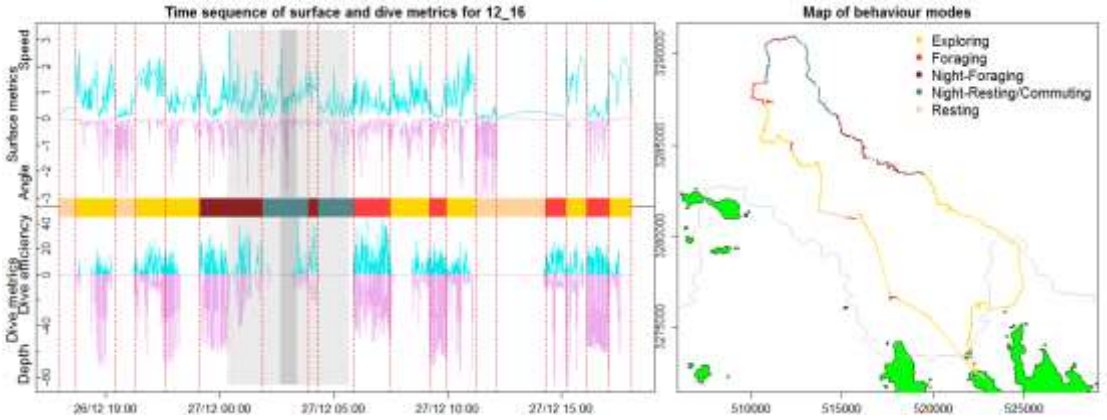
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
11_14	27-12 (13)	28-12 (15)	26.3	21.4	AC	12.4	20%	9%	0.33	24%	0.05
11_15	29-12 (12)	30-12 (11)	22.9	NA	AC	11.1	24%	11%	0.34	15%	0.04





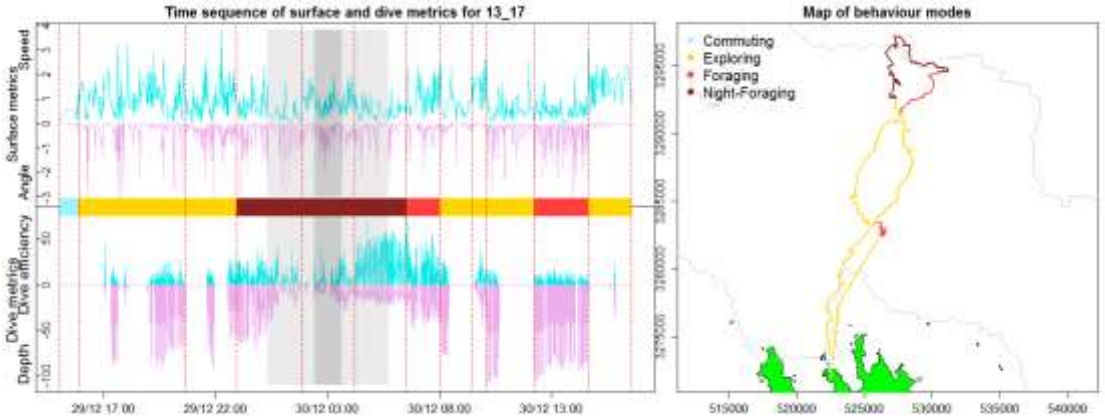
Deployment	**12**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	50.2x17.7
Sex	female
Weight (kg)	3.6 (0.5)
Offspring	1

Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
12_16	26-12 (16)	27-12 (18)	25.2	NA	AC	22.0	21%	18%	0.31	29%	0.10



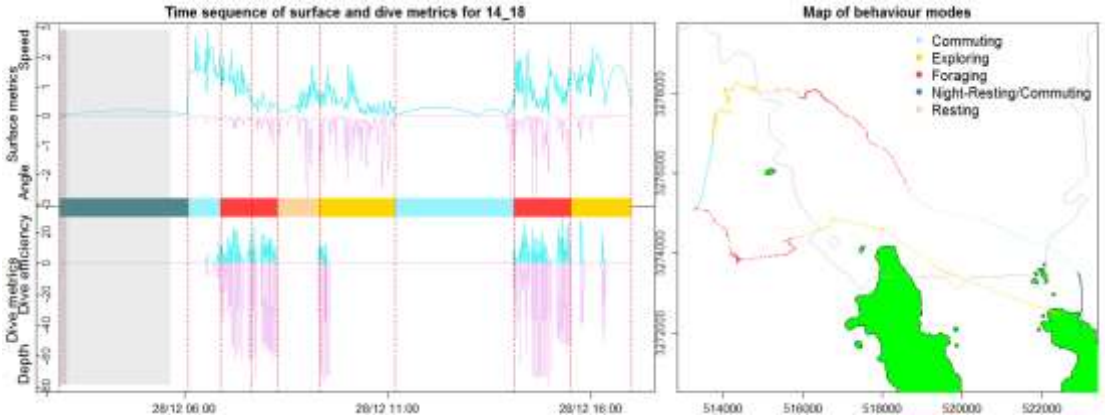
Deployment	**13**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	50.9x19
Sex	unsure
Weight (kg)	3.7 (1.3)
Offspring	2

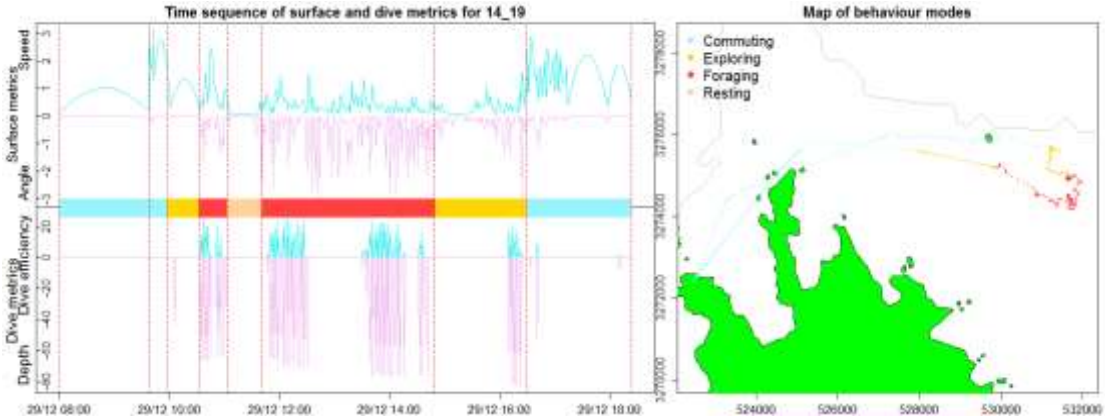
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
13_17	29-12 (15)	30-12 (16)	25.6	NA		25.3	21%	38%	0.38	45%	0.14

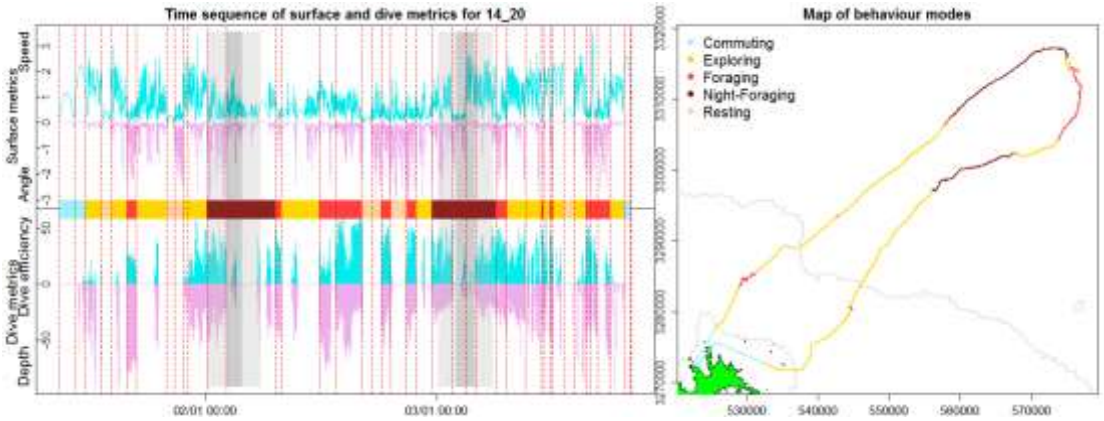


Deployment	**14**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	46.6x17.25
Sex	female
Weight (kg)	3 (1.2)
Offspring	2

Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
14_18	28-12 (02)	28-12 (17)	14.1	15.0	AC	10.8	20%	0%	0.26	20%	0.05
14_19	29-12 (08)	29-12 (18)	10.4	62.4	AC	9.8	0%	0%	0.22	35%	0.03
14_20	01-01 (08)	03-01 (20)	59.5	NA	AC	68.4	19%	30%	0.27	44%	0.28

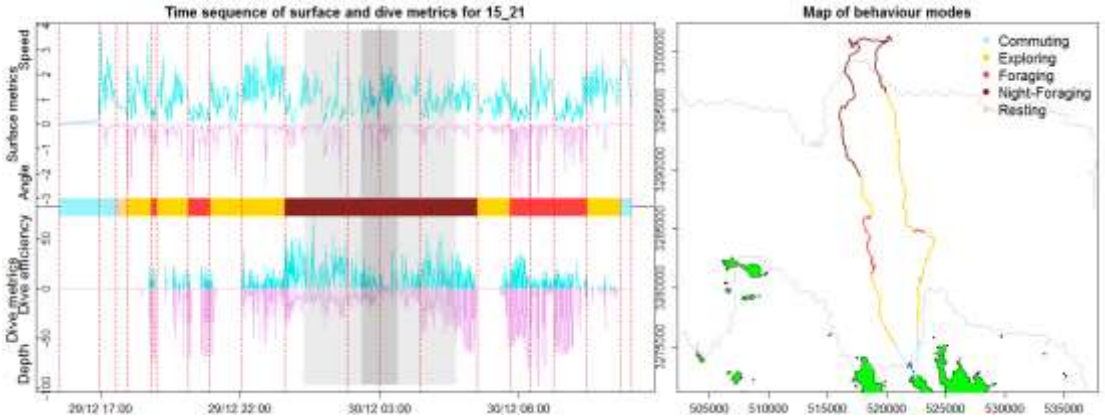





Time sequence of surface and dive metrics for 14_20
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
02/01 00:00
03/01 00:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Foraging
Resting
530000
540000
550000
560000
570000

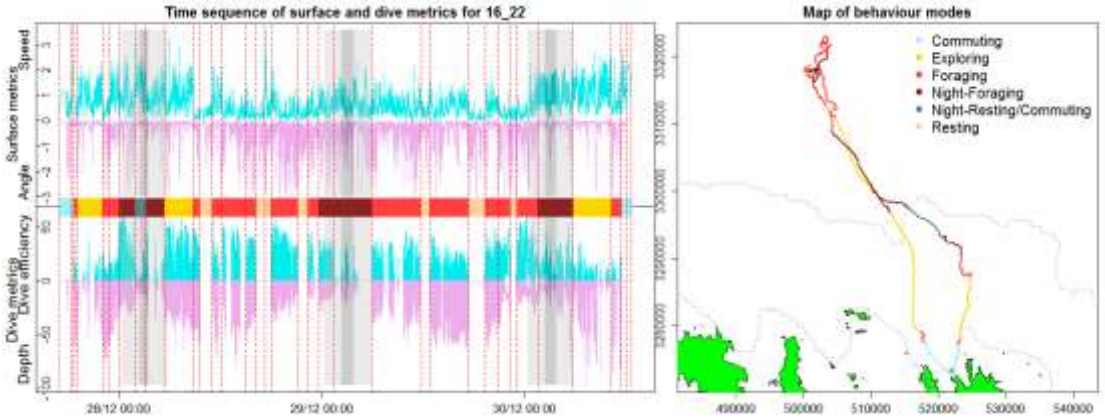
Deployment	**15**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	46.3x16.7
Sex	female
Weight (kg)	3.7 (0.5)
Offspring	2

Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
15_21	29-12 (15)	30-12 (12)	20.6	NA	AC	29.2	27%	48%	0.26	52%	0.13



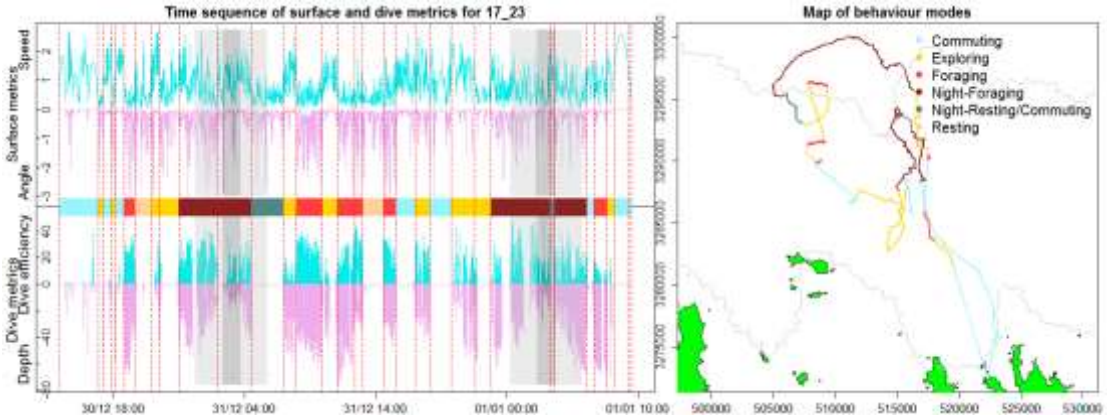
Deployment	**16**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	52.75x18.9
Sex	unsure
Weight (kg)	2.9 (1.8)
Offspring	2

Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
16_22	27-12 (16)	30-12 (12)	67.7	NA	AC	54.1	24%	32%	0.38	65%	0.30



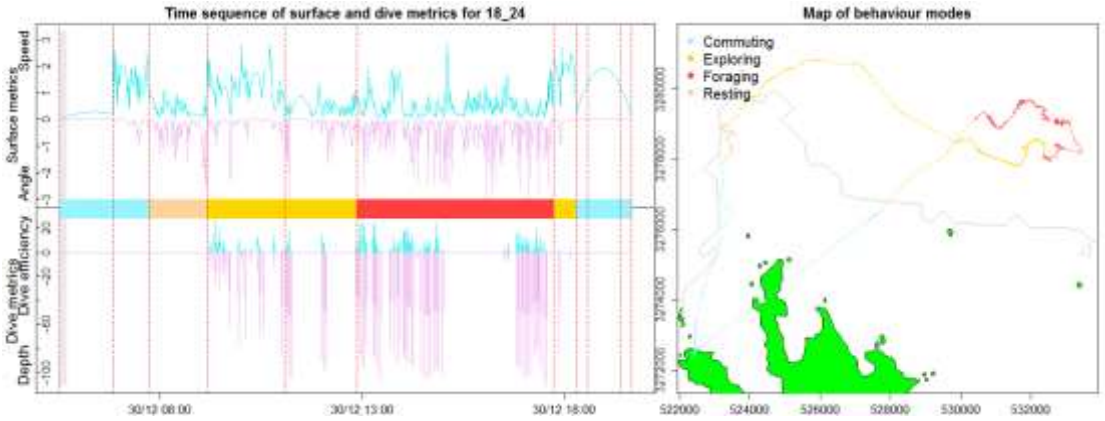
Deployment	**17**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	46.5x18.7
Sex	female
Weight (kg)	3.5 (0.7)
Offspring	2

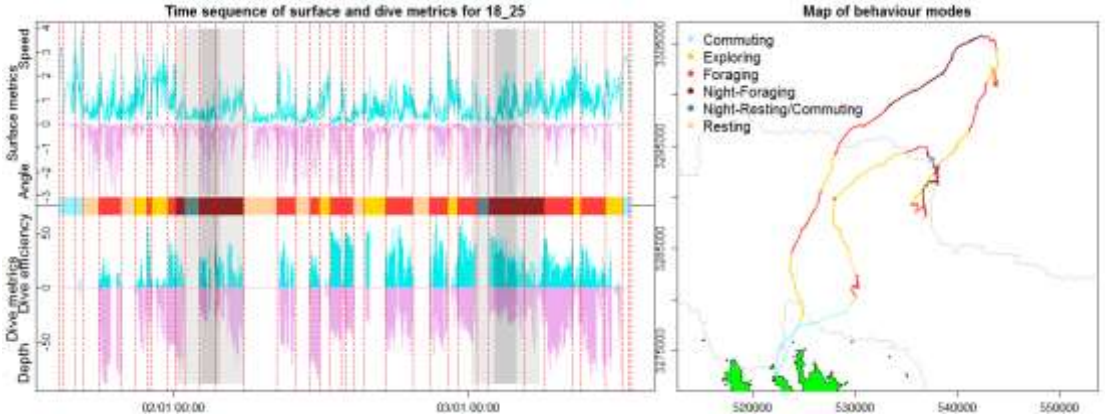
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
17_23	30-12 (13)	01-01 (09)	43.7	NA	AC	30.3	25%	41%	0.26	44%	0.17



Deployment	**18**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	52.1x17.7
Sex	female
Weight (kg)	3.7 (0.7)
Offspring	2

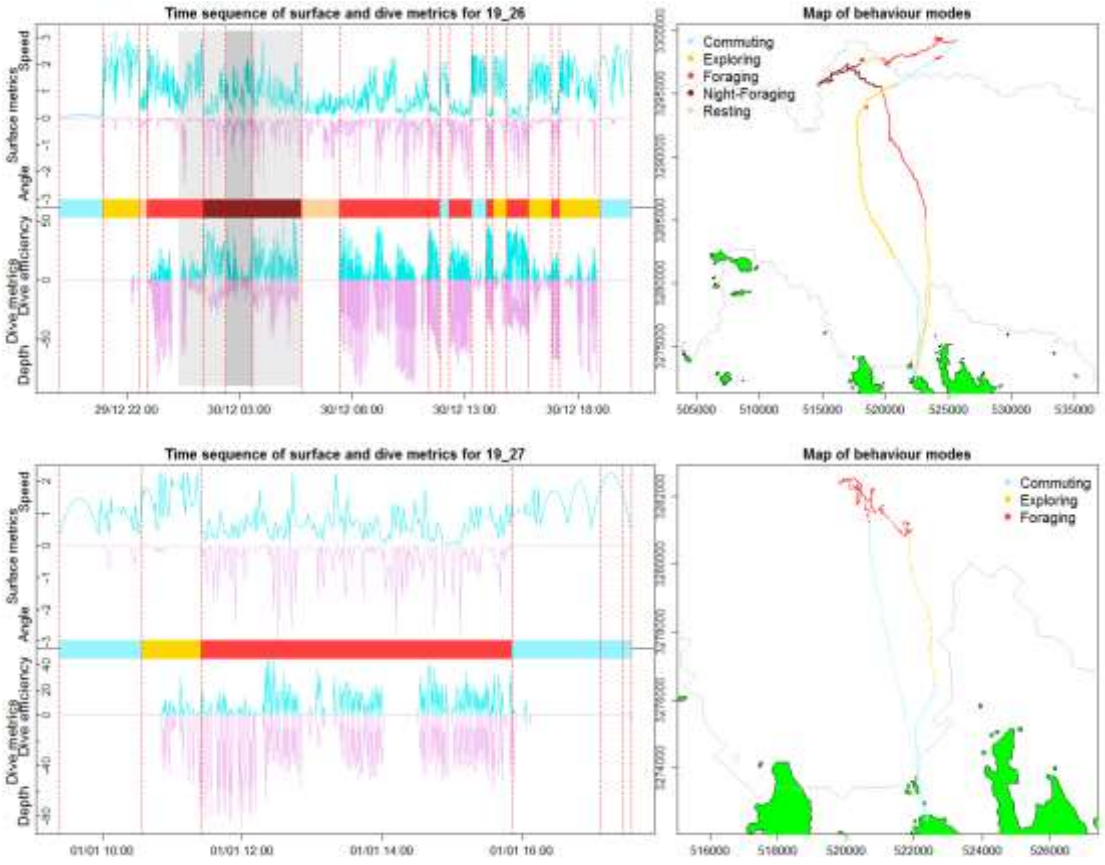
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
18_24	30-12 (05)	30-12 (19)	14.2	43.0	C	12.6	1%	0%	0.24	34%	0.09
18_25	01-01 (14)	03-01 (13)	46.6	NA	AC	39.2	24%	34%	0.38	55%	0.24



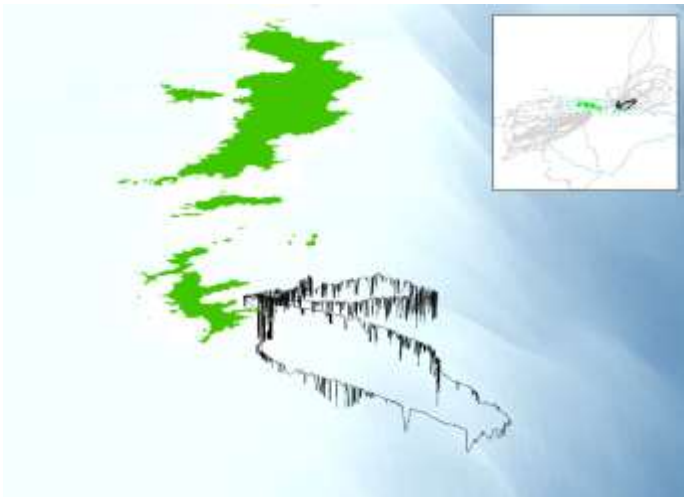


Deployment	**19**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	48.7x18.9
Sex	unsure
Weight (kg)	3.9 (0.4)
Offspring	2

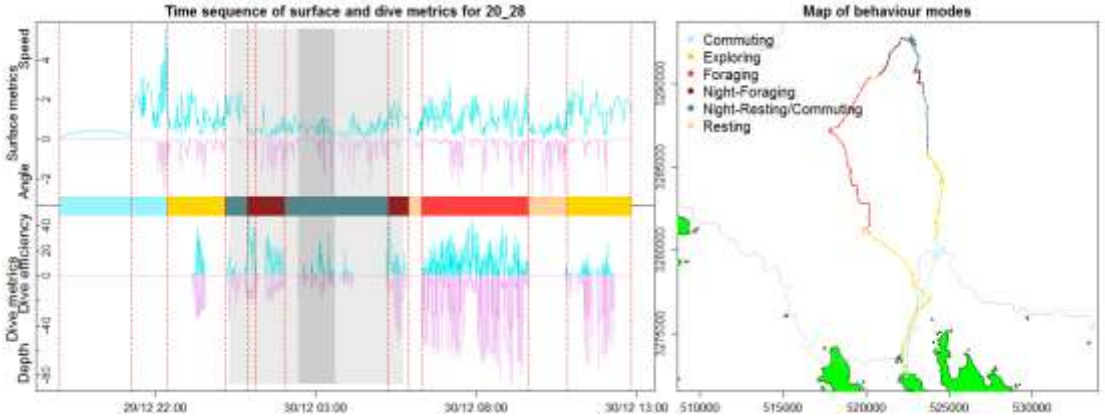
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
19_26	29-12 (19)	30-12 (20)	25.4	37.0	AC	27.2	22%	43%	0.30	55%	0.17
19_27	01-01 (09)	01-01 (17)	8.2	NA	AC	10.3	0%	0%	0.32	54%	0.06

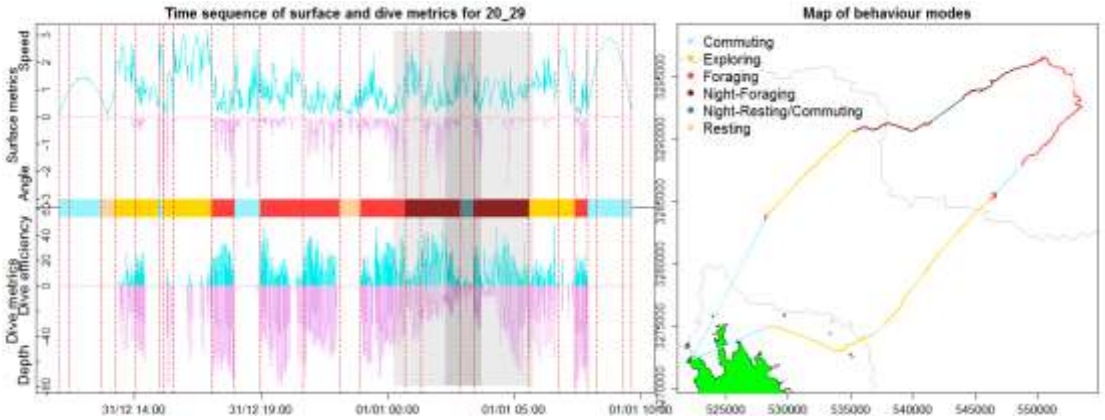


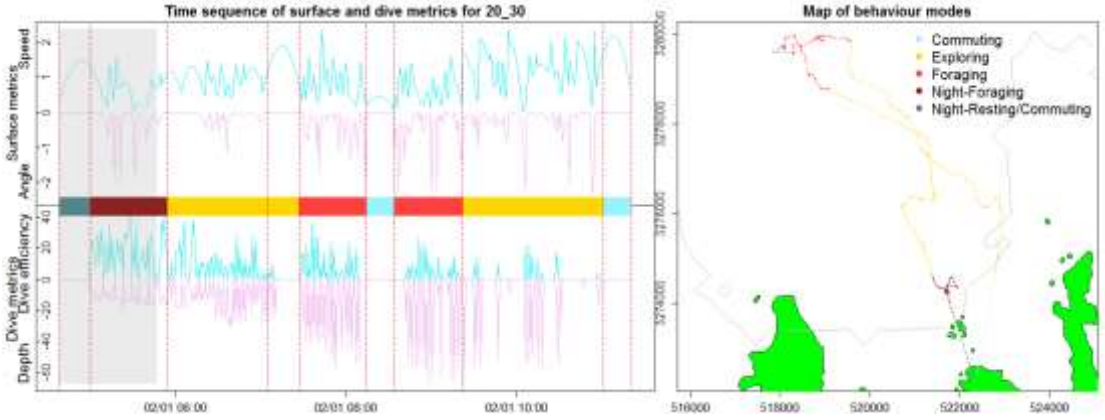
Deployment	**20**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	44.9x16.5
Sex	female
Weight (kg)	3.6 (0.5)
Offspring	2



Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
20_28	29-12 (19)	30-12 (12)	17.8	22.2	AC	20.6	30%	40%	0.19	29%	0.09
20_29	31-12 (11)	01-01 (09)	22.6	19.0	AC	38.0	24%	47%	0.27	47%	0.23
20_30	02-01 (04)	02-01 (11)	6.7	NA	C	8.6	17%	29%	0.27	37%	0.04

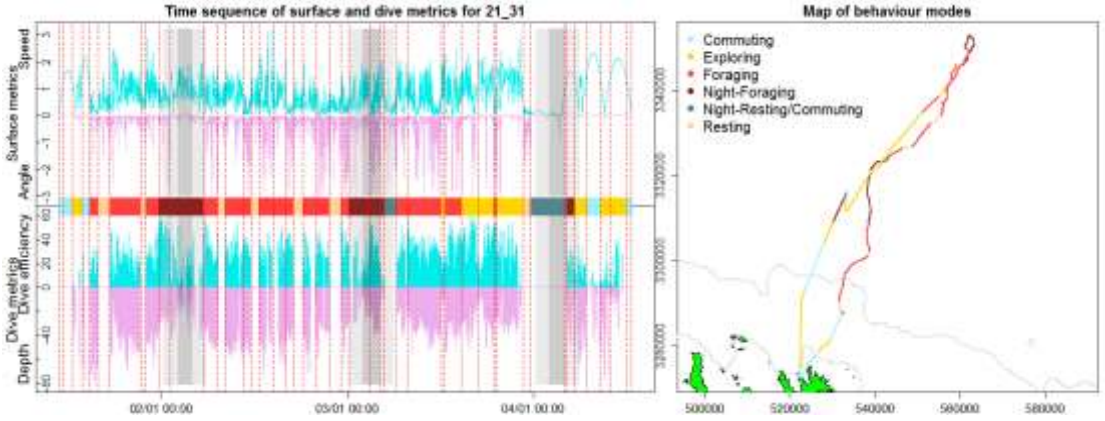





Time sequence of surface and dive metrics for 20_30
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
02/01 06:00
02/01 08:00
02/01 10:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Foraging
Night-Resting/Commuting
516000
518000
520000
522000
524000

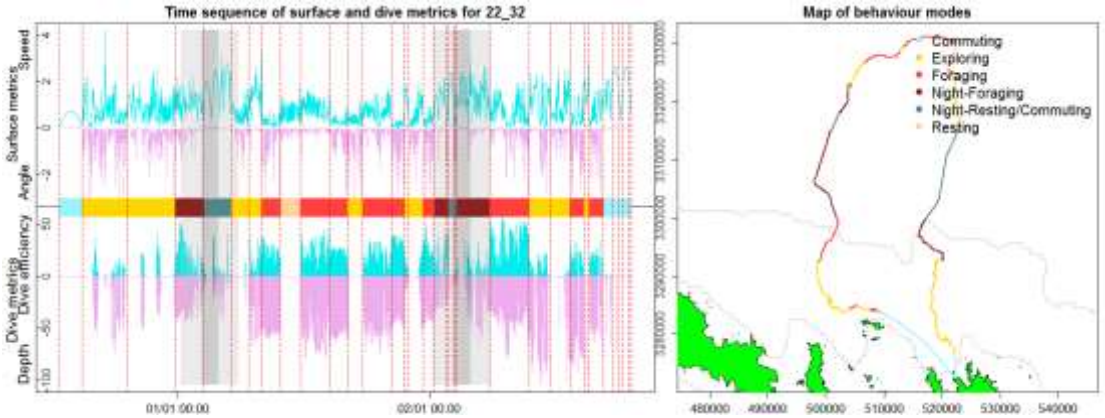
Deployment	**21**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	48.9x17.9
Sex	female
Weight (kg)	4.2 (0.3)
Offspring	2

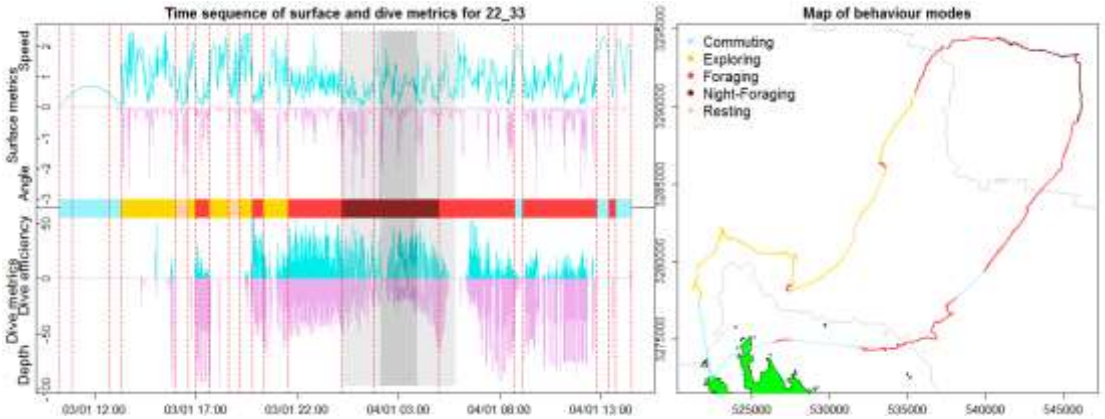
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
21_31	01-01 (10)	04-01 (12)	73.9	NA	AC	89.8	23%	22%	0.36	55%	0.32



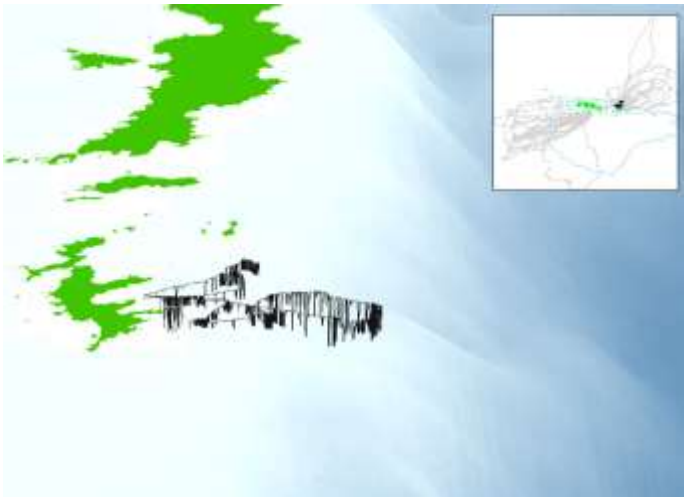
Deployment	**22**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	49.9x17.6
Sex	female
Weight (kg)	4 (-0.1)
Offspring	2

Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
22_32	31-12 (12)	02-01 (19)	54.6	15.0	AC	59.1	20%	24%	0.35	46%	0.24
22_33	03-01 (10)	04-01 (14)	28.3	NA	C	31.5	20%	40%	0.35	58%	0.16

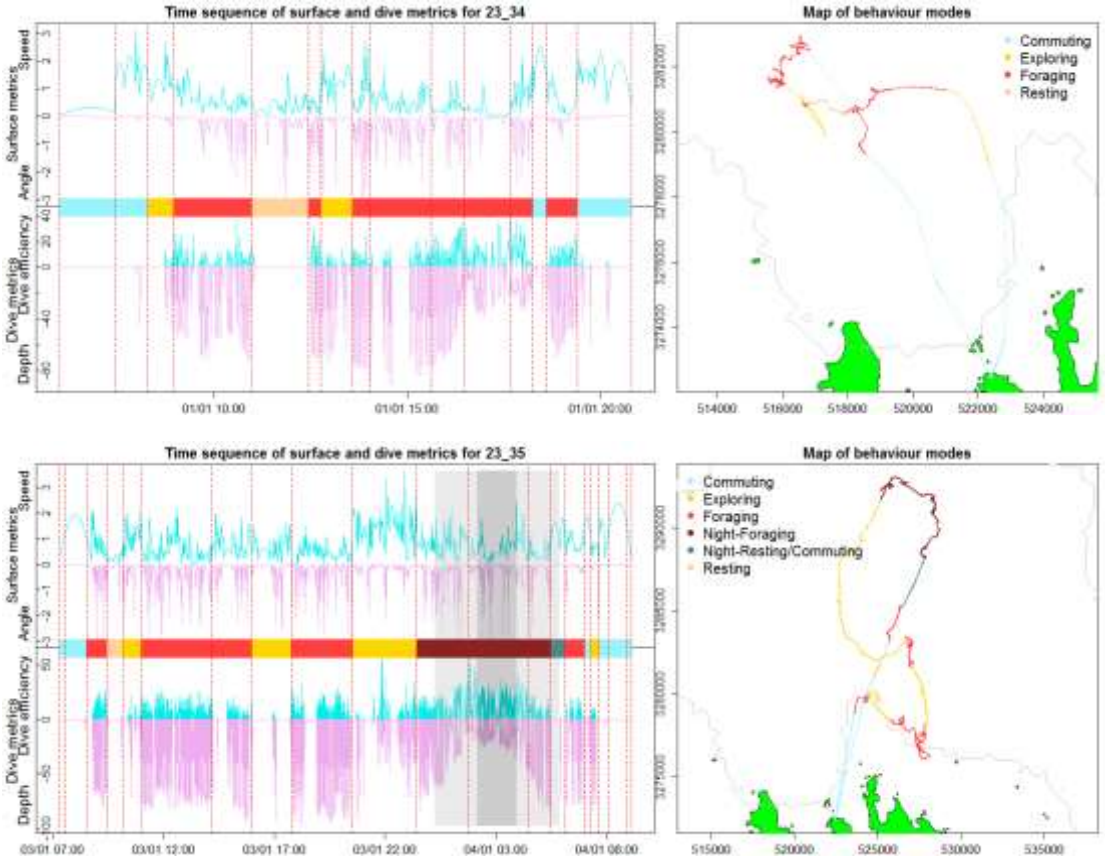




Deployment	**23**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	48.9x14.5
Sex	female
Weight (kg)	4.3 (0.2)
Offspring	2

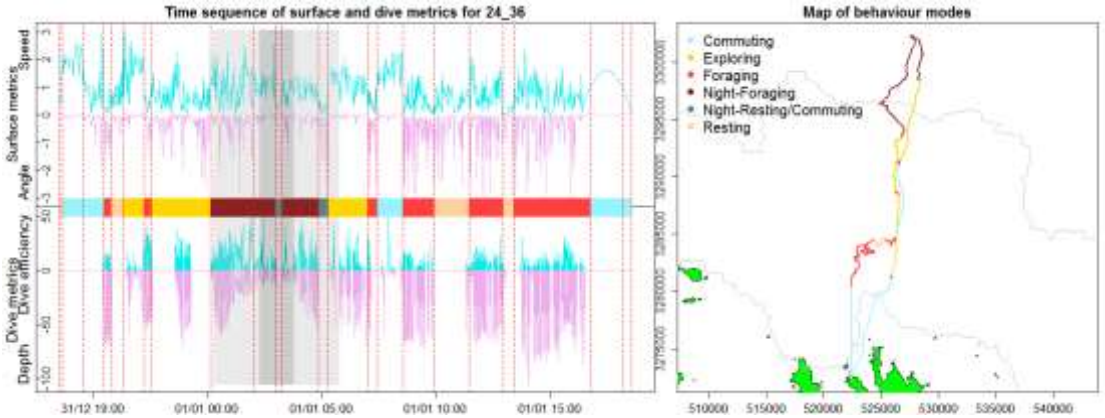


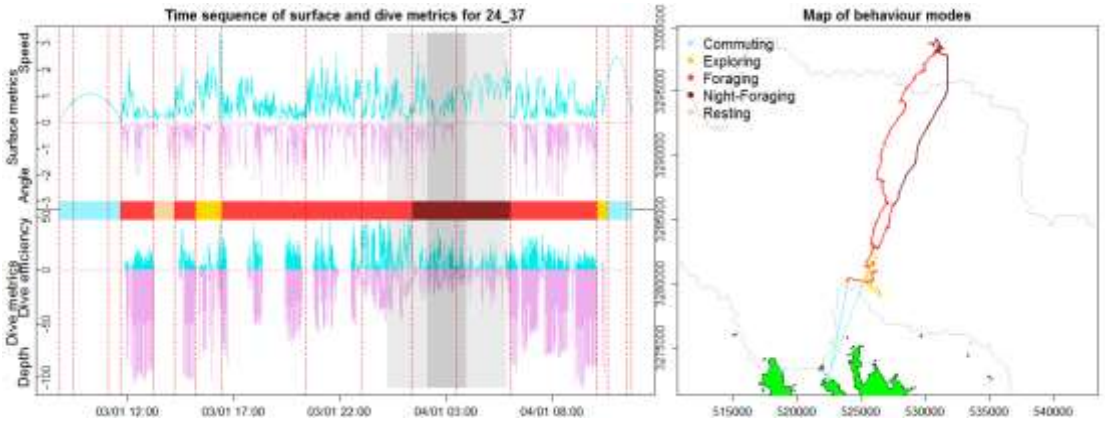
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
23_34	01-01 (06)	01-01 (20)	14.8	34.5	AC	12.0	0%	0%	0.43	53%	0.08
23_35	03-01 (07)	04-01 (09)	25.9	NA	C	20.8	22%	40%	0.51	60%	0.08



Deployment	**24**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	58.3x18.85
Sex	male
Weight (kg)	4.6 (-0.1)
Offspring	2

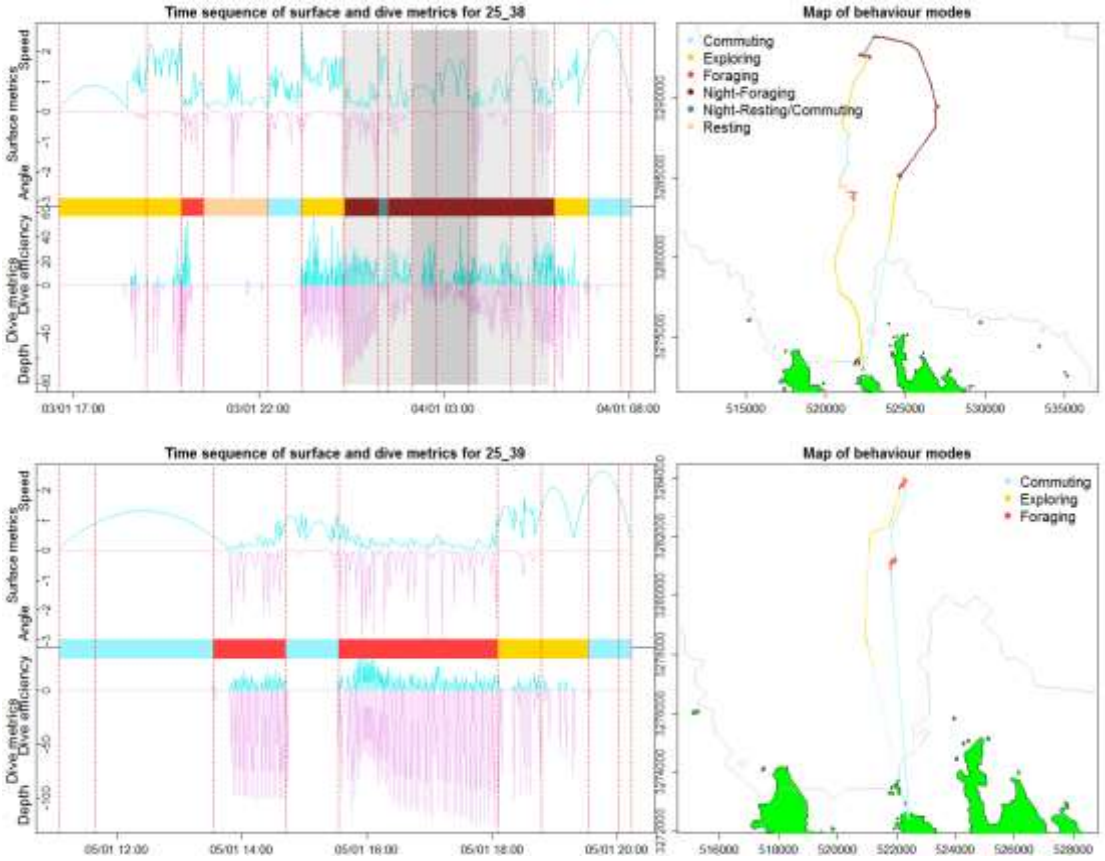
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
24_36	31-12 (17)	01-01 (18)	25.1	38.2	AC	30.2	22%	38%	0.31	47%	0.14
24_37	03-01 (08)	04-01 (11)	27.0	NA	C	28.0	21%	34%	0.41	75%	0.13





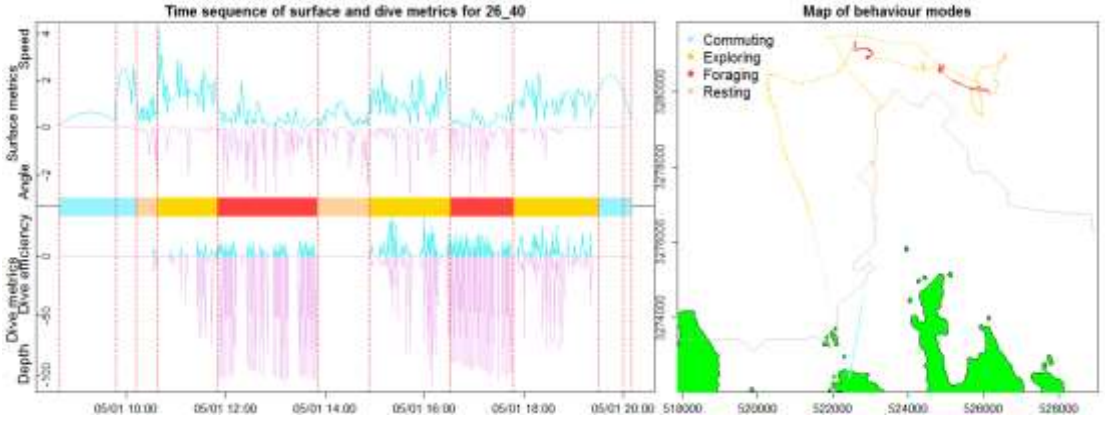
Deployment	**25**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	46.1x18.8
Sex	female
Weight (kg)	4.6 (-0.6)
Offspring	2

Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
25_38	03-01 (16)	04-01 (08)	15.5	27.0	C	21.5	36%	68%	0.26	39%	0.10
25_39	05-01 (11)	05-01 (20)	9.2	NA	AC	11.6	0%	0%	0.59	40%	0.09



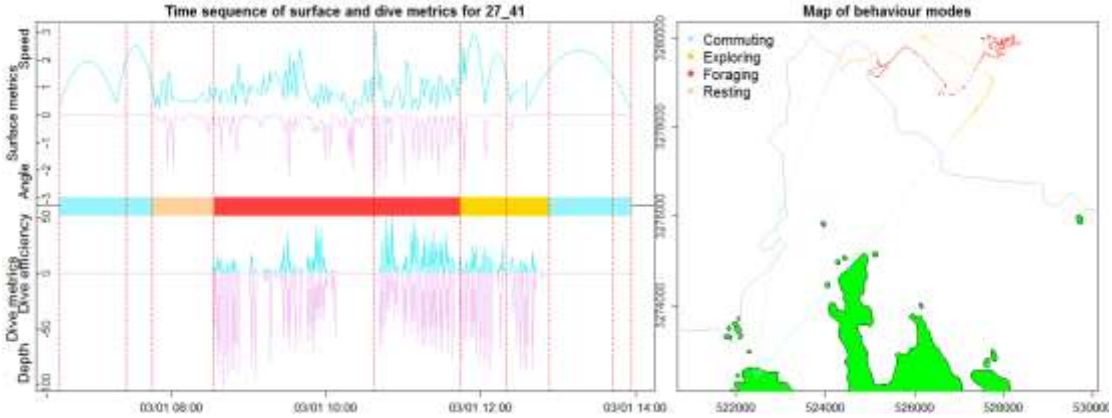
Deployment	**26**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	45.5x17.2
Sex	female
Weight (kg)	3.9 (-0.7)
Offspring	2

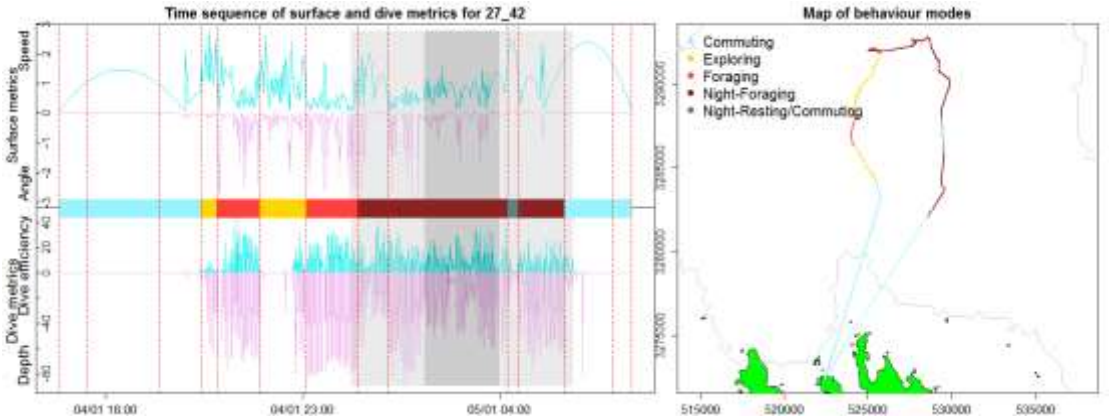
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
26_40	05-01 (08)	05-01 (20)	11.5	NA	AC	9.6	0%	0%	0.40	28%	0.07

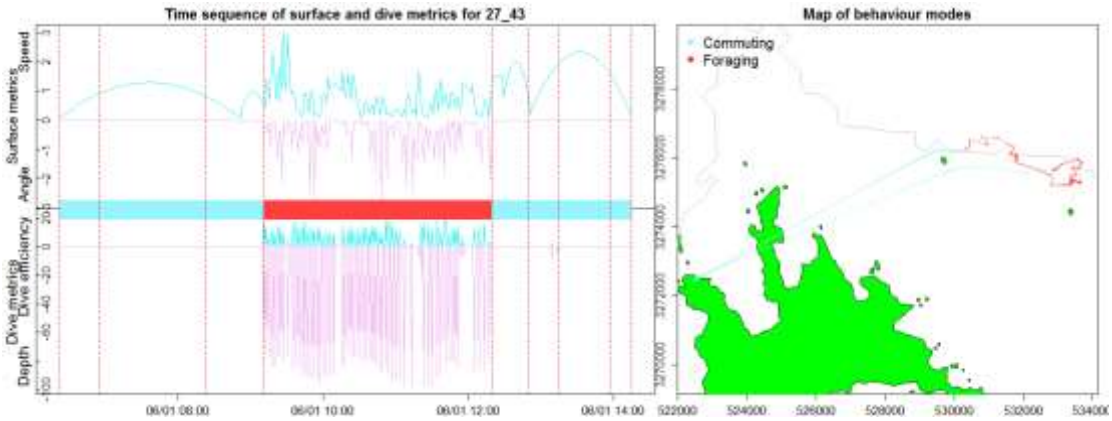


Deployment	**27**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	48.8x19.5
Sex	male
Weight (kg)	5 (-0.1)
Offspring	2

Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
27_41	03-01 (06)	03-01 (13)	7.4	26.9	C	9.6	0%	0%	0.26	43%	0.05
27_42	04-01 (16)	05-01 (07)	14.6	23.0	C	21.3	39%	68%	0.38	50%	0.09
27_43	06-01 (06)	06-01 (14)	7.9	NA	C	11.8	0%	0%	0.34	40%	0.04

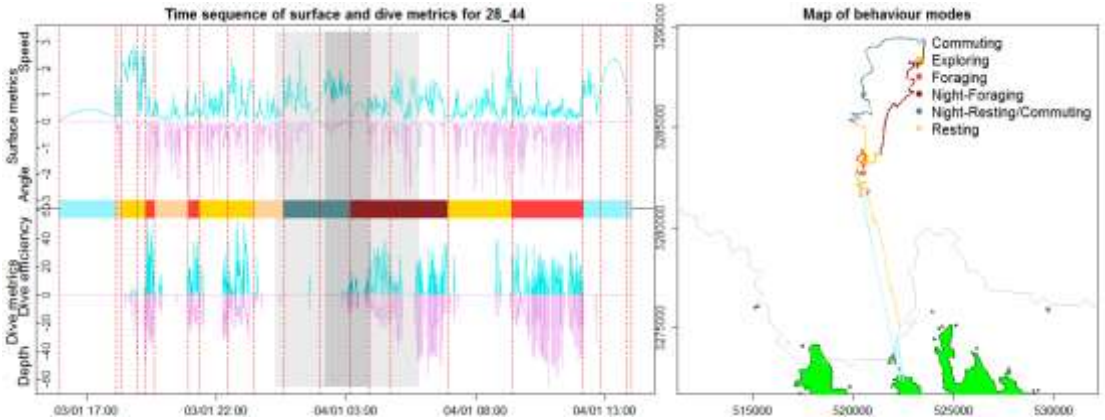


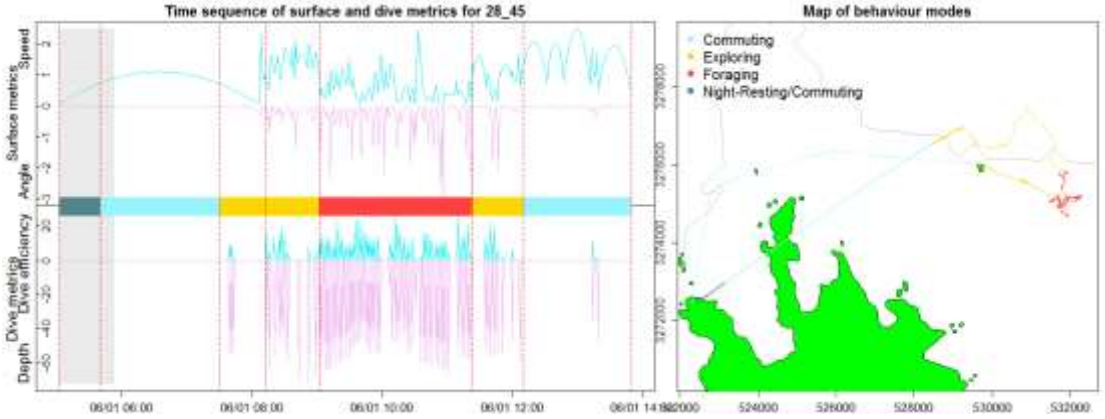



Time sequence of surface and dive metrics for 27_43
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
06/01 08:00
06/01 10:00
06/01 12:00
06/01 14:00
Map of behaviour modes
Commuting
Foraging
522000
524000
526000
528000
530000
532000

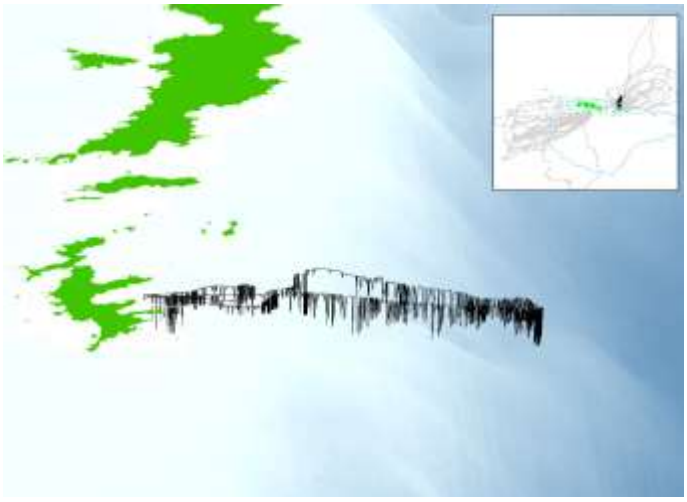
Deployment	**28**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	48.9x19.6
Sex	male
Weight (kg)	3.8 (0.1)
Offspring	2

Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
28_44	03-01 (15)	04-01 (14)	22.1	39.0	AC	17.0	25%	28%	0.18	33%	0.11
28_45	06-01 (05)	06-01 (13)	8.8	NA	C	10.3	10%	0%	0.25	27%	0.03

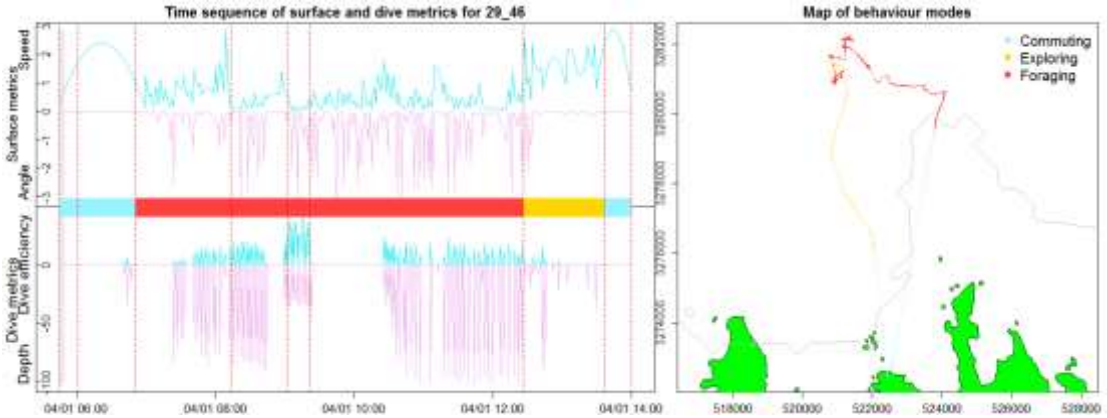


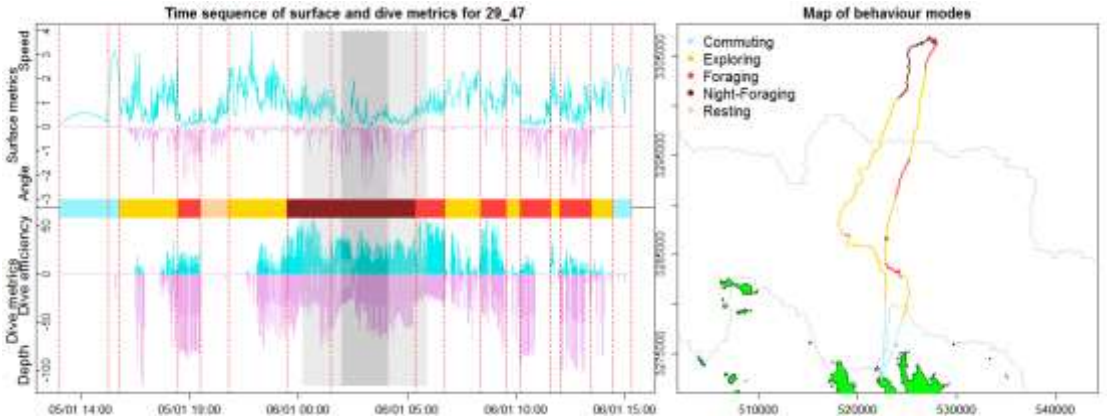


Deployment	**29**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	50.7x16.9
Sex	female
Weight (kg)	4.2 (-0.1)
Offspring	2

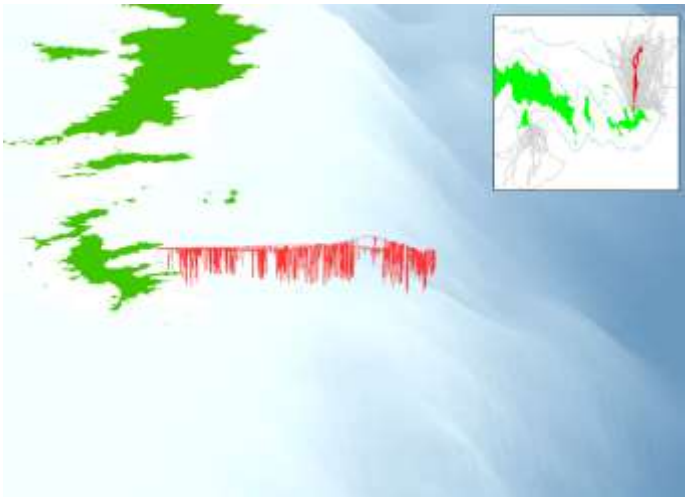


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
29_46	04-01 (05)	04-01 (14)	8.3	23.0	AC	9.7	1%	0%	0.39	68%	0.07
29_47	05-01 (13)	06-01 (15)	26.3	NA	C	34.9	22%	40%	0.42	46%	0.17

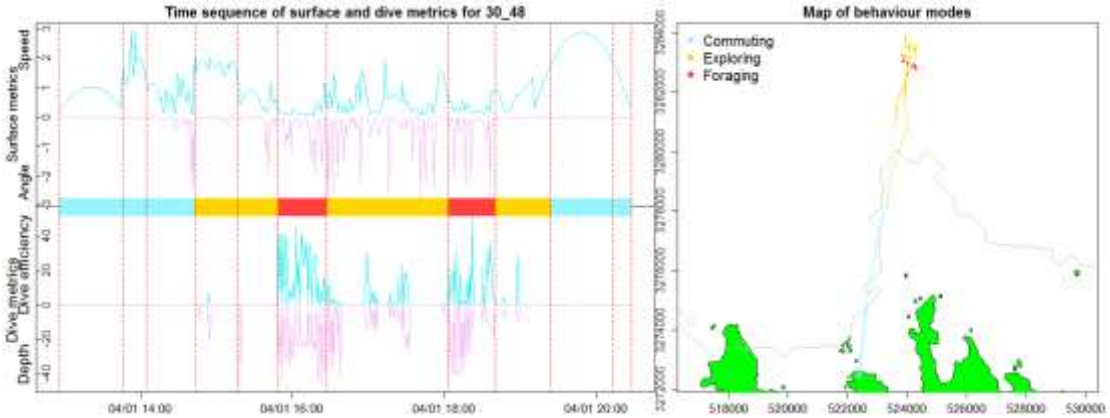


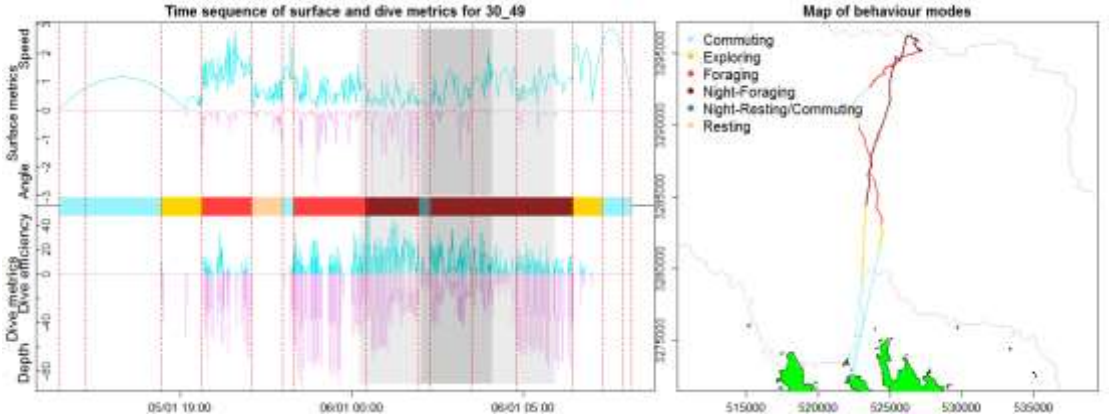


Deployment	**30**
Site	Geddes
Season	2011-12
Stage	Brood
Bill (mm)	48.8x17.9
Sex	female
Weight (kg)	4.7 (0)
Offspring	2



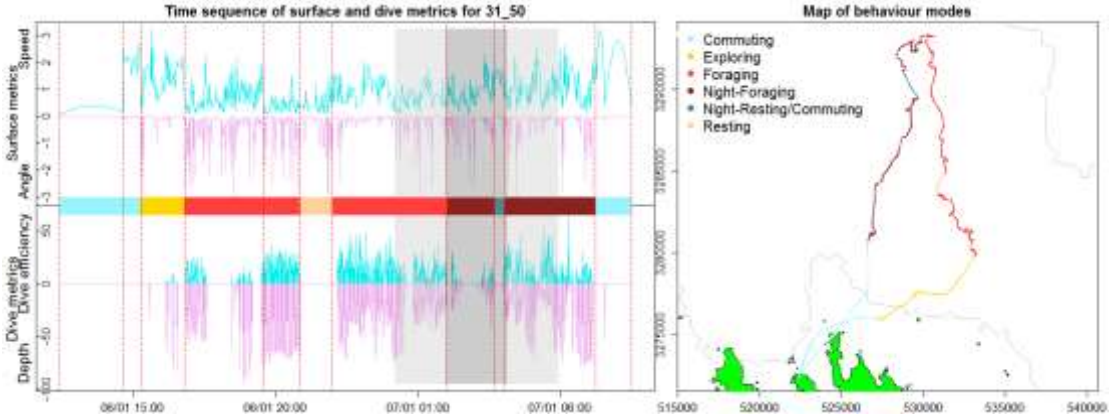
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
30_48	04-01 (12)	04-01 (20)	7.5	19.0	C	11.6	0%	0%	0.12	17%	0.23
30_49	05-01 (15)	06-01 (08)	16.7	NA	AC	24.2	34%	72%	0.33	56%	0.31

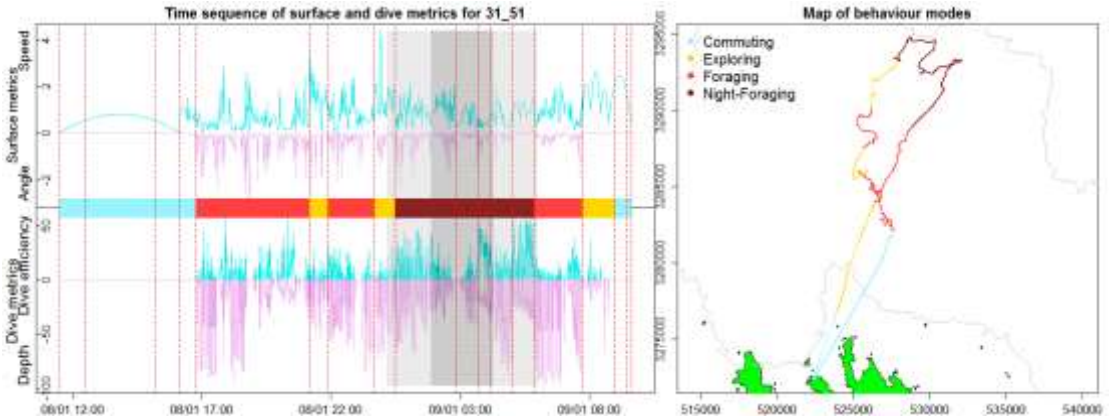


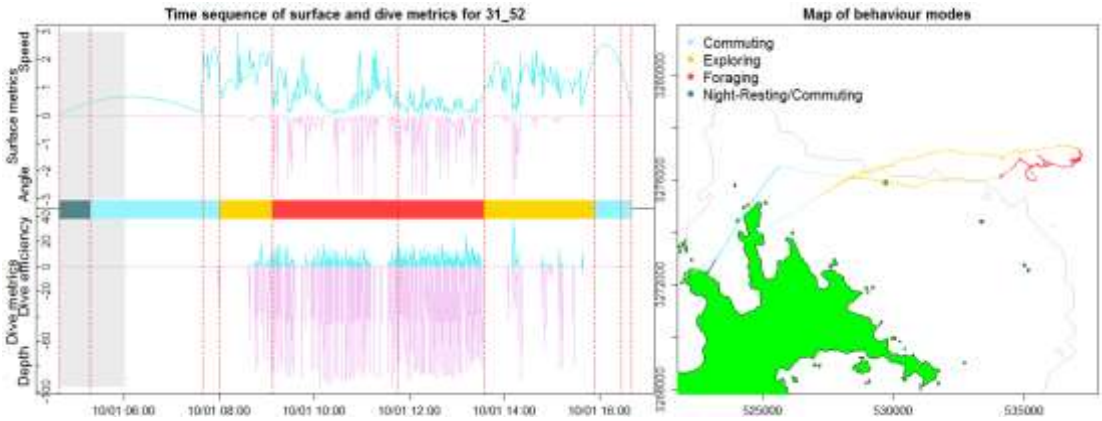


Deployment	**31**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	53.3x17.3
Sex	female
Weight (kg)	4.2 (-0.5)
Offspring	1

Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
31_50	06-01 (12)	07-01 (08)	20.1	27.0	AC	22.4	29%	46%	0.35	64%	0.10
31_51	08-01 (11)	09-01 (09)	22.2	19.0	C	23.6	26%	42%	0.39	61%	0.10
31_52	10-01 (04)	10-01 (16)	12.0	NA	AC	15.0	12%	0%	0.40	37%	0.10

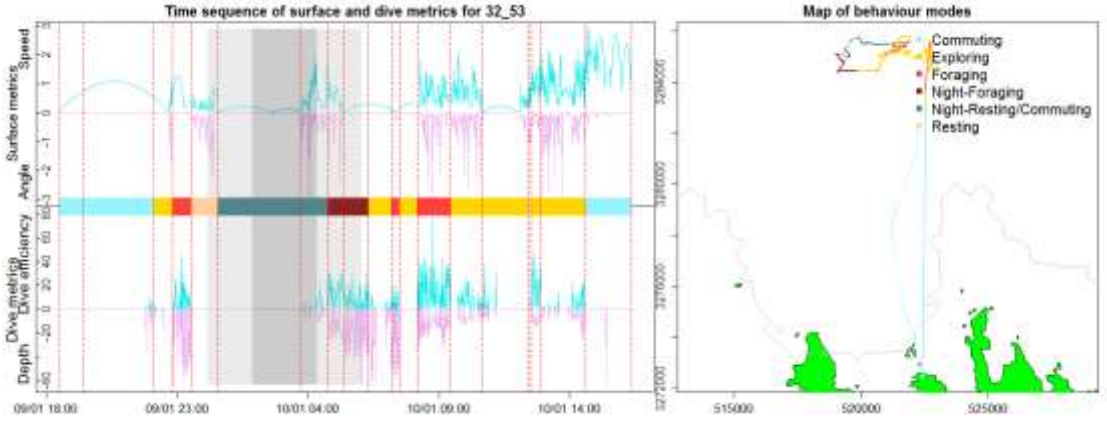




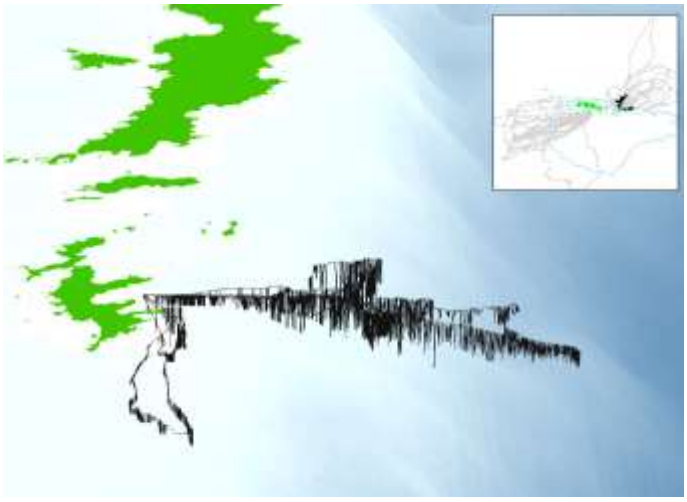

Time sequence of surface and dive metrics for 31_52
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
10/01 06:00
10/01 08:00
10/01 10:00
10/01 12:00
10/01 14:00
10/01 16:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Resting/Commuting
525000
530000
535000

Deployment	**32**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	52.1x18.4
Sex	unsure
Weight (kg)	4.4 (-0.6)
Offspring	2

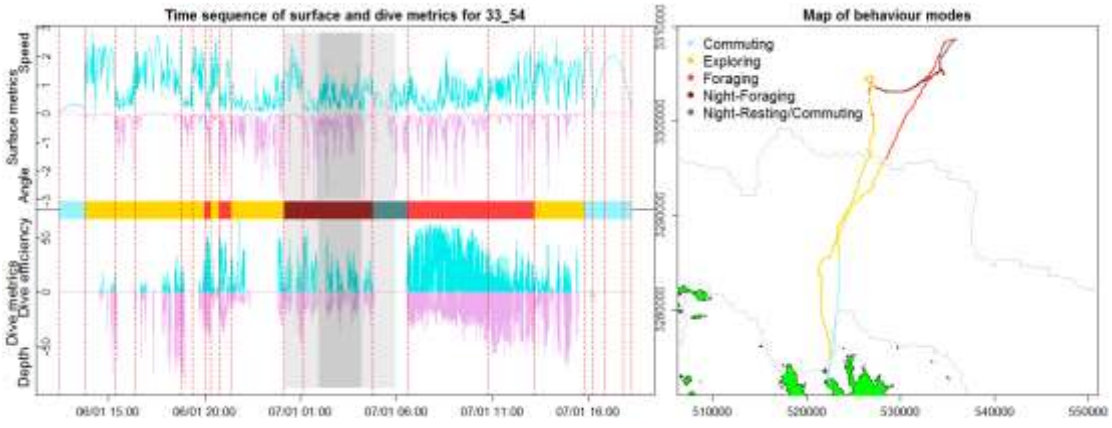
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
32_53	09-01 (18)	10-01 (16)	21.9	NA	AC	13.6	27%	24%	0.18	17%	0.13

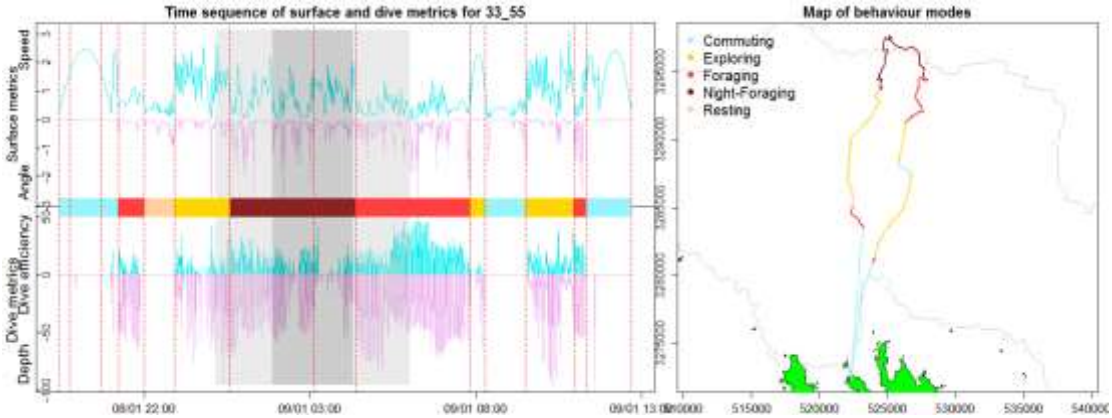


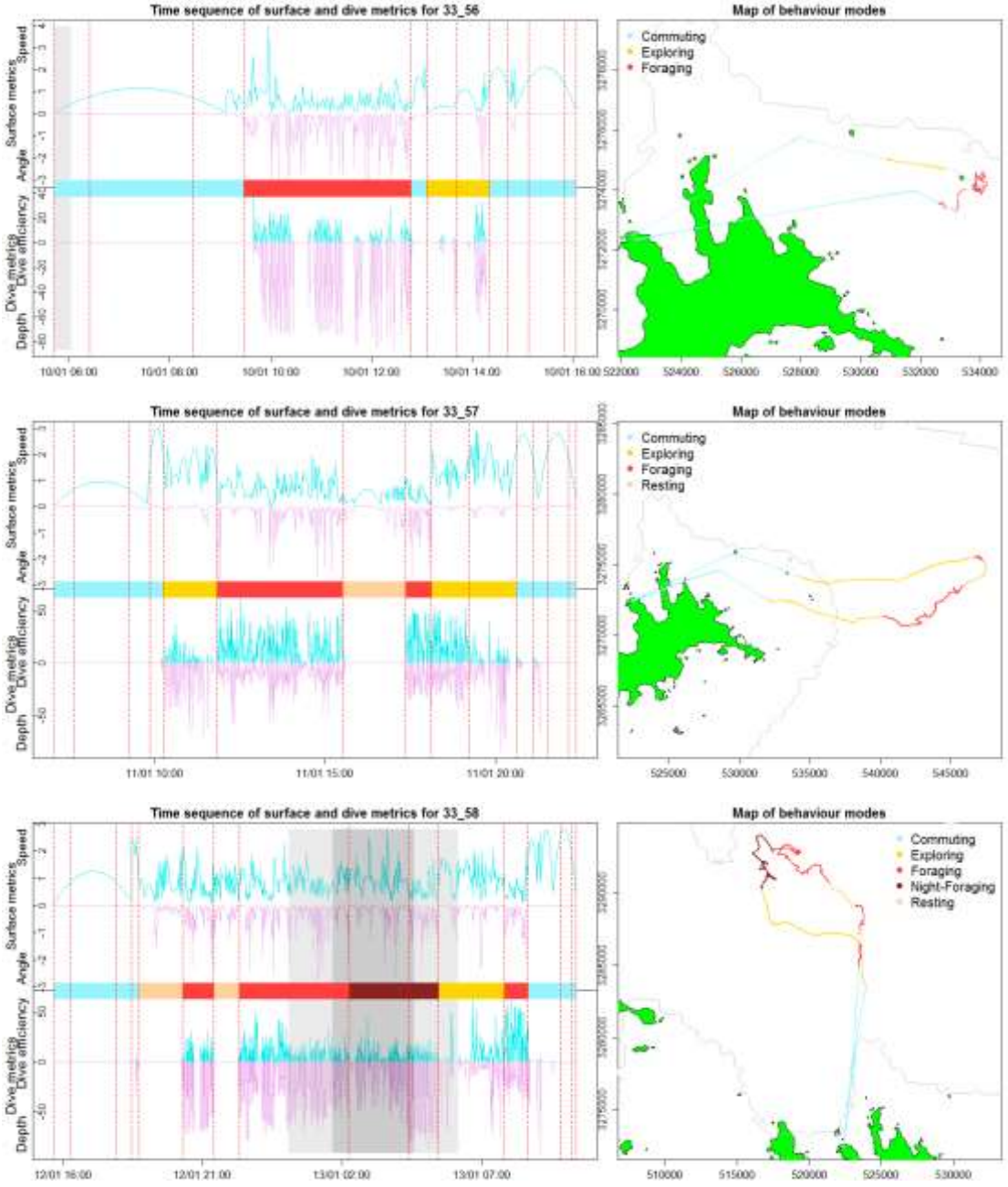
Deployment	**33**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	44.5x18.3
Sex	female
Weight (kg)	3.6 (-0.4)
Offspring	2



Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
33_54	06-01 (12)	07-01 (18)	29.8	25.2	C	38.7	19%	26%	0.24	40%	0.25
33_55	08-01 (19)	09-01 (12)	17.3	17.0	C	25.3	34%	46%	0.38	48%	0.13
33_56	10-01 (05)	10-01 (16)	10.4	15.0	AC	11.9	3%	0%	0.22	32%	0.04
33_57	11-01 (07)	11-01 (22)	15.3	17.3	AC	25.2	0%	0%	0.17	29%	0.11
33_58	12-01 (15)	13-01 (10)	18.7	NA	AC	22.3	33%	46%	0.34	49%	0.11

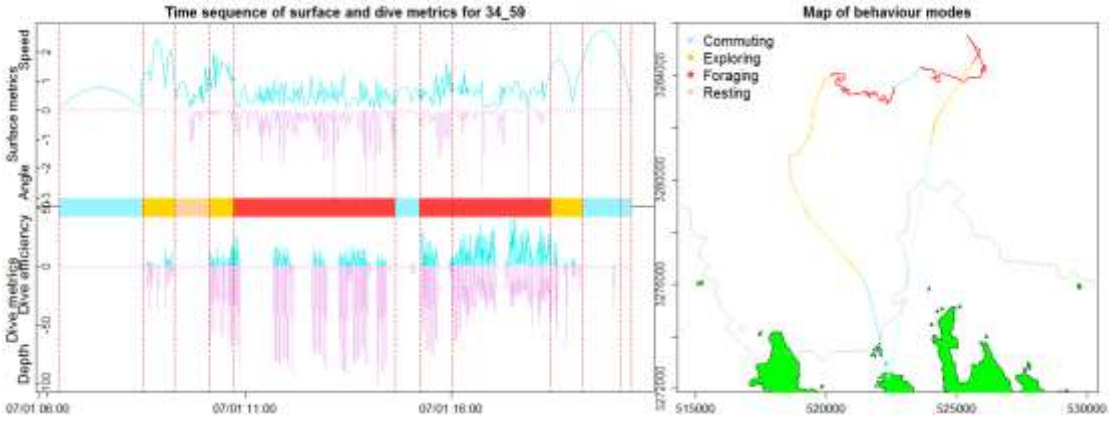


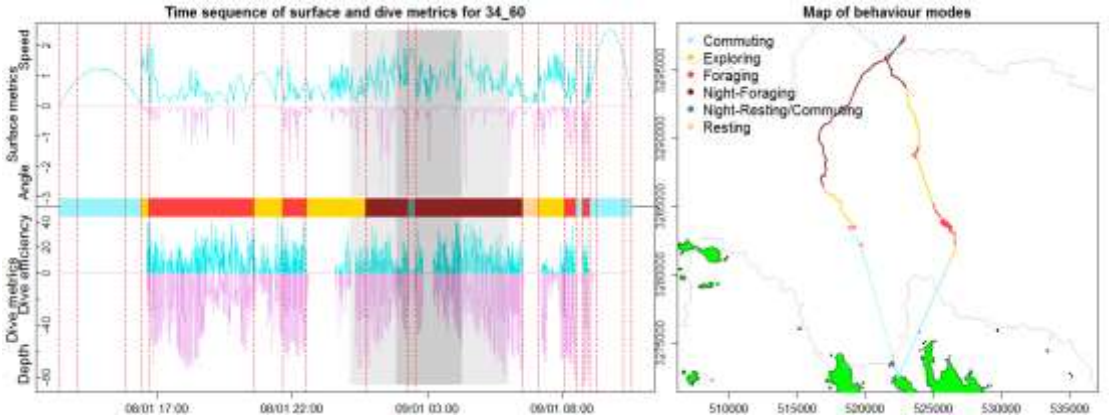


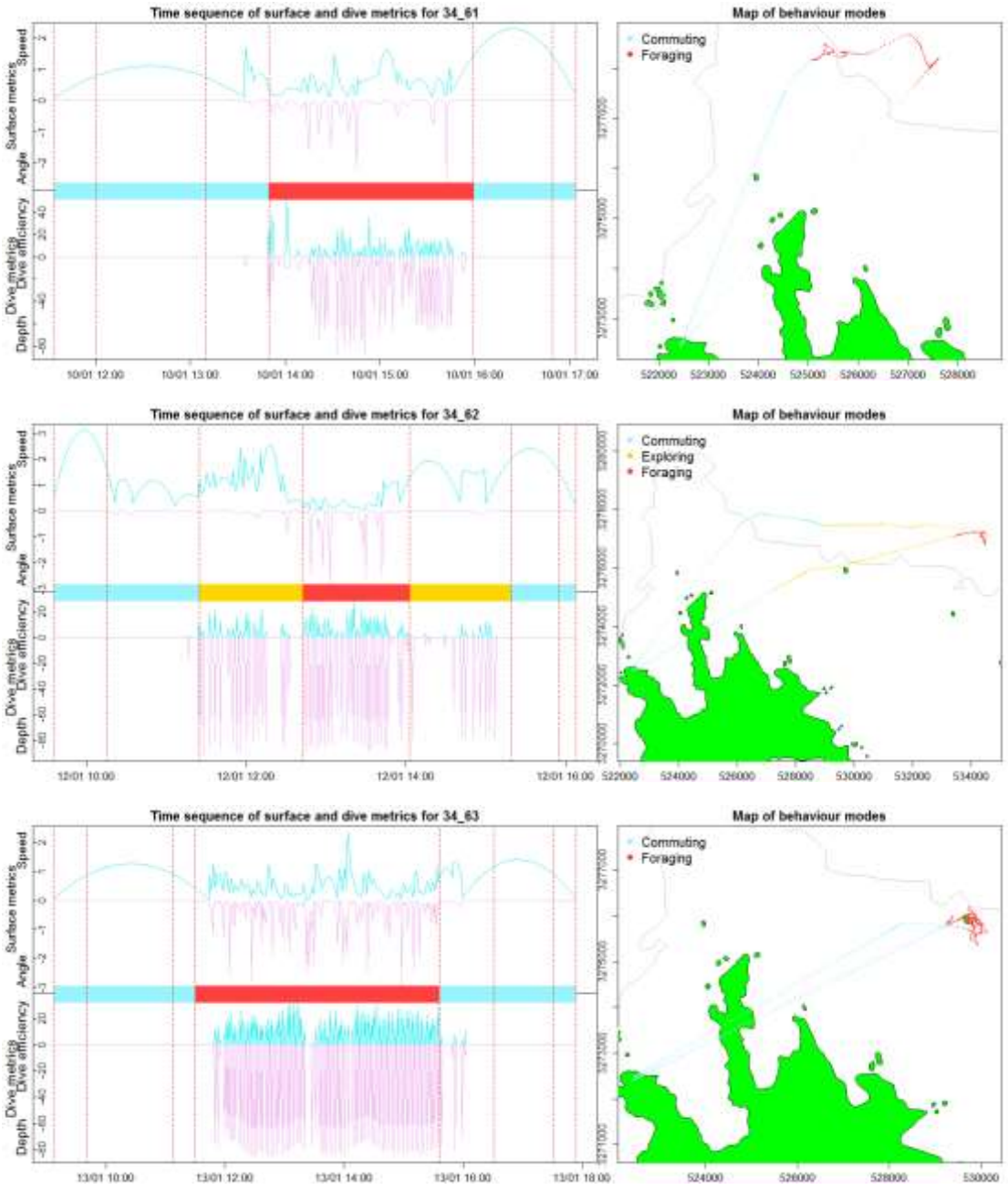

Time sequence of surface and dive metrics for 33_56
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
10/01 06:00
10/01 08:00
10/01 10:00
10/01 12:00
10/01 14:00
10/01 16:00
Map of behaviour modes
Commuting
Exploring
Foraging
Time sequence of surface and dive metrics for 33_57
11/01 10:00
11/01 15:00
11/01 20:00
Map of behaviour modes
Commuting
Exploring
Foraging
Resting
Time sequence of surface and dive metrics for 33_58
12/01 16:00
12/01 21:00
13/01 02:00
13/01 07:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Foraging
Resting

Deployment	**34**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	51.7x18.3
Sex	unsure
Weight (kg)	4.35 (-1.1)
Offspring	2

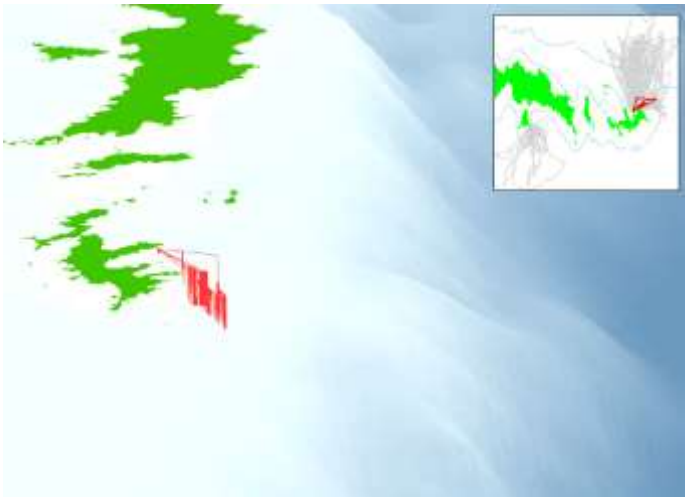
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
34_59	07-01 (06)	07-01 (20)	13.9	17.0	C	13.4	0%	0%	0.33	51%	0.11
34_60	08-01 (13)	09-01 (10)	21.2	25.0	AC	25.1	28%	38%	0.43	52%	0.11
34_61	10-01 (11)	10-01 (17)	5.5	40.5	C	7.8	0%	0%	0.23	39%	0.04
34_62	12-01 (09)	12-01 (16)	6.5	17.0	C	12.9	0%	0%	0.29	21%	0.07
34_63	13-01 (09)	13-01 (17)	8.8	NA	AC	8.4	0%	0%	0.56	47%	0.03



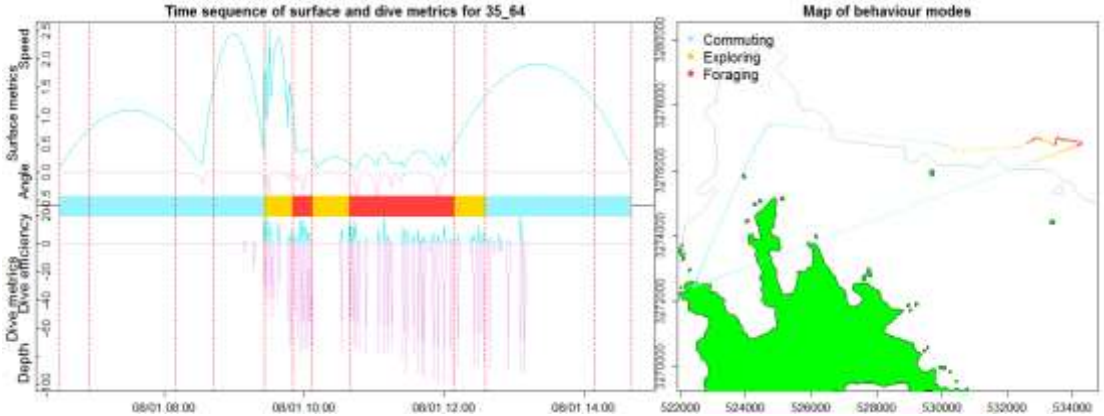


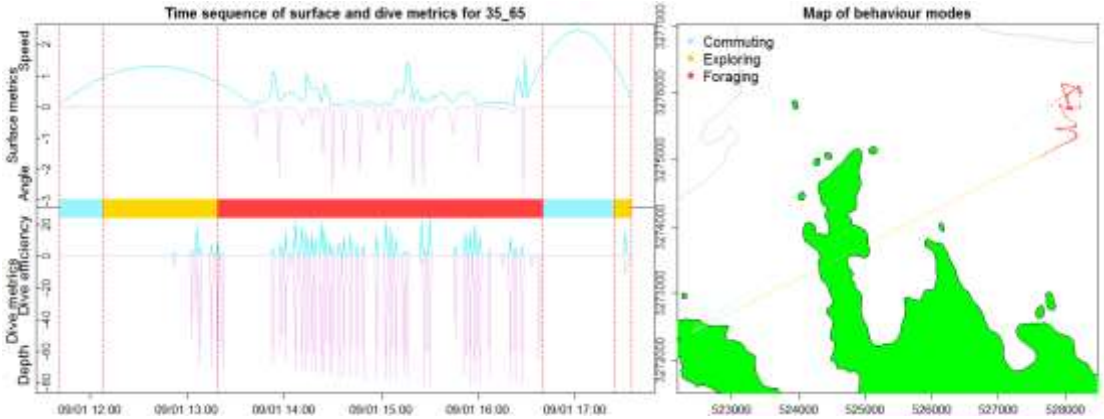

Time sequence of surface and dive metrics for 34_61
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
10/01 12:00
10/01 13:00
10/01 14:00
10/01 15:00
10/01 16:00
10/01 17:00
Map of behaviour modes
Commuting
Foraging
Time sequence of surface and dive metrics for 34_62
12/01 10:00
12/01 12:00
12/01 14:00
12/01 16:00
Map of behaviour modes
Commuting
Exploring
Foraging
Time sequence of surface and dive metrics for 34_63
13/01 10:00
13/01 12:00
13/01 14:00
13/01 16:00
13/01 18:00
Map of behaviour modes
Commuting
Foraging

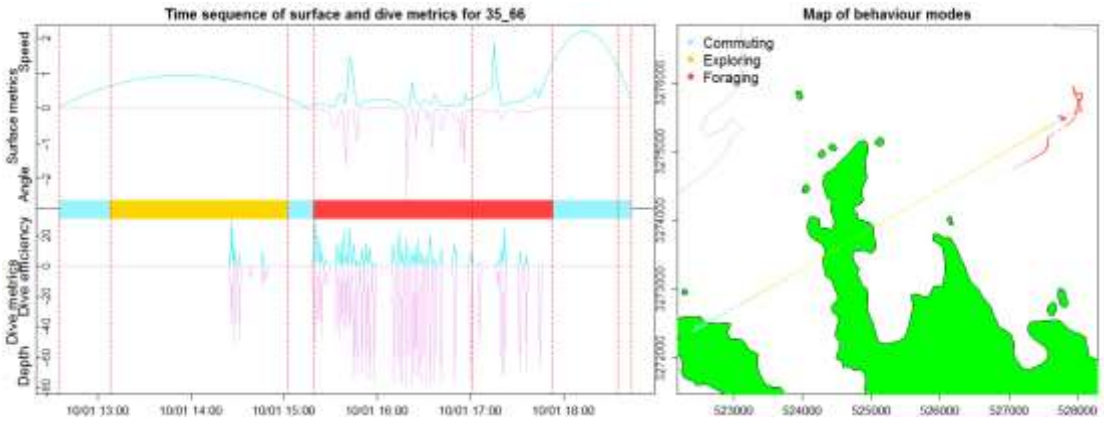
Deployment	**35**
Site	Geddes
Season	2011-12
Stage	Brood
Bill (mm)	47.6x17.8
Sex	female
Weight (kg)	3.85 (-0.6)
Offspring	2



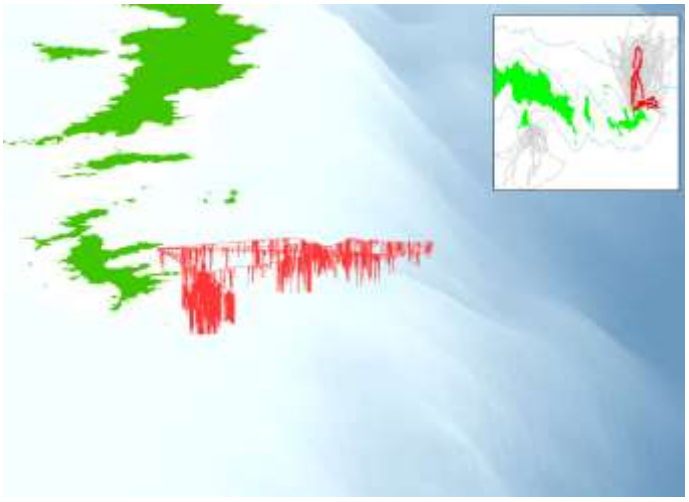
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
35_64	08-01 (06)	08-01 (14)	8.2	21.0	C	12.7	0%	0%	0.22	22%	0.21
35_65	09-01 (11)	09-01 (17)	5.9	19.0	AC	6.9	0%	0%	0.36	57%	0.14
35_66	10-01 (12)	10-01 (18)	6.2	NA	C	6.6	0%	0%	0.34	42%	0.14



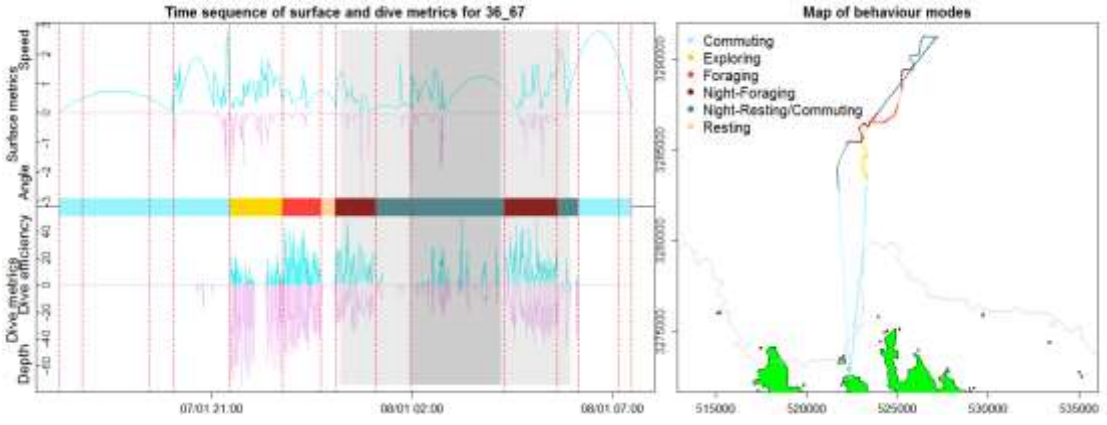


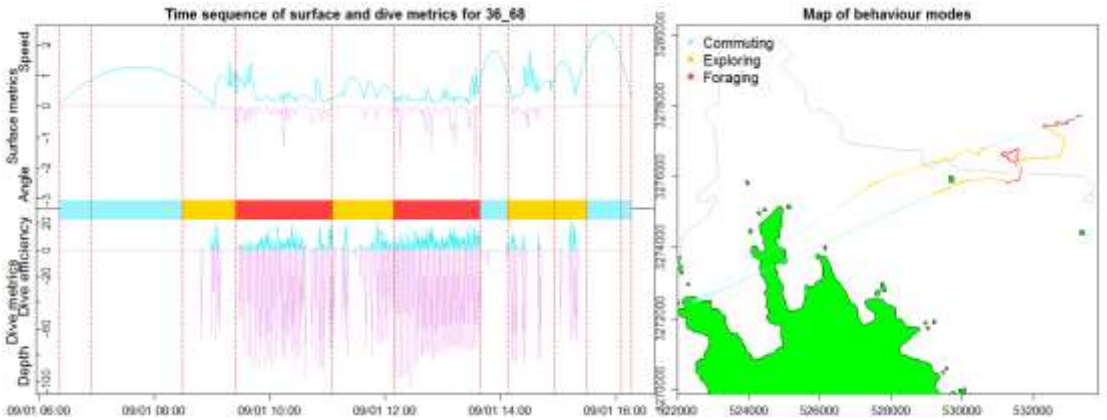

Time sequence of surface and dive metrics for 35_66
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
10/01 13:00
10/01 14:00
10/01 15:00
10/01 16:00
10/01 17:00
10/01 18:00
Map of behaviour modes
Commuting
Exploring
Foraging
523000
524000
525000
526000
527000
528000

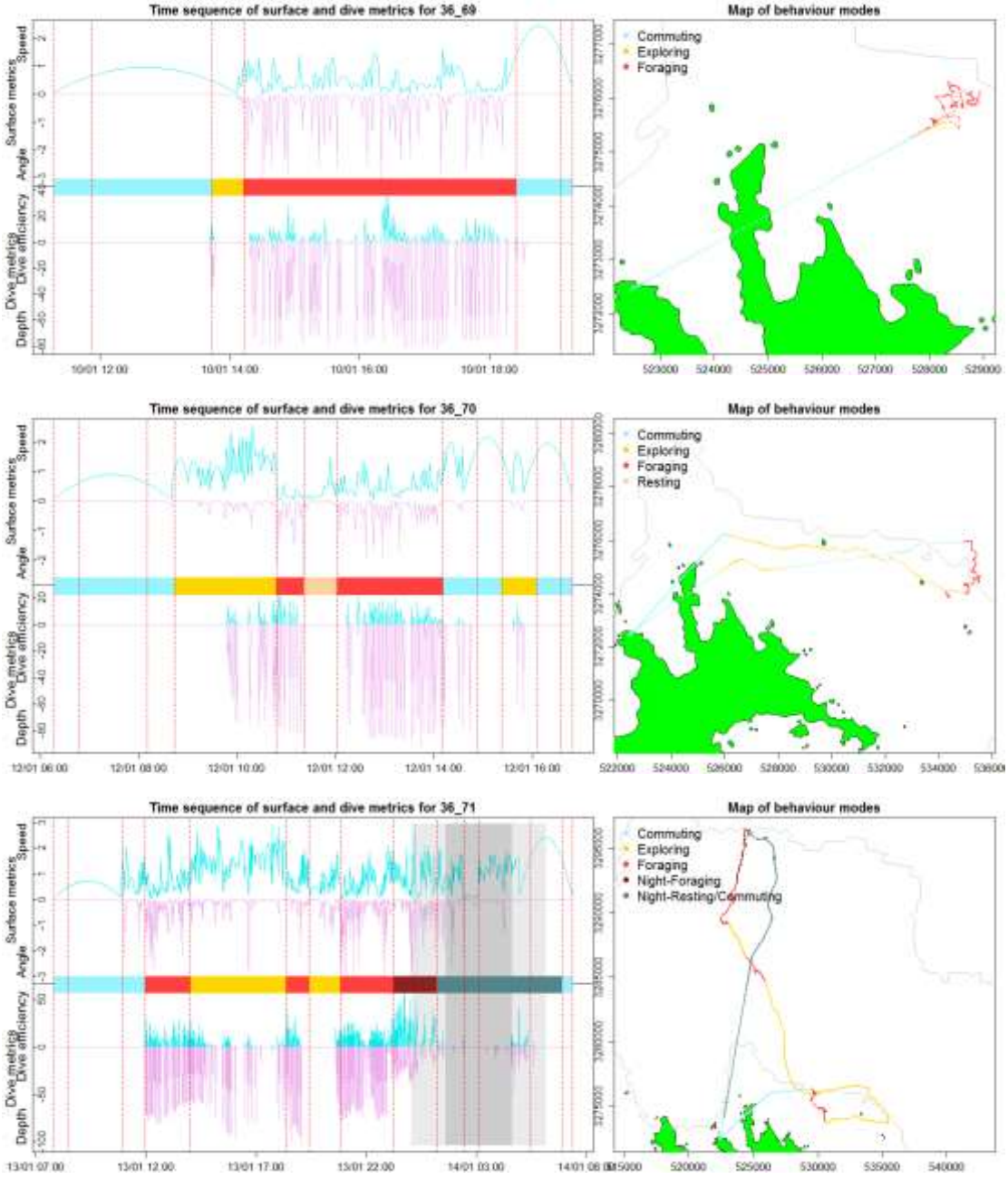
Deployment	**36**
Site	Geddes
Season	2011-12
Stage	Brood
Bill (mm)	51.6x17.6
Sex	female
Weight (kg)	4.4 (-0.7)
Offspring	1



Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
36_67	07-01 (17)	08-01 (07)	14.3	22.9	AC	19.4	40%	69%	0.22	23%	0.24
36_68	09-01 (06)	09-01 (16)	9.9	19.0	AC	12.2	0%	0%	0.53	32%	0.23
36_69	10-01 (11)	10-01 (19)	8.0	35.0		7.5	0%	0%	0.42	52%	0.15
36_70	12-01 (06)	12-01 (16)	10.5	15.0	AC	13.4	0%	0%	0.24	26%	0.21
36_71	13-01 (07)	14-01 (07)	23.6	NA	AC	24.1	26%	28%	0.26	32%	0.27

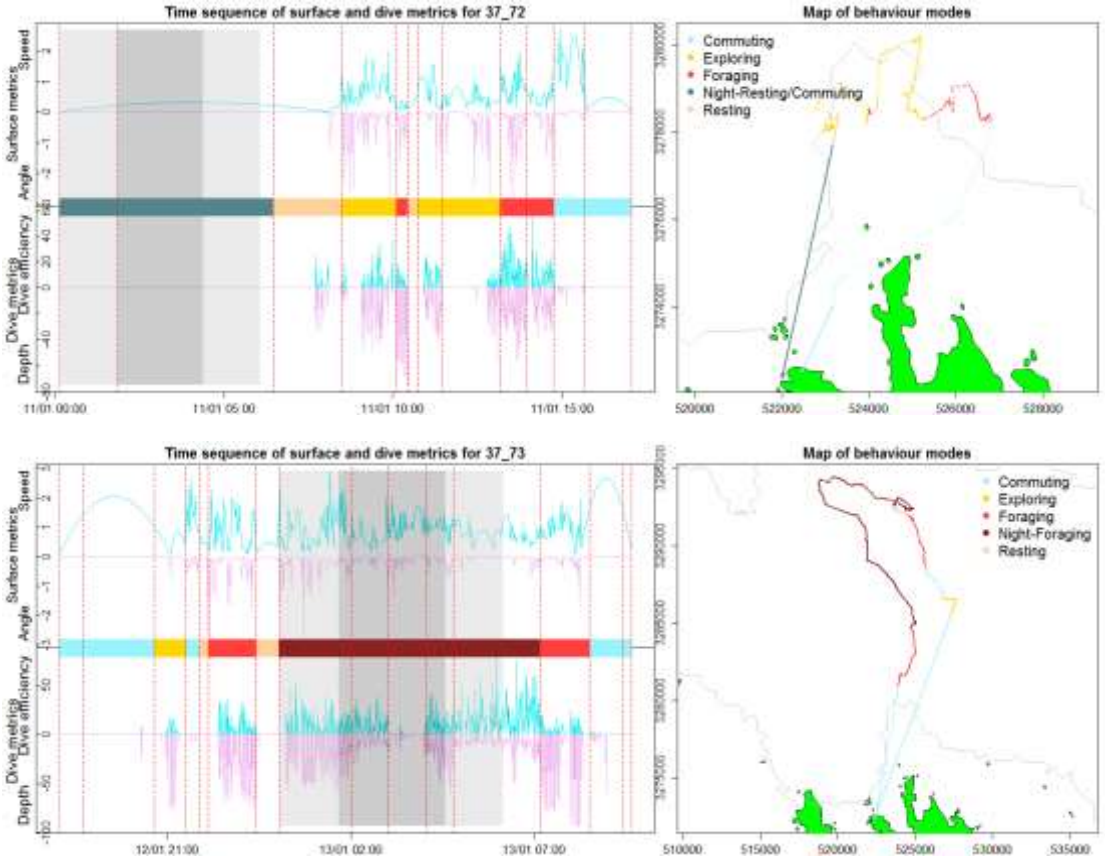




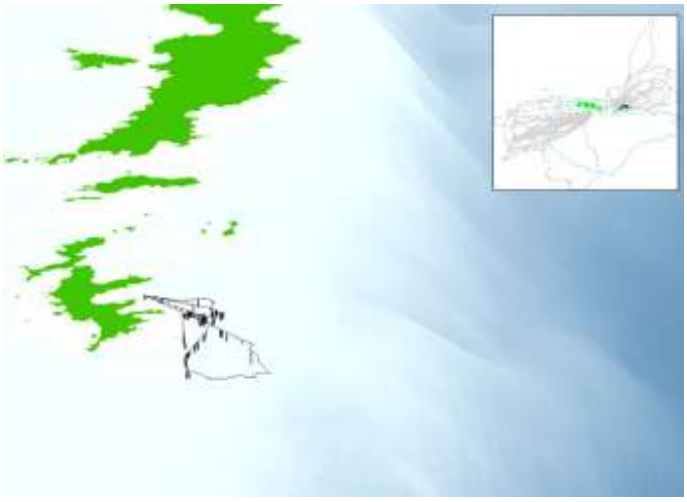

Time sequence of surface and dive metrics for 36_69
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
10/01 12:00
10/01 14:00
10/01 16:00
10/01 18:00
Map of behaviour modes
Commuting
Exploring
Foraging
Time sequence of surface and dive metrics for 36_70
12/01 06:00
12/01 08:00
12/01 10:00
12/01 12:00
12/01 14:00
12/01 16:00
Map of behaviour modes
Commuting
Exploring
Foraging
Resting
Time sequence of surface and dive metrics for 36_71
13/01 07:00
13/01 12:00
13/01 17:00
13/01 22:00
14/01 03:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Foraging
Night-Resting/Commuting

Deployment	**37**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	53.3x15
Sex	female
Weight (kg)	3.8 (-0.6)
Offspring	2

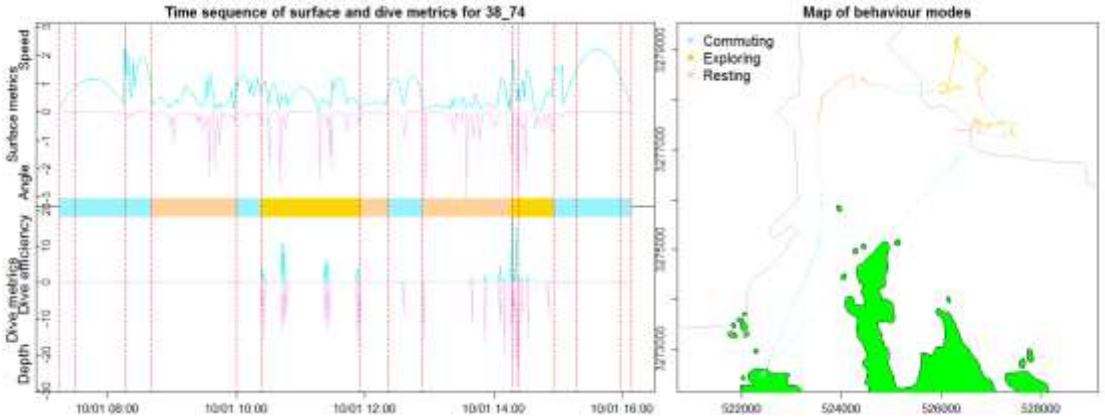
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
37_72	11-01 (00)	11-01 (17)	16.9	25.0	C	8.5	35%	0%	0.22	11%	0.04
37_73	12-01 (18)	13-01 (09)	15.6	NA	AC	22.2	39%	62%	0.25	63%	0.10

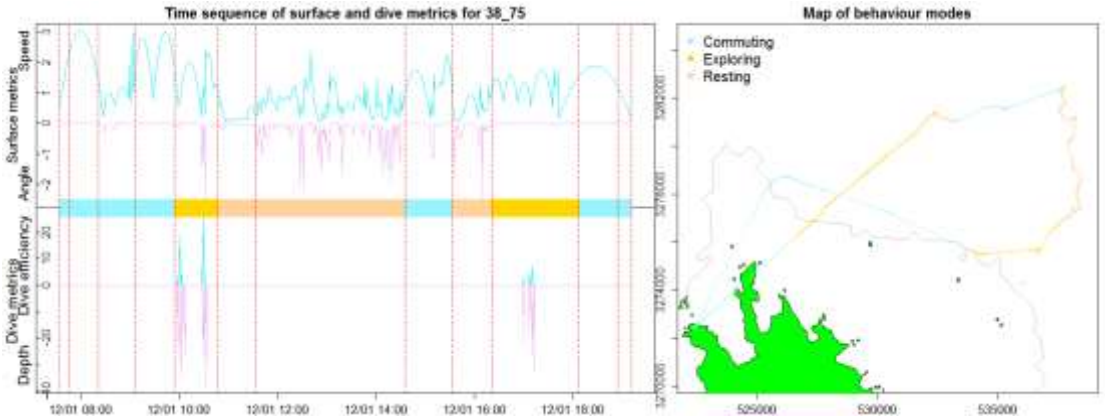


Deployment	**38**
Site	Geddes
Season	2011-12
Stage	Incubation
Bill (mm)	46.4x16.4
Sex	female
Weight (kg)	3.4 (-0.5)
Offspring	2

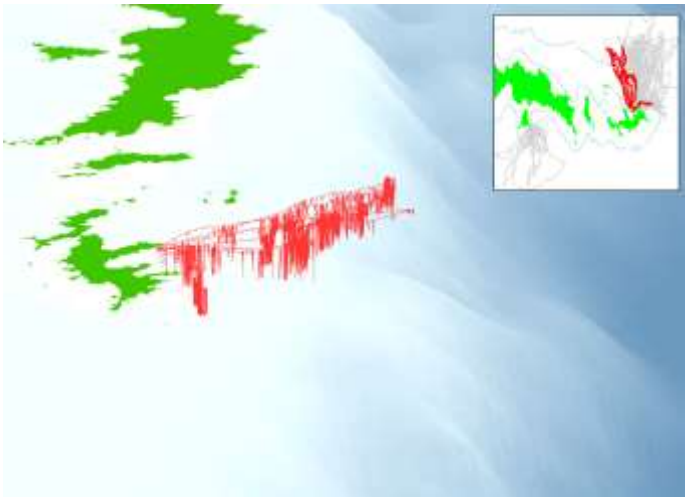


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
38_74	10-01 (07)	10-01 (16)	8.9	39.4	C	7.9	0%	0%	0.02	0%	0.04
38_75	12-01 (07)	12-01 (19)	11.6	NA	AC	18.4	0%	0%	0.01	0%	0.12

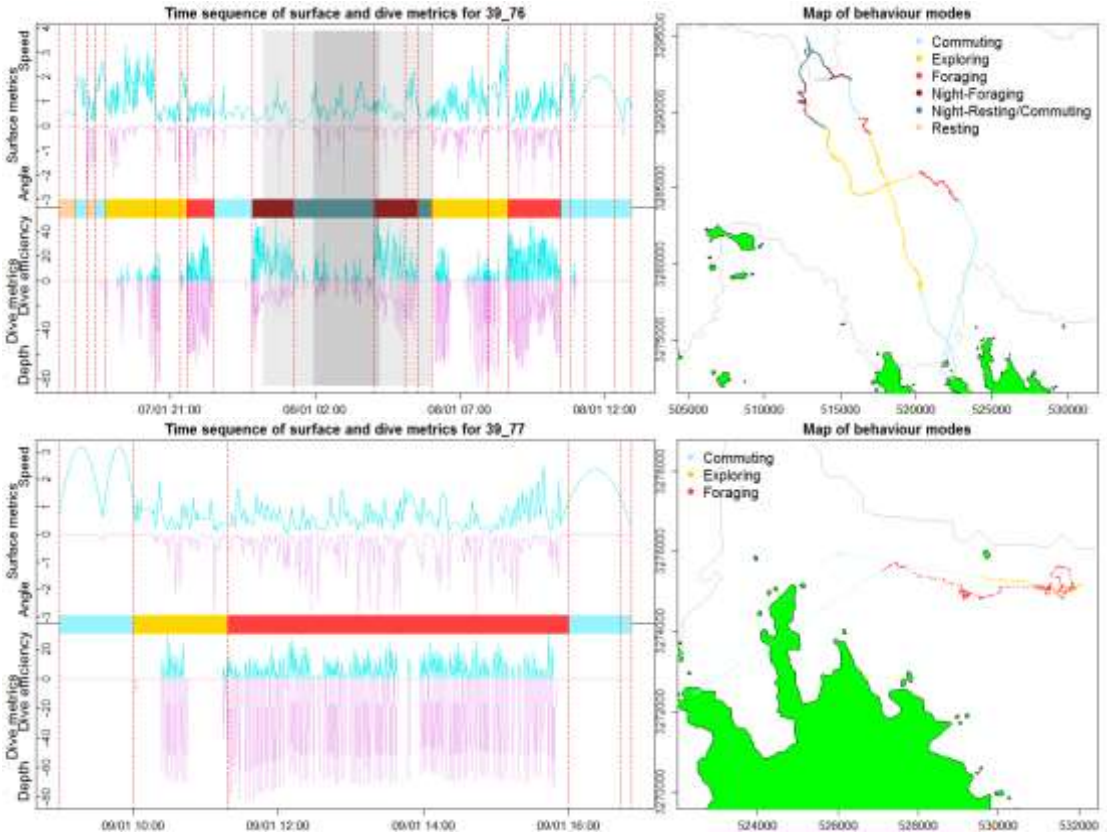


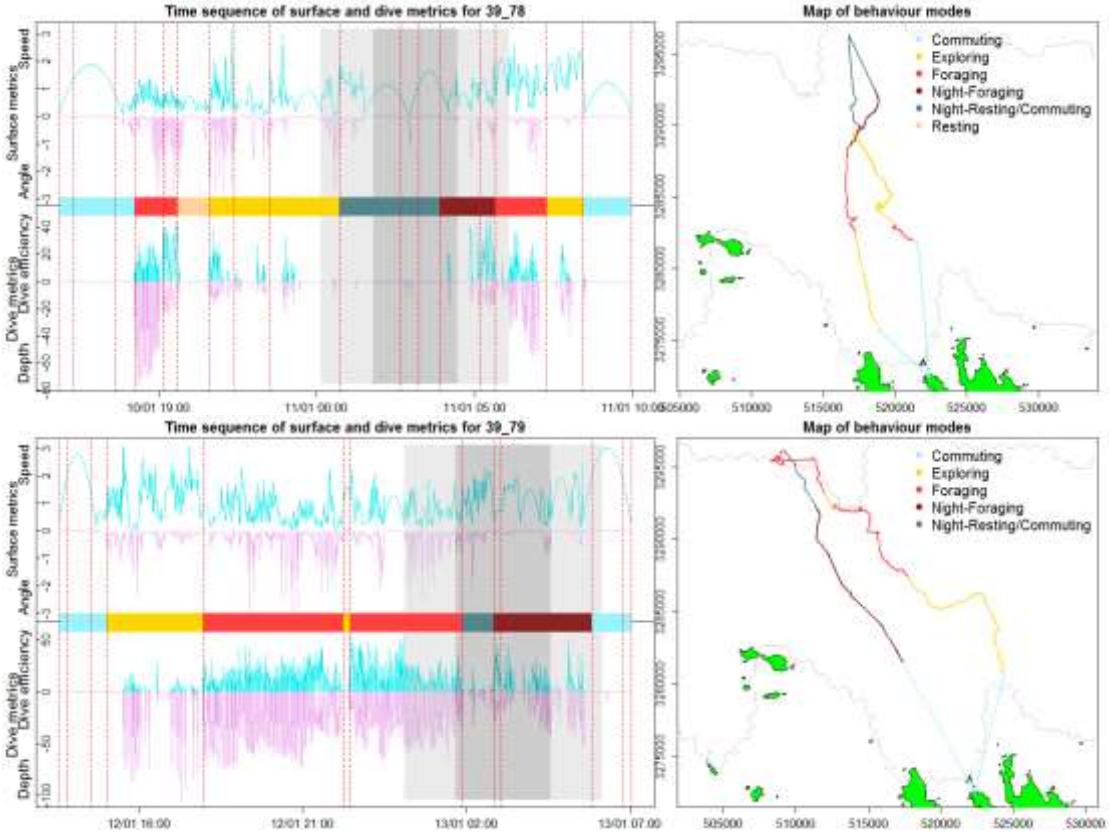


Deployment	**39**
Site	Geddes
Season	2011-12
Stage	Brood
Bill (mm)	47.2x17.3
Sex	female
Weight (kg)	3.9 (0.1)
Offspring	2

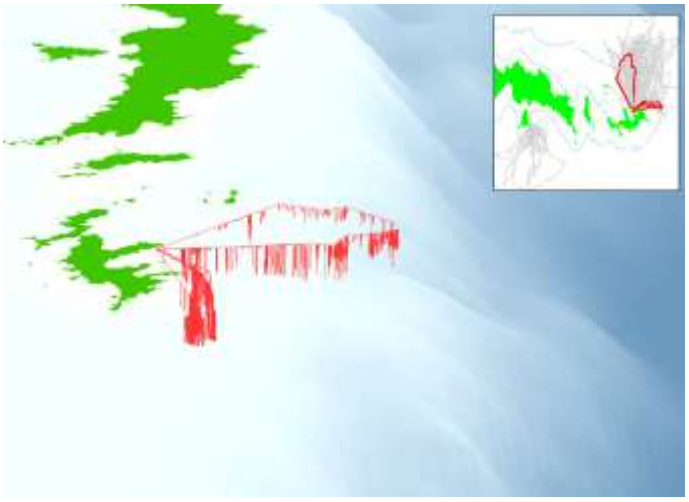


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
39_76	07-01 (17)	08-01 (12)	19.7	20.1	AC	24.4	30%	50%	0.26	29%	0.27
39_77	09-01 (08)	09-01 (16)	7.9	23.0	C	10.0	0%	0%	0.47	59%	0.15
39_78	10-01 (15)	11-01 (09)	18.1	27.6	AC	24.5	33%	27%	0.10	26%	0.25
39_79	12-01 (13)	13-01 (07)	17.5	NA	AC	27.0	35%	38%	0.35	61%	0.33

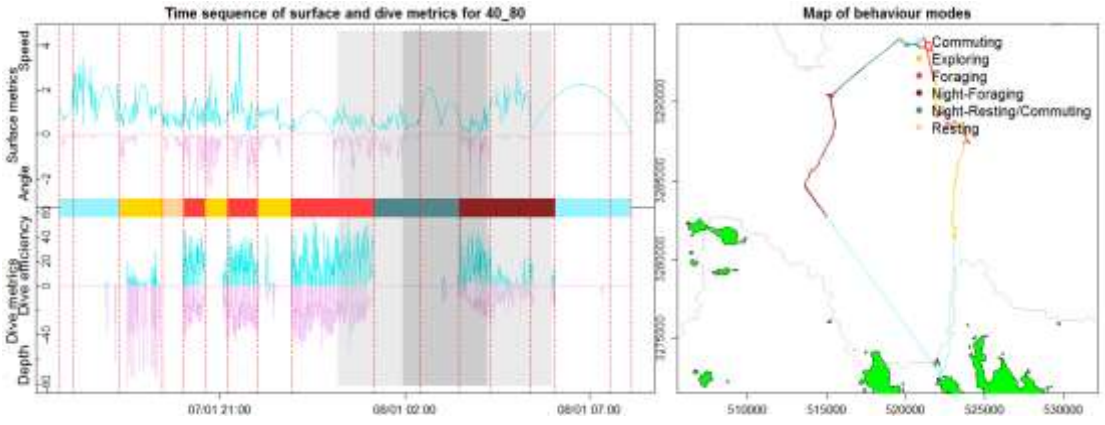


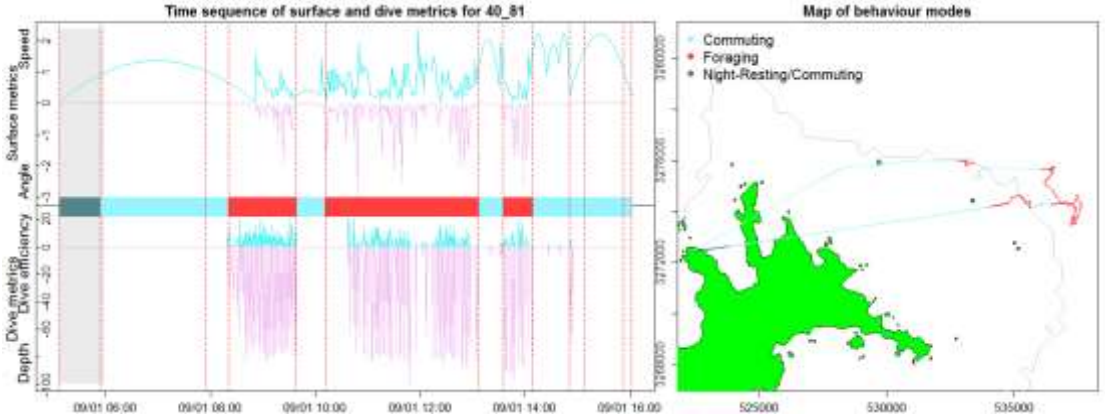

Time sequence of surface and dive metrics for 39_78
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Foraging
Night-Resting/Commuting
Resting
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
10/01 19:00
11/01 00:00
11/01 05:00
505000
510000
515000
520000
525000
530000
Time sequence of surface and dive metrics for 39_79
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Foraging
Night-Resting/Commuting
12/01 16:00
12/01 21:00
13/01 02:00
13/01 07:00

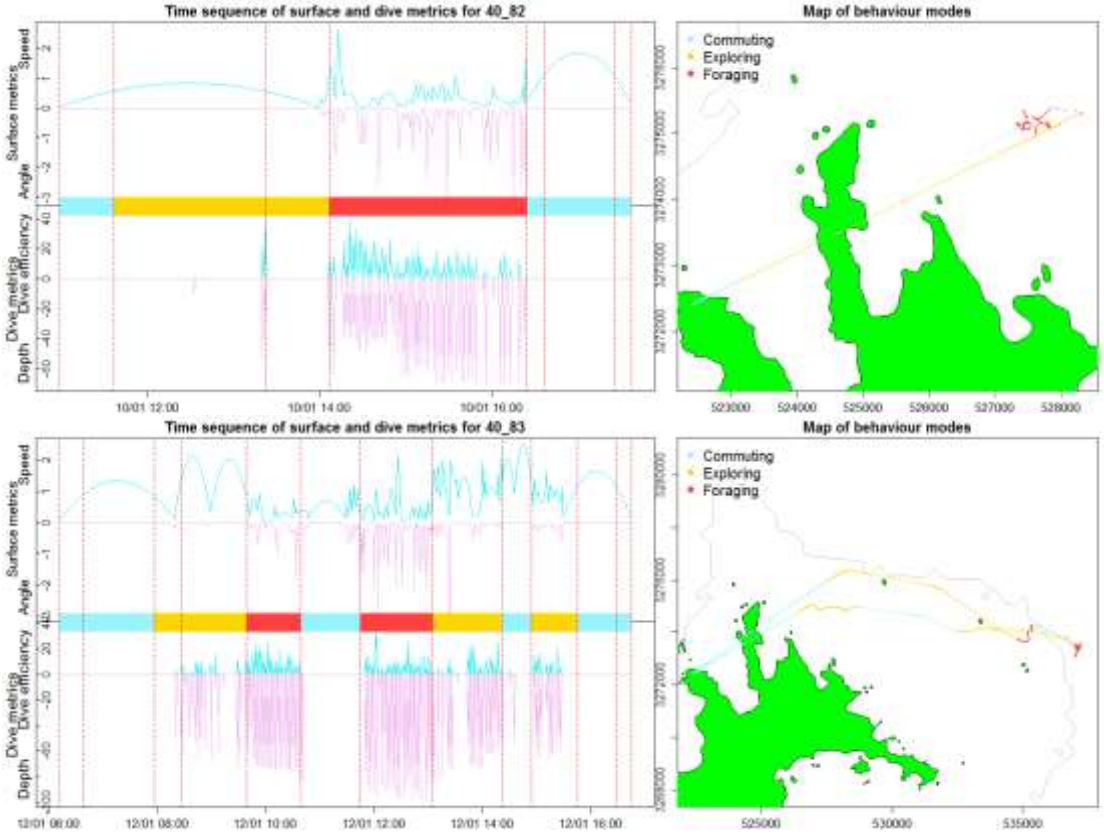
Deployment	**40**
Site	Geddes
Season	2011-12
Stage	Brood
Bill (mm)	50.8x17.5
Sex	female
Weight (kg)	3.4 (-0.4)
Offspring	1



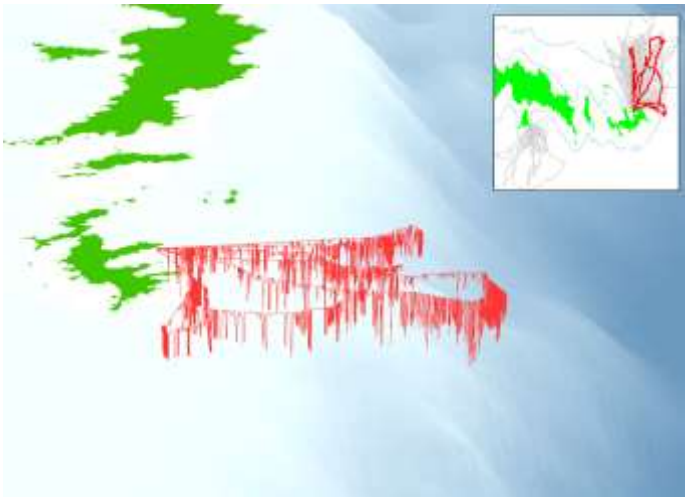
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
40_80	07-01 (16)	08-01 (08)	15.5	21.0	AC	21.7	38%	48%	0.19	40%	0.30
40_81	09-01 (05)	09-01 (16)	10.9	18.9	AC	15.3	8%	0%	0.33	44%	0.25
40_82	10-01 (10)	10-01 (17)	6.7	36.6	AC	6.6	0%	0%	0.36	34%	0.14
40_83	12-01 (06)	12-01 (16)	10.6	NA	C	14.9	0%	0%	0.37	22%	0.23



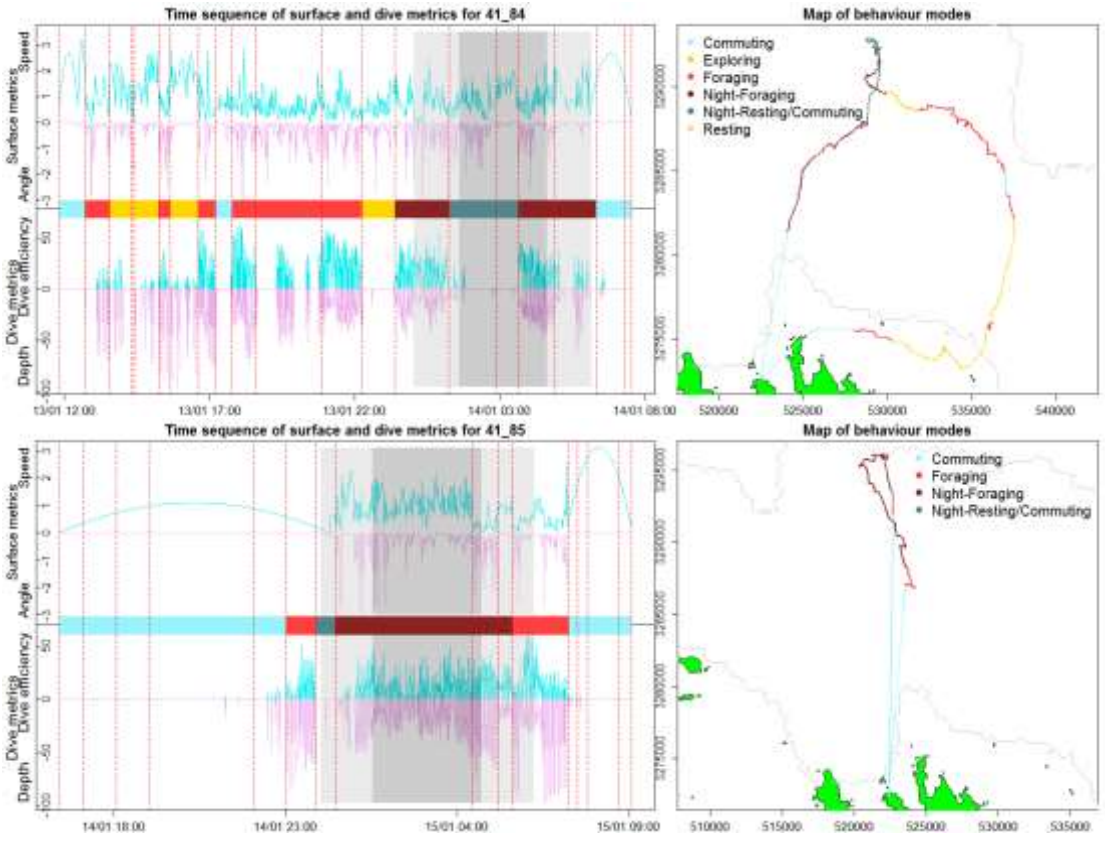


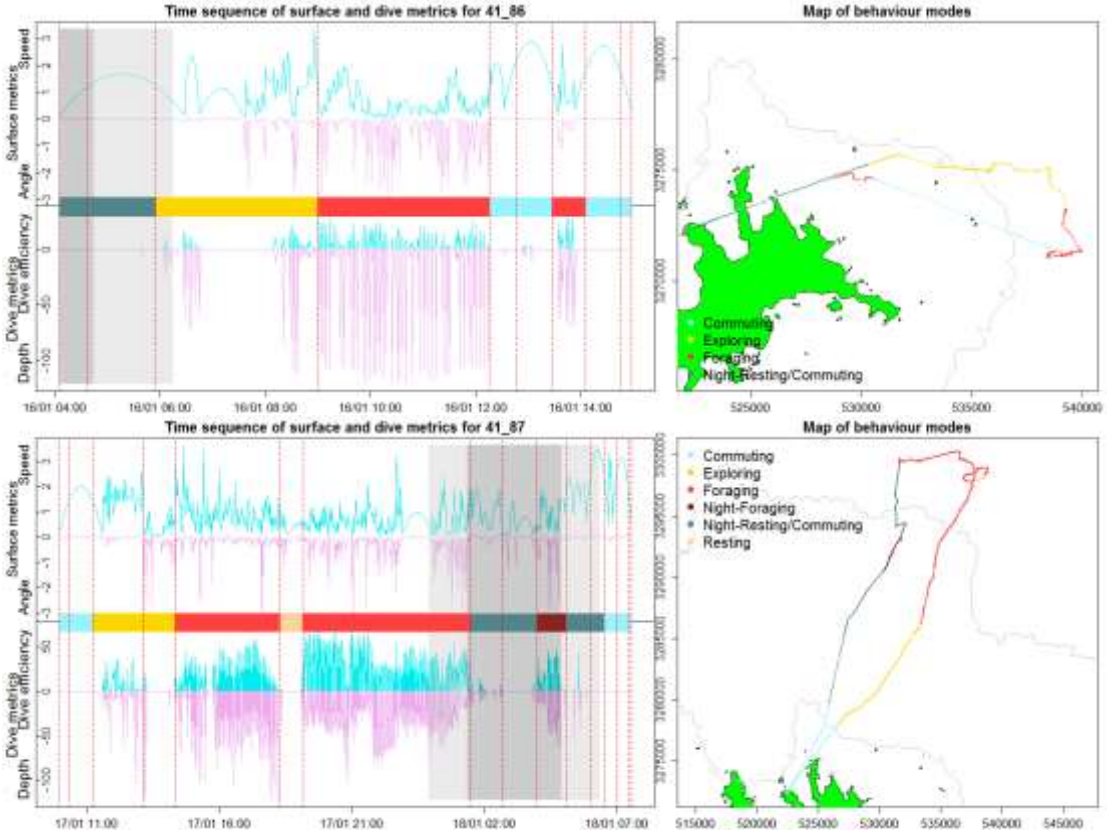

Time sequence of surface and dive metrics for 40_82
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
10/01 12:00
10/01 14:00
10/01 16:00
Map of behaviour modes
Commuting
Exploring
Foraging
523000
524000
525000
526000
527000
528000
Time sequence of surface and dive metrics for 40_83
12/01 08:00
12/01 10:00
12/01 12:00
12/01 14:00
12/01 16:00
Map of behaviour modes
525000
530000
535000

Deployment	**41**
Site	Geddes
Season	2011-12
Stage	Brood
Bill (mm)	46.2x17.5
Sex	female
Weight (kg)	3.2 (0)
Offspring	2

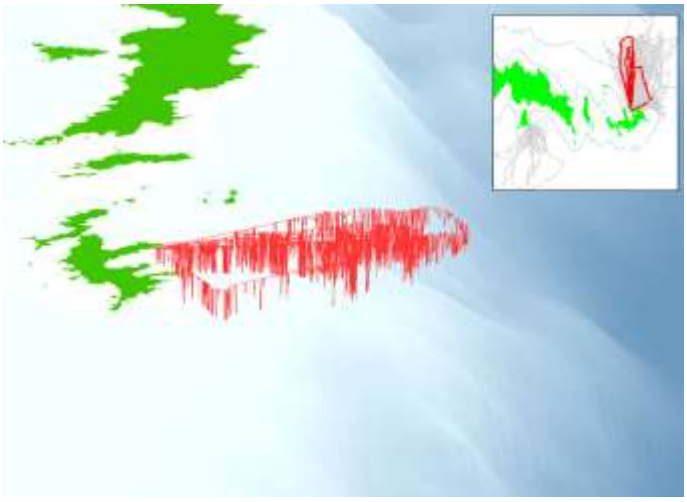


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
41_84	13-01 (11)	14-01 (07)	19.7	8.9	AC	21.4	31%	44%	0.25	55%	0.33
41_85	14-01 (16)	15-01 (09)	16.7	19.0	AC	23.7	37%	77%	0.28	46%	0.28
41_86	16-01 (04)	16-01 (14)	10.9	19.0	C	17.6	20%	4%	0.26	36%	0.26
41_87	17-01 (09)	18-01 (07)	21.6	NA	AC	31.3	30%	29%	0.34	52%	0.42

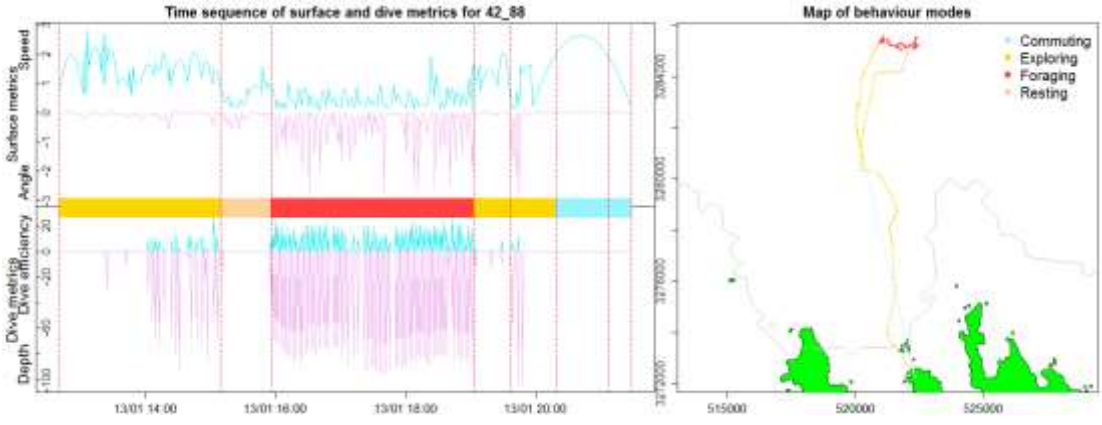


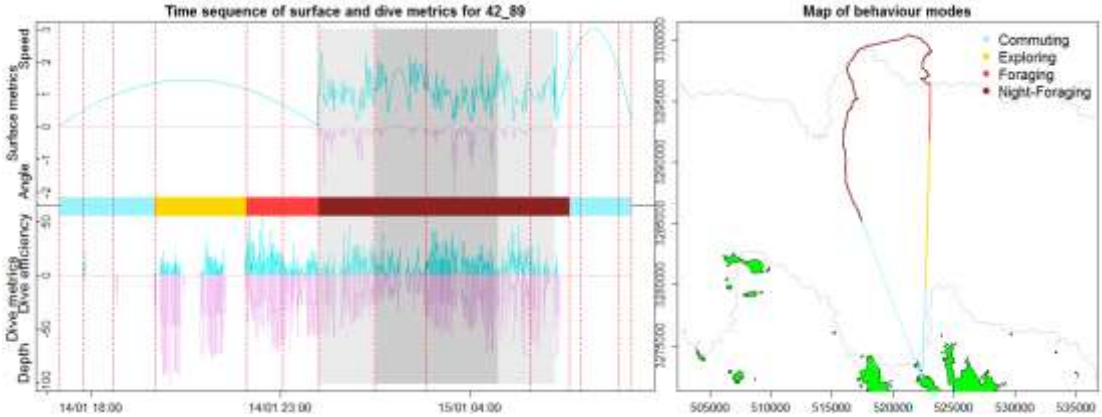

Time sequence of surface and dive metrics for 41_86
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
16/01 04:00
16/01 06:00
16/01 08:00
16/01 10:00
16/01 12:00
16/01 14:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Resting/Commuting
525000
530000
535000
540000
Time sequence of surface and dive metrics for 41_87
17/01 11:00
17/01 16:00
17/01 21:00
18/01 02:00
18/01 07:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Foraging
Night-Resting/Commuting
Resting
515000
520000
525000
530000
535000
540000
545000

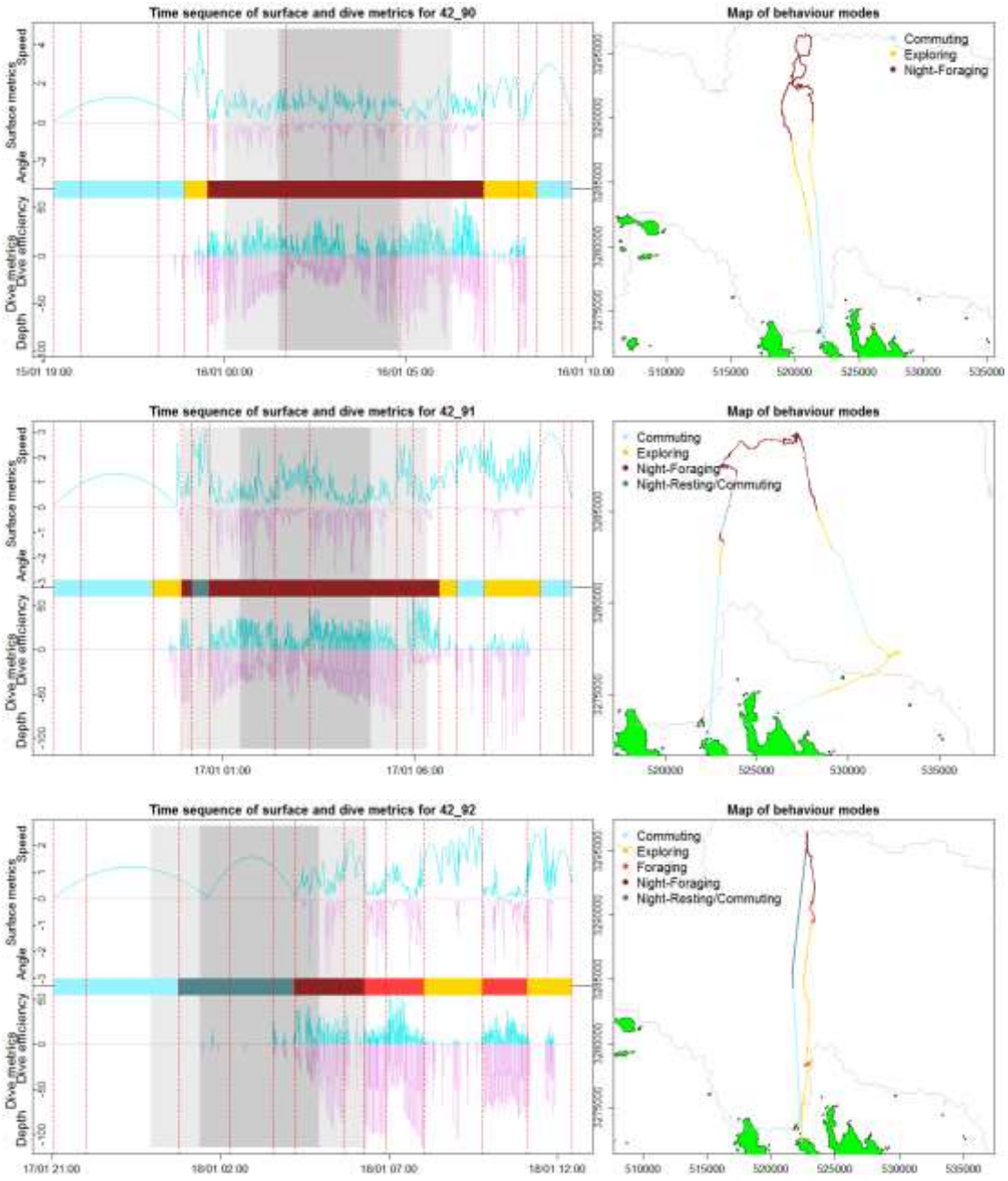
Deployment	**42**
Site	Geddes
Season	2011-12
Stage	Brood
Bill (mm)	52x19
Sex	unsure
Weight (kg)	3.7 (-0.1)
Offspring	2



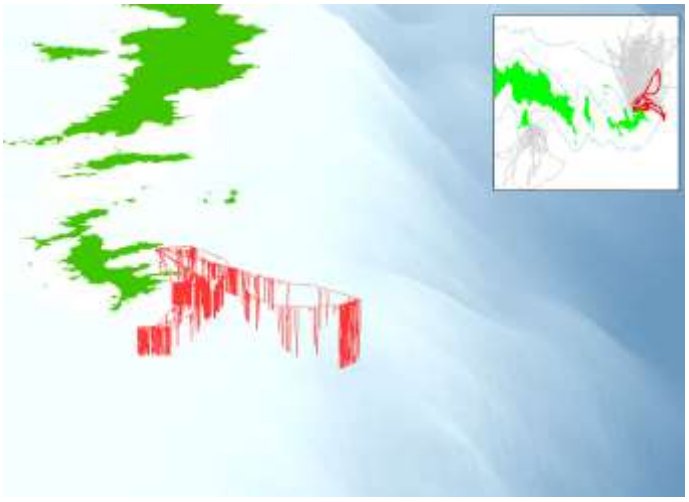
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
42_88	13-01 (12)	13-01 (21)	8.8	19.7	AC	13.3	0%	0%	0.38	35%	0.17
42_89	14-01 (17)	15-01 (08)	15.1	11.0	AC	28.0	41%	67%	0.29	57%	0.33
42_90	15-01 (19)	16-01 (09)	14.4	11.0	AC	24.2	44%	76%	0.31	53%	0.31
42_91	16-01 (20)	17-01 (10)	13.5	11.0	C	17.6	47%	79%	0.33	47%	0.25
42_92	17-01 (21)	18-01 (12)	15.4	NA	C	24.1	42%	39%	0.34	33%	0.25



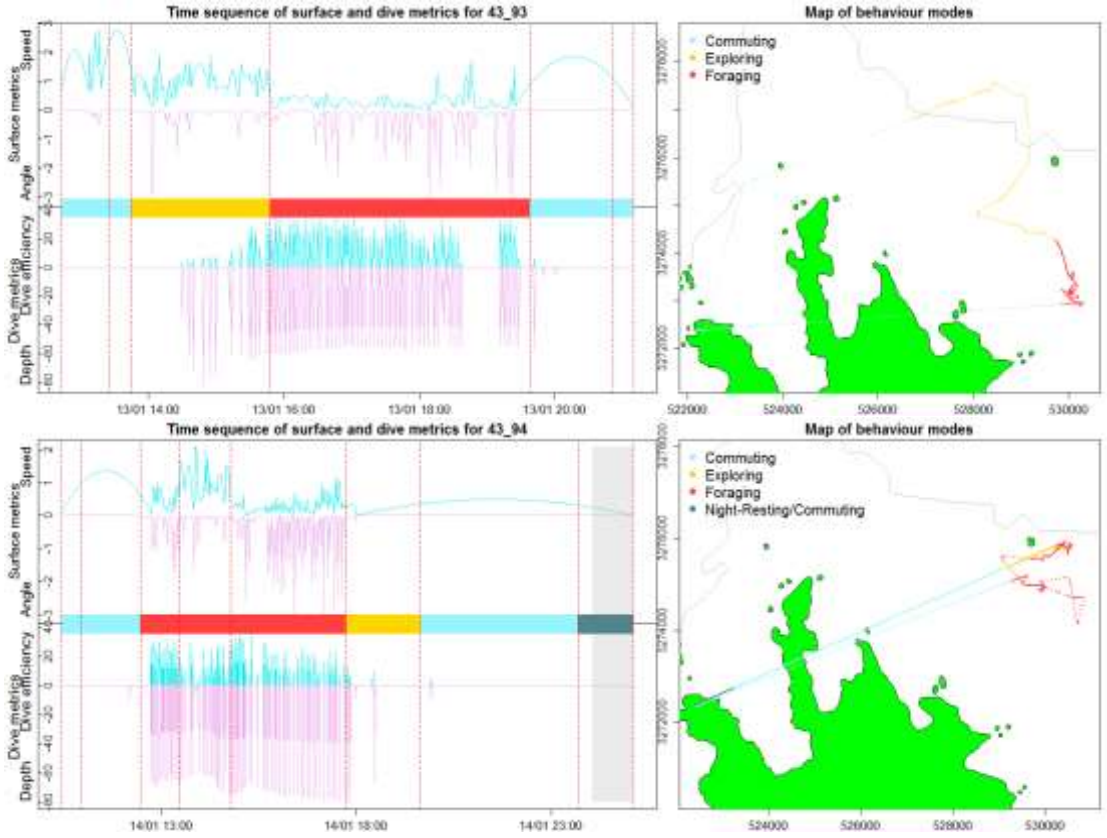


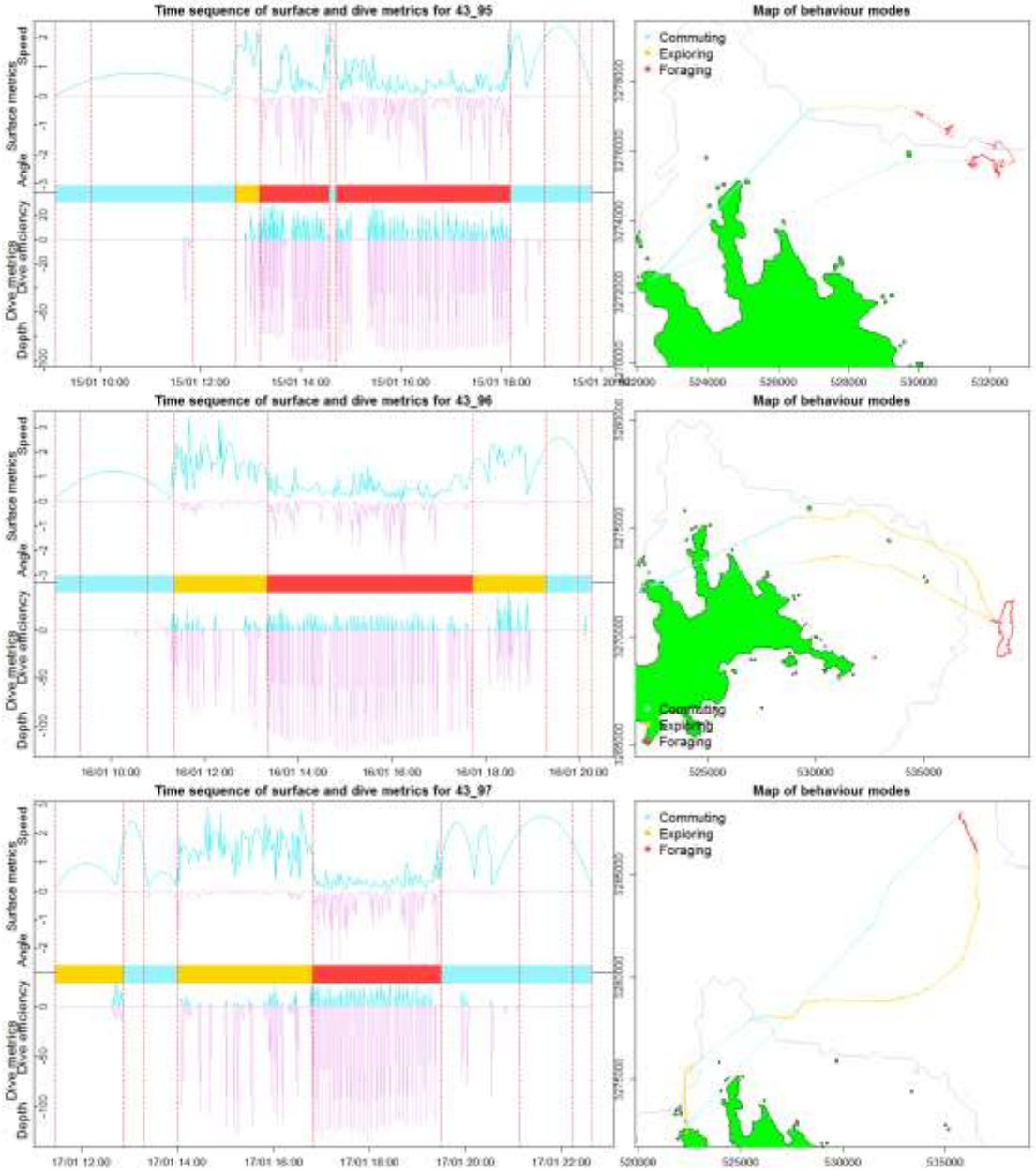

Time sequence of surface and dive metrics for 42_90
Map of behaviour modes
Commuting
Exploring
Night-Foraging
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
15/01 19:00
16/01 00:00
16/01 05:00
16/01 10:00
510000
515000
520000
525000
530000
535000
Time sequence of surface and dive metrics for 42_91
Map of behaviour modes
Commuting
Exploring
Night-Foraging
Night-Resting/Commuting
17/01 01:00
17/01 06:00
520000
525000
530000
535000
Time sequence of surface and dive metrics for 42_92
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Foraging
Night-Resting/Commuting
17/01 21:00
18/01 02:00
18/01 07:00
18/01 12:00
510000
515000
520000
525000
530000
535000

Deployment	**43**
Site	Geddes
Season	2011-12
Stage	Brood
Bill (mm)	48.6x18.6
Sex	female
Weight (kg)	3.2 (0)
Offspring	2

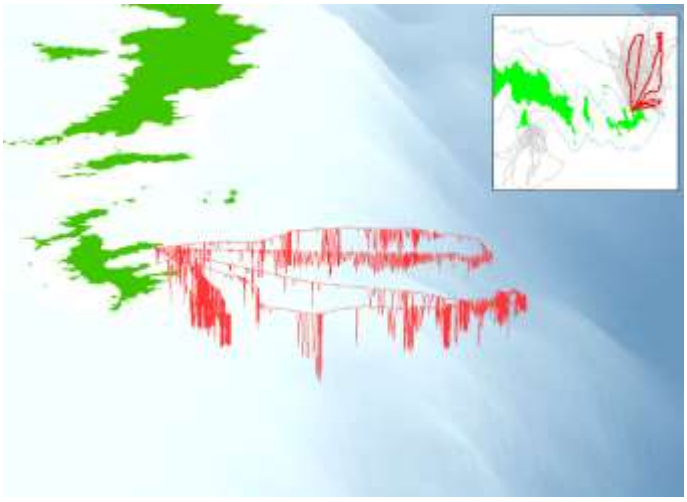


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
43_93	13-01 (12)	13-01 (21)	8.5	13.3	C	8.3	0%	0%	0.34	45%	0.16
43_94	14-01 (10)	15-01 (01)	14.7	8.0	AC	8.9	7%	0%	0.42	36%	0.15
43_95	15-01 (09)	15-01 (19)	10.7	13.0	C	10.8	0%	0%	0.44	45%	0.20
43_96	16-01 (08)	16-01 (20)	11.5	15.2	C	16.9	0%	0%	0.33	38%	0.26
43_97	17-01 (11)	17-01 (22)	11.2	NA	AC	20.6	0%	0%	0.24	24%	0.27

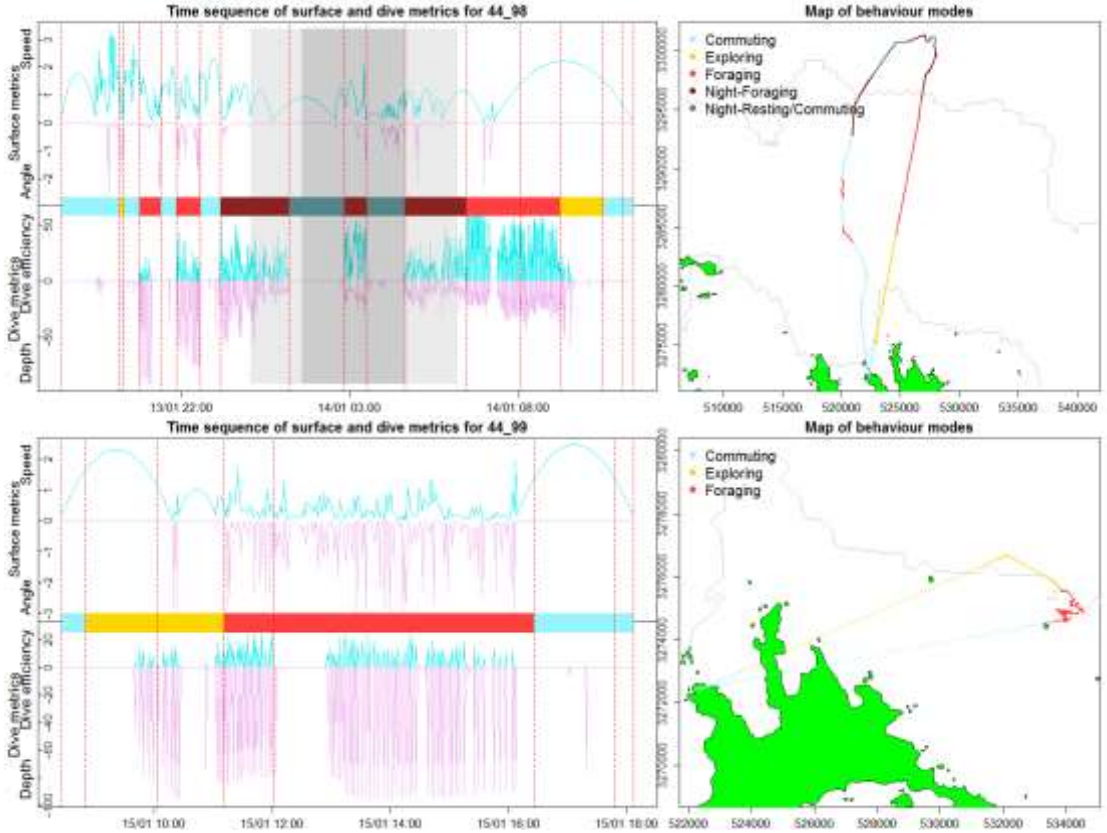


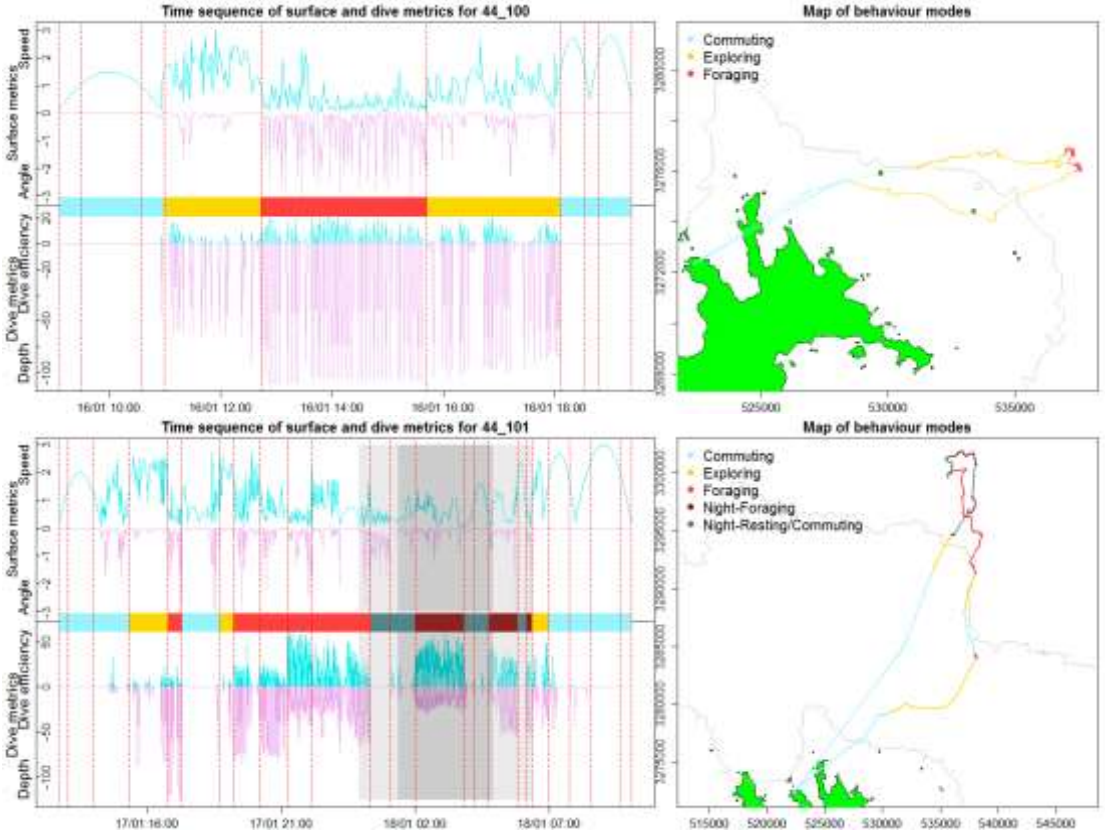

Time sequence of surface and dive metrics for 43_95
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
15/01 10:00
15/01 12:00
15/01 14:00
15/01 16:00
15/01 18:00
Map of behaviour modes
Commuting
Exploring
Foraging
Time sequence of surface and dive metrics for 43_96
16/01 10:00
16/01 12:00
16/01 14:00
16/01 16:00
16/01 18:00
16/01 20:00
Time sequence of surface and dive metrics for 43_97
17/01 12:00
17/01 14:00
17/01 16:00
17/01 18:00
17/01 20:00
17/01 22:00

Deployment	**44**
Site	Geddes
Season	2011-12
Stage	Brood
Bill (mm)	48.3x15
Sex	female
Weight (kg)	2.8 (0)
Offspring	2

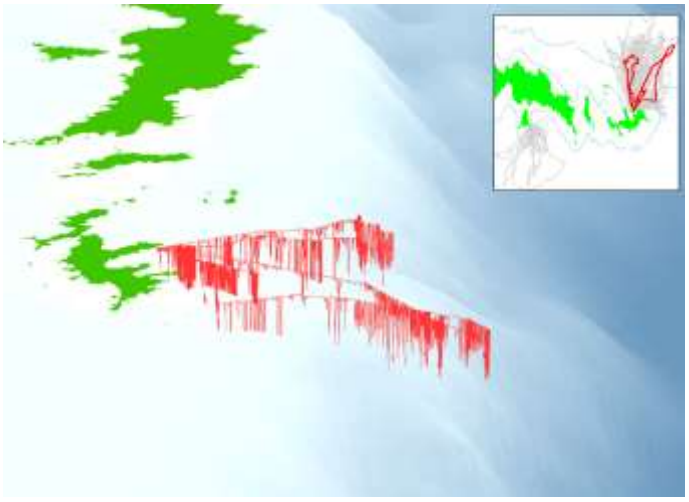


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
44_98	13-01 (18)	14-01 (11)	17.0	21.0	C	29.3	37%	47%	0.20	51%	0.36
44_99	15-01 (08)	15-01 (18)	9.7	15.0	C	12.4	0%	0%	0.44	54%	0.26
44_100	16-01 (09)	16-01 (19)	10.3	17.4	AC	15.7	0%	0%	0.39	29%	0.22
44_101	17-01 (12)	18-01 (10)	21.4	NA	AC	33.3	30%	45%	0.25	41%	0.41

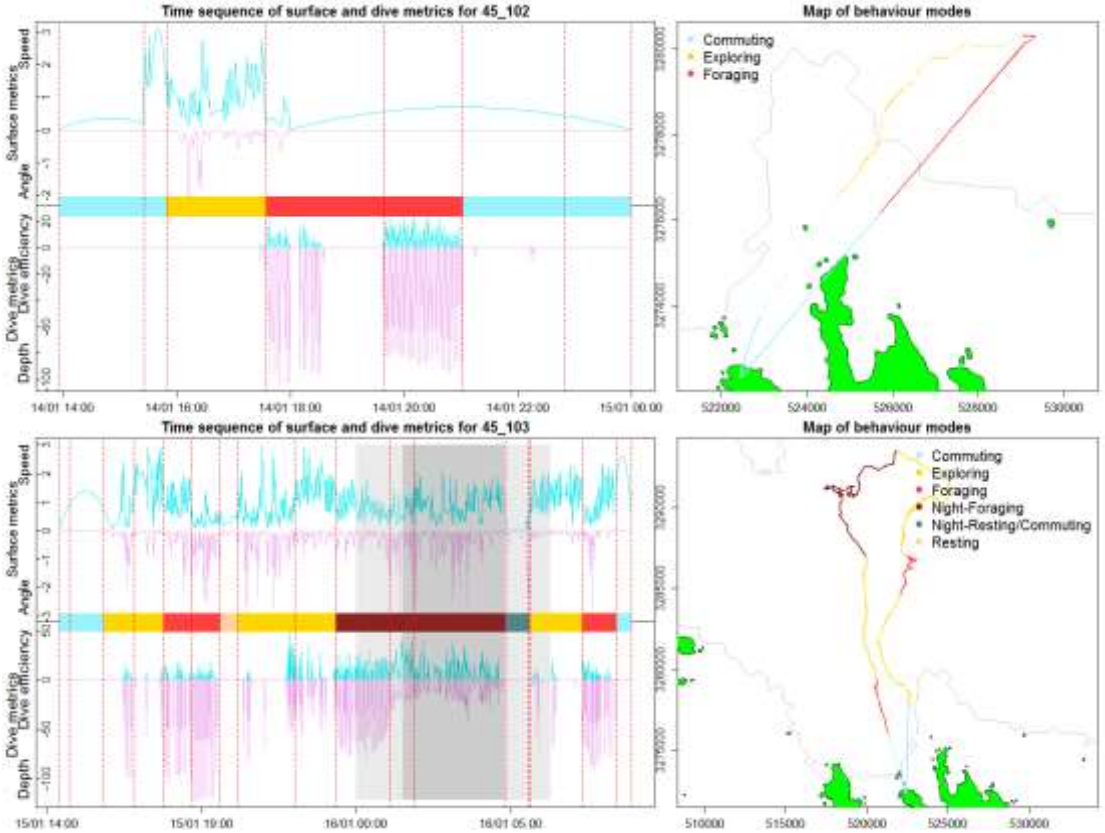


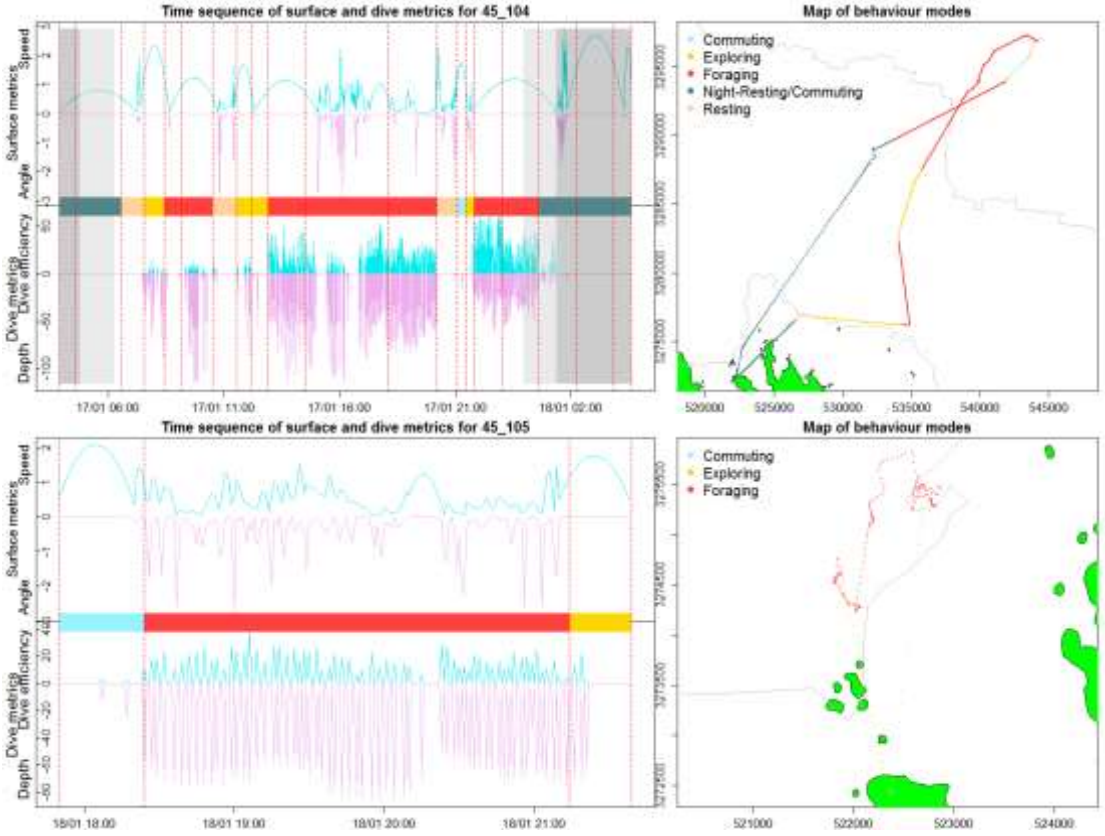

Time sequence of surface and dive metrics for 44_100
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
16/01 10:00
16/01 12:00
16/01 14:00
16/01 16:00
16/01 18:00
Map of behaviour modes
Commuting
Exploring
Foraging
525000
530000
535000
Time sequence of surface and dive metrics for 44_101
17/01 16:00
17/01 21:00
18/01 02:00
18/01 07:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Foraging
Night-Resting/Commuting
515000
520000
525000
530000
535000
540000
545000

Deployment	**45**
Site	Geddes
Season	2011-12
Stage	Brood
Bill (mm)	48.5x18.9
Sex	unsure
Weight (kg)	3 (0.4)
Offspring	1

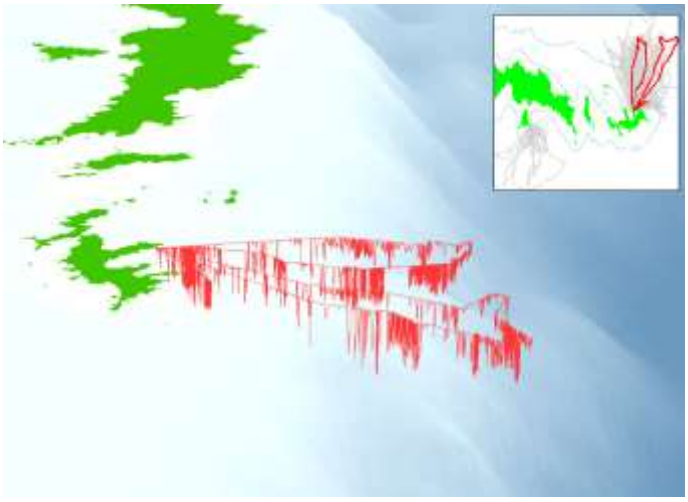


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
45_102	14-01 (13)	15-01 (00)	10.1	14.4	C	10.5	0%	0%	0.36	34%	0.18
45_103	15-01 (14)	16-01 (08)	18.5	19.0	AC	21.1	34%	60%	0.31	45%	0.27
45_104	17-01 (03)	18-01 (04)	24.7	13.2	AC	32.8	29%	13%	0.34	49%	0.37
45_105	18-01 (17)	18-01 (21)	3.8	NA	AC	3.4	0%	0%	0.89	74%	0.12

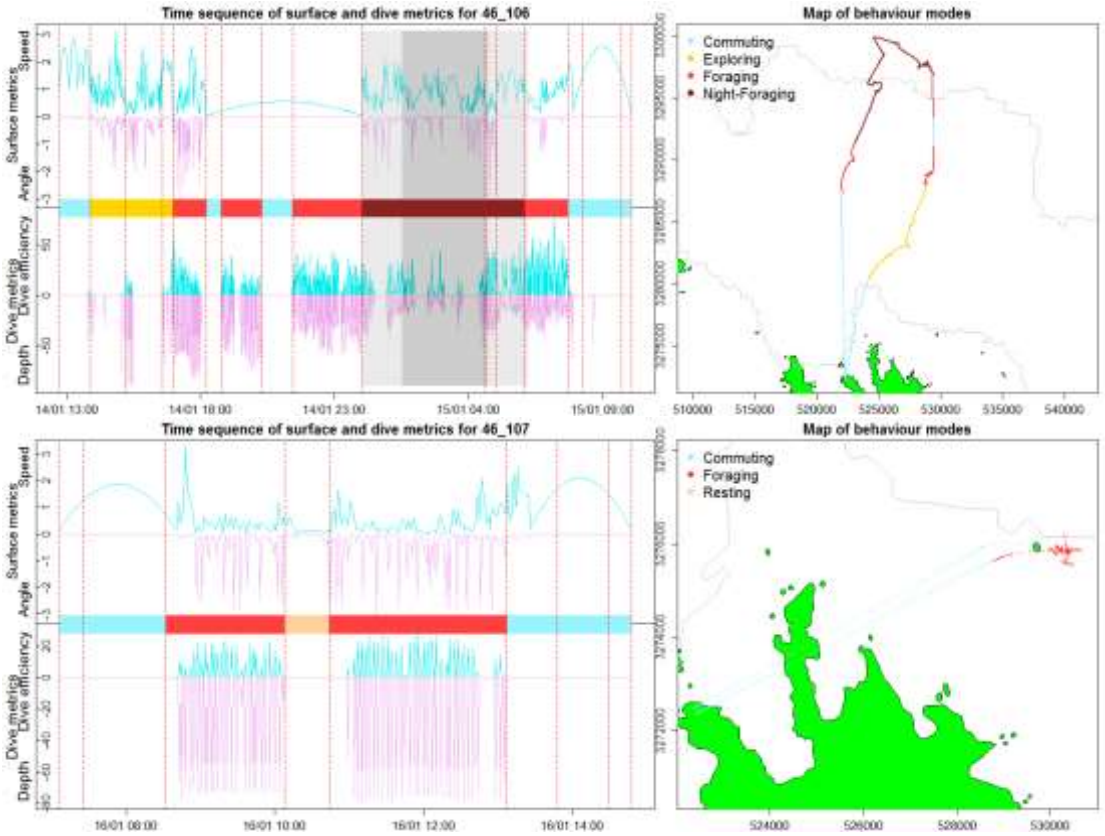


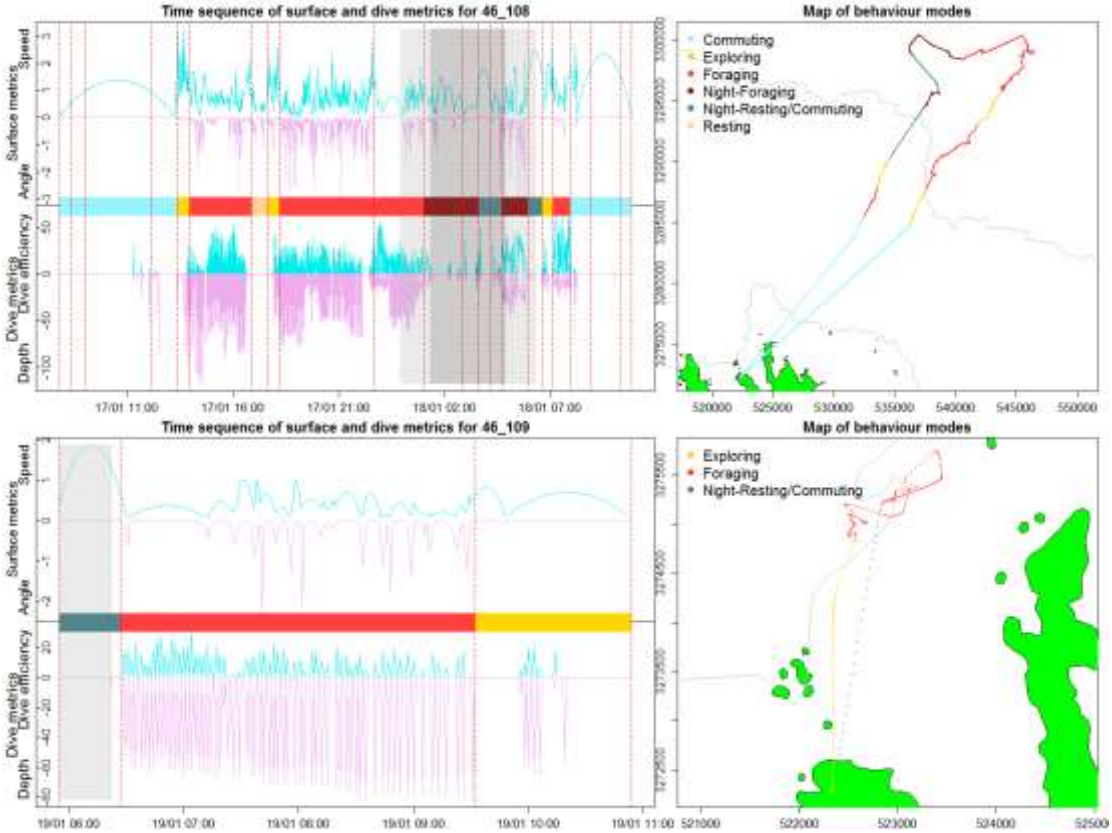

Time sequence of surface and dive metrics for 45_104
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
17/01 06:00
17/01 11:00
17/01 16:00
17/01 21:00
18/01 02:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Resting/Commuting
Resting
520000
525000
530000
535000
540000
545000
Time sequence of surface and dive metrics for 45_105
18/01 18:00
18/01 19:00
18/01 20:00
18/01 21:00
Map of behaviour modes
Commuting
Exploring
Foraging
521000
522000
523000
524000

Deployment	**46**
Site	Geddes
Season	2011-12
Stage	Brood
Bill (mm)	50x17.8
Sex	female
Weight (kg)	2.8 (0.4)
Offspring	1

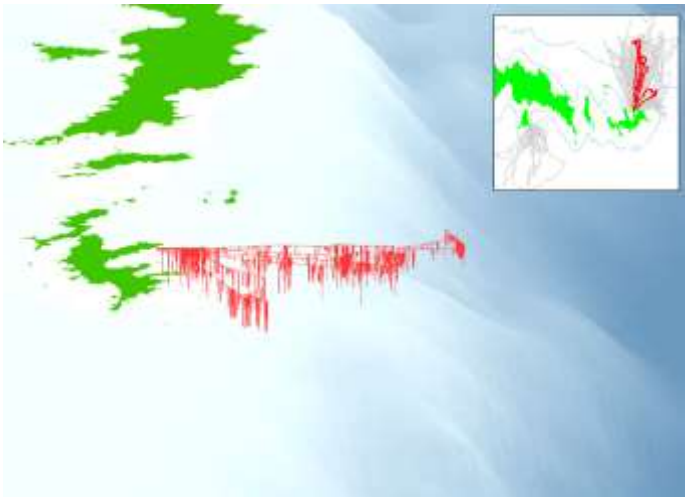


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
46_106	14-01 (12)	15-01 (10)	21.4	21.0	AC	27.7	29%	43%	0.31	61%	0.38
46_107	16-01 (07)	16-01 (14)	7.7	17.0	AC	8.9	0%	0%	0.36	52%	0.15
46_108	17-01 (07)	18-01 (10)	27.1	19.1	AC	36.3	24%	32%	0.29	53%	0.41
46_109	19-01 (05)	19-01 (10)	5.0	NA	AC	3.5	9%	1%	0.99	62%	0.10

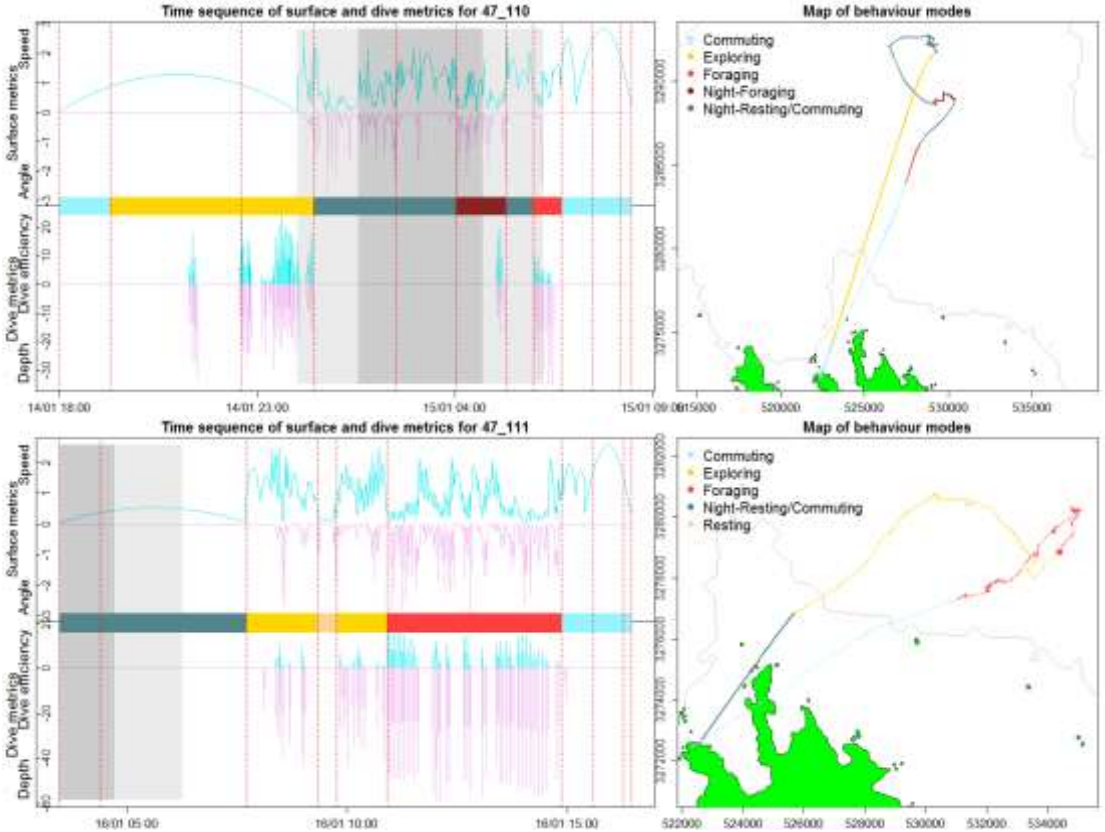


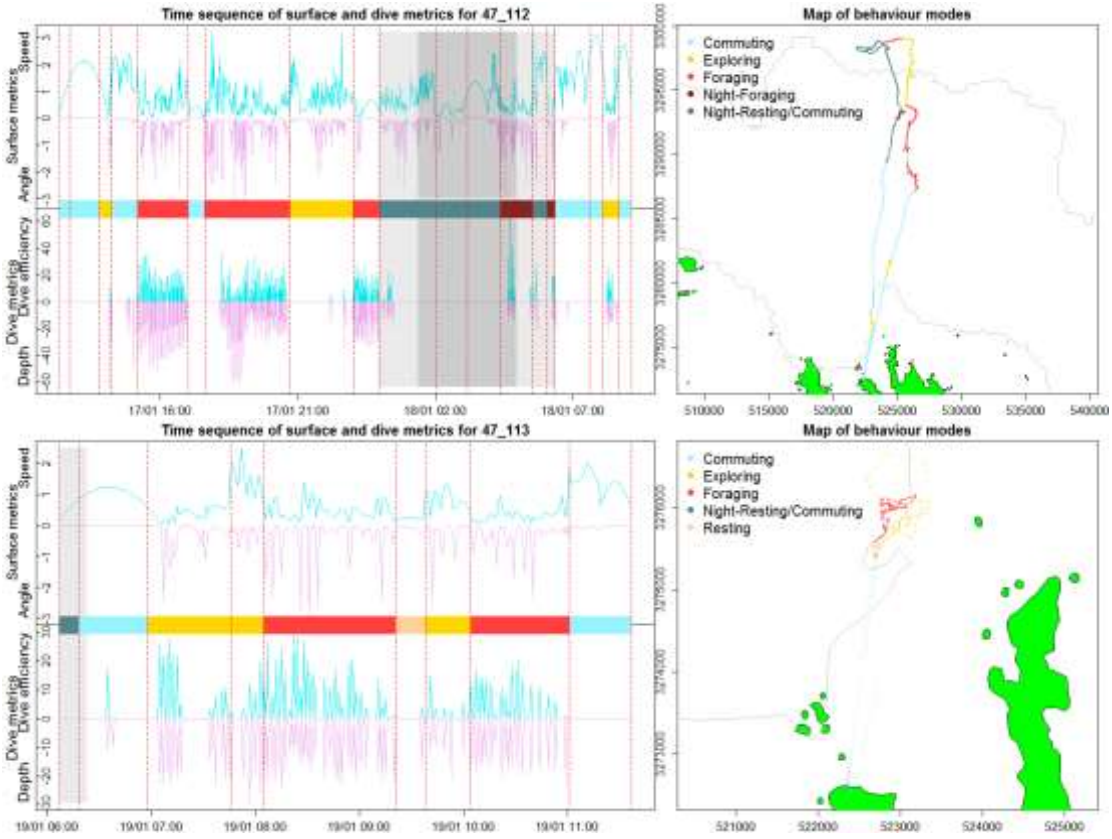

Time sequence of surface and dive metrics for 46_108
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
17/01 11:00
17/01 16:00
17/01 21:00
18/01 02:00
18/01 07:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Foraging
Night-Resting/Commuting
Resting
520000
525000
530000
535000
540000
545000
550000
Time sequence of surface and dive metrics for 46_109
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
19/01 06:00
19/01 07:00
19/01 08:00
19/01 09:00
19/01 10:00
19/01 11:00
Map of behaviour modes
Exploring
Foraging
Night-Resting/Commuting
521000
522000
523000
524000
525000

Deployment	**47**
Site	Geddes
Season	2011-12
Stage	Brood
Bill (mm)	51.4x16.5
Sex	female
Weight (kg)	2.7 (0.4)
Offspring	2

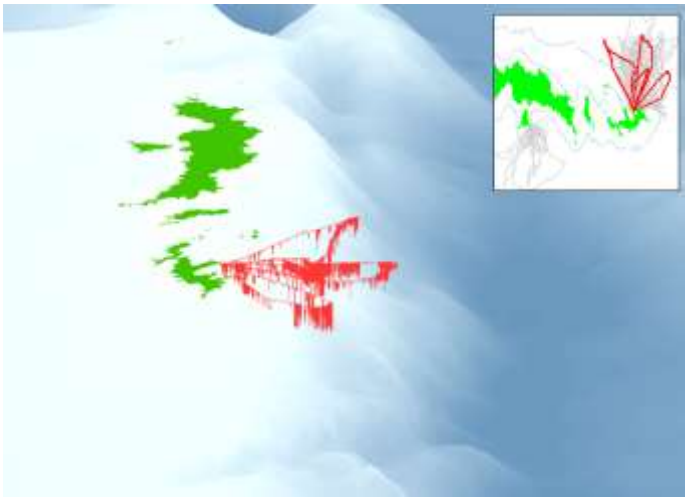


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
47_110	14-01 (18)	15-01 (08)	14.5	19.0	AC	21.3	43%	33%	0.03	14%	0.30
47_111	16-01 (03)	16-01 (16)	13.0	19.9	C	14.9	22%	0%	0.12	30%	0.19
47_112	17-01 (12)	18-01 (09)	20.8	21.0	AC	26.8	31%	22%	0.09	35%	0.37
47_113	19-01 (06)	19-01 (11)	5.5	NA	AC	4.2	5%	0%	0.15	40%	0.14

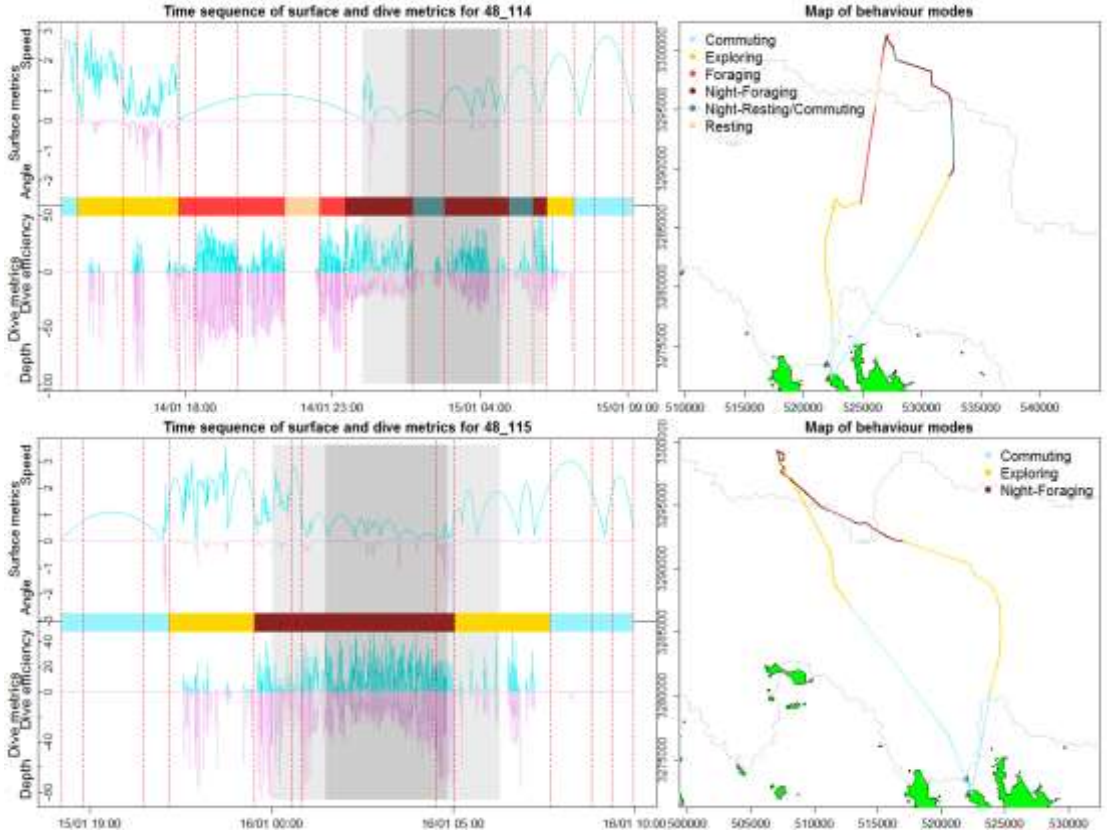


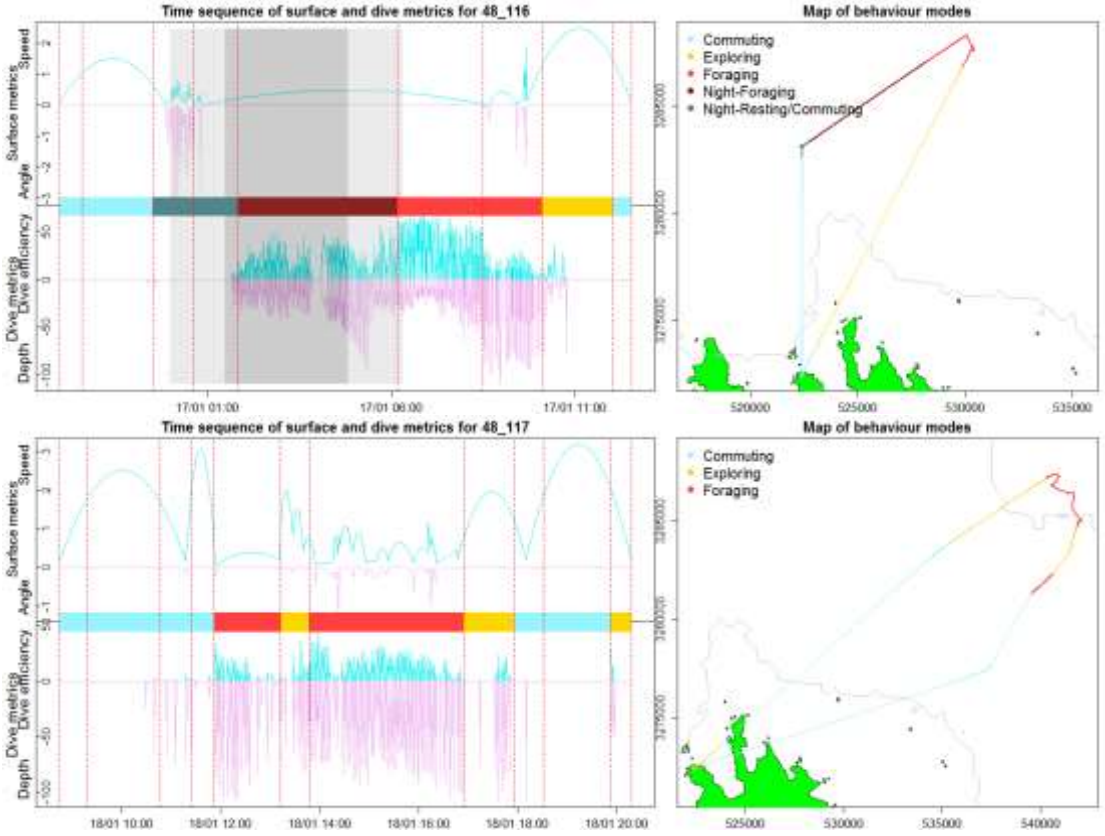

Time sequence of surface and dive metrics for 47_112
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
17/01 16:00
17/01 21:00
18/01 02:00
18/01 07:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Foraging
Night-Resting/Commuting
510000
515000
520000
525000
530000
535000
540000
Time sequence of surface and dive metrics for 47_113
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
19/01 06:00
19/01 07:00
19/01 08:00
19/01 09:00
19/01 10:00
19/01 11:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Resting/Commuting
Resting
521000
522000
523000
524000
525000

Deployment	**48**
Site	Geddes
Season	2011-12
Stage	Brood
Bill (mm)	48.6x17.3
Sex	female
Weight (kg)	3.1 (-0.1)
Offspring	2

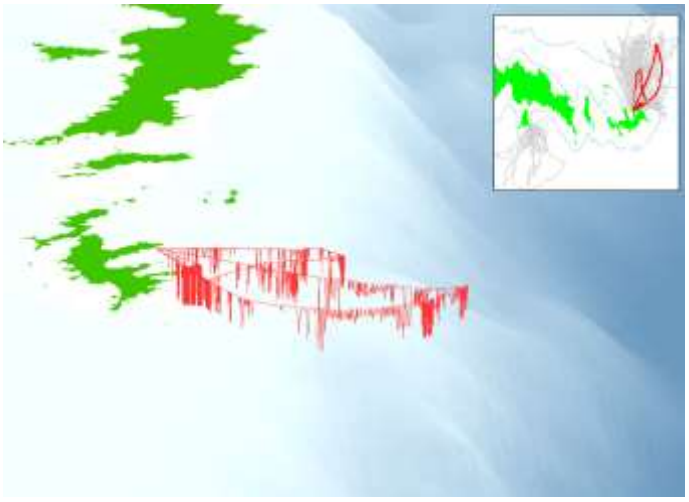


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
48_114	14-01 (13)	15-01 (09)	19.4	9.0	C	29.1	32%	52%	0.27	48%	0.39
48_115	15-01 (18)	16-01 (09)	15.8	11.0	AC	30.9	40%	80%	0.18	35%	0.35
48_116	16-01 (20)	17-01 (12)	15.6	20.2	C	17.7	41%	53%	0.51	53%	0.24
48_117	18-01 (08)	18-01 (20)	11.6	NA	AC	23.8	0%	0%	0.31	39%	0.32

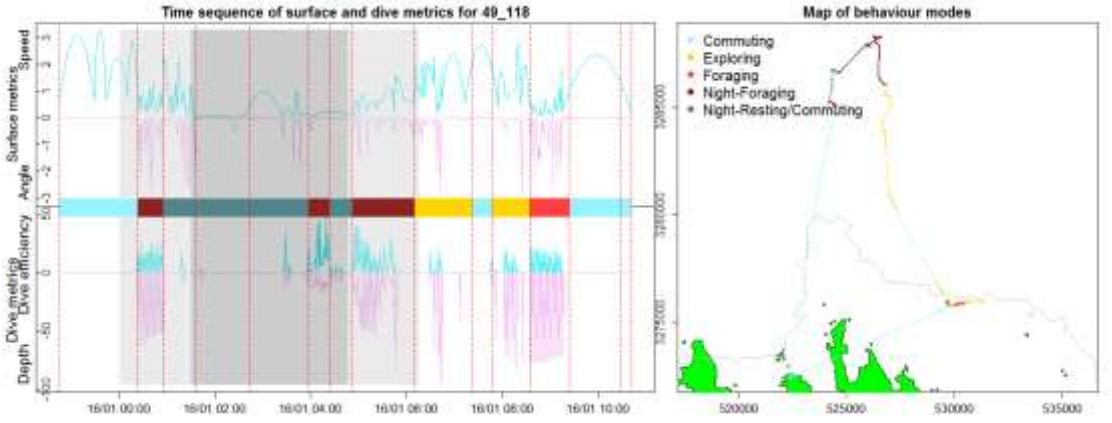


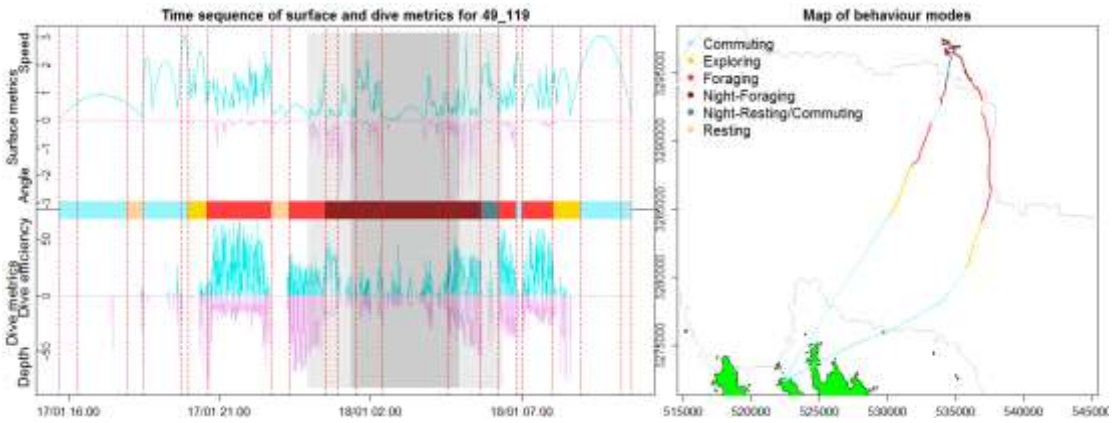

Time sequence of surface and dive metrics for 48_116
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
17/01 01:00
17/01 06:00
17/01 11:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Foraging
Night-Resting/Commuting
520000
525000
530000
535000
Time sequence of surface and dive metrics for 48_117
18/01 10:00
18/01 12:00
18/01 14:00
18/01 16:00
18/01 18:00
18/01 20:00
Map of behaviour modes
Commuting
Exploring
Foraging
525000
530000
535000
540000

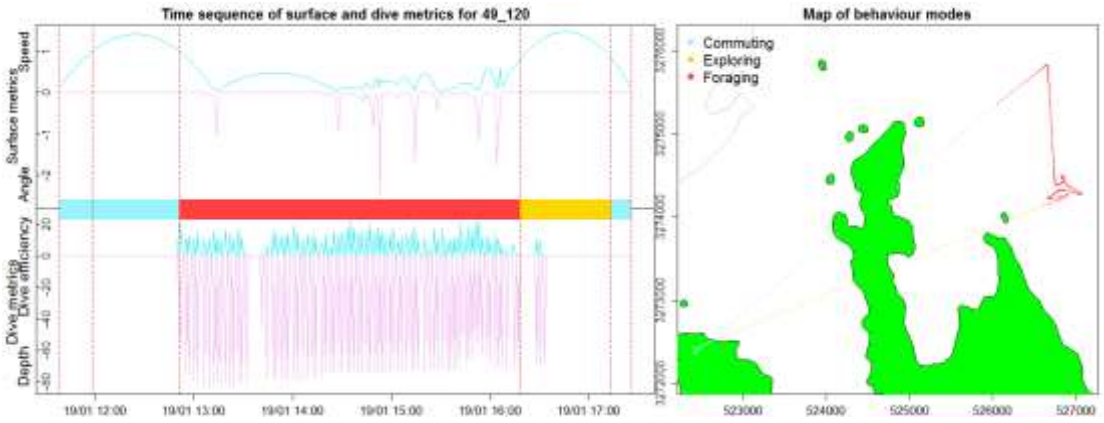
Deployment	**49**
Site	Geddes
Season	2011-12
Stage	Brood
Bill (mm)	45.9x17.1
Sex	female
Weight (kg)	2.7 (0.5)
Offspring	2



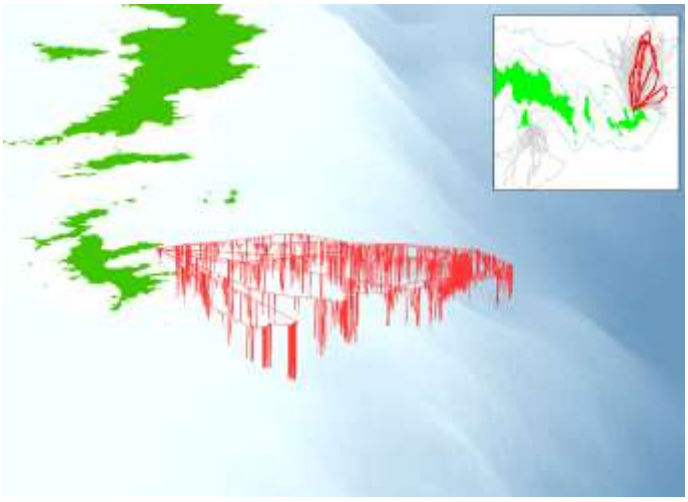
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
49_118	15-01 (22)	16-01 (10)	12.0	29.0	C	16.3	53%	74%	0.19	26%	0.24
49_119	17-01 (15)	18-01 (10)	18.9	25.0	AC	27.8	34%	49%	0.23	53%	0.38
49_120	19-01 (11)	19-01 (17)	5.8	NA	C	5.5	0%	0%	0.89	59%	0.13



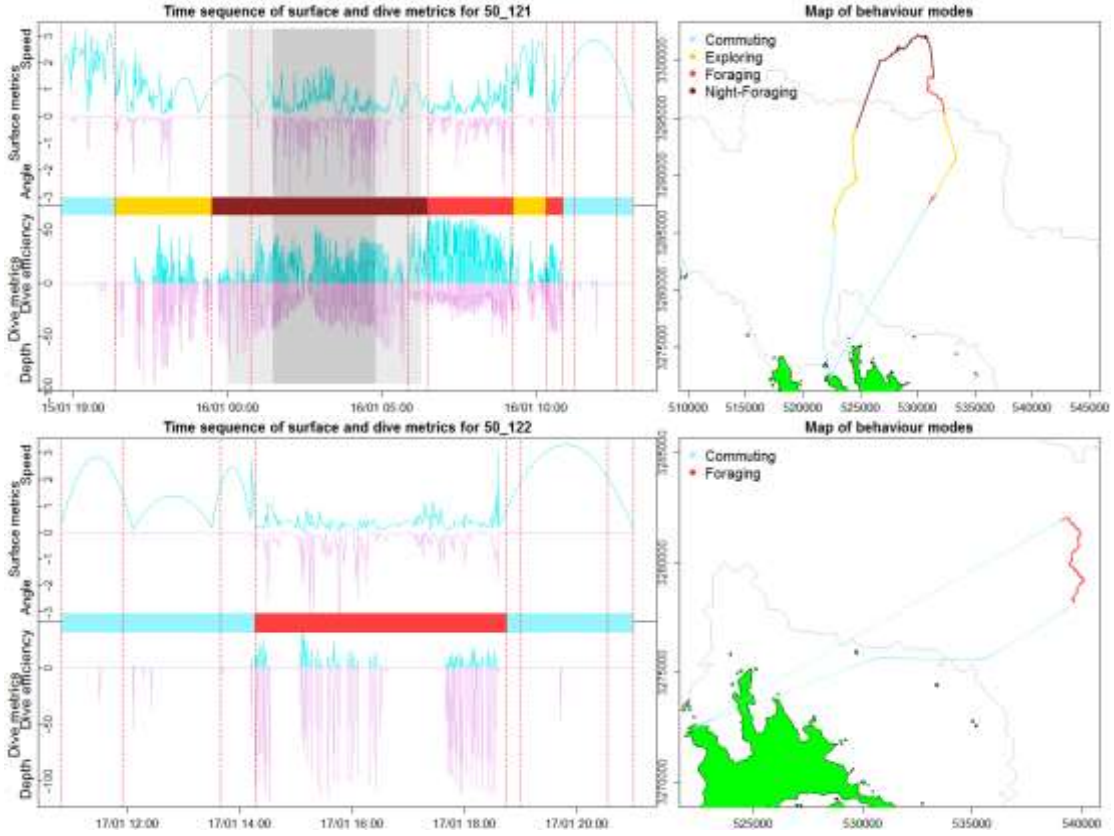


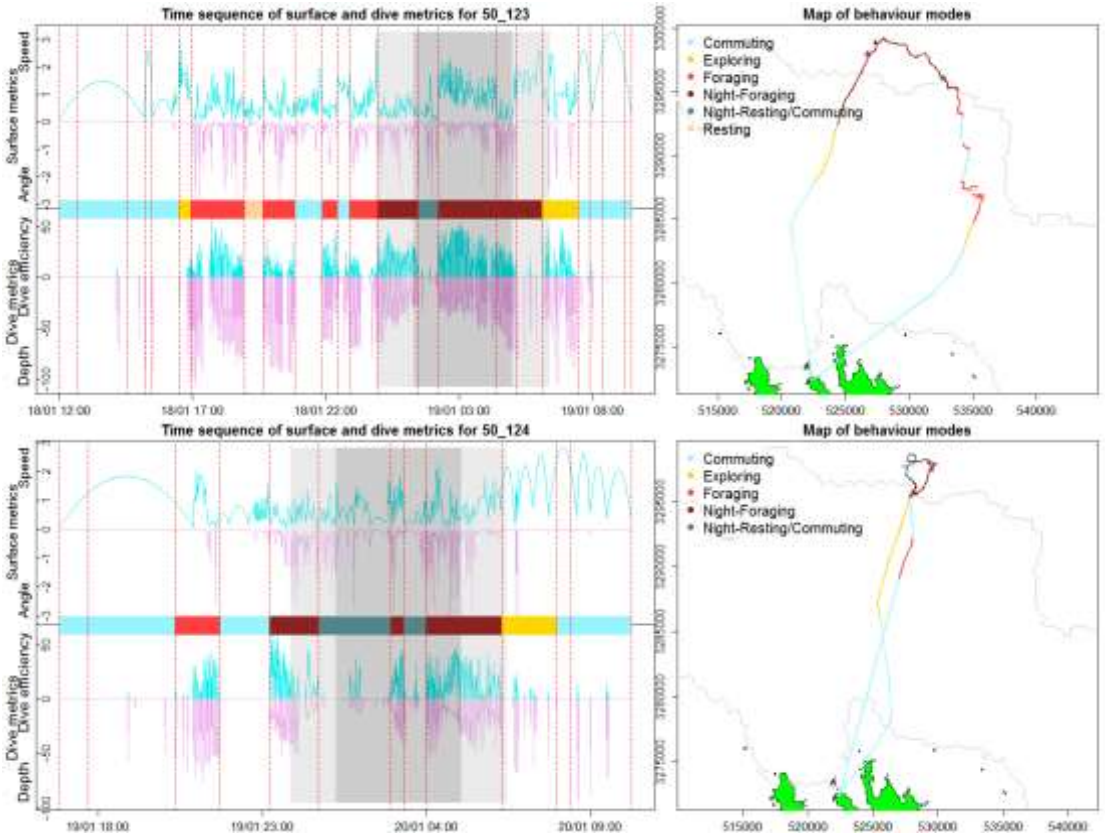

Time sequence of surface and dive metrics for 49_120
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
19/01 12:00
19/01 13:00
19/01 14:00
19/01 15:00
19/01 16:00
19/01 17:00
Map of behaviour modes
Commuting
Exploring
Foraging
523000
524000
525000
526000
527000

Deployment	**50**
Site	Geddes
Season	2011-12
Stage	Brood
Bill (mm)	48x17.65
Sex	female
Weight (kg)	2.9 (-0.3)
Offspring	2

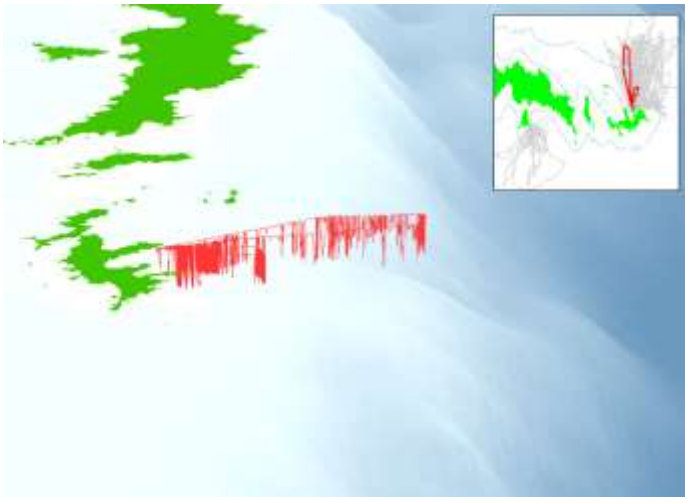


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
50_121	15-01 (18)	16-01 (13)	18.5	21.7	C	30.9	34%	49%	0.32	55%	0.41
50_122	17-01 (10)	17-01 (21)	10.2	15.0	AC	19.7	0%	0%	0.16	44%	0.27
50_123	18-01 (12)	19-01 (09)	21.5	7.4	AC	27.4	30%	52%	0.37	48%	0.38
50_124	19-01 (16)	20-01 (10)	17.4	NA	C	26.8	38%	71%	0.18	32%	0.38

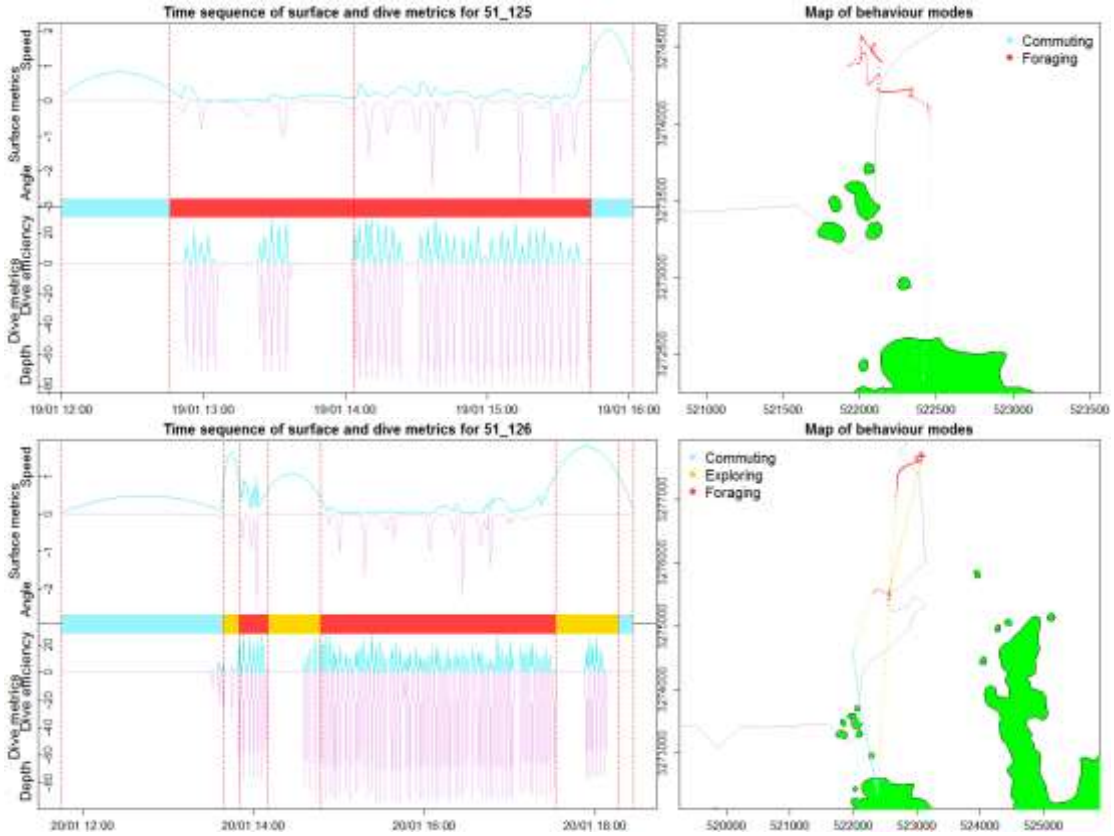


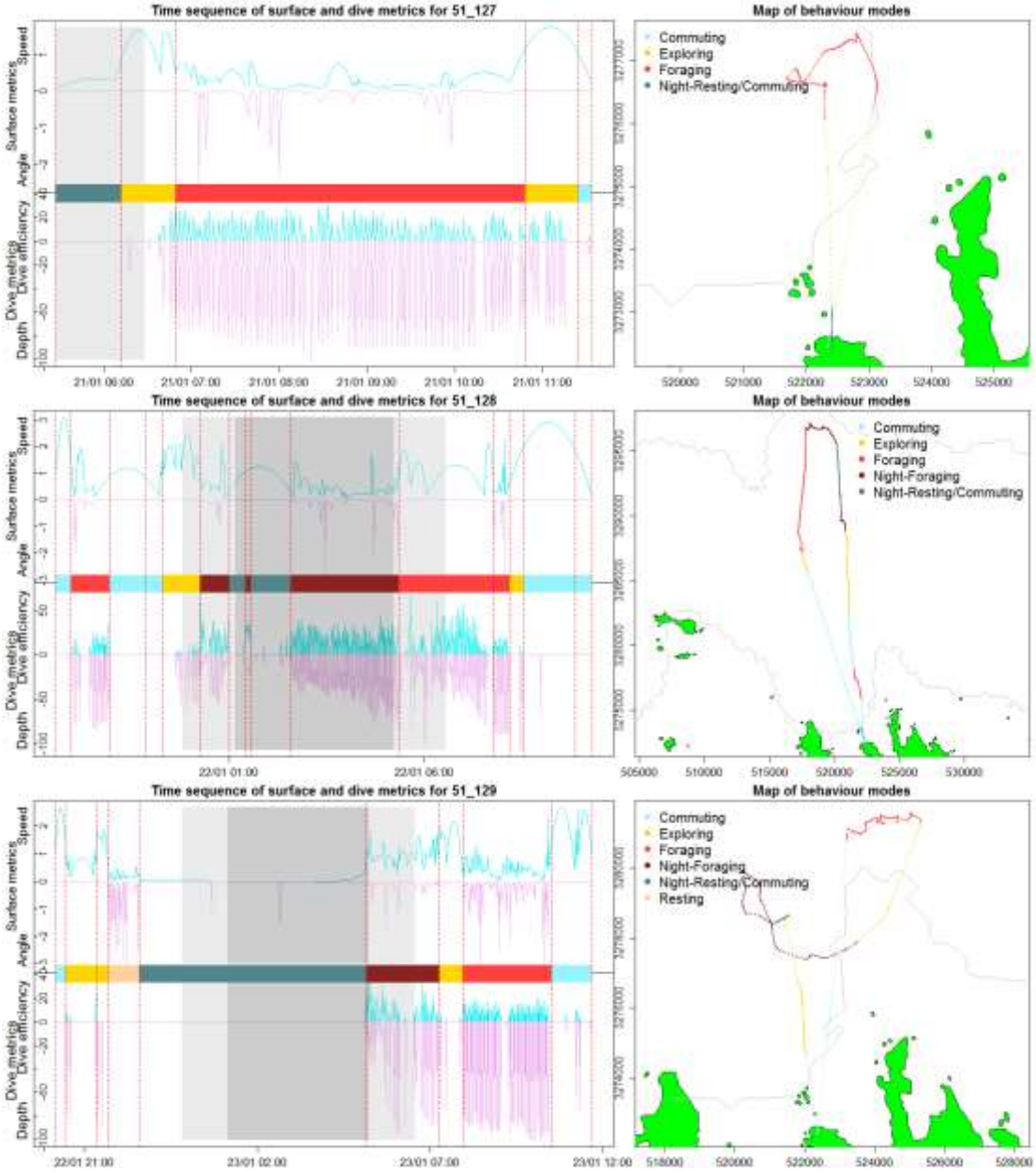

Time sequence of surface and dive metrics for 50_123
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
18/01 12:00
18/01 17:00
18/01 22:00
19/01 03:00
19/01 08:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Foraging
Night-Resting/Commuting
Resting
515000
520000
525000
530000
535000
540000
Time sequence of surface and dive metrics for 50_124
19/01 18:00
19/01 23:00
20/01 04:00
20/01 09:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Foraging
Night-Resting/Commuting

Deployment	**51**
Site	Geddes
Season	2011-12
Stage	Brood
Bill (mm)	52.9x19.2
Sex	male
Weight (kg)	3.8 (-0.3)
Offspring	2

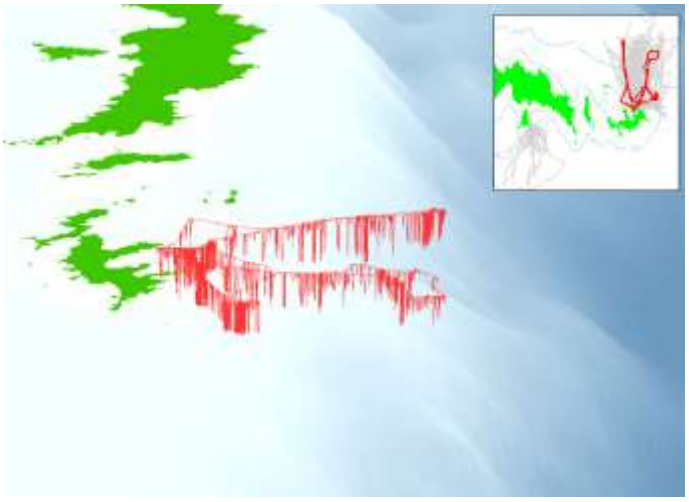


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
51_125	19-01 (12)	19-01 (16)	4.0	19.7	AC	2.3	0%	0%	1.12	73%	0.08
51_126	20-01 (11)	20-01 (18)	6.7	11.0		5.4	0%	0%	1.06	46%	0.11
51_127	21-01 (05)	21-01 (11)	6.1	9.0	C	5.1	17%	1%	1.19	65%	0.12
51_128	21-01 (20)	22-01 (10)	13.7	9.9	AC	25.0	49%	72%	0.37	54%	0.32
51_129	22-01 (20)	23-01 (11)	15.6	NA	C	9.5	44%	27%	0.48	30%	0.15

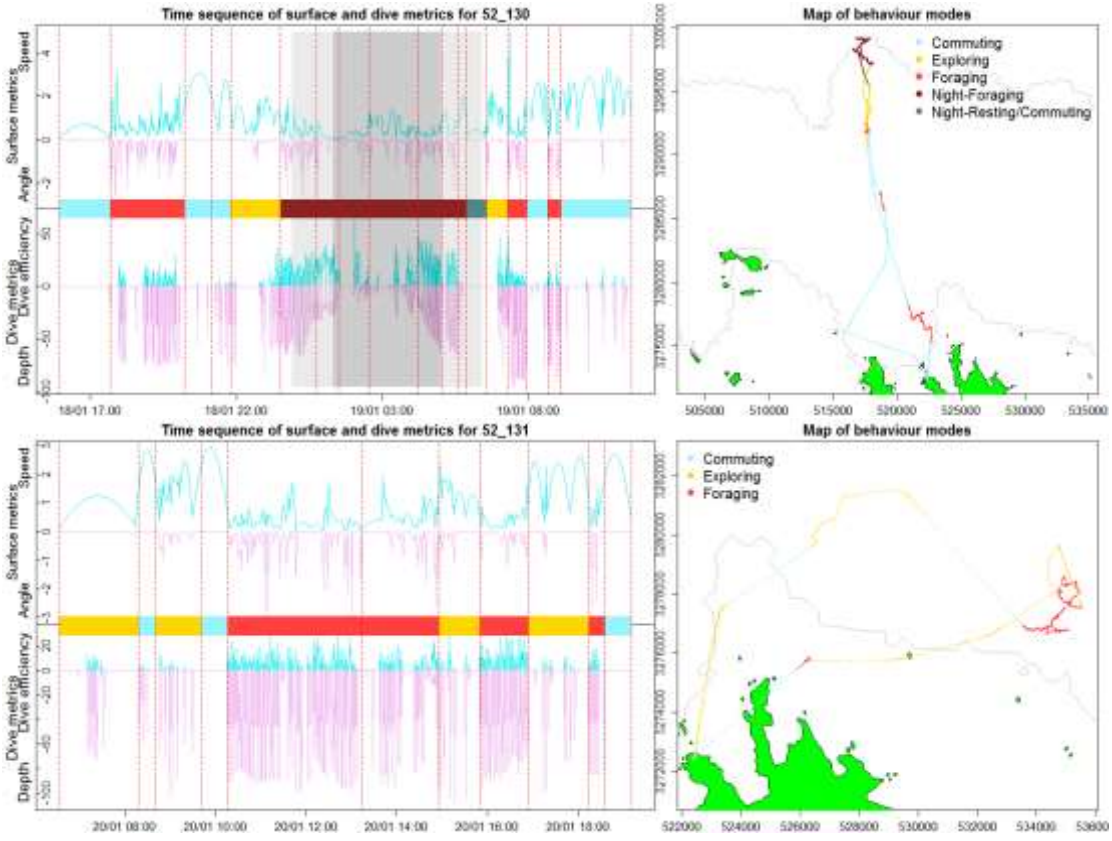


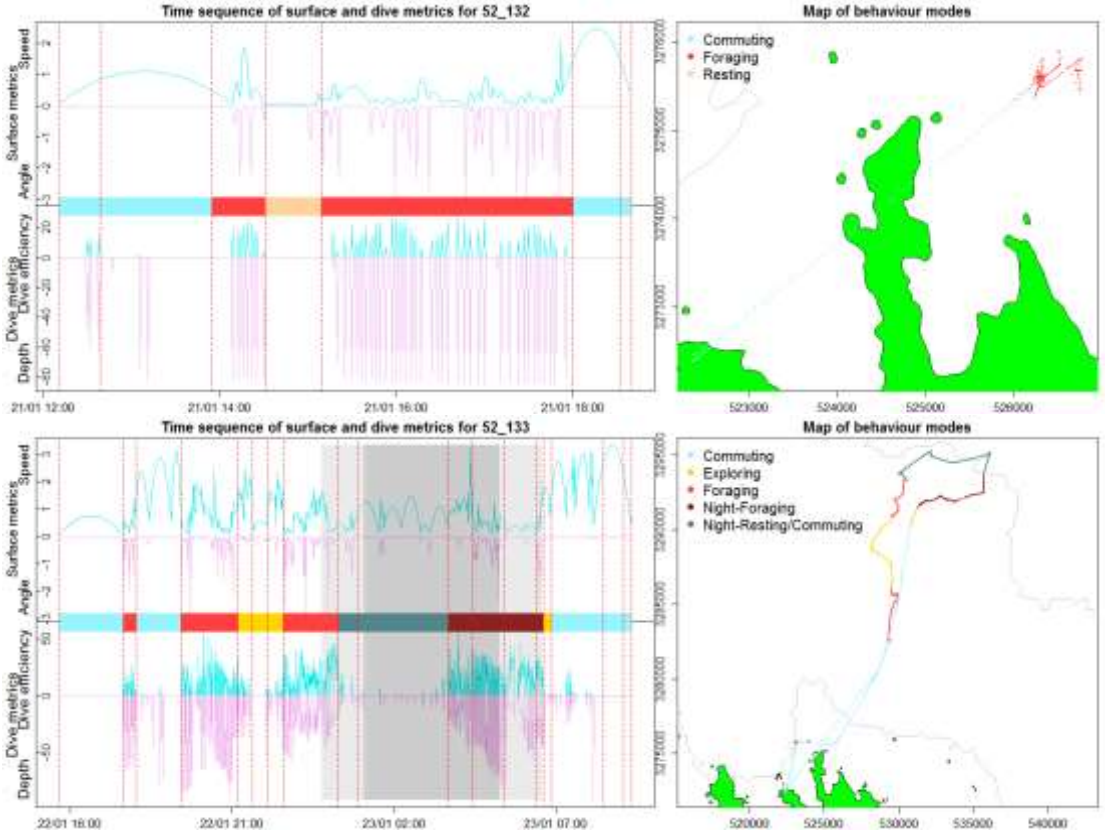

Time sequence of surface and dive metrics for 51_127
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
21/01 06:00
21/01 07:00
21/01 08:00
21/01 09:00
21/01 10:00
21/01 11:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Resting/Commuting
520000
521000
522000
523000
524000
525000
Time sequence of surface and dive metrics for 51_128
22/01 01:00
22/01 06:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Foraging
Night-Resting/Commuting
505000
510000
515000
520000
525000
530000
Time sequence of surface and dive metrics for 51_129
22/01 21:00
23/01 02:00
23/01 07:00
23/01 12:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Foraging
Night-Resting/Commuting
Resting
518000
520000
522000
524000
526000
528000

Deployment	**52**
Site	Geddes
Season	2011-12
Stage	Brood
Bill (mm)	56.7x19.8
Sex	male
Weight (kg)	3.5 (0.7)
Offspring	2

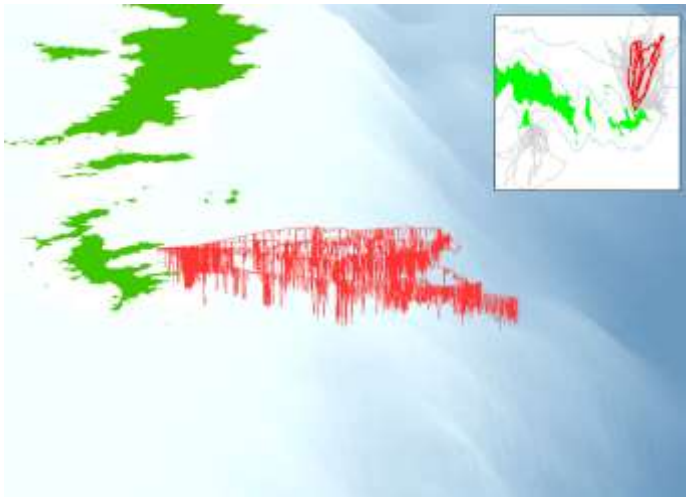


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
52_130	18-01 (15)	19-01 (11)	19.6	19.0		27.3	33%	58%	0.32	51%	0.35
52_131	20-01 (06)	20-01 (19)	12.6	17.0	C	14.3	0%	0%	0.46	48%	0.23
52_132	21-01 (12)	21-01 (18)	6.5	21.0		5.6	0%	0%	0.55	53%	0.10
52_133	22-01 (15)	23-01 (09)	17.7	NA	C	26.6	39%	55%	0.28	39%	0.35

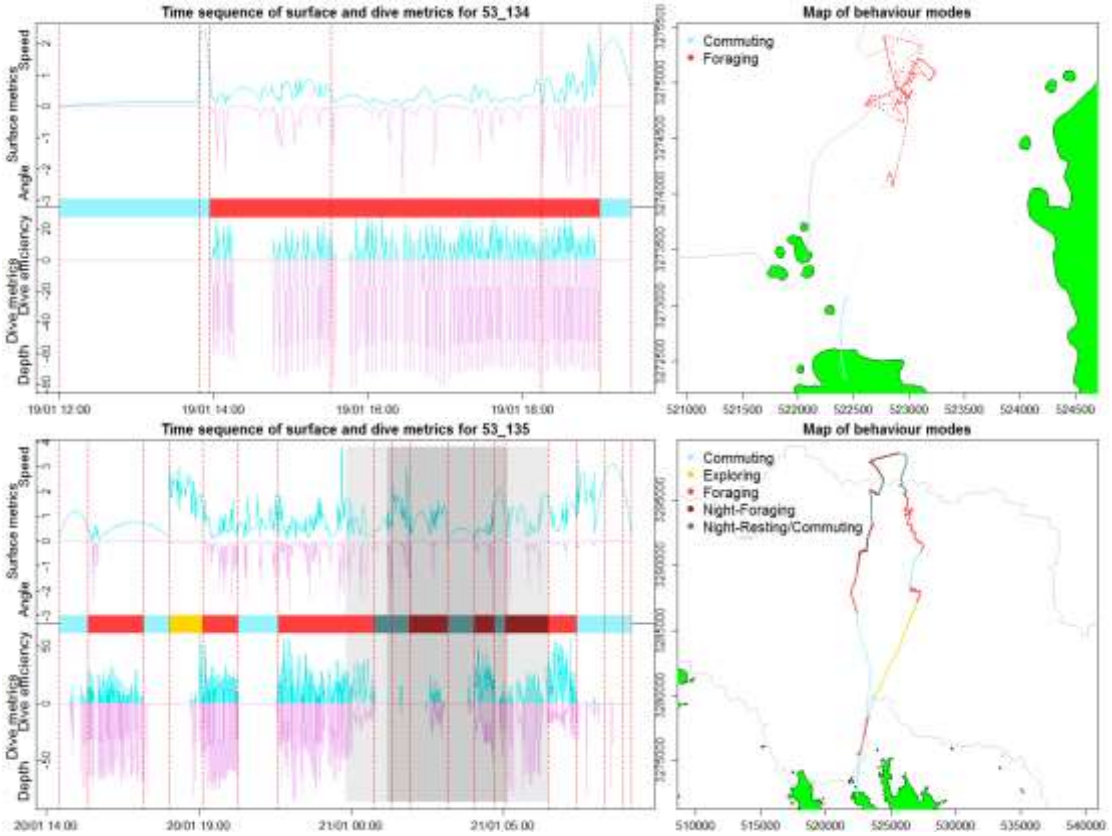


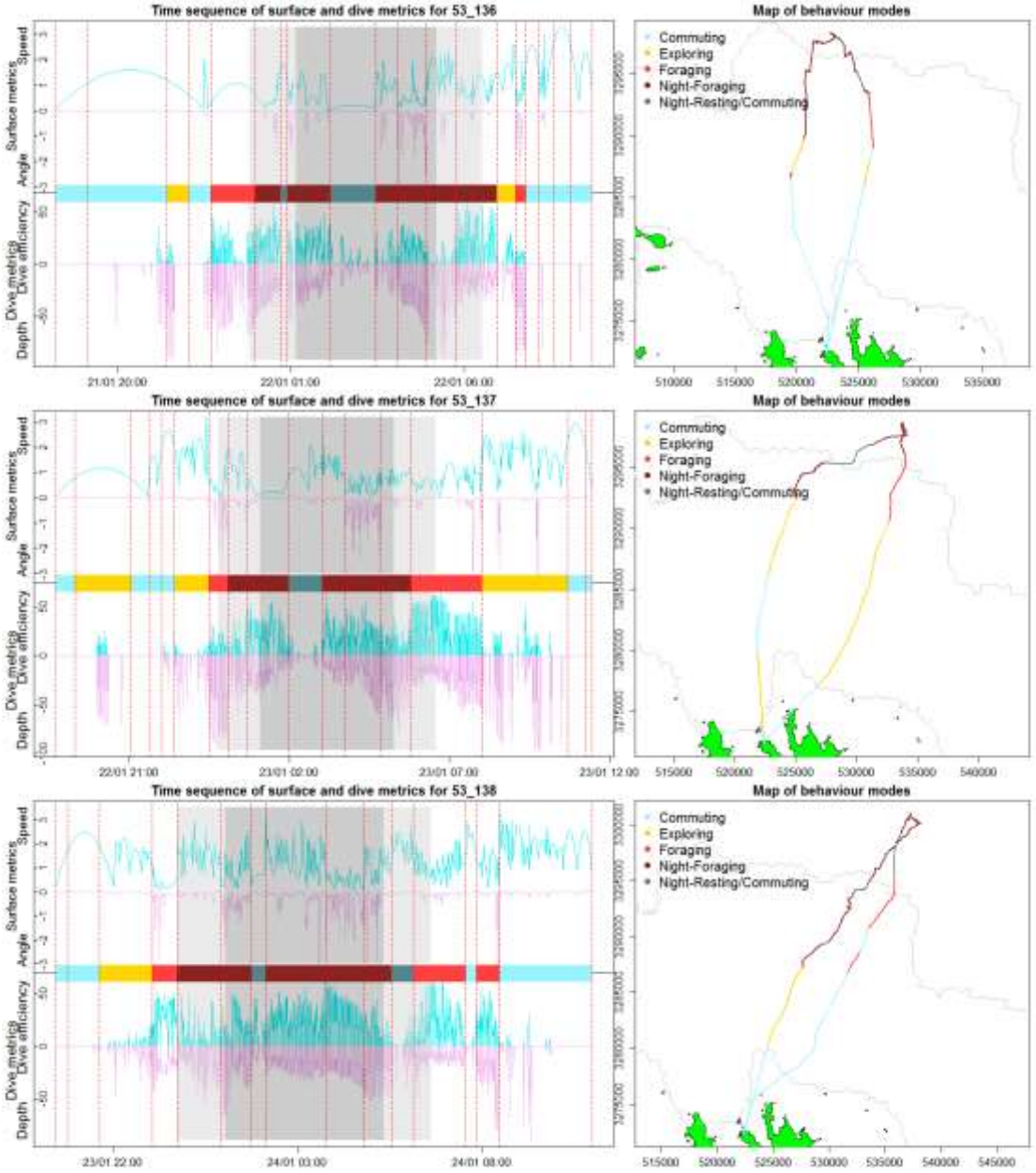

Time sequence of surface and dive metrics for 52_132
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
21/01 12:00
21/01 14:00
21/01 16:00
21/01 18:00
Map of behaviour modes
Commuting
Foraging
Resting
523000
524000
525000
526000
Time sequence of surface and dive metrics for 52_133
22/01 16:00
22/01 21:00
23/01 02:00
23/01 07:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Foraging
Night-Resting/Commuting
520000
525000
530000
535000
540000

Deployment	**53**
Site	Geddes
Season	2011-12
Stage	Brood
Bill (mm)	49.3x18
Sex	female
Weight (kg)	3.3 (-0.1)
Offspring	2

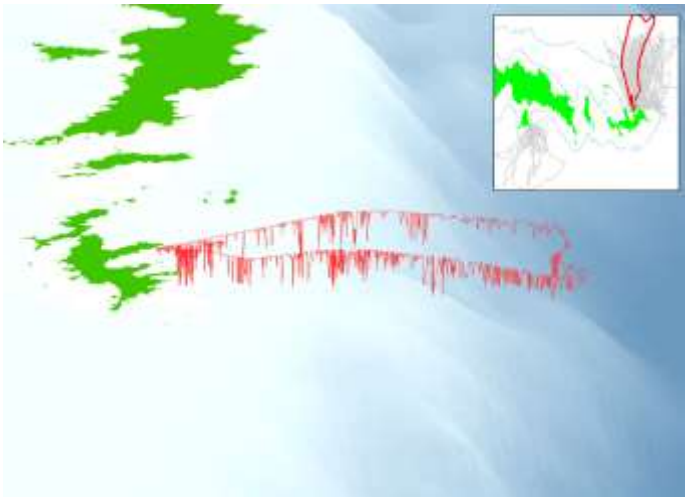


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
53_134	19-01 (12)	19-01 (19)	7.4	19.0	AC	3.1	0%	0%	1.06	68%	0.09
53_135	20-01 (14)	21-01 (09)	18.8	9.0	AC	26.4	35%	42%	0.35	55%	0.33
53_136	21-01 (18)	22-01 (09)	15.5	9.0	AC	26.0	43%	69%	0.29	45%	0.34
53_137	22-01 (18)	23-01 (11)	16.8	9.0	C	28.6	40%	65%	0.33	44%	0.35
53_138	23-01 (20)	24-01 (10)	14.5	NA	C	32.3	47%	61%	0.22	56%	0.38

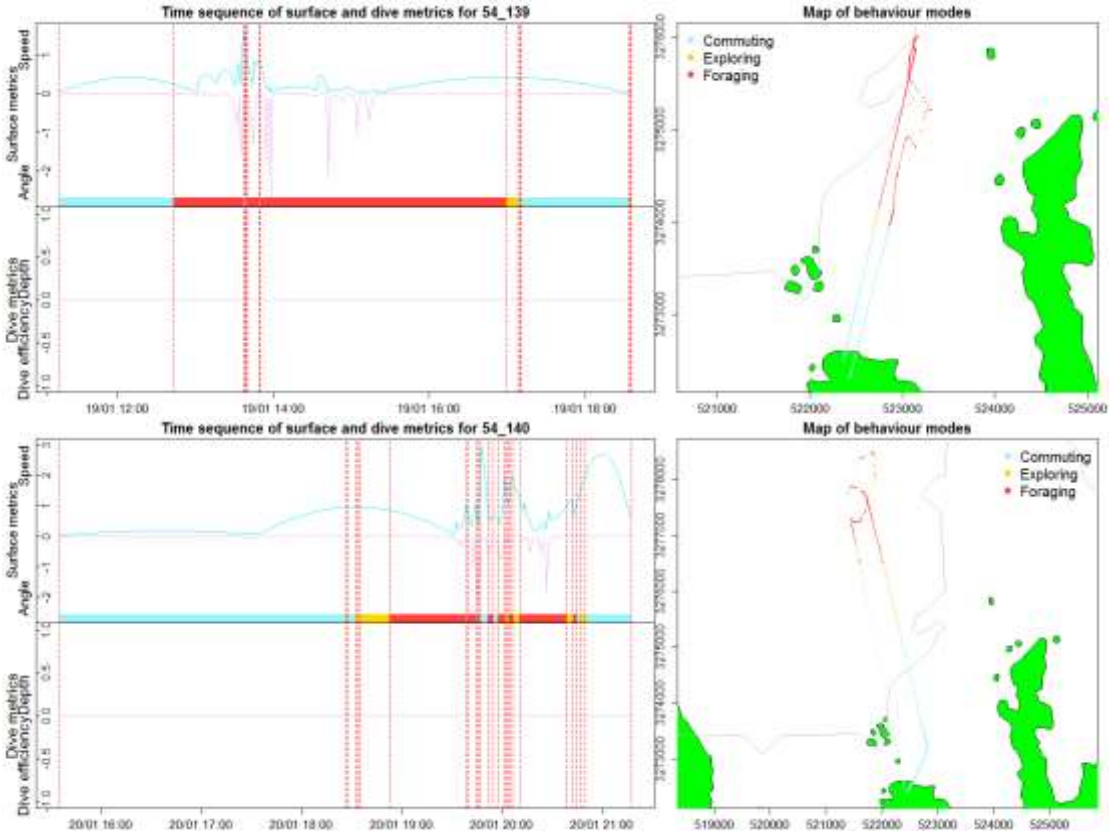


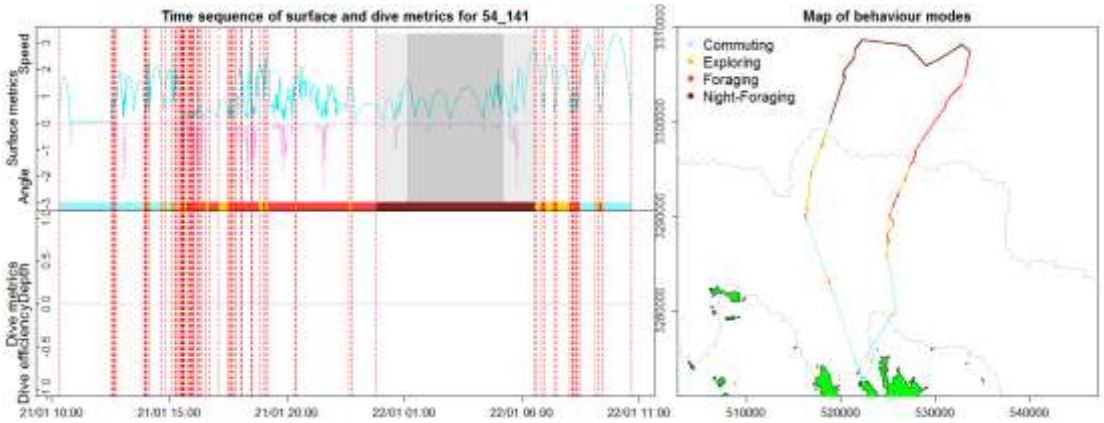

Time sequence of surface and dive metrics for 53_136
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
21/01 20:00
22/01 01:00
22/01 06:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Foraging
Night-Resting/Commuting
510000
515000
520000
525000
530000
535000
Time sequence of surface and dive metrics for 53_137
22/01 21:00
23/01 02:00
23/01 07:00
23/01 12:00
515000
520000
525000
530000
535000
540000
Time sequence of surface and dive metrics for 53_138
23/01 22:00
24/01 03:00
24/01 08:00
515000
520000
525000
530000
535000
540000
545000

Deployment	**54**
Site	Geddes
Season	2011-12
Stage	Brood
Bill (mm)	49.9x19.1
Sex	unsure
Weight (kg)	3.5 (-0.6)
Offspring	2

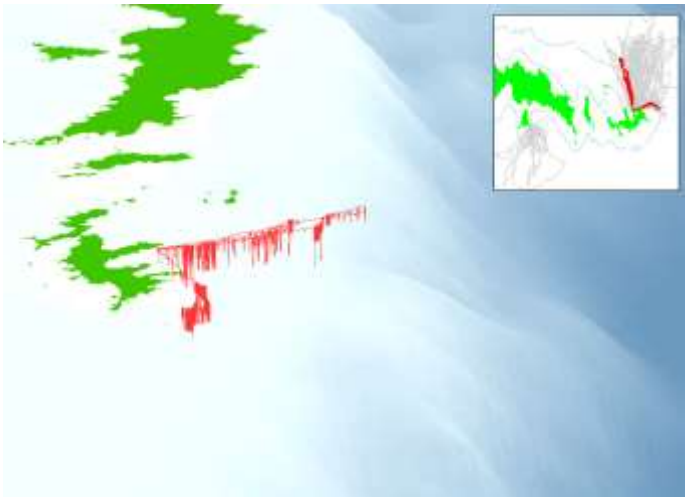


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
54_139	19-01 (11)	19-01 (18)	7.4	21.0		3.8	0%	NA	NA	57%	0.10
54_140	20-01 (15)	20-01 (21)	5.7	13.0		6.1	0%	NA	NA	26%	0.10
54_141	21-01 (10)	22-01 (10)	24.4	NA	AC	37.2	28%	NA	NA	59%	0.33

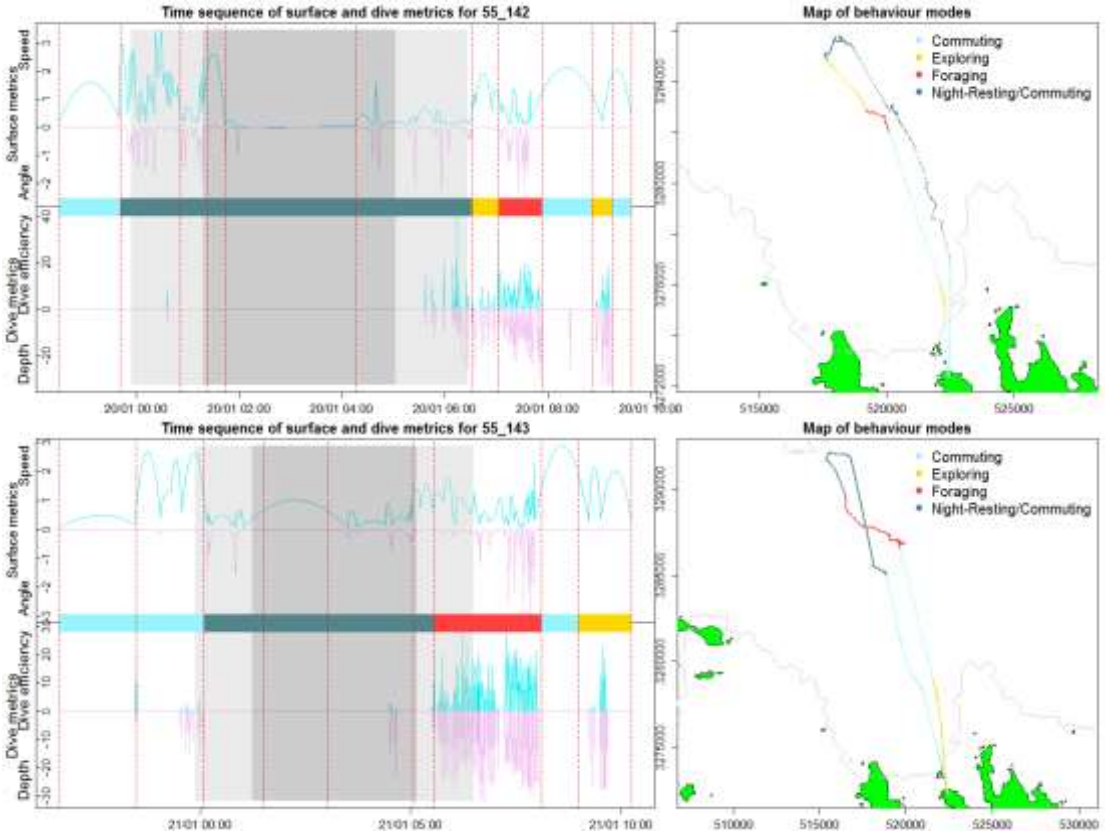


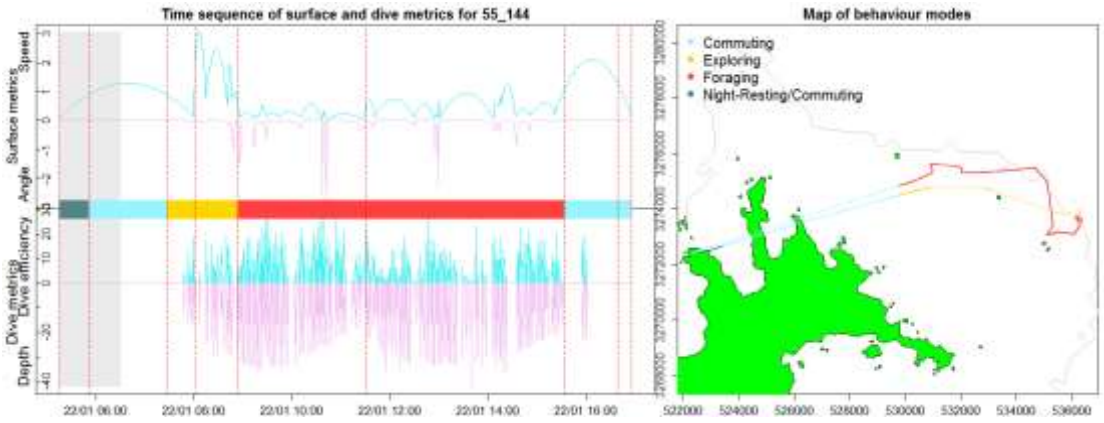

Time sequence of surface and dive metrics for 54_141
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
21/01 10:00
21/01 15:00
21/01 20:00
22/01 01:00
22/01 06:00
22/01 11:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Foraging
510000
520000
530000
540000

Deployment	**55**
Site	Geddes
Season	2011-12
Stage	Brood
Bill (mm)	44.2x17.3
Sex	female
Weight (kg)	3.2 (-0.2)
Offspring	1



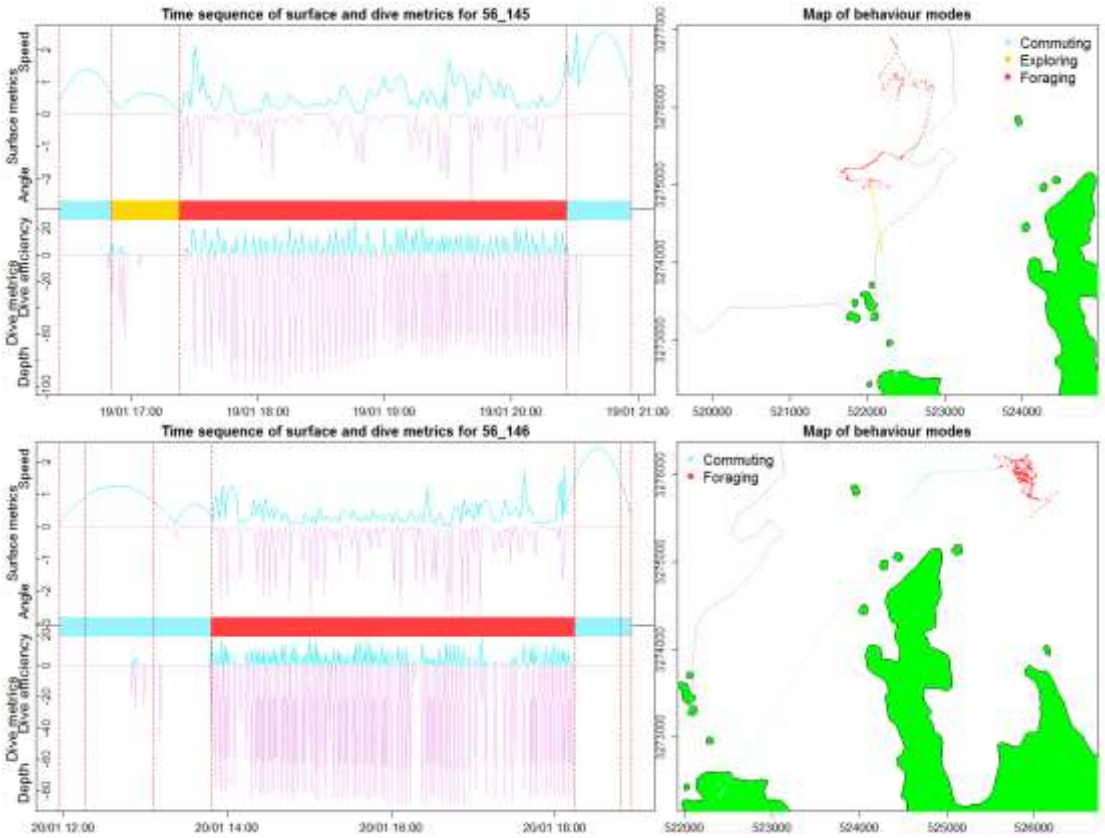
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
55_142	19-01 (22)	20-01 (09)	11.1	11.0	AC	14.1	59%	26%	0.04	7%	0.16
55_143	20-01 (20)	21-01 (10)	13.6	19.0	C	21.0	49%	34%	0.06	19%	0.21
55_144	22-01 (05)	22-01 (16)	11.7	NA		14.0	11%	0%	0.20	57%	0.24

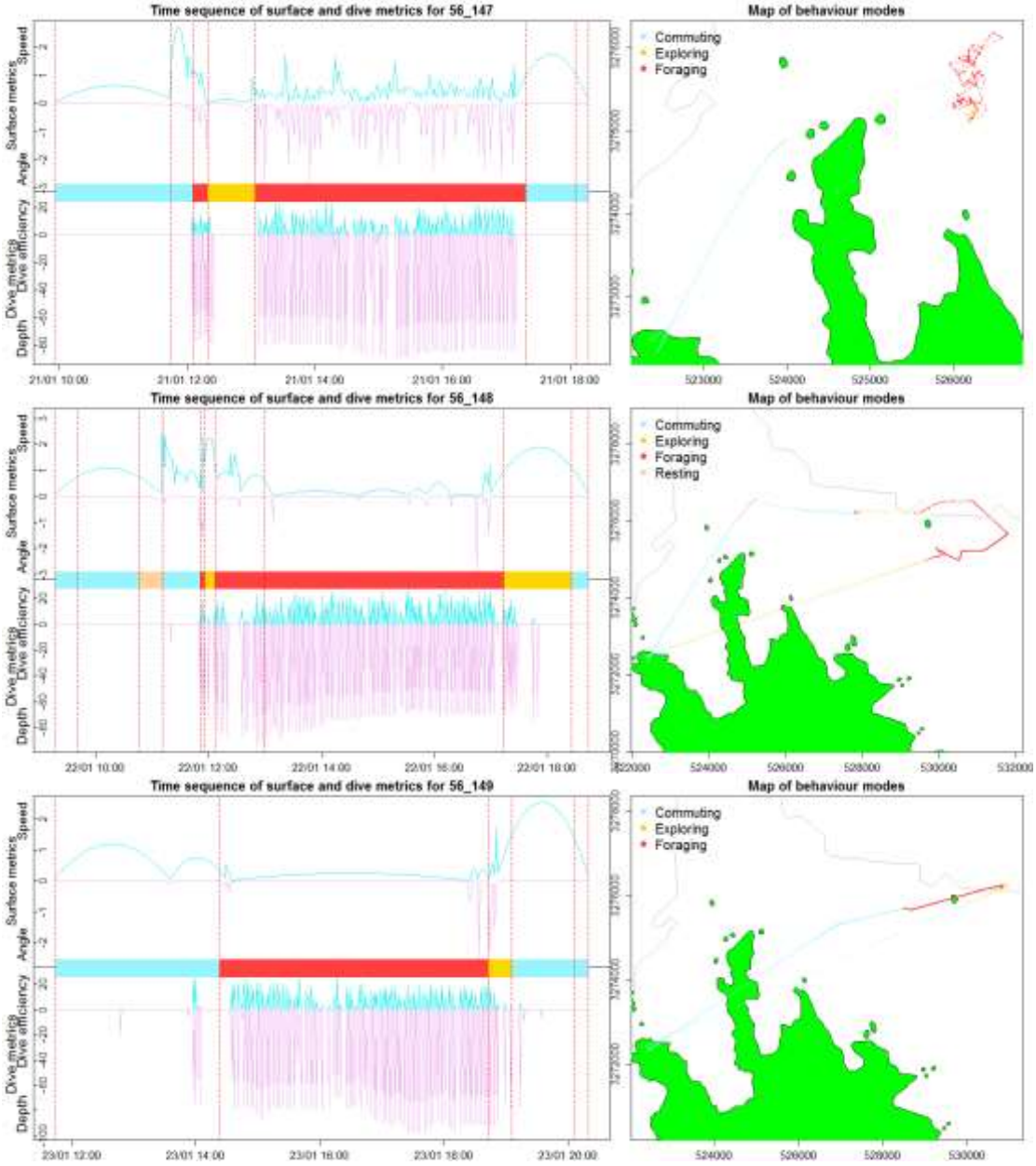



Time sequence of surface and dive metrics for 55_144
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
22/01 06:00
22/01 08:00
22/01 10:00
22/01 12:00
22/01 14:00
22/01 16:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Resting/Commuting
522000
524000
526000
528000
530000
532000
534000
536000

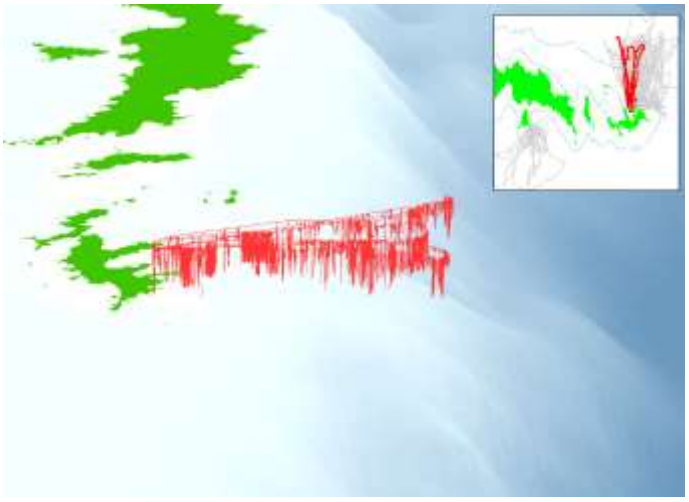
Deployment	**56**
Site	Geddes
Season	2011-12
Stage	Brood
Bill (mm)	43.1x17.2
Sex	female
Weight (kg)	2.65 (0.1)
Offspring	2

Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
56_145	19-01 (16)	19-01 (20)	4.5	15.0		4.4	0%	0%	0.85	67%	0.13
56_146	20-01 (11)	20-01 (18)	7.0	15.0	C	5.3	0%	0%	0.83	63%	0.08
56_147	21-01 (09)	21-01 (18)	8.4	15.0		5.6	0%	0%	0.71	53%	0.10
56_148	22-01 (09)	22-01 (18)	9.5	17.0	C	9.9	0%	0%	0.66	55%	0.15
56_149	23-01 (11)	23-01 (20)	8.6	NA		9.4	0%	0%	0.73	50%	0.17

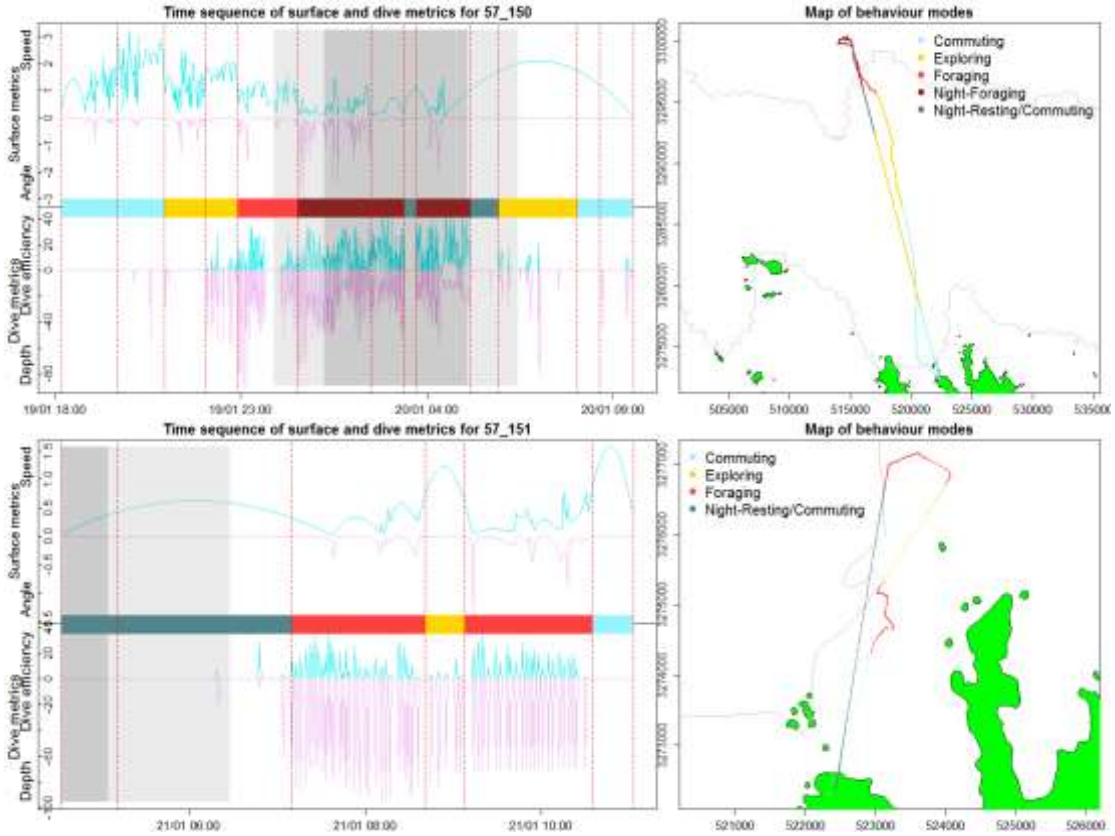


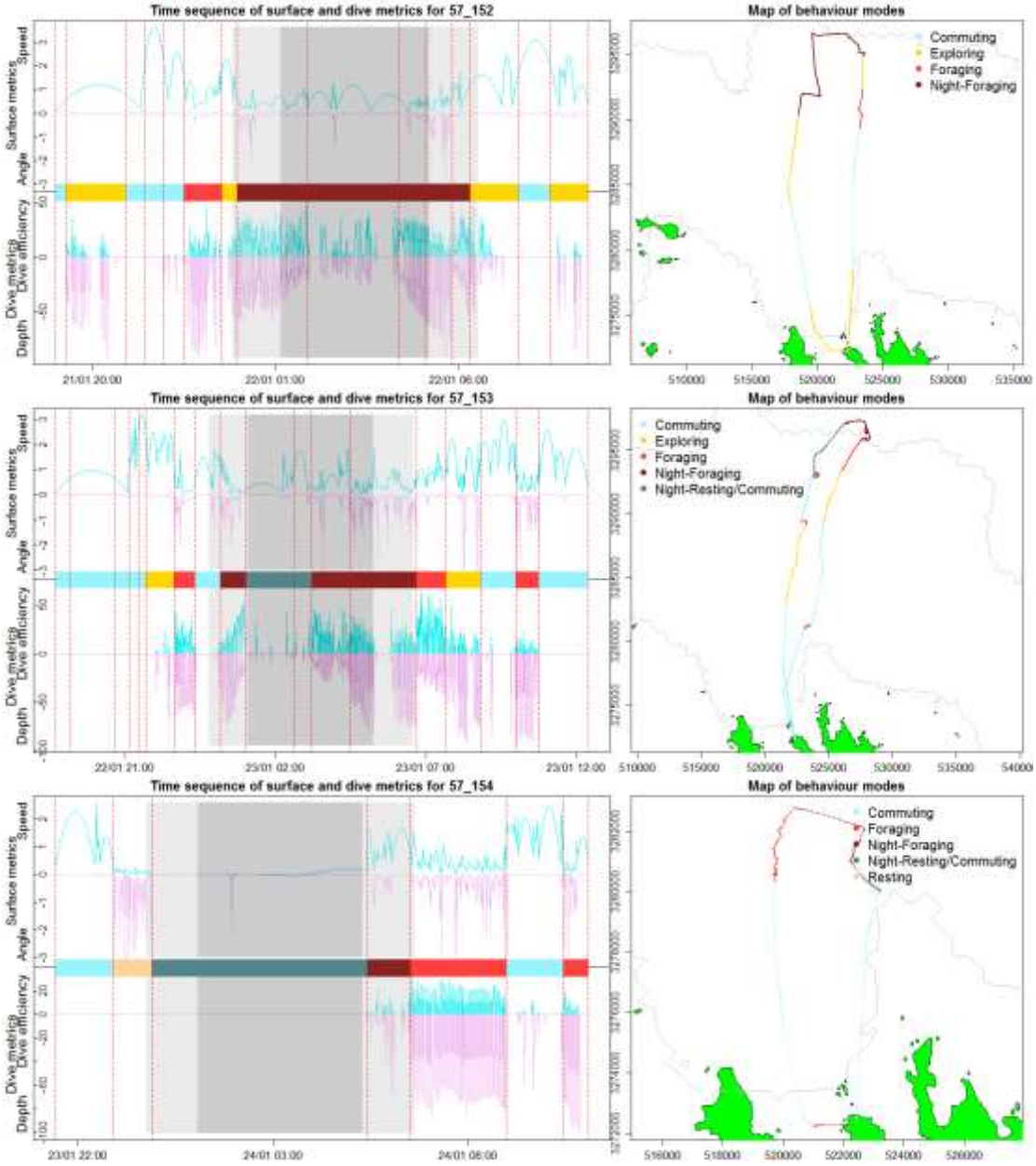

Time sequence of surface and dive metrics for 56_147
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
21/01 10:00
21/01 12:00
21/01 14:00
21/01 16:00
21/01 18:00
Map of behaviour modes
Commuting
Exploring
Foraging
523000
524000
525000
526000
Time sequence of surface and dive metrics for 56_148
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
22/01 10:00
22/01 12:00
22/01 14:00
22/01 16:00
22/01 18:00
Map of behaviour modes
Commuting
Exploring
Foraging
Resting
522000
524000
526000
528000
530000
532000
Time sequence of surface and dive metrics for 56_149
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
23/01 12:00
23/01 14:00
23/01 16:00
23/01 18:00
23/01 20:00
Map of behaviour modes
Commuting
Exploring
Foraging
524000
526000
528000
530000

Deployment	**57**
Site	Geddes
Season	2011-12
Stage	Brood
Bill (mm)	44.3x18.1
Sex	female
Weight (kg)	2.8 (0.1)
Offspring	2

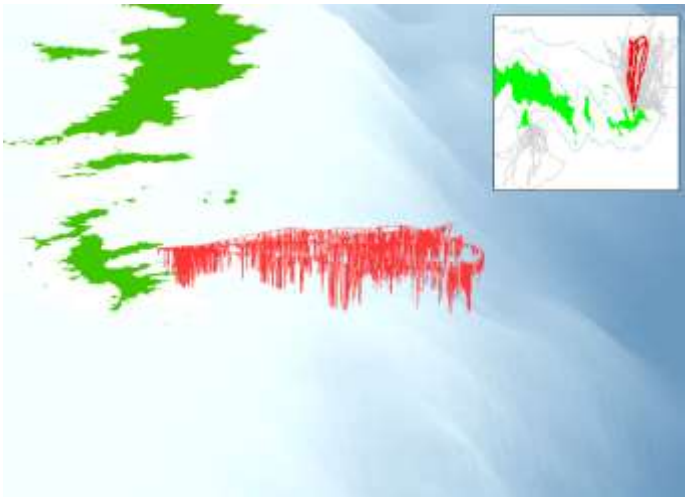


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
57_150	19-01 (18)	20-01 (09)	15.4	19.0		29.1	43%	81%	0.19	39%	0.36
57_151	21-01 (04)	21-01 (11)	6.5	7.9	C	5.0	29%	3%	0.82	46%	0.11
57_152	21-01 (18)	22-01 (09)	14.6	9.1	AC	24.5	46%	75%	0.31	51%	0.32
57_153	22-01 (18)	23-01 (12)	17.7	9.0	C	25.5	38%	55%	0.32	38%	0.33
57_154	23-01 (21)	24-01 (11)	13.7	NA	AC	10.6	50%	20%	0.39	31%	0.21

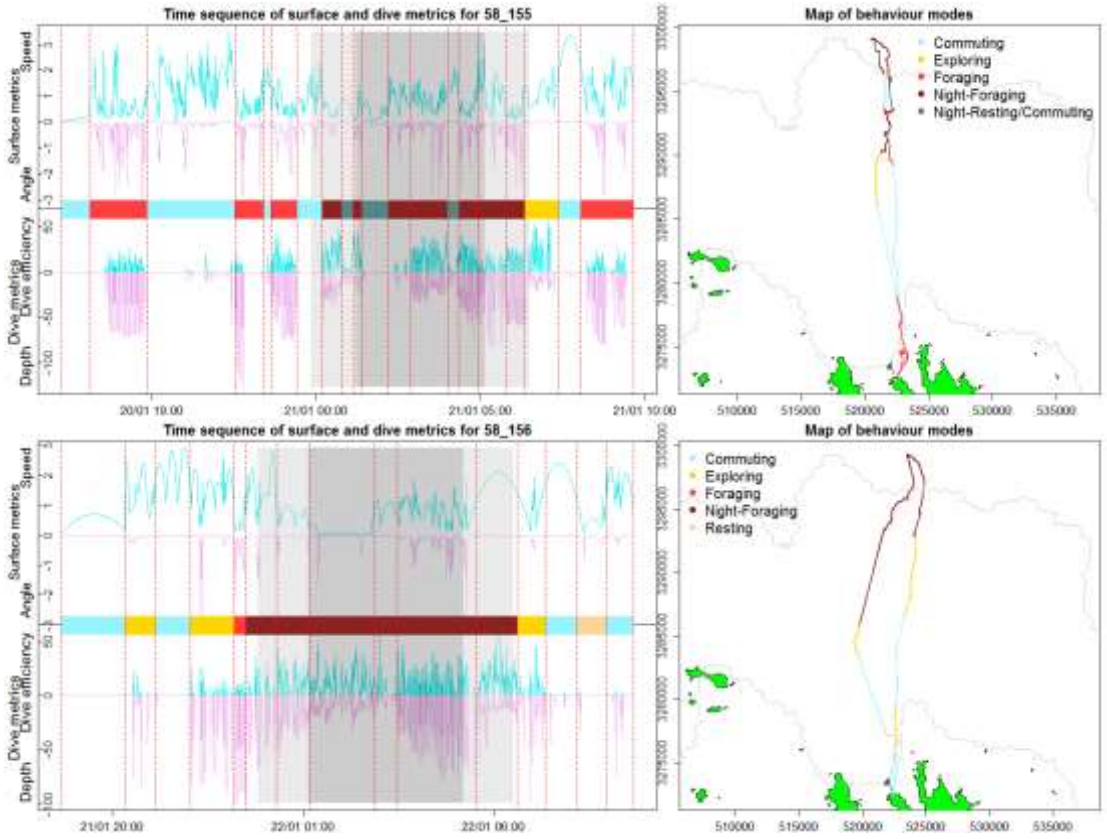


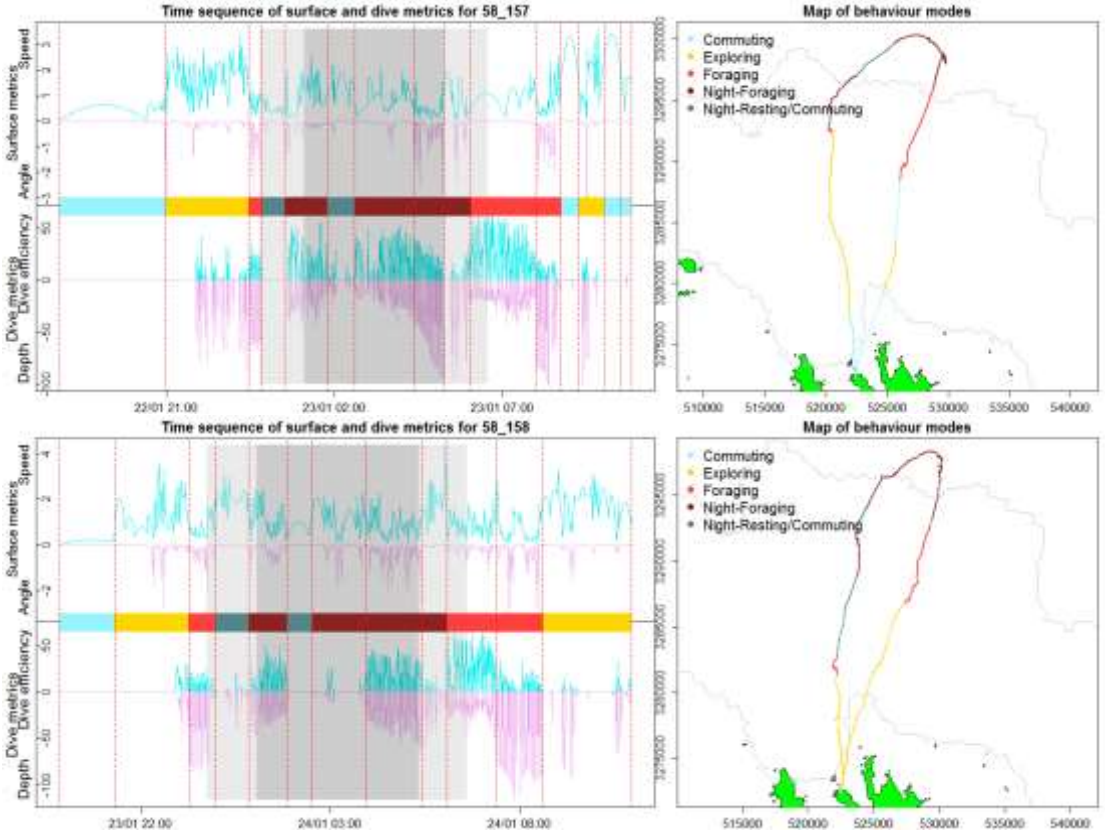

Time sequence of surface and dive metrics for 57_152
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
21/01 20:00
22/01 01:00
22/01 06:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Foraging
Time sequence of surface and dive metrics for 57_153
22/01 21:00
23/01 02:00
23/01 07:00
23/01 12:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Foraging
Night-Resting/Commuting
Time sequence of surface and dive metrics for 57_154
23/01 22:00
24/01 03:00
24/01 08:00
Map of behaviour modes
Commuting
Foraging
Night-Foraging
Night-Resting/Commuting
Resting

Deployment	**58**
Site	Geddes
Season	2011-12
Stage	Brood
Bill (mm)	45.5x19.6
Sex	unsure
Weight (kg)	3.2 (0)
Offspring	2

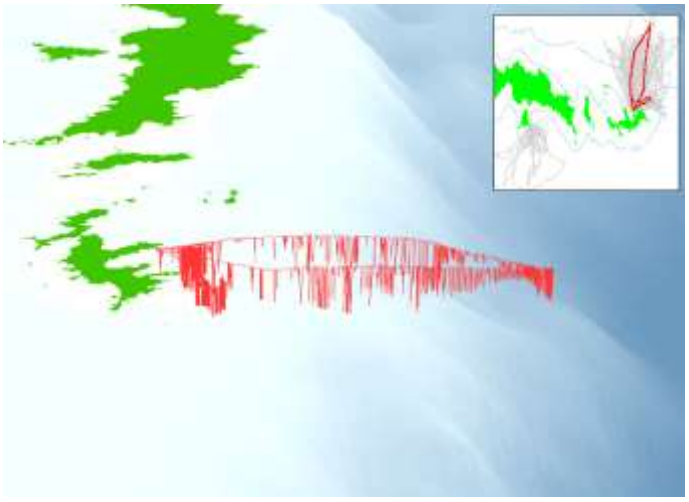


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
58_155	20-01 (16)	21-01 (09)	17.4	9.0		26.9	38%	60%	0.31	55%	0.32
58_156	21-01 (18)	22-01 (09)	15.0	8.1	AC	26.9	45%	77%	0.26	50%	0.32
58_157	22-01 (17)	23-01 (10)	17.0	9.0	C	28.5	40%	60%	0.28	46%	0.35
58_158	23-01 (19)	24-01 (10)	15.1	NA	C	27.0	45%	56%	0.28	51%	0.31

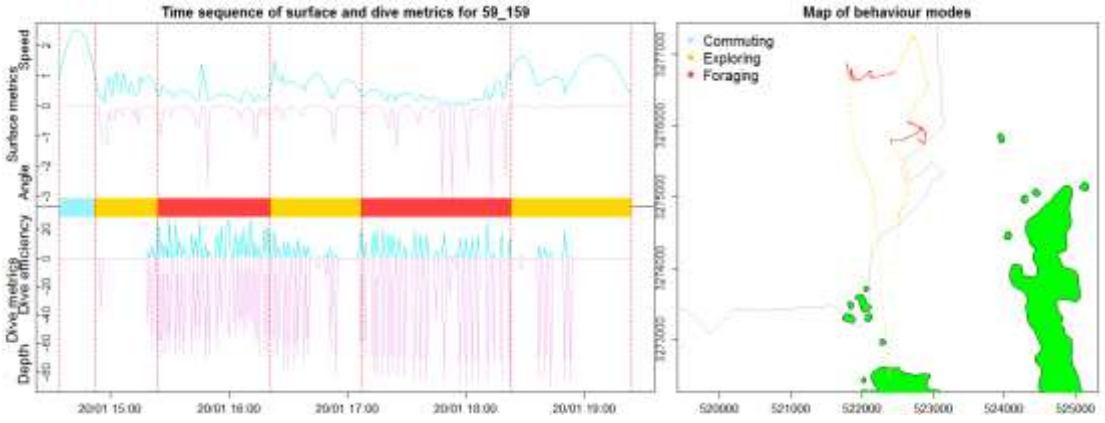


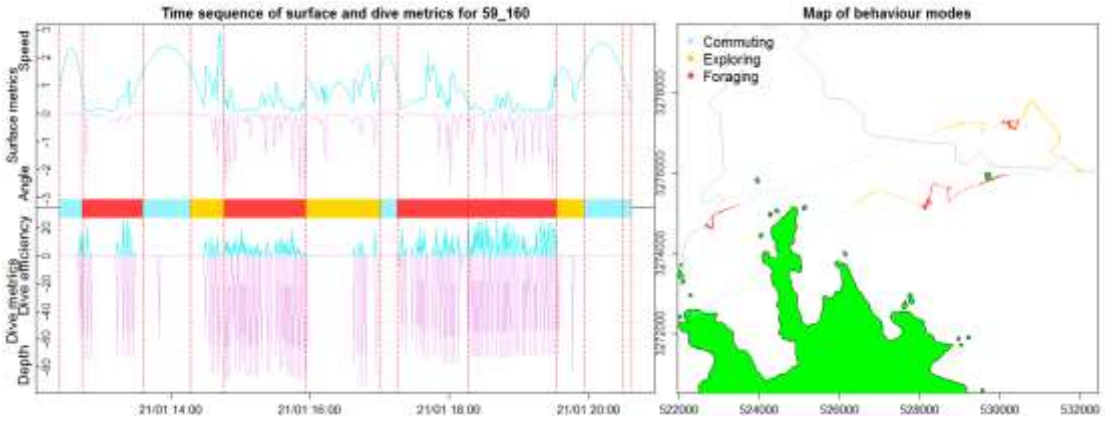

Time sequence of surface and dive metrics for 58_157
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
23/01 21:00
23/01 02:00
23/01 07:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Foraging
Night-Resting/Commuting
510000
515000
520000
525000
530000
535000
540000
Time sequence of surface and dive metrics for 58_158
23/01 22:00
24/01 03:00
24/01 08:00
Map of behaviour modes

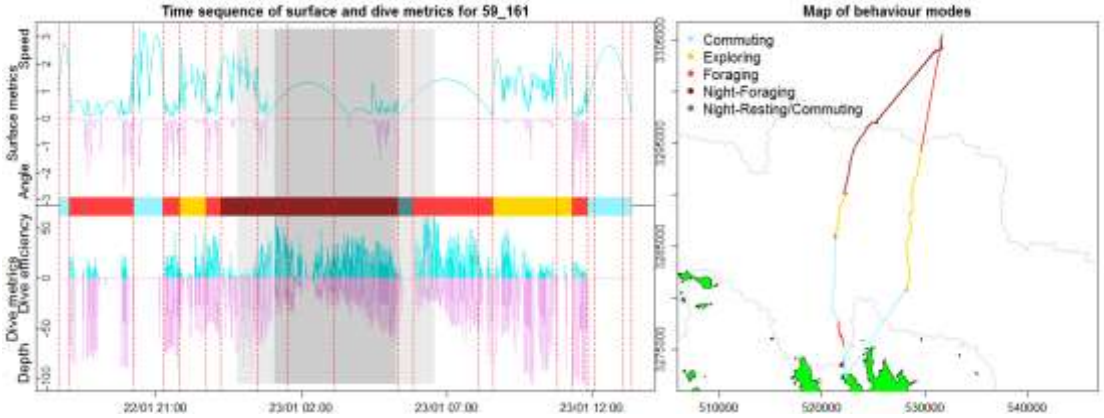
Deployment	**59**
Site	Geddes
Season	2011-12
Stage	Brood
Bill (mm)	49.2x18.7
Sex	female
Weight (kg)	3 (0.6)
Offspring	2



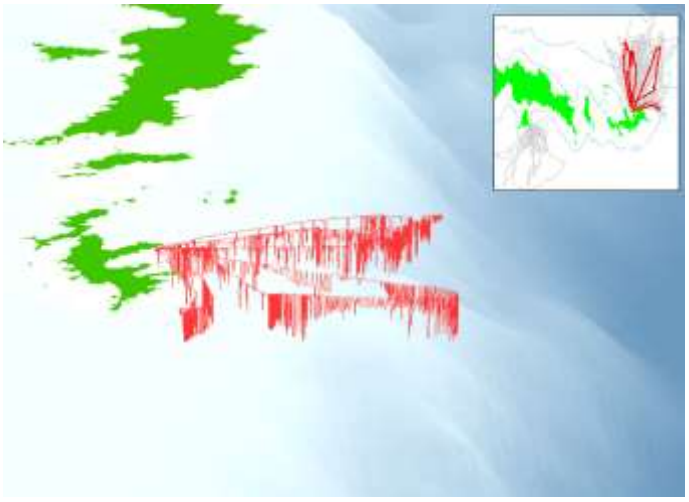
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
59_159	20-01 (14)	20-01 (19)	4.8	17.0	AC	4.8	0%	0%	0.73	46%	0.13
59_160	21-01 (12)	21-01 (20)	8.2	21.1	C	10.3	0%	0%	0.51	52%	0.19
59_161	22-01 (17)	23-01 (13)	19.7	NA	C	34.3	35%	49%	0.39	64%	0.35



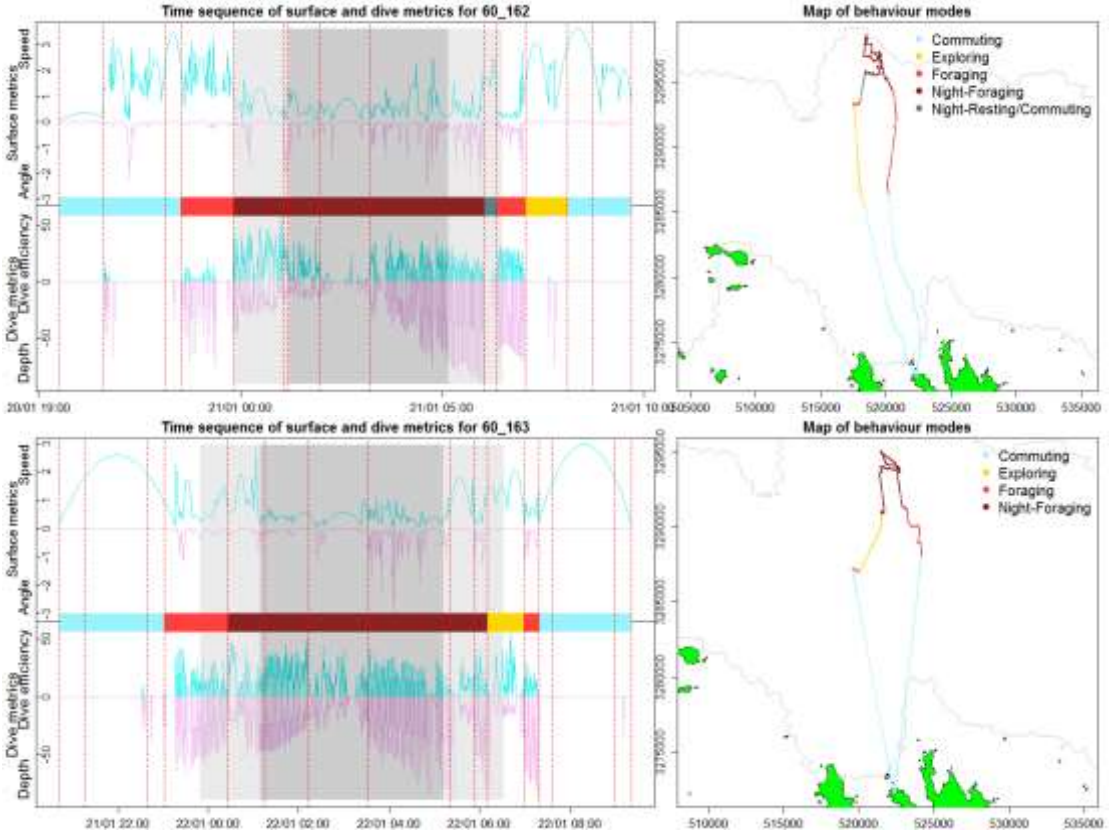


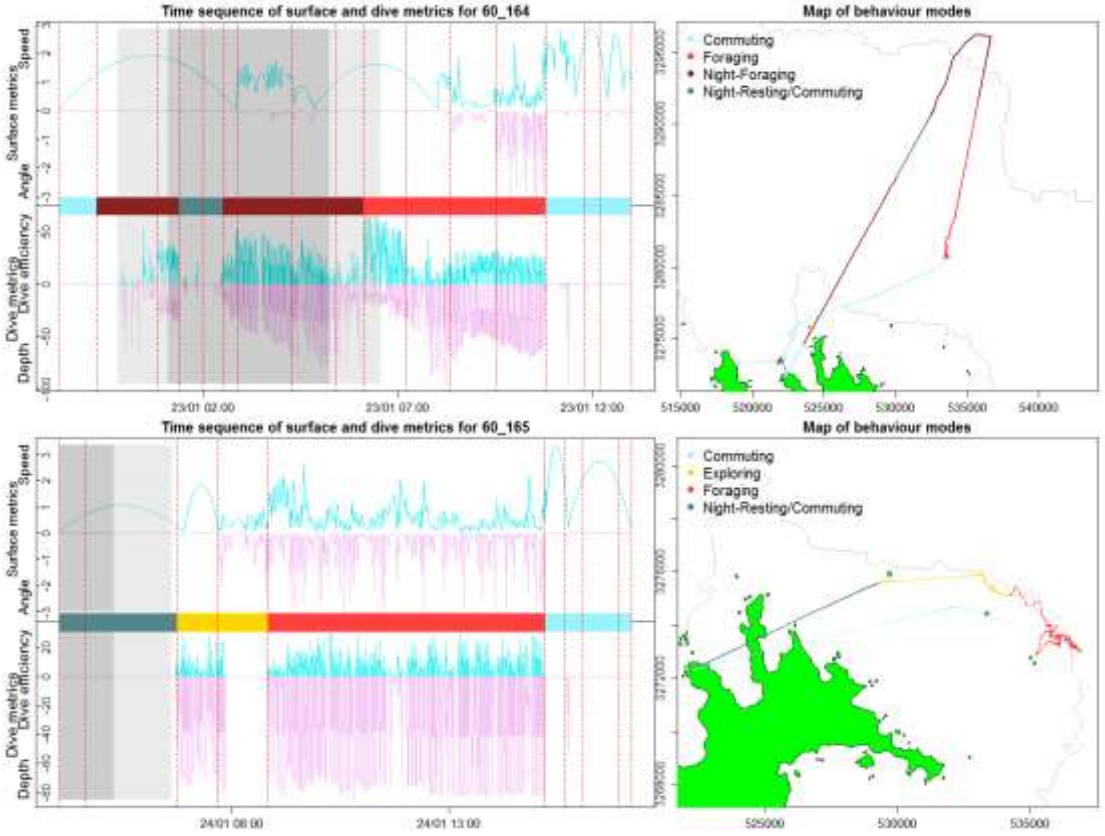

Time sequence of surface and dive metrics for 59_161
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
22/01 21:00
23/01 02:00
23/01 07:00
23/01 12:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Foraging
Night-Resting/Commuting
510000
520000
530000
540000

Deployment	**60**
Site	Geddes
Season	2011-12
Stage	Brood
Bill (mm)	49.9x19.3
Sex	male
Weight (kg)	3.2 (0.2)
Offspring	2

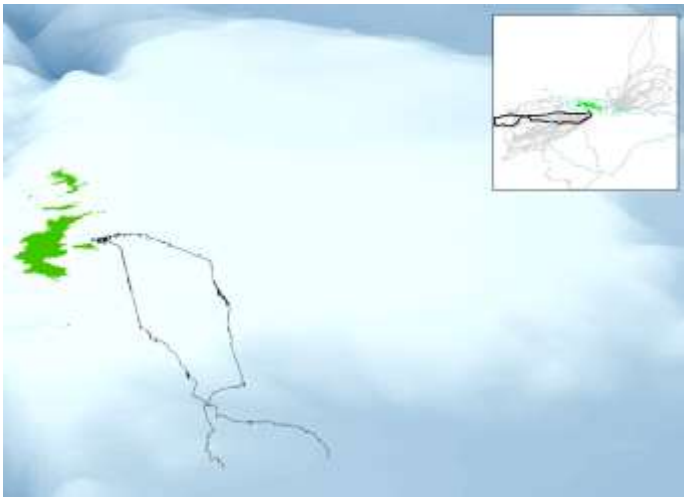


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
60_162	20-01 (19)	21-01 (09)	14.2	11.0	AC	26.5	47%	84%	0.25	59%	0.37
60_163	21-01 (20)	22-01 (09)	12.7	12.9	AC	22.7	53%	82%	0.33	59%	0.30
60_164	22-01 (22)	23-01 (13)	14.7	15.0	C	27.6	46%	55%	0.35	71%	0.31
60_165	24-01 (04)	24-01 (17)	13.2	NA	C	14.5	20%	0%	0.48	48%	0.26

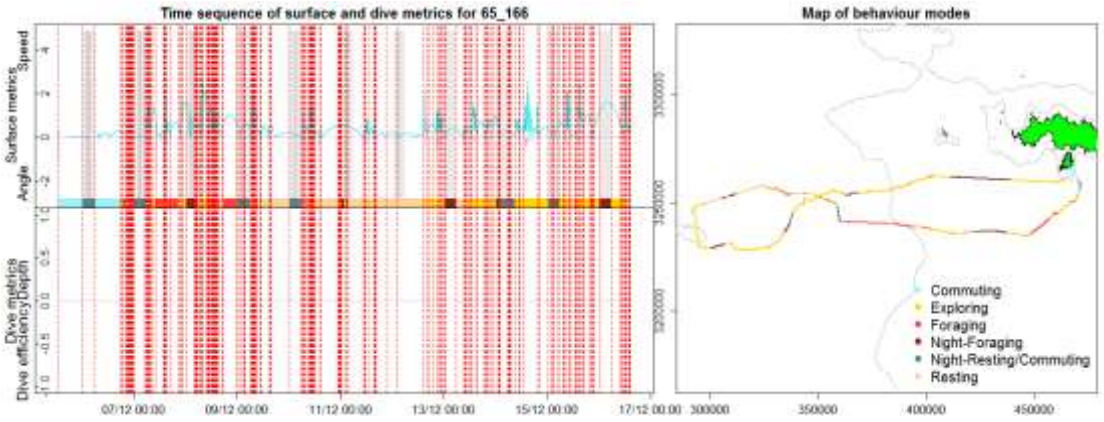



Time sequence of surface and dive metrics for 60_164
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
23/01 02:00
23/01 07:00
23/01 12:00
Map of behaviour modes
Commuting
Foraging
Night-Foraging
Night-Resting/Commuting
515000
520000
525000
530000
535000
540000
Time sequence of surface and dive metrics for 60_165
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
24/01 08:00
24/01 13:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Resting/Commuting
525000
530000
535000

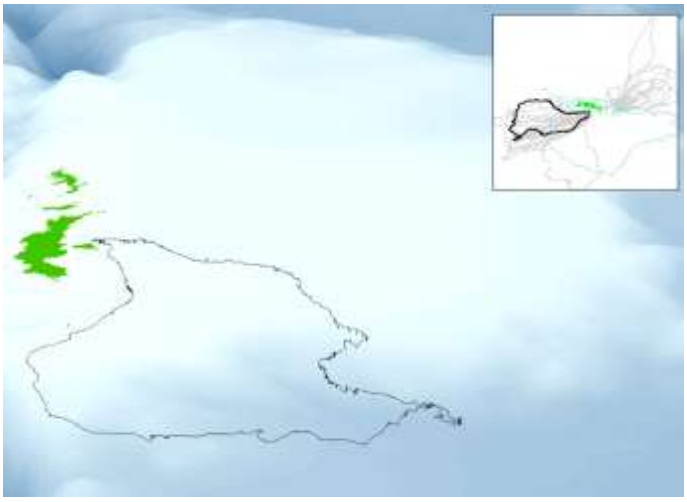
Deployment	**65**
Site	Gourlay
Season	2013-14
Stage	Incubation
Bill (mm)	59.6x19.4
Sex	male
Weight (kg)	3.7 (NA)
Offspring	1



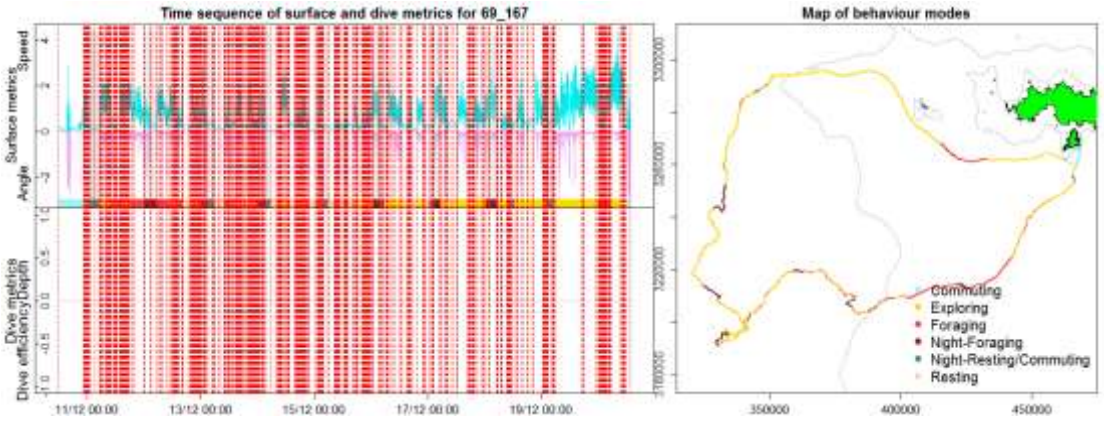
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
65_166	05-12 (12)	16-12 (14)	266.2	NA	C	177.4	22%	NA	NA	20%	0.19



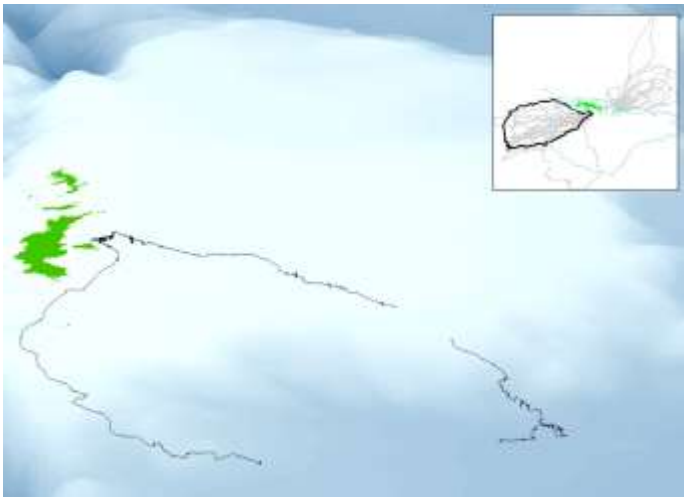
Deployment	**69**
Site	Gourlay
Season	2013-14
Stage	Incubation
Bill (mm)	51.7x18.8
Sex	unsure
Weight (kg)	3.75 (NA)
Offspring	1



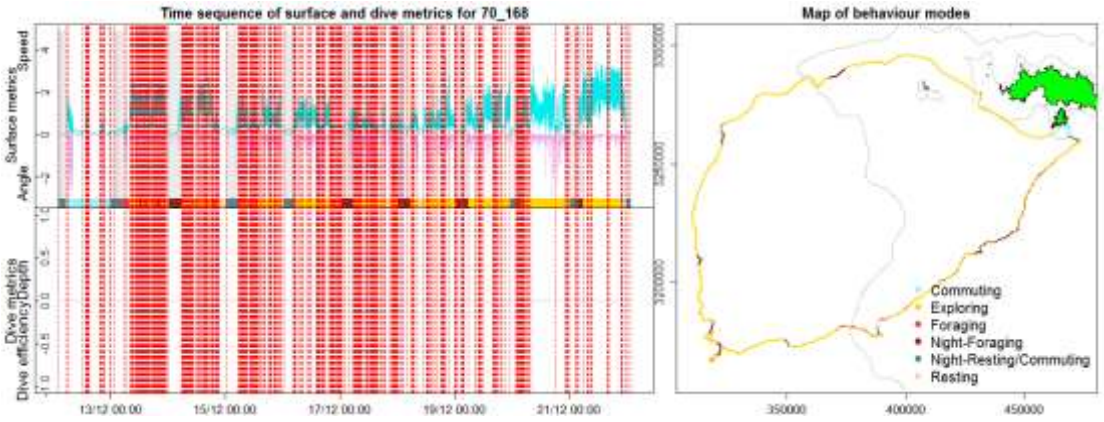
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
69_167	10-12 (11)	20-12 (13)	242.2	NA	C	157.8	21%	NA	NA	32%	0.19



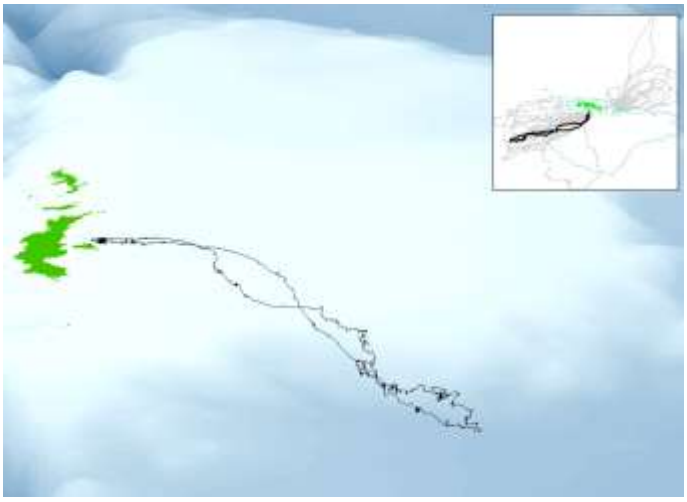
Deployment	**70**
Site	Gourlay
Season	2013-14
Stage	Incubation
Bill (mm)	51.4x18.1
Sex	female
Weight (kg)	3.7 (NA)
Offspring	1



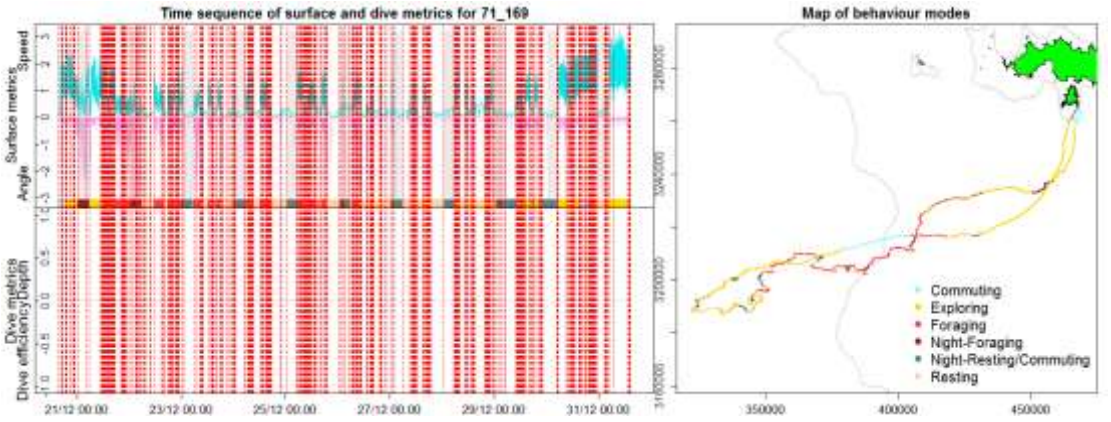
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
70_168	12-12 (02)	22-12 (01)	239.8	NA	C	181.2	21%	NA	NA	21%	0.17



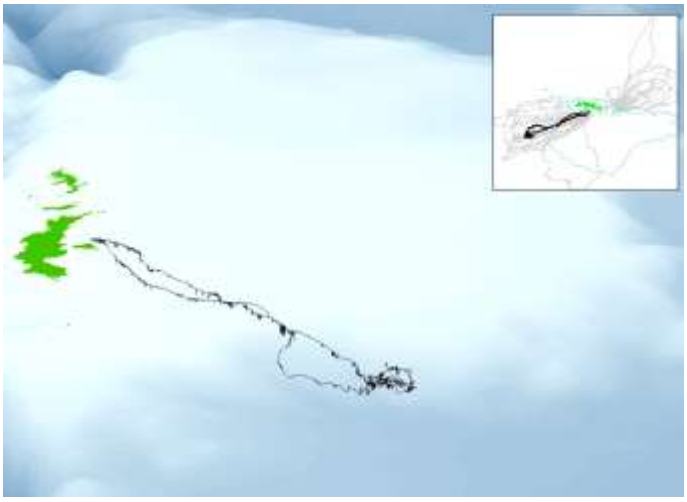
Deployment	**71**
Site	Gourlay
Season	2013-14
Stage	Incubation
Bill (mm)	48.6x18.1
Sex	female
Weight (kg)	3.15 (NA)
Offspring	2



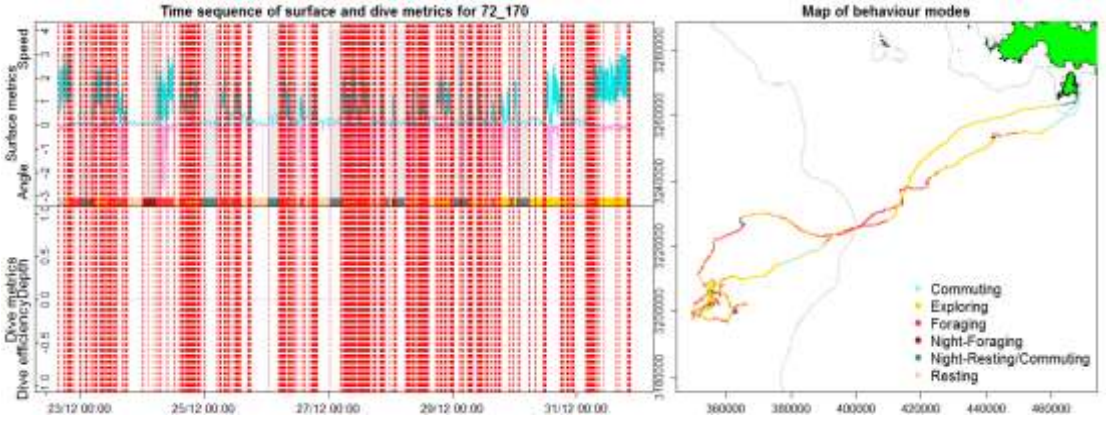
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
71_169	20-12 (15)	31-12 (14)	263.3	NA	C	165.8	21%	NA	NA	28%	0.21



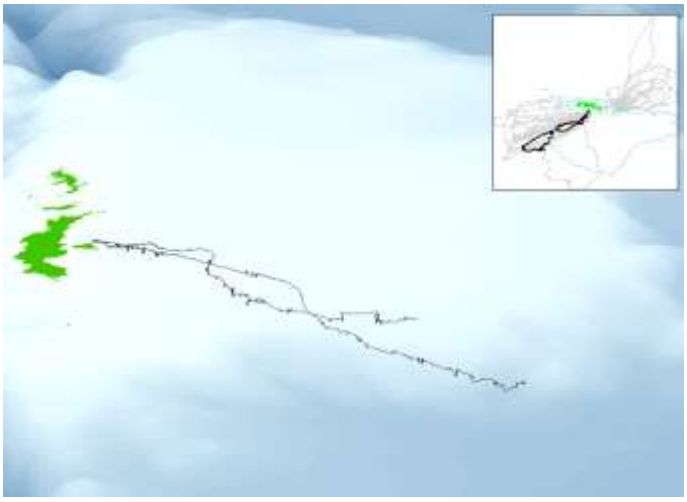
Deployment	**72**
Site	Gourlay
Season	2013-14
Stage	Incubation
Bill (mm)	52.5x20.3
Sex	male
Weight (kg)	3.15 (NA)
Offspring	1



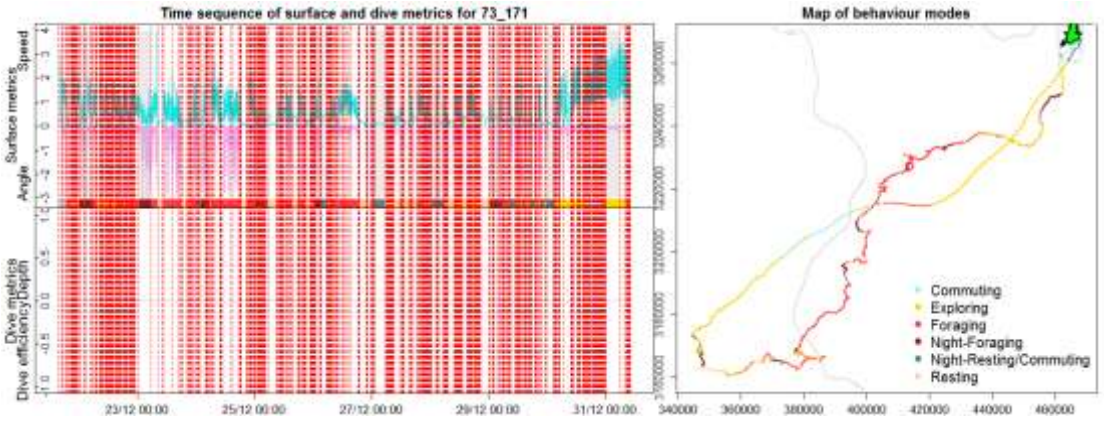
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
72_170	22-12 (15)	31-12 (20)	221.1	NA	C	137.5	21%	NA	NA	30%	0.22



Deployment	**73**
Site	Gourlay
Season	2013-14
Stage	Incubation
Bill (mm)	48.5x20.3
Sex	male
Weight (kg)	4.1 (NA)
Offspring	1

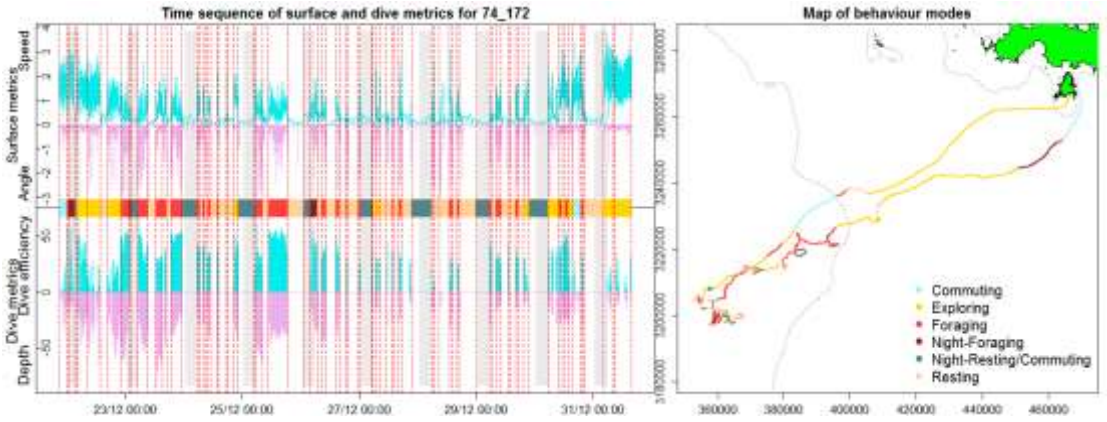


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
73_171	21-12 (15)	31-12 (10)	234.9	NA	C	158.8	22%	NA	NA	43%	0.19



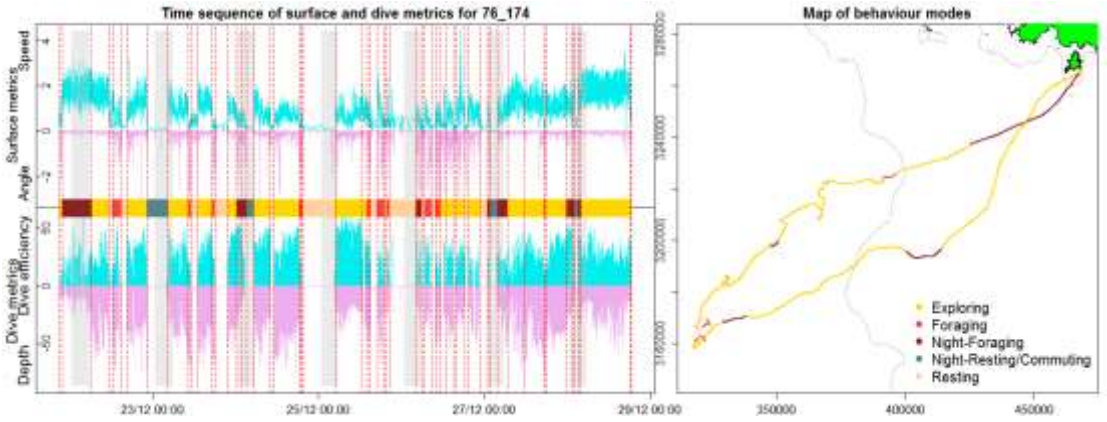
Deployment	**74**
Site	Gourlay
Season	2013-14
Stage	Incubation
Bill (mm)	47.8x17.5
Sex	female
Weight (kg)	3.1 (NA)
Offspring	1

Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
74_172	21-12 (20)	31-12 (15)	234.9	NA	C	131.6	22%	14%	0.21	23%	0.24

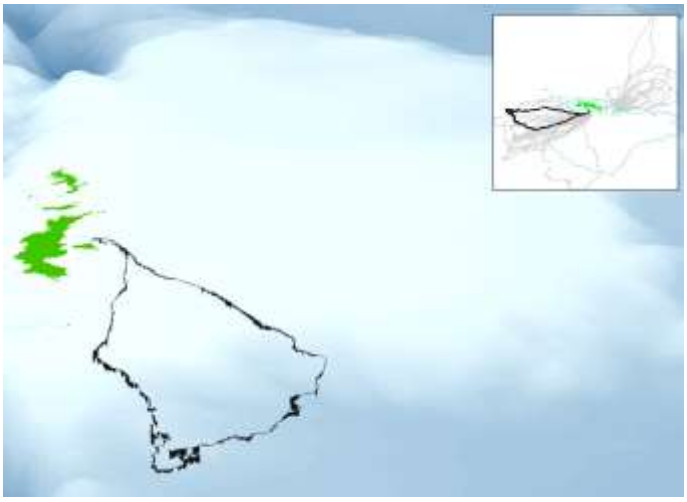


Deployment	**76**
Site	Gourlay
Season	2013-14
Stage	Incubation
Bill (mm)	45.1x18.6
Sex	female
Weight (kg)	3.35 (NA)
Offspring	1

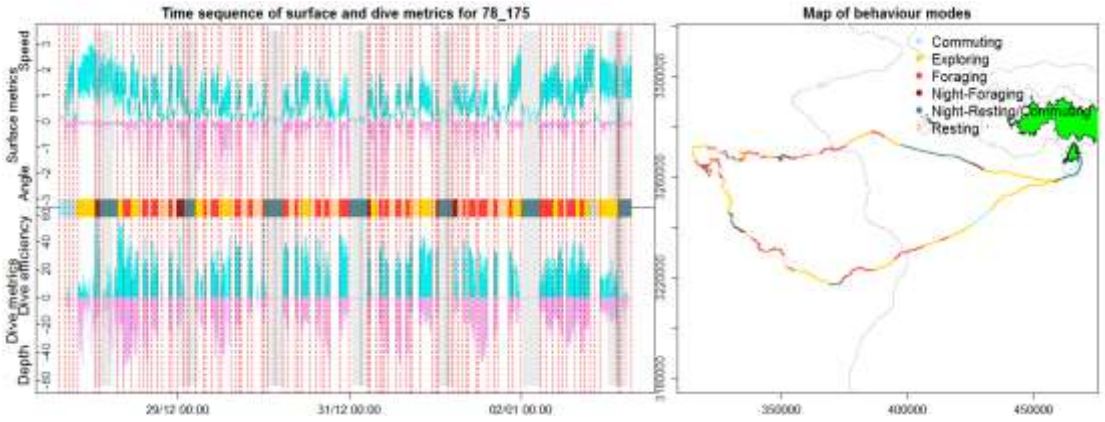
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
76_174	21-12 (20)	28-12 (18)	165.8	NA	C	185.9	21%	16%	0.29	20%	0.19



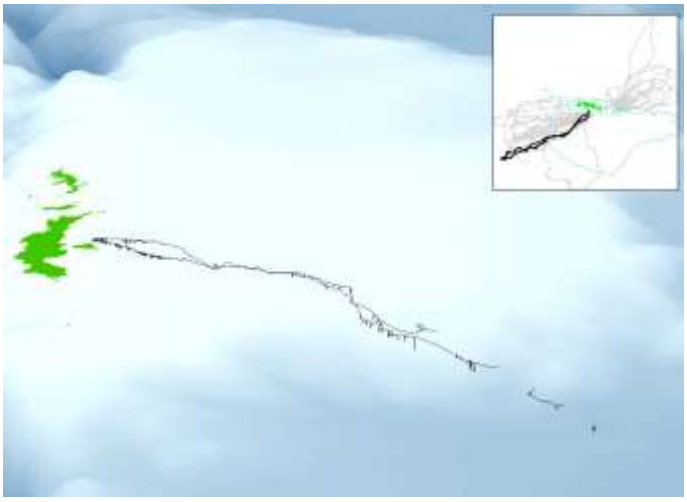
Deployment	**78**
Site	Gourlay
Season	2013-14
Stage	Incubation
Bill (mm)	54x18.3
Sex	unsure
Weight (kg)	3.65 (NA)
Offspring	2



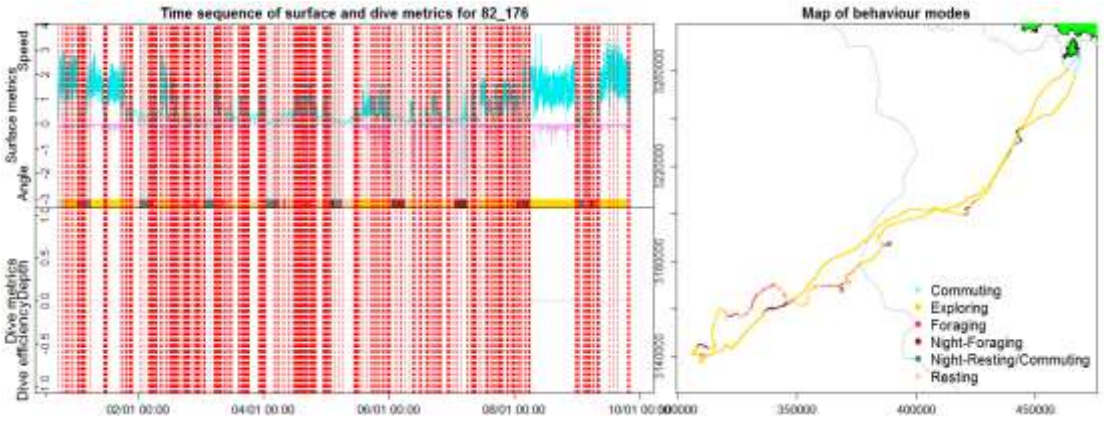
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
78_175	27-12 (14)	03-01 (07)	160.2	NA	AC	152.8	23%	12%	0.15	29%	0.19



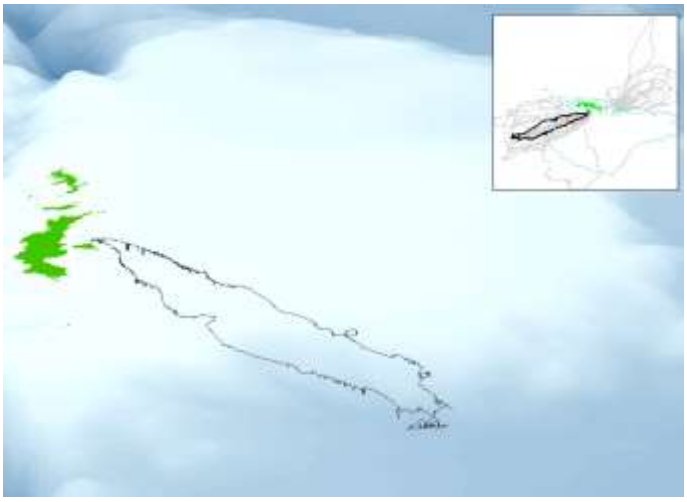
Deployment	**82**
Site	Gourlay
Season	2013-14
Stage	Incubation
Bill (mm)	43.47x17.2
Sex	female
Weight (kg)	3.15 (NA)
Offspring	1



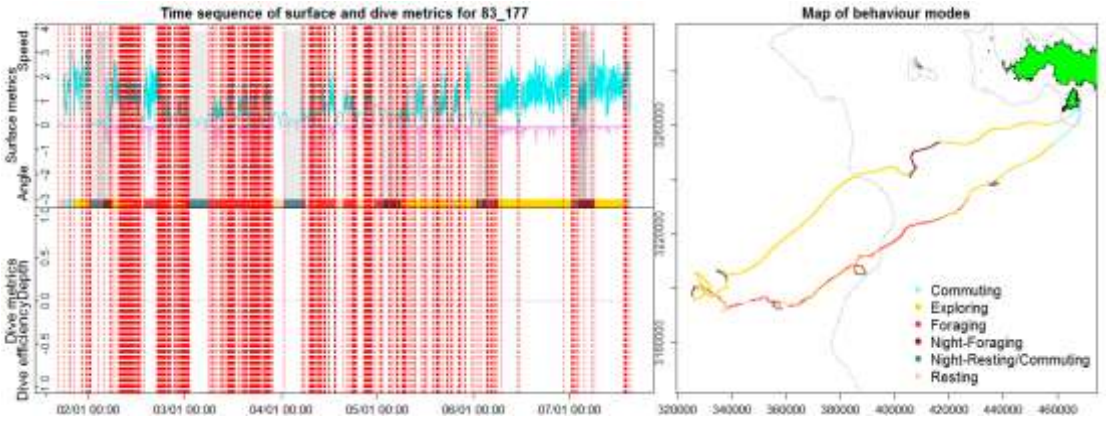
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
82_176	31-12 (17)	09-01 (20)	219.0	NA		205.5	22%	NA	NA	20%	0.18



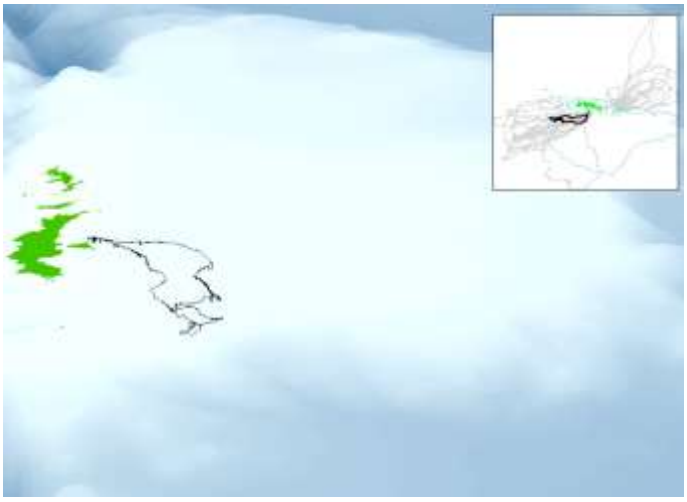
Deployment	**83**
Site	Gourlay
Season	2013-14
Stage	Incubation
Bill (mm)	48.1x18
Sex	female
Weight (kg)	3.95 (NA)
Offspring	1



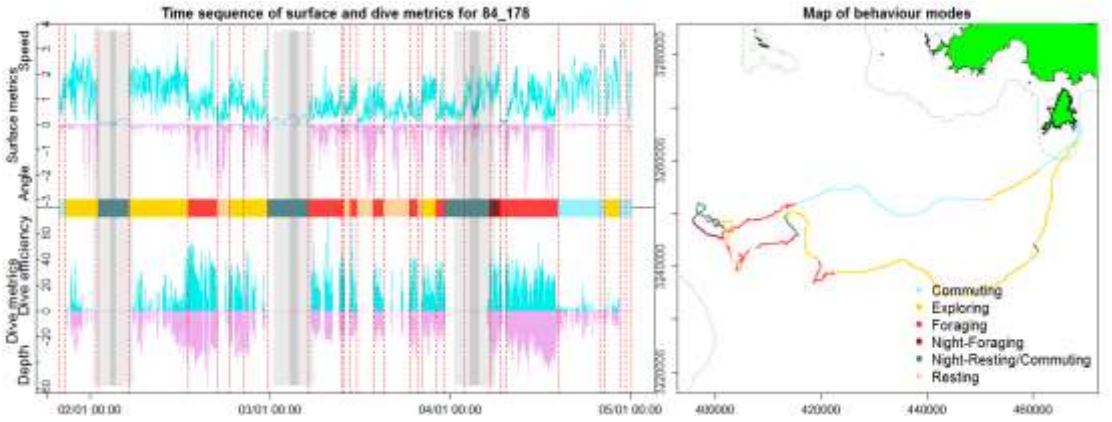
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
83_177	01-01 (16)	07-01 (15)	142.7	NA	C	159.0	23%	NA	NA	34%	0.20



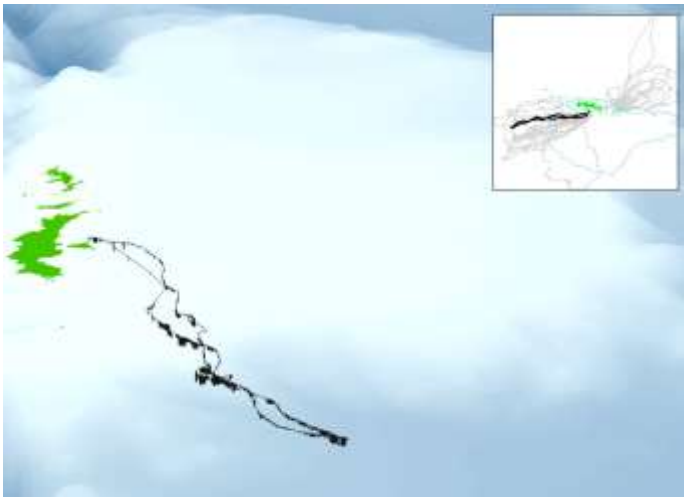
Deployment	**84**
Site	Gourlay
Season	2013-14
Stage	Incubation
Bill (mm)	52x19.5
Sex	male
Weight (kg)	3.8 (NA)
Offspring	2



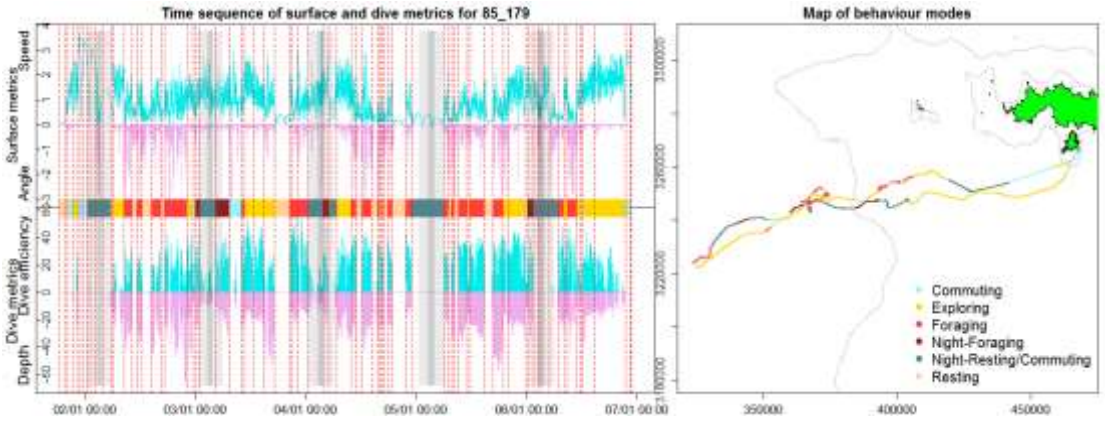
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
84_178	01-01 (19)	05-01 (00)	76.2	NA	C	74.5	21%	5%	0.12	29%	0.09



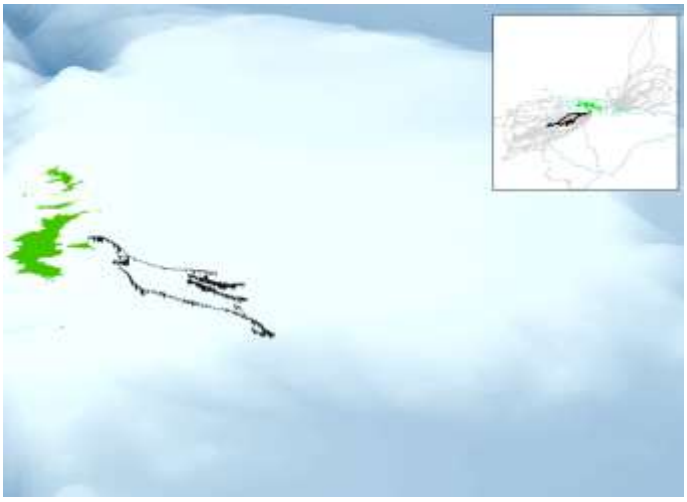
Deployment	**85**
Site	Gourlay
Season	2013-14
Stage	Incubation
Bill (mm)	46.6x17.6
Sex	female
Weight (kg)	3.2 (NA)
Offspring	1



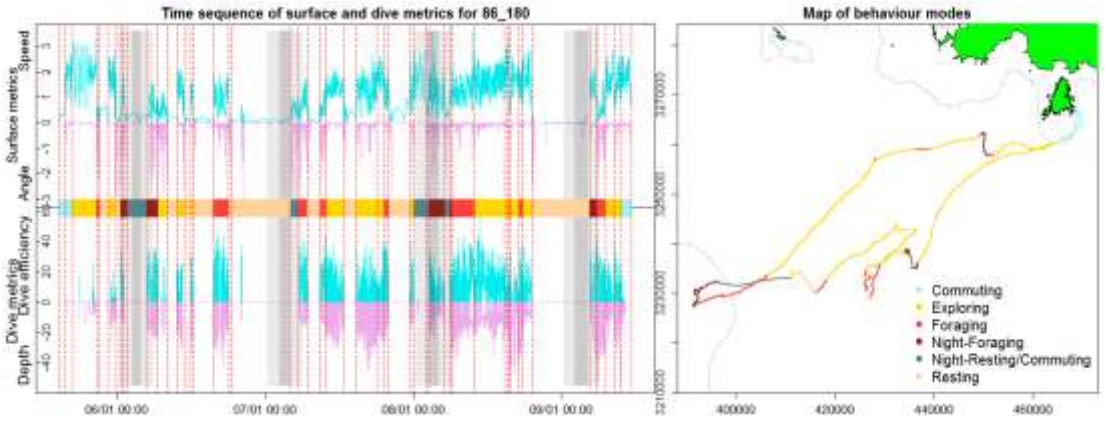
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
85_179	01-01 (18)	06-01 (22)	124.4	NA		150.7	22%	12%	0.14	31%	0.16



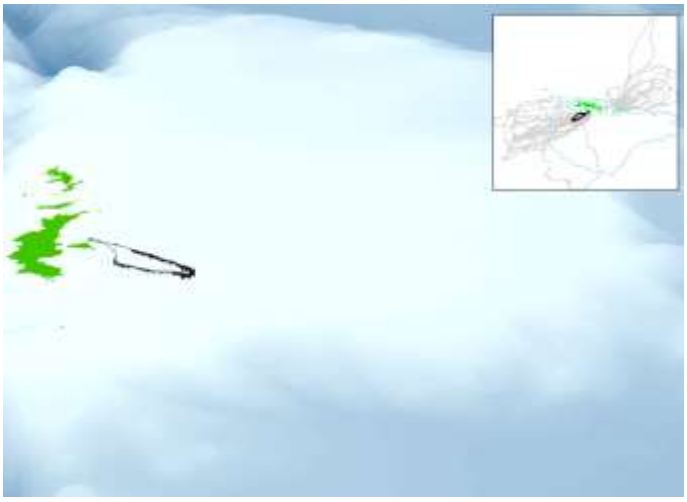
Deployment	**86**
Site	Gourlay
Season	2013-14
Stage	Incubation
Bill (mm)	51.4x19.2
Sex	male
Weight (kg)	3.7 (NA)
Offspring	1



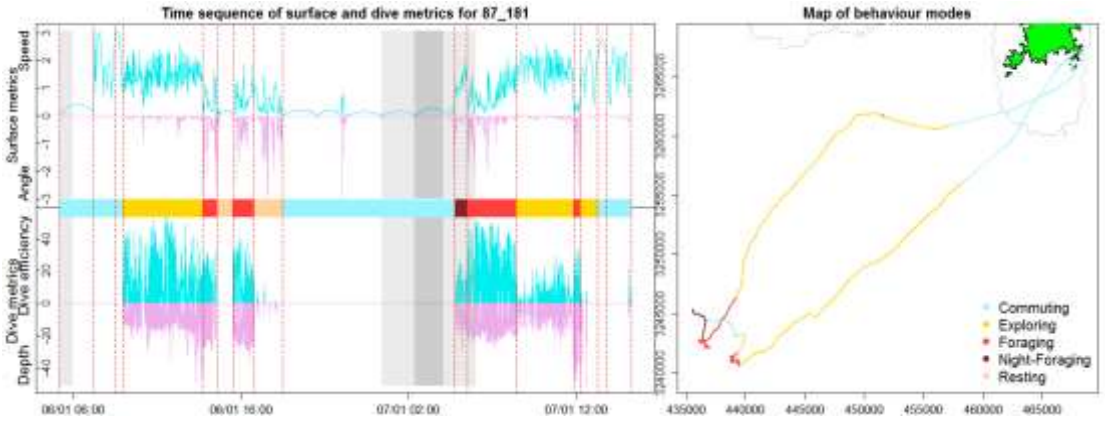
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
86_180	05-01 (14)	09-01 (11)	92.6	NA	C	86.3	24%	16%	0.14	20%	0.10



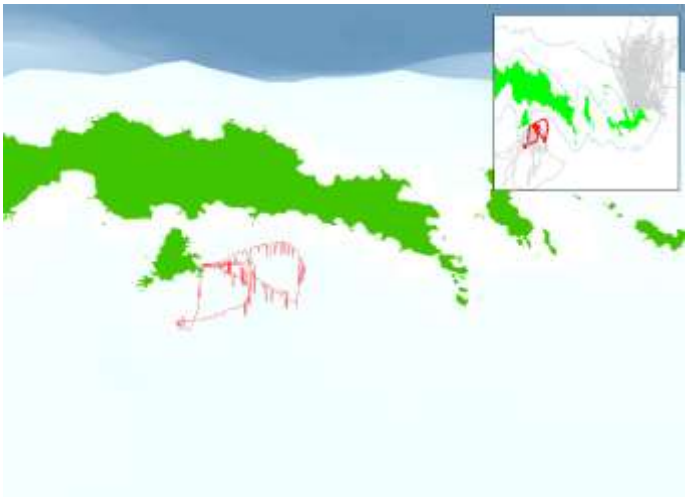
Deployment	**87**
Site	Gourlay
Season	2013-14
Stage	Incubation
Bill (mm)	52.9x19.9
Sex	male
Weight (kg)	4.65 (NA)
Offspring	1



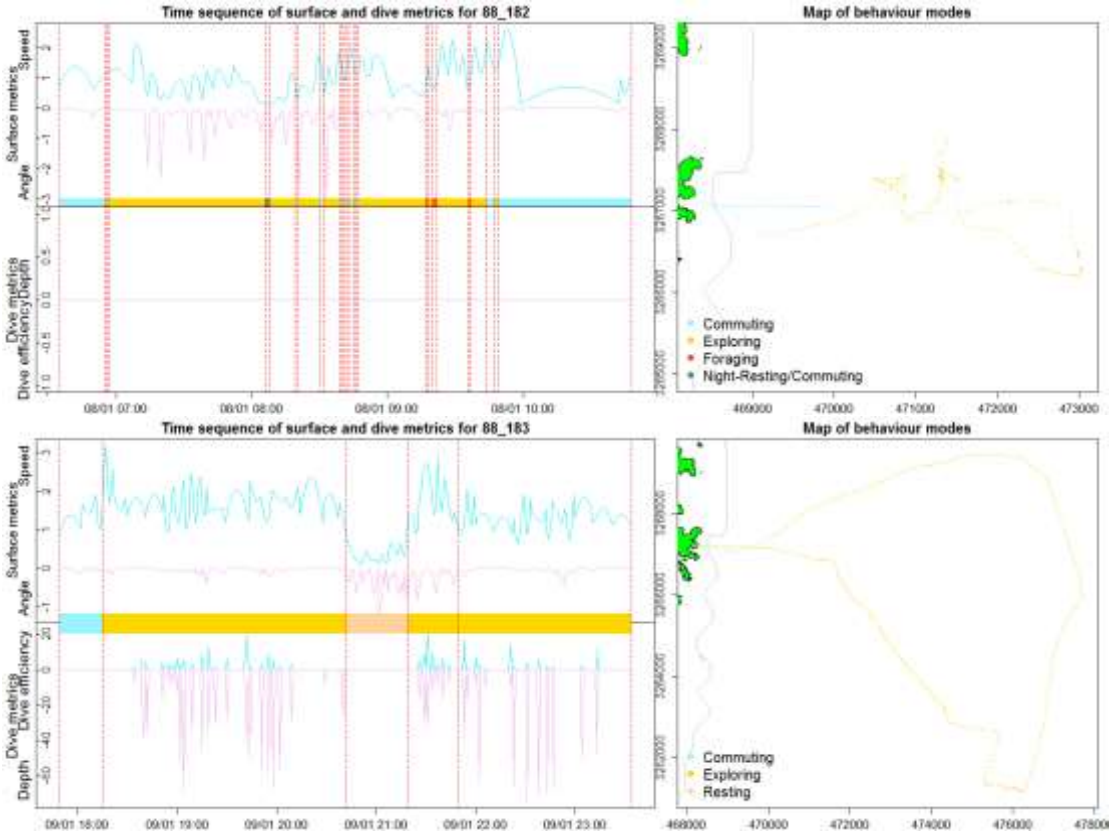
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
87_181	06-01 (05)	07-01 (15)	34.2	NA	C	40.2	19%	8%	0.13	18%	0.06

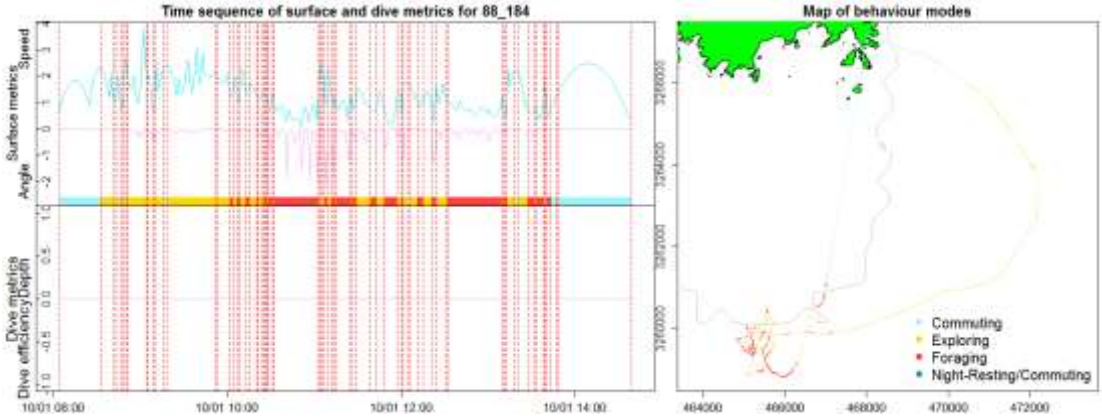


Deployment	**88**
Site	Gourlay
Season	2013-14
Stage	Brood
Bill (mm)	45.1x17.6
Sex	female
Weight (kg)	4.15 (NA)
Offspring	2

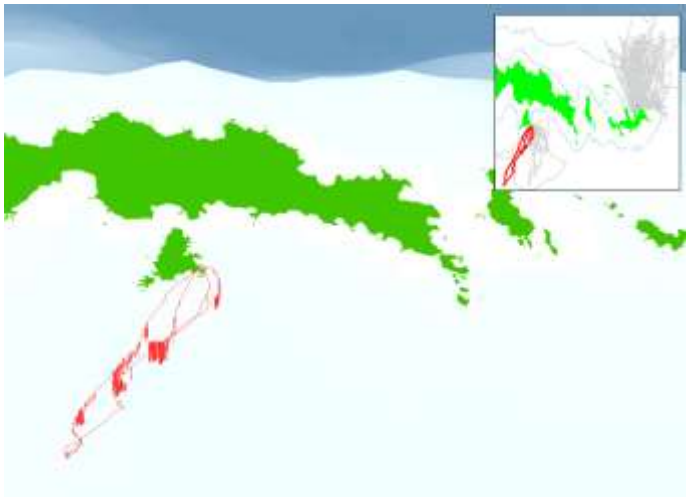


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
88_182	08-01 (06)	08-01 (10)	4.2	31.0		4.8	0%	NA	NA	2%	0.15
88_183	09-01 (17)	09-01 (23)	5.8	8.5	C	10.0	0%	0%	0.09	0%	0.18
88_184	10-01 (08)	10-01 (14)	6.6	NA	C	8.8	0%	NA	NA	34%	0.21

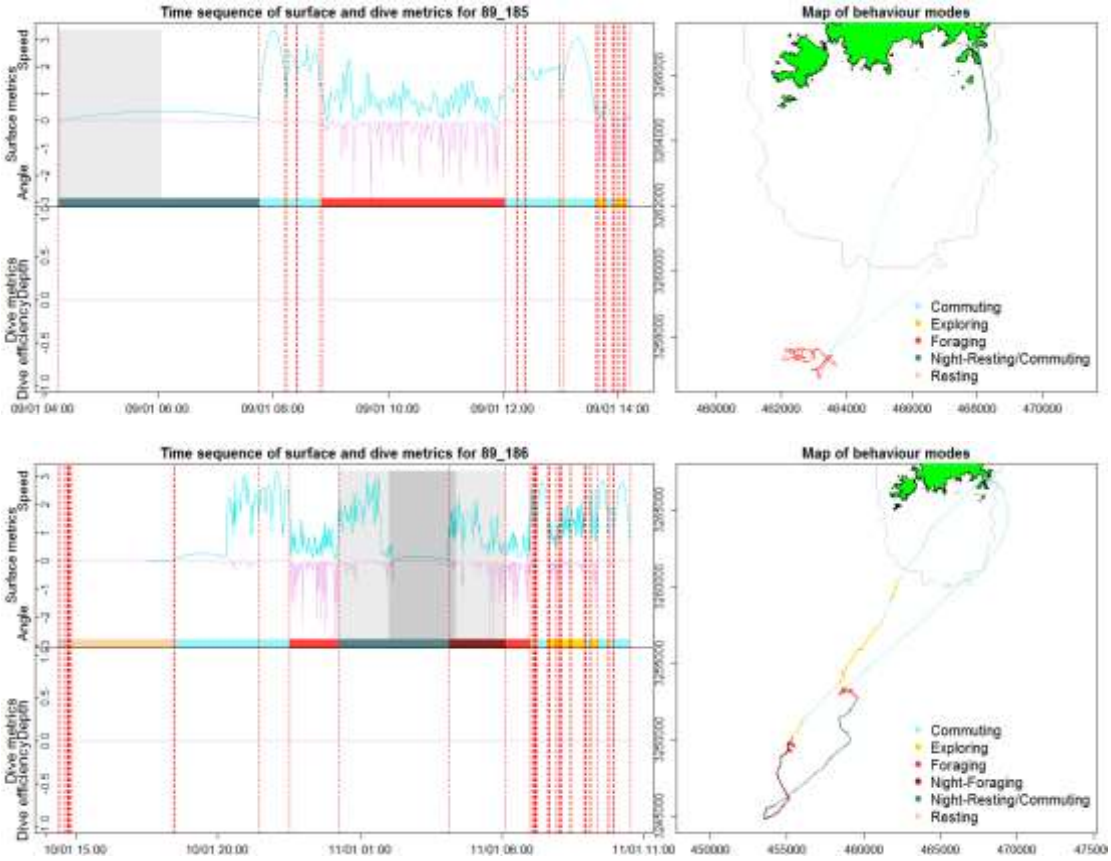



Time sequence of surface and dive metrics for 88_184
Surface metrics
Speed
Angle
Dive metrics
Depth
Dive efficiency
10/01 08:00
10/01 10:00
10/01 12:00
10/01 14:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Resting/Commuting
464000
466000
468000
470000
472000

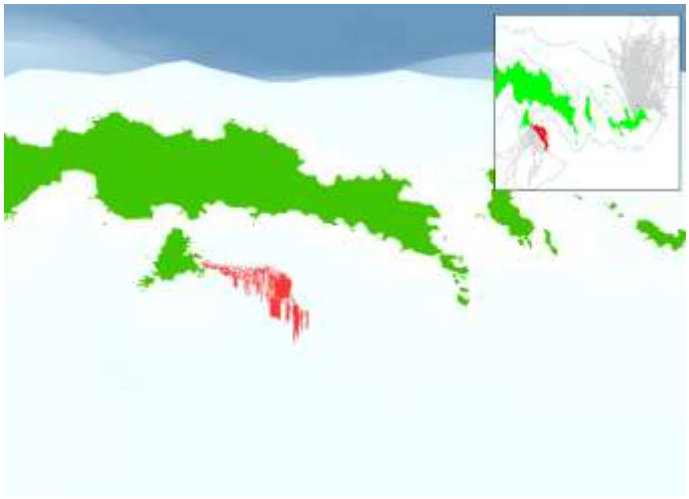
Deployment	**89**
Site	Gourlay
Season	2013-14
Stage	Brood
Bill (mm)	54.4x19
Sex	male
Weight (kg)	4.05 (NA)
Offspring	2



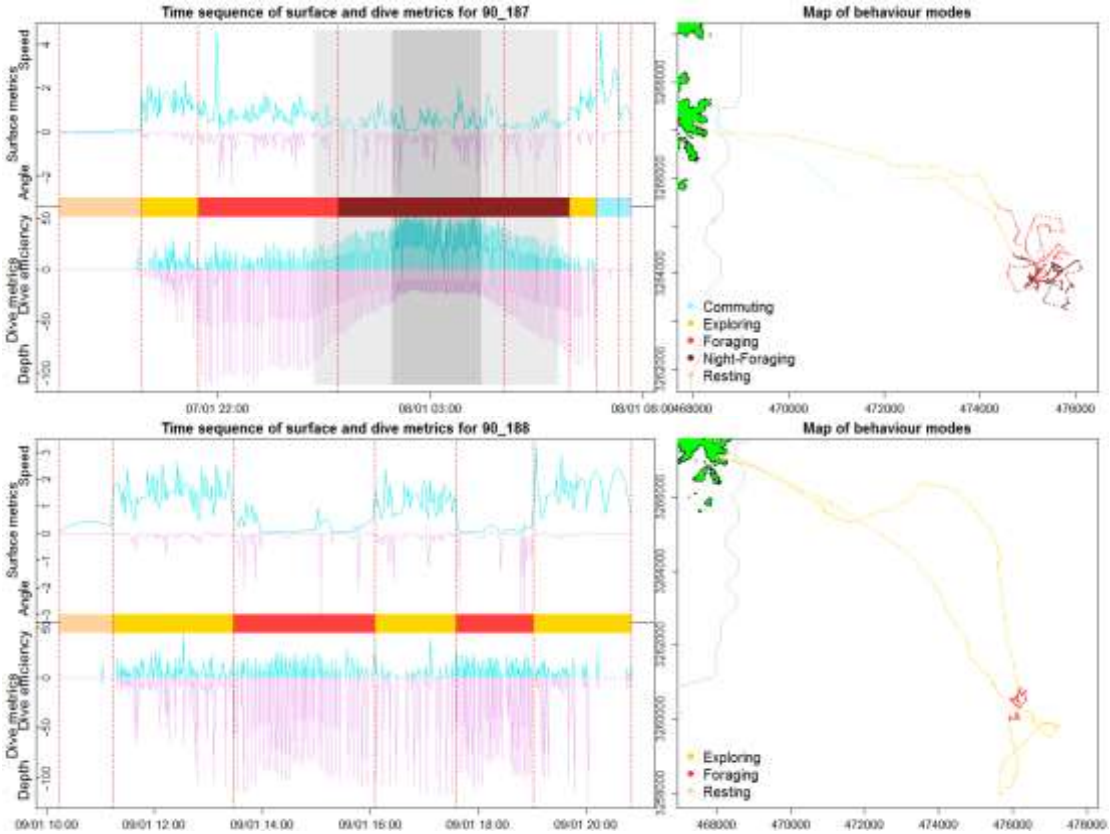
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
89_185	09-01 (04)	09-01 (14)	10.0	24.2	C	11.6	18%	NA	NA	32%	0.17
89_186	10-01 (14)	11-01 (10)	20.2	NA	C	26.5	29%	NA	NA	24%	0.24

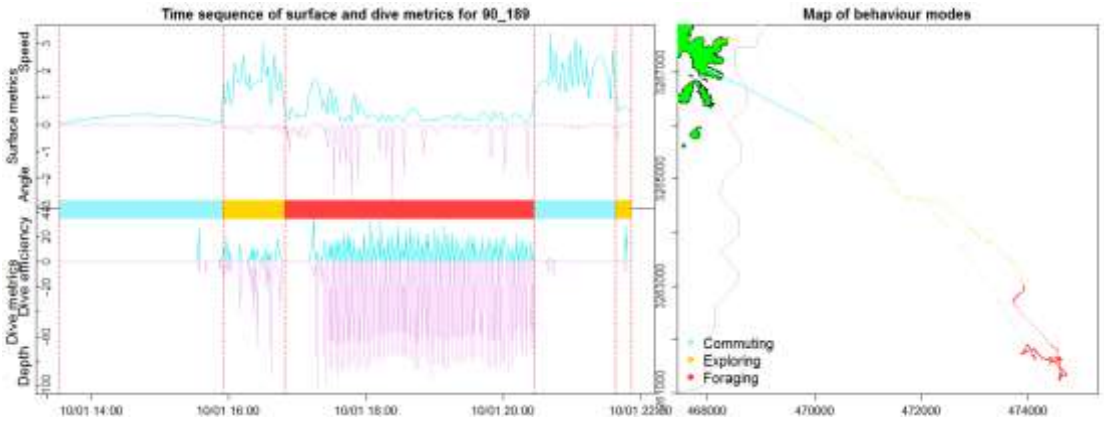


Deployment	**90**
Site	Gourlay
Season	2013-14
Stage	Brood
Bill (mm)	NAxNA
Sex	NA
Weight (kg)	NA (NA)
Offspring	1

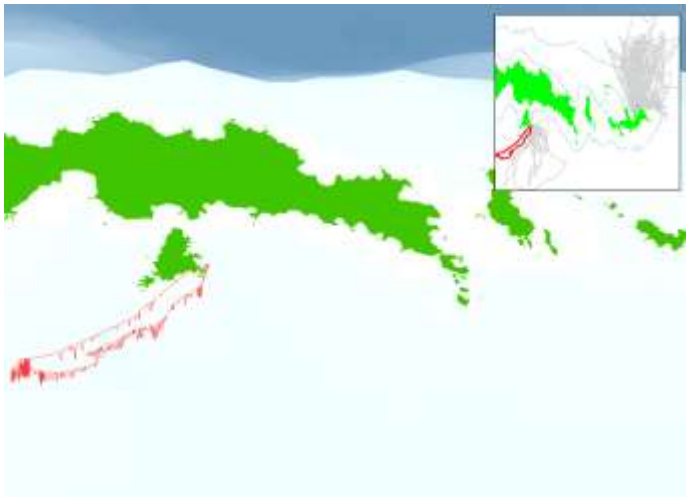


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
90_187	07-01 (18)	08-01 (07)	13.5	26.5	C	8.7	43%	63%	0.59	65%	0.21
90_188	09-01 (10)	09-01 (20)	10.6	16.7	C	11.9	0%	0%	0.54	38%	0.18
90_189	10-01 (13)	10-01 (21)	8.3	NA	C	8.8	0%	0%	0.52	43%	0.20

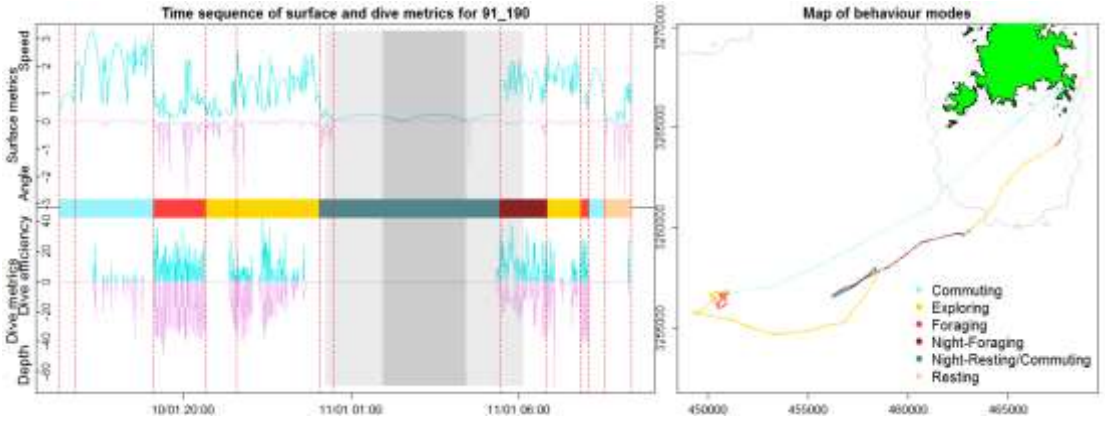



Time sequence of surface and dive metrics for 90_189
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
10/01 14:00
10/01 16:00
10/01 18:00
10/01 20:00
Map of behaviour modes
Commuting
Exploring
Foraging
468000
470000
472000
474000

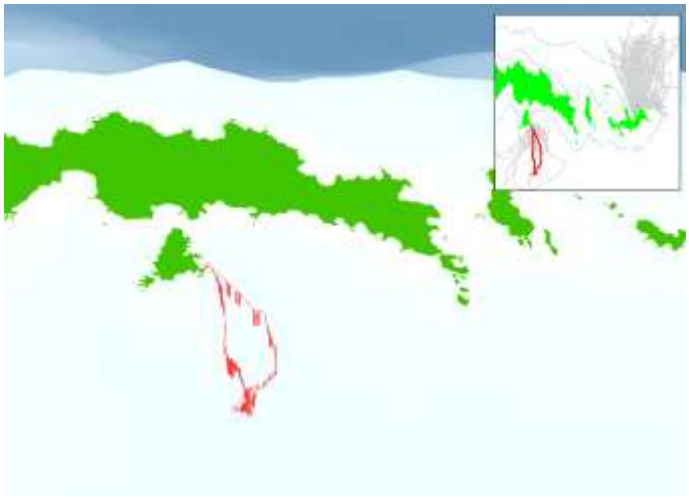
Deployment	**91**
Site	Gourlay
Season	2013-14
Stage	Brood
Bill (mm)	48x17
Sex	female
Weight (kg)	3.65 (NA)
Offspring	2



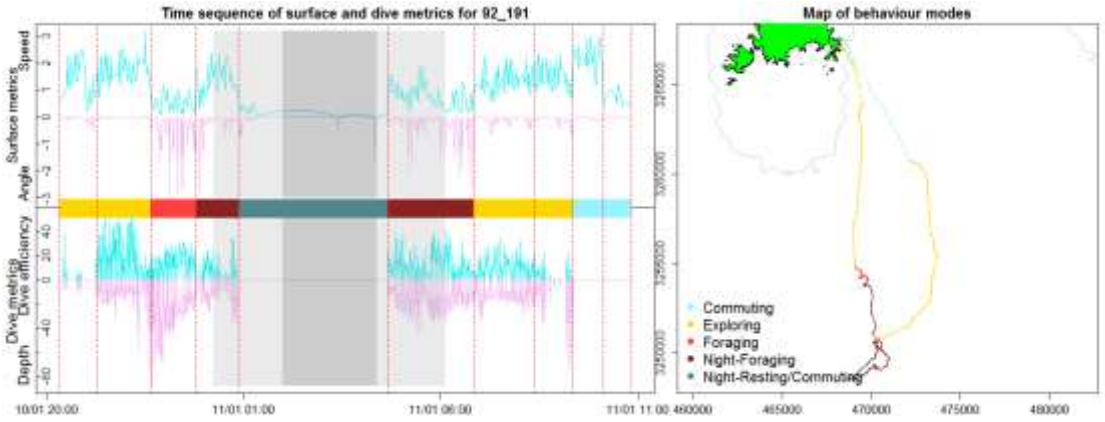
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
91_190	10-01 (16)	11-01 (09)	17.1	NA	AC	21.8	34%	19%	0.13	19%	0.17



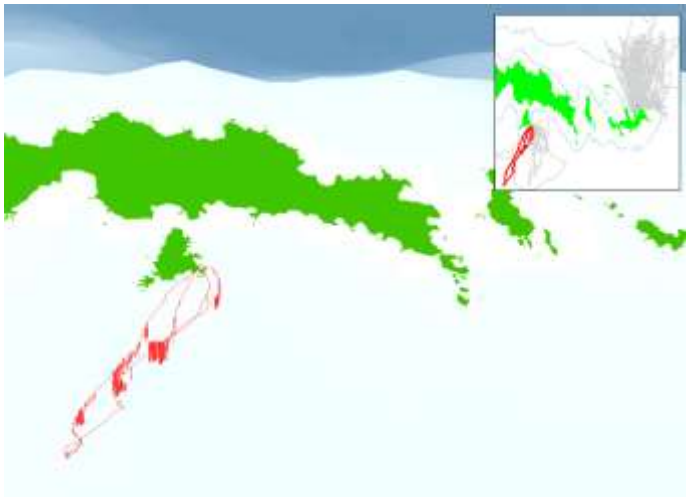
Deployment	**92**
Site	Gourlay
Season	2013-14
Stage	Brood
Bill (mm)	47x18.9
Sex	female
Weight (kg)	3.65 (NA)
Offspring	2



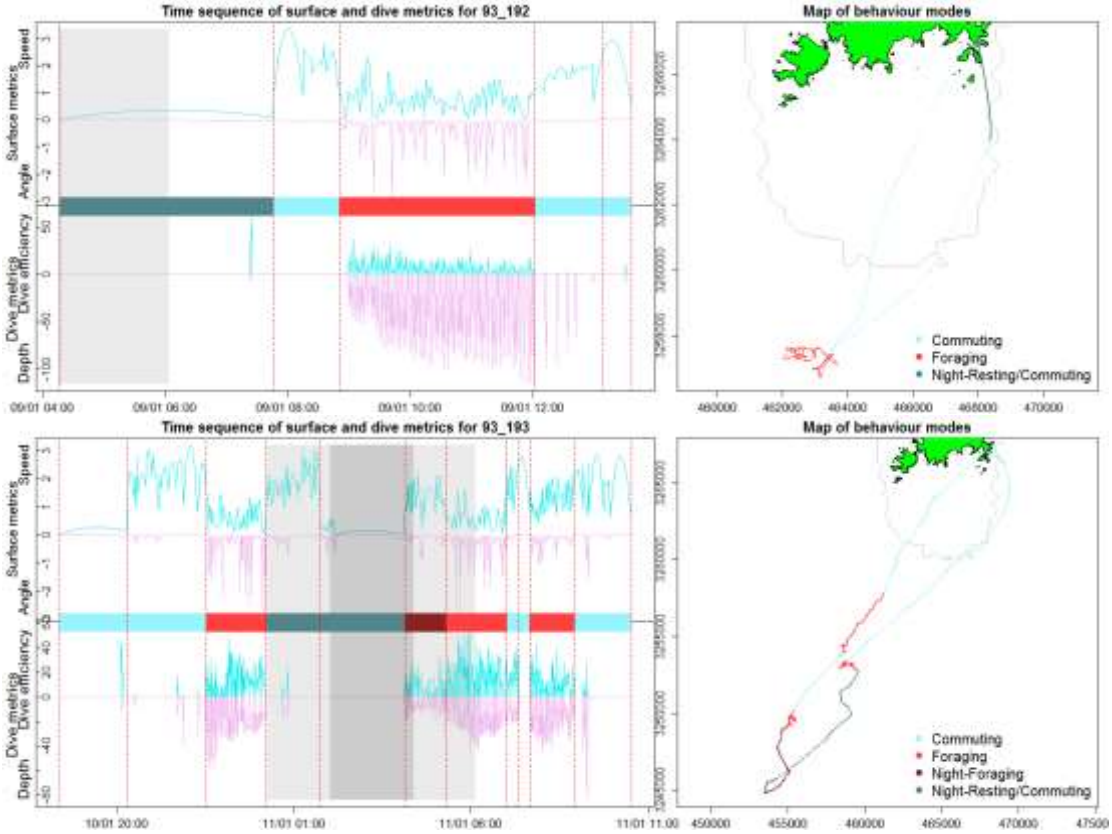
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
92_191	10-01 (20)	11-01 (10)	14.5	NA	AC	18.7	40%	24%	0.23	30%	0.19



Deployment	**93**
Site	Gourlay
Season	2013-14
Stage	Brood
Bill (mm)	46x18.6
Sex	female
Weight (kg)	4 (NA)
Offspring	2

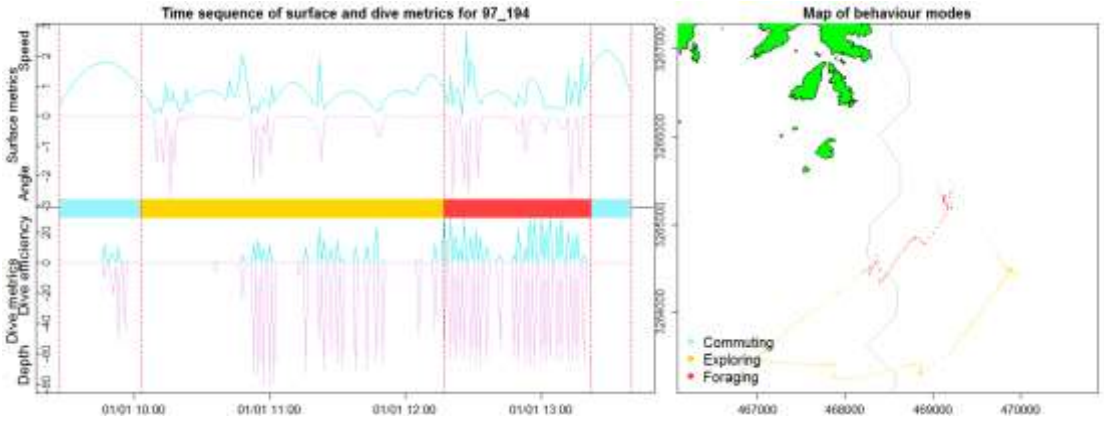


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
93_192	09-01 (04)	09-01 (13)	9.4	28.8	C	11.6	19%	0%	0.37	34%	0.17
93_193	10-01 (18)	11-01 (10)	16.2	NA	C	26.5	36%	28%	0.16	36%	0.24

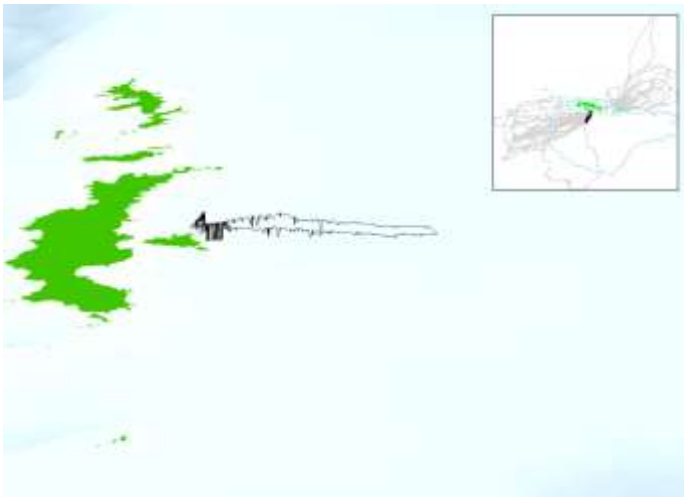


Deployment	**97**
Site	Gourlay
Season	2011-12
Stage	Incubation
Bill (mm)	54.6xNA
Sex	NA
Weight (kg)	4.1 (0.1)
Offspring	NA

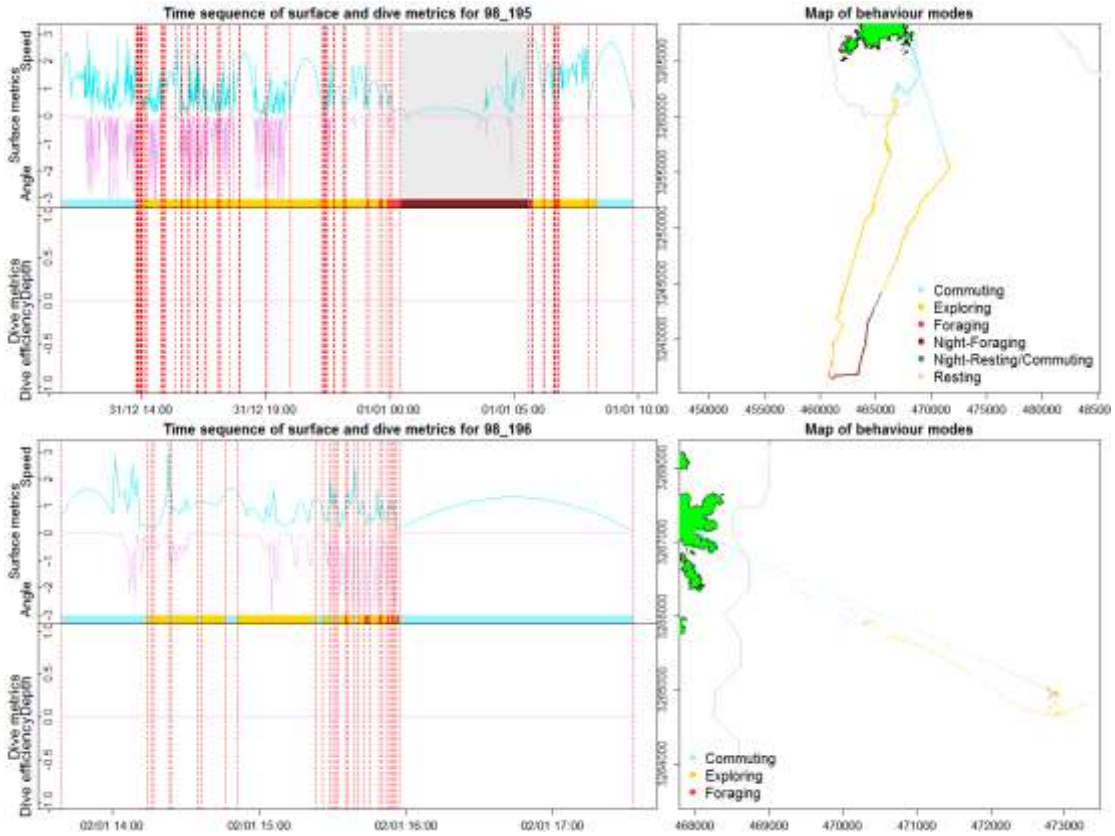
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
97_194	01-01 (09)	01-01 (13)	4.2	NA	C	3.9	0%	0%	0.41	26%	0.05



Deployment	**98**
Site	Gourlay
Season	2011-12
Stage	Incubation
Bill (mm)	46.5xNA
Sex	NA
Weight (kg)	4.15 (0)
Offspring	NA

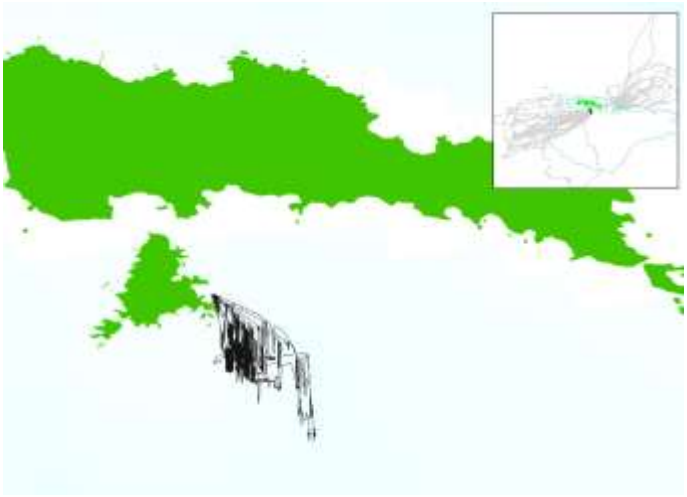


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
98_195	31-12 (10)	01-01 (09)	23.1	27.8	AC	31.5	23%	NA	NA	28%	0.11
98_196	02-01 (13)	02-01 (17)	3.9	NA	AC	5.6	0%	NA	NA	2%	0.05

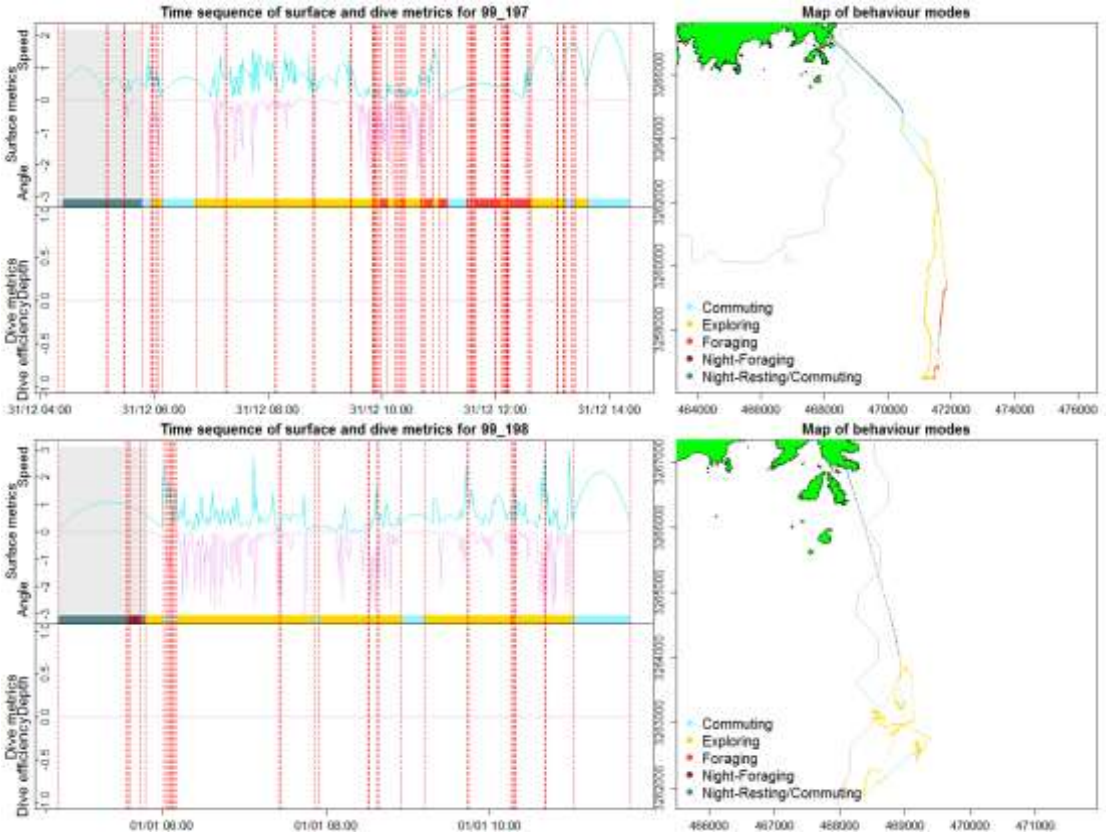


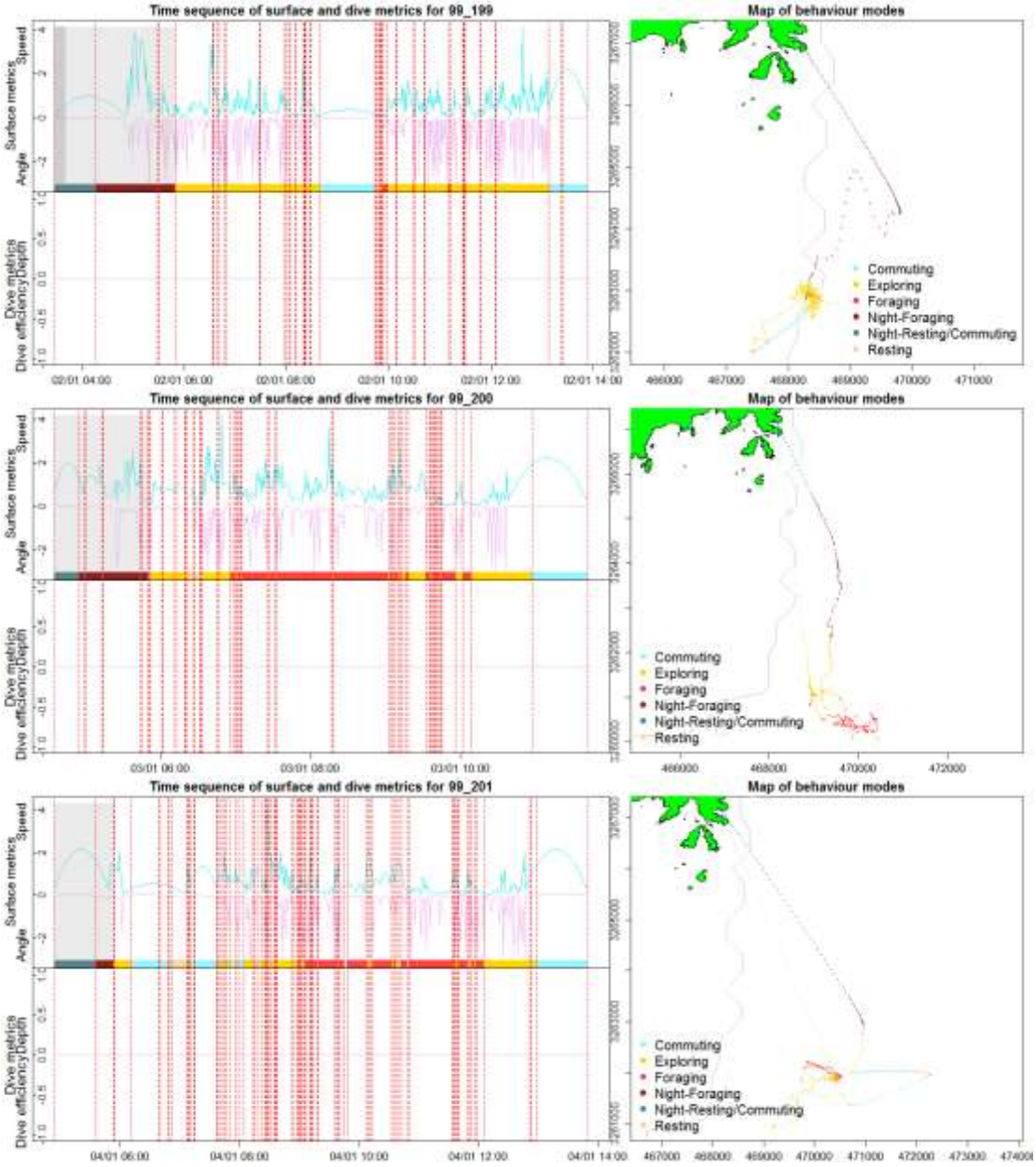
Deployment 99

Site	Gourlay
Season	2011-12
Stage	Incubation
Bill (mm)	47.3xNA
Sex	NA
Weight (kg)	3.2 (NA)
Offspring	NA

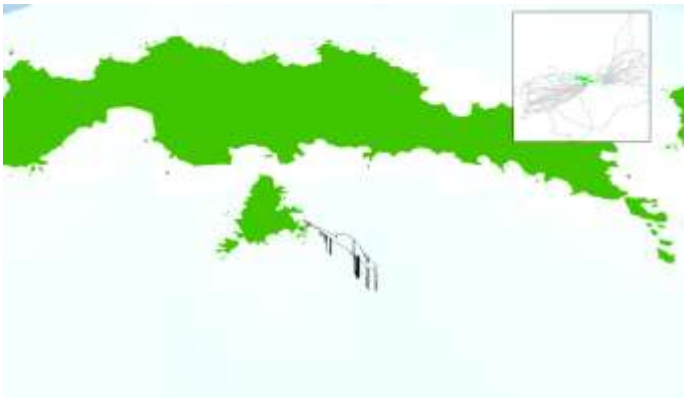


Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
99_197	31-12 (04)	31-12 (14)	10.1	14.4		11.2	15%	NA	NA	18%	0.10
99_198	01-01 (04)	01-01 (11)	7.0	15.8		5.2	15%	NA	NA	3%	0.05
99_199	02-01 (03)	02-01 (13)	10.4	14.7	C	5.2	23%	NA	NA	17%	0.04
99_200	03-01 (04)	03-01 (11)	7.1	17.2	C	7.5	18%	NA	NA	48%	0.08
99_201	04-01 (04)	04-01 (13)	8.9	NA	C	6.7	11%	NA	NA	31%	0.08

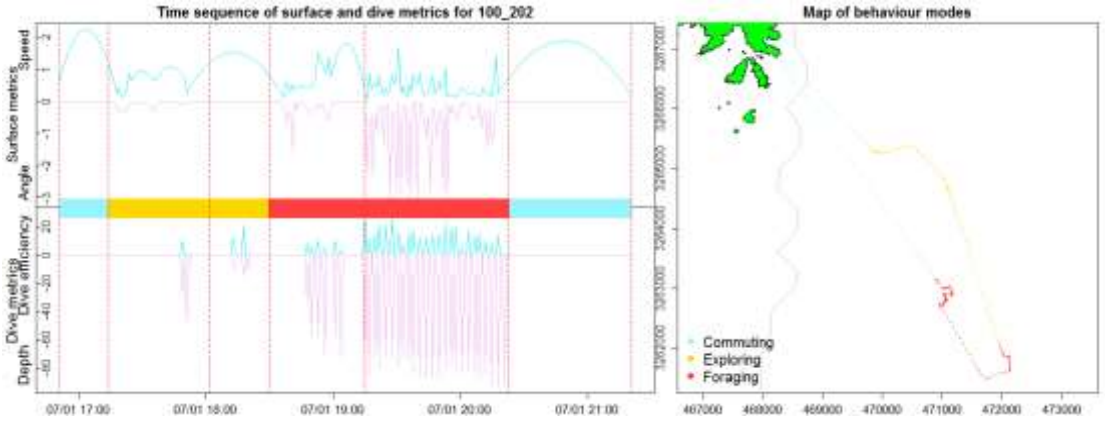



Time sequence of surface and dive metrics for 99_199
Map of behaviour modes
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
Commuting
Exploring
Foraging
Night-Foraging
Night-Resting/Commuting
Resting
Time sequence of surface and dive metrics for 99_200
Map of behaviour modes
Time sequence of surface and dive metrics for 99_201
Map of behaviour modes

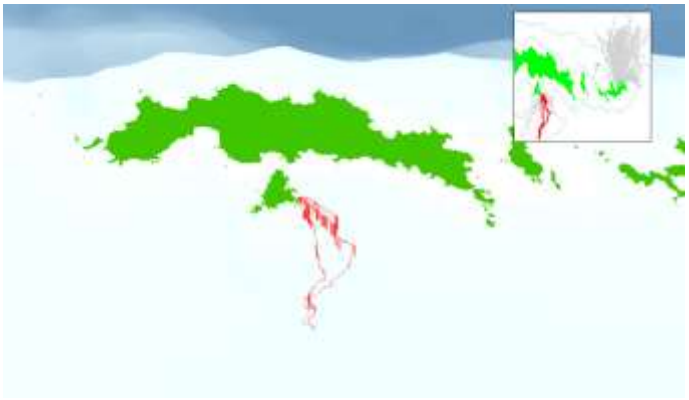
Deployment	**100**
Site	Gourlay
Season	2011-12
Stage	Incubation
Bill (mm)	51.4xNA
Sex	NA
Weight (kg)	4.8 (-0.1)
Offspring	NA



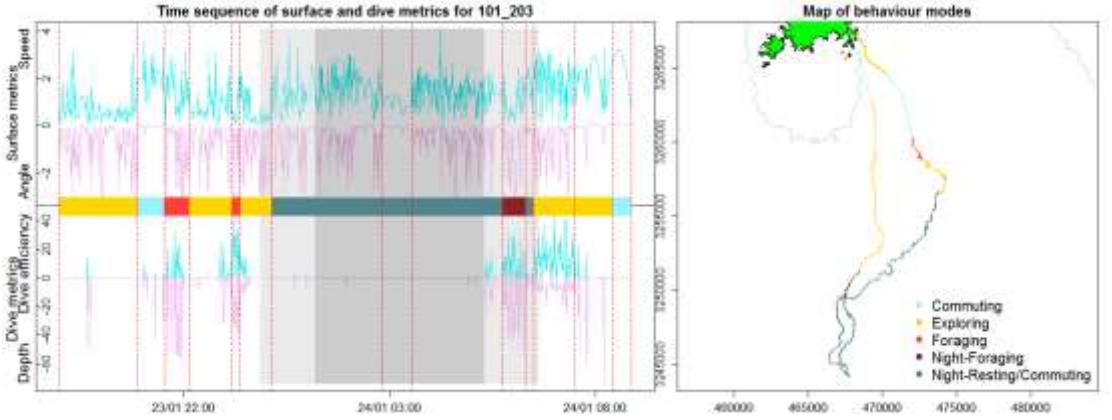
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
100_202	07-01 (16)	07-01 (21)	4.5	NA		6.9	0%	0%	0.30	42%	0.06

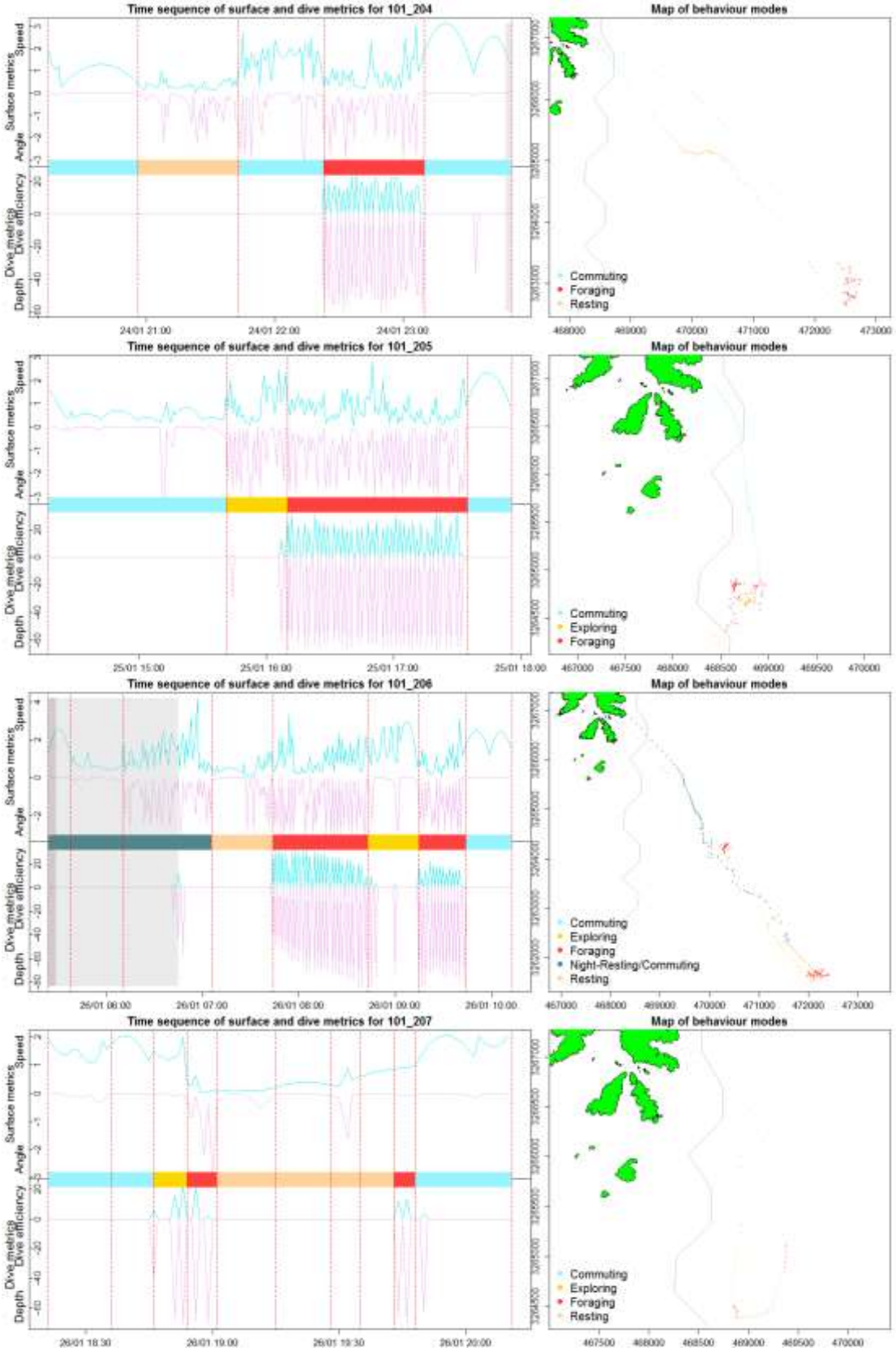


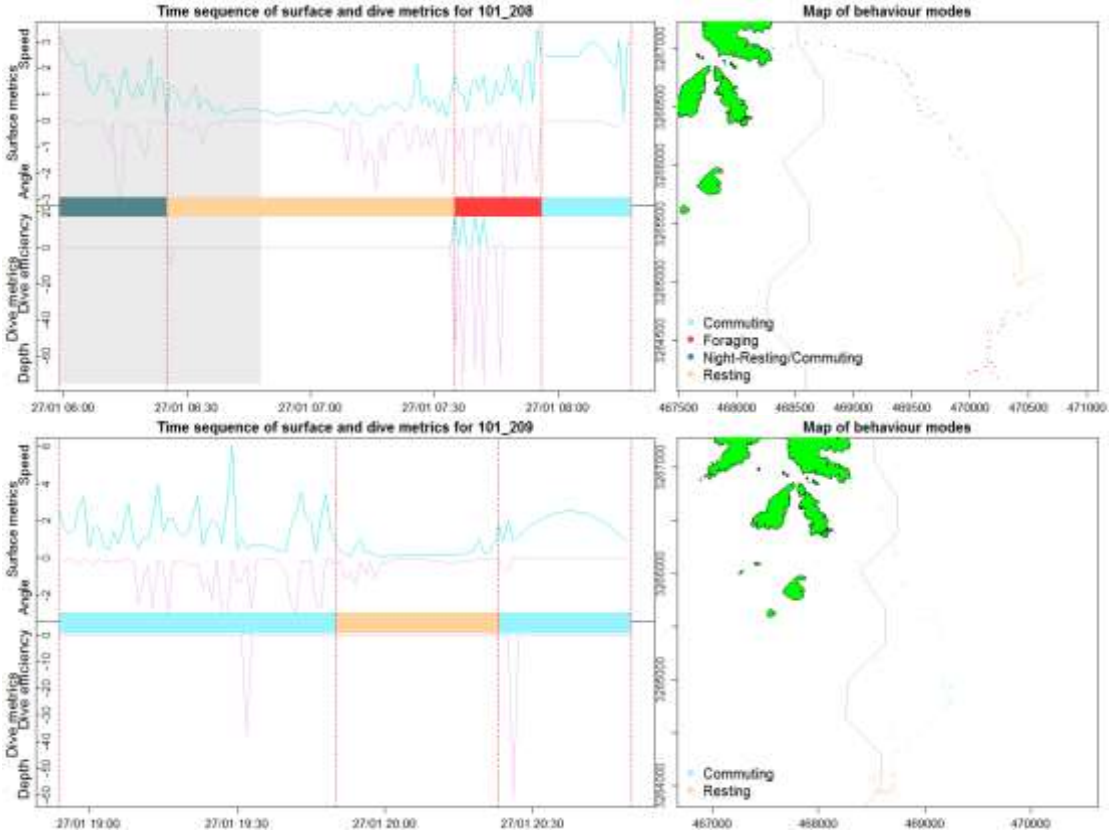
Deployment	**101**
Site	Gourlay
Season	2011-12
Stage	Brood
Bill (mm)	45.5x17.8
Sex	female
Weight (kg)	3.6 (0.1)
Offspring	NA



Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
101_203	23-01 (18)	24-01 (08)	13.9	11.4	C	23.0	49%	32%	0.06	10%	0.19
101_204	24-01 (20)	24-01 (23)	3.6	14.4		6.3	2%	0%	0.17	22%	0.18
101_205	25-01 (14)	25-01 (17)	3.7	11.5		2.9	0%	0%	0.46	39%	0.12
101_206	26-01 (05)	26-01 (10)	4.8	8.1		7.0	28%	2%	0.30	30%	0.19
101_207	26-01 (18)	26-01 (20)	1.8	9.8		2.9	0%	0%	0.16	11%	0.13
101_208	27-01 (05)	27-01 (08)	2.3	10.6	C	3.6	35%	17%	0.07	15%	0.16
101_209	27-01 (18)	27-01 (20)	1.9	NA		3.2	0%	0%	0.02	0%	0.13

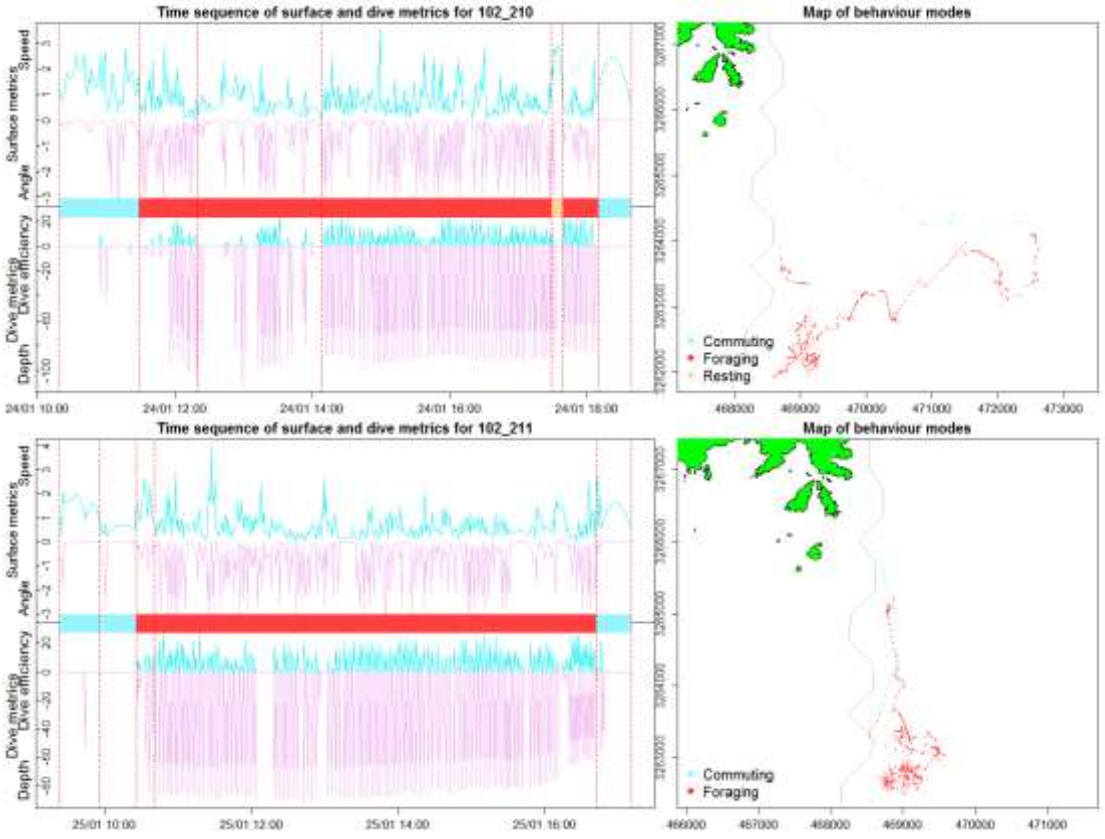


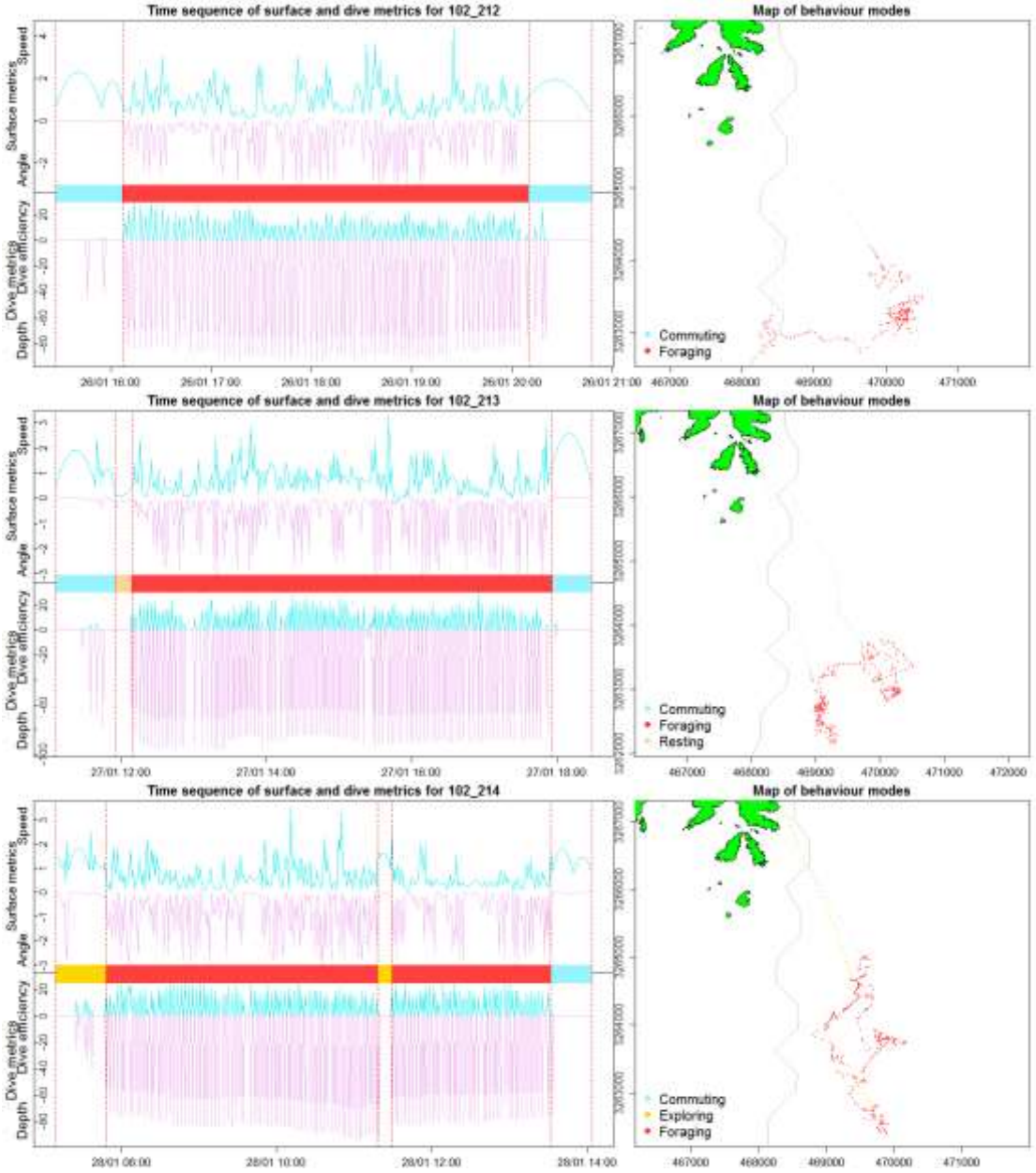

Time sequence of surface and dive metrics for 101_204
Map of behaviour modes
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
24/01 21:00
24/01 22:00
24/01 23:00
Commuting
Foraging
Resting
Time sequence of surface and dive metrics for 101_205
Map of behaviour modes
25/01 15:00
25/01 16:00
25/01 17:00
25/01 18:00
Commuting
Exploring
Foraging
Time sequence of surface and dive metrics for 101_206
Map of behaviour modes
26/01 06:00
26/01 07:00
26/01 08:00
26/01 09:00
26/01 10:00
Commuting
Exploring
Foraging
Night-Resting/Commuting
Resting
Time sequence of surface and dive metrics for 101_207
Map of behaviour modes
26/01 18:30
26/01 19:00
26/01 19:30
26/01 20:00
Commuting
Exploring
Foraging
Resting


Time sequence of surface and dive metrics for 101_208
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
27/01 06:00
27/01 06:30
27/01 07:00
27/01 07:30
27/01 08:00
Map of behaviour modes
Commuting
Foraging
Night-Resting/Commuting
Resting
467500
468000
468500
469000
469500
470000
470500
471000
Time sequence of surface and dive metrics for 101_209
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
27/01 19:00
27/01 19:30
27/01 20:00
27/01 20:30
Map of behaviour modes
Commuting
Resting
467000
468000
469000
470000

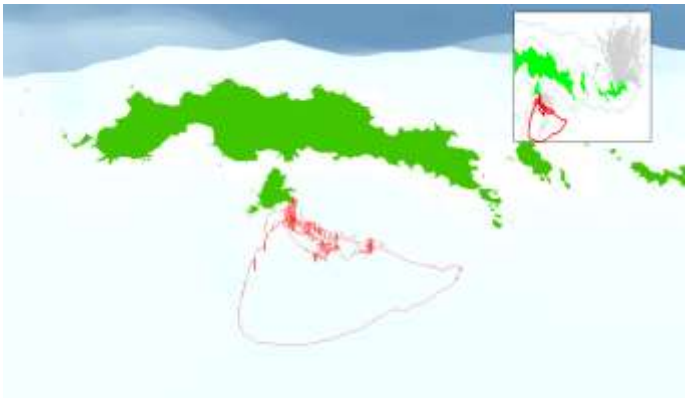
Deployment	**102**
Site	Gourlay
Season	2011-12
Stage	Brood
Bill (mm)	48.2x18.6
Sex	female
Weight (kg)	4.5 (0.1)
Offspring	NA

Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
102_210	24-01 (10)	24-01 (18)	8.3	14.7	C	5.9	0%	0%	0.64	78%	0.18
102_211	25-01 (09)	25-01 (17)	7.8	22.3		4.7	0%	0%	0.94	80%	0.15
102_212	26-01 (15)	26-01 (20)	5.4	14.3	AC	4.8	0%	0%	0.71	76%	0.16
102_213	27-01 (11)	27-01 (18)	7.4	12.7	C	5.1	0%	0%	0.84	78%	0.16
102_214	28-01 (07)	28-01 (14)	6.9	NA		5.1	0%	0%	1.03	80%	0.16

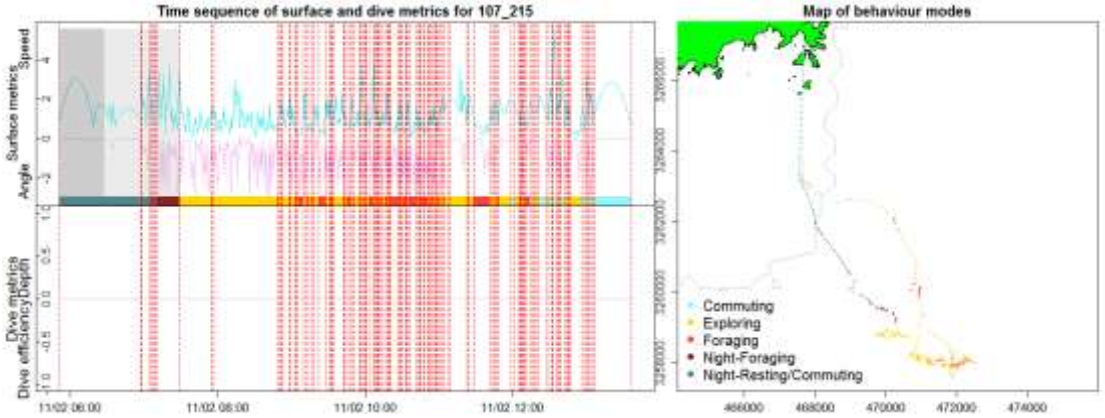


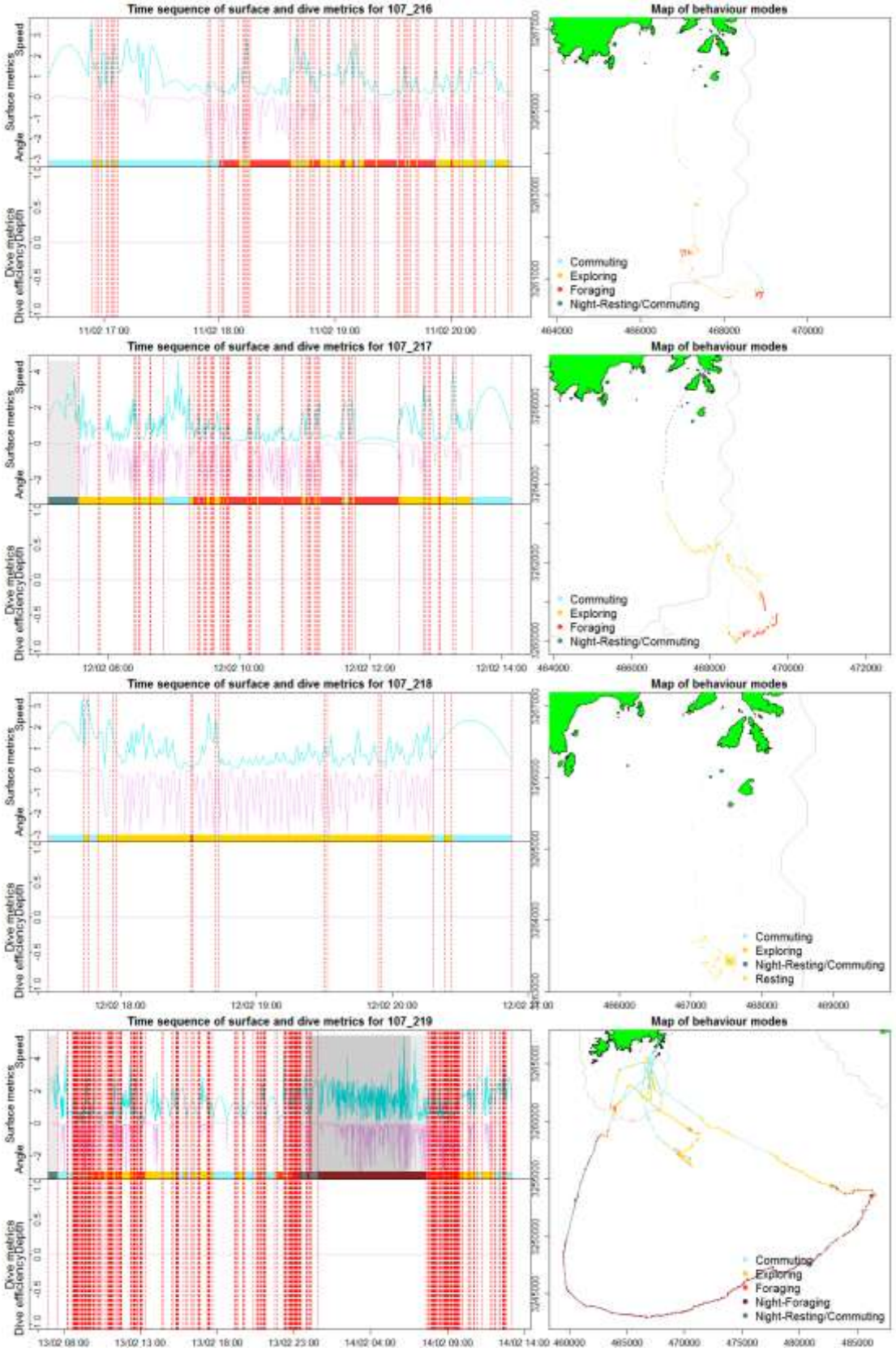

Time sequence of surface and dive metrics for 102_212
Map of behaviour modes
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
Commuting
Foraging
Time sequence of surface and dive metrics for 102_213
Map of behaviour modes
Commuting
Foraging
Resting
Time sequence of surface and dive metrics for 102_214
Map of behaviour modes
Commuting
Exploring
Foraging

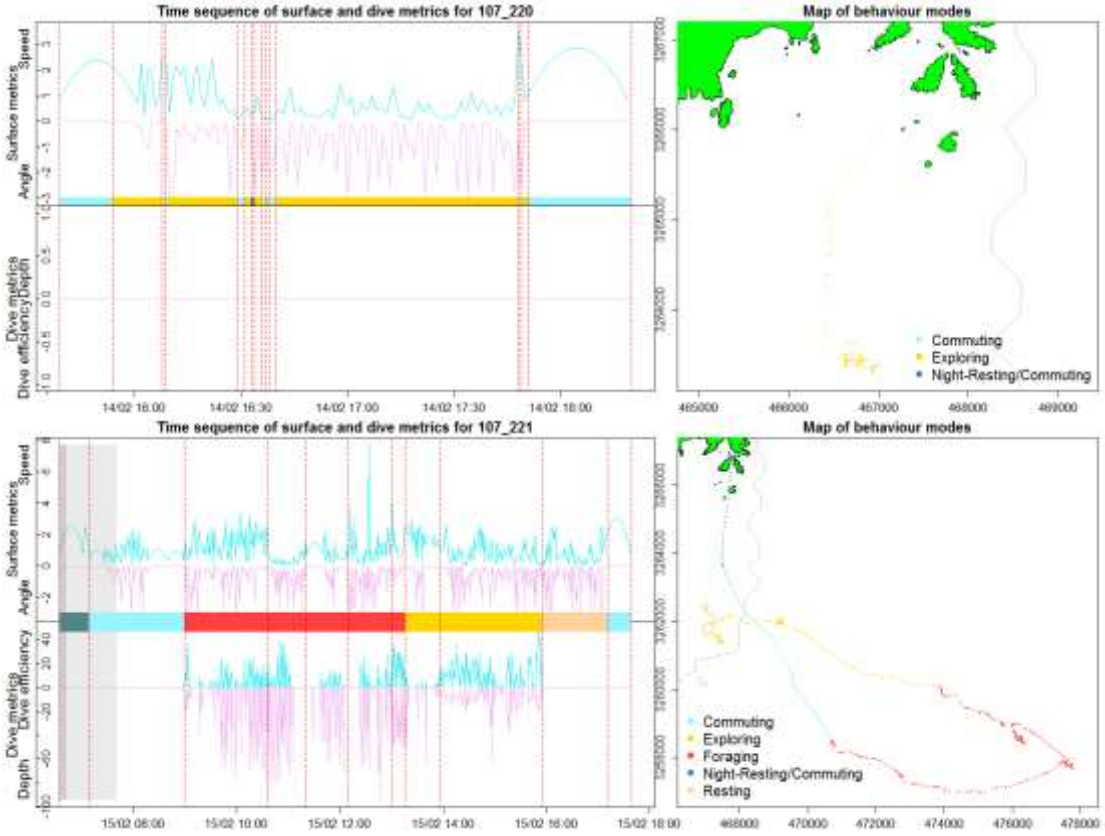
Deployment	**107**
Site	Gourlay
Season	2011-12
Stage	Brood
Bill (mm)	47.2x17.6
Sex	female
Weight (kg)	3.9 (-0.4)
Offspring	NA



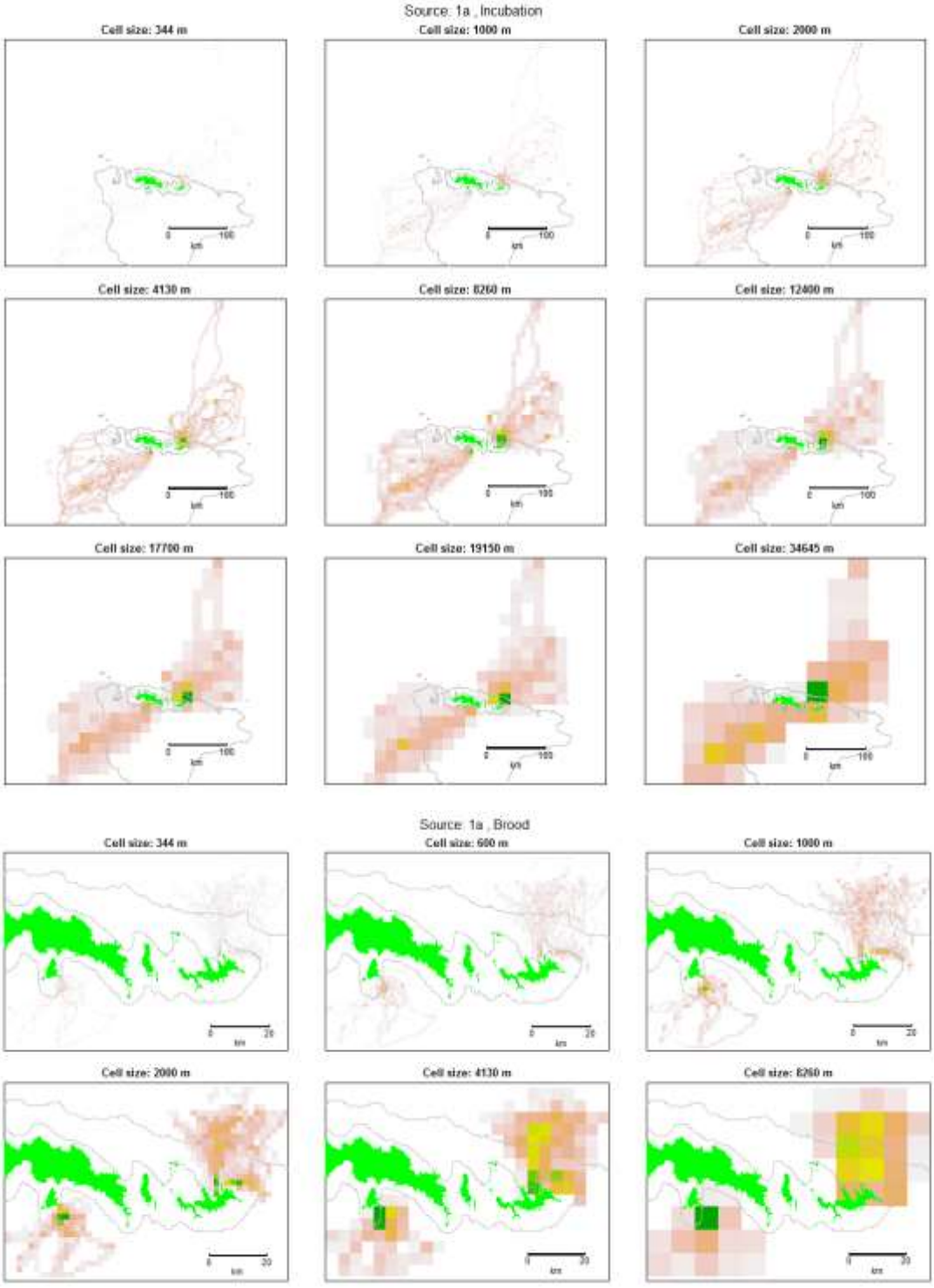
Trip ID	Start date (hour)	End date (hour)	Trip duration (h)	Post trip duration (h)	Direction	Maximum range (km)	Percentage of night activity	Percentage of night dives	Vertical/horizontal distances	Percentage of foraging	Weighted habitat use
107_215	11-02 (05)	11-02 (13)	7.8	2.9	AC	10.3	21%	NA	NA	25%	0.24
107_216	11-02 (16)	11-02 (20)	4.0	10.6	AC	6.7	0%	NA	NA	31%	0.18
107_217	12-02 (07)	12-02 (14)	7.1	3.3	AC	7.1	7%	NA	NA	35%	0.21
107_218	12-02 (17)	12-02 (20)	3.4	10.1	AC	3.9	0%	NA	NA	0%	0.13
107_219	13-02 (06)	14-02 (13)	30.2	2.4	AC	24.1	31%	NA	NA	38%	0.21
107_220	14-02 (15)	14-02 (18)	2.7	12.2	AC	4.0	0%	NA	NA	0%	0.13
107_221	15-02 (06)	15-02 (17)	11.1	NA	AC	13.6	10%	0%	0.18	39%	0.20

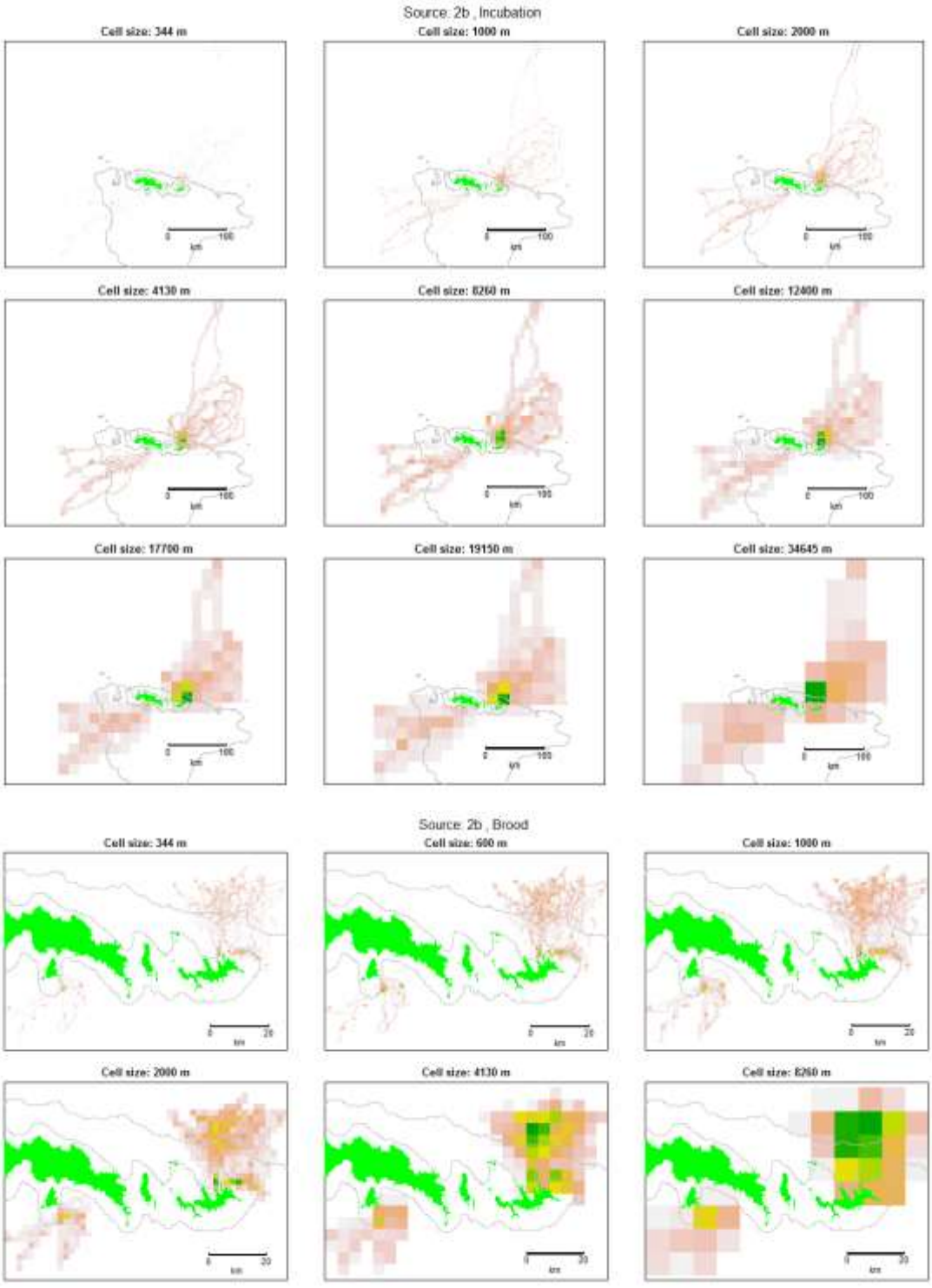


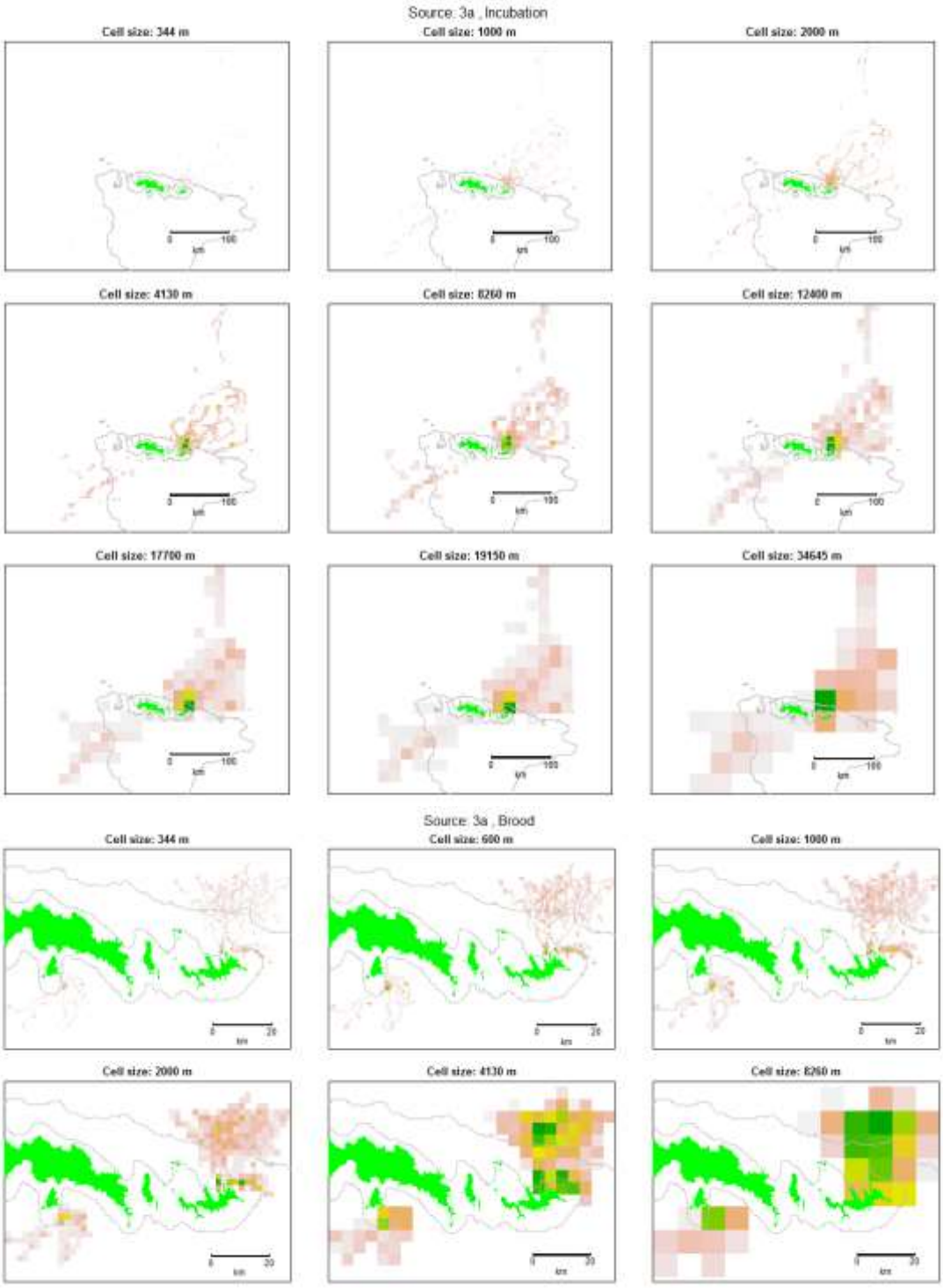

Time sequence of surface and dive metrics for 107_216
Map of behaviour modes
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
11/02 17:00
11/02 18:00
11/02 19:00
11/02 20:00
Commuting
Exploring
Foraging
Night-Resting/Commuting
Time sequence of surface and dive metrics for 107_217
Map of behaviour modes
12/02 08:00
12/02 10:00
12/02 12:00
12/02 14:00
Commuting
Exploring
Foraging
Night-Resting/Commuting
Time sequence of surface and dive metrics for 107_218
Map of behaviour modes
12/02 18:00
12/02 19:00
12/02 20:00
Commuting
Exploring
Night-Resting/Commuting
Resting
Time sequence of surface and dive metrics for 107_219
Map of behaviour modes
13/02 08:00
13/02 13:00
13/02 18:00
13/02 23:00
14/02 04:00
14/02 09:00
14/02 14:00
Commuting
Exploring
Foraging
Night-Foraging
Night-Resting/Commuting

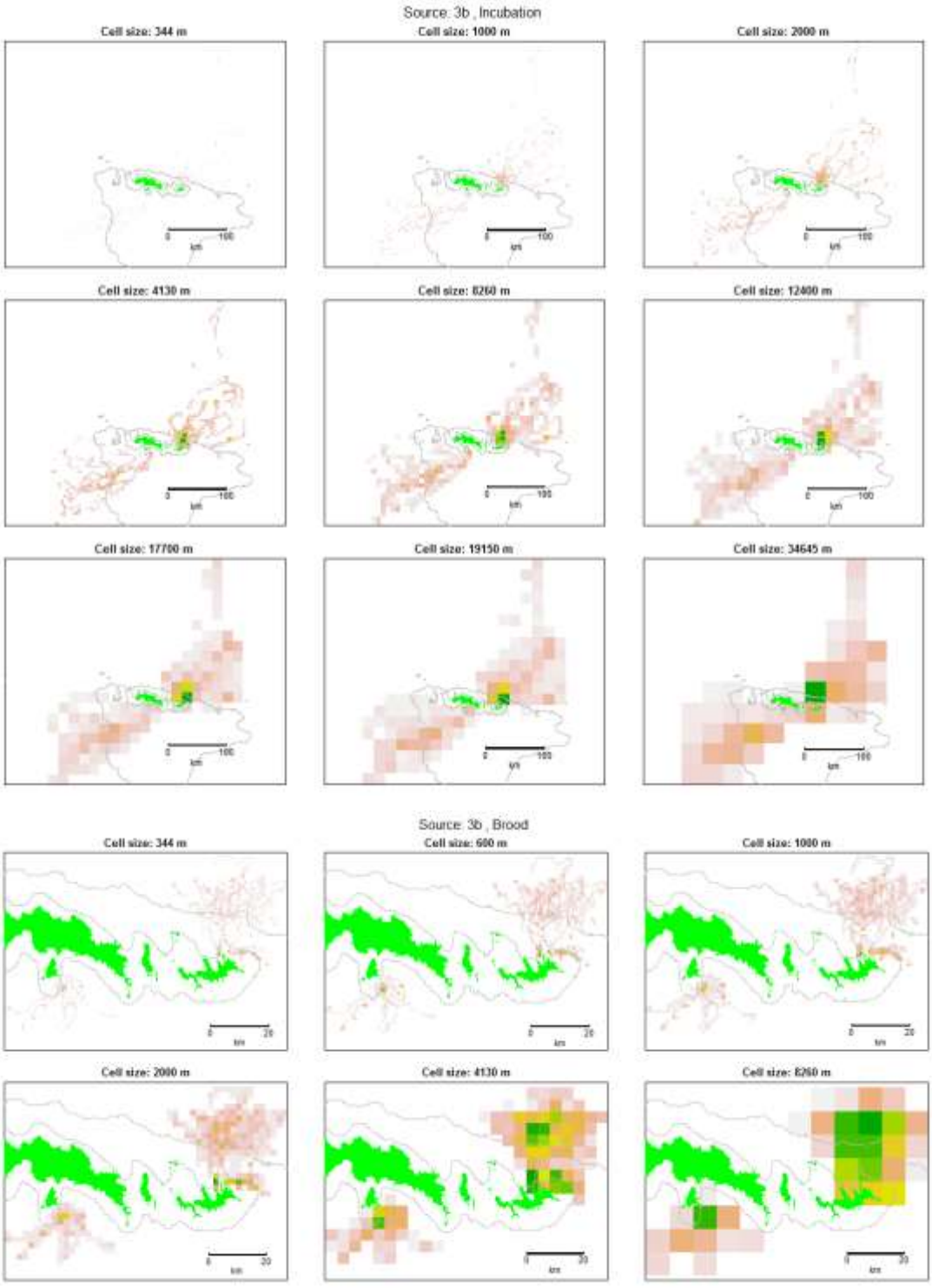

Time sequence of surface and dive metrics for 107_220
Surface metrics
Speed
Angle
Dive metrics
Dive efficiency
Depth
14/02 16:00
14/02 16:30
14/02 17:00
14/02 17:30
14/02 18:00
Map of behaviour modes
Commuting
Exploring
Night-Resting/Commuting
Time sequence of surface and dive metrics for 107_221
15/02 08:00
15/02 10:00
15/02 12:00
15/02 14:00
15/02 16:00
15/02 18:00
Map of behaviour modes
Commuting
Exploring
Foraging
Night-Resting/Commuting
Resting

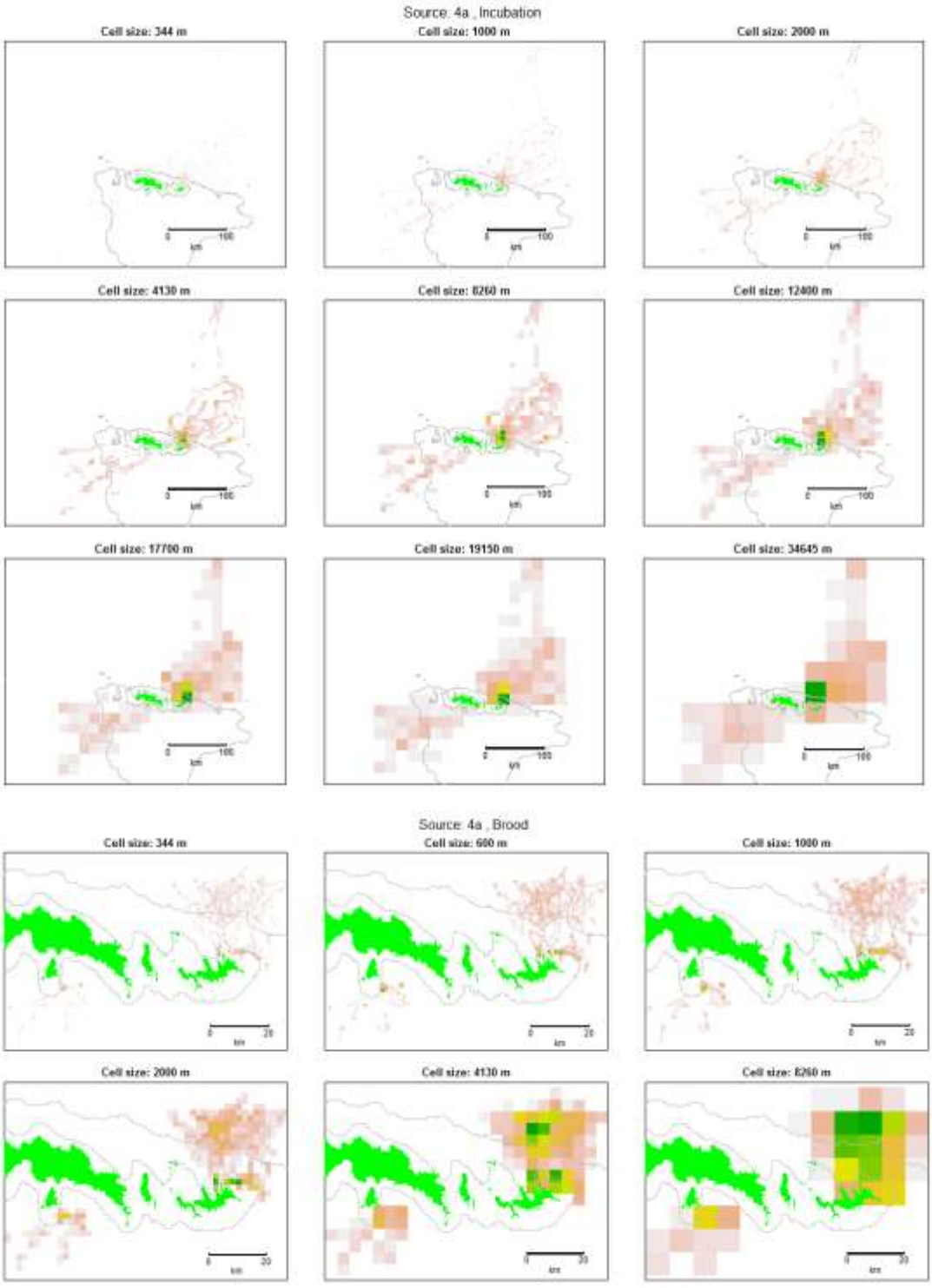
APPENDIX III

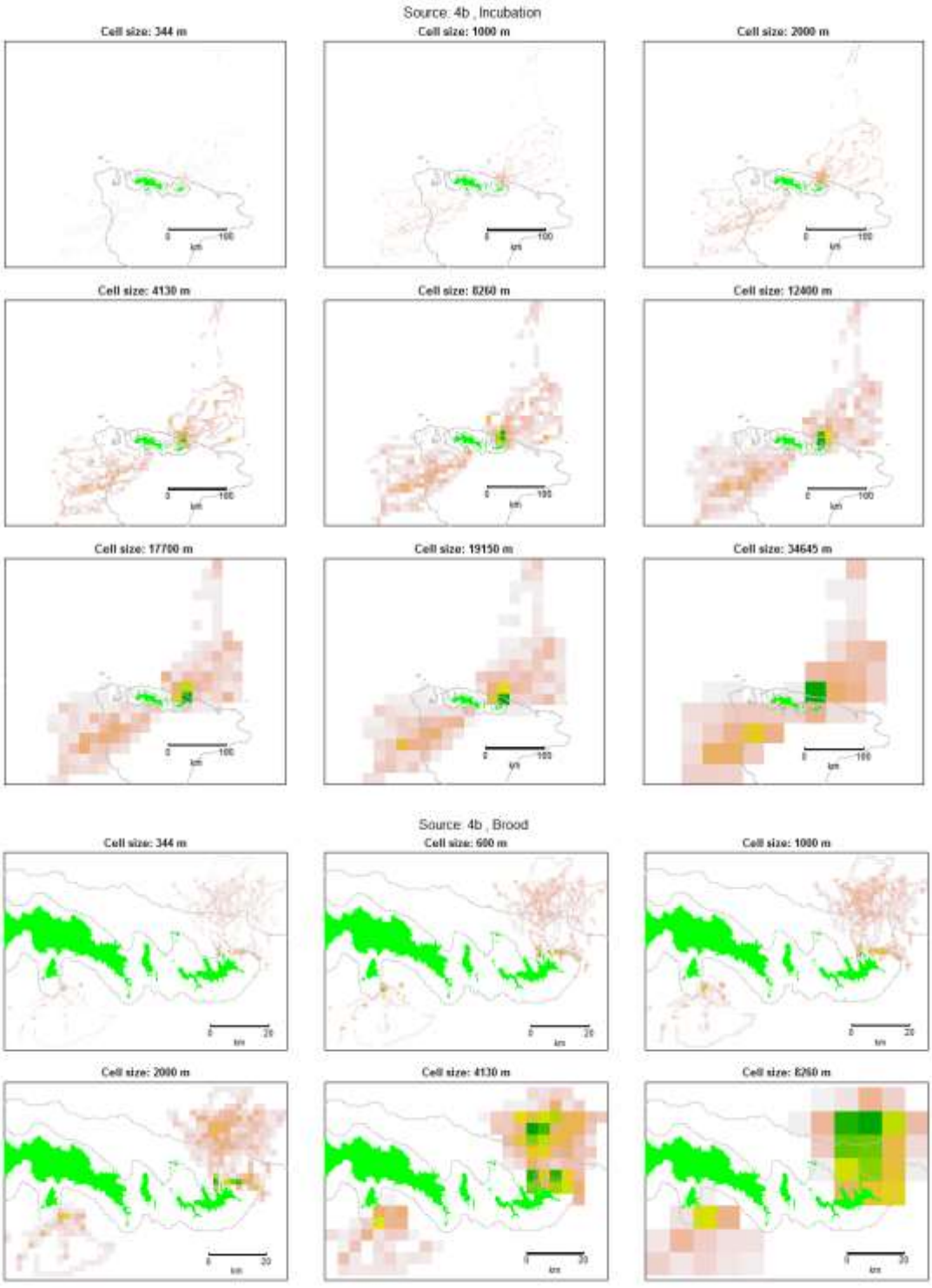



Source: 2b , Incubation
Cell size: 344 m
Cell size: 1000 m
Cell size: 2000 m
Cell size: 4130 m
Cell size: 8260 m
Cell size: 12400 m
Cell size: 17700 m
Cell size: 19150 m
Cell size: 34645 m
Source: 2b , Brood
Cell size: 344 m
Cell size: 600 m
Cell size: 1000 m
Cell size: 2000 m
Cell size: 4130 m
Cell size: 8260 m


Source: 3a , Incubation
Cell size: 344 m
Cell size: 1000 m
Cell size: 2000 m
Cell size: 4130 m
Cell size: 8260 m
Cell size: 12400 m
Cell size: 17700 m
Cell size: 19150 m
Cell size: 34645 m
Source: 3a , Brood
Cell size: 344 m
Cell size: 600 m
Cell size: 1000 m
Cell size: 2000 m
Cell size: 4130 m
Cell size: 8260 m

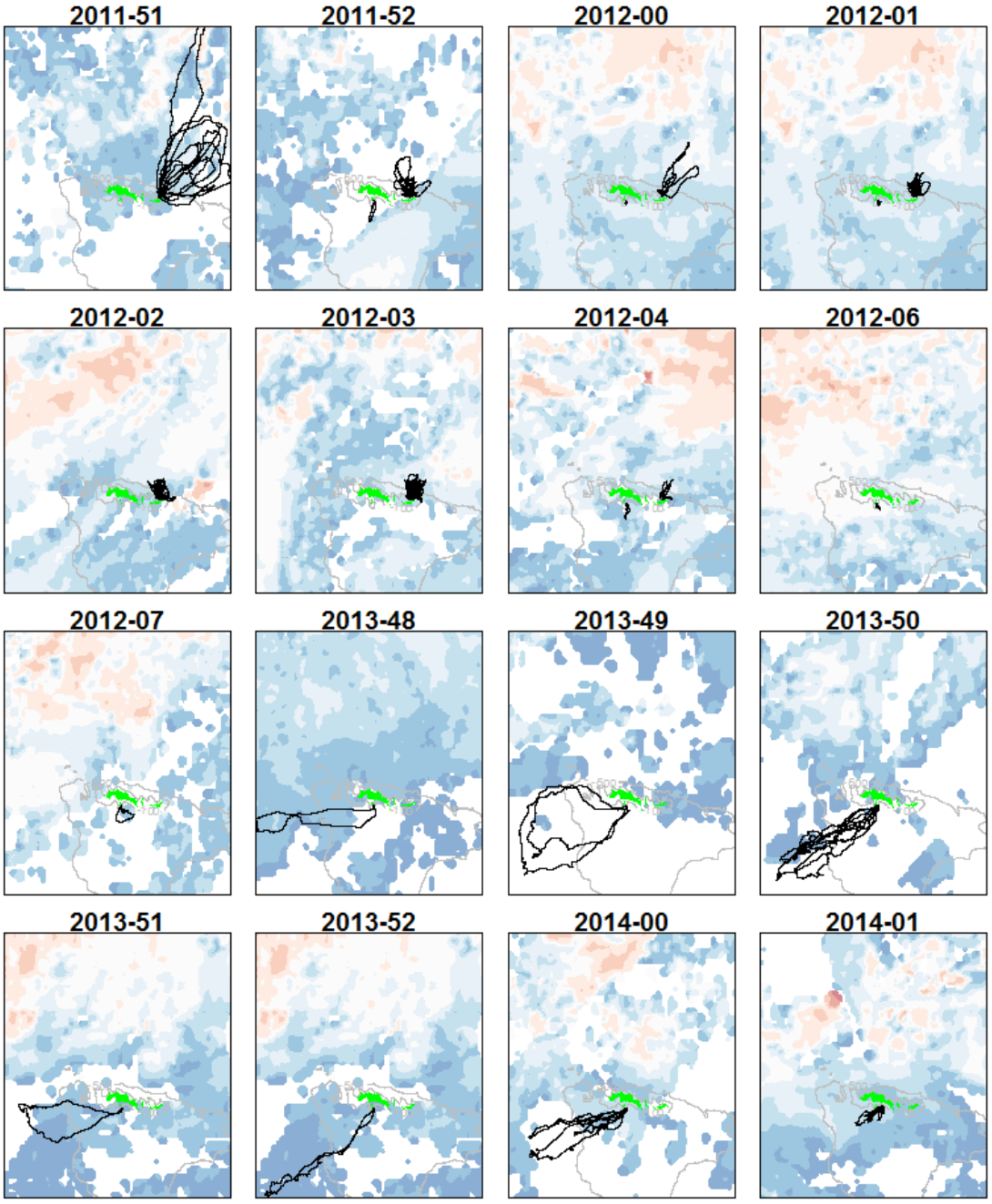

Source: 3b , Incubation
Cell size: 344 m
Cell size: 1000 m
Cell size: 2000 m
Cell size: 4130 m
Cell size: 8260 m
Cell size: 12400 m
Cell size: 17700 m
Cell size: 19150 m
Cell size: 34645 m
Source: 3b , Brood
Cell size: 344 m
Cell size: 600 m
Cell size: 1000 m
Cell size: 2000 m
Cell size: 4130 m
Cell size: 8260 m


Source: 4a , Incubation
Cell size: 344 m
Cell size: 1000 m
Cell size: 2000 m
Cell size: 4130 m
Cell size: 8260 m
Cell size: 12400 m
Cell size: 17700 m
Cell size: 19150 m
Cell size: 34645 m
Source: 4a , Brood
Cell size: 344 m
Cell size: 600 m
Cell size: 1000 m
Cell size: 2000 m
Cell size: 4130 m
Cell size: 8260 m

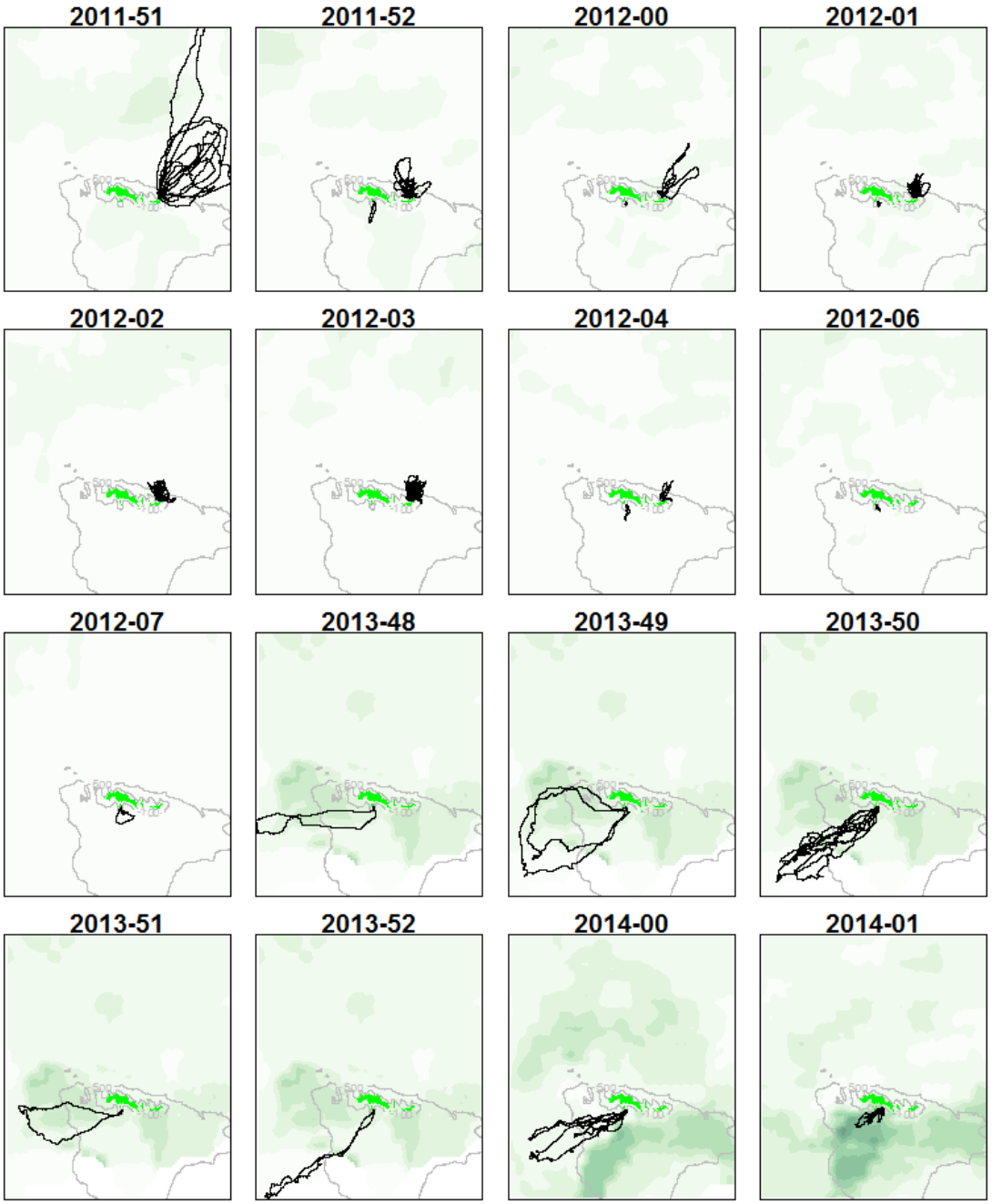

Source: 4b , Incubation
Cell size: 344 m
Cell size: 1000 m
Cell size: 2000 m
Cell size: 4130 m
Cell size: 8260 m
Cell size: 12400 m
Cell size: 17700 m
Cell size: 19150 m
Cell size: 34645 m
Source: 4b , Brood
Cell size: 344 m
Cell size: 600 m
Cell size: 1000 m
Cell size: 2000 m
Cell size: 4130 m
Cell size: 8260 m

APPENDIX IV

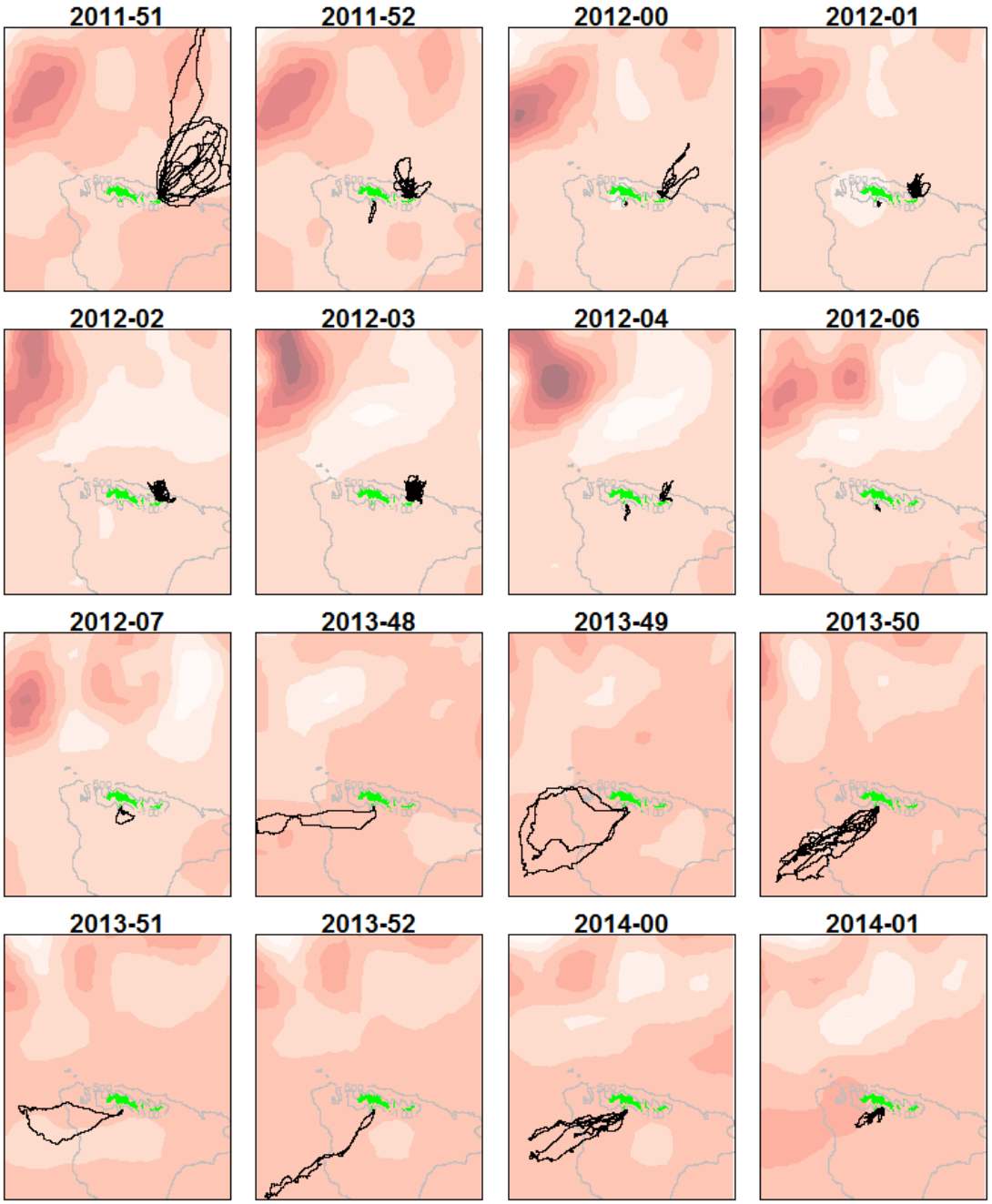
Weekly variations in sea surface temperature (SST)



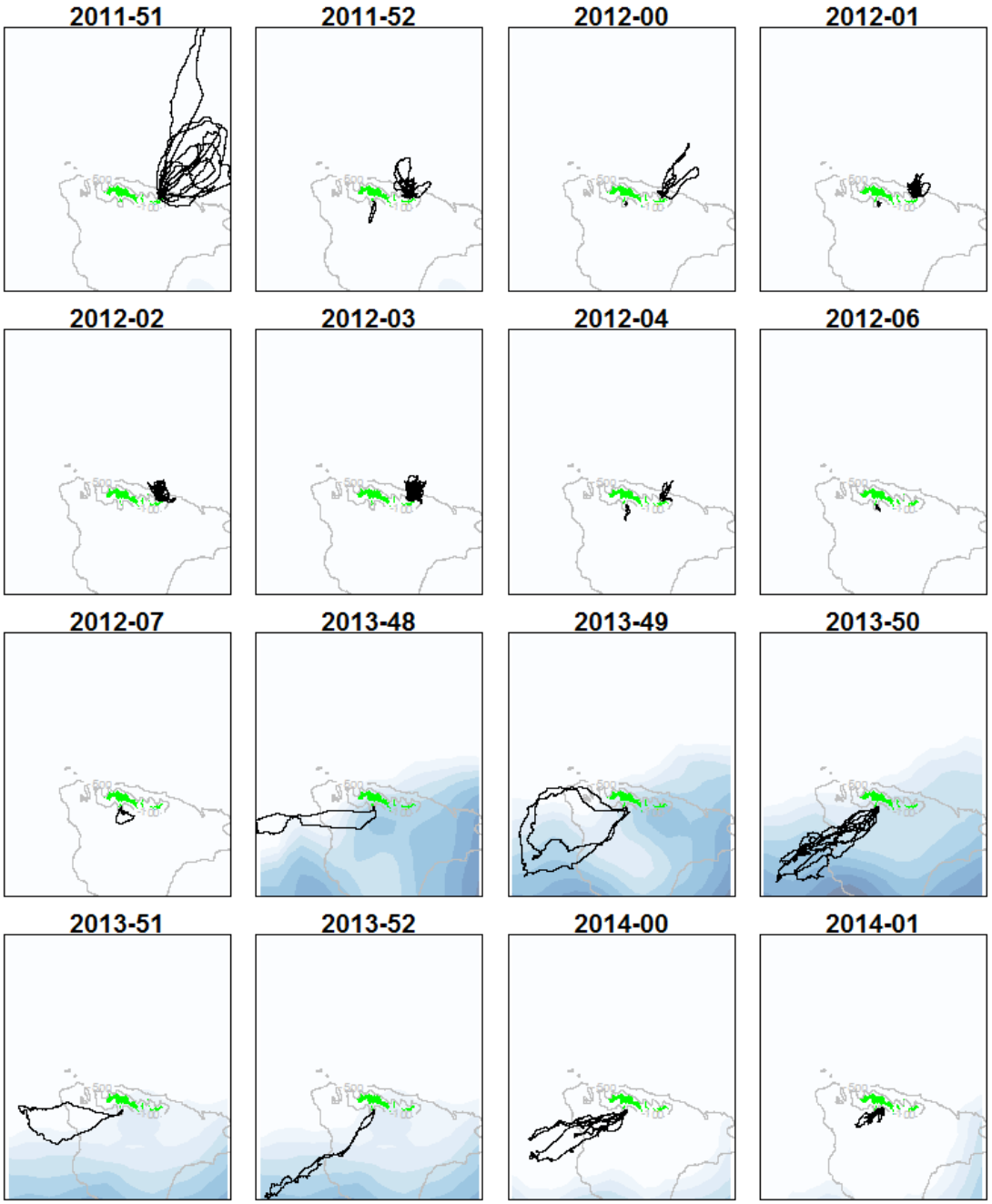
Weekly variations in net primary productivity (NPP)



Weekly variations in mean sea level anomaly (MSLA)



Weekly variations in sea ice cover



Weekly variations in surface currents

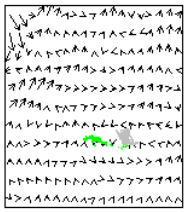
2011-51

2011-52

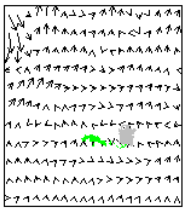
2012-00

2012-01

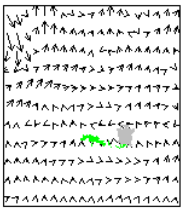
2012-02



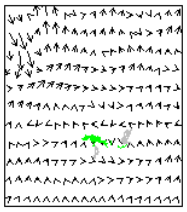
2012-03



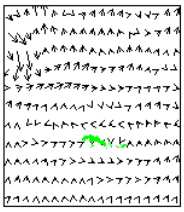
2012-03



2012-04



2012-05



2012-05

2012-06

2013-47

2013-48

2013-49

2013-50

2013-50

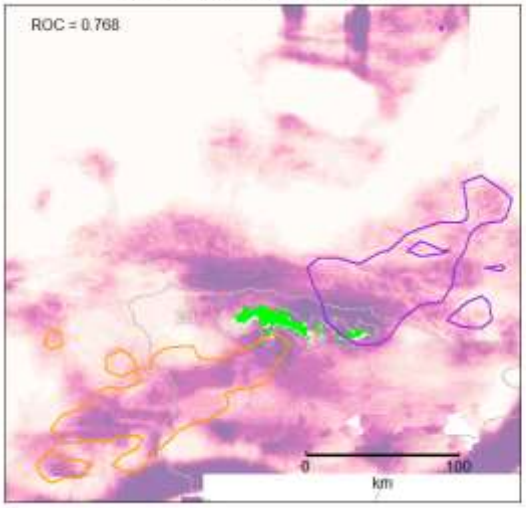
2013-51

2014-00

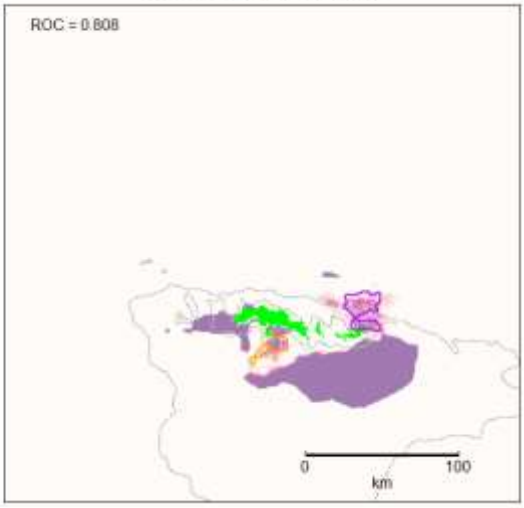
2014-01

APPENDIX V

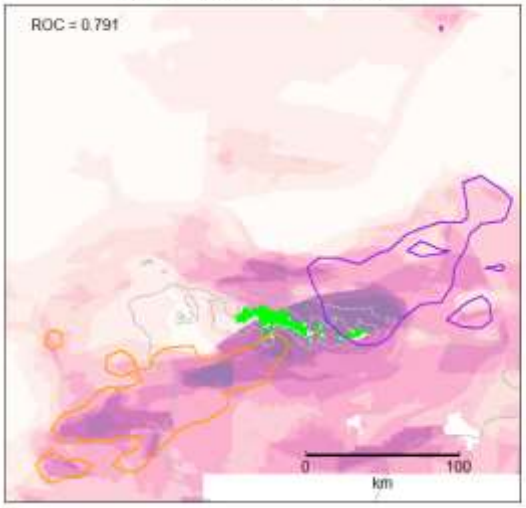
Round 1: 1a - GAM (Incubation)



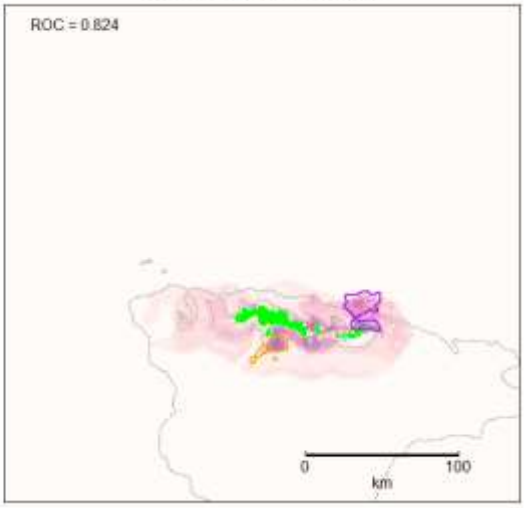
Round 1: 1a - GAM (Brood)



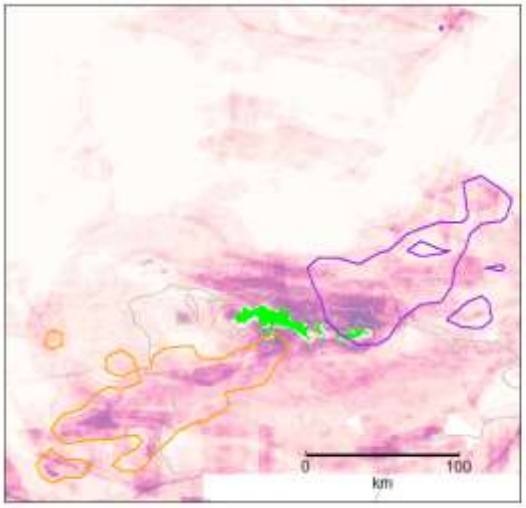
Round 1: 1a - GBM (Incubation)



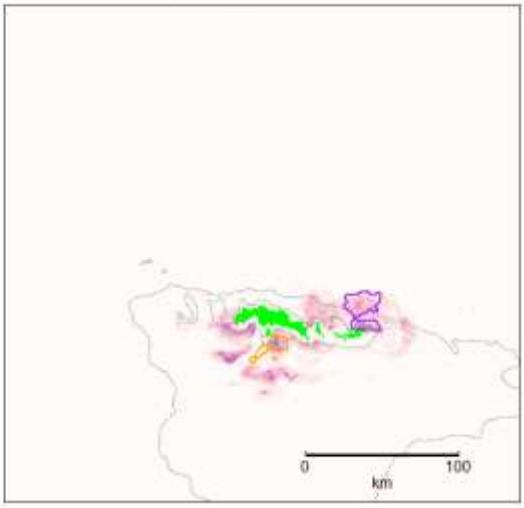
Round 1: 1a - GBM (Brood)



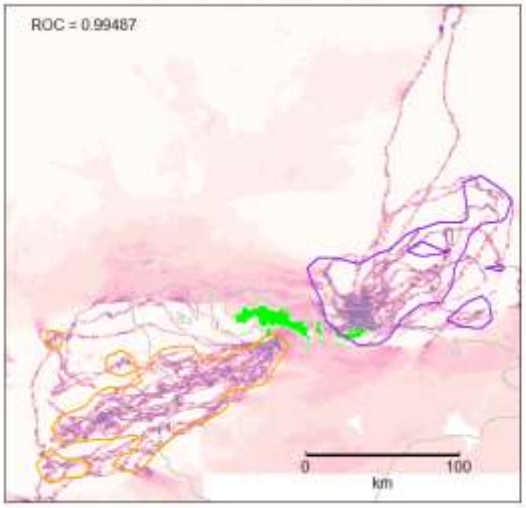
Round 1: 1a - MaxEnt (Incubation)



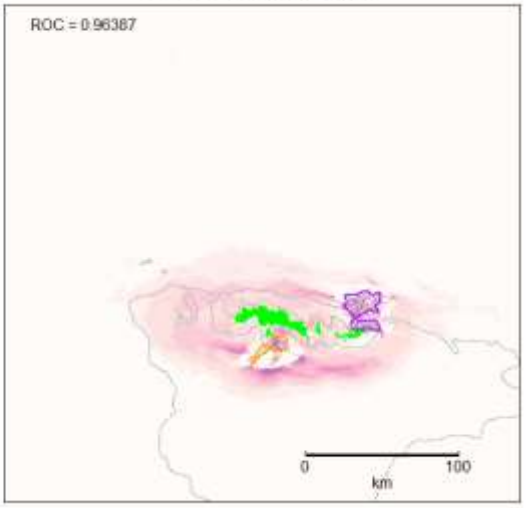
Round 1: 1a - MaxEnt (Brood)



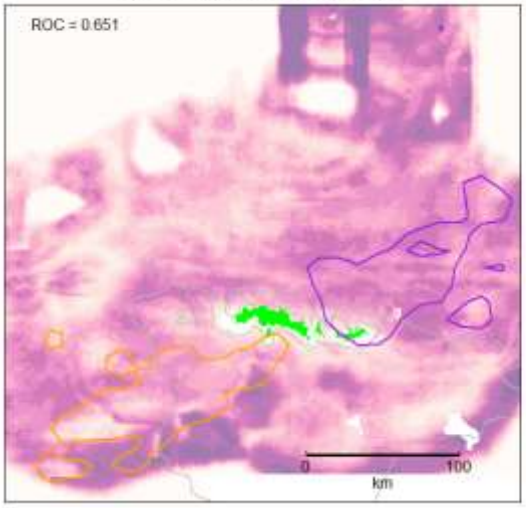
Round 1: 1a - RF (Incubation)



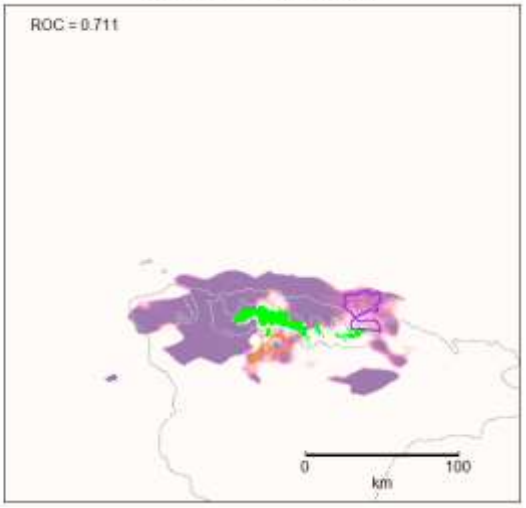
Round 1: 1a - RF (Brood)



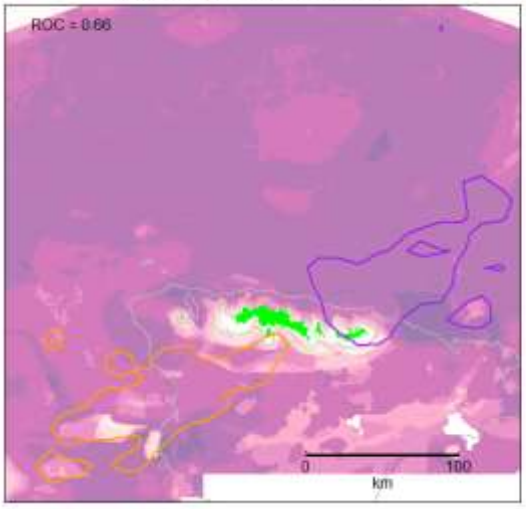
Round 1: 2b - GAM (Incubation)



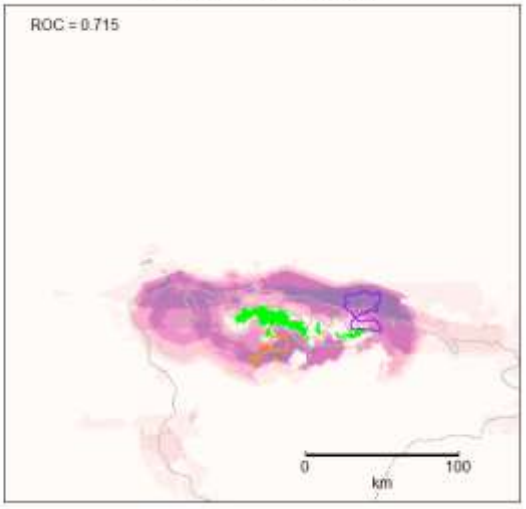
Round 1: 2b - GAM (Brood)



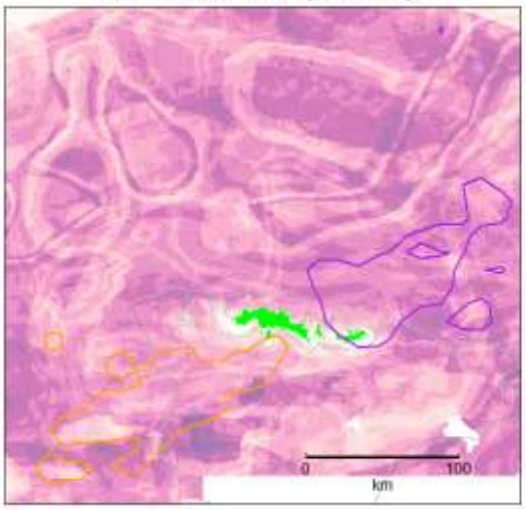
Round 1: 2b - GBM (Incubation)



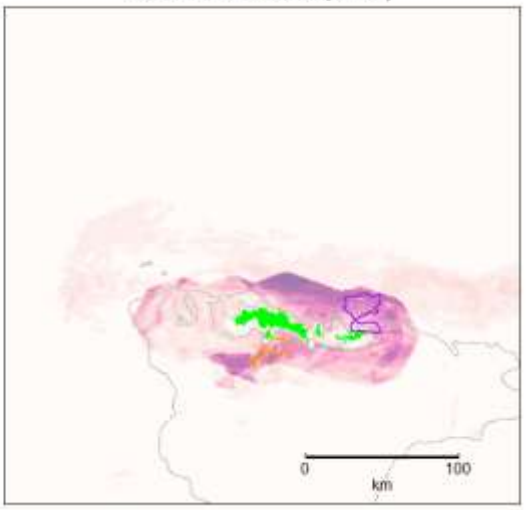
Round 1: 2b - GBM (Brood)



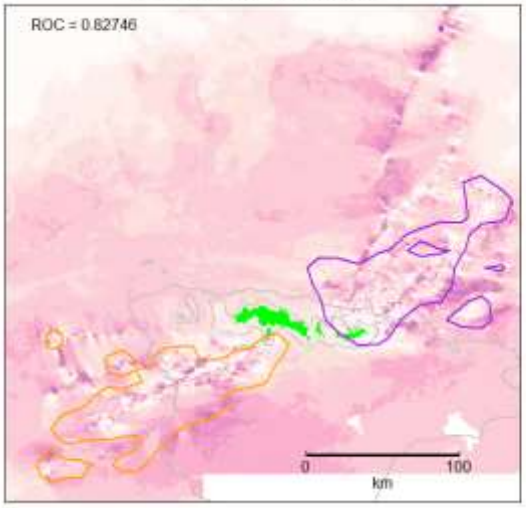
Round 1: 2b - MaxEnt (Incubation)



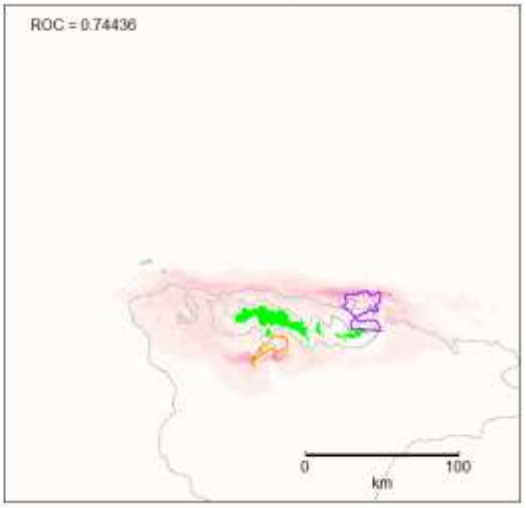
Round 1: 2b - MaxEnt (Brood)



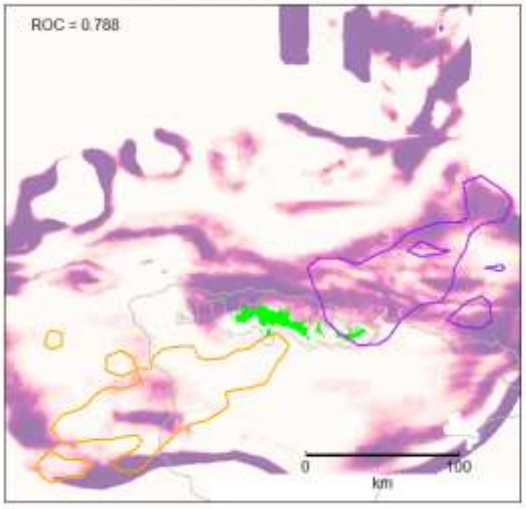
Round 1: 2b - RF (Incubation)



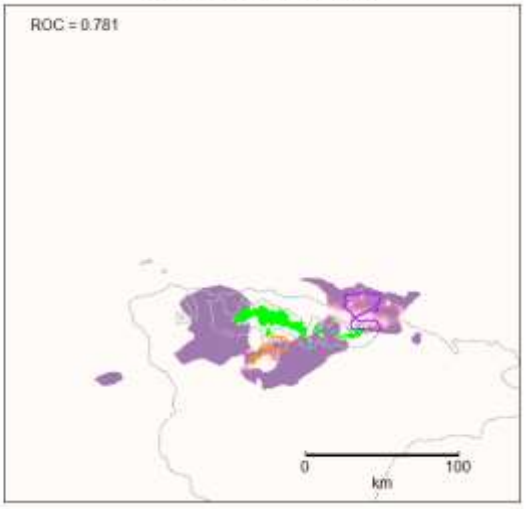
Round 1: 2b - RF (Brood)



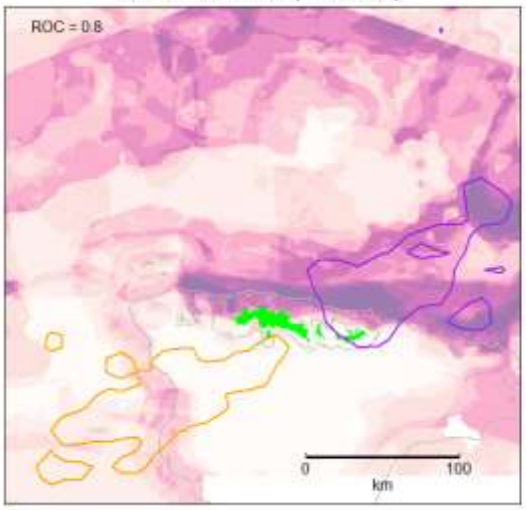
Round 1: 3a - GAM (Incubation)



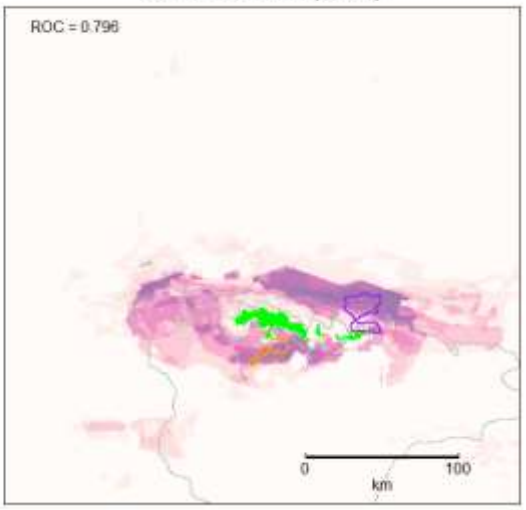
Round 1: 3a - GAM (Brood)



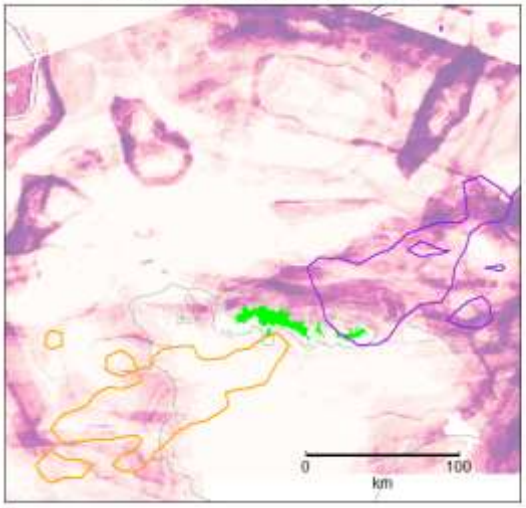
Round 1: 3a - GBM (Incubation)



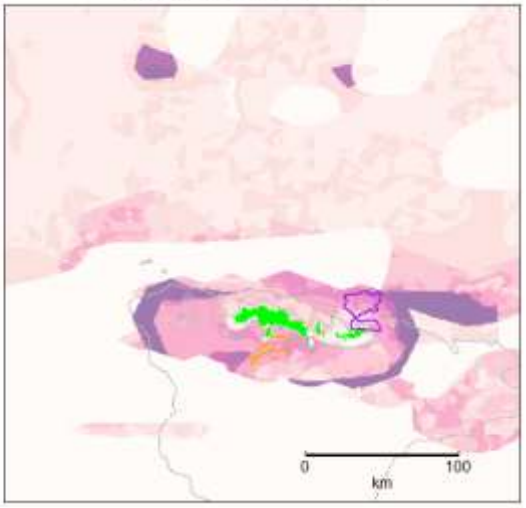
Round 1: 3a - GBM (Brood)



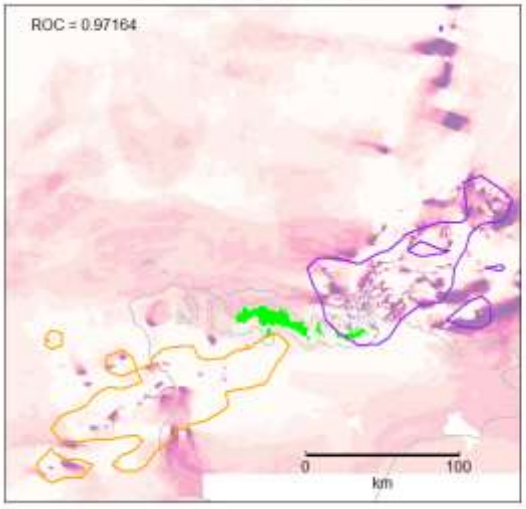
Round 1: 3a - MaxEnt (Incubation)



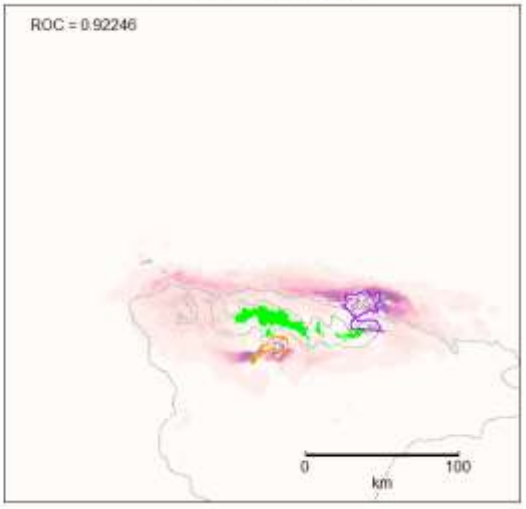
Round 1: 3a - MaxEnt (Brood)



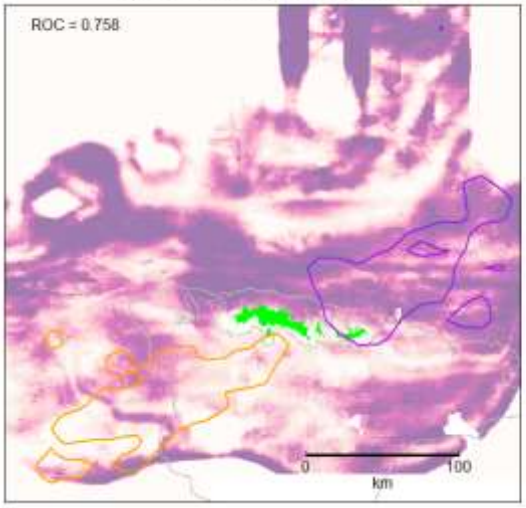
Round 1: 3a - RF (Incubation)



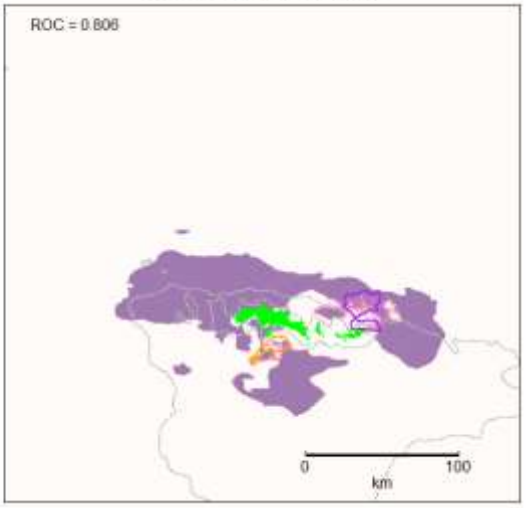
Round 1: 3a - RF (Brood)



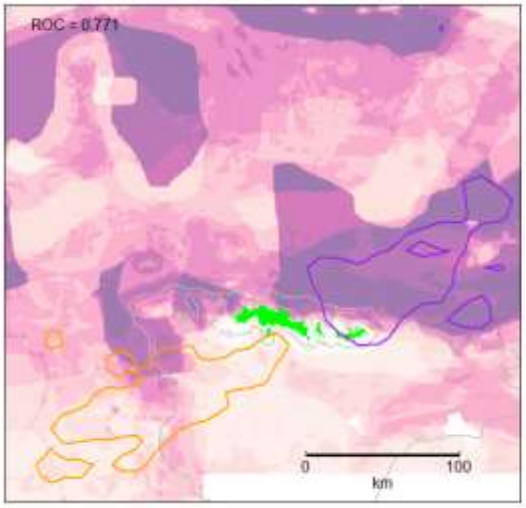
Round 1: 4a - GAM (Incubation)



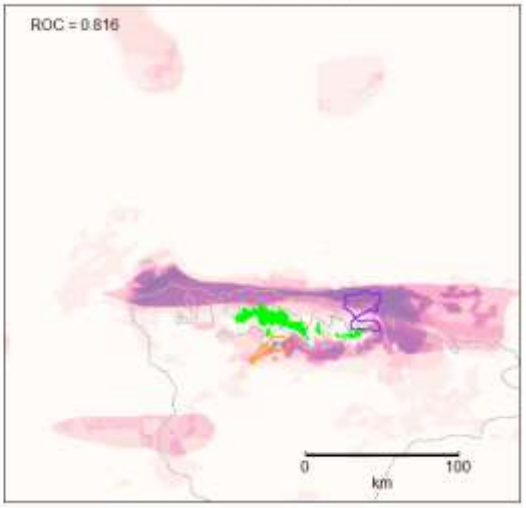
Round 1: 4a - GAM (Brood)



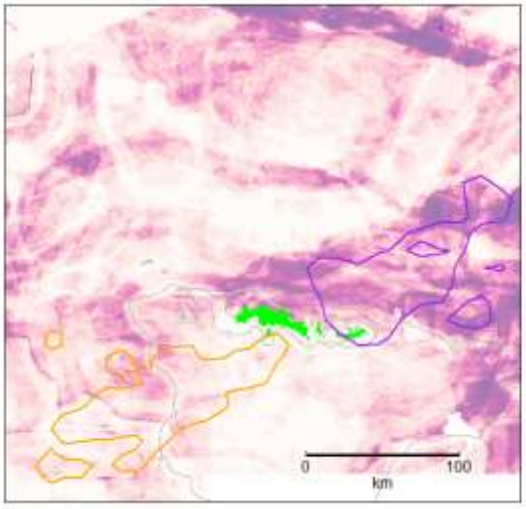
Round 1: 4a - GBM (Incubation)



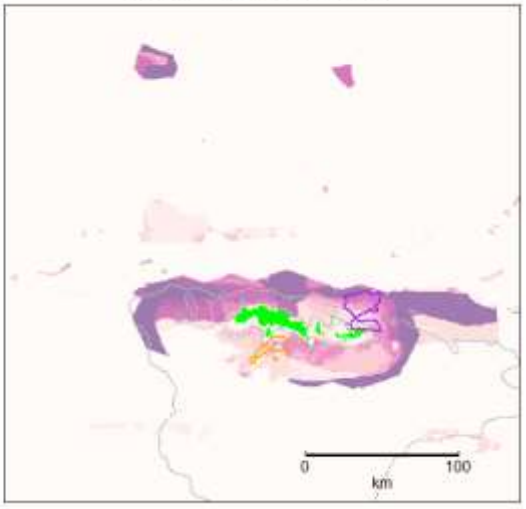
Round 1: 4a - GBM (Brood)



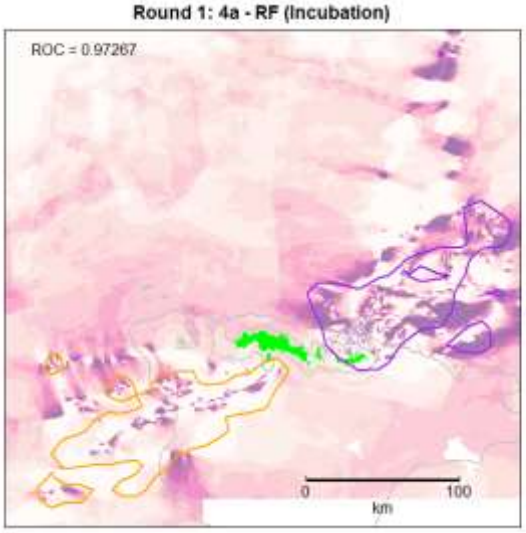
Round 1: 4a - MaxEnt (Incubation)



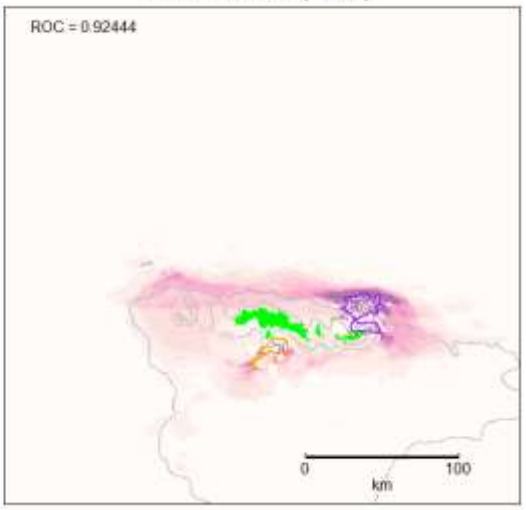
Round 1: 4a - MaxEnt (Brood)



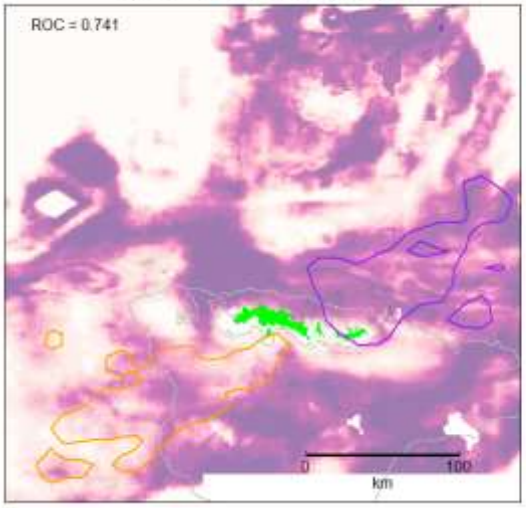
Round 1: 4a - RF (Incubation)



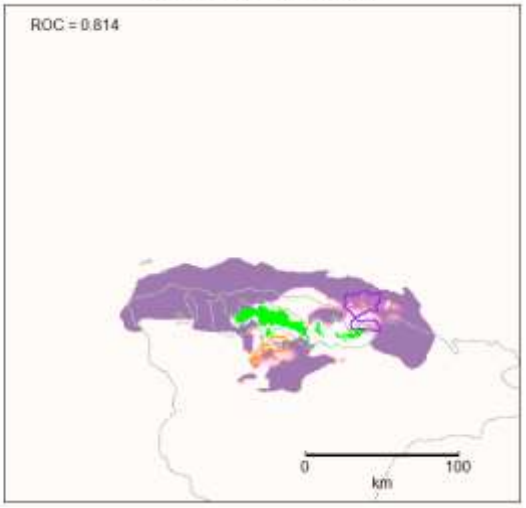
Round 1: 4a - RF (Brood)



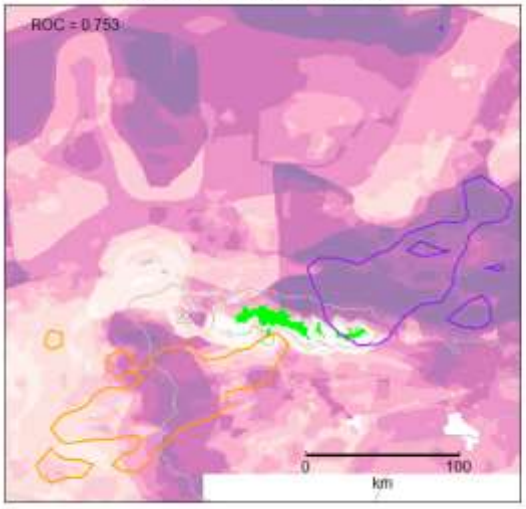
Round 1: 4b - GAM (Incubation)



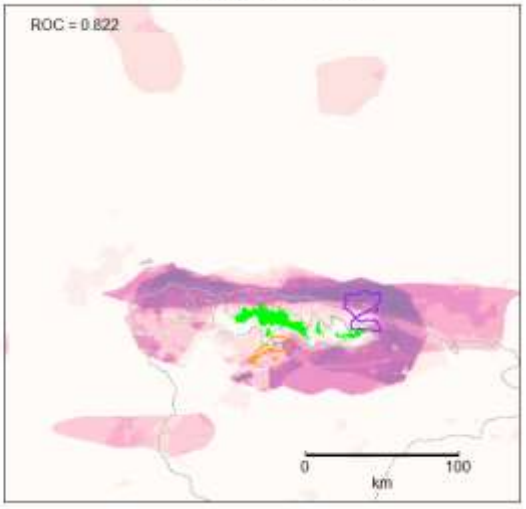
Round 1: 4b - GAM (Brood)



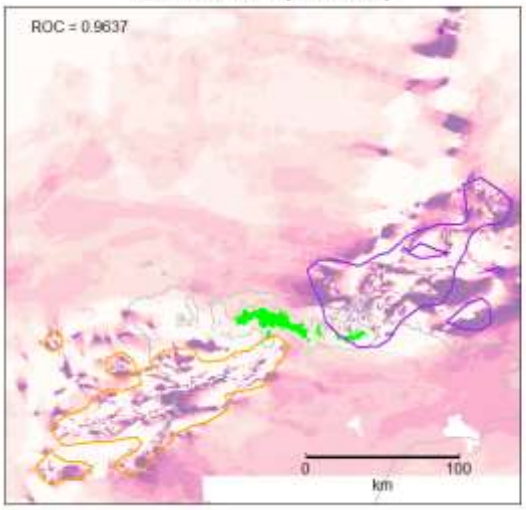
Round 1: 4b - GBM (Incubation)



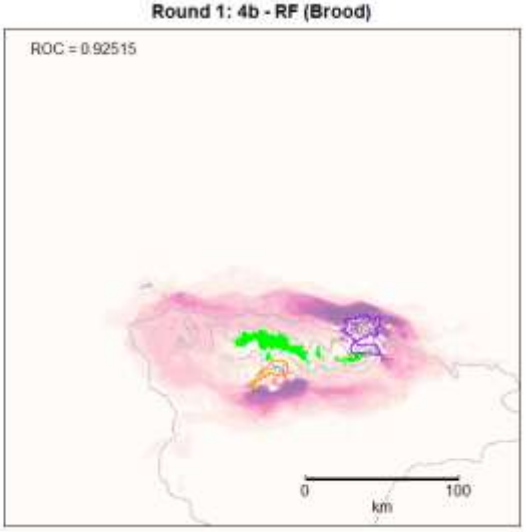
Round 1: 4b - GBM (Brood)



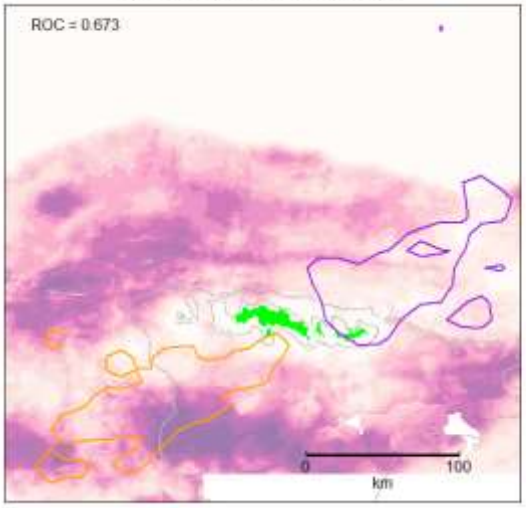
Round 1: 4b - RF (Incubation)



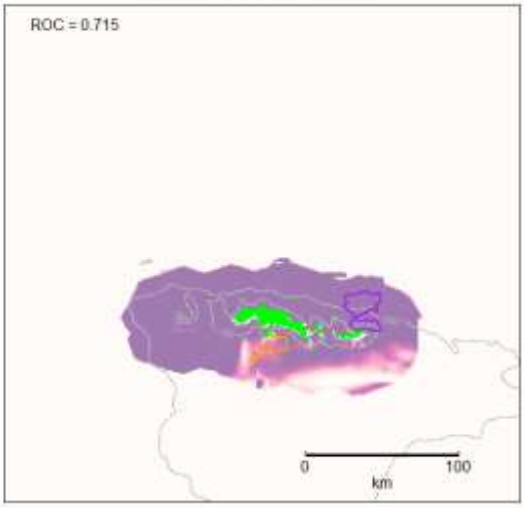
Round 1: 4b - RF (Brood)



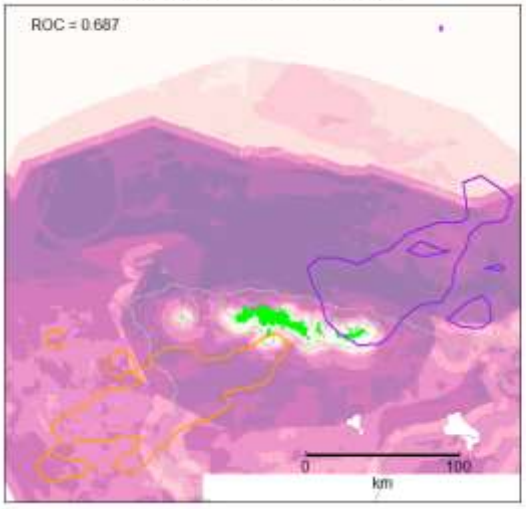
Round 2: 2b - GAM (Incubation)



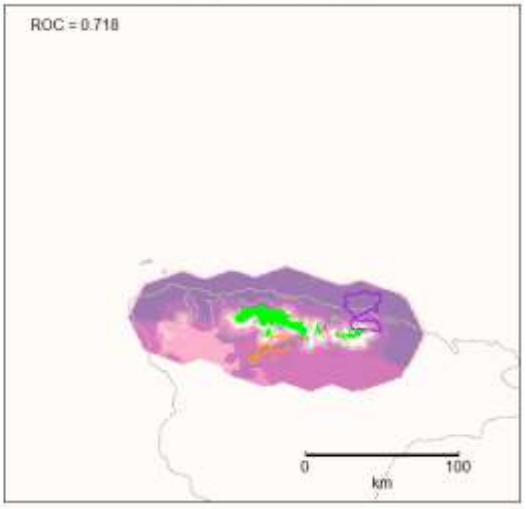
Round 2: 2b - GAM (Brood)



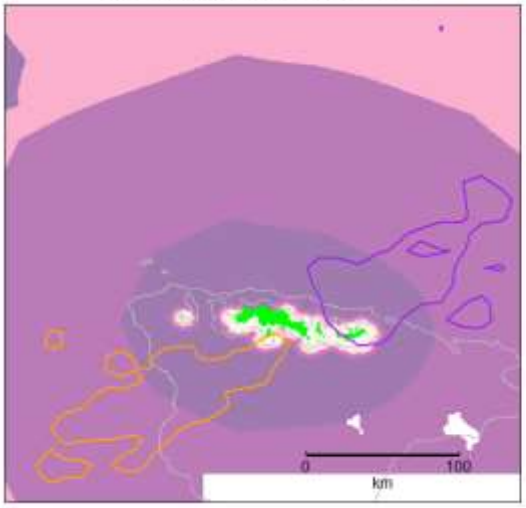
Round 2: 2b - GBM (Incubation)



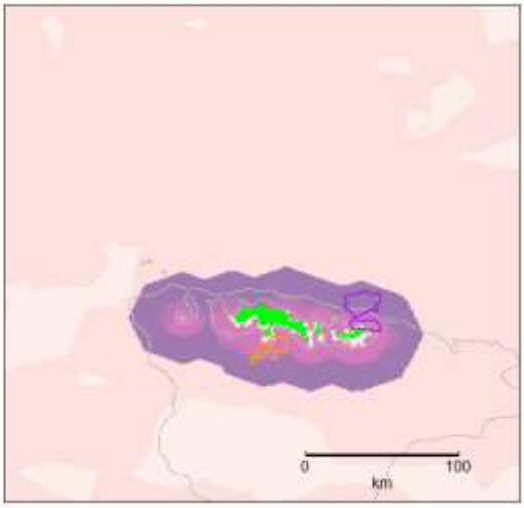
Round 2: 2b - GBM (Brood)



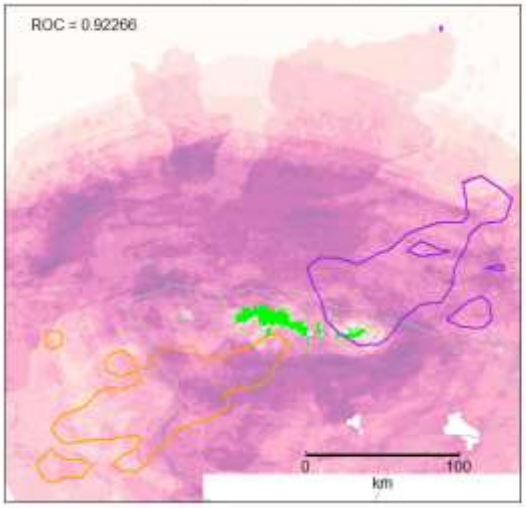
Round 2: 2b - MaxEnt (Incubation)



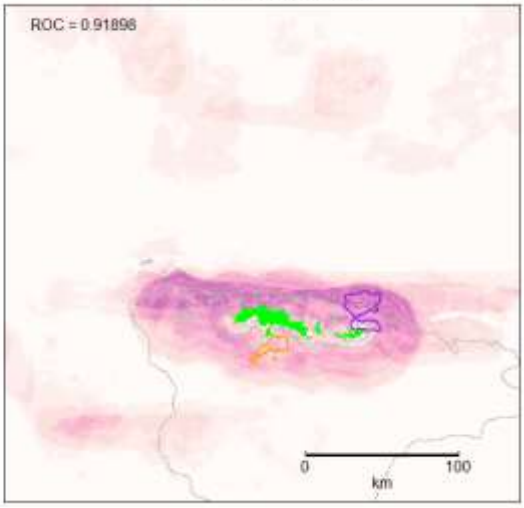
Round 2: 2b - MaxEnt (Brood)



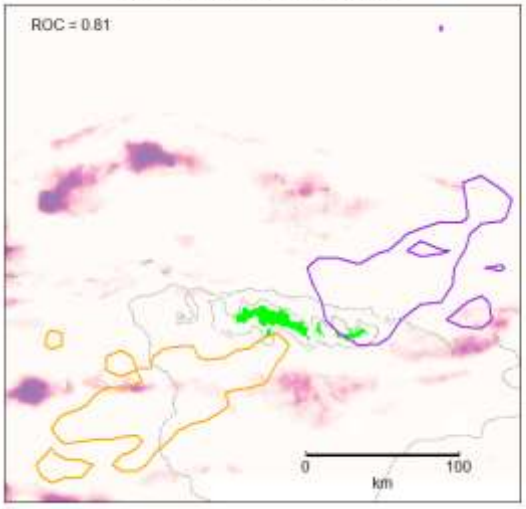
Round 2: 2b - RF (Incubation)



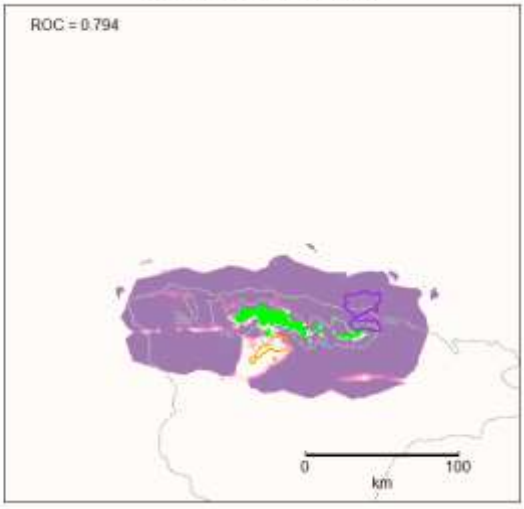
Round 2: 2b - RF (Brood)



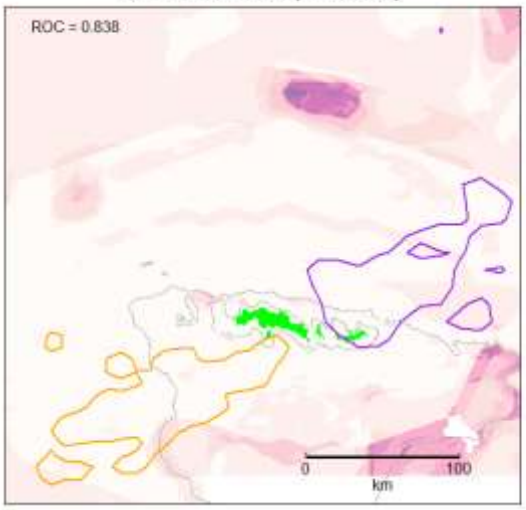
Round 2: 3a - GAM (Incubation)



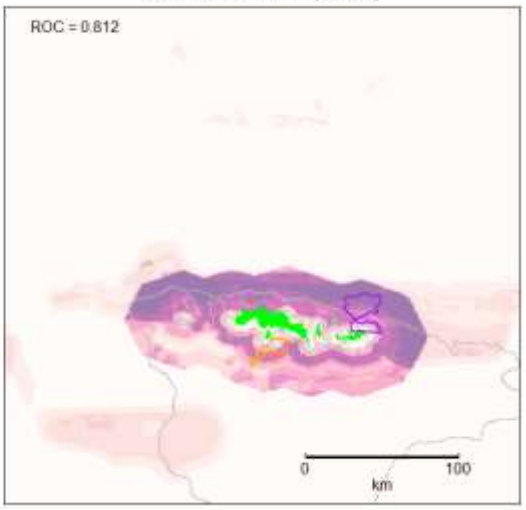
Round 2: 3a - GAM (Brood)



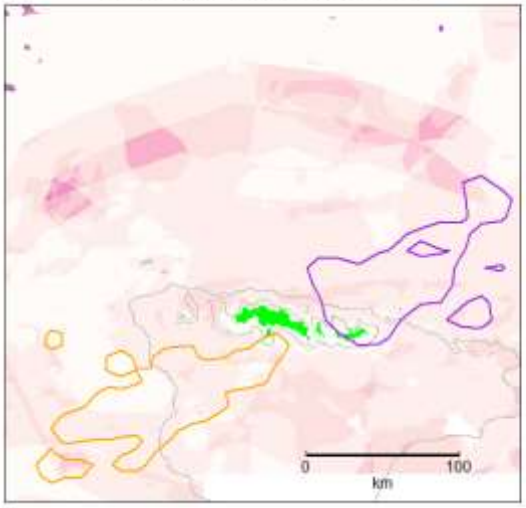
Round 2: 3a - GBM (Incubation)



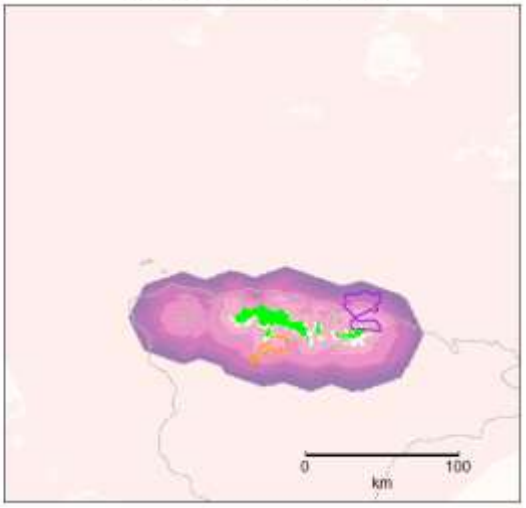
Round 2: 3a - GBM (Brood)



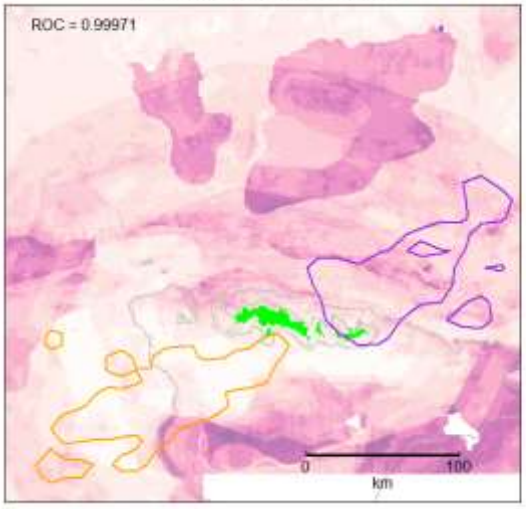
Round 2: 3a - MaxEnt (Incubation)



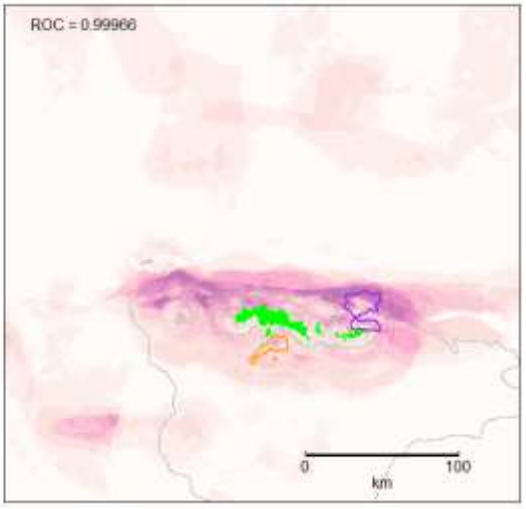
Round 2: 3a - MaxEnt (Brood)



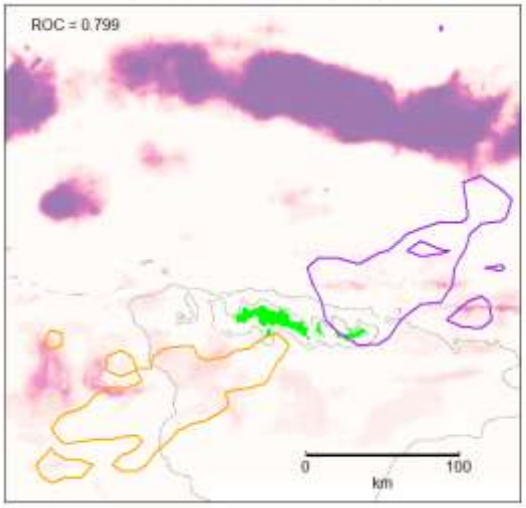
Round 2: 3a - RF (Incubation)



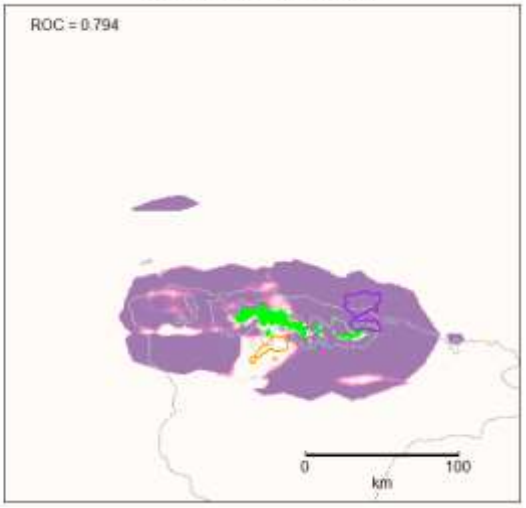
Round 2: 3a - RF (Brood)



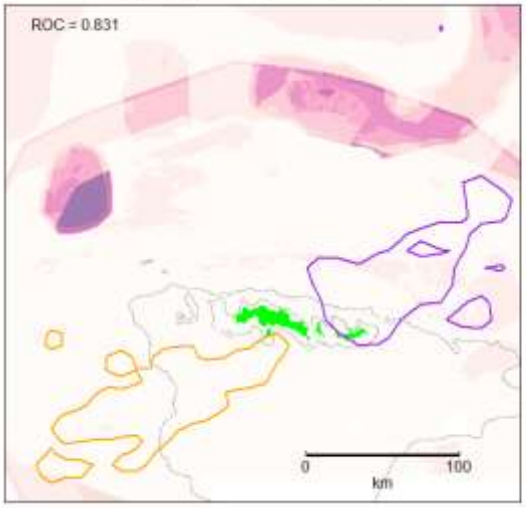
Round 2: 3b - GAM (Incubation)



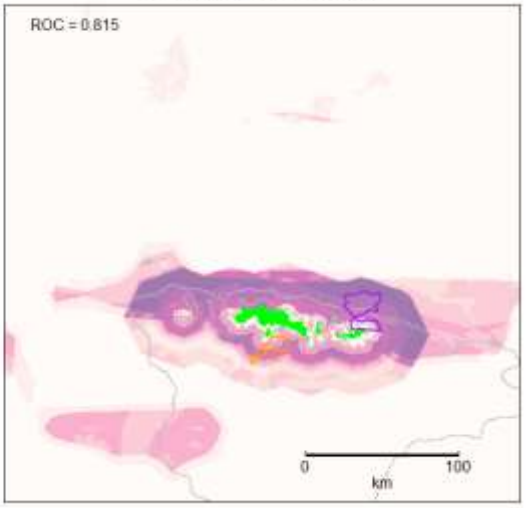
Round 2: 3b - GAM (Brood)



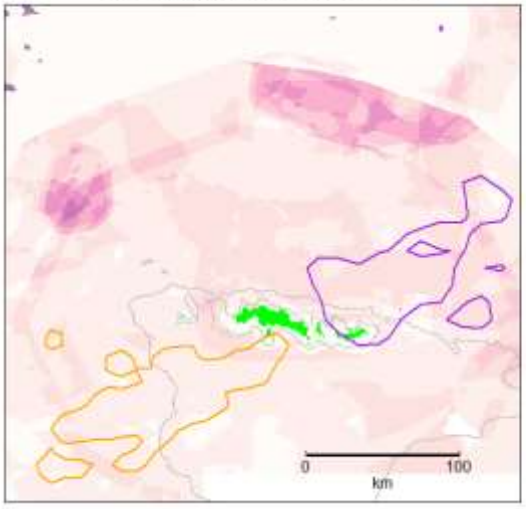
Round 2: 3b - GBM (Incubation)



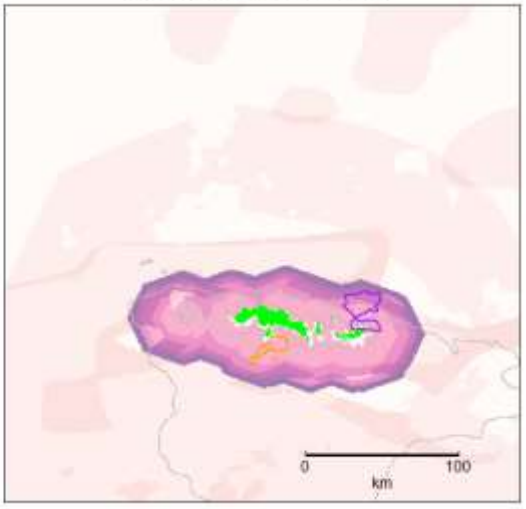
Round 2: 3b - GBM (Brood)



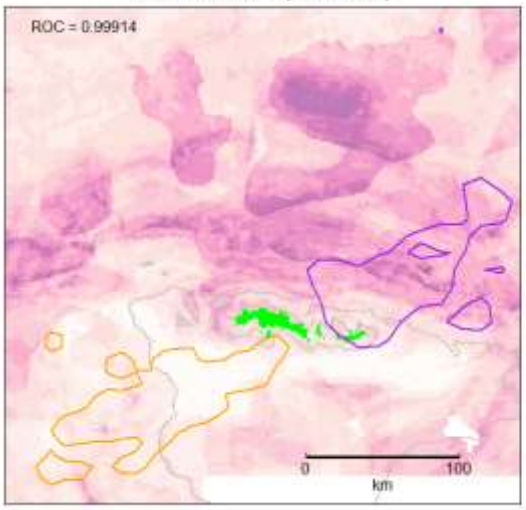
Round 2: 3b - MaxEnt (Incubation)



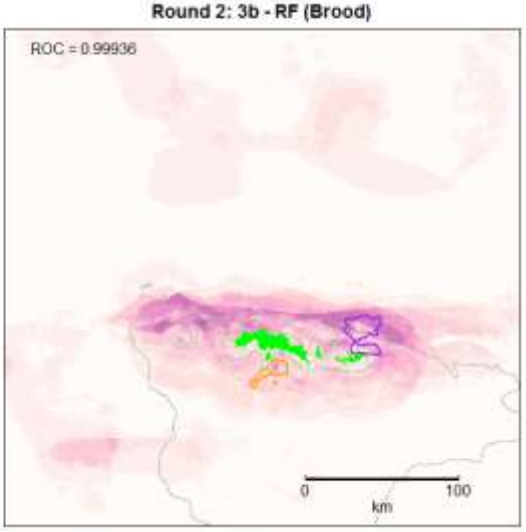
Round 2: 3b - MaxEnt (Brood)



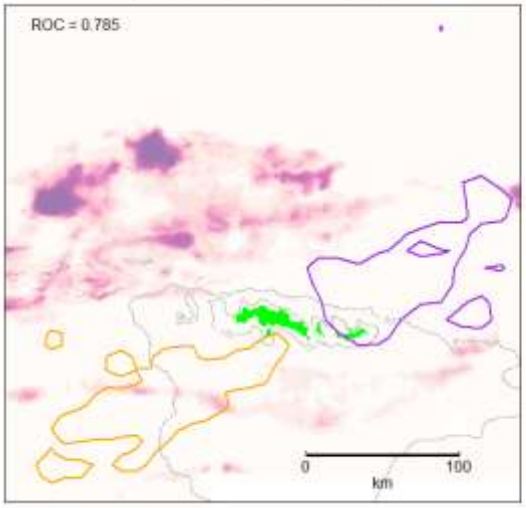
Round 2: 3b - RF (Incubation)



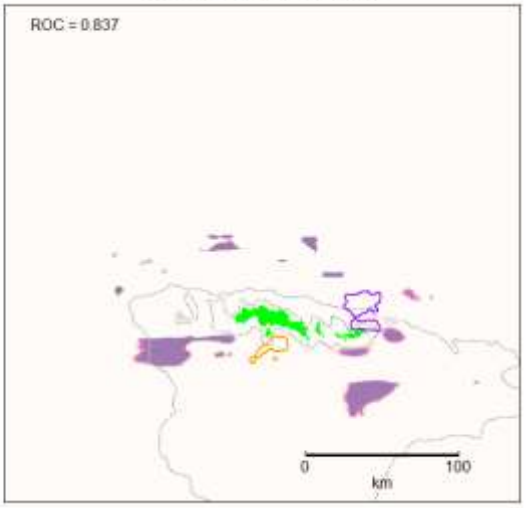
Round 2: 3b - RF (Brood)



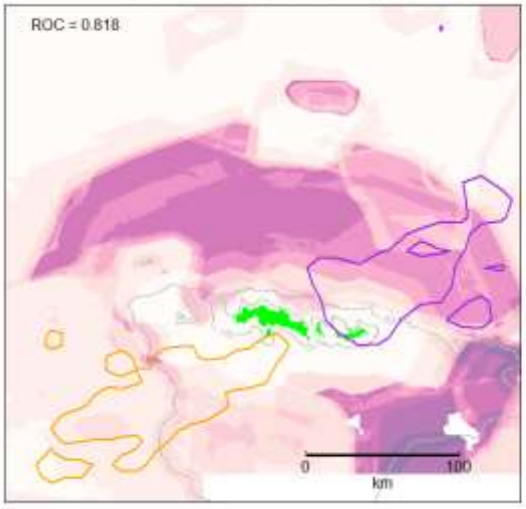
Round 2: 4a - GAM (Incubation)



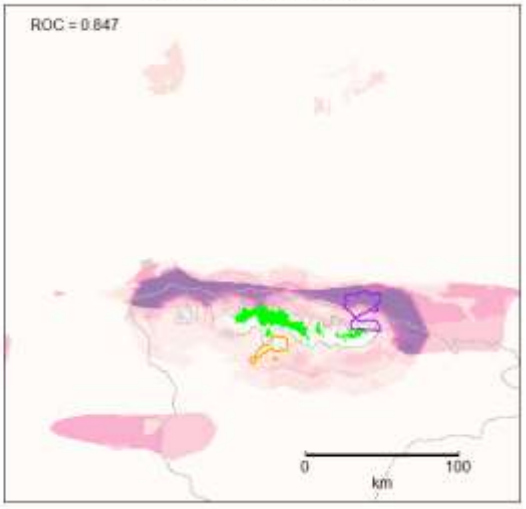
Round 2: 4a - GAM (Brood)



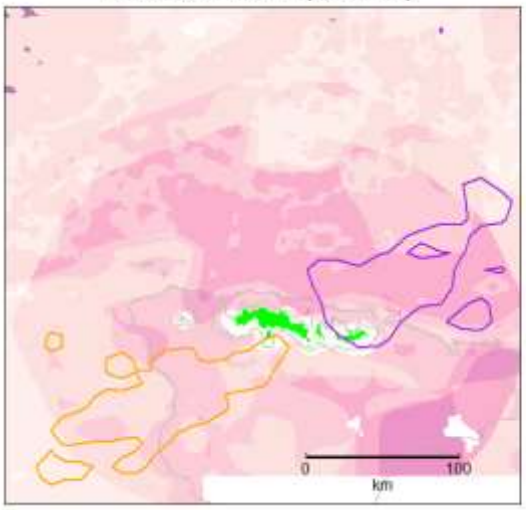
Round 2: 4a - GBM (Incubation)



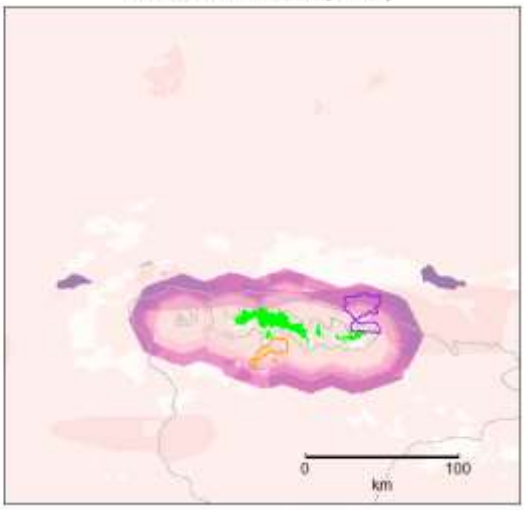
Round 2: 4a - GBM (Brood)



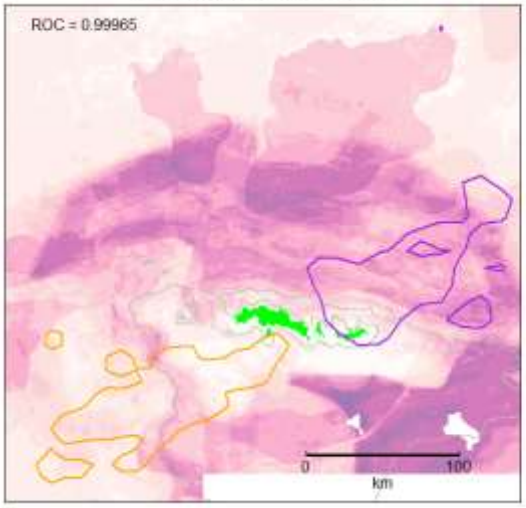
Round 2: 4a - MaxEnt (Incubation)



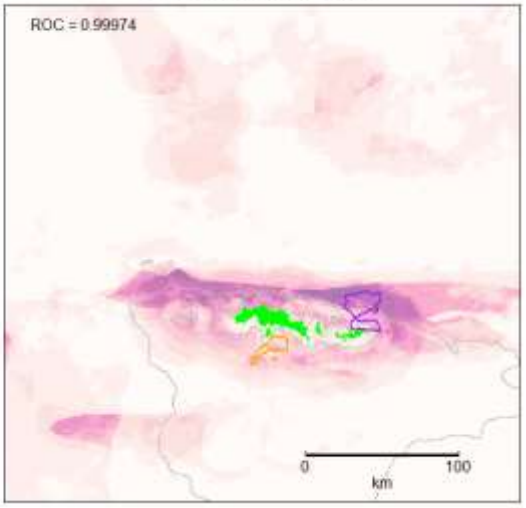
Round 2: 4a - MaxEnt (Brood)



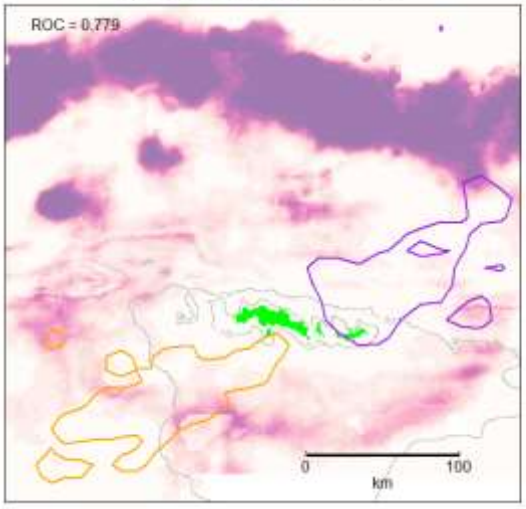
Round 2: 4a - RF (Incubation)



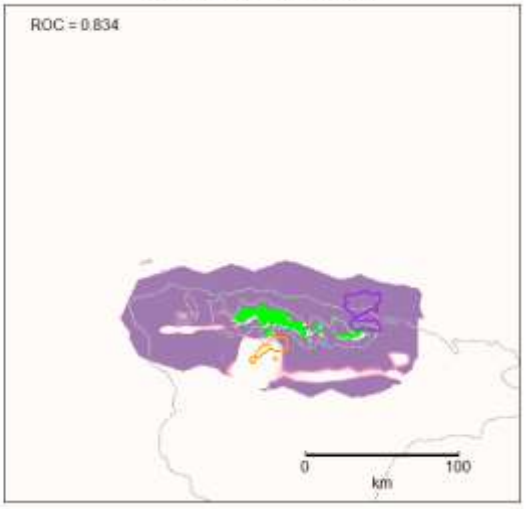
Round 2: 4a - RF (Brood)



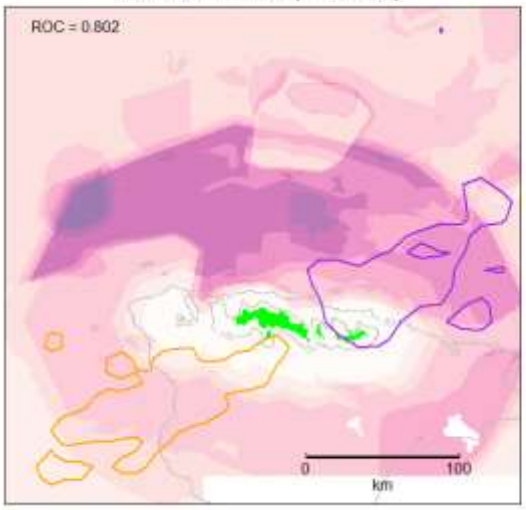
Round 2: 4b - GAM (Incubation)



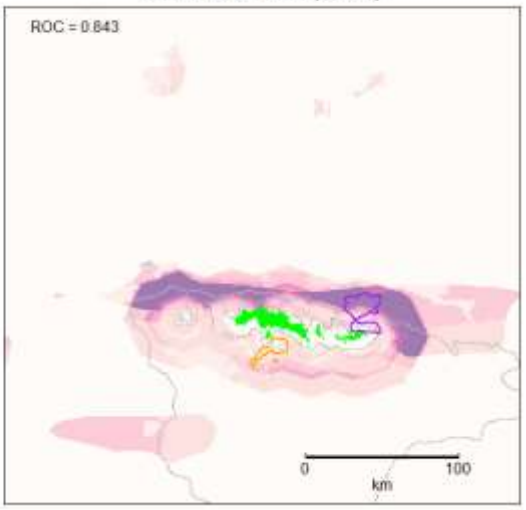
Round 2: 4b - GAM (Brood)



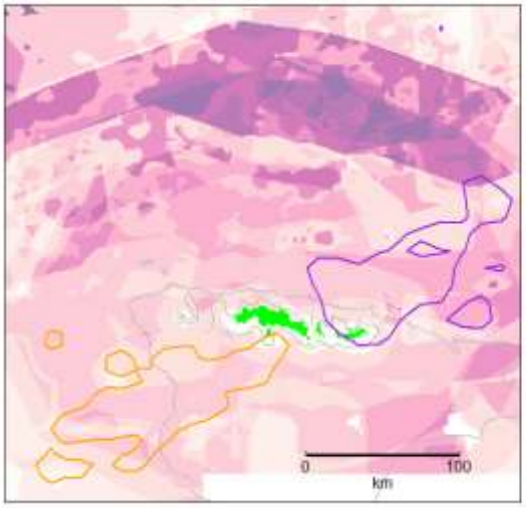
Round 2: 4b - GBM (Incubation)



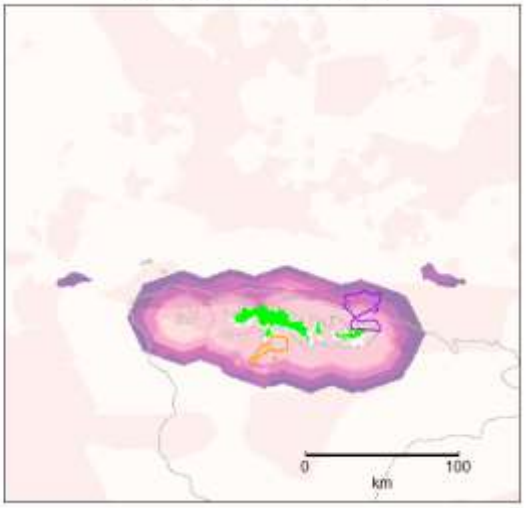
Round 2: 4b - GBM (Brood)



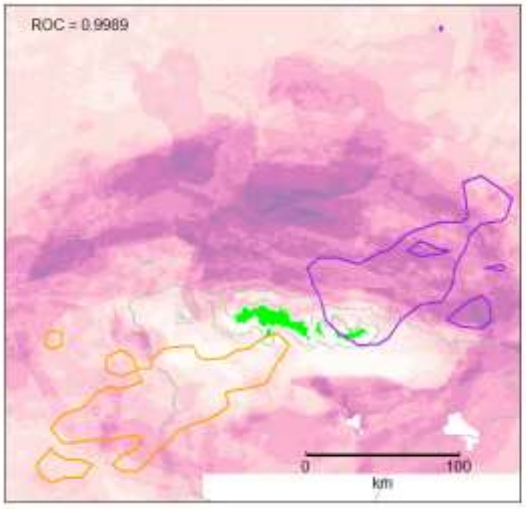
Round 2: 4b - MaxEnt (Incubation)



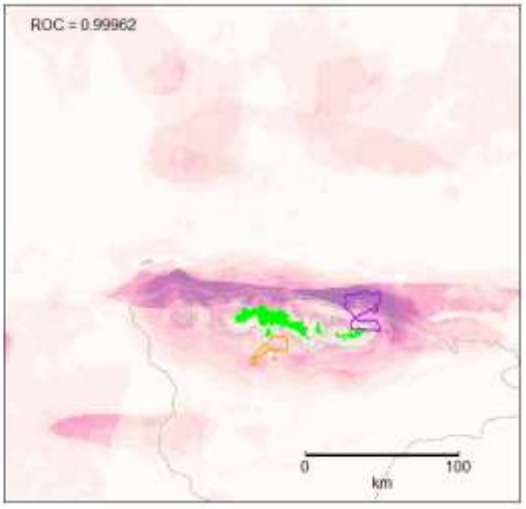
Round 2: 4b - MaxEnt (Brood)



Round 2: 4b - RF (Incubation)



Round 2: 4b - RF (Brood)



APPENDIX VI

Round-Input-Model	Model performance AUC	Rank	Krill validation Correlation	Rank	Site cross-validation AUC	Rank	Correlation	Rank	Final Rank
INCUBATION									
2-4a- RF	0.9996	2	0.27 +	4	0.6241	2	0.30 +	9	17
2-4b-RF	**0.9989**	**4**	**0.29 +**	**2**	**0.5701**	**7**	**0.22 +**	**10**	**23**
1-1a-RF	0.9949	5	0.11 -	19	0.6647	1	0.53 +	4	29
2-2b-RF	0.9227	10	0.21 +	9	0.5571	16	0.45 +	8	43
2-3b-RF	0.9991	3	0.27 +	3	0.5261	28	0.20 +	11	45
2-4b-GBM	0.8020	16	0.19 +	11	0.5855	4	0.11 +	16	47
1-1a-GBM	0.7910	19	0.30 -	1	0.5661	9	0.02 +	20	49
2-3a-RF	0.9997	1	0.21 +	10	0.5276	27	0.12 +	14	52
2-4a-GBM	0.8180	14	0.22 +	7	0.5528	20	0.17 +	12	53
1-3a-RF	0.9716	7	0.02 +	28	0.5536	18	0.62 +	1	54
1-4a-RF	0.9727	6	0.01 -	31	0.5574	15	0.61 +	2	54
2-2b-GBM	0.6870	30	0.24 +	6	0.5605	13	0.48 +	7	56
1-3b-RF	0.9659	8	0.00 -	33	0.5640	11	0.52 +	5	57
1-4b-RF	0.9637	9	0.05 -	23	0.5529	19	0.52 +	6	57
2-3a-GAM	0.8100	15	0.18 +	12	0.5548	17	0.10 +	17	61
2-3a-GBM	0.8380	11	0.04 -	24	0.5777	6	0.02 -	23	64
1-3b-GBM	0.7800	22	0.17 +	13	0.6068	3	0.50 -	31	69
1-3a-GAM	0.7880	20	0.06 +	22	0.5841	5	0.04 -	24	71
1-2b-RF	0.8275	13	0.02 -	29	0.5367	26	0.55 +	3	71
1-3a-GBM	0.8000	17	0.24 +	5	0.5482	23	0.23 -	29	74
2-4a-GAM	0.7850	21	0.15 +	17	0.5602	14	0.11 -	25	77
2-4b-GAM	0.7790	23	0.09 -	21	0.5660	10	0.15 -	28	82
2-2b-GAM	0.6730	31	0.10 -	20	0.5606	12	0.02 +	22	85
1-4a-GBM	0.7710	24	0.15 +	18	0.5261	29	0.12 +	15	86
1-4b-GAM	0.7410	29	0.00 +	32	0.5697	8	0.06 +	18	87
1-2b-GBM	0.6600	32	0.22 +	8	0.5493	21	0.14 -	27	88
2-3b-GAM	0.7990	18	0.16 -	15	0.4869	33	0.14 -	26	92
2-3b-GBM	0.8310	12	0.02 -	30	0.5170	30	0.02 +	21	93
1-1a-GAM	0.7680	25	0.17 -	14	0.5427	24	0.28 -	30	93
1-4a-GAM	0.7580	27	0.16 +	16	0.4933	32	0.03 +	19	94
1-3b-GAM	0.7650	26	0.03 +	25	0.5099	31	0.12 +	13	95
1-4b-GBM	0.7530	28	0.03 -	26	0.5416	25	0.57 -	33	112
1-2b-GAM	0.6510	33	0.03 +	27	0.5489	22	0.52 -	32	114

Round-Input-Model	Model performance AUC	Rank	Krill validation Correlation	Rank	Site cross-validation AUC	Rank	Correlation	Rank	Final Rank
BROOD									
2-4b-RF	**0.9996**	**3**	**0.36 +**	**3**	**0.6425**	**3**	**0.60 +**	**2**	**11**
2-3a-RF	0.9997	2	0.31 +	7	0.6470	2	0.42 +	9	20
1-1a-RF	0.9639	5	0.28 +	17	0.7914	1	0.81 +	1	24
2-4a-RF	0.9997	1	0.34 +	4	0.6197	8	0.36 +	12	25
2-3b-RF	0.9994	4	0.31 +	9	0.6162	9	0.46 +	7	29
2-2b-RF	0.9190	10	0.32 +	6	0.6017	11	0.51 +	4	31
2-4b-GBM	0.8430	12	0.36 +	2	0.6141	10	0.01 +	21	45
1-4a-RF	0.9244	7	0.27 +	18	0.5891	16	0.48 +	5	46
2-4a-GBM	0.8470	11	0.36 +	1	0.5760	20	0.14 +	17	49
1-2b-RF	0.7444	29	0.29 +	14	0.6216	7	0.48 +	6	56
1-3a-RF	0.9225	8	0.24 +	24	0.5919	14	0.37 +	11	57
1-1a-GBM	0.8240	15	0.32 +	5	0.5941	13	0.14 -	28	61
2-4b-GAM	0.8340	14	0.24 +	22	0.6387	4	0.07 -	25	65
1-4b-RF	0.9252	6	0.23 +	25	0.5540	24	0.41 +	10	65
1-3b-RF	0.9210	9	0.20 +	27	0.5846	18	0.29 +	13	67
1-4a-GBM	0.8160	17	0.29 +	12	0.6268	6	0.30 -	33	68
1-2b-GBM	0.7150	31	0.21 +	26	0.5912	15	0.52 +	3	75
1-4b-GAM	0.8140	19	0.29 +	11	0.5000	32	0.18 +	15	77
1-4b-GBM	0.8220	16	0.29 +	13	0.5859	17	0.25 -	31	77
2-3b-GBM	0.8150	18	0.26 +	20	0.5647	21	0.03 +	19	78
1-3a-GBM	0.7960	23	0.13 +	29	0.5953	12	0.23 +	14	78
2-3a-GBM	0.8120	20	0.30 +	10	0.5844	19	0.30 -	32	81
2-2b-GBM	0.7180	30	0.31 +	8	0.5622	22	0.02 -	23	83
2-4a-GAM	0.8370	13	0.03 -	32	0.5541	23	0.18 +	16	84
1-3b-GBM	0.7830	26	0.11 +	30	0.6300	5	0.09 -	26	87
1-4a-GAM	0.8060	22	0.29 +	15	0.5067	29	0.00 +	22	88
1-2b-GAM	0.7110	33	0.25 +	21	0.5000	31	0.45 +	8	93
2-3b-GAM	0.7940	25	0.28 +	16	0.5356	27	0.15 -	29	97
2-3a-GAM	0.7940	24	0.26 +	19	0.5417	25	0.24 -	30	98
1-1a-GAM	0.8080	21	0.04 +	31	0.5000	30	0.02 +	20	102
2-2b-GAM	0.7150	32	0.24 +	23	0.5386	26	0.02 -	24	105
1-3b-GAM	0.7700	28	0.19 +	28	0.4523	33	0.05 +	18	107
1-3a-GAM	0.7810	27	0.02 -	33	0.5078	28	0.11 -	27	115