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From Pup to Predator: Ontogeny of Foraging Behaviour in Grey Seal (Halichoerus grypus) Pups

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From pup to predator: ontogeny of foraging behaviour in grey seal (*Halichoerus grypus*) pups

by

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Supervisory Committee: Dr Clare Embling (Director of Studies),
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“Many a trip continues long after movement in time and space have ceased.”

- *John Steinbeck*
Travels with Charley

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Author's Declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other university award without the prior agreement of the Doctoral College Sub-Committee.

Work submitted for this research degree at the University of Plymouth has not formed part of any other degree either at the University of Plymouth or at another establishment.

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Publications are detailed on page xxi.

Presentations at conferences are detailed on page xxi.

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From pup to predator: ontogeny of foraging behaviour in grey seal (*Halichoerus grypus*) pups

Matt Ian Daniel Carter

ABSTRACT

For young animals, surviving the first year of nutritional independence requires rapid development of effective foraging behaviour before the onset of terminal starvation. Grey seal (*Halichoerus grypus*) pups are abandoned on the natal colony after a brief (15-21 days) suckling period and must learn to dive and forage without parental instruction. Regional and sex-specific differences in diet and foraging behaviour have been described for adults and juveniles, but the early-life behaviour of pups during the critical first months at sea remains poorly understood. This thesis investigates sources of intrinsic and extrinsic variation in the development of foraging behaviour and resource selection in grey seal pups. The studies presented here feature tracking and dive data collected from 52 recently-weaned pups, tagged at six different breeding colonies in two geographically-distinct regions of the United Kingdom (UK). Original aspects of this thesis include: (Chapter I) a comprehensive review of analytical methods for inferring foraging behaviour from tracking and dive data in pinnipeds; (Chapter II) description and comparison of regional and sex differences in movements and diving characteristics of recently-weaned pups during their first trips at sea; (Chapter III) implementation of a novel generalized hidden Markov modelling (HMM) technique to investigate the development of foraging movement patterns whilst accounting for sources of intrinsic (age, sex) and extrinsic (regional) variation; and (Chapter IV) the first analysis of grey seal pup foraging habitat preference, incorporating behavioural inferences from HMMs and investigating changes in preference through time.

In Chapter II, I demonstrate that pups undertake an initial exploratory phase during the first two months, developing their benthic diving ability and foraging trip behaviour. I show that male and female pups exhibit sex-specific early-life behaviours, with females diving in shallower water than males, but that these differences are not equal among regions. In Chapter III, I show that pup travelling and foraging movement patterns become increasingly distinct throughout the initial four months after leaving the natal colony. I demonstrate that travelling behaviour becomes faster and more directed, and that foraging behaviour becomes more tortuous, suggesting an increase in travel efficiency and decrease in scale of foraging search behaviour as pups learn the location of foraging grounds and haulout sites. In Chapter IV, I present regional differences in foraging habitat preference, and find that individuals in Northeast Scotland select foraging resources in shallow sandy areas close to haulouts, consistent with predation on overwintering sandeels (*Ammodytes spp.*). I show that pups in West Wales display evidence of sex-specific foraging strategies before sexual size dimorphism; females select foraging habitat in shallower areas closer to haulouts than males. The methods implemented here have broad application to analyses of animal tracking data, and the findings have implications for foraging ecology, the study of behavioural ontogeny, and conservation management based on juvenile rather than adult behaviour.

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List of Abbreviations

ACF: autocorrelation function

ADL: aerobic dive limit

AIC: Akaike information criterion

ARGOS: Advanced Research and Global Observation Satellite

ARS: area-restricted search

BGS: British Geological Survey

BODC: British Oceanographic Data Centre

CIS: Celtic and Irish Seas

CLS: Collecte Localisation Satellites

CTD: conductivity temperature depth

DTM: Digital Terrain Model

EMODnet: European Marine Observation and Data Network

EU: European Union

FCS: Favourable Conservation Status

FPT: first-passage time

FTP: file transfer protocol

GAM: generalized additive model

GAMM: generalized additive mixed effects model

GEE: generalized estimating equation

GLS: Global Location Sensor

GPS: Global Positioning System

GSI: Geological Survey of Ireland

GSM: Global System for Mobile Communications

HMM: hidden Markov model

IQR: inter-quartile range

KF: Kalman filter

LAT: lowest astronomical tide

LC: location class

LS: least squares

ML: maximum likelihood

MPA: marine protected area

MREI: marine renewable energy installation

NERC: Natural Environment Research Council

NOAA: National Oceanographic and Atmospheric Administration

NS: North Sea

ODT: optimal dive theory

OFT: optimal foraging theory

PODAAC: Physical Oceanography Distributed Active Archive Center

RT: residence time

SCOS: Special Committee on Seals

SD: standard deviation

SMRU: Sea Mammal Research Unit, University of St Andrews

SRDL: Satellite Relay Data Logger

SSB: spawning stock biomass

SSM: state-space model

SST: sea surface temperature

STT: stomach temperature telemetry

TAD: time allocation at depth

TDR: time-depth recorder

UHF: ultra-high frequency

VHF: very-high frequency

VIF: variance inflation factor

YOY: young-of-the-year

Summary of Research Output

Peer-reviewed publications:

Carter, M.I.D.; Bennett, K.A.; Embling, C.B.; Hosegood, P.J.; Russell, D.J.F. (2016) Navigating uncertain waters: a critical review of inferring foraging behaviour from tracking and dive data in pinnipeds. *Movement Ecology* 4:25.

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Conference presentations & seminars:

Carter, M.I.D.; Embling, C.B.; McClintock, B.T.; Bennett, K.A.; Thompson, D.T.; Russell, D.J.F. "Investigating the temporal dynamics of foraging behaviour in a highly-mobile naïve marine predator: grey seal pups". Plymouth Marine Science Education Fund Postgraduate Conference 2018. Plymouth Marine Laboratory, UK. *Oral presentation.*

Carter, M.I.D.; Grecian, W.J.; Russell, D.J.F.; Bennett, K.A.; Thompson, D.; Hosegood, P.J.; Embling, C.B. "Foraging habitat preference of grey seal pups revealed from GPS tracking data". Society for Marine Mammalogy Biennial Conference 2017. Halifax, Canada. *Poster presentation.*

Carter, M.I.D.; Grecian, W.J.; Russell, D.J.F.; Bennett, K.A.; Thompson, D.; Hosegood, P.J.; Embling, C.B. "Foraging habitat preference of grey seal pups revealed from GPS tracking data". Bio-Logging Symposium 2017. Konstanz, Germany. *Poster presentation.*

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Carter, M.I.D.; Russell, D.J.F.; Embling, C.B.; Blight, C.; Thompson, D.; Hosegood, P.J.; Bennett, K.A. "From pup to predator: sex and regional differences in the ontogeny of movement and dive behaviour of grey seal (*Halichoerus grypus*) pups in their first months at sea". Dec 2016. Sea Mammal Research Unit, University of St Andrews, UK. *Seminar.*

Carter, M.I.D.; Russell, D.J.F.; Bennett, K.A.; Thompson, D.; Hosegood, P.J.; Embling, C.B. "From pup to predator: first year movements of grey seal (*Halichoerus grypus*) pups". UK and Ireland Regional Student Chapter of the Society for Marine Mammalogy Annual Meeting 2016. Sea Mammal Research Unit, University of St Andrews, UK. *Oral presentation.*

Carter, M.I.D.; Russell, D.J.F.; Bennett, K.A.; Thompson, D.; Hosegood, P.J.; Embling, C.B. "From pup to predator: ontogeny of foraging behaviour in grey seal (*Halichoerus grypus*) pups". Society for Marine Mammalogy Biennial Conference 2015. San Francisco, USA. *Poster presentation.*

Carter, M.I.D.; Russell, D.J.F.; Bennett, K.A.; Thompson, D.; Hosegood, P.J.; Embling, C.B. "From pup to predator: ontogeny of foraging behaviour in grey seal (*Halichoerus grypus*) pups". Marine Biology and Ecology Research Centre researcher seminar. Nov 2015. University of Plymouth, UK. *Seminar.*

Carter, M.I.D.; Russell, D.J.F.; Bennett, K.A.; Thompson, D.; Hosegood, P.J.; Embling, C.B. "Ontogeny of foraging in grey seal (*Halichoerus grypus*) pups". UK and Ireland Regional Student Chapter of the Society for Marine Mammalogy Annual Meeting 2015. Bangor University, Bangor, UK. *Speed talk.*

Other scientific contributions:

- January 2018. Invited article for Biosphere Magazine: Issue 30, pp 35-47: *"Pup to predator"*. Co-authored with Dr Kimberley Bennett.
- April 2017. Consultation and interview for BBC The One Show feature: *"Scratching Seals: why do seals scratch their backs on the seabed?".* http://www.bbc.co.uk/programmes/p04zrw16
- Aug 2015. Consultation and interview for BBC Natural History Unit documentary: *"Big Blue UK: Seals"*. http://www.bbc.co.uk/programmes/b0684sqb

Professional Development & Research Training

Conference organising committees:

- Feb 2017. *Plymouth Marine Science and Education Foundation (PlyMSEF) Postgraduate Conference*. Plymouth Marine Laboratory, UK.

- Jan 2017. *UK and Ireland Regional Student Chapter of the Society for Marine Mammalogy Annual Meeting*. University of Plymouth, UK.
- Jan 2016. *UK and Ireland Regional Student Chapter of the Society for Marine Mammalogy Annual Meeting*. St Andrews University, UK.

Internal training course attendance:

- Sep 2016. "University Website CMS; Creating and Publishing Content".
- Mar 2016. "The Transfer Process".
- Feb 2016. "Immersive Writing Workshop".
- Jun 2015. "GAM Workshop", Dr Clare Embling.

External training course attendance:

- Aug 2017. Hidden Markov Models for Animal Movement Data (Prof. Roland Langrock), Centre for Research into Ecological and Environmental Modelling, St. Andrews, UK.
- Nov 2015. Spatial Statistics in R for Ecologists, PR Statistics (Prof. Jason Matthiopoulos), Scottish Centre for Ecology & the Natural Environment, Loch Lomond, UK.
- Aug 2015. Environmental Statistics and Data Analytics Training (NERC), University of Glasgow, UK.
- Feb 2015. State-Space Model Workshop (Dr Debbie Russell), University of Exeter, Cornwall Campus, UK.
- Oct 2014. Learning and Teaching in Higher Education (LTHE), University of Exeter, Cornwall Campus, UK.

Introduction

Project Rationale

For young animals, development of an effective foraging strategy is critical to surviving the transition from dependence upon parental provisioning to independent feeding (Lindström 1999, Daunt et al. 2007, Riotte-Lambert and Weimerskirch 2013). Many long-lived vertebrate species exhibit delayed recruitment to the breeding population, undergoing a prolonged period of immaturity (Lindström 1999). During this time some species learn to forage alongside adult conspecifics, often during a protracted dependency period (Rapaport and Brown 2008, Bender et al. 2009), whereas others are weaned abruptly, and must learn to forage alone (Boness and Bowen 1996, Riotte-Lambert and Weimerskirch 2013). The challenges of foraging ontogeny are particularly acute for such naïve animals (Lindström 1999, Riotte-Lambert and Weimerskirch 2013). First-year mortality of long-lived vertebrates is often high, and juvenile survival can have a profound effect on population dynamics (Lack 1954, Harwood and Prime 1978, Sæther et al. 2013). Consequently, the early-life behaviour of long-lived species is of key research interest (Shillinger et al. 2012). For highly-mobile aquatic animals, such as marine vertebrate predators, quantifying behaviour is problematic because individuals spend most of their time at sea, frequently below the surface (Hazen et al. 2012). However, the development of animal tracking devices has allowed ecologists to collect detailed movement data from remote subjects around the world (Block et al. 2011). The refinement and miniaturisation of such devices has facilitated investigation of complex questions about how young animals learn to exploit their environment (Blanchet et al. 2016, Orgeret et al. 2016, Rotics et al. 2016, de Grissac et al. 2017).

Grey seals (*Halichoerus grypus*) are among the most-studied of marine predator species. They occupy coastal and shelf seas of the North Atlantic, and their pupping and foraging grounds often overlap considerably with areas of human activity (Hewer 1974, Kelly et al. 2004, Russell et al. 2013, 2014). This overlap is particularly evident in the United Kingdom (UK), which is home to around 38% of the global population (SCOS 2017), and where human-seal conflict has been a feature of wildlife management for centuries (Lambert 2001). Legislation for the conservation of grey seal populations was first introduced in the UK in 1914. Today, the species is protected under the Conservation of Seals Act 1970 (England and Wales), the Marine (Scotland) Act 2010 and the Wildlife (Northern Ireland) Order 1985. Furthermore, grey seals are listed under Annex II of the European Union (EU) Habitats Directive (92/43/EEC 1992), requiring member states to maintain ‘Favourable Conservation Status’ (FCS). As such, a great deal of research effort has been dedicated to grey seal ecology in the UK, including long-term annual population monitoring (SCOS 2017). Improvements to the resolution and quantity of data obtainable from tracking devices, and refinements to the analytical techniques for such data, have allowed ecologists to map important at-sea habitat for grey seals in the UK (Aarts et al. 2008, Jones et al. 2015), investigate intrinsic and extrinsic drivers of variation in foraging behaviour (Russell et al. 2015), and assess the potential impacts of anthropogenic activities (Russell et al. 2014, Cronin et al. 2016). However, this work has predominantly focussed on adults of reproductive age, captured after the annual moult. Grey seals exhibit a prolonged period of sexual immaturity (females: 6 years; males: 10 years) (Harwood and Prime 1978). Therefore, any disturbance to pups during their first months of nutritional independence could have serious population-level consequences that would only be manifested after a considerable time lag. Moreover, grey seals are exposed to a growing range of anthropogenic threats, including fisheries interactions (Bjørge et al. 2002), resource competition (Cronin et al. 2016), vessel traffic (Jones et al. 2017a) and offshore construction (Edrén et al. 2010). As such, there is an urgent need to investigate the biological and physical factors that shape pup behaviour as they learn to forage.

Grey seal pups are weaned abruptly after 15-21 days and abandoned on the natal colony (Fedak and Anderson 1982), and must learn to dive and find food without parental instruction before their metabolic fuel reserves are exhausted (Reilly 1991, Bennett et al. 2007). The development of successful foraging behaviour is therefore critical to surviving the first months at sea, and starvation is a major cause of first-year mortality (Baker et al. 1998). The challenges of finding and capturing prey for recently-weaned seal pups are confounded by physiological constraints on their ability to dive and remain at depth. Unlike adults, juvenile seals may need to continually dive up to their physiological limits in order to forage (Burns 1999). The physiological challenge of breath-hold diving for a small animal with limited oxygen storage capacity, and a high mass-specific metabolic rate, may be further exacerbated by competition with adults. Young animals may be excluded from foraging grounds closer to haulouts, and consequently have to make longer trips into deeper water (Breed et al. 2011a, 2013). Other published studies have investigated foraging in grey seal juveniles (>1 year old) (Breed et al. 2011a, Russell et al. 2015) and young-of-the-year (YOY; > 5 months old) (Breed et al. 2011a). For example, Breed et al. (2011a) showed that sex-differences in foraging behaviour are present in YOY animals before sexual size dimorphism, but the timing and drivers of their onset are unclear. The critical first months of at-sea behaviour remain poorly studied; only Bennett et al. (2010) have investigated early-life behaviour in recently-weaned grey seal pups. The authors found that pups from a colony in the North Sea developed their diving capability rapidly in the initial months after leaving the colony (Bennett et al. 2010). However, it is not clear how this relates to foraging behaviour, or how behavioural ontogeny may vary in relation to regional differences in the environment. Furthermore, conservation management of this species is largely informed by our understanding of adult behaviour (SCOS 2017), and may be inappropriate for pups as they may have different habitat requirements to adults. There is, therefore, a clear need to build on existing work and to assess the biological and environmental factors that shape the development of foraging behaviour and habitat preference in grey seal pups on their first trips at sea.

This project utilises a unique, large tracking dataset of 52 recently-weaned grey seal pups from six colonies around the UK. In the following chapters, I review analytical approaches to inferring foraging behaviour from location and dive data in seals, examine the intrinsic and extrinsic drivers of variation in foraging ontogeny and habitat preference in grey seal pups using robust modelling techniques, discuss the implications for foraging ecology and conservation management, and highlight priorities for future research.

Objectives

This thesis aims to describe the spatial and temporal dynamics of foraging behaviour in UK grey seal pups during their first months at sea, and identify sources of intrinsic and extrinsic variation in the ontogenetic process. Specifically, the main objectives of this thesis are to:

1) review the commonly-used devices for tracking pinniped locations and dives, and evaluate the methods for inferring foraging behaviour from the data they generate.
2) identify changes in early-life at-sea behaviours over time related to ontogeny of foraging, examining sources of intrinsic and extrinsic variation in this process.
3) develop a robust analytical approach to identify discrete movement states (foraging, resting and travelling) from tracking data in naïve animals, accounting for temporal changes in foraging movement patterns.
4) explore how pups develop foraging habitat preference by relating foraging behaviour (identified in (3)) to potential oceanographic and habitat drivers.
5) evaluate the significance of the key findings in the context of foraging ecology and conservation management and provide recommendations for future work.

Thesis Structure

This thesis comprises a series of chapters, each written as an individual piece of research addressing the aforementioned objectives. Whilst each chapter may be read and considered in isolation, the overall thesis structure presents a detailed body of work examining the ontogeny of foraging behaviour and habitat preference in grey seal pups during their first months of nutritional independence.

Chapter I is a comprehensive critical synthetic review of analytical methods for inferring foraging behaviour from location and dive data in pinnipeds. The first section outlines the development of technological options for tracking pinnipeds at sea, and discusses the merits and limitations of the data they generate with regards to identifying and quantifying foraging activity. The second section evaluates different methods of inferring foraging behaviour using (i) dive metrics, (ii) track metrics, and (iii) a combination of both. The review considers both traditional and emerging approaches, highlighting the caveats associated with each. The final part of the review provides an outline of current limitations and knowledge gaps in the field, and highlights that current foraging models designed for adults may be inappropriate for young animals. The review offers guidance for future studies, based on a framework of considerations relating to the study species, data type and research question. This chapter was published as a review article in *Movement Ecology* in October 2016 as:

> Carter, M.I.D.; Bennett, K.A.; Embling, C.B.; Hosegood, P.J.; Russell, D.J.F. (2016) Navigating uncertain waters: a critical review of inferring foraging behaviour from tracking and dive data in pinnipeds. *Movement Ecology* 4: 25. DOI: 10.1186/s40462-016-0090-9

Chapter II presents an investigation of intrinsic (sex) and extrinsic (regional) variation in the ontogeny of trip and dive behaviour in grey seal pups during their first four months of independent life at sea. Key findings show that pups develop adult-like behaviour rapidly over the first 40 days, commuting between haulout sites and known foraging areas after an initial exploratory phase. The chapter also reveals that male and female pups behave differently soon after leaving the colony, and that these differences are likely mediated by extrinsic (regional) factors. This chapter was published as an original research article in *Scientific Reports* in November 2017 as:

> Carter, M.I.D.; Russell, D.J.F.; Embling, C.B.; Blight, C.B.; Thompson, D.; Hosegood, P.J.; Bennett, K.A. (2017) Intrinsic and extrinsic factors drive ontogeny of early-life at-sea behaviour in a marine top predator. *Scientific Reports* 17: 15505. DOI: 10.1038/s41598-017-15859-8

Chapter III presents a novel application of hidden Markov models (HMMs) to animal movement data, in which movement characteristics (speed and path tortuosity) of states (foraging and travelling) can vary as a function of intrinsic (age, sex) and extrinsic (region) covariates. To our knowledge, this is the first such application to animal movement data. Using this method, the chapter demonstrates how foraging and travelling movement patterns become increasingly distinct over the first four months at sea. Key findings show that pup travelling movements become faster and more directed with age, and the scale of foraging search behaviour decreases, likely due to individuals learning the location of foraging grounds and haulout sites. This chapter is in the final stages of preparation for submission as an original research article.

Chapter IV models the relationship between pup foraging locations, obtained from the HMM implemented in Chapter III, and environmental predictor variables. This chapter presents a novel approach to habitat preference, whereby foraging locations are first identified with an HMM, then modelled against environmental covariates in a use-availability design to account for the relative availability of habitat. Key findings show that pups exhibit strong regional differences in habitat preference, and that the specific habitat features associated with foraging change throughout the first four months of nutritional independence.

Chapter V is a summary of the conservation relevance of the main findings of the thesis that serves as a non-technical briefing document for conservation organisations and marine management bodies. This chapter identifies concerns for conservation management, highlights knowledge gaps, and makes recommendations for future research based on the findings of this thesis.

Summary of Collaborator Contributions

Chapter I: This chapter is a literature review prepared by myself, in consultation with the supervisory committee. Each of the supervisors provided comments on chapter drafts.

Chapter II: Pup tracking data used in this chapter were provided by Dr Kimberley Bennett (Abertay University) and Dr Dave Thompson (SMRU). Dr Debbie Russell (SMRU) provided guidance in cleaning and processing the data as per SMRU protocol. Statistical advice was provided by Dr Clare Embling (University of Plymouth), Dr Russell and Dr Bennett. Analysis in this chapter involved matching dive locations to bathymetric depth data. Mr Clint Blight (SMRU) assisted in providing a raster of bathymetric depth data compiled from the European Marine Observation Data Network (EMODnet) Digital Terrain Model. Mr Blight also provided useful consultation on technical aspects of geospatial data analysis. All collaborators provided comments on chapter drafts, together with the supervisory team.

Chapter III: Pup tracking data used in this chapter were provided by Dr Dave Thompson (SMRU). Analysis in this chapter involved implementing a statistical framework for investigating changes to foraging movement patterns through time. Dr Brett McClintock (National Oceanographic and Atmospheric Administration, USA) was consulted on technical aspects of modelling, and has subsequently developed an R package "momentuHMM" capable of implementing generalized HMMs. However, it was necessary to make some extensions to the package to adapt it specifically for application to diving predators. Dr McClintock provided those extensions in the form of a bespoke version of the package. Dr Russell provided guidance in analysis and both Dr Russell and Dr Embling advised on results interpretation. Dr McClintock provided comments on chapter drafts, together with the supervisory team.

Chapter IV: Pup tracking data used in this chapter were provided by Dr Dave Thompson (SMRU). Dr W. James Grecian (SMRU) and Dr Russell provided consultation in the design of the use-availability framework and modelling approach implemented in this chapter. Dr Embling and Dr Russell provided advice on analysis and results interpretation. All supervisors provided comments on chapter drafts.

Chapter V: This chapter is a non-technical summary of the conservation relevance of the main findings, prepared by myself. Supervisors provided comments on chapter drafts.

The following chapters were created in collaboration with those mentioned above. I use the term "we" throughout the chapters as per publication standard practise and for consistency. It is not intended to suggest that any part of this thesis is not my own work.

Chapter I

Navigating uncertain waters: a critical review of inferring foraging behaviour from location and dive data in pinnipeds

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ABSTRACT

In the last thirty years, the emergence and progression of biologging technology has led to great advances in marine predator ecology. Large databases of location and dive observations from biologging devices have been compiled for an increasing number of diving predator species (such as pinnipeds, sea turtles, seabirds and cetaceans), enabling complex questions about animal activity budgets and habitat use to be addressed. Central to answering these questions is our ability to correctly identify and quantify the frequency of essential behaviours, such as foraging. Despite technological advances that have increased the quality and resolution of location and dive data, accurately interpreting behaviour from such data remains a challenge, and analytical methods are only beginning to unlock the full potential of existing datasets. This review evaluates both traditional and emerging methods and presents a starting platform of options for future studies of marine predator foraging ecology, particularly from location and two-dimensional (time-depth) dive data. We outline the different devices and data types available, discuss the limitations and advantages of commonly-used analytical techniques, and highlight key areas for future research. We focus our review on pinnipeds - one of the most studied taxa of marine predators - but offer insights that will be applicable to other air-breathing marine predator tracking studies. We highlight that traditionally-used methods for inferring foraging from location and dive data, such as first-passage time and dive shape analysis, have important caveats and limitations depending on the nature of the data and the research question. We suggest that more holistic statistical techniques, such as state-space models, which can synthesise multiple track, dive and environmental metrics whilst simultaneously accounting for measurement error, offer more robust alternatives. Finally, we identify a need for more research to elucidate the role of physical oceanography, device effects, study animal selection, and developmental stages in predator behaviour and data interpretation.

1.1 Introduction

The need to find food is a fundamental pressure that drives the evolution of animal physiology, behaviour, and life histories (Stephens and Krebs 1986). A key question for ecologists is how animals exploit their environment to optimise prey intake and maximise fitness (Stephens and Krebs 1986). For air-breathing diving predators, such as marine mammals, sea turtles, and seabirds, foraging poses a unique challenge: within the physiological constraints of breath-hold, individuals must find patchily-distributed prey resources in a three dimensional (3D) dynamic environment (Kooyman and Ponganis 1998). Observing and measuring such behaviour in the field is inherently problematic. However, in recent years, a suite of devices and analytical techniques dedicated to tackling this challenge has emerged (Cooke et al. 2004, Rutz and Hays 2009, Ropert-Coudert et al. 2009, Hart and Hyrenbach 2009, Evans et al. 2013, Hussey et al. 2015).

Biologging (the "use of miniaturized animal-attached tags for logging and/or relaying data about an animal's movements, behaviour, physiology and/or environment"; Rutz and Hays (2009)) is changing the way we observe and interpret the behaviour of marine predators (Cooke et al. 2004, Hart and Hyrenbach 2009, Evans et al. 2013, Hussey et al. 2015). Devices allow us to collect an increasing range of data that can be either archived and later retrieved, or autonomously transmitted via acoustic or satellite telemetry, or mobile phone technology (biotelemetry; see Cooke et al. (2004)). Such data include empirical observations of feeding attempts from fine-scale body movements such as jaw opening (Wilson et al. 2002, Fossette et al. 2008, Naito et al. 2013) and lunges measured using accelerometers (Goldbogen et al. 2006, Carroll et al. 2014, Volpov et al. 2015), and even physiological measurements of feeding, such as changes in stomach temperature (Ancel et al. 1997, Kuhn et al. 2009, Lee et al. 2014). Animal-mounted cameras have complemented such information and contributed substantially to our understanding of how diving predators (both captive and in the wild) search for, capture and handle prey (Davis et al.

1999, Hooker et al. 2002, Naito et al. 2013, Votier et al. 2013). However, datasets from devices such as cameras, jaw magnets, accelerometers and stomach temperature telemetry (STT) loggers are generally limited by small sample sizes and short sampling periods. Moreover, high demands on memory and battery, the need to recover archival tags, or complex attachment procedures limit the use of such devices on wild animals, and thus leave little opportunity for long-term studies with population-level inferences. Nevertheless, direct observations of foraging from these devices can allow us to ground-truth inferences of foraging behaviour made from location and dive (time-depth) data (Austin et al. 2006a, Kuhn et al. 2009, Heaslip et al. 2014, Viviant et al. 2014, Volpov et al. 2016). Studies using positional tracking devices and pressure sensors (calculating depth) to measure movement are prevalent, and this type of data has been collected in abundance since the 1980s. However, interpreting behaviour from these data can be challenging. A variety of analytical techniques to infer foraging have been advocated, based on assumptions about physiological constraints, behavioural choices and optimal foraging theory (OFT; see Appendix A1.1: Glossary). Most commonly-used approaches have important caveats, depending on the study species and data quality, which we will discuss in detail below.

Many reviews exist of the development, capabilities and applications of biologging devices (Cooke et al. 2004, Rutz and Hays 2009, Ropert-Coudert et al. 2009, Hart and Hyrenbach 2009, Hazen et al. 2012, Evans et al. 2013, Hussey et al. 2015, Wilmers et al. 2015). However, little synthesis has been offered on the data they each collect, which can influence the choice and power of subsequent analysis, and the limitations of commonly-used analytical methods to reliably infer foraging. The purpose of this review, therefore, is to: (i) discuss the range of devices available for tracking horizontal and vertical foraging movements in the marine environment, and the constraints and opportunities presented by the data collected, (ii) discuss the assumptions and relative merits of different approaches to inferring foraging from location and two-dimensional (2D; time-depth) dive data, and (iii) highlight knowledge gaps, providing a point of reference for future studies. The range of devices and analytical techniques used in foraging studies is extensive across marine vertebrate taxa, especially for seabirds and pinnipeds, for which biologging studies are particularly prevalent (Ropert-Coudert et al. 2009). Here, we discuss inference of foraging behaviour in pinnipeds. Although insights may be applicable to other air-breathing marine predator tracking studies, differences in behaviour and device constraints mean that discussion relating to other taxa is outside the scope of this review.

1.2 Devices and Data

For many years knowledge of pinniped movements was limited to re-sightings of coded mark-recapture flipper tags or brandings (Hewer 1974) (Fig. 1.1a-b). These observations allow long-term monitoring of survival and dispersal, but offer little insight into where individuals go between hauling-out. Many technological options are now available for tracking animal movement at sea (Table 1.1; Fig. 1.1). In this review we focus on devices capable of collecting fine-scale information on foraging movements. Whilst global location sensors (GLS) and smart position or temperature transmitters (SPOT) have been used in foraging studies, they are generally deployed to track migration or broad-scale movement, and foraging inferences are made from behavioural data or higher resolution location data from simultaneously-deployed devices (Staniland et al. 2012, Labrousse et al. 2015, Arthur et al. 2016). GLS and SPOT tags are therefore excluded from this review.

Pioneering, early pinniped foraging studies used acoustic telemetry such as very high frequency (VHF) radio transmitters to describe at-sea movements (Thompson and Miller 1990, Thompson et al. 1991) and formed the basis of our understanding of pinniped foraging. Feeding was inferred from breaks in the VHF signal from diving, assuming that dives equated to foraging (Thompson and Miller 1990), or from dive depth data indicating swimming on or near the sea bed (Thompson et al. 1991). The scope of this technique was limited by the need for proximity of the animal to an observer or multiple receiver stations in order to triangulate its position (Thompson and Miller 1990, Thompson et al. 1991).

Early time-depth recorders (TDRs) were deployed on several pinniped species in the first diving studies (Kooyman 1966, Gentry and Kooyman 1986, Le Boeuf et al. 1988). These devices recorded depth readings over time, providing important insight into pinniped diving capabilities. TDRs are archival devices, and have to be retrieved in order to access the data. Archival TDRs and positional loggers (collecting high-resolution Global Positioning System (GPS)-derived location data) are used widely today, but studies are limited to life stages and/or species in which individuals are easily re-encountered and re-captured. For example, many studies use archival devices to track the movements and dive behaviour of lactating otariids (eared seals) (Gentry and Kooyman 1986, Jeglinski et al. 2013, Riet-Sapriza et al. 2013). Unlike many phocid (true seal) species, otariid pups have a protracted dependency period, during which they remain on the colony whilst the mother makes repeated foraging trips offshore. As otariid mothers must return to the colony to provision their pups over a longer time period, archival devices can be retrieved with relative confidence. Although some phocid mothers, such as harbour (*Phoca vitulina*) and bearded (*Erignathus barbatus*) seals also make foraging excursions during lactation (Bowen et al. 1999, Gjertz et al. 2000), pups generally spend more time in the water than otariids (Bekkby and Bjørge 2000), and may even suckle in the water and move between haulout sites (Schreer et al. 2010), making the re-capture of a specific individual more challenging. In seminal work, Kooyman (1966) studied the dive capabilities of Weddell seals (*Leptonychotes weddellii*) in Antarctica, and translocated them to an area of fast-ice with just one breathing hole, thus ensuring an opportunity to recapture individuals and recover the TDRs. Alternatively, for some species, animals can be re-encountered by predicting the timing and location of their life-history events. For example, Le Boeuf et al. (1988) glued archival loggers to the fur of northern elephant seals (*Mirounga angustirostris*) that return to the same colony to moult. Unlike other species in which moulting can be prolonged, elephant seals undergo an annual catastrophic moult, shedding a large quantity of fur at once, during which time they avoid entering the water. Tags are therefore released with the moulted fur on the colony, rather than in the sea, and can be later retrieved. VHF transmitters can be deployed in addition to archival loggers to aid re-encounter of the individual on the colony (Fig. 1.1a) (Jeglinski et al. 2013, Riet-Sapriza et al. 2013). For other species, tracking their offshore movements requires a transmitting tag (Fig. 1.1c-d).

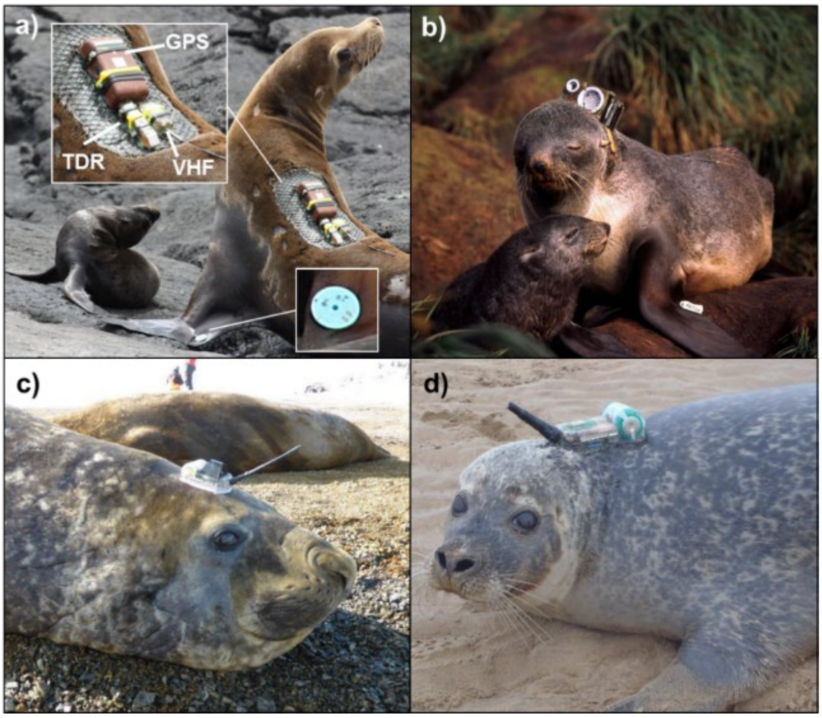

Figure 1.1: Biologging device deployments. *(a) Lactating female Galápagos sea lion (Zalophus wollebaeki) with archival GPS and TDR loggers. Archival loggers are favoured for tropical species as ARGOS satellite coverage is poor near the equator. VHF transmitter aids re-encounter on the colony for device retrieval. Picture also shows coded mark-recapture tag in the fore-flipper (photo: Jana Jeglinski). (b) Lactating female Antarctic fur seal (Arctocephalus gazella) with archival video camera. Note mark-recapture flipper tag (photo: Sascha Hooker). (c) ARGOS-CTD telemetry tag deployed on a southern elephant seal (Mirounga leonina) in West Antarctica. This device records both movement and environmental data simultaneously and transmits the data via polar-orbiting satellites, offering valuable data for ecologists and oceanographers alike (photo: Mike Fedak). (d) GPS-GSM phone telemetry tag deployed on a harbour seal (Phoca vitulina) in the North Sea. These devices are a good option for species that frequent coastal waters in less-remote regions (photo: Sea Mammal Research Unit). Note: for scale, devices pictured in (c) and (d) are roughly the same size.*

Satellite telemetry devices, such as Satellite Relay Data Loggers (SRDLs) were developed in the late 1980s, allowing data to be recorded and transmitted autonomously from anywhere in the world, revolutionising the study of marine predator movements at sea (Stewart et al. 1989, McConnell et al. 1992a, b, Photopoulou et al. 2015a). These tags are particularly useful for long-ranging pelagic species, such as southern elephant seals (*Mirounga leonina*; McConnell et al. (1992b)), in which VHF tracking in the open ocean is not possible, and re-encountering individuals for device retrieval is difficult or expensive due to the remoteness of their habitat. These satellite tags were developed to determine location estimates, and transmit data via the Advanced Research and Global Observation Satellite (ARGOS) system, which calculates the tag's position using the Doppler-shift in frequencies between the transmitter and low-orbiting polar satellites (Fig. 1.2a; CLS (2015)), relaying the information to a receiver station on land. An important consideration with ARGOS-derived location data is that location estimates are associated with high uncertainty; the level of which is dependent on how many satellite links are achieved whilst the tag is at the surface (Fig. 1.2a). Therefore, for species that make long dives with short inter-dive surface durations, such as elephant seals, location quality can be consistently poor (Costa et al. 2010). The ARGOS data-processing system produces location estimates with an associated location class (LC). Poor-quality LCs do not have a measure of spatial uncertainty, and in reality this could range to hundreds of kilometres (CLS 2015). As a high-resolution alternative to ARGOS-derived location data, Fastloc® GPS tags have now been developed, allowing faster location estimation with greater spatial accuracy. Once the antenna is exposed at the surface, it takes less than 100 ms for these devices to collect the data required to estimate a location (Bryant 2007, Costa et al. 2010). Double-tagging individuals with both ARGOS and Fastloc® GPS technology has allowed more accurate assessment of spatial error and behavioural inferences from ARGOS data (Vincent et al. 2002, Patterson et al. 2014, Silva et al. 2014, Lowther et al. 2015). GPS data can be transmitted via the ARGOS system (Table 1.1).

With the advent of ARGOS tags, developers began to incorporate other sensors such as wet-dry and pressure sensors or conductivity-temperature-depth (CTD) sensors alongside accelerometers (measuring tri-axial movement), light intensity meters (detecting bioluminescence in the deep ocean), and fluorometers (to estimate chlorophyll *a* concentration), capable of collecting and transmitting environmental and behavioural covariates simultaneously. In this way, pinnipeds contribute valuable information to both ecological and oceanographic datasets (Boehlert et al. 2001, Charrassin et al. 2008, Boehme et al. 2009, Fedak 2013). When deployed on long-ranging, deep-diving species such as southern elephant seals (Fig. 1.1c), these devices can collect environmental data from the entire water column in areas that were previously difficult or expensive to reach (e.g. remote areas of Antarctic water, or areas covered by sea ice; (Charrassin et al. 2008)). However, a key limitation of transmission via the ARGOS system is that data are only transmitted if a satellite is passing overhead while the tag is at the surface, resulting in 'snapshots' of location, behavioural and/or environmental data at irregular intervals. For example, Fastloc® GPS tags can record location data at every surfacing, and devices with integrated pressure sensors can record all dives. These data are stored in the device's buffer memory, but only a random subset will be successfully transmitted, resulting in patchy datasets (Fedak et al. 2002). In addition, equatorial regions are likely to receive poorer satellite coverage than polar regions, resulting in sparser data (Patterson and Hartmann 2011). The impact of these limitations on the analysis of behaviour will depend on the scale of movement of the study species and the specific research question (Vincent et al. 2002, Costa et al. 2010).

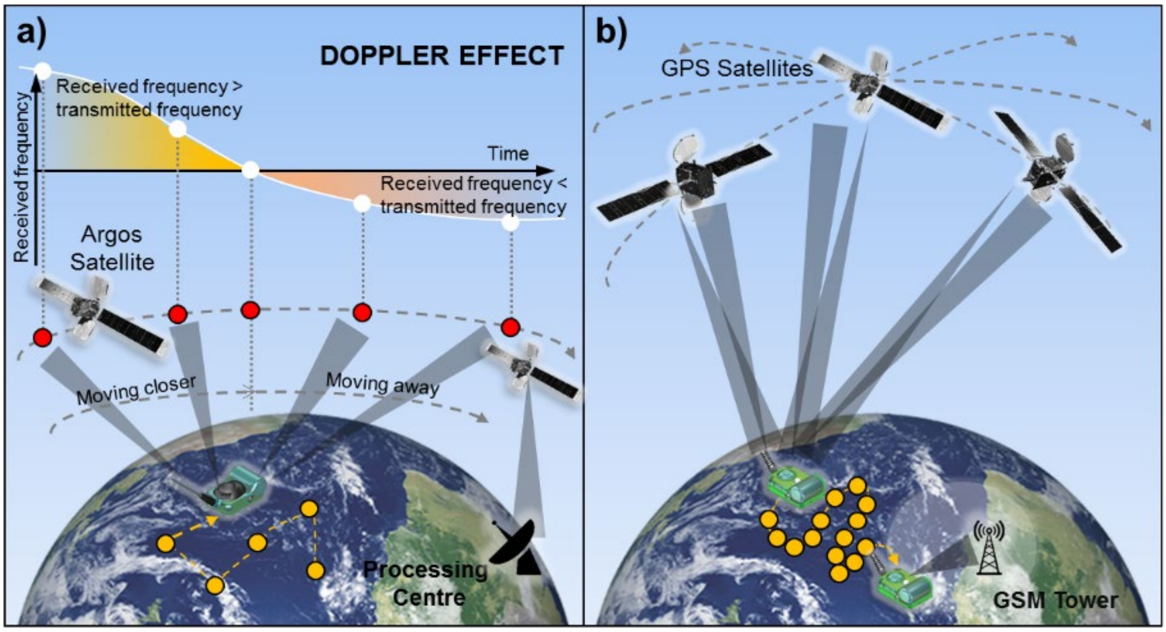

Figure 1.2: Location detection and transmission methods *for (a) ARGOS satellite relay data loggers (SRDL) (adapted from (CLS 2015)) and (b) GPS-GSM phone tags. Yellow dots represent locations where the tag is at the surface and a location fix is derived. Tag graphics: SMRU Instrumentation.*

A potential solution to the limitations of ARGOS transmission has emerged in recent years; the option now exists for Fastloc® GPS location data and high-resolution dive data to be archived at-sea and later transmitted via the Global System for Mobile Communications (GSM) phone network (Fig. 1.1d) (McConnell et al. 2004). GPS-GSM tags can store data for up to six months in the buffer memory, and as the tagged individual returns to coastal waters (and GSM range) to haul-out and rest, the stored data are sent via file transfer protocol (FTP) or short message service (SMS; text message) (Fig. 1.2b). Greater volumes of dive and haulout data can therefore be obtained, offering better application for fine-scale behavioural studies and recording of rare behaviour (Bailey et al. 2014). This transmission method also allows higher resolution behavioural covariates to be collected. For example, ARGOS relay tags and GPS-GSM tags both sample pressure at regular intervals throughout a dive. These data are then abstracted (reduced) to a number of depth inflection points before transmission, from which a 2D depth profile through time can be reconstructed (Fedak et al. 2001, Photopoulou et al. 2015b). The number of inflection points per dive varies depending on tag programming: ARGOS tags typically attempt to transmit four points per dive, whilst GPS-GSM tags transmit many more, giving a much more detailed picture of an individual's movements underwater (Fig. 1.3a).

In comparison to ARGOS, the increased temporal resolution of GPS-GSM technology offers greater potential to recreate spatially accurate animal movements in three dimensions, improving our ability to determine foraging behaviour, and allowing researchers to tackle more complex questions of fine-scale movement and habitat use. Nevertheless, studies in areas without a receiver network must rely on archival loggers or transmission via the ARGOS system. Despite the higher location accuracy of Fastloc® GPS devices, many researchers still use ARGOS-derived location data because tags are more economical in terms of battery demand and satellite costs, allowing longer study durations at lower cost (Breed et al. 2011b). Whilst ARGOS coverage is poor around the equator, satellite passes are much more frequent towards the poles, making them a good option for polar species (Breed et al. 2011b, Patterson and Hartmann 2011). Furthermore, for some species that are wide-ranging, such as southern elephant seals, mapping movements at high frequency and spatial accuracy may be less important in order to successfully identify foraging behaviour.

Table 1.1: Commonly-used tracking devices. *Battery duration and tag weights are given as a rough indication but are highly dependent on device configuration. References are given to indicate some examples of the application of each device. This table aims to give an overview of commonly-used tagging systems but is in no way exhaustive. Note: most devices, if recovered, can be re-charged, re-programmed and re-deployed. However, due to the low probability of retrieval in many cases, relay devices are generally considered single-use.*

Device	Examples	Location Derivation	Data Transmission	Common Applications	Typical Batt. Dur.	Approx. Weight (g)	Advantages	Disadvantages	References
Radio tag (Fig. 1.1a)	Mariner Radar (early studies); Advanced Telemetry Systems MM100 Series	Very High Frequency (VHF) or Ultra High Frequency (UHF)	Acoustic telemetry: radio signal (VHF/UHF)	Early pinniped studies. Short range studies. Relocation for data logger retrieval.	6-12 months	80-200 (early studies); 30	Smaller & lighter than ARGOS / GPS units. No need to retrieve. Can be used to re-encounter specific individuals on a colony for recovery of archival devices (Fig. 1.1a).	Device must be in line-of-sight range of base station(s) and/or mobile receiver(s) to record locations. Signal can be interrupted by terrain.	(Thompson and Miller 1990, Thompson et al. 1991, Robinson et al. 2010, Jeglinski et al. 2013, Riet-Sapriza et al. 2013)
GPS Logger (Fig. 1.1a)	Sirtrack F1G	Fastloc® GPS	Archival	Mainly individuals with restricted ranges (e.g. lactating female otariids during pup provisioning).	3 weeks – 6 months	215	Fast and accurate location estimates. Lighter than telemetry units. Salt-water switch turns the tag off when the animal dives / hauls out to extend battery life.	Must be recovered to extract data, therefore often needs to be deployed in conjunction with VHF transmitter to facilitate re-encounter on the colony. Study limited to specific timescales (e.g. pre-moult / breeding season).	(Jeglinski et al. 2013, Riet-Sapriza et al. 2013, Hoskins et al. 2015)
ARGOS relay tags (Fig. 1.1c)	SMRU 9000x SRDL; Wildlife Computers Mk10 SPLASH Tag; Sirtrack KiwiSat 101; Telonics ST-10 PTT	ARGOS	ARGOS	Very widely used. Long-ranging pelagic pinnipeds in remote locations.	12 months (depending on power options and duty cycle).	370	Can integrate other sensors such as wet-dry, CTD, or accelerometer. Useful in remote areas where no GSM coverage available. Complete data record can be retrieved if tag recovered. Better coverage in polar regions.	Not all locations & dives transmitted. Data often patchy due to interrupted transmissions. Location estimates can carry high spatial error. Fine-scale reconstruction of movement not possible. ARGOS coverage poor in areas closer to equator.	(McConnell et al. 1992a, b, Thompson et al. 1998b, Le Boeuf et al. 2000, Bestley et al. 2015)
GPS relay tags	SMRU GPS SRDL; Wildlife Computers Mk10 SPLASH Tag	Fastloc® GPS	ARGOS	Individuals in remote locations with no GSM coverage or prospect of device retrieval.	3-6 months (depending on power options and duty cycle).	370	As ARGOS relay tag (above). Solar powered option for extended battery life. Fast and accurate location estimates across most of the globe. Can integrate TDR.	Not all locations & dives transmitted. Data often patchy due to interrupted transmissions. ARGOS coverage poor in areas closer to equator.	(Kuhn et al. 2010, Patterson et al. 2014)
GPS-GSM (Fig. 1.1d)	SMRU GPS Phone Tag	Fastloc® GPS	GSM (FTP/SMS)	Pinnipeds in non-remote locations (with GSM coverage).	1-12 months (depending on power options and duty cycle).	370	Many power options including solar panel. All dives and locations can be transmitted. Fast and accurate location estimates across most of the globe.	Individual must enter GSM range to transmit data (time lag in data retrieval). Not useful in remote locations. If tag detached at sea before entering GSM range data are lost.	(Russell et al. 2014, 2015, Huon et al. 2015, Ramasco et al. 2015)

1.3 Inferring Foraging

Methods of inferring foraging from the data described above generally fall into three categories: (i) use of dive data, (ii) use of location data, and (iii) consideration of movements in three dimensions.

1.3.1 Inferring foraging from dive data

In VHF studies during the early 1990s, the presence of diving was used to infer foraging activity in pinnipeds (Thompson and Miller 1990). However, seals may dive for reasons other than searching for prey. For example, individuals may dive for efficient travel (Thompson et al. 1991), and some species also perform resting or digestion dives (Le Boeuf et al. 1988, Thompson et al. 1991, Baechler et al. 2002, Watanabe et al. 2015). Diving datasets collected using pressure sensors can be applied in various ways to infer foraging. From each dive, a number of empirical and geometric measurements can be calculated, including the duration of the dive; duration of bottom time; maximum depth; duration of surface interval; ascent and descent rates; distribution of time allocation across depths (Time Allocation at Depth (TAD) index; see Glossary); and 2D dive profile shapes (Fig. 1.3). The application of each of these metrics depends on the resolution of the data, the temporal scale of analysis, and the specific research question (i.e. whether the study aims to quantify search activity, successful foraging or other aspects of behaviour and physiology).

To quantify foraging in terms of search behaviour at the scale of individual dives, ecologists have proposed that specific 2D dive profile shapes (representing depth over time) can be attributed to different behaviours (i.e. foraging, travelling and resting; Fig. 1.3b; (Le Boeuf et al. 1988, Wilson et al. 1996, Martin et al. 1998, Schreer et al. 2001)). However, ground-truthing with direct metrics has revealed that the assumed link between dive shape and behaviour may not be consistent between species, age classes or life-history stages (Baechler et al. 2002, Kuhn et al. 2009). The approach was first applied with northern elephant seals (Le Boeuf et al. 1988), and has subsequently been used for other species (Thompson et al. 1991, Schreer and Testa 1996, Baechler et al. 2002). Benthic U-shaped dive profiles are thought to represent either stationary behaviour on, or movement along, the seabed, which have been interpreted as searching for or pursuing prey in benthic-feeding species (Kuhn et al. 2009), or resting at depth (Thompson et al. 1991). The presence of vertical 'wiggles' (sinuosity) during the bottom phase of U-shaped dives could also indicate active search behaviour, or pursuit of pelagic prey depending on the proximity to the seabed, and can be used to identify prey capture attempts within dives (Heerah et al. 2014, Arthur et al. 2016). However, the ability to detect these movements may be restricted to high-resolution datasets, and determining the proximity of an individual to the seabed is often not possible with ARGOS-derived location data; accurately matching dive depth to the bathymetric depth of the location where that dive occurred requires a high frequency of accurate location estimates and high-resolution bathymetric data. Skewed shapes may represent drift-dives related to food processing, in which the seal is passively drifting through the water column (Le Boeuf et al. 1988, Hindell et al. 1991, Crocker et al. 1997). V-shaped dives with no bottom time are often taken to represent travelling, or sampling the underwater environment (Thompson et al. 1991, Baechler et al. 2002). However, the geometry of a dive is affected by maximum dive depth; dives of similar bottom time may appear as either U or V-shaped depending on the depth. For example, elephant seals forage benthically on deep seamounts (Maxwell et al. 2012), and deep foraging dives may appear as V-shaped dives due to the extended time spent in descent and ascent relative to the bottom phase. A dive of similar bottom time at shallower depth with shorter ascent and descent phases would appear as a U-shaped dive.

Direct metrics of feeding have been used to evaluate the accuracy of dive profile shape analysis for identification of foraging. Kuhn et al. (2009) used STT loggers to validate assumptions of behaviour from dive profiles for northern elephant seals (Fig. 1.3c) and found that, although most common on U-shaped wiggle dives (74.2% of feeding events), feeding occurred on dives of all shapes. Baechler et al. (2002) used animal-borne cameras coupled with TDRs, to observe search behaviour in both male and female harbour seals of varying age class. They found that U-shaped dives were a reasonable predictor of search activity for most individuals. However, the accuracy of predicting search behaviour from dive shapes varied for males during the breeding season. Matching video footage with TDR data revealed adult males producing U-shaped dive profiles whilst searching for prey, travelling and roaring underwater (a vocalisation behaviour associated with reproduction) (Baechler et al. 2002). 2D profiles do not account for lateral displacement underwater; i.e. if an individual remains at constant depth, from a 2D shape we cannot deduce whether they are actively searching or remaining stationary (due to resting, vocalisation, or waiting to ambush prey for example). 3D reconstruction of dives using acoustic positioning arrays, video recorders and accelerometers has revealed that pinniped foraging behaviour during a dive can be remarkably varied and complex (Davis et al. 1999, Simpkins et al. 2001, Hindell et al. 2002). Reconstruction suggests that, if used as the sole analytical technique, 2D profiles may be overly simplistic, introducing a degree of subjectivity to classification of behaviours. Triaxial accelerometers can be particularly helpful to improve our understanding of 3D movement underwater. Head-mounted accelerometers have been used to identify prey-capture attempts in multiple species (Heerah et al. 2014, Ydesen et al. 2014, Volpov et al. 2015). However, they can also be used to determine body position and horizontal displacement, and potentially elucidate the particular behaviours associated with individual dives (Sala et al. 2011). For example, Sala et al. (2011) deployed TDRs with integrated accelerometers on elephant seals to assess the accuracy of behavioural assumptions from 2D dive shapes. By including data on pitch and roll, the authors were able to visualise the body position of individuals at all phases of dives, and differentiate more effectively between passive drift dives, and active search dives (Sala et al. 2011). Moving forwards, combining accelerometer data with dive and location data will increase our ability to infer search behaviour and feeding attempts in 3D. However, accelerometers generate large volumes of data, and the successful transmission of such a quantity of data is currently challenging (Cox et al. 2018). Therefore, the deployment of accelerometers is largely restricted to scenarios where they can be recovered. Although recent advances in abstraction of accelerometery data onboard the device may help to resolve this issue (Cox et al. 2018).

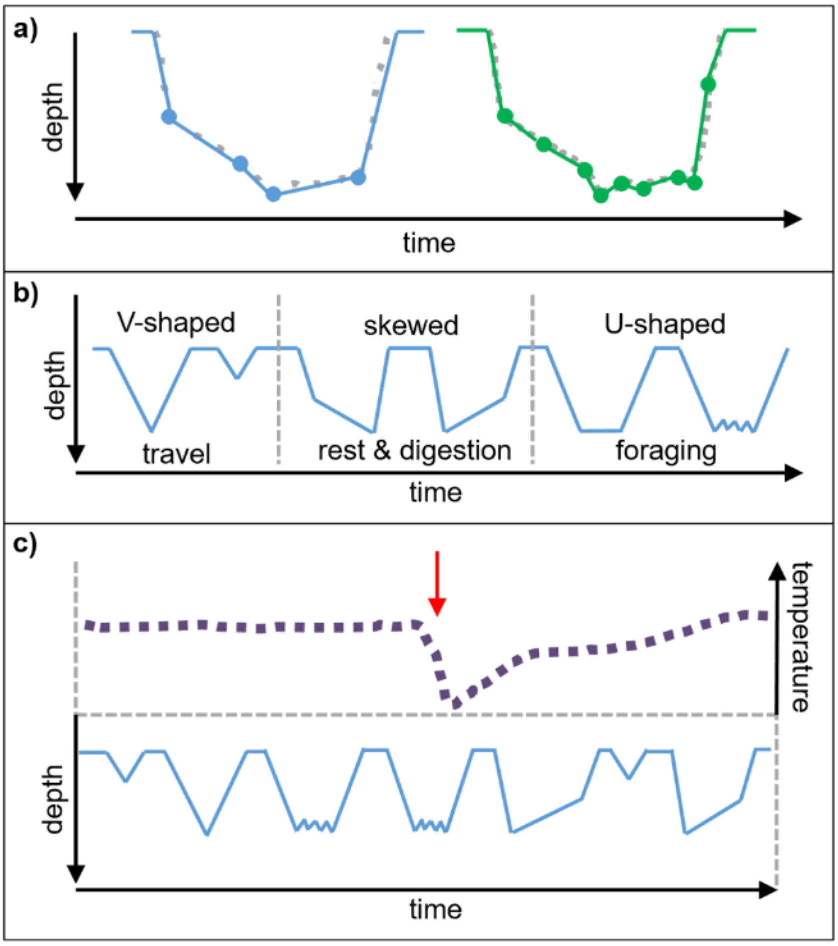

Figure 1.3: Dive data. *(a) Diagram of depth data collected at regular intervals throughout a dive (grey dashed line) and abstracted to inflection points for low resolution (blue dots) and high resolution (green dots) data. This abstraction may be performed using an algorithm on-board the device to reduce the amount of data stored and transmitted. (b) Different 2D dive profiles abstracted from dive data are often used to infer behaviour in seals. (c) Hypothetical example of how stomach temperature telemetry (STT) (top trace) can be used to validate assumptions of foraging inferred from dive profiles (bottom trace). Based on* Kuhn et al. (2009)*, Fig. 1. Arrow denotes feeding event, identified by sharp drop in stomach temperature.*

Whilst U-shaped dives have been used to infer search behaviour at the scale of individual dives, resting dives (with a right or left-skewed shape) may be useful for identifying successful foraging over a broader temporal scale. Drift-rate during rest dives is correlated with an individual's buoyancy in elephant seals, allowing the inference of body mass gain due to successful foraging (Biuw et al. 2003). In this way, areas of successful foraging can be mapped (Bailleul et al. 2007, Dragon et al. 2012a) and other methods of inferring foraging success from location and dive data can be evaluated (Robinson et al. 2007, Dragon et al. 2012b). Although similar right and left-skewed dive profiles have been reported in other species (Baechler et al. 2002, Watanabe et al. 2015), comparable relationships between drift-rate and mass gain are yet to be described. This discovery has yielded a relatively simple method of assessing foraging success for long-ranging animals without the need for identifying foraging behaviour. However, phocid seals experience dramatic changes in body mass and composition in response to life-history events, such as fasting (i.e. the post-weaning fast in pups, or due to being hauled-out for moulting or reproduction in adults), pupping, and season (Beck et al. 2000). Following a period of mass loss, an individual may gain lean mass rather than blubber (Condit and Ortiz 1987, Hall and McConnell 2007). Changes in pinniped body composition may also be affected by the lipid content of their prey-type (Rosen and Trites 2005, Kumagai et al. 2006), or by seasonal changes in the amount of blubber needed for thermoregulation (Rosen and Renouf 1997). In this case, although the individual may be foraging successfully, it is unlikely to experience a positive buoyancy change because lean mass is denser than water (Condit and Ortiz 1987, Beck et al. 2000). Using drift dives to infer foraging success thus has the potential to overlook successful foraging in some circumstances.

In addition to using dive profiles, ecologists have built theoretical foraging models using dive metrics such as dive frequency, depth, bottom duration, ascent and descent rates, as well as duration of post-dive intervals. Using these models, foraging success is inferred based on assumptions drawn from OFT. Pinnipeds must dive in order to search for food, and the descent and ascent phases of a dive represent the transit to and from a prey patch (Houston and McNamara 1985). OFT dictates that individuals will concentrate their time in areas of successful feeding (Stephens and Krebs 1986). Following this, and based on the assumption that foraging occurs during the bottom phase of dives (Thompson and Fedak 2001, Austin et al. 2006b, Kuhn et al. 2009), optimal diving theory (ODT) suggests that divers will maximise their time at the bottom phase of a foraging dive (Carbone and Houston 1996). By maximising time spent at foraging depth, and minimising the time spent in transit (descent and ascent) and recovery (post-dive surface interval), individuals increase their chances of prey capture, offsetting the energetic costs of transit between the surface and the prey patch (Carbone and Houston 1996). Importantly, from this perspective, time underwater is maximised over bouts (a succession of foraging dives with minimal surface interval) rather than individual dives (Carbone and Houston 1996). Exceeding the aerobic dive limit (ADL; the point at which lactate begins to build up in the blood (Butler 2006)) on a single dive, or successive short aerobic dives, will result in anaerobic metabolism, increasing recovery time at the surface and potentially decreasing net energetic gain (Boyd 1997, Kooyman and Ponganis 1998, Rosen et al. 2007). Theoretical foraging models based on ODT predict that oxygen will be the limiting factor in dive behaviour (Rosen et al. 2007), and that individuals will consistently dive up to their calculated ADL during foraging dives in order to maximise prey-capture opportunities. Such models therefore predict that foraging success increases with dive duration, bottom time and dive frequency (Robinson et al. 2007).

Such theoretical foraging models do not account for many of the ecological and physiological complexities that may regulate predator diving. For example, an individual's physiological capacity to dive to, and remain at depth may vary on a seasonal and diurnal scale (Bennett et al. 2001). Therefore, predators may adapt their foraging strategies to account for this physiological plasticity. Furthermore, ODT models assume that prey patches are of a uniform density and quality. In reality this is not the case, and depending on the quality and depth of a prey patch, and the level of competition from other predators, maximising time at foraging depth may not always be the most energy-efficient foraging strategy (Thompson and Fedak 2001, Sparling et al. 2007). For example, in an area with a high density of good quality prey patches where prey capture rates are high, the need to stay at depth is less acute; individuals may surface and move on to a new prey patch with lower energetic consequences. The decision to move on may be driven by localised depletion of the food resource, competition, or the need to rest and digest (Charnov 1976). Likewise, Sparling et al. (2007) have shown that individuals that abandon search and move on early in areas of low prey density maximise net energetic gain. Therefore, in these scenarios, increased bottom time is not correlated with foraging success. Direct observations of feeding attempts have been used to test the performance of ODT models as predictors of foraging success. Such studies have shown that the accuracy of different predictor variables may vary between species, habitats and temporal scale of analysis (Austin et al. 2006a, Gallon et al. 2013, Heaslip et al. 2014, Viviant et al. 2014, Volpov et al. 2016). Viviant et al. (2014) deployed accelerometers (measuring jaw-openings as a proxy for prey capture attempts) in conjunction with TDRs on Antarctic fur seals (*Arctocephalus gazella*). They tested a combination of metrics including bottom duration, ascent and descent rates and maximum dive depth as predictors of foraging success. Ground-truthing with accelerometer data revealed that the best predictors varied depending on the temporal scale of analysis, ranging from individual dives to several hours (Viviant et al. 2014). This suggests that data resolution is likely to be a key factor in the accuracy of different methods of identifying foraging success from dive metrics; the best predictor of foraging success for a particular dive bout may not perform as well when applied across an entire foraging trip. With this in mind, current theoretical foraging models using dive metrics may be too simplistic to accurately describe the dynamics of decision-making in foraging behaviour.

Overall, dive data are a powerful resource when attempting to quantify foraging effort in pinnipeds, in which direct observations of search behaviour or feeding attempts are not available, but should be used with a clear understanding of their limitations. Recent studies suggest that high-resolution dive datasets can be used to inform the best analytical approach for low-resolution data (Heerah et al. 2015, Labrousse et al. 2015). Moving forwards, tagging a sub-sample of animals with high-resolution devices, cameras or accelerometers where possible may be a good option for future studies in order to identify appropriate analytical techniques.

1.3.2 Inferring foraging from location data

Animal location data can be used to identify and quantify foraging. For central place foragers that make discrete foraging trips to sea, returning to land to rest and digest, or provision young, the duration and extent of these trips are used to make broad observations of foraging effort (Thompson et al. 1998a, Takahashi et al. 2003, Cronin et al. 2013). However, in isolation, trip duration and extent give no information about where individuals are searching for prey, how they are exploiting their environment in order to find it, what proportion of the time at sea is spent foraging in relation to other behaviours such as resting and travelling, and if they are foraging successfully. Within the trip itself, the distribution of time along the track can be analysed, and movement patterns that may relate to specific behaviours can be identified (Boyd 1996). The simplest way to deconstruct a horizontal track and identify movement patterns is to divide it into segments of straight lines interrupted by turns. In order to quantify the distribution of time along a track, it is often necessary to regularise ‘fixes’ (locations) to a constant time step (Fig. 1.4a). By interpolating between temporally-regularised locations, the displacement distance and change in bearing between fixes can then be extracted (Fig. 1.4b). Displacement gives a measure of ground speed, whilst change in bearing (turning angle) can show track sinuosity. Predator movements are often classified into two broad strategies; (1) 'directed' travel with little or no meandering, and (2) 'resident' behaviour with slower, meandering movement (Fig. 1.5a) (Boyd 1996, Le Boeuf et al. 2000). In the context of OFT, these slower movements are commonly attributed to area-restricted search (ARS) behaviour, indicative of foraging effort within a prey patch (Boyd 1996, Fauchald and Tveraa 2003, Barraquand and Benhamou 2008). Studies commonly use track metrics to distinguish between directed and resident movement patterns. For example, travel to and from, or between, foraging patches is associated with high displacement between fixes, and small changes in bearing. In contrast, ARS behaviour is characterised by a more sinuous track section with lower displacement (Boyd 1996). Although opportunistic foraging may occur during directed travel (Thompson et al. 1991, McConnell et al. 2002, Kuhn et al. 2009), and individuals may search for prey on multiple spatial scales (Barraquand and Benhamou 2008, Pinaud 2008), ARS behaviour is often used to quantify when and where predators concentrate foraging effort. Methods of quantifying ARS from track metrics range from simple descriptive approaches (e.g. plotting variable distributions through time and defining a threshold (Le Boeuf et al. 2000)) to sophisticated mechanistic models that can incorporate multiple movement metrics at different data resolutions and account for spatial uncertainty of location estimates (Patterson et al. 2008).

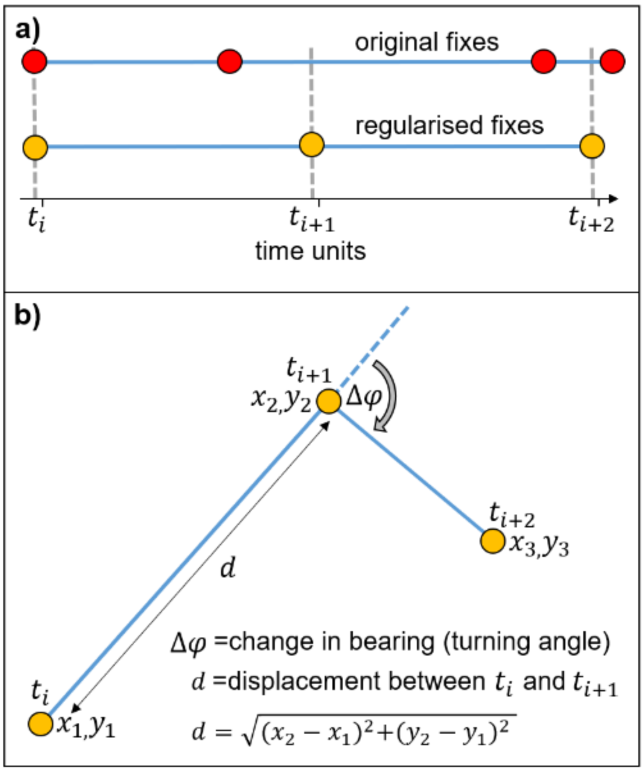

Figure 1.4: Track metrics. *Diagram of successive hypothetical location fixes through (a) time and (b) space. (a) In order to calculate changes in track metrics through time, it is often necessary to regularise recorded 'fixes' (locations) to a constant time step. The resulting regularised fixes are normally connected in space with linear interpolation. (b) Diagram shows two metrics commonly used in movement analyses. Change in bearing (turning angle) is a measure of path sinuosity, whilst the displacement distance between temporally-regularised location fixes can give an estimate of ground speed. By examining changes to these metrics over time different movement patterns can be identified.*

As an alternative to the use of displacement and turning angle, first-passage time (FPT) can be used to distinguish between ARS and directed movement (Fauchald and Tveraa 2003). The FPT is defined as the time taken for an individual to cross a virtual circle of given radius (Fauchald and Tveraa 2003). The circle is centred on the location fix, and the FPT is calculated by summing the number of temporally-regularised time steps taken to leave the circle boundary in both forward and backward directions (Fig. 1.5b). The areas in which individuals concentrate their time can be identified by sliding this circle along the track (Fig. 1.5c). FPT analysis is conceptually simple and relatively straightforward to implement. Nevertheless, certain limitations restrict its accuracy for pinnipeds. For example, Fauchald and Tveraa (2003) proposed that the chosen radius of the circle should be equal to the diameter of a typical prey patch. This, however, assumes that all prey patches will be circular, and of equal density, and that predators are repelled by patch boundaries. In reality, the density and distribution of pinniped prey resources is rarely known, and may vary along a single track. Seals may access multiple habitats, and target different prey types during a foraging trip, with subsequent effects on foraging behaviour and the scale of search (Biuw et al. 2007, Barraquand and Benhamou 2008). The circle radius chosen for FPT analysis will therefore be somewhat arbitrary, and defining one scale for the entire track may be inappropriate (Barraquand and Benhamou 2008).

'Residence time' (RT) analysis was developed as an adaptation of the FPT concept to attempt to overcome the aforementioned limitation. It can take account of previous time spent in the same circle (Fig. 1.5b) (Barraquand and Benhamou 2008). This means that the analysis is more effective at identifying foraging areas in heterogeneous environments, as it gives a cumulative measure of habitat use (Barraquand and Benhamou 2008). Furthermore, RT analysis uses a statistical approach (penalised contrast algorithm; Lavielle (2005)) to identify ARS, rather than relying on visual inspection of model output (Barraquand and Benhamou 2008). Barraquand and Benhamou (2008) show that the RT approach is also less influenced by data resolution than FPT analysis. Whilst this method represents a step forward from FPT analysis, it still relies on the user to define certain parameters (i.e. the amount of time an animal is out of the circle before that path segment is discounted; Fig. 1.5b). Furthermore, as with FPT, RT analysis cannot account for the uncertainty related to location estimates, or give a measure of uncertainty related to assumptions of foraging behaviour. In recent years, sophisticated modelling techniques have been developed that can perform these functions in a more objective manner (Patterson et al. 2008).

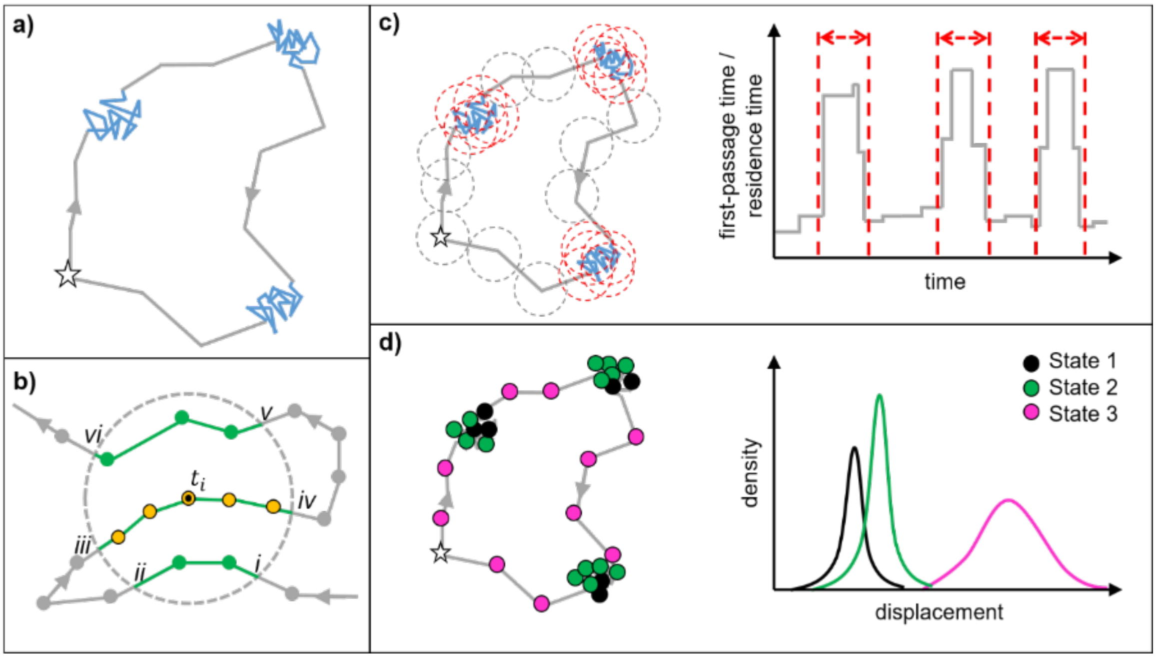

Figure 1.5: Analytical methods for horizontal movement data. *Diagrams show hypothetical track of a central place forager, star represents central place. (a) Two patterns of movement can typically be detected in predator tracks; extensive movements with high displacement and low turning angle (grey lines) and intensive movements with low displacement and high turning angles (blue lines). Intensive movements are commonly taken to represent area-restricted search (ARS) behaviour. (b) Fist-passage time (FPT) is the sum of temporally-regularised location fixes required to leave a circle of given radius in both forward and backward directions from time point* t_i *(yellow dots). Residence time (RT) includes total time spent in the circle from present (iii-iv), previous (i-ii) and future (v-vi) time steps (green lines), provided that time outside the circle (gap between intersection points ii-iii or between iv-v) is not above a user-defined threshold. (c) Areas of high FPT / RT can be identified by sliding the circle along the track at each time step. Red dashes denote the areas in space (left) and time (right) taken to represent ARS. (d) Demonstration of a three-state HMM output. Right-hand plot shows posterior probability distributions of displacement for three discrete states. Using biological rationale, movement states can be used to infer behaviours (e.g. state 3 with high displacement may be travelling, states 1 and 2 may be either foraging or resting). Presence/absence of diving can be included in the model to distinguish between foraging and resting at the surface* (Russell et al. 2015).

State-space models (SSMs) have multiple applications for animal movement studies (Patterson et al. 2008, Schick et al. 2008). SSMs can be used to improve the spatial accuracy of location estimates, and/or estimate movement modes (Jonsen et al. 2003). Location estimates can be processed with an SSM (e.g. Kalman filter; KF) to reduce spatial errors

(Jones et al. 2015). The SSM predicts the current state (location) together with its associated spatial error. Since 2011, ARGOS have offered the option to receive location estimates derived by a KF, rather than the original least squares (LS) algorithm (CLS 2015). Once a prediction for a location is made, the algorithm updates all predictions of previous locations using a weighted average, giving more weight to estimates with higher certainty. Recent studies have tested the accuracy of both KF-derived and LS-derived ARGOS locations for phocids using simultaneously collected high-resolution Fastloc® GPS data as a measure of 'true' location (Silva et al. 2014, Lowther et al. 2015). Silva et al. (2014) found that 82% of KF-derived harbour seal locations were within 5km of the 'true' GPS positions, compared with 73% of LS-derived locations. By improving location accuracy, SSMs can increase the potential of low resolution telemetry datasets for investigation of behaviours (Silva et al. 2014, Lowther et al. 2015).

SSMs have been developed that can estimate movement modes from location data. The cleaning of the location data, to improve accuracy, can be combined with state estimation (Jonsen et al. 2003, 2005). Alternatively, data are used directly for state estimation within a hidden Markov model (HMMs); such data must be spatially accurate (GPS-derived), or already cleaned using an SSM to improve accuracy (Patterson et al. 2008). HMMs are SSMs in which a finite number of discrete states are defined. States are estimated based on the distribution of movement metrics through time (Langrock et al. 2012). HMMs take input movement metrics, such as displacement and consistency in travel direction, and generate unique posterior distributions for each, based on a specified or estimated number of behavioural states (Fig. 1.5d). A recently-developed R package "moveHMM" makes building simple HMMs accessible for researchers outside the field of statistics (Michelot et al. 2016).

SSMs represent a powerful tool for foraging analysis in that they can combine multiple movement metrics from tracking data and estimate movement states with a higher degree of statistical robustness than other commonly-used methods (Jonsen et al. 2005, Patterson et al. 2008, Bestley et al. 2015). For example, unlike FPT and RT approaches, SSMs can distinguish between multiple movement patterns without needing to apply thresholds to movement metrics or analytical scale (Jonsen et al. 2005). Using biological rationale, ecologists infer behaviours from the discrete movement states identified by the SSM. SSMs enable us to quantify foraging behaviour in relation to other behaviours such as resting and travelling, and thus tackle more complex questions of how these activities interact through time and space (Jonsen et al. 2005, Breed et al. 2009, 2011b, Russell et al. 2015). Importantly, models can test the influence of explanatory covariates on the probability of switching into a certain movement state. For example, Morales et al. (2004) demonstrated how SSMs can be used to investigate the influence of environmental factors on foraging decisions. Furthermore, models can be applied in either a frequentist Maximum Likelihood (ML) or Bayesian framework. Although ML models are more tractable and computationally less costly, they typically require data to be in uniform time steps with little associated error in order to make the calculation (Langrock et al. 2012). Bayesian models do not have such constraints, and therefore can account for spatial uncertainty and irregular time series arising from coarse tracking data (Schick et al. 2008). This makes them a good option for data collected via the ARGOS system. However, processing time for Bayesian models is greatly increased due to the associated computational demand.

Pinniped location data has been an important resource for developing and testing the utility of SSMs for animal movement studies (Jonsen et al. 2005). SSMs have now been applied to large datasets to investigate diverse questions including intrinsic and extrinsic drivers of variation in foraging behaviour (Breed et al. 2009, Russell et al. 2015). However, despite the relative advantages of SSM approaches over other commonly-used analytical methods, they share a common limitation if only applied to location data. Using only horizontal movements, these techniques assume that individuals make discrete journeys in order to forage, but return to the central place to rest. This paradigm therefore assumes only two behavioural modes at sea; travelling and foraging, and attributes all slow, sinuous movements to ARS behaviour (Jonsen et al. 2005, Breed et al. 2009). However, many pinniped species rest at sea during foraging trips either at the surface (Thompson et al. 1991, Boyd 1996, Ramasco et al. 2015, Russell et al. 2015), or beneath it (Crocker et al. 1997, Watanabe et al. 2015), producing similar movement patterns to ARS. Therefore, using location data in this way may over-estimate foraging behaviour. In order to overcome these limitations, it is necessary to consider movement in three dimensions.

1.3.3 Combining dive and location data to improve foraging models

Recently, Russell et al. (2015) used an SSM to investigate the possible drivers of contrasting population trajectories for sympatric grey (*Halichoerus grypus*) and harbour seals in the North Sea. They combined location data with simultaneously-collected dive data. Using consistency in travel direction and displacement distance between temporally-regularised location fixes, the model identified between high transit rate with small changes in direction, and slower, more sinuous movement (Russell et al. 2015). However, incorporating presence/absence of diving in the model allowed the authors to infer two behavioural states from slow movements; ‘foraging’, and ‘resting at surface’ (Russell et al. 2015). Moreover, where previous studies had excluded data within proximity of the coast to avoid classifying time spent hauled-out on land as foraging, using the ancillary behavioural data, they were able to include resting on land as a further behaviour in their analysis of activity budgets (Russell et al. 2015). In this way, the analysis was able to capture coastal foraging that may have been excluded by applying a coastal buffer (Russell et al. 2015). Importantly, the study found that >10% of the seals’ activity was attributed to resting at the surface whilst at sea, highlighting the importance of combining track metrics with dive data to ensure that resting behaviour is not mistakenly classified as foraging (Russell et al. 2015). For species that commonly rest underwater, however, such as elephant seals, incorporation of presence/absence of diving would not be a satisfactory method of distinguishing between resting and foraging. In this case, models could attempt to distinguish resting dives by their shape, duration or vertical displacement rate compared to foraging or travelling dives, and thus inform behavioural states in the same way.

Although either dive or location data may be used in isolation to identify foraging with traditional methods or SSMs, the accuracy of analysis is often scale-dependent and highly influenced by data resolution. Furthermore, using one of these data types alone may over-simplify at-sea behaviours, leading to over or under-estimation of foraging activity. Including both dive and location metrics in analytical models lends more information, and therefore more power to foraging analysis (Photopoulou et al. 2014). Bestley et al. (2015) incorporated dive depth and duration, as well as post-dive surface interval into an SSM with horizontal track metrics to describe foraging for multiple Antarctic pinniped species. The use of vertical data improved the capacity of the model to identify where foraging bouts occurred (Bestley et al. 2015). Increasing the accuracy of foraging models in this way will allow ecologists to identify important foraging habitat with greater certainty, and improve the effectiveness of conservation management. Moving forwards, SSMs represent a powerful tool for tackling complex questions of both the spatial and energetic dynamics of foraging. Furthermore, the ability to incorporate environmental covariates in SSMs may prove vital in unravelling how oceanographic processes drive spatial and temporal patterns of foraging behaviour (Eckert et al. 2008, Schick et al. 2008, Patterson et al. 2009). SSMs have great potential for maximising the utility of tracking datasets, and the combined advantages they offer cannot currently be equalled by any other approach that we know of. SSM techniques not only allow us to identify foraging behaviour in a more statistically robust manner than traditional methods, but they allow us to do so by combining multiple data types (e.g. dive and location data) and qualities (e.g. ARGOS and GPS data) in the same analysis, thus maximising the application of available data resources (Bailey et al. 2014, Russell et al. 2015). However, a trade-off exists between the computational tractability and simplicity of models, and biological realism. For example, combining multiple data types will improve the biological realism of inferred behavioural states, but will increase computational demand and technical complexity. Nevertheless, SSMs for animal tracking data continue to be refined and developed, and these models represent our best option for improving our understanding of pinniped foraging dynamics as multi-year tracking datasets grow in abundance. However, this progress will depend on ecologists collaborating closely with statisticians, sharing their code openly alongside published studies.

1.4 Future Directions

1.4.1 Data resolution

Foraging can be classified at the scale of surface movement patterns, individual dives, or even parts of dives. With all attempts to infer foraging from tracking data there are important considerations to be made. Firstly, models should ideally detect foraging on the scale of search of the individual. For animals with small ranges of movement, detecting search behaviour may require data at high levels of spatial and temporal resolution. The scale of movement may therefore be too fine to detect with data transmitted via ARGOS, and researchers may find that model parameters are defined by the data resolution rather than the biology (Robinson et al. 2007, Pinaud 2008, Breed et al. 2011b). This may result in under/over-estimation of foraging. For example, a recent study used SSMs to compare activity budgets for grey and harbour seals (Russell et al. 2015). The study combined ARGOS SRDL data with GPS-GSM data. In order to utilise both data types, SSMs were fitted to assign movement states to 6 hour intervals. Whilst the resolution was suitable to quantify activity budgets for grey seals, determining between travel and foraging proved problematic for harbour seals, probably because they typically forage closer to shore, and thus do not exhibit long periods of travelling (Russell et al. 2015). The SSM models for harbour seals performed better when GPS data were used on a 2 hour resolution interval (Russell 2015a). Secondly, the research question will also dictate the resolution of data required; in order to investigate the fine-scale movements of harbour seals within an offshore windfarm, Russell et al. (2014) used an SSM with fifteen minute intervals. In this case, with a 2 hour interval, it would not be possible to determine if individuals trace specific structures, or to distinguish between foraging and travelling around and between these structures. For long-ranging species moving across ocean basins, in which behaviour may switch between migration and residency, a small number of location fixes per day may be enough to detect discrete behaviours. Therefore, when designing tagging studies, researchers should be mindful of the spatial and temporal data resolution required to accurately identify changes in movement patterns for their study species and research question, and choose a device and sampling rate that will capture this signal (Fig. 1.6; Breed et al. (2011b)). Nevertheless, increasing duty cycles will likely have a negative effect on the duration of the battery, and so, the trade-off between sampling frequency and duration needs to be carefully considered.

Biologging device deployments are normally costly and logistically demanding. With all devices, the quantity and quality of the data transmitted will depend on the battery life, transmission opportunities, duty cycle, satellite coverage and animal behaviour (Patterson and Hartmann 2011). However, Patterson and Hartmann (2011) pointed out that researchers often rely on trial and error to optimize sampling regimes, resulting in unhelpful datasets. They suggest that pooling datasets across species and regions to compare tag performance could help in designing optimal data collection strategies. Moreover, they showed that synchronizing transmission attempts with satellite passes can improve data throughput and battery performance (Patterson and Hartmann 2011). Studies of this technical nature are extremely helpful, but have received little acknowledgment in subsequent published studies. We suggest that such theoretical research should be consulted before selecting and programming devices to avoid incomplete datasets and to maximise the utility of the data. Furthermore, improving biologging data utility will depend upon ecologists collaborating with technicians and engineers to improve device battery performance and maximise data capture.

1.4.2 Device effects

Although technological advances are allowing us to minimise the size and weight of biologging devices, there is substantial evidence to suggest that some methods of handling animals for tag application, and the physical effects of the tag itself, may alter the subsequent behaviour of the individual, and perhaps its prey (Heaslip and Hooker 2008, Hazekamp et al. 2010, Walker et al. 2012, Blanchet et al. 2014). For example, head-mounted cameras with strobe flashes have been reported to affect the diving behaviour of their pinniped carriers, and/or the prey on which they forage (Heaslip and Hooker 2008). In contrast to flying seabirds, where device weight can have a large effect on the energetics of flight (Vandenabeele et al. 2012), drag caused by tag placement is a greater concern in pinnipeds (Suzuki et al. 2014). Hazekamp et al. (2010) showed that externally-attached devices such as SRDLs can change an animal's hydrodynamics and potentially alter their physiology and behaviour. Tag designers face a challenge in that a device's antenna must break the surface in order to receive a location estimate and/or transmit data. This often requires tag placement on the head, neck or back. Attaching tags in a caudal position would likely reduce device-induced turbulence (Bannasch et al. 1994), but this may compromise data collection and transmission. Whilst the effects on animals will only last as long as the device is attached, ecologists should be mindful that the movement patterns observed in their data may carry some bias. In addition to these concerns, device effects raise ethical considerations about the welfare of the individual, particularly for juveniles and smaller species, in which drag may be more severe (McKnight et al. 2015). As we continue to rely on biologging data to inform the conservation management of species, more research is urgently needed in this field in order to assess the potential bias in existing datasets, refine capture and tag application methods, and improve the hydrodynamic footprint of externally-attached devices.

1.4.3 Considering the environment

The vast majority of marine predator studies that recreate animal movements from tracking data do so in geographical space; i.e. they assume that the individual is moving through a still medium with no physical forces acting upon them. The reality is that ocean tides and currents can have a strong and dynamic influence on movement and therefore how we infer behaviour (Gaspar et al. 2006). Gaspar et al. (2006) reconstructed the movements of a migrating leatherback turtle (*Dermochelys coriacea*) in both geographical and hydrographical space (accounting for ocean currents). They showed that currents can have a large influence on how we interpret track tortuosity, and therefore identify ARS. The study demonstrated how overlooking ocean currents can compromise our ability to successfully identify foraging activity, particularly in areas of high turbulence which are normally associated with high prey density and productivity (Gaspar et al. 2006). Moving forwards, it is vital that researchers consider the dynamic physical nature of the individual's environment before attempting to interpret behaviour from location data alone. For example, an individual foraging on pelagic prey in the water column may be moving with the current, whilst a benthic-foraging animal may be attempting to remain in one place, actively swimming against the current. This has important implications for the way data are interpreted and how researchers assign behaviours to observed patterns. In the latter scenario, if we do not consider currents, an individual may appear to be stationary or resting underwater when in fact it is foraging, and perhaps expending significant energy in maintaining position. One way to avoid this error is to exclude data in areas of high tidal flow (Russell et al. 2015). However, it is not understood exactly how predators exploit ocean currents, and this approach may fail to identify potentially important foraging habitat (Zamon 2001, Johnston et al. 2005, Bailey and Thompson 2010, Hastie et al. 2016, Hays et al. 2016). Therefore, for foraging studies, other approaches that capture the influence of currents on the movement of the instrumented animal should be explored. For example, a drift covariate may be incorporated in hierarchical models of animal movement to account for ocean currents (Johnson et al. 2008). We suggest that studies similar to that of Gaspar et al. (2006) should be conducted with multiple pinniped species in varied oceanographic conditions to assess the effect of currents on detection of ARS for commonly-used methods. Deploying STT devices or accelerometers in conjunction with tracking devices may help to inform researchers about how their study species exploits ocean currents during foraging (Della Penna et al. 2015).

Considering the environment in which the study species exists is important not only for the accurate identification of foraging, but also for understanding how abiotic (i.e. oceanographic) covariates may be driving observed behaviour (Schick et al. 2008, Patterson et al. 2009). Bailleul et al. (2007) used data from animal-borne CTD sensors in conjunction with drift-dive analysis to determine the unique oceanographic features of important foraging zones for southern elephant seals. Studies such as this may provide key information to aid conservation managers and marine spatial planners in designing effective protection for marine predators. A major advantage of environmental sensors deployed on free-ranging marine predators is that they provide valuable information for ecologists and oceanographers alike (Boehlert et al. 2001, Boehme et al. 2009, Fedak 2013). In addition to data from animal-borne sensors, a comprehensive suite of remotely-sensed, and buoy-recorded physical oceanographic data is available to give a more complete picture of oceanographic processes, (for example from the Physical Oceanography Distributed Active Archive Center (PODAAC), the British Oceanographic Data Centre (BODC), the National Oceanographic and Atmospheric Administration

(NOAA), and the NERC Earth Observation Data Acquisition and Analysis Service (NEODAAS)). Data on sea surface temperature (SST), bathymetry, tidal vectors, sea-ice coverage and wind shear stress, used in conjunction with tracking datasets, are now allowing ecologists to build a greater understanding of how populations may respond to climate anomalies (Lea et al. 2006), and potentially exploit dynamic oceanographic features, (Biuw et al. 2007, Bost et al. 2009, Scales et al. 2014, Della Penna et al. 2015, Labrousse et al. 2015, Miller et al. 2015). Moreover, incorporating environmental covariates in SSMs may allow us to simultaneously improve our ability to identify foraging behaviour and determine habitat preference, whilst taking into account the uncertainty in locations and assumptions about classifying foraging (Morales et al. 2004, Schick et al. 2008, Patterson et al. 2009). Moving forwards, combining data sources to improve our ability to identify and predict behaviours from marine species in this way could inform novel conservation approaches such as Dynamic Ocean Management; "management that rapidly changes in space and time in response to changes in the ocean and its users through the integration of near real-time biological, oceanographic, social and/or economic data" (Maxwell et al. 2015).

1.4.4 Population-level inferences

Although we are drawing an increasingly detailed picture of marine predator foraging behaviour, research has tended to be heavily focussed on a handful of species and demographic classes (Hazen et al. 2012, McIntyre 2014). In pinniped tracking studies, there is a general bias towards reproductive females (McIntyre 2014), as many species are tied to land throughout the pupping and provisioning phase of the breeding cycle, and are thus easier to catch for tag application and retrieval. This is most notable in the otariid literature. Nevertheless, foraging strategies are known to vary seasonally, between the sexes (Thompson et al. 1998a, Beck et al. 2003a, 2007, Breed et al. 2009, Sharples et al.

2012) , age classes (Fowler et al. 2006, Bennett et al. 2010, Breed et al. 2011a, Jeglinski et al. 2012), and indeed between individuals in general (Tollit et al. 1998, Austin et al. 2006b, Biuw et al. 2007). Due to cost and logistics, tagging studies are often constrained by relatively small sample sizes. However, in order to answer research questions that will have some benefit to the conservation management of species, it is often necessary to make population-level inferences about foraging and habitat use (Aarts et al. 2008). Fully understanding population dynamics and potential threats may therefore depend on examining the behaviour of individuals from across their range, sexes and age classes (Aarts et al. 2008). A further consideration is that the individuals selected for a tagging study may not always be representative of the wider population. Logistical constraints mean that tagged animals are rarely selected at random. For example, it may be necessary to select individuals from the periphery of a colony in order to minimise disturbance, or known animals may be preferentially selected based on their contribution to long-term datasets, or robustness to handling. However, it is not known how the capture or selection method may introduce bias to population-level inferences of behaviour; i.e. animals taken from the periphery of a colony may be in poorer condition, which may be reflected in their behaviour at sea. Moving forwards, when investigating population-level foraging, researchers should consider the number of tags that need to be deployed, and whether they can logistically obtain a balanced and representative sample (Fig. 1.6). For a more detailed discussion on representativeness of study sample in population-level tracking studies, see Aarts et al. (2008).

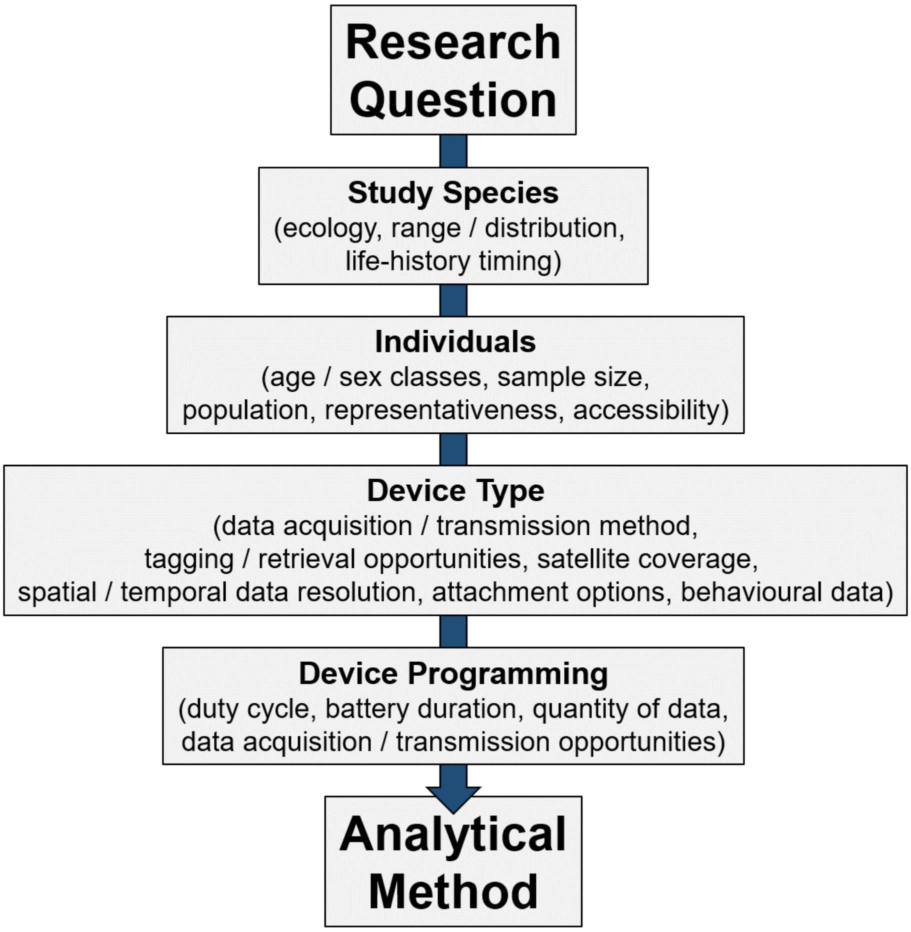

Figure 1.6: Choosing the right analytical method. *Choosing the appropriate analytical method will depend upon careful consideration of some key aspects of the study. Key aspects are given in bold, subsequent considerations are shown in parentheses.*

Animal movement studies face the inherent challenge that the quantity of data may be disproportionate between individuals or groups (Aarts et al. 2008). Furthermore, location and dive observations are autocorrelated, and the use of multiple observations per individual is considered pseudo-replication (Zuur et al. 2009). Whilst detailed discussion of this is beyond the scope of this review, they are important considerations when analysing such datasets, and researchers should select the most robust statistical tools available to them. In recent years, mixed effects models and generalized estimating equations with correlation structures have become more prevalent in pinniped studies, and can help to overcome these challenges. For more discussion on this, see (Aarts et al. 2008, Zuur et al. 2009, Pirotta et al. 2011).

To discover how individual differences in foraging strategies arise, we must focus more research attention on ontogeny (Hays et al. 2016). First-year survival in pinnipeds is naturally low, and variable between years, and has an important effect on population dynamics (Harwood and Prime 1978, Hall et al. 2002, Baker and Thompson 2007, de Little et al. 2007). However, a dearth of information exists on the factors that affect the development of successful foraging behaviour (Hazen et al. 2012). In order to address this knowledge gap, researchers should attempt to track recently-weaned pups as they explore their environment, learning how to dive and find food (Bennett et al. 2010). Numerous studies have used pup movement data to address the ontogeny of diving from a physiological perspective (Lydersen et al. 1993, Bekkby and Bjørge 2000, Bennett et al. 2010, Jenssen et al. 2010), and comparatively fewer investigate the ontogeny of foraging strategies (Fowler et al. 2007, Breed et al. 2011a, Jeglinski et al. 2012). For otariids, and some phocid species, pups may learn to dive (and potentially forage) alongside their mother (Bowen et al. 1999, Gjertz et al. 2000, Lee et al. 2014). However, some phocid species, such as elephant and grey seals, undergo a post-weaning fast, often on land, and must learn to dive and find food without parental supervision before their energy stores are exhausted (Reilly 1991, Bennett et al. 2007). Breed et al. (2011a) modelled movement data for young-of-the-year (YOY; captured at five months of age) and sub-adult grey seals using an SSM and found evidence that sex-related differences in foraging may develop before sexual dimorphism emerges. They also found that YOY animals travelled up to three times further to foraging patches than sub-adults and adults, requiring greater transit time and energetic investment (Breed et al. 2011a). Given that pups are already constrained in terms of accessible foraging habitat by their limited physiological capacity to dive to, and remain at depth, this has potentially important ramifications for survival (Burns 1999, Bennett et al. 2010). Pups gain lean mass rather than blubber in their first year of independent feeding (Hall and McConnell 2007). Failure or delay in successful foraging after leaving the natal colony is likely to result in depletion of limited protein, and ultimately starvation (Bennett et al. 2007). Therefore, smaller pups with more limited fuel reserves may not develop the necessary physiological capability to exploit foraging grounds before their protein stores are diminished (Bennett et al. 2007, 2010). More research is needed to fully understand the challenges facing pups as they leave the colony and learn to find food in a rapidly-changing marine environment, so that important foraging areas can be identified and potential anthropogenic impacts can be assessed and effectively mitigated at this critical life stage. Furthermore, integrating more movement sensors such as accelerometers in tags deployed on pups will allow better classification of movement states from location and dive data. Given that pups have different physiological capabilities and energy requirements to adults, and their behaviour will likely change over time, the assumptions of behavioural modes from adult foraging models may be inaccurate.

1.5 Concluding Remarks

As we continue to impact marine ecosystems with over-fishing, increased vessel traffic, habitat modification, pollution, and anthropogenic climate change, rates of biodiversity loss may pass a critical threshold of extinction (McCauley et al. 2015). In addition to these pressures, the ramifications for marine fauna of policy changes such as fisheries discard reforms, and the switch from hydrocarbon extraction to marine renewable energy installations, remain unknown. Assessing the significance of these changes for marine ecosystems will be of chief importance for conservation management (Inger et al. 2009, McCauley et al. 2015). Among the species likely to be most immediately and obviously affected are marine predators (Votier et al. 2013, Russell et al. 2014, Sydeman et al. 2015). Accurately reconstructing predator foraging movements will be crucial to identifying critical habitat for marine species and designing effective marine protected areas (MPAs) that will benefit entire ecosystems (Hooker and Gerber 2004, Hooker et al. 2011, Montevecchi et al. 2012, Allen and Singh 2016). Moreover, marine mammals represent a valuable resource as sentinels of ecosystem health, and expanding our knowledge of their foraging behaviour will allow us to assess how marine systems may respond under global environmental change (Ross 2000, Reddy et al. 2001, Moore 2008, Bossart 2011). Biologging data will no doubt play a leading role in this process, and further refining analytical techniques of these data should be given high priority (Hays et al. 2016). There remain inherent limitations in inferring animal behaviour from location and dive data. No one analytical approach can capture foraging from these data with complete accuracy. However, ecologists can select the best analytical method based upon several key considerations; the research question, the study species, the number and class of individuals required, the device type, and device programming (Fig. 1.6). Depending on the range of movement of the individual, the resolution of the data and the complexity of the analysis, some techniques may over or under-estimate foraging. Nevertheless, SSMs represent a rapidly-developing holistic statistical method that has the capacity to incorporate multiple data types and allows more robust behavioural inferences to be made (Patterson et al. 2008). SSMs will allow ecologists to create a more complete picture of activity budgets and population dynamics (Breed et al. 2009, Russell et al. 2015), with the potential to draw links between predator behaviours and environmental phenomena (Patterson et al. 2009). The priority for future work is to focus on incorporating oceanographic information into analyses to better understand patterns of habitat use, to determine the physical and behavioural consequences of specific tags to the study animal, and to develop an understanding of the ontogeny of foraging strategies in naïve pups. This will lead to more accurate population-level assessment of habitat use and will therefore benefit our ability to mitigate the effects of anthropogenic activity on the marine environment.

Chapter II

Intrinsic and extrinsic factors drive ontogeny of early-life at-sea behaviour in a marine top predator

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ABSTRACT

Young animals must learn to forage effectively to survive the transition from parental provisioning to independent feeding. Rapid development of successful foraging strategies is particularly important for capital breeders that do not receive parental guidance after weaning. The intrinsic and extrinsic drivers of variation in ontogeny of foraging are poorly understood for many species. Grey seals (*Halichoerus grypus*) are typical capital breeders; pups are abandoned on the natal site after a brief suckling phase and must develop foraging skills without external input. We collected location and dive data from recently-weaned grey seal pups from two regions of the United Kingdom (the North Sea and the Celtic and Irish Seas) using animal-borne telemetry devices during their first months of independence at sea. Dive duration, depth, bottom-time, and benthic diving increased over the first 40 days. The shape and magnitude of changes differed between regions. Females consistently had longer bottom-times, and in the Celtic and Irish Seas they used shallower water than males. Regional sex differences suggest that extrinsic factors, such as water depth, contribute to behavioural sexual segregation. We recommend that conservation strategies consider movements of young naïve animals in addition to those of adults to account for developmental behavioural changes.

2.1 Introduction

Transition from dependence on parental provisioning to independent feeding is a critical time in the life of all animal species that receive parental care. For slow-maturing species, the first months of independent life are crucial in determining survival to recruitment, and therefore sustaining stable populations (Lindström 1999, Sæther et al. 2013, Orgeret et al. 2016). Survival depends on developing the ability to successfully find, compete for, capture and handle food resources whilst avoiding predation (Sullivan 1989, Daunt et al. 2007). Juvenile behaviour, and its relationship with the development of successful feeding strategies, is receiving increasing research interest given the influence of early-life survival on population dynamics (Lindström 1999, Shillinger et al. 2012, Riotte-Lambert and Weimerskirch 2013, Orgeret et al. 2016, Rotics et al. 2016, de Grissac et al. 2017). Unpicking the intrinsic and extrinsic factors that affect the development of foraging skills is key to understanding population trajectories and identifying critical habitat for species during their most vulnerable life stages.

For air-breathing marine diving predators, such as marine mammals, sea turtles, and seabirds, the challenge of developing effective foraging strategies is particularly acute. Individuals must locate and exploit patchily-distributed prey resources in a dynamic environment, within the physiological constraints of breath-hold diving (Boyd 1997). Studying ontogeny in wild marine predators is problematic, not least because a considerable proportion of their lives is spent at sea, often underwater, where direct observations of behaviour are difficult or impossible (Shillinger et al. 2012). Acoustic, satellite and Global System for Mobile communication (GSM) telemetry devices have allowed ecologists to track diving predators at sea, building an increasingly clear picture of their movements and dive behaviour (Ropert-Coudert et al. 2009, Hussey et al. 2015). Logistical and practical constraints, such as high mortality rates and low re-encounter probability, mean that behavioural datasets for young animals are sparse (Hazen et al.

2012). Pinnipeds and seabirds are dependent on terrestrial habitat for reproduction, and young animals are large enough to carry biologging devices, therefore providing tractable opportunities to record location and behavioural data spanning the initial months of independence (Hazen et al. 2012).

Many pinniped species, including otariids and walruses (odobenids), are income breeders (Boness and Bowen 1996): they have protracted dependency periods, during which the young learn diving and foraging skills before weaning (Fowler et al. 2006, Jeglinski et al. 2012). The nursing period may last many months, or even years (Boness and Bowen 1996). Other pinnipeds (phocids), exhibit a range of breeding strategies. Some small phocids, such as harbour seals (*Phoca vitulina*), are also income breeders, but, in contrast to otariids, pups can dive within hours of birth. Despite short dependency periods (< 1 month (Thompson and Wheeler 2008)), harbour seal pups can develop diving skills during suckling and may accompany their mothers on foraging excursions (Bekkby and Bjørge 2000). Synchronous diving of mothers and pups during lactation also occurs in some ice-breeding phocids (Sato et al. 2006). Larger phocid species, such as elephant (*Mirounga spp.*), hooded (*Cystophora cristata*) and grey (*Halichoerus grypus*) seals, are usually capital breeders, and pups are abruptly abandoned at the natal site after a brief nursing period (Boness and Bowen 1996). Grey seals, for example, suckle for 15-21 days (Pomeroy et al. 1999). Pups then undergo a post-weaning fast, usually on land, of between nine and 40 days, during which time they lose up to 25% of their body mass (Bennett et al. 2007, Noren et al. 2008). After departure from the natal colony, they must learn to dive and find food without maternal provisioning, or the benefit of observing the foraging behaviour of their mother (Hewer 1974). Furthermore, they must do this before their remaining blubber and protein reserves are depleted to critical levels and terminal starvation begins (Bennett et al. 2010).

Swimming in cold water and diving to depth is energetically costly, and seal pups have a higher surface area to volume ratio, higher mass-specific metabolic rate and lower mass-specific oxygen storage capacity than adults (Burns and Castellini 1996, Noren et al. 2005). In contrast to adults, young seals repeatedly dive up to their physiological limits and foraging efficiency is therefore lower because they must spend longer at the surface to recover (Burns 1999, Fowler et al. 2006). Maximum diving capability increases in grey seal pups during the first months at sea (Bennett et al. 2010), but little is known about the development of their routine behaviours. First year mortality is high and variable between years for grey seals (Hall et al. 2001, 2002, 2009), which has a profound effect on population dynamics (Harwood and Prime 1978). Moreover, first year survival probability appears to be three times greater for females than males, regardless of body condition at weaning (Hall et al. 2001). Differences in survival between male and female pups could be linked to development of sex-specific diving behaviour, leading to the sex difference in foraging strategies underpinned by sexual size dimorphism in adults (Beck et al. 2003a). In general, adult grey seals make repeated, short duration (3-10 days) foraging trips offshore within shelf seas, diving to the bottom to exploit benthic and demersal prey, and returning to coastal 'haulout' sites (Thompson et al. 1991, McConnell et al. 1999). Most research has focussed on adult movements and foraging strategies. Whilst some work has investigated foraging in grey seal juveniles (> 12 months old) and young-of-the-year (YOY; > 5 months old) (Breed et al. 2011a, Russell et al. 2015), and others have studied pup behaviour on and around the colony (Kovacs 1987, Jenssen et al. 2010), only Bennett et al. (2010) have examined the ontogeny of at-sea behaviour in recently-weaned pups across their first months of nutritional independence. Previous studies have demonstrated sex differences in the foraging behaviour of grey seal adults (seals of reproductive age) (Beck et al. 2003a, Russell et al. 2015), juveniles (Russell et al. 2015), and YOY (Breed et al. 2011a). Sex differences in behaviour thus emerge from an early age (Breed et al. 2011a), but the timing of their onset is unknown. Development of diving and learning of successful foraging behaviour is also likely to be shaped by local experience, and the environment that pups encounter when they first go to sea. Oceanographic conditions and prey availability vary among regions, presenting different challenges for different subpopulations. Together, these factors may confer regional differences in the ontogeny of diving behaviour and thus the development of successful foraging strategies for grey seal pups.

The United Kingdom (UK) is home to ~38% of the world grey seal population (SCOS 2017) and has an obligation under European Union (EU) legislation to maintain this population in "Favourable Conservation Status" (FCS; EU Habitats Directive 92/43/EEC 1992). As part of this obligation, critical habitat must be identified for this species both on land and at sea to assess and mitigate anthropogenic disturbance. Current UK conservation management for grey seals at sea is largely based upon observations of adult movement (SCOS 2017). Foraging behaviour has not yet been described for grey seal pups, but, given that they undergo profound physiological development during their initial months of independent life (Noren et al. 2005, Bennett et al. 2010), coupled with a need to explore their environment and develop knowledge of potential foraging areas, we should not expect their behaviour and habitat requirements to be the same as for adults. As pups develop diving skills, grow larger and acquire knowledge of their surroundings, we might expect that their behaviour begins to converge on that of adults, since adult behaviour represents successful foraging patterns. The main aim of this study, therefore, was not to quantify foraging in grey seal pups, but to investigate changes in at-sea behaviours relevant to the development of successful foraging skills during their first four months of independent life at sea. We used a unique, large (*n* = 52 individuals) animal-borne satellite and GSM telemetry dataset of location and dive (time-depth) data from recently-weaned pups born at six different colonies around the UK (Table 2.1). Ontogeny of foraging behaviour has been characterised in young seals by reductions in trip metrics (duration and distance), and increases in dive metrics (depth, duration, proportion of dives that are benthic, bottom time and proportion of day spent diving) with age (Baylis et al. 2005, Fowler et al. 2006, Bennett et al. 2010, Blanchet et al. 2016). Such changes in these metrics are indicative of an individual's ability to maximise foraging opportunities within individual dives and/or over foraging trips, and are thus representative of greater foraging efficiency (Baylis et al. 2005, Fowler et al. 2006, Bennett et al. 2010, Blanchet et al. 2016). Thus, using generalized estimating equations in a generalized additive model framework (GEE-GAM), we investigated how these variables changed over time and compared the trajectories between the sexes and two distinct geographic regions (Celtic and Irish Seas (hereafter CIS) and North Sea (hereafter NS); Fig. 2.1). Furthermore, sexual segregation of foraging habitat may be manifested in the depth of water where males and females dive (Breed et al. 2011a). We therefore examined differences in the bathymetric depth of dive locations in the same way.

Table 2.1: Device deployment summary information. *Tagged pup sample sizes and tag duration by deployment site and year. Trip and dive numbers given are those included in the analysis after data cleaning and restriction to 120 days after leaving the colony. Although SRDL devices recorded dives, these could not be matched to bathymetric depth data and so were excluded from dive analysis. Colonies were assigned to two geographic regions; NS = North Sea, CIS = Celtic and Irish Seas.*

			No. tagged seals			Mean no. locations		
Deployment site (year)	**Region**	**Device type**	**f**	**m**	**Total**	**day^{-1} ± SD**	**Total no. trips**	**Total no. dives**
Isle of May (2001)	NS	SRDL	5	6	11	4.5 ± 2.3	109	N/A
Isle of May (2002)	NS	SRDL	5	5	10	5.2 ± 1.7	67	N/A
Bardsey (2009)	CIS	GPS-GSM	2	0	2	35.5 ± 5.4	23	3871
The Skerries (2009)	CIS	GPS-GSM	1	2	3	33.1 ± 5.7	141	9373
The Skerries (2010)	CIS	GPS-GSM	4	1	5	57.2 ± 13.8	212	46589
Ramsey (2010)	CIS	GPS-GSM	3	4	7	37.3 ± 9.7	162	27609
Muckle Green Holm (2010)	NS	GPS-GSM	4	3	7	22.5 ± 9.6	38	7417
Stroma (2010)	NS	GPS-GSM	5	2	7	24.4 ± 4	84	7941
		Total:	**29**	**23**	**52**		**836**	**102800**

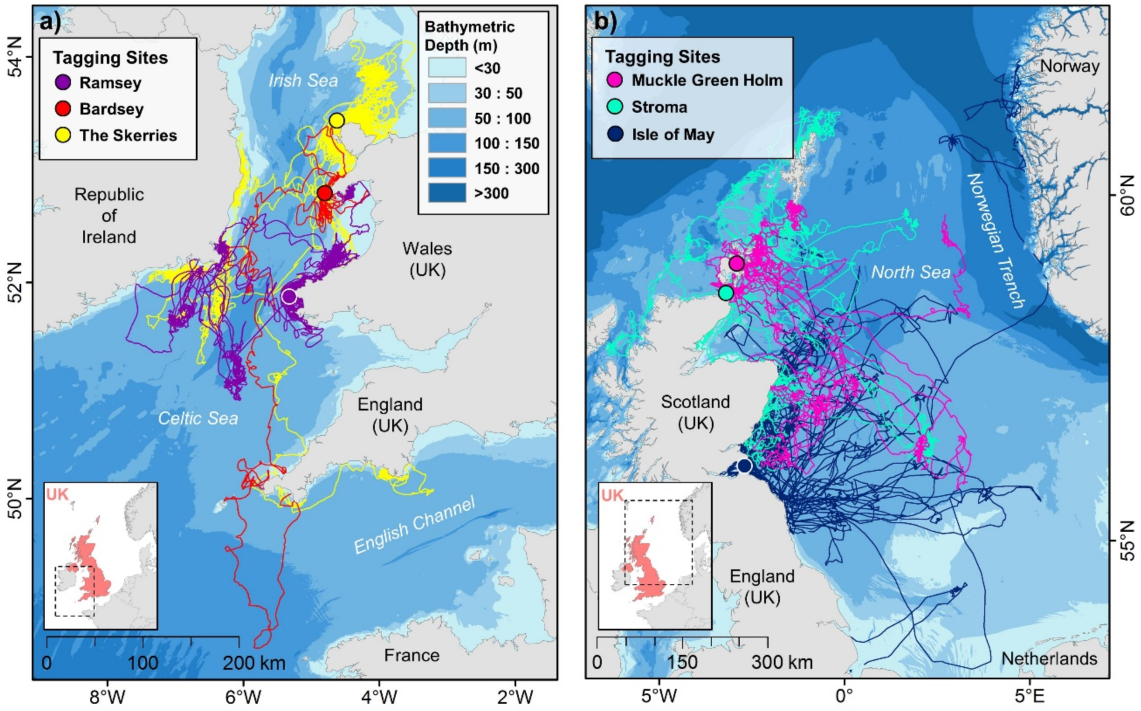

Figure 2.1: Pup tagging sites and trips at sea. *Pups were tagged at six colonies in the United Kingdom (UK). Colonies were assigned to one of two geographic regions; (a) Celtic and Irish Seas (CIS), and (b) North Sea (NS). Tracks show pup trips (n = 836) during the initial four months after leaving the colony.*

2.2 Methods

2.2.1 Instrumentation

Two different telemetry device models were deployed on 52 recently-weaned grey seal pups at six UK breeding sites in 2001 and 2002 (Bennett et al. 2010), and in 2009 and 2010 (Thompson 2012) (Table 2.1). Earlier deployments (2001-2002; *n* = 21) were ARGOS Satellite Relay Data Loggers (SRDL; Sea Mammal Research Unit, UK), and later deployments (*n* = 31) were Fastloc® GPS-GSM tags (GPS phone tags; Sea Mammal Research Unit, UK). Individuals were captured post-weaning for device application. When anaesthesia was required (due to additional procedures not related to this study; CIS 2010 and all Isle of May deployments), pups were administered with 0.025 mg kg^{-1} intravenous Zoletil$_{100}$® (Virbac, France) (Bennett et al. 2010, Thompson 2012). Following McConnell et al. (1999), a tag was glued to cleaned, dried fur at the base of the skull using RS Quick-Set Epoxy Adhesive (RS Components Ltd., UK; 2001-2009), or Loctite® 422™ cyanoacrylate adhesive (Henkel, UK; 2010). All experimental protocols were carried out with UK Home Office approval under project licences #60/2589 (2001-2002), and #60/4009 (2009-2010), in accordance with the Animals (Scientific Procedures) Act 1986. In total, 7057 days of data were recorded from 52 pups (for information on tag duration see Appendix A2.1: Tag duration).

2.2.2 Telemetry data processing

(a) Horizontal movement data

Whilst both SRDL and GPS-GSM devices transmitted location data at irregular intervals, mean number of location fixes achieved per day was much higher for GPS-GSM tags (Table 2.1). ARGOS-derived location estimates from SRDLs also carry a greater spatial error, ranging from 50 m to > 2.5 km (Vincent et al. 2002). Erroneous ARGOS location observations were eliminated using the standard technique of filtering with a maximum speed threshold of 2 ms^{-1} (McConnell et al. 1992a). Remaining locations were then processed with a Kalman filter to improve location accuracy (Jones et al. 2015). Kalman filter observation model parameters were taken from Vincent et al. (2002), and process model parameters were based on average speeds of 142 seal GPS tracks (Jones et al. 2015). Erroneous GPS locations were identified and excluded using residual error thresholds and number of satellites (Russell et al. 2015).

Devices also recorded dive and haulout data derived from integrated conductivity and pressure sensors. Following Russell et al. (2015), a seal's location during a haulout event was taken as the mean of all latitude and longitude estimates during the time hauled-out. If no location estimates were recorded during the haulout interval, the location was derived using linear interpolation to a midpoint between the pre and post observed location fixes. Interpolated haulout locations were flagged as unreliable if there was no adjacent observed location within 6 h. The location data were then restricted to discrete 'trips' between haulout events. Trips were only included in the analysis if they had a reliable haulout location on land at both the beginning and end. One individual hauled-out repeatedly on an offshore oil rig in the central North Sea > 250 km from land; these haulouts were classed as on land and the associated trips were included in the analysis. Seals often wait in the water between haulout events for tidal sites to become available, when they may sleep either on the seabed or at the surface (Thompson 1989). To exclude this behaviour, as it is not relevant to foraging, trips < 8 hr in duration and with a maximum distance < 500 m from the coast were also omitted from the analysis (Russell 2015b). Finally, as tag duration varied between individuals (from 13 to 337 days; see Appendix A2.1: Tag duration), data were clipped at 120 days after leaving the colony to ensure a robust sample size throughout the time series for statistical analysis (Zuur et al. 2010). The resulting dataset comprised location and haulout data from 52 individuals; 23 males and 29 females (Table 2.1; Fig. 2.1; 836 trips). The duration and total distance of each trip was calculated alongside days since first leaving the natal colony at the mid-point of the trip. Total distance was calculated as the sum of all step lengths between successive location fixes during a trip, regularised to 30 min intervals. Days since leaving colony was used to give a measure of the at-sea experience of the pup.

(b) Dive data

GPS-GSM tags classified dives as periods when the pressure sensor recorded depths > 1.5 m for > 8 s. These devices recorded depth readings at 4 s intervals throughout a dive, which were then abstracted to 11 inflection points by an algorithm onboard the device before data transmission (Fedak et al. 2001). Although SRDLs also recorded dive data, tag parametrisation was different to that of GPS-GSM tags (SRDLs only recorded dives > 6 m depth with four inflection points). Furthermore, the lower frequency of successful transmissions and higher spatial error of concomitant ARGOS-derived location estimates meant that SRDL dive data could not be accurately matched to a location, and thus to bathymetric depth, and were therefore excluded from all dive analyses. For GPS-GSM dive data, the maximum dive depth and total dive duration were extracted for each dive. A dive was treated as any time below the depth threshold (1.5 m). Devices also transmitted two-hourly summaries of data, detailing the proportion of time the device was in either "haulout", "dive" or "cruise" (device is wet and above 1.5 m) mode. These data were used to calculate the total number of hours spent diving per individual per day. Only days with data for all twelve summary intervals were used.

To investigate changes in the proportion of benthic dives performed by pups, and the bathymetric depth of dive locations, dives were first matched to adjacent location fixes in time using the mid-point between dive start and end times. The location for each dive mid-point was then calculated using linear interpolation between prior and post location fixes. Interpolated dive locations with no adjacent observed location fix within 15 min could not be accurately matched with bathymetric depth data and were therefore excluded from the analysis. Bathymetric depth was extracted for each dive location from the harmonised 1/8 arc minute * 1/8 arc minute (~230 m) gridded Digital Terrain Model (DTM) for European Waters which is freely-available through the European Marine Observation and Data Network (EMODnet) Portal for Bathymetry (http://www.emodnet-bathymetry.eu/). Benthic dives were classified following Ramasco et al. (2015), using a mixture distribution model approach (see Appendix A2.2: Classification of benthic dives). The bathymetric depth range of the study area is shown in Fig. 2.1. After filtering, a number of dives (15%) recorded a null or positive bathymetric depth value, due to interpolated dive locations falling too close to the coast and were subsequently removed. As with trip data, the resulting dive dataset was clipped to 120 days after leaving the colony to ensure a robust sample size throughout the time series. Lastly, as seals may perform successive shallow dives while resting close to haulouts, and this is not related to foraging behaviour, any dive with a maximum depth < 5 m was excluded. The final dataset comprised 102,800 dives from 31 individuals (Table 2.1).

2.2.3 Statistical analysis

Trip (duration and distance) and dive metrics (depth, bathymetric depth of dive locations, proportion of dives that were benthic, duration, bottom time and proportion of day spent diving) were analysed using generalised estimating equations within a generalized additive model framework (GEE-GAMs) using the "geepack" and "splines" packages (Halekoh et al. 2006) in R version 3.2.5 (R Core Team 2016a). The GAM approach allows the inclusion of smoothed terms to investigate non-linear relationships (Wood 2006). However, GAMs are not robust to the serial autocorrelation within individuals that is inherent in longitudinal telemetry datasets. GAMs can be extended to include autocorrelation structures and random effects, but the GEE approach allows the inclusion of an unstructured correlation coefficient, which is more appropriate for telemetry data as it estimates all correlations between within-individual observations independently (Zuur et al. 2009). Furthermore, this method allows the prediction of population mean responses by averaging across individuals. This approach has been previously applied to study temporal movement trends in seal telemetry datasets (Russell et al. 2015).

We investigated ontogeny in pup dive behaviour using a number of metrics, at a temporal resolution of one day by calculating daily means per individual per day. As pups grow, their muscular and cardio-vascular systems develop, and their ratio of blubber to lean mass decreases, becoming less buoyant (Noren et al. 2005, Hall and McConnell 2007). Their ability to dive to, and remain at depth should therefore increase over time (Bennett et al. 2010). Daily mean dive maximum depth and duration were used to track changes in diving ability over time. For air-breathing benthic foragers, the depth of water in which dives occur is also relevant to their ability to dive to and remain at foraging depth. The bathymetric depth of water where dives occurred was also modelled in the same way. Optimal diving theory (ODT) suggests that benthic foragers will maximise time at the seabed (and therefore probability of successful foraging), and minimise time spent in the ascent and descent phases of a dive and at the surface (Carbone and Houston 1996). We therefore investigated changes in the proportion of dives that were benthic, and in dive bottom time (the proportion of a dive's duration spent at > 80% of the maximum dive depth; a measure of time spent at foraging depth relative to descent and ascent phases of a dive) (Lesage et al. 1999). Lastly, pups may maximise time spent underwater (and therefore foraging opportunities) over bouts of short dives, rather than individual long dives (Boyd 1997, Sparling et al. 2007). We therefore investigated changes in the mean proportion of time spent diving per individual per day (24 h period).

Pup behaviour may change through time, and the dynamics of this change may differ between the sexes, and/or geographic regions (due to differences in habitat features such as coastal geography, prey availability and bathymetry). Therefore, response variables were analysed in separate models as a function of *time since leaving colony* (days; as a smoothed term), *sex* (as a categorical term) and *region* (as a categorical term) in a three-way interaction. Model selection was performed by backwards hypothesis testing from GEE-based P-values until arriving at a minimal adequate model. Colonies were assigned to one of two geographic regions (Table 2.1; North Sea or Celtic and Irish Seas). There was considerable spatial overlap of areas used by pups from colonies within each of the two wider geographic regions (Fig. 2.1), such that region rather than colony was used in the models for the sake of parsimony, and to maximise statistical power. 95% confidence intervals around model-predicted means were calculated by parametric bootstrapping using GEE-based uncertainty parameters (Jones et al. 2015). Scale-corrected Pearson's residuals were checked for normal distribution by visual inspection in all models. For models with continuous response variables (all except bottom time, benthic diving and proportion of day spent diving), gamma and Poisson error structures were considered in order to improve normality, but in all cases a Gaussian error structure with log-link function proved superior. Proportion data (bottom time, proportion of dives that were benthic and proportion of day spent diving) were modelled with a binomial error structure with logit-link function.

2.3 Results

2.3.1 Trip behaviour

All pups remained within the limits of the continental shelf, but NS individuals had a much wider dispersal pattern, and several pups travelled along the shelf break (Fig. 2.1). Although NS pups travelled far from their natal colonies on individual trips, all returned to haulout locations on the east coast of Scotland and England. No pup crossed the shelf break into waters > 200 m deep. However, one male from the Isle of May travelled between the UK and Norway on multiple occasions, diving to the bottom of the Norwegian Trench (Fig. 2.1b; > 200 m). In general, pups from both regions explored new areas before settling into repeated trip behaviour, hauling-out in one or more locations and commuting back and forth to foraging grounds, as observed in adults (McConnell et al. 1999) (Fig. 2.2). Many NS pups undertook a prolonged exploratory phase shortly after leaving the colony, with 69% of pups (n = 24) spending > 20 days offshore without returning to the coast, and some individuals exceeding 60 days offshore, which is substantially greater than typical trip durations seen in adults (McConnell et al. 1999). Only 18% of CIS pups (n = 3) performed a trip with duration > 20 days. CIS pups remained much closer to land, generally dispersing along the coast of Wales and the Republic of Ireland (Fig. 2.1a). One female travelled south towards the north coast of France before returning to the south coast of England. Some individuals made repeated trips into the middle of the Celtic Sea, while others remained within 30 km of the coastline, and never travelled > 50 km from their natal colony (Fig. 2.3).

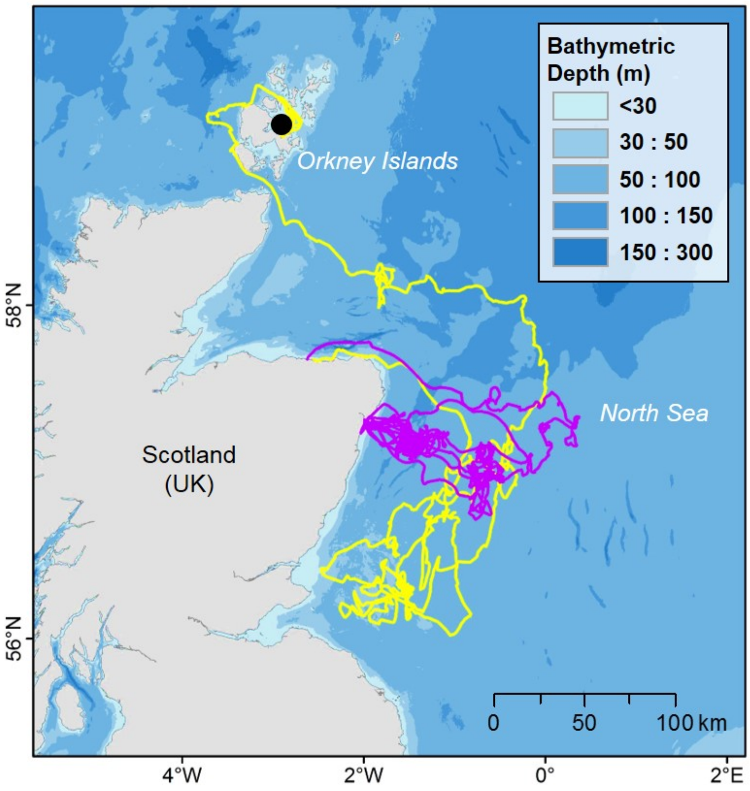

Figure 2.2: Changes in NS pup trip behaviour with time since departing the colony. *Map shows initial exploratory trip of a pup from Muckle Green Holm, Orkney Isles (black dot), during which it did not haul-out for 64 days (yellow track). During the following 56 days, the pup performed repeated short-duration (5-14 days) foraging trips (purple tracks), travelling between the haulout site and specific putative foraging areas.*

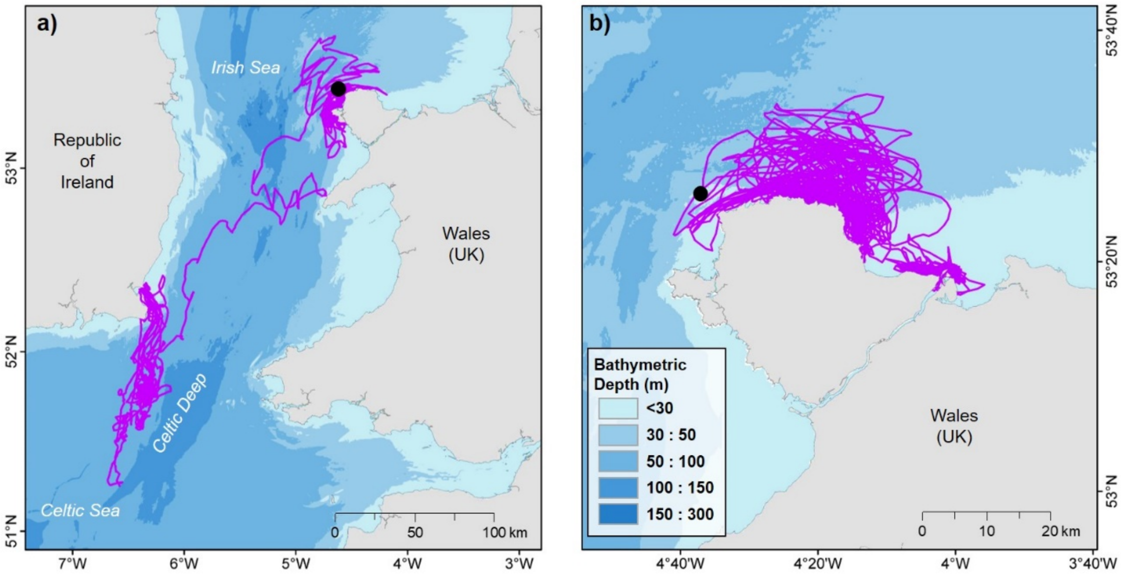

Figure 2.3: Differences in dispersal of CIS pups. *Maps show trips of two pups from The Skerries over the first 4 months of independence. Pup (a) remains in areas adjacent to the colony (black dot) for ~50 days before dispersing to the southeast coast of Ireland, hauling-out at a popular grey seal haulout site, and subsequently making repeated trips to putative foraging grounds on the edge of the Celtic Deep. Pup (b) remains in areas adjacent to the colony (black dot) for the entire 4 months.*

Trip duration increased significantly with time after leaving the colony for pups from both regions (Table 2.2; GEE-GAM; $\chi^2_3 = 15.2$, $p = 0.002$), peaking at around 70 days before declining (Fig. 2.4a-b). However, trip duration was significantly longer for NS pups than CIS pups (Fig. 2.4a-b; GEE-GAM; $\chi^2_1 = 66.1$, $p < 0.001$). There was no significant difference in trip duration between males and females in either region (GEE-GAM; $\chi^2_1 = 1.4$, $p = 0.233$). Trip distance was also significantly affected by time since departure for pups from both regions (Table 2.2; GEE-GAM; $\chi^2_3 = 8.2$, $p = 0.042$), peaking at around 70 days then declining (Fig. 2.4c-d). However, there was a significant effect of an interaction between region and sex on trip duration (Fig 2.4d; GEE-GAM; $\chi^2_1 = 4.73$, $p = 0.03$); NS pups travelled consistently further than CIS pups. CIS males travelled further than females, whilst there was no obvious sex difference in trip distance for NS pups.

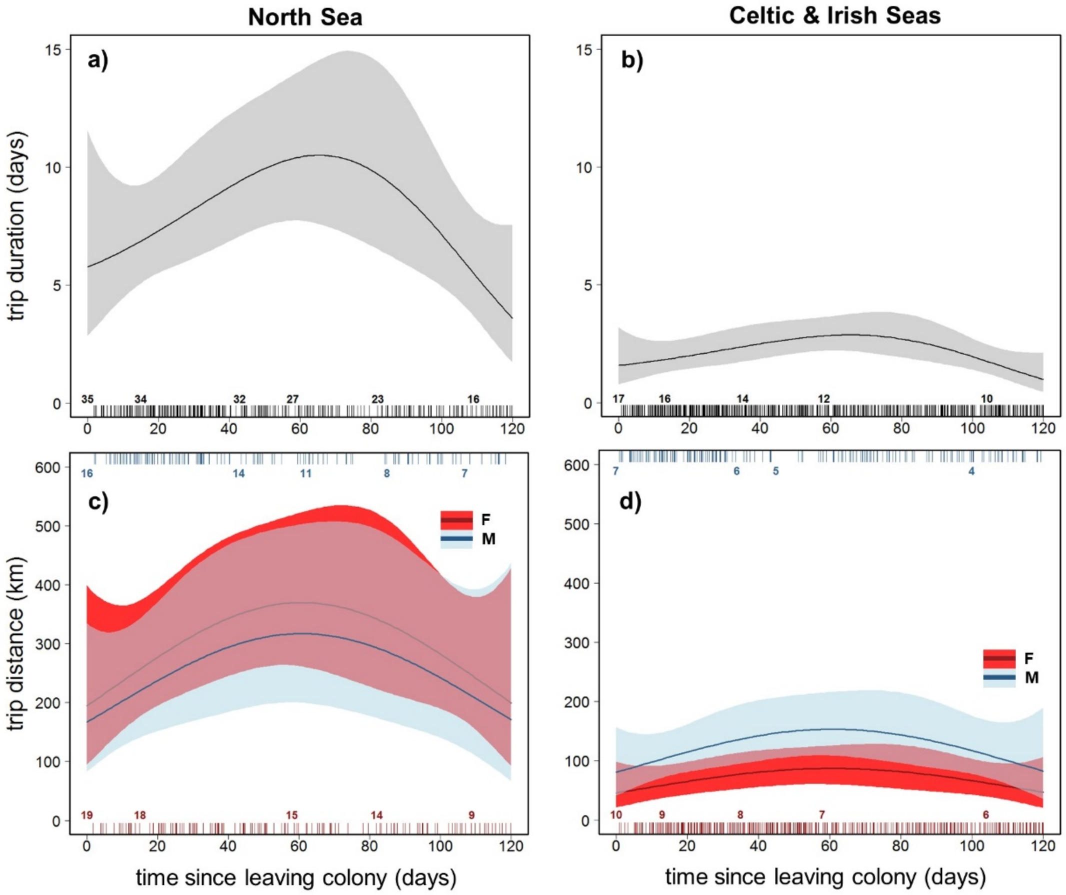

__Figure 2.4: Sex and region differences in ontogeny of trip behaviour.__ Model-fitted values for trip duration (a-b) and trip distance (c-d) over time since leaving the colony. Solid lines show population mean responses by region (North Sea (NS) left, Celtic and Irish Seas (CIS) right), with associated GEE-based 95% confidence intervals (shaded areas). Pup trip behaviour changed significantly with time since departure. NS pups performed longer duration trips than CIS pups, however there was no sex difference (a-b). CIS males (d; blue) travelled further than females (red). Rug plots top and bottom show the distribution of data, colour-coded by sex, and associated numbers indicate pup sample size.

Table 2.2: Model output. *Results of model simplification using backwards hypothesis testing with GEE-GAMs. Predictor variables: T = Time, R = Region, S = Sex. Significant ($p < 0.05$) terms are shown with "*". Interactions between variables are denoted by ":". Where a variable was significant in an interaction, the significance of component interactions and/or individual fixed effects is not reported.*

Predictor Variables	**Response Variables**							
	Trips		**Dives (daily means)**					
	Duration (Fig. 2.4a-b)	**Distance** (Fig. 2.4c-d)	**Max. Depth** (Fig. 2.5a-b)	**Bathy. Depth** (Fig. 2.5c-d)	**Prop. Benthic** (Fig. 2.5e-f)	**Duration** (Fig. 2.6a-b)	**Prop. Bottom Time** (Fig. 2.6c-d)	**Prop. Time Diving** (Fig. 2.6e-f)
T	$\chi^2_3 = 15.2$, $p = 0.002$*	$\chi^2_3 = 8.2$, $p = 0.042$*	-	-	-	-	-	-
S	$\chi^2_1 = 1.4$, $p = 0.233$	-	-	-	$\chi^2_1 = 5.2$, $p = 0.023$*	$\chi^2_1 = 2.5$, $p = 0.117$	-	-
R	$\chi^2_1 = 66.1$, $p < 0.001$*	-	-	-	-	-	-	-
T : S	$\chi^2_3 = 3.9$, $p = 0.268$	$\chi^2_3 = 6.2$, $p = 0.1$	-	-	$\chi^2_3 = 1.1$, $p = 0.774$	$\chi^2_3 = 3.1$, $p = 0.369$	$\chi^2_3 = 3.1$, $p = 0.378$	$\chi^2_3 = 13.9$, $p = 0.003$*
T : R	$\chi^2_3 = 4.1$, $p = 0.254$	$\chi^2_3 = 3.3$, $p = 0.346$	-	-	$\chi^2_3 = 13.1$, $p = 0.004$*	$\chi^2_3 = 16.4$, $p < 0.001$*	$\chi^2_3 = 14.9$, $p = 0.002$*	$\chi^2_3 = 15$, $p = 0.002$*
R : S	$\chi^2_1 = 2.7$, $p = 0.099$	$\chi^2_1 = 4.7$, $p = 0.03$*	-	-	$\chi^2_1 = 0.1$, $p = 0.767$	$\chi^2_1 = 0$, $p = 0.875$	$\chi^2_1 = 9.3$, $p = 0.002$*	$\chi^2_1 = 0.02$, $p = 0.885$
T : R : S	$\chi^2_3 = 0.8$, $p = 0.852$	$\chi^2_3 = 1.4$, $p = 0.708$	$\chi^2_3 = 13.6$, $p = 0.003$*	$\chi^2_3 = 10.4$, $p = 0.016$*	$\chi^2_3 = 1.3$, $p = 0.74$	$\chi^2_3 = 1.9$, $p = 0.591$	$\chi^2_3 = 7.24$, $p = 0.065$	$\chi^2_3 = 4.5$, $p = 0.215$

2.3.2 Dive behaviour

A three-way interaction between time since departure, region and sex best explained variation in daily mean maximum dive depth (Table 2.2; GEE-GAM; $\chi^2_3 = 13.6$, $p = 0.003$). Pups increased their dive depth rapidly over the first 40 days, except for CIS females, which showed a prolonged, more moderate increase (Fig. 2.5a-b). Sex differences in the change in dive depth over time were apparent in CIS pups, with males diving significantly deeper than females from 20-60 days after leaving the colony (Fig. 2.5b). The population mean maximum depth for CIS males during this period reached ~40 m, whilst females achieved ~25 m. Throughout the time series, NS pups dived significantly deeper than CIS pups, with both males and females reaching a maximum daily mean of ~50 m.

A three-way interaction between time since departure, region and sex best explained variation in daily mean bathymetric depth of dive locations (Table 2.2; GEE-GAM; $\chi^2_3 = 10.4$, $p = 0.016$). NS pups and CIS males dived in increasingly deep water over the first 40 days after departure from the colony (Fig. 2.5c). CIS females remained in shallower water than males throughout the first four months at sea, averaging depths of ~30 m whilst mean bathymetric depth for male dives reached up to ~60 m (Fig. 2.5d). No significant sex difference was evident in bathymetric depth of dive locations for NS pups. Both male and female NS pups dived in significantly deeper water than CIS pups, reaching a maximum daily mean of ~80 m.

The daily mean proportion of dives that were benthic changed with time since departure, and the dynamic of this change was different between the regions (Table 2.2; GEE-GAM; $\chi^2_3 = 13.1$, $p = 0.004$). Pups from both regions increased the proportion of benthic dives rapidly over the initial 40 days. This reached an asymptote for NS pups (Fig. 2.5e), but continued to increase for CIS pups (Fig. 2.5f). The trend showed some evidence of a decline in the latter half of the time series for NS pups, but confidence intervals were wide (Fig. 2.5e). Females performed a greater proportion of benthic dives than males throughout the time series in both regions (GEE-GAM; $\chi^2_1 = 5.2$, $p = 0.023$). The daily mean proportion of benthic dives reached a peak at ~0.5 for NS females, ~0.6 for CIS females, ~0.4 for NS males, and ~0.5 for CIS males. Confidence intervals for the sexes overlapped in both regions. The effect of bathymetric depth on the proportion of dives that were benthic is presented in Appendix A2.3.

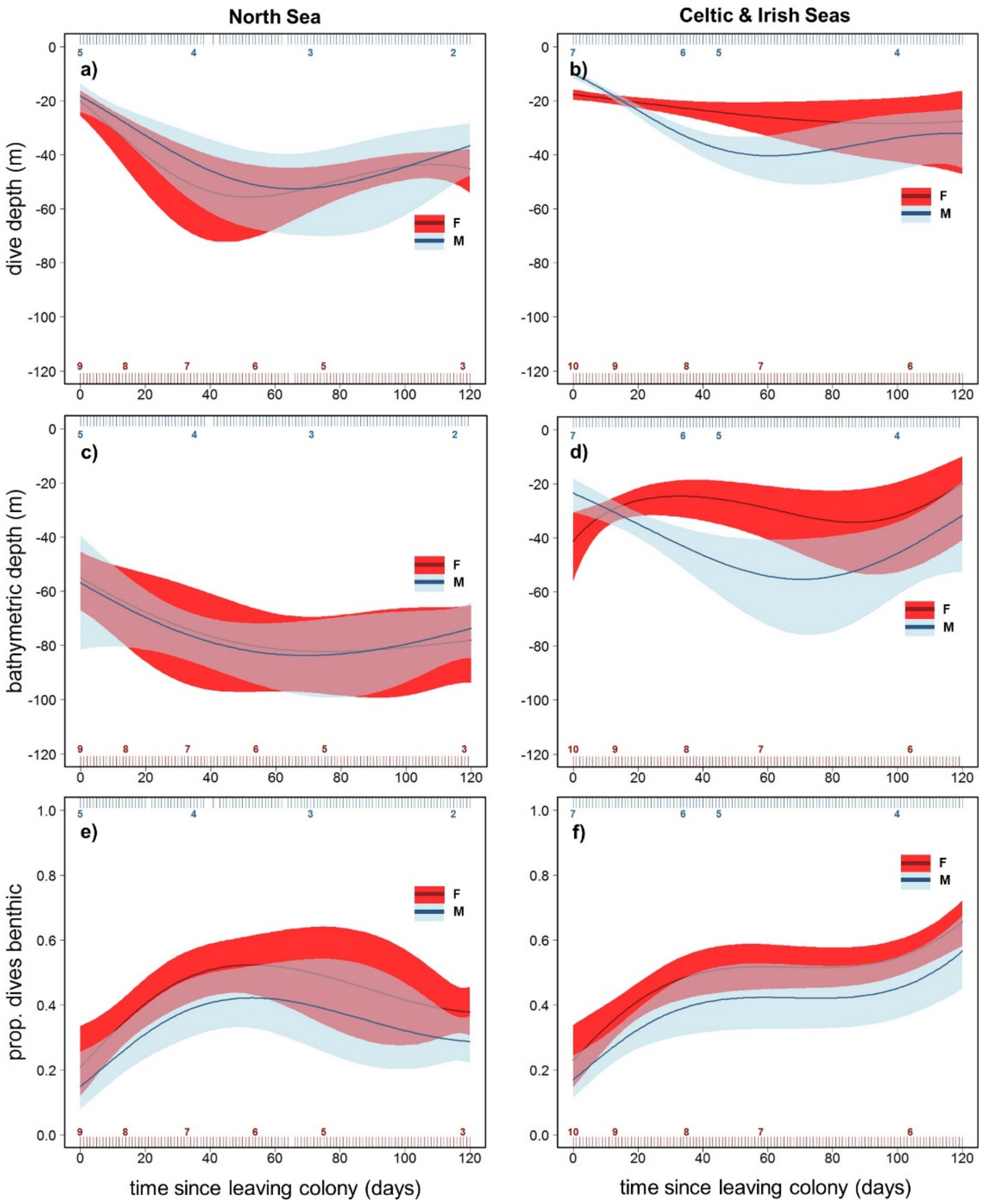

Figure 2.5: Sex and region differences in ontogeny of dive depth. *Model-fitted values for daily mean maximum dive depth (a-b) and bathymetric depth of dive locations (c-d) over time since leaving the colony. Solid lines show population mean responses by region (North Sea (NS) left, Celtic and Irish Seas (CIS) right), with associated GEE-based 95% confidence intervals (shaded areas). Pups increased their dive depth rapidly over the initial 40 days (a-b), except for CIS females (b). NS pups dived in deeper water throughout (c). Sex differences in bathymetric depth of dive locations emerged from the outset in CIS pups, as females (red) dived in shallower areas (d). The proportion of dives that were benthic increased rapidly for all pups over the initial 40 days. However, females recorded marginally higher mean values than males in both regions (e-f). Rug plots top and bottom show the distribution of data, colour-coded by sex, and associated numbers indicate pup sample size.*

Daily mean dive duration was best explained by an interaction between time since departure and region (Table 2.2; GEE-GAM; $\chi^2_3 = 16.4$, $p < 0.001$). There was no significant effect of sex on this metric (GEE-GAM; $\chi^2_1 = 2.5$, $p = 0.117$). Similar to dive depth and bathymetric depth, pup dive duration increased rapidly over the initial 40 days at sea for both regions, before declining over the following 60 days (Fig. 2.6a-b). Peak mean dive duration for NS pups was marginally longer than for CIS pups (NS: ~140 s, CIS ~130 s).

Temporal patterns in bottom time differed between regions (Table 2.2; GEE-GAM; $\chi^2_3 = 14.9$, $p = 0.002$). CIS pups showed a strong increase in bottom time over the initial 40 days at sea, before levelling off, then a further increase at ~100 days. NS pups showed a moderate increase over the whole time series, with bottom time remaining between 40-50% of dive duration (Fig. 2.6c-d). In addition, sex differences in bottom time differed between the regions (GEE-GAM; $\chi^2_1 = 9.3$, $p = 0.002$). In both regions, females achieved higher bottom times than males (although 95% confidence intervals overlapped for NS pups; Fig. 2.6c). The difference between males and females was more pronounced in CIS pups: females achieved a maximum mean of ~70% of the dive spent in the bottom phase, whilst males achieved a maximum mean of ~55% (Fig. 2.6c-d).

Time spent diving per day varied significantly with time since departure, and the shape of this relationship was affected by sex (Table 2.2; GEE-GAM; $\chi^2_3 = 13.9$, $p = 0.003$) and region (GEE-GAM; $\chi^2_3 = 15$, $p = 0.002$). The sex difference was comparable between both regions (GEE-GAM; $\chi^2_1 = 0.02$, $p = 0.885$). NS pups began diving ~14 hrs per day, then reduced time spent diving in the third month to ~10 hrs for males and ~12 hrs for females (Fig. 2.6e). CIS females initially spent ~11 hrs diving per day, which rose steadily to ~13 hrs in the third month (Fig. 2.6f). CIS males initially spent ~10 hrs per day diving, which rose steeply to ~13 hrs in the first month before declining back to ~11 hrs in the third month (Fig. 2.6f).

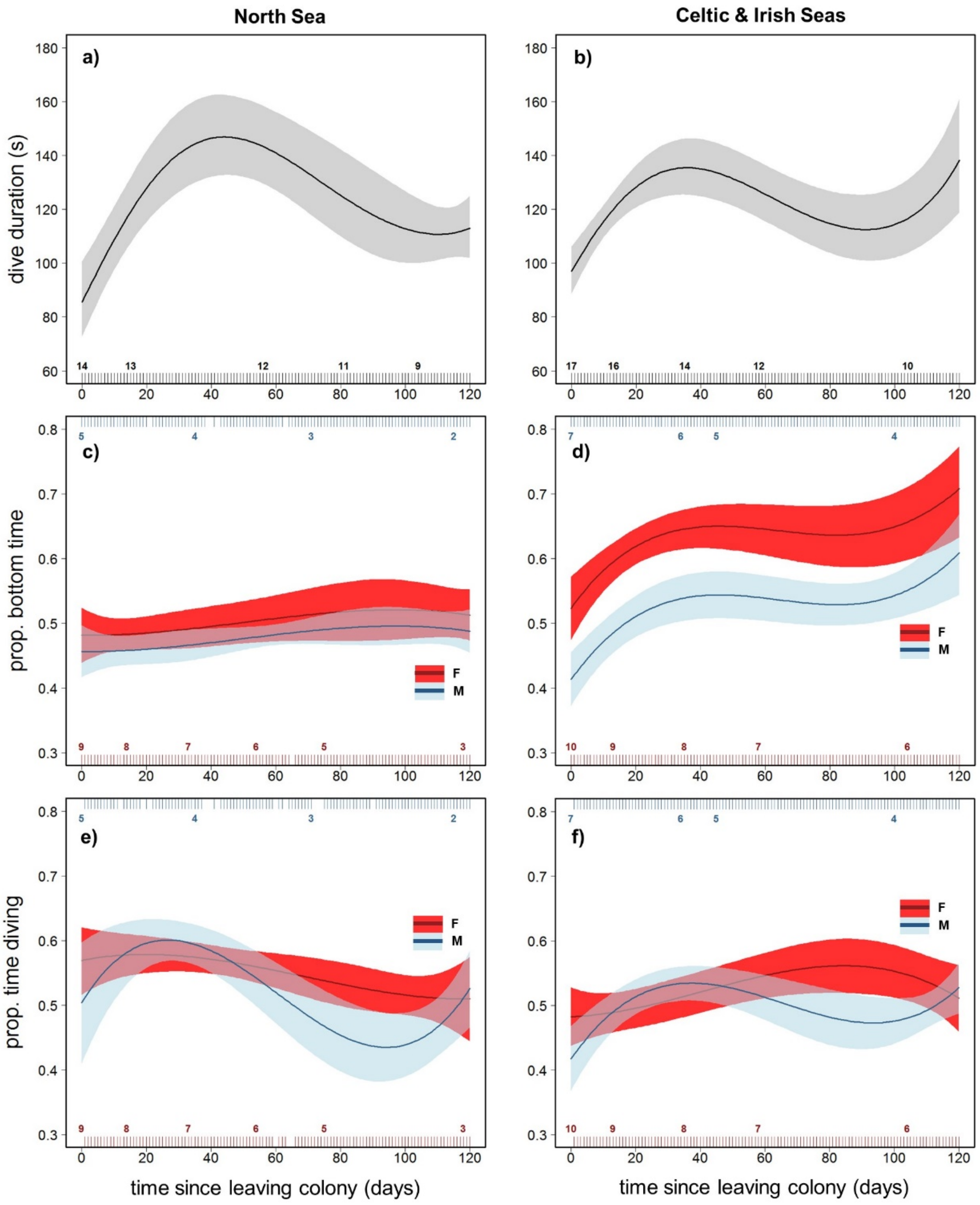

__Figure 2.6: Sex and region differences in ontogeny of dive duration.__ Model-fitted values for daily mean total dive duration (a-b), bottom time (as proportion of total dive duration; c-d), and time spent diving (as proportion of 24 h period; e-f) over time since leaving the colony. Solid lines show population mean responses by region (North Sea (NS) left, Celtic and Irish Seas (CIS) right), with associated GEE-based 95% confidence intervals (shaded areas). Pups increased their dive duration rapidly over the initial 40 days (a-b), and there was no sex difference in dive duration. Females (red) had higher bottom time than males (blue) (c-d), although this was more marked in CIS pups (d). Females spent more time diving than males in the third month (e-f). Rug plots top and bottom show the distribution of data, colour-coded by sex, and associated numbers indicate pup sample size

2.4 Discussion

This study reveals that sexual segregation of behaviour can be exhibited as early as nutritional independence in capital breeders. Female pups from both regions spent more time diving per day than males. CIS females made shorter distance trips than males, diving in shallower water and achieving a higher proportion of the dive duration in the bottom phase. The same level of sexual segregation in depth, proportion bottom time and trip duration was not observed in NS pups, suggesting that sex differences in the ontogeny of foraging behaviour may be mediated by extrinsic factors. In both regions, pup behaviour changed rapidly: dive duration, depth, bottom time and benthic diving increased over the first 40 days after leaving the colony. These findings are important in the context of both foraging ecology and conservation management, as we outline below.

Grey seal adults exhibit substantial sexual size dimorphism (Hewer 1974), which is thought to drive differences in feeding areas (Beck et al. 2003a). Grey seal pups are not size-dimorphic (Bennett et al. 2010), but seal pups and juveniles may experience differences in energy requirements before overt size and body composition differences emerge (Kelso et al. 2012). Kelso et al. (2012) found that male northern elephant seal (*M. angustirostris*) pups had higher rates of energy expenditure than females during the post-weaning fast, but were more effective at sparing protein reserves. These differences are likely related to the development of sex-specific metabolic strategies required for successful breeding (Kelso et al. 2012). Differences in metabolic demand during the ontogeny of foraging behaviour could therefore drive sex-specific feeding strategies and habitat requirements. Our findings support this possibility; we found that females from both regions spent longer performing behaviours consistent with foraging across two different temporal scales (individual dives and 24 h period). At the individual dive scale, time in the bottom phase is indicative of time at potential foraging depth, with the descent and ascent phases of the dive representing the transit to and from any potential prey patch (Boyd 1997). Despite the lack of sex difference in total dive duration, females spent longer in the bottom phase than males relative to total dive duration. At the 24 h scale, females spent on average 2 h more diving than males in both regions. We also found a moderate sex difference in the proportion of dives that reached the seabed, with females performing more benthic dives than males. Females may therefore have increased chance of prey capture during individual dives, which could represent an energetic advantage (Boyd 1997, Sparling et al. 2007), and contribute to higher survival probability of female pups (Hall et al. 2001). However, we cannot exclude the possibility that females spend more time diving because they are searching and are unsuccessful. Using direct observations of prey capture (i.e. stomach temperature telemetry, accelerometers or video cameras) to ground-truth putative foraging as identified from location and dive data would help to evaluate foraging success (Carter et al. 2016; Chapter I), and draw links between differences in ontogeny of foraging behaviour and survival probability.

Sex differences in bottom time, proportion of benthic dives, and time spent diving per day may be related to differences in the type and quality of prey items consumed by male and female pups. For example, if females target lower energy prey items, they will need to spend longer foraging than males for the same energetic gain. Grey seal adults are benthic foragers with a broad diet that varies between the sexes (Hammond et al. 1994, Beck et al. 2007). Beck et al. (2007) used quantitative fatty acid analysis to investigate niche breadth in grey seals in the northwest Atlantic. They found that the diet composition of YOY animals was significantly broader than that of adults, but found no sex differences for young animals. However, grey seal diet varies regionally and seasonally (Hammond et al. 1994, Beck et al. 2007), and therefore extrinsic factors unique to certain locations may shape sex differences in diet for young animals. No specific information currently exists on the diet of recently-weaned grey seal pups in the UK once they have left the colony due to the logistical constraints of collecting tissue and/or faecal samples specifically from this age-class. However, a recent study of grey seals in the North Sea presented ontogenetic changes in stable isotope ratios obtained from samples of tooth material, deposited during juvenile and adult life stages (Hanson et al. 2018). The study suggests that juveniles feed on a wider variety of lower trophic level, benthic prey closer to shore than adults (Hanson et al. 2018). The sharp increase in proportion of benthic dives over the first 40 days, and the subsequent reduction in trip distance, may therefore be indicative of pups learning to exploit benthic prey, and finding foraging grounds closer to shore where they can effectively reach the bottom. Additional dive analysis also suggests that shallow waters < 20 m deep may represent important foraging habitat for grey seal pups (see Appendix A2.3: Effects of bathymetric depth on benthic diving).

Water depth is an important regulating factor in foraging behaviour and habitat preference in older grey seals (Austin et al. 2006b, Aarts et al. 2008). Breed et al. (2011a) reported that adult and YOY females in the northwest Atlantic population forage in shallower water than males. Our data from CIS pups, showing that females dived in significantly shallower water than males, support these findings and suggest that water depth may play a key role in the development of habitat (and possibly diet) segregation among the sexes in some regions. We also found a moderate sex difference in trip distance for CIS pups, with males travelling further than females. Given that there was no sex difference in trip duration, this may mean that CIS males travel further offshore to forage compared to females, accessing deeper water, and potentially spending longer travelling per unit of time spent foraging than females. CIS females performed a greater proportion of benthic dives in shallow water (< 20 m) than males (see Appendix A2.3). The fact that CIS pups dived in shallower water than NS pups likely means that they were able to achieve greater dive bottom time and proportion of benthic dives as they spent less time in the ascent and descent phases of the dive. Sex differences in trip distance and water depth of dive locations were not strongly evident for NS pups. As with other metrics, sex differences may be mediated by extrinsic factors that vary among regions, such as prey distribution, physical oceanography, and the diversity of available habitats. In general, the North Sea is a more homogeneous ecosystem, with less variation in bathymetry and habitat types than the Celtic and Irish Seas (EMODnet Seabed Habitats Consortium 2016), which may reduce sexual niche separation in NS pups.

Intra and inter-specific competition may impact trip distance and duration in central place foragers. Juvenile grey seals in the northwest Atlantic travel further and for longer on foraging trips than adults, likely as a result of competitive exclusion from the best foraging grounds closer to shore (Breed et al. 2013). Age-related segregation has also been reported for other phocid species (Hamilton et al. 2016). We found that NS pups travelled further offshore and performed longer trips than CIS individuals. Population density of grey seal adults is much higher on the east coast of Scotland compared to the Celtic and Irish Seas (Jones et al. 2015, SCOS 2017). Moreover, Russell et al. (2015) showed that adult males in the North Sea reduce their time spent travelling to foraging locations in winter, whilst juveniles show an increase. Given that NS pups leave the colony during the winter months, and we see the longest trips performed during this time, competitive exclusion by conspecifics may be a feature of movement patterns specifically during the winter, forcing pups to make longer trips further offshore. In addition, harbour seals are present in coastal regions of the North Sea, but not in the Celtic and Irish Seas (Jones et al. 2015). Inter-specific competition may also contribute to NS pups travelling further offshore than CIS pups.

Our results show that NS pups can make trips of over two months in duration, travelling greater distances than commonly observed in adult foraging trips and hauling out less frequently (McConnell et al. 1999). We also found that pups significantly reduced their trip duration and distance in the third month (Fig. 2.2). A similar temporal dynamic has been observed in other phocids, with young seals reducing trip duration after an initial increase (Blanchet et al. 2016), and may be indicative of an increase in foraging efficiency, or a change in foraging strategy as pups get older. Moreover, the higher initial trip duration and distance may represent an exploration phase in the development of NS pups. Votier et al. (2017) found that immature northern gannets (*Morus bassanus*) develop knowledge of foraging grounds during early-life exploratory trips. This may also be the case for grey seal pups, as, like gannets, they receive no parental guidance in the location of foraging resources. Furthermore, we found that some pups returned to forage repeatedly in areas that they had previously discovered during their initial exploratory trip (Fig. 2.2). Exploration may therefore be an important behaviour in determining future foraging success (de Grissac et al. 2017).

CIS pups also performed exploratory trips, although their duration and distance was lower than those performed by NS pups. Individuals from NS colonies are not as geographically constrained as CIS pups by the proximity of land and shelf edge and therefore have more marine space to explore. Upon leaving the colony, CIS pups are more likely to encounter coastline, and therefore suitable haulout locations, than pups in the North Sea. Alternatively, the offshore phase could be driven by environmental variables not measured in this study. For example, tidal currents may direct pups further from land in the North Sea. The reduction in trip distance after 60 days for NS pups may therefore be related to a seasonal change in physical oceanography, or an increase in their ability to resist surface currents as muscle strength improves. Grey seals are known to rest at sea (Russell et al. 2015), and this study provides further evidence that they do not need to return to shore to rest, even when very young.

Our results show that pup movements can change rapidly throughout the initial months at sea. Therefore, accurately quantifying foraging effort from these data may require extension of current analytical techniques, such as state-space models (SSMs), to account for temporal changes in movement patterns (Carter et al. 2016; Chapter I). Moreover, as a priority for future work, analysis of pup foraging habitat preference may allow us to infer potential prey species based on habitat features such as seabed substrate type, and further assess the implications of early-life sexual segregation in movement patterns for foraging ecology.

In addition to ontogenetic changes in muscular and cardio-vascular systems, oxygen storage capacity and metabolic rate, and the development of knowledge of profitable foraging areas, there are likely to be seasonal changes in foraging habitat and prey distribution which may further explain differences in pup behaviour over time. Given that pups leave the colony on different dates in both regions (see Appendix A2.4: Colony departure dates), local conditions may dictate some of the patterns observed here. Bennett et al. (2001) have shown that maximum dive depth of adult southern elephant seals may be regulated by seasonally-mediated factors. However, due to a paucity of tracking data from post-breeding adult grey seals in the UK, such seasonal changes in at-sea behaviour are unclear. It was therefore not possible to disentangle ontogeny from seasonal effects on pup behaviour. Furthermore, some of the varition in early-life behavioural ontogeny may be explained by the fact that post-weaning fast duration varies among individuals (Bennett et al. 2010), and age at the point of departure from the colony is not equal for all pups. Natal and weaning dates were not known for all pups in this study, and time since departing colony was therefore used as a measure of at-sea experience. Future research should aim to achieve simultaneous tagging of adults, juveniles and pups, coupled with colony-based monitoring, which will allow us to further tease apart intrinsic and extrinsic drivers of variation in grey seal foraging behaviour and investigate the potential for competitive exclusion (Russell et al. 2015).

Investigating the factors that affect the ontogeny of early-life behaviours is key to understanding how populations may respond to natural and anthropogenic threats. Bennett et al. (2007) suggested that grey seal pups have an average of 36 days in which to find food after leaving the colony before their protein reserves are critically depleted and starvation occurs. Our results show that profound changes in pup behaviour happen during the first 40 days after departure from the colony, indicating this initial period at sea is likely of particular importance for development of effective foraging strategies. Consequently, pups may be most vulnerable to disturbance from a number of growing anthropogenic activities, such as increased vessel traffic (Jones et al. 2017a), intensive fishing practices (Bjørge et al. 2002) and offshore construction (Hastie et al. 2015) during this period, with substantial consequences for survival. Given the importance of early-life survival for maintaining stable populations (Harwood and Prime 1978), and the rapid development of key behaviours during this period, conservation managers should make special considerations for pups during their initial months at sea to effectively mitigate these threats and avoid population-level impacts. With continuing development of biologging technology and analytical techniques, further work is urgently needed to fully explore and describe the ontogeny of fundamental behaviours in naïve marine predators and identify critical habitat for young animals during their most vulnerable life stage.

Chapter III

Investigating ontogeny of foraging behaviour from animal movement data using generalized hidden Markov models

ABSTRACT

Foraging behaviour is central to many questions in ecology and conservation. Hidden Markov models (HMMs) have emerged as a useful tool for inferring behavioural states such as travelling and foraging from animal movement data. By including covariates, such as environmental variables, on the probability of transitioning between these states, HMMs allow investigation of factors affecting the timing and duration of particular movement behaviours. However, such models typically assume that the movement characteristics of behavioural states are not affected by covariates (i.e. state-dependent probability distributions are stationary). In reality, movement characteristics for any given behavioural state may be influenced by dynamic intrinsic and extrinsic factors. For example, in young animals learning to forage, we might expect the movement patterns generated by foraging behaviour to change through time as a function of age and experience. Using GPS tracking data, we investigated ontogenetic changes in movement state characteristics for 29 recently-weaned, naïve grey seal (*Halichoerus grypus*) pups from colonies in Northeast Scotland and West Wales (United Kingdom) during their first four months of independent life at sea. Using generalized HMMs, we allowed the expected movement characteristics of foraging and travelling states to change through time, between the sexes and among geographic regions. Specifically, we examined the effects of intrinsic (*time since leaving colony*, *sex*) and extrinsic (*region*) covariates on the probability distribution parameters of step lengths (i.e. speed) and turn angles (i.e. directional persistence) for foraging and travelling states. As pups got older, foraging movements became more tortuous and travelling became faster and more directed, indicating an increase in travel efficiency as they progressed from exploration to commuting between known haul-out sites and foraging grounds. Females showed greater changes in these movement parameters than males, particularly in Welsh pups. Comparing results with a conventional movement HMM (assuming stationarity in state-dependent movement characteristics) revealed differences of up to 12.6% in the estimated amount of foraging

activity. Model selection overwhelmingly favoured the generalized HMM. This study demonstrates that ontogenetic changes in animal movement can be readily addressed using generalized HMMs. It also demonstrates the sensitivity of state-assignments to the assumption of stationarity in state-dependent movement characteristics. Such sensitivities could have serious implications for conservation efforts, particularly when HMM outputs are used to define protected areas.

3.1 Introduction

Identification and quantification of foraging activity is essential to understand how animals interact with their environment to survive and maximise Darwinian fitness (Pyke 1983). The foraging areas of highly-mobile species are often associated with high biodiversity and ecosystem productivity, and are therefore frequently the focus of spatial conservation management (Worm et al. 2003, Grecian et al. 2016). However, direct observation of foraging behaviour in highly-mobile species is challenging. Animal-borne telemetry devices have allowed ecologists to collect detailed, high-resolution movement datasets from both terrestrial and marine species from which foraging behaviour can be inferred (Cooke et al. 2004).

Decoding animal movement data into discrete behaviours has become an increasingly active area of research over the past two decades (Turchin 1998, Fauchald and Tveraa 2003, Barraquand and Benhamou 2008). With location data, researchers generally use track characteristics (e.g. step lengths and turn angles between successive locations) to classify two or more modes of movement (Turchin 1998). In this context, foraging is inferred by slow, tortuous movements indicative of area-restricted search (ARS) (Carter et al. 2016; Chapter I). Based on this assumption, a speed threshold is often used to separate faster travelling behaviour from ARS (Turchin 1998). However, this approach is limited to one movement characteristic. Hidden Markov models (HMMs) are more sophisticated statistical models of animal movement, offering greater potential for robust ecological inferences (Patterson et al. 2008). HMMs are mixture distribution models, capable of identifying a finite number of probability distributions for multiple movement characteristics (Zucchini et al. 2016). Ecologists can then use biological rationale to attribute those distributions to behavioural states. HMMs offer a flexible and tractable statistical framework for quantifying behaviours from high-resolution (i.e. Global Positioning System, GPS) tracking data (Patterson et al. 2008, Langrock et al. 2012), and have also been applied to vertical movement (Langrock et al. 2014, Isojunno and Miller 2015) and accelerometery data (Leos-Barajas et al. 2016). HMMs frequently outperform conventional analytical methods for accurately inferring foraging behaviour in highly-mobile animals (Dragon et al. 2012b, Bennison et al. 2018), and are increasingly used to identify important foraging grounds for spatial conservation management (Maxwell et al. 2011, Patterson et al. 2016). The R package "moveHMM" makes fitting simple HMMs to animal movement data relatively straightforward and computationally-efficient for non-statisticians (Michelot et al. 2016).

A key benefit of HMMs is that they can incorporate multiple data streams (e.g. step length and turn angle, dive activity, accelerometery) and environmental covariates, simultaneously increasing confidence in foraging inferences and allowing investigation of environmental drivers of foraging decisions (Morales et al. 2004, Patterson et al. 2009, McClintock et al. 2017). Integrating data from multiple biologging sensors in a multivariate HMM can increase the number of identifiable behavioural states (McClintock et al. 2013, 2017), and is now facilitated with the R package "momentuHMM" (McClintock and Michelot 2018). Moreover, HMMs can be used to model the effects of environmental covariates on state transition probabilities, and therefore investigate the influence of extrinsic factors on resource selection (Morales et al. 2004, Patterson et al. 2009). For example, Morales et al. (2004) demonstrated how elk (*Cervus elaphus*) switch from an "exploratory" to "encamped" state with increasing proximity to open habitat.

A limitation of the HMMs typically implemented in animal movement studies is that they assume that the probability distributions that characterise each movement state are stationary. This assumption may be violated in many ecological scenarios. Specifically, for naïve juvenile animals learning to forage independently, the state-dependent distributions of movement metrics (e.g. step lengths and turn angles) will likely change through time. We might expect to see an increase in the speed and directional persistence of travelling as individuals gain knowledge of their environment and begin to adopt an optimal movement strategy (Osborne et al. 2013). There may also be a reduction in the scale of ARS, which may be reflected in the tortuosity of foraging movements. Ontogeny of behaviour in juvenile long-lived vertebrates is of key research interest given the influence of first-year survival on population dynamics (Harwood and Prime 1978, Orgeret et al. 2016, Rotics et al. 2016). However, accurately quantifying foraging behaviour from tracking data in young animals remains a substantial obstacle because most foraging models are based on adult behaviour (Jonsen et al. 2005, Carter et al. 2016, Bennison et al. 2018). Consequently, there is a need for a more generalized analytical approach to study foraging activity from tracking data in the context of juvenile movement.

Grey seals (*Halichoerus grypus*) undergo a prolonged period of sexual immaturity before recruitment to the breeding population (females: 6 years, males: 10 years) (Harwood and Prime 1978). Pups are abandoned on the natal colony after a brief (15-21 days) suckling period (Pomeroy et al. 1999) and receive no parental instruction in foraging tactics. Pups must learn to dive and find food rapidly before their fasting fuel reserves are depleted and terminal starvation begins (Bennett et al. 2010), and they experience substantial ontogenetic changes in behaviour throughout their initial months of life (Bennett et al. 2010, Carter et al. 2017; Chapter II). We therefore expect movement characteristics of foraging and travelling to change with age during this time. Moreover, in the United Kingdom (UK), the development of foraging skills in grey seal pups differs between the sexes and regional sub-populations (Carter et al. 2017; Chapter II). This may lead to sex and region differences in the ontogeny of behaviour-specific movement patterns. Using location and pressure sensor data from recently-weaned grey seal pups in the UK, we examine how foraging and travelling movement patterns change throughout the first four months of nutritional independence at sea. To investigate these ontogenetic hypotheses within the HMM framework, we incorporated intrinsic (*time since leaving colony, sex*), and extrinsic (*region*) covariate effects on the probability distribution parameters of movement characteristics (Fig. 3.1). In the spirit of generalized linear models (McCullagh and Nelder 1989), we refer to an HMM that relaxes the stationarity assumption of data stream probability distributions as a "generalized HMM". To test the sensitivity of state assignments to violating the stationarity assumption, we compared the generalized HMM results to a conventional HMM, assuming stationarity in the state-dependent probability distributions for movement characteristics. Finally, we provide insights into further applications of this technique that extend the utility of HMMs for studies of foraging ecology from animal movement datasets.

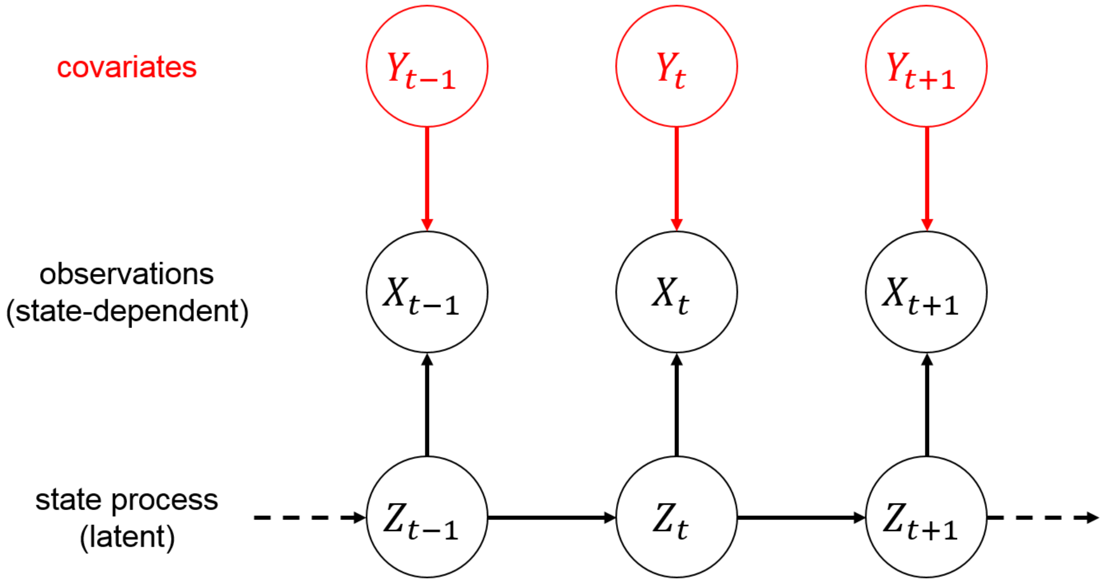

Figure 3.1: HMM structure. *In a conventional movement HMM (black), observed movement data stream parameter(s) (X_t; e.g. step length and change in bearing) are a stochastic product of latent states (Z_t; e.g. resting, foraging and travelling). However, this framework assumes that animal movement patterns associated with discrete states are not affected by covariates. By modelling state-dependent distribution parameter(s) (e.g. mean step length) as additionally dependent on covariate(s) (Y_t; e.g. time) in a generalized HMM, we can create models of animal movement in which state-dependent movement behaviours change as a function of intrinsic and extrinsic factors (e.g. as juveniles develop foraging skills with age).*

3.2 Methods

3.2.1 Telemetry data

Fastloc® GPS phone tags (SMRU Instrumentation, St. Andrews, UK) were deployed on 29 grey seal pups at five UK breeding sites in 2009 and 2010 (Table 3.1; Fig. 3.2). Pups were caught post-weaning before leaving the natal colony and devices were glued to the fur at the base of the skull (Carter et al. 2017; Chapter II). All capture and handling protocols were carried out under UK Home Office license #60/4009 in accordance with the Animals (Scientific Procedures) Act 1986.

Table 3.1: Grey seal pup sample size by tagging site and year. *Tag deployment sites were assigned to one of two distinct geographic regions (West Wales and Northeast Scotland).*

		No. tagged seals		
Tag deployment site (year)	**Region**	**f**	**m**	**Total**
Bardsey (2009)	W Wales	1	0	1
The Skerries (2009)	W Wales	1	2	3
The Skerries (2010)	W Wales	4	1	5
Ramsey (2010)	W Wales	3	4	7
Muckle Green Holm (2010)	NE Scotland	3	3	6
Stroma (2010)	NE Scotland	5	2	7
	Total:	**17**	**12**	**29**

Erroneous GPS location estimates were identified and excluded using residual error threshold and number of satellites (Russell et al. 2015). In addition to location fixes, devices transmitted two-hourly summaries of data, beginning at midnight (GMT), including percentage of time spent diving, as determined by the integrated pressure sensor. A dive started when the sensor recorded depth > 1.5 m for > 8 s, and ended when it recorded a depth of < 1.5 m. Data were transmitted via the Global System for Mobile communication (GSM) phone network (McConnell et al. 2004). Location fixes were interpolated to a constant time step of 2 h, falling at the midpoint of each summary interval. Any interval with missing summary data, or for which there was a gap > 6 h between the surrounding observed location fixes, was flagged as “unreliable”.

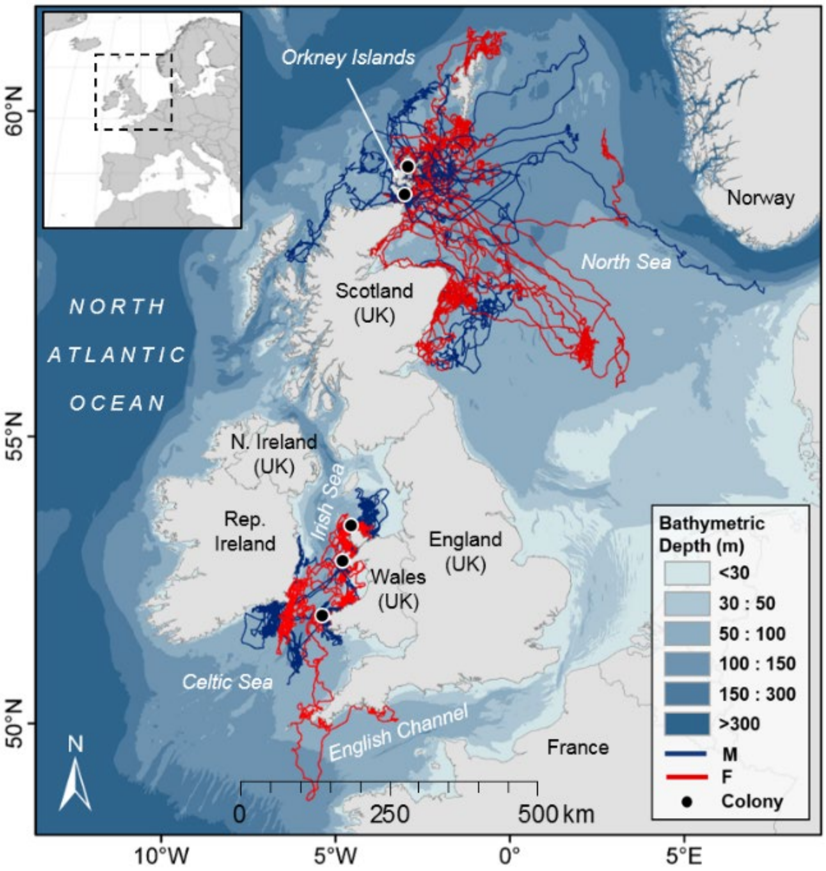

Figure 3.2: Pup tagging locations and tracks. *Tracks show pup movements during the first 120 days after leaving the colony. Colonies are shown with black dots (NE Scotland: North – South; Muckle Green Holm, Stroma), (W Wales: North – South; The Skerries, Bardsey and Ramsey). Tracks of males (n = 12) are shown in blue and females (n = 17) in red. Map created in Esri ArcMap™ 10.4. Bathymetric data extracted from the Digital Terrain Model for European Waters (European Marine Observation and Data Network).*

Natal dates were not known. Time since leaving colony (days) was therefore calculated for each interval and used as a measure of at-sea experience. Tag duration varied among individuals (from 34 to 337 days). Data were clipped to 120 days after first leaving the colony to ensure a comparable sample size for all sex-region groups throughout the time series (Zuur et al. 2010). Grey seal pups in the UK exhibit regional differences in the scale of at-sea movement during their initial months of life (Carter et al. 2017; Chapter II). We therefore grouped adjacent colonies into two geographically-distinct regions (Northeast

Scotland and West Wales) to investigate regional differences in the ontogeny of behavioural movement characteristics (Table 3.1).

3.2.2 Hidden Markov model

(a) State assignment

Time intervals ($t = 1, \dots, T$) were assigned to one of three latent states: $Z_t \in \{R, F, Tr\}$, where R denotes "resting", F denotes "foraging", and Tr denotes "travelling". Grey seals dive while foraging and travelling, but also spend prolonged periods at the surface (Thompson et al. 1991, Russell et al. 2015). For diving predators, horizontal movements during prolonged resting at the surface may be conflated with ARS if only location data are used to determine movement states (McClintock et al. 2013). Following Russell et al. (2015), we distinguished between time spent at the surface (resting state) and diving using the proportion of a time interval spent diving ($\omega_{d,t}$) from the tag summary data. Pups may dive continuously throughout a 2 h time interval, but the maximum proportion of any time interval spent underwater was 0.888. This is because pups must surface to breathe. Based on a majority rule, the threshold for an interval to be assigned to diving states was set at half of the maximum possible proportion of time spent diving, such that $Z_t = R$ when $\omega_{d,t} < 0.444$ and $Z_t \in \{F, Tr\}$ when $\omega_{d,t} > 0.444$ (Russell et al. 2015). Diving intervals were then attributed to either foraging or travelling based on step length (s_t; the Euclidian distance travelled in a 2 h time interval) and bearing (φ_t) in a multivariate, discrete-time HMM (Zucchini et al. 2016).

Following McClintock et al. (2017), we assumed step length $s_t | Z_t = i \sim \text{Gamma}(\mu_i/\sigma_i, \sigma_i)$ with the state-dependent mean step parameter $\mu_Z > 0$ and shape parameter $\sigma_Z > 0$ for $Z_t \in \{R, F, Tr\}$. For bearing, we assumed $\varphi_t | Z_t = i \sim \text{wCauchy}(\varphi_{t-1}, \gamma_i)$: a wrapped Cauchy distribution with state-dependent directional persistence parameter $0 < \gamma_Z < 1$

for $Z_t \in \{R, F, Tr\}$ (McClintock et al. 2017). Following Russell et al. (2015), states were assigned for "unreliable" intervals (see above) based solely on the Markov property of the state transition probabilities. State assignments for "unreliable" intervals were excluded from all further analyses.

Maximum likelihood estimation was performed using the forward algorithm (Zucchini et al. 2016). Poor state-dependent parameter starting values for numerical maximisation may affect the ability of the HMM to find the global optimum of the likelihood function ($\mathcal{L}$), resulting in numerical instability (Zucchini et al. 2016). Starting values were selected by testing 50 iterations of random combinations of parameter values $0.25 \leq \mu_Z \leq 14$ and $0.1 \leq \sigma_Z \leq 10$ and $0.01 \leq \gamma_Z \leq 0.9$. We assumed that mean step length (μ_Z) and directional persistence (γ_Z) would be higher for $Z = Tr$ than for $Z \in \{R, F\}$. The best starting values were identified by comparing the maximum log $\mathcal{L}$ estimate for each iteration of the model, and these values were then used throughout model selection. All modelling and subsequent analyses were performed in R version 3.3.2 (R Core Team 2016b).

(b) Generalized HMM

We fitted the HMM described above, allowing covariates to affect both the state-dependent probability distribution parameters of the movement characteristics (s_t, φ_t), and the state transition probabilities. The maximal model comprised a three-way interaction of covariates – *time since leaving colony* (continuous), *region* (two level factor) and *sex* (two level factor) - on the distribution of; (i) foraging and travelling mean step lengths ($\mu_{Z \in \{F,Tr\}}$), (ii) foraging and travelling directional persistence parameter ($\gamma_{Z \in \{F,Tr\}}$), and (iii) the state transition probabilities. The movements of naïve young animals may converge on adult-like patterns early in life (Osborne et al. 2013, de Grissac et al. 2017), and state-dependent distributions may therefore reach an optimum, arriving at a constant mean step length or directional persistence parameter value. This maximal model was therefore fitted with an asymptote on each of the state-dependent data stream probability distribution parameters (mean step length and directional persistence parameter). For details on implementation of covariate effects, see Appendix A3.1. To arrive at the minimal adequate model, backwards model selection was conducted by removing covariate effects from the maximal model based on Akaike information criterion (AIC) score (threshold for covariate exclusion $\Delta\mathrm{AIC} < 2$ (Burnham and Anderson 2002)). The most probable state sequence was then decoded using the Viterbi algorithm (Zucchini et al. 2016). Models were validated by visual inspection of pseudo-residual plots (Appendix A3.2).

(c) Comparison to conventional movement HMM

To test the effect of relaxing the assumption of stationarity on the data stream probability distributions, we compared the state-assignments from the minimal adequate generalized HMM described above against those from a minimal adequate “conventional” movement HMM with no covariate effects on the data stream probability distribution parameters (but with covariate effects on state transition probabilities). For model selection, the maximal conventional model comprised a three-way interaction of *time since leaving colony*, *region* and *sex* acting on the state transition probabilities. In other words, within the maximal conventional model, the covariates (including *time*) could affect the probability of switching between states (i.e. frequency of states), but not the distribution of movement metrics that inform the states, which remain stationary. As with the generalized HMM, backwards model selection was conducted to arrive at a minimal adequate model, the states of which were then decoded for each 2 h time interval using the Viterbi algorithm.

We tested if the proportion of state-assignments attributed to foraging (for the entire dataset, and at sex-region group level) was significantly different between the minimal adequate generalized and conventional HMMs using two-sample tests for equality of proportions (i.e. binomial tests).

3.3 Results

In both the generalized and conventional HMMs, the two states identified by the model were presumed to represent foraging and travelling, based on their respective characteristics. The state with lower mean step length and directional persistence values was attributed to foraging (Fig. 3.3). Resting intervals were pre-determined by the threshold of diving activity, and so were not assigned by the HMM in a probabilistic manner (see "Methods"). Therefore, covariate effects on resting state-dependent parameters did not affect state assignment and are not reported.

3.3.1 Generalized HMM

The minimal adequate generalized HMM included covariate effects of time since leaving colony, sex and region in a three-way interaction on the; (i) mean step length, (ii) directional persistence parameter and (iii) state transition probabilities (Table 3.2). An asymptotic relationship was retained in the model for the effect of time since leaving colony on mean step length (Table 3.2).

The mean step length associated with travelling increased with time since leaving colony, whereas it remained constant in the foraging state (Fig. 3.3a-d). The mean step length attributed to foraging showed no significant change over time for any of the sex-region groups, remaining at around 2.2 km (± 0.2; 95% confidence intervals) per 2 h interval (Fig. 3.3a-d). The magnitude of the increase in travelling speed differed by sex in a region-specific manner. For females in both regions, mean step length of travelling intervals began at 5 km (± 0.8 NE Scotland; ± 2 W Wales) and increased to 7 km (± 0.8 NE Scotland;

± 2 W Wales) by the end of the time series (Fig. 3.3b,d). In contrast, mean travelling step length for males increased from 5 km (± 0.2) to 6 km (± 0.2) in NE Scotland, but remained at a constant 5 km (± 1) in Wales (Fig. 3.3a,c).

Table 3.2: Generalized HMM backwards selection by AIC. *ΔAIC shows the change in score compared to the best model (lowest AIC) of the previous round. Threshold for covariate removal = ΔAIC < 2 (shown in bold). The combination of covariate effects on movement parameters is shown for each model. "T" denotes time (continuous), "R" denotes region (two-level factor) and "S" denotes sex (factor). Interactions between covariates are shown with ":". "Asym" Indicates if an asymptotic relationship was permitted for the parameter. k denotes the number of parameters in the model. The minimal adequate model is shown with "*".*

		Covariate effects								
		Mean step length ($\mu_{z\in\{F,Tr\}}$)		**Dir. persistence ($\gamma_{z\in\{F,Tr\}}$)**		**State transition prob.**				
Round	**Model**	**Covs**	**Asym**	**Covs**	**Asym**	**Covs**	***k***	**log $\mathcal{L}$**	**AIC**	**ΔAIC**
Maximal		T:R:S	Y	T:R:S	Y	T:R:S	110	-117603.7	235427.3	0.0
1	a	T:R:S	Y	T:R:S	N	T:R:S	107	-117606.2	**235426.5**	**-0.8***
	b	T:R:S	N	T:R:S	Y	T:R:S	107	-117608.6	235431.2	3.9
2	a	T:R:S	N	T:R:S	N	T:R:S	104	-117611.1	235430.2	3.7
	b	T:R+T:S+R:S	Y	T:R:S	N	T:R:S	104	-117614.2	235436.4	9.9
	c	T:R:S	Y	T:R+T:S+R:S	N	T:R:S	104	-117616.5	235440.9	14.4
	d	T:R:S	Y	T:R:S	N	T:R+T:S+R:S	101	-117636.4	235474.9	48.4

The tortuosity of both foraging and travelling movements changed significantly with time since leaving colony. Foraging movements became more tortuous over time for all sex-region groups; the wrapped Cauchy distribution directional persistence parameter γ_F (scaled from 0 to 1) decreased over time for foraging intervals (Fig. 3.3e-h). Females showed greater changes than males in both regions. For males in both regions, γ_F was approximately 0.35 (± 0.06 NE Scotland; ± 0.1 W Wales) upon leaving the colony, and declined to approximately 0.25 (± 0.06 NE Scotland; ± 0.1 W Wales) by the end of the time series (Fig. 3.3e,g). Foraging movements of Scottish females were less tortuous than those of males upon leaving the colony, at 0.55 (± 0.15), but declined to a similar value of 0.3 (± 0.15) by the end of the time series (Fig. 3.3f). Foraging movements of Welsh females were the least tortuous of all sex-region groups at the beginning of the time series, at 0.8 (± 0.22) and showed the steepest decline, to around 0.2 (± 0.22) (Fig. 3.3h). However, 95% confidence intervals were much wider for Welsh females than for other sex-region groups.

Travelling movements became more directed with time since leaving the colony for all sex-region groups, indicated by an increase in γ_{Tr} values (Fig. 3.3e-h). For Scottish pups, γ_{Tr} was approximately 0.5 (± 0.02 M; ± 0.08 F) when pups left the colony and increased to approximately 0.7 (± 0.02) for males, and 0.8 (± 0.08) for females by the end of the time series (Fig. 3.3e-f). Travelling movements of Welsh pups were more tortuous than those of Scottish pups at the beginning of the time series, at approximately 0.3 (± 0.09 M; ± 0.2 F), but γ_{Tr} values increased to 0.6 (± 0.09) for males (Fig. 3.3g) and 0.7 (± 0.2) for females (Fig. 3.3h).

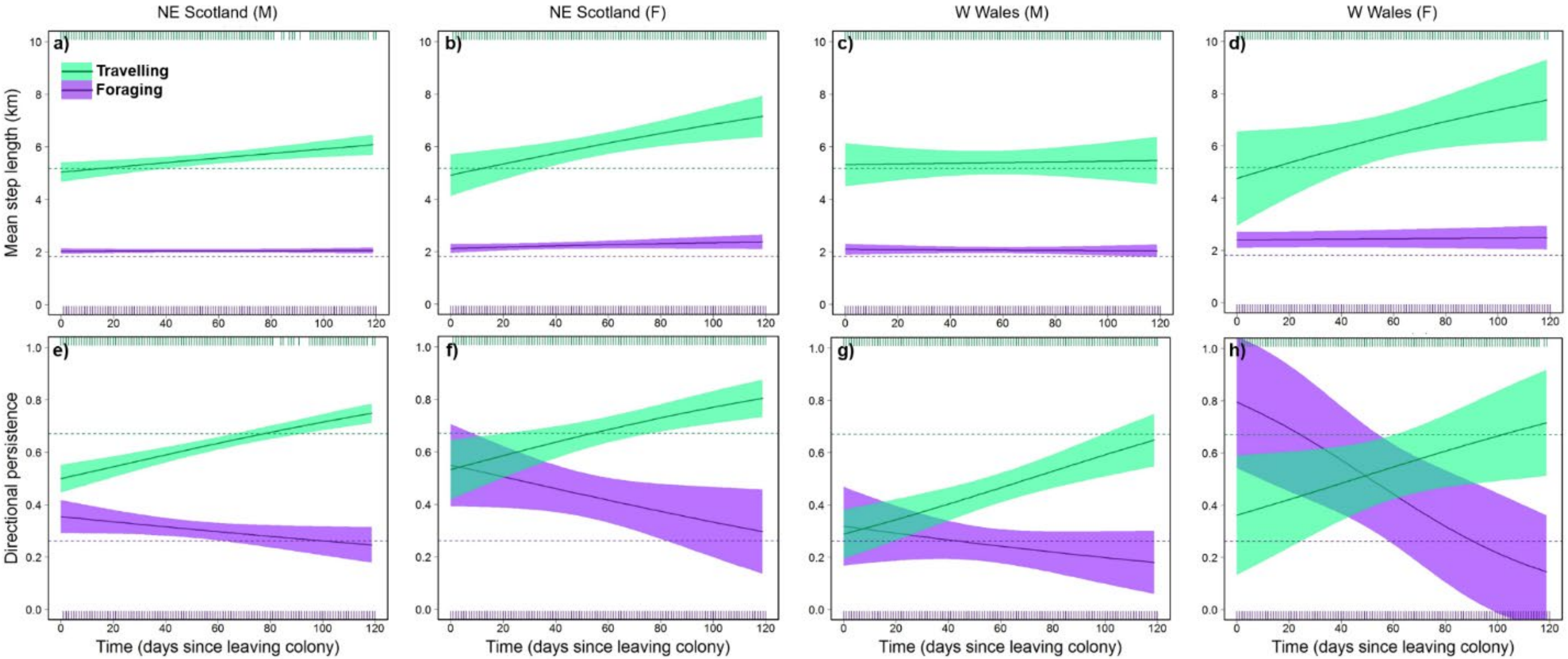

Figure 3.3: Covariate effects on state movement parameters. *Solid lines represent sample mean estimates of covariate effects with associated 95% confidence intervals (shaded areas), colour-coded by state. Horizontal axis rug plots show the distribution of data, colour-coded by state. Horizontal dashed lines show conventional HMM model parameter estimates, colour-coded by state. Movement parameters are given as values for 2 h time intervals. Directional persistence parameter values (path straightness) are scaled from 0 to 1.*

3.3.2 Frequency of behaviours

Disregarding “unreliable” time intervals (see “Methods”), the proportion of time spent in a foraging state for the entire dataset was 0.44, compared with 0.29 for travelling and 0.27 for resting, as decoded by the Viterbi algorithm for the minimal adequate generalized HMM. Fig. 3.4a shows example state predictions from the generalized HMM, highlighting that foraging occurs in bouts, interspersed with meandering travel during initial exploratory movements, and that pups develop adult-like behaviour, commuting between haulout sites and foraging grounds within the first four months of independence.

The state transition probabilities changed as a function of time since leaving colony. However, the strength and direction of this change was not equal among sex-region groups. Welsh females experienced an increase in the probability of switching from resting to foraging over time, from 0.24 (± 0.03) to 0.4 (± 0.03), whereas males experienced a decrease from 0.32 (± 0.05) to 0.25 (± 0.05) (Fig. 3.5a). The probability of remaining in a foraging state increased over time for Welsh females from 0.69 (± 0.04) to 0.85 (± 0.02), whilst Welsh males showed a slight decline from 0.74 (± 0.04) to 0.67 (± 0.04) (Fig. 3.5b). In Scottish pups, the probability of remaining in a foraging state was stable at around 0.7 (± 0.04), and no significant sex difference in foraging state transition probabilities was detected.

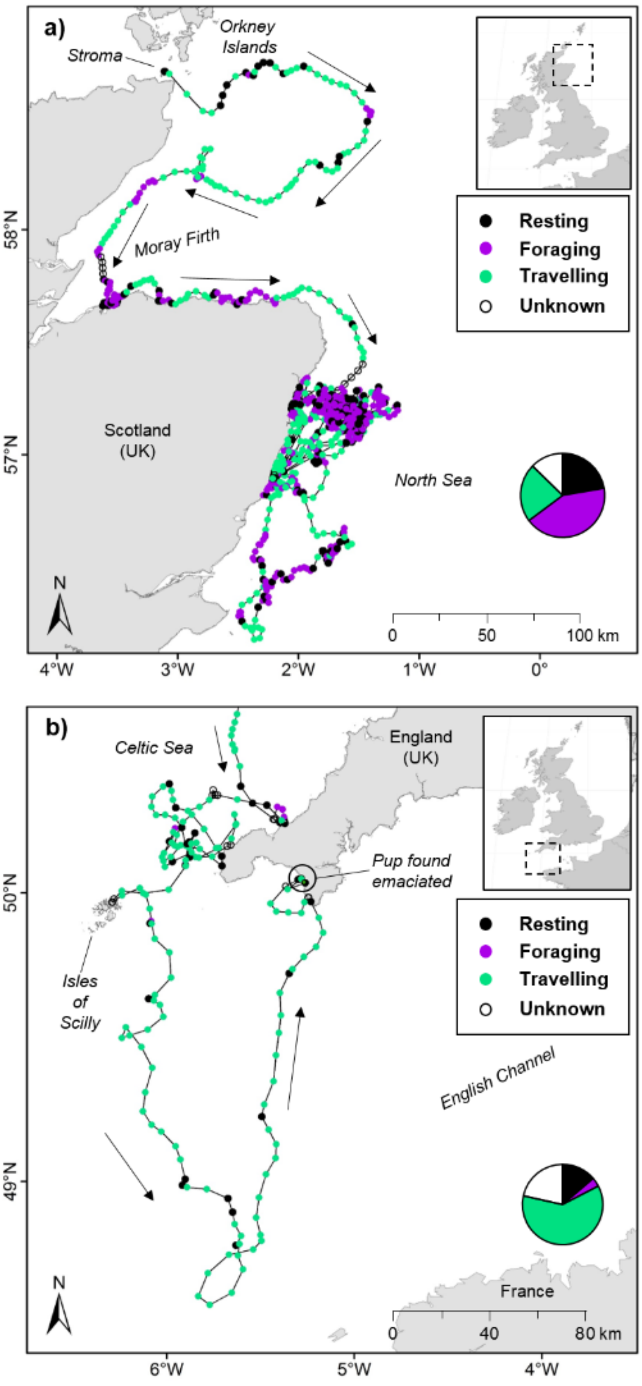

Figure 3.4: Example generalized HMM state predictions. *Map (a) shows all state assignments for an example pup track from Stroma (NE Scotland) during the initial 120 days after leaving the colony. The pup performs an exploratory phase as it leaves the colony and travels along the coast of the Moray Firth before switching to more directed trips to foraging grounds off the east coast of mainland Scotland. Arrows show direction of travel. Each point represents a 2 h time interval. Pie charts show proportion of activity across the time series. Map (b) shows a pup from Bardsey (W Wales) during the final 16 days of the track. The model predicts only 7% of the time was spent foraging, and the pup subsequently stranded in an emaciated condition in south-west England, 58 days after leaving the colony. Maps created in Esri ArcMap™ 10.4.*

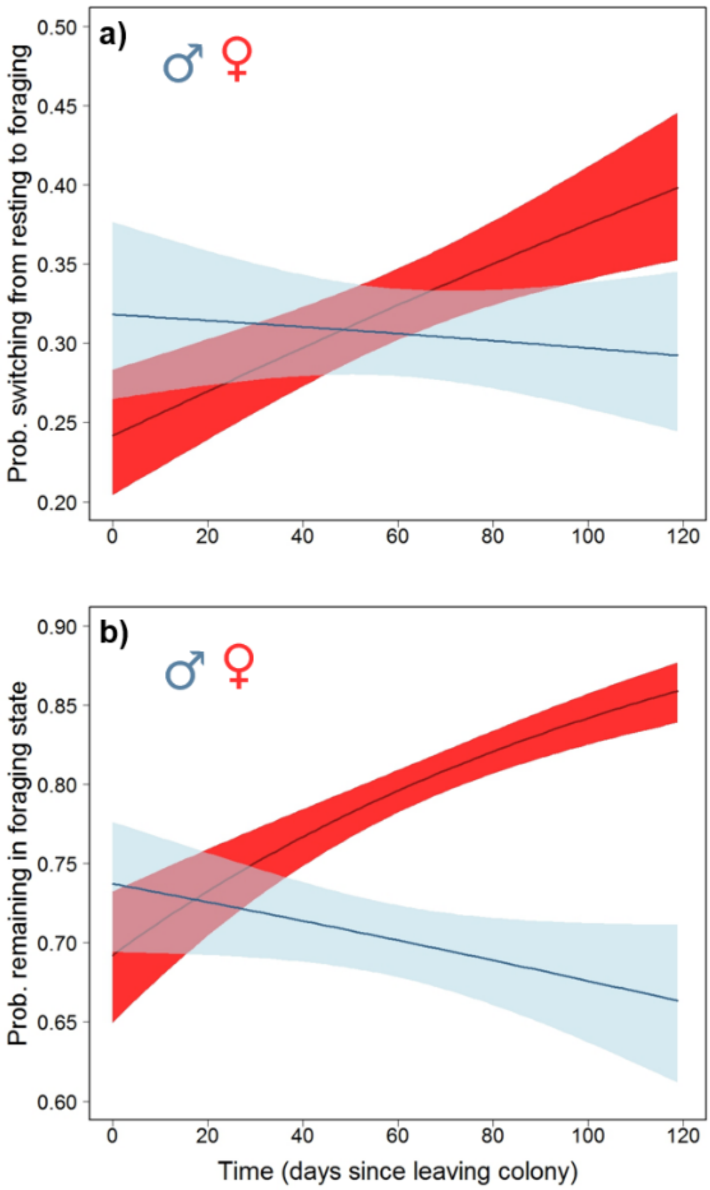

Figure 3.5: Sex differences in state-transition probabilities of Welsh pups. *Welsh females (red) spent more time foraging than males (blue) as they got older, indicated by an increased probability of switching from resting to foraging over time (a), and an increased probability of remaining in foraging state (b). Solid lines are sample mean responses, shaded areas are 95% confidence intervals.*

3.3.3 Comparison to conventional HMM

The minimal adequate generalized HMM was deemed superior to the minimal adequate conventional HMM, which had a three-way interaction of covariates on the state transition probabilities (Tables 3.2-3.3; ΔAIC = -1418.2). The proportion of time estimated to be foraging differed between the two models; 8.4% (n = 1770) of non-resting state assignments conflicted. For the entire dataset, the proportion of all time intervals attributed to foraging by the generalized HMM was significantly higher than for the conventional HMM (binomial test; χ^2_1= 112.83, p < 0.001). Moreover, the difference was not equal for all sex-region sample groups. The proportion of intervals assigned as foraging was significantly higher for the generalized HMM in all sex-region groups except Welsh females (Fig. 3.6a: NE Scotland males; binomial test; χ^2_1 = 65.67, p < 0.001, NE Scotland females; χ^2_1 = 114.82, p < 0.001, W Wales males; χ^2_1 = 54.67, p < 0.001, W Wales females; χ^2_1 = 7.08, p = 0.996). The maximum difference was for a male from Scotland, in which the conventional HMM recorded 12.6% fewer foraging intervals than the generalized HMM (Fig. 3.6a). In some instances, intervals that were assigned as travelling by the stationary model, and as foraging by the non-stationary model, were clustered in space (Fig. 3.6b).

Table 3.3: Conventional HMM backwards selection by AIC. *ΔAIC shows the change in score compared to the best model (lowest AIC) of the previous round. Threshold for covariate removal = ΔAIC < 2. The combination of covariate effects on state transition probabilities is shown for each model. "T" denotes time (continuous), "R" denotes region (two-level factor) and "S" denotes sex (factor). Interactions between covariates are shown with ":". k denotes the number of parameters in the model. The minimal adequate model is shown with "*".*

Round	**State transition prob. covs**	***k***	**log $\mathcal{L}$**	**AIC**	**ΔAIC**
Maximal	T:R:S	62	-118360.3	**236844.7**	**0.0***
1	T:R+T:S+R:S	56	-118385.3	236882.5	37.8

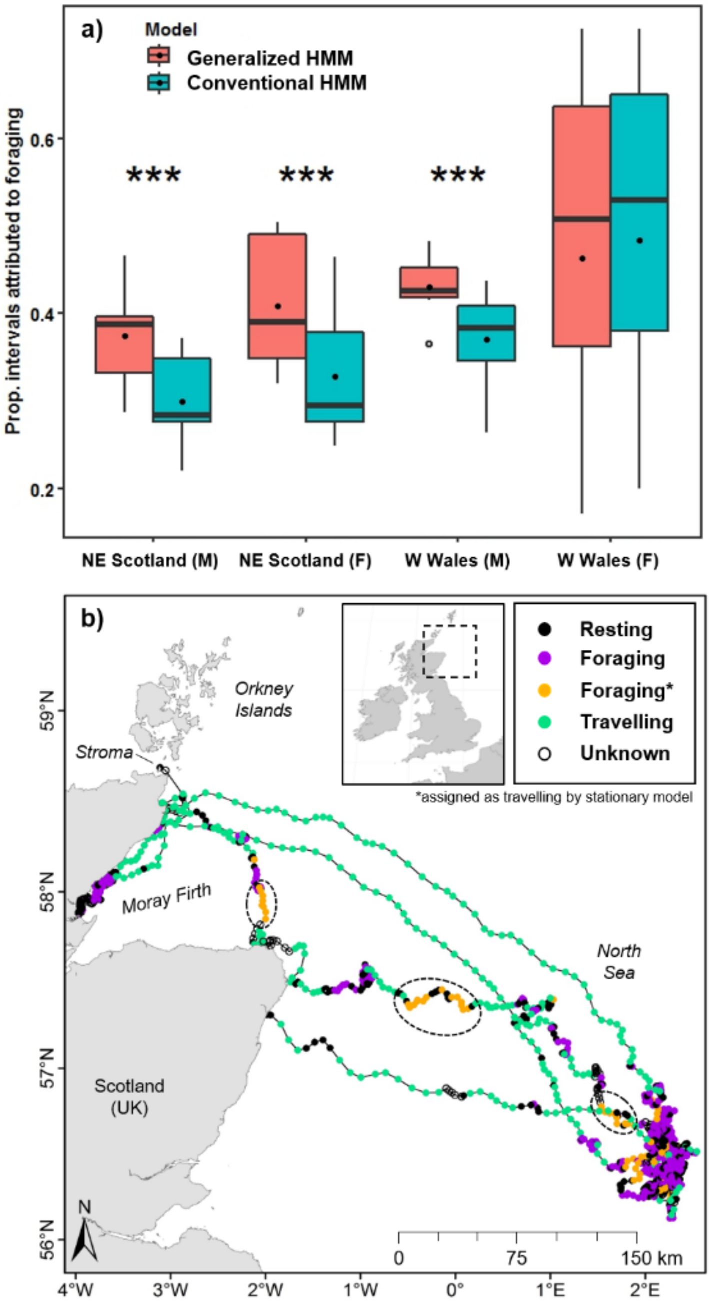

Figure 3.6: Differences between generalized and conventional HMMs. *Boxplot (a) shows the difference in proportion of total non-resting time intervals (n = 21,062) assigned as foraging between the best generalized and best conventional model. The conventional model estimated significantly less foraging than the generalized model for all sex-region groups apart from Welsh females ("***" indicates p < 0.001). Thick black lines are median values, black dots are sample means, boxes show interquartile ranges (IQRs), lines show minimum and maximum values, open circles are outliers (> 1.5*IQR <). Map (b) shows state assignments for a Scottish pup. Each point represents a 2 h time interval. Gold points show intervals that were assigned as foraging by the generalized HMM, but as travelling by the conventional HMM. Potentially important foraging areas may be under-estimated or overlooked by not accounting for covariate effects on state-dependent movement parameters (dashed ovals). Map created in Esri ArcMap™ 10.4.*

3.4 Discussion

By relaxing the assumption of stationarity in the data stream probability distributions associated with typical animal movement HMMs (e.g. Patterson et al. 2009; Langrock et al. 2012), we have demonstrated how foraging and travelling behaviour develops with age in a naïve marine top predator. Grey seal pups' travelling behaviour became faster and more directed over the first four months after leaving the colony (Fig 3.3), indicating an increase in travel efficiency. In contrast, foraging movements became more tortuous, indicating a decrease in the spatial scale of ARS. Despite a lack of obvious sexual size dimorphism at this age (Bennett et al. 2010), the magnitude of these changes varied with sex. This sex-specific temporal relationship differed between geographic regions, indicating that extrinsic factors can also influence foraging and travelling movement characteristics. To better understand the implications of assuming stationarity in the movement characteristic probability distributions, we compared the estimated behavioural states from our generalized HMM with those from a conventional movement HMM, within which the same covariates (a three-way interaction between *time since leaving colony*, *sex* and *region*) were included, but could only impact the state transition probabilities. Our comparison revealed significant differences in the estimated amount of foraging activity of up to 12.6%, and our model selection procedure overwhelmingly supported the generalized HMM.

3.4.1 Temporal changes in movement characteristics

The temporal changes in state-dependent movement characteristics of grey seal pups reported here are likely related to ontogenetic changes driven by an increase in experience and physiological development. Changes likely occur as pups shift from slow, meandering exploratory movements to more directed travel, commuting between known haul-out sites and known foraging locations, which is consistent with adult behaviour (McConnell et al. 1999, Breed et al. 2011a). Travelling and foraging state-dependent parameter values diverged over time (Fig. 3.3), indicating that state-specific movements become increasingly distinct with age as pups gain experience and shift from opportunistic foraging towards a more focussed search strategy. This insight would not have been obtained using a conventional HMM. Carter et al. (2017; Chapter II) found a reduction in trip duration in the third month after leaving the colony in UK grey seal pups, suggesting that pups developed adult-like foraging trip behaviour during this time. A study using HMMs to compare behaviour in young of the year (YOY; > 5 months old) grey seals to that of adults in the northwest Atlantic population found no difference between the two age classes in the speed and tortuosity of outbound travelling movements on foraging trips, and concluded that young seals navigated between haul-out sites and foraging grounds as effectively as adults (Breed et al. 2011a). Our findings build on this and suggest that pups acquire spatial knowledge of productive foraging grounds during exploration, leading to the development of adult-like foraging trip behaviour within four months of leaving the colony. Despite this rapid increase in travel efficiency and search behaviour, it seems likely that pup foraging efficiency remains below that of adults because juveniles spend more time travelling per unit of time spent foraging compared to adults (Breed et al. 2011a, Russell et al. 2015). The initial four months of independence at sea are therefore likely important for the development of routine behavioural patterns in grey seals, which are refined over subsequent years. Nevertheless, rapid acquisition of foraging skills in naïve animals is critical for survival (Daunt et al. 2007, Orgeret et al. 2016). For grey seals, starvation is the primary cause of mortality during the first year (Baker et al. 1998). Indeed, one of the pups included in this study was found ashore in an emaciated condition, 58 days after leaving the colony. During the last 16 days of its track, the model reveals that only 7% of time intervals were spent foraging (Fig. 3.4b). Reduced foraging activity may be an indicator of poor nutritional condition preceding mortality, as in juvenile seabirds (Daunt et al. 2007).

In addition to gaining experience, grey seals also undergo profound physiological development during the initial months of life after weaning, which likely contributes to the observed temporal changes in state-dependent movement characteristics. Oxygen storage capacity and muscle strength improves throughout the early months of life (Noren et al. 2005), and pups convert blubber into lean mass (Hall and McConnell 2007), becoming less buoyant, which likely facilitates an observed increase in dive duration (Bennett et al. 2010, Carter et al. 2017; Chapter II). Similar early-life increases in dive performance have been reported for penguins (Orgeret et al. 2016) and other pinniped species (Baylis et al. 2005, Blanchet et al. 2016). Grey seal adults dive continuously during travel to minimise surface drag (Thompson and Fedak 1993), and an increased ability to remain submerged is therefore likely a feature of the observed increase in travel speed and directional persistence reported here. Physical oceanography and extreme weather events can shape the dispersal and early-life movements of terrestrial-breeding marine predators (Lea et al. 2009, Mansfield et al. 2014). Although the influence of such factors on grey seal pup movements in the UK is unknown, pups are likely more able to overcome the effects of surface currents as diving capacity increases. Further research is needed to elucidate the impact of contemporaneous surface currents on state-dependent movement metrics. Generalized HMMs and user-friendly software for implementing these models (e.g. McClintock and Michelot (2018)) should provide a platform for future studies of how movement-specific behaviours develop in relation to environmental factors for highly-mobile animals.

3.4.2 Sex and region effects

In both regions, we found sex differences in development of foraging and travelling behaviour for grey seal pups. Sex-specific foraging behaviour is common in size-dimorphic vertebrates, such as terrestrial herbivores (Ruckstuhl and Neuhaus 2000, Shannon et al.

2006), seabirds (Gonzalez-Solis et al. 2000) and pinnipeds (Staniland 2005). Here, sex-specific foraging behaviour precedes overt sexual size dimorphism. Females showed greater changes in step length and directional persistence than males over time. Our study supports previous evidence of sex-specific foraging behaviour soon after departing the colony in grey seal pups (Carter et al. 2017; Chapter II). Indeed, previous studies have shown that sex differences in energy storage strategies are present in young seals before independent feeding (Arnould et al. 1996, Kelso et al. 2012), but a link to subsequent at-sea behaviour has not previously been established. In Antarctic fur seals (*Arctocephalus gazella*) male pups develop more lean mass, whilst females store more energy as blubber (Arnould et al. 1996). Similarly, Kelso et al. (2012) showed that male southern elephant seal (*Mirounga leonina*) pups are more efficient at sparing protein when fasting than females. Adult female grey seals prioritise accumulation of lipid mass which they must convert into milk to provision pups, whilst males put on lean mass in order to compete effectively for females (Beck et al. 2003a).

Adult and YOY female grey seals spend more time exhibiting foraging behaviour than males (Breed et al. 2009, 2011a). Similarly, Carter et al. (2017; Chapter II) found that female pups spent longer performing diving behaviours consistent with foraging than male pups in Wales. Our results confirm that Welsh females consistently spent more time engaged in foraging behaviour than males (Fig. 3.5). These differences may be driven by sex-specific prey preferences that underpin dimorphism of body size and body composition in adults (Beck et al. 2003b, 2007). If females pursue smaller, more patchily-distributed prey than males, they must spend longer foraging per unit of energetic gain. Given the high risk of starvation to seal pups (Baker et al. 1998), early foraging niche separation may be important for minimising competition, and maximising survival chances. The sex differences were not observed in the NE Scotland population, indicating the influence of environmental factors on foraging ontogeny. Regional sex-specific foraging strategies were recently described for adult Weddell seals (*Leptonychotes* *weddellii*) in Antarctica (Langley et al. 2017). Although the environmental drivers of behavioural sex differences are difficult to identify, our study provides further evidence of this phenomenon in phocid seals and shows that it emerges early in life. Possible causal factors might include regional differences in the diversity of available foraging habitat, or prey availability and distribution. Formal diet studies have not been conducted on the Welsh population of grey seals, but previous work comparing scat samples from seals in east and west Scotland revealed regional differences in diet composition (Wilson and Hammond 2016).

3.4.3 Conclusions and wider implications

Here we have demonstrated an extension of HMMs to investigate how intrinsic and extrinsic covariates affect behaviour-specific movement patterns. This generalized HMM approach has revealed new information about how grey seal pups develop foraging behaviour that would not have been detected within the conventional HMM framework. Understanding how animals learn to find and exploit patchy food resources is critical to predicting how they might respond to future environmental change and habitat modification. A growing body of literature suggests that, for naïve animals, search behaviour is optimised following an initial exploratory phase (Osborne et al. 2013, de Grissac et al. 2017, Votier et al. 2017). For example, Osborne et al. (2013) radar-tracked naïve bumblebees (*Bombus terrestris*) from their first foraging trip and found that the speed and directional persistence of their tracks increased with experience as they developed knowledge of the spatial distribution of foraging resources. Our findings support this and provide further evidence for the importance of early-life exploration for the development of optimal search strategies, and the need for analytical approaches to account for it.

The techniques implemented here have broader applications within the study of foraging ontogeny. Indeed, the transition to independent feeding is also a critical time in the life of animals that receive prolonged parental care. For example, despite remaining with their parents for up to 40 days post-fledging, juvenile European shags (*Phalacrocorax aristotelis*) are at high risk of starvation during their first year (Daunt et al. 2007). Daunt et al. (2007) found that juveniles spent longer foraging per day than adults to compensate for inferior foraging proficiency. In such cases, the generalized HMM method represents a tool to investigate the drivers of variation in foraging ontogeny. Moreover, we have highlighted the importance of considering how interacting intrinsic and extrinsic covariates impact the decoding of discrete behaviours using animal movement HMMs. Until now, researchers have either modelled different sex or regional groups separately, or assumed no variation among groups in state-dependent parameters (Russell et al. 2015). However, the integrative approach presented here demonstrates that the inclusion of covariate effects on state-dependent parameters can act as a grouping (partial-pooling) mechanism (Zucchini et al. 2016), to increase the ecological insights achievable from one model.

In addition to ontogenetic changes, animals experience temporal changes in their reproductive status (Weimerskirch et al. 1993) and energetic requirements (Pirotta et al. 2018), along with changes in the physical environment (Lea et al. 2006) and prey distribution (Kuhn et al. 2015), which may all affect their foraging strategy. The generalized HMM approach presented here therefore has wide application to investigate how mobile species adapt their foraging movements to cope with such dynamic factors. In particular, there has been increasing research interest in the environmental drivers of variation in foraging behaviour for highly-mobile species (Scales et al. 2014, Bon et al. 2015, Della Penna et al. 2015, Cox et al. 2016). Whilst conventional HMMs can uncover how habitat features affect behavioural state transitions (Patterson et al. 2009), incorporating extrinsic covariate effects on data stream parameters will improve our understanding of how animals adjust their behaviour-specific movement patterns in response to environmental cues. Furthermore, our results suggest that, in cases where the stationarity assumption is violated, not accounting for temporal covariate effects on foraging movement patterns may lead to inaccurate estimations of activity budgets, and, may translate to sub-optimal designation of conservation resources. Moving forwards, this generalized HMM technique will allow ecologists to tackle more complex questions and reveal how behaviour-specific animal movement relates to changes in the individual and in the environment.

Chapter IV

Ontogeny of foraging habitat preference in a naïve marine top predator; the grey seal

ABSTRACT

Naïve juvenile animals that learn to forage without parental instruction must do so before their energy reserves are depleted, and terminal starvation occurs. For slow-maturing long-lived vertebrates, first-year survival is often low and has a large influence on population dynamics. Identifying important habitat for the development of foraging behaviour in young animals should therefore be a conservation priority. Much research effort has sought to uncover the environmental and biological drivers of foraging resource selection in adult animals, but the development of habitat preference in young animals is seldom studied. Here, we investigated the ontogeny of foraging resource selection in a marine top predator; grey seal (*Halichoerus grypus*) pups. We used a GPS tracking dataset from 29 recently-weaned pups, instrumented at colonies in two geographically-distinct regions of the United Kingdom (UK); Northeast Scotland and West Wales. We modelled the relationship between putative foraging locations and candidate environmental variables in a use-availability framework with generalized additive mixed models (GAMMs). To investigate ontogeny of foraging habitat preference, this relationship was allowed to vary with time (*days since leaving colony*). Pups from NE Scotland developed preference for sandy areas of cold (5 - 6.5^{0}C) lagged mean sea surface temperature (previous winter), between 40 – 80 m depth; habitat consistent with overwintering sandeels (*Ammodytes spp.*). Pups preferentially foraged closer to shore (< 100 km from haulouts) after the first two months. In W Wales, preference was less clearly-defined, indicating a more generalist diet, and more individual variation in foraging resource selection. However, we found evidence of sex-specific foraging strategies before sexual size dimorphism, with Welsh females preferring shallower areas than males. This study illustrates the utility of incorporating behavioural inferences from hidden Markov models to investigate resource selection in the context of foraging. It highlights the importance of considering intrinsic (e.g. age, sex) and extrinsic (e.g. regional) sources of variation in habitat preference, which may be important in conservation management decisions.

4.1 Introduction

Unpicking the physical and biological processes that shape animal habitat preference is critical to assessing how populations may be affected by anthropogenic habitat modification (Sawyer et al. 2006, Russell et al. 2016) and climate change (Hindell et al. 2017), and in designing effective conservation management (Embling et al. 2010). One of the principal factors influencing how animals interact with their environment is the need to find and exploit food resources (Pyke 1983). Individuals must optimise their foraging behaviour in order to survive and maximise fitness (Stephens and Krebs 1986). For marine species, a large area of research focusses on how highly-mobile animals, such as large vertebrate predators, locate patchily-distributed prey resources in a dynamic environment (Bailey and Thompson 2010, Embling et al. 2012, Cox et al. 2016, Hastie et al. 2016). Such research has revealed the importance of tidal channels as habitat corridors, providing foraging opportunities for dolphins (Hastie et al. 2004) and seals (Hastie et al. 2016), and oceanographic fronts as prey aggregation sites for seabirds (Scales et al. 2014, Cox et al. 2016), and planktivorous sharks (Miller et al. 2015). However, the vast majority of resource selection studies have focussed on adults, and few studies have addressed the ontogeny of habitat preference in young animals, which may be different to that of adult conspecifics (Riotte-Lambert and Weimerskirch 2013, Cameron et al. 2018, Frans et al. 2018).

Understanding the intrinsic and extrinsic factors that shape the development of habitat preference is especially important for slow-maturing, long-lived species, such as seabirds and marine mammals, since first-year survival can have a profound effect on population dynamics (Harwood and Prime 1978, Lindström 1999, Sæther et al. 2013). Foraging efficiency is often lower for juveniles due to lack of experience and greater physiological limitations compared with adults (Goss-Custard and Durell 1987, Burns 1999, Daunt et al. 2007, Riotte-Lambert and Weimerskirch 2013). These challenges are particularly acute for naïve solitary foragers that do not receive prolonged parental provisioning, or the chance to learn foraging strategies alongside adult conspecifics (Lindström 1999). For example, many large phocid seals, such as elephant (*Mirounga spp.*), hooded (*Cystophora cristata*) and grey seals (*Halichoerus grypus*), are weaned abruptly on the breeding colony, and must learn to dive and forage without maternal instruction (Boness and Bowen 1996). Early-life survival of naïve animals therefore depends upon rapid acquisition of effective foraging skills before metabolic fuel is critically depleted and terminal starvation begins (Baker et al. 1998, Daunt et al. 2007, Bennett et al. 2007, Orgeret et al. 2016). The behavioural strategies employed by young naïve animals to overcome these challenges remain poorly studied for many species. Nevertheless, studies of early-life behaviour in young highly-mobile animals are becoming more frequent, facilitated by the continued refinement and miniaturisation of animal-attached telemetry devices (Shillinger et al. 2012). The next challenge in this field of study is to identify important habitat features for the ontogeny of foraging behaviour in young animals during this vulnerable life stage (Cameron et al. 2018).

Grey seals are among the most studied of marine predator species. Adults inhabit shelf seas in the North Atlantic (Breed et al. 2006, Jones et al. 2015). The United Kingdom (UK) represents a globally-important population centre for grey seals, encompassing approximately 38% of the world's population (SCOS 2017). Under Annex II of the European Union (EU) Habitats Directive (92/43/EEC 1992), the UK has a responsibility to maintain this species in "Favourable Conservation Status" (FCS). Grey seals exhibit delayed recruitment to the breeding population (females: 6 years, males: 10 years) (Harwood and Prime 1978), and first year mortality is high (up to 80%; (Hall et al. 2001)). Whilst the UK population appears to be stable or increasing (SCOS 2017), any disturbance to pups at sea may have ramifications for population dynamics that will only be manifested after a considerable time lag. With increasing anthropogenic activity in the marine environment (i.e. marine renewable energy installations, intensive vessel traffic and fisheries), there is growing interest in the at-sea distribution and foraging behaviour of this apex predator species in order to assess and mitigate potential population-level threats (Russell et al. 2013, 2015, 2017, Jones et al. 2015, 2017a).

Grey seals have a generalist diet that varies between the sexes and among geographic regions, comprised primarily of benthic and demersal prey species (Bowen and Harrison 1994, Beck et al. 2007, Gosch et al. 2014, Wilson and Hammond 2016). However, juveniles appear to feed at a lower trophic level than adults (Hanson et al. 2018). Pups must learn to forage alone because they are abandoned after a brief (15-21 days) suckling period (Pomeroy et al. 1999), and are therefore naïve when they leave the colony. Recent research has shown that the initial months of nutritional independence are of key importance for the development of foraging skills, such as benthic diving (Bennett et al. 2010, Carter et al. 2017; Chapter II). Moreover, pups exhibit sex-differences in the ontogeny of diving behaviour, which may be related to sex-specific prey preferences (Carter et al. 2017; Chapter II). These sex-differences are not equal among regions, suggesting the influence of extrinsic factors on sex-specific foraging strategies (Carter et al. 2017; Chapter II, Chapter III). However, the foraging habitat requirements of male and female pups remain unknown. There is therefore a need to evaluate the specific habitat features required by pups as they learn to forage.

We investigated the ontogeny of foraging habitat preference in grey seal pups during their first four months of nutritional independence after leaving the colony. We used Global Positioning System (GPS) location data collected from 29 recently-weaned pups, tagged at breeding sites in two geographically-distinct regions of the UK (West Wales and Northeast Scotland). We modelled the relationship between putative foraging locations (identified using a generalized hidden Markov model (HMM) in Chapter III) and candidate environmental predictor variables: seabed gradient, substrate type, water depth, distance from haulouts, and mean winter sea surface temperature (SST), using generalized additive mixed models (GAMMs). Foraging habitat preference was modelled under a use-availability design, relating habitat use to the availability of accessible resources in the environment (Manly et al. 2002). Importantly, we considered the influence of time (*days since leaving colony*) on preference for predictor variables to quantify ontogenetic changes in foraging resource selection. We also compared results between the sexes and geographic regions to investigate the existence of regional and sex-specific habitat requirements during this developmental phase. This represents the first assessment of grey seal pup habitat requirements at sea, which has important implications for the conservation management of this species.

4.2 Methods

4.2.1 Putative foraging locations

Grey seal pups (*n* = 29) were instrumented with Fastloc® GPS phone tags (SMRU Instrumentation, St. Andrews, UK) at five UK breeding sites in Northeast Scotland (2010) and West Wales (2009 and 2010) (Table 4.1). Pups were captured during the post-weaning fast, before leaving the natal colony. Devices were glued to the fur at the base of the skull (Carter et al. 2017; Chapter II, Chapter III). All capture and handling procedures were carried out under UK Home Office license #60/4009 in accordance with the Animals (Scientific Procedures) Act 1986. Devices recorded GPS location estimates, dive (time-depth) data, and haulout information, and transmitted the data via the Global System for Mobile communication (GSM) phone network (McConnell et al. 2004). Erroneous location estimates were identified and excluded using residual error threshold and number of satellites (Russell et al. 2015). Putative foraging behaviour was identified in Chapter III for these data using a generalized HMM, accounting for intrinsic (age, sex) and extrinsic (regional) variation in foraging movement patterns.

Table 4.1: Grey seal pup sample size by tagging site and year. *Tag deployment sites were assigned to one of two distinct geographic regions (W Wales and NE Scotland).*

		No. tagged seals		
Tag deployment site (year)	**Region**	**f**	**m**	**Total**
Bardsey (2009)	W Wales	1	0	1
The Skerries (2009)	W Wales	1	2	3
The Skerries (2010)	W Wales	4	1	5
Ramsey (2010)	W Wales	3	4	7
Muckle Green Holm (2010)	NE Scotland	3	3	6
Stroma (2010)	NE Scotland	5	2	7
	Total:	**17**	**12**	**29**

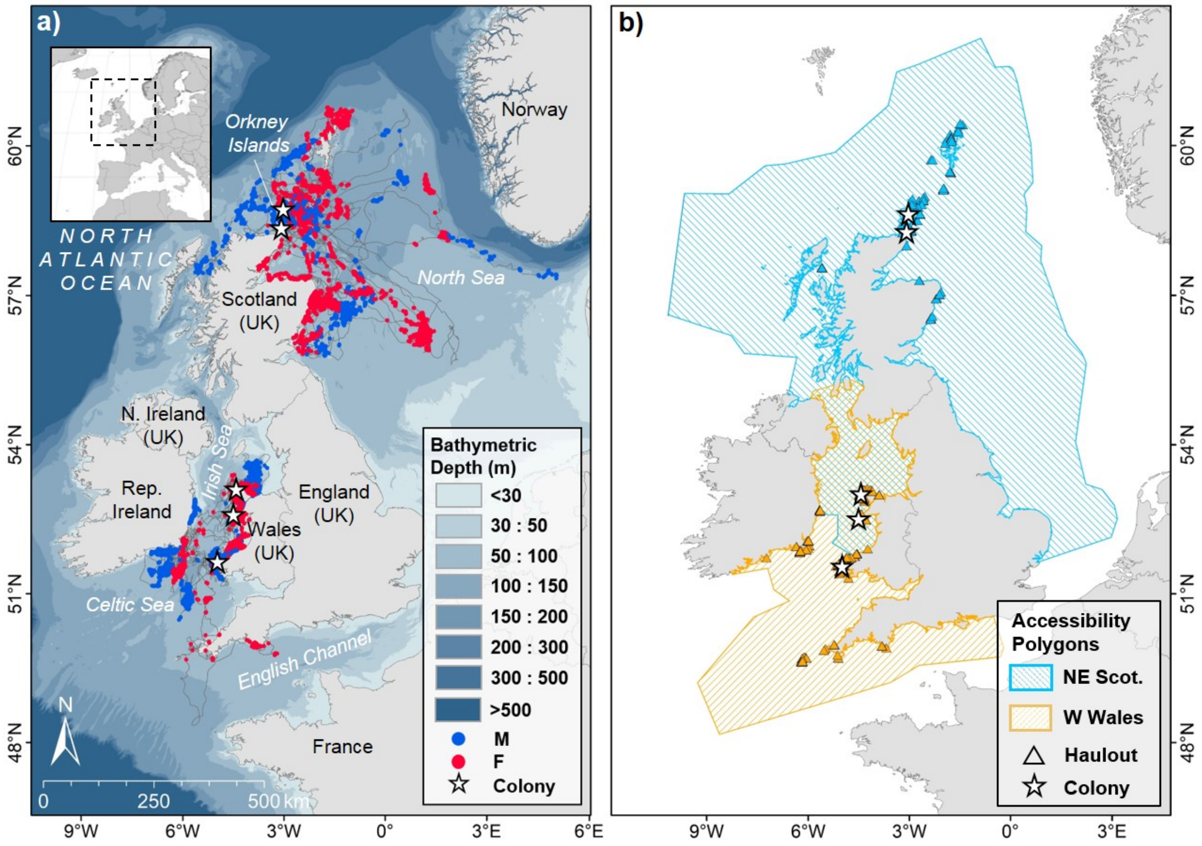

Figure 4.1: Pup foraging locations and accessibility polygons. *Map (a) shows putative foraging locations for male (blue) and female (red) pups. Pups were tagged on five UK colonies in NE Scotland and W Wales (North-South: Muckle Green Holm, Stroma, The Skerries, Bardsey, Ramsey). Map (b) shows the regional accessibility polygons, based on maximum foraging range, used as sampling areas for candidate environmental variables.*

We mapped the putative foraging locations (on a 2 h temporal resolution) (Fig. 4.1a), and the haulout sites used between foraging trips (Fig. 4.1b). Previous analysis showed regional differences in movement behaviour (Chapters II and III). Colonies were therefore aggregated into two distinct geographic regions (W Wales and NE Scotland). Since tag duration varied among individuals (from 34 to 337 days), the data were clipped to 120 days after leaving the colony to ensure a robust sample size from each regional dataset throughout the time series (Zuur et al. 2010), as in Chapters II and III.

4.2.2 Use-availability framework

(a) Accounting for accessibility

For central-place foragers, selection of foraging resources is mediated by distance (accessibility) from the central place (Matthiopoulos 2003). For example, grey seals must return to terrestrial haulout sites between foraging trips (McConnell et al. 1999), and thus we expect resource selection to decline with increasing distance. We must therefore control for the effect of accessibility on usage before inferences of preference can be made (Matthiopoulos 2003). We generated an accessibility polygon for each region based on the maximum geodesic distance (shortest path at sea without crossing land) between foraging locations and haulout sites (Russell et al. 2016). The maximum distance value for each region (NE Scotland: 670.6 km; W Wales: 266.4 km), was taken as the radius of the regional accessibility polygon, as a proxy for the maximum foraging range of that regional population. Polygon boundaries were defined by demarcating the areas accessible to pups from any of the haulout sites used during the time series, up to the maximum foraging range (without crossing land). The polygon boundaries were then clipped to account for the availability of environmental data (Fig. 4.1b). Any foraging locations that fell outside of the polygon boundaries (*n* = 676; 5.28%) were then excluded from the study. All maps were created in Esri ArcMap™ 10.4.

(b) Accounting for availability

To make statistically-robust inferences of animal habitat preference from presence-only telemetry data, usage (e.g. foraging locations) must be modelled alongside information on the availability of accessible resources (Manly et al. 2002). Preference is therefore calculated as the ratio of habitat use to availability (Aarts et al. 2008). To give an accurate representation of the available habitat accessible to the pups, each foraging point (presence) was matched to five control points (pseudo-absences) which were spaced randomly within the corresponding regional accessibility polygons (Koper and Manseau 2009, Bailey et al. 2014). These pseudo-absences were then weighted in the habitat models such that each set of five contributed the same as one presence.

(c) Predictor variables

Candidate predictor variables were selected based on possible biological relevance and data availability (Aarts et al. 2008). A list of data sources and calculation / extraction methods is presented in Table 4.2. Values were calculated or extracted for each presence and pseudo-absence. Firstly, we calculated distance to haulout (i.e. the combined geodesic distance from the previous and next haulout site to the presence / pseudo-absence point). Distance to haulout was included in all models to control for decreasing accessibility with increased distance (Matthiopoulos 2003). Secondly, we included bathymetric depth; for diving benthic or demersal predators, water depth is potentially a key factor limiting the suitability of foraging habitat (Aarts et al. 2008), as individuals must forage whilst diving within their physiological limits (Boyd 1997). Seabed gradient (slope) is an important predictor of foraging habitat in some marine predators (Bailey and Thompson 2010, Pirotta et al. 2011). For example, bottlenose dolphins (*Tursiops truncatus*) forage in steep gradient areas, and likely use the seabed topography as a physical barrier to herd prey (Hastie et al. 2004, Bailey and Thompson 2010). We included slope in the models to investigate the importance of seabed gradient for grey seal pup foraging areas. In the absence of detailed data on the distribution of potential prey species, we estimated the relative percentage fractions of seabed sediment type (sand, mud and gravel). Such data have been used in previous studies to characterise habitat preference in the UK for seals (McConnell et al. 1992b, Aarts et al. 2008, Jones et al. 2017b) and cetaceans (Bailey and Thompson 2010, Embling et al. 2010).

Table 4.2: Candidate predictor variables. *Data ranges for presences and pseudo-absences, (median values) and sources / calculation methods for the sampled availability areas.*

Var.	Unit	Range (Median)		Description	Data source / calculation method
		NE Scotland	**W Wales**		
Depth	m	-2498 : -1 (-91.2)	-253 : -1 (-68.5)	Bathymetric depth	Extracted from harmonised European Marine Observation and Data Network (EMODnet) Digital Terrain Model for European Waters at ~250 m^2 resolution http://www.emodnet-bathymetry.eu
Distance	km	1 : 2320 (711.1)	1 : 2828 (530.3)	Combined geodesic distance to pre and post haulout locations	Calculated with R package "gdsitance" (van Etten 2015)
% Mud	%	0 : 99 (4.9)	0 : 99.2 (4.1)	Predicted mud / gravel / sand fraction of sediment at seabed	Fractions extracted from seabed grab and trawl samples from British Geological Survey (BGS; http://www.bgs.ac.uk) and Geological Survey of Ireland (GSI; https://www.gsi.ie) databases and kriged to 1 km^2 resolution rasters in Esri ArcMap™ 10.4. Rock areas were extracted from the from EMODnet broad-scale seabed habitat map for Europe (EUSeaMap; http://www.emodnet.eu/seabed-habitats) and areas underlying rock were set to 0
% Gravel	%	0 : 87.2 (4.2)	0 : 88.6 (12.9)		
% Sand	%	0 : 99.5 (77.8)	0 : 99.4 (70.3)		
Winter SST Lag1	°C	3.2 : 10.2 (7.2)	3.2 : 11.3 (8.4)	Mean sea surface temperature of Jan-Mar prior to pup data	Averaged from daily mean predictions, extracted from Met Office NW Shelf Re-Analysis FOAM AMM7 model ~7km^2 resolution http://marine.copernicus.eu
Slope	°	0 : 40 (0.2)	0 : 12.5 (0.1)	Seabed gradient	Calculated from bathymetry data using "terrain" function in R package "raster" (Hijmans 2016)

Previous studies have indicated the importance of sandeels (*Ammodytes spp.*), particularly lesser sandeels (*A. marinus*), in the diet of marine predators in the North Sea, including seals (Hammond et al. 1994), porpoises (MacLeod et al. 2007), and breeding seabirds (Furness and Tasker 2000, Carroll et al. 2017). Carroll et al. (2017) found an inverse relationship between lagged mean winter sea surface temperature (previous winter; Lag1) and lesser sandeel spawning stock biomass (SSB) in the North Sea. This suggests that adult sandeels overwintering in seabed sediments should be more abundant in areas that experienced a lower mean SST during the previous winter (Carroll et al. 2017). Overwintering sandeels may represent an important prey resource for grey seal pups in the UK (especially in Northeast Scotland) during their initial months of nutritional independence. To investigate this, we calculated the mean winter (January – March) SST values for all locations (presences and pseudo-absences). As tags were deployed late in the year (W Wales: October – November; NE Scotland: December), we took SST values from January – March of the deployment year, corresponding to the previous winter. For maps of the distribution of environmental covariates within the accessibility polygons, see Appendix A4.1.

4.2.3 Habitat preference modelling

(a) Model formulation

GAMMs were fitted using the package "mgcv" (Wood 2006) in R version 3.3.2 (R Core Team 2016b). The response variable was binary presence / pseudo-absence. Data were therefore modelled with a binomial error structure with logit-link function. Individual was included as a random effect in all models to control for multiple observations per pup. Each smoothed predictor variable was fitted with a shrinkage spline, such that terms can be penalised to zero, making no contribution to the model, and could be subsequently eliminated during model selection (Wood 2006). To avoid over-fitting of smooth functions to the data, for each term biological rationale was used to restrict the maximum number of knots (depth = 6; distance = 6; substrate = 4; slope = 4; SST = 3) (Wood 2006). Variance Inflation Factors (VIFs) were calculated for all variables using the "car" package in R (Fox and Weisberg 2011), and correlated variables (VIF > 3) were not modelled together (Zuur et al. 2010). A maximum of two substrate variables were retained during model selection to further limit issues of collinearity (Aarts et al. 2008).

(b) Model selection protocol

We modelled data from each region separately, as they represent distinct ecosystems, and, based on the findings of Chapters II and III, there was no justification for an assumption that preference will be the same in different regions. We also expected *a priori* that male and female pups may have different habitat preferences based on the findings of Chapters II and III. Therefore, model selection was initially carried out separately for each sex-region group. However, initial model selection resulted in the same combination of predictor variables for male and female pups from NE Scotland, with extremely similar preference relationships (see Appendix A4.2). Both sexes were subsequently modelled together for NE Scotland to maximise analytical power. Forwards model selection by minimising the Akaike information criterion (AIC) score, was performed in rounds by step-wise addition of candidate predictor variables. In each round, the most important variable (largest reduction in AIC score) was retained in the model. The threshold for covariate inclusion was ΔAIC < 2 (Burnham and Anderson 2002). The resulting models were trained using a random subset of approximately 75% of individuals for each group. Following Aarts et al. (2008), we then used cross-validation for final model selection by fitting the GAMMs to the remaining individuals in the group dataset and comparing the model fit (negative log-likelihood / number of observations) with the addition of each selected predictor variable, allowing us to pick the most parsimonious model for each group (see Appendix A4.3).

The best model was then extended in a further round of model selection by offering a temporal covariate (*time since leaving colony*) in a tensor product interaction smooth with each predictor variable in turn to investigate changes in habitat preference with age. As natal age was not known for all pups, *time since leaving colony* was used instead. Models were then cross-validated as described above. The final (minimal adequate) model for each group was further validated by visual inspection of residuals to check for spatial and temporal autocorrelation. Population mean responses were predicted for each variable in turn using the “predict” function in “mgcv” (Wood 2006), keeping all other variables constant at the median value from the presence data. Model-predicted covariate plots are presented on the scale of the link function, as transformation to the response scale is not appropriate for use-availability designs (Boyce 2006).

4.3 Results

Foraging habitat preference of grey seal pups showed regional differences, with pups in NE Scotland selecting shallow, sandy areas of low lagged mean winter SST, whilst pups in W Wales exhibited sex-specific foraging strategies, with females showing stronger preference for shallow areas than males. The results of model selection are shown in Table 4.3.

Table 4.3: Model selection results. *Significant variables (ΔAIC < 2) are shown, ranked in order of importance. Smooths are given with the number of effective degrees of freedom in parentheses. “te” indicates a tensor product smooth. ΔAIC is the change in AIC score caused by the addition of the variable to the model. Interactions with Time (days since leaving colony) are denoted with “:”. Variables shown with “*” were later dropped during cross-validation.*

		NE Scotland (M + F)		**W Wales (M)**		**W Wales (F)**	
	Rank	**Smooth (e.d.f.)**	**ΔAIC**	**Smooth (e.d.f.)**	**ΔAIC**	**Smooth (e.d.f.)**	**ΔAIC**
Main Effects	1	s(Dist, 2.98)	-2562.87	s(Dist, 2.76)	-2036.85	s(Dist, 3.11)	-2311.9
	2	s(SST, 2.54)	-192.81	s(%Mud, 2.91)	-128.4	s(Depth, 3.89)	-141.09
	3	s(%Sand, 1.71)	-11.09	s(%Gravel, 2.87)	-6.29	s(%Sand, 2.71)	-28.34
	4	s(Depth, 1.01)	-8.36	s(Depth, 3.56)	-2.21	s(%Gravel, 1.63)*	-8.88
Time Effect	1	te(SST:Time, 8.08)	-111.56	te(%Mud:Time, 12.39)	-44.78	te(Dist:Time, 11.47)	-125.31
	2	te(Dist:Time, 11.85)	-18.31			te(Depth:Time, 12.09)	-8.81
	3	te(Depth:Time, 8.91)	-13.93				

4.3.1 NE Scotland

Grey seal pups tagged in NE Scotland foraged primarily around Orkney and Shetland, and within the northwest North Sea (Fig. 4.1a). The best model of foraging habitat preference included distance to haulout, lagged mean winter SST (previous winter), % sand and water depth, but did not include slope or % gravel (Table 4.3). Percentage mud was collinear with depth (VIF = 3.4), and so was excluded from model selection once depth was selected in the model. Cross-validation did not result in exclusion of any selected variables (Appendix A4.3). Preference for SST, distance and water depth changed as pups got older, showing an interaction with *time since leaving colony* (Table 4.3). Of the candidate predictor variables, distance to haulout was the most important (Table 4.3). As expected, preference declined with increasing distance, with pups selecting foraging areas up to 200 km from haulout sites. However, this relationship changed over time, and the distance associated with selected foraging areas decreased in the third and fourth months after leaving the colony, when strongest preference was shown for areas close to haulouts (< 50 km) (Fig. 4.2a).

Lagged mean winter SST was the second most important predictor variable (Table 4.3). Preference declined with increasing mean winter SST during the first three months after leaving the colony, with strongest preference shown for areas that experienced a mean winter SST of between 5 - 7.5^{0}C (Fig. 4.2b). However, this trend disappeared in the fourth month, as preference switched to areas that had experienced warmer mean winter SST (7.5 - 9^{0}C). Percentage sand was also selected in the model, but there was no evidence for a change in this relationship over time (Table 4.3). Preference increased monotonically with increasing sand content in seabed sediments (Fig. 4.2c). Finally, water depth was selected in the model (Table 4.3). Pups showed strongest preference for water < 40 m deep in the first two months, but also foraged in areas > 160 m deep (Fig. 4.2d). However, in the third and fourth months, foraging habitat preference was focussed in areas of intermediate

(40 – 80 m) depth, and pups did not select foraging areas in deep or shallow water. No sex difference was detected in the habitat preference of grey seal pups in NE Scotland (see Appendix A4.2).

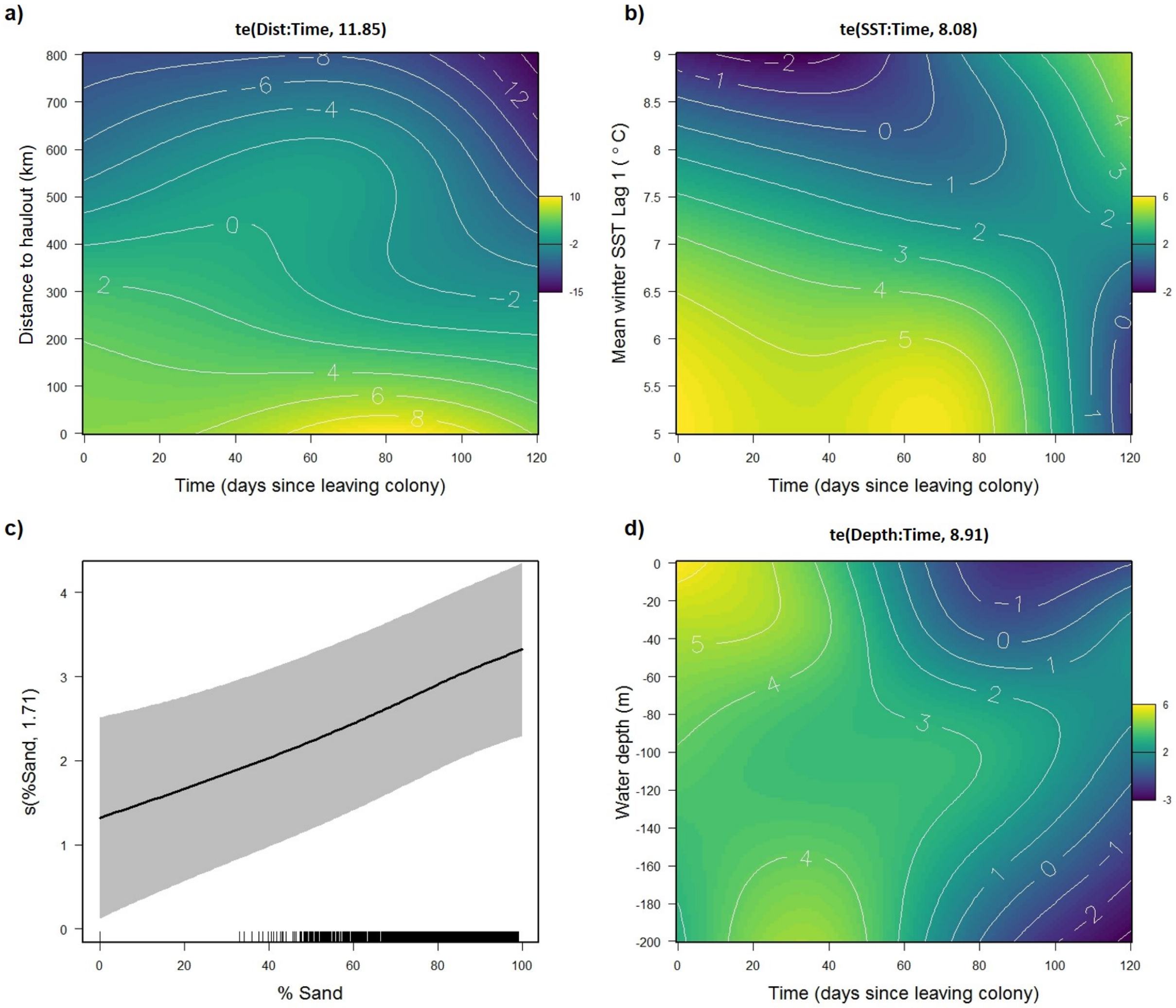

Figure 4.2: NE Scotland pup forging habitat preference. *Plots show population mean effect of modelled covariates on pup foraging habitat preference, on the scale of the link function. Contour plots (a, b and d) show the interaction between the main covariate and time since leaving colony. Estimates of uncertainty for these plots are presented in Appendix A4.4. 95% confidence intervals around model predictions are indicated in (c) by a shaded area, rugs show the distribution of presence data. Number of effective degrees of freedom for each smooth are shown in parentheses.*

4.3.2 W Wales

Pups tagged in W Wales foraged primarily along the coast of Wales and southeast Ireland, and within the Celtic Sea (Fig. 4.1a). Male and female pups displayed sex-specific foraging habitat preference from the beginning of the time series.

(a) Males

The best model of foraging habitat preference for male pups in W Wales included distance to haulout, % mud, % gravel, and water depth, but did not include slope (Table 4.3). Cross-validation did not result in exclusion of any selected variables (Appendix A4.3). Lagged mean winter SST was collinear with depth (VIF = 3.8), and so was excluded from model selection once depth was selected. Similarly, % sand was excluded from model selection once % mud and % gravel were selected in the model. Only percentage mud of preferred foraging areas changed as pups got older, showing an interaction with *time since leaving colony* (Table 4.3).

As with Scottish pups, distance to haulout was the most important of the candidate predictor variables (Table 4.3). As expected, preference declined monotonically with increasing distance from haulouts, and strongest preference was shown for areas < 25 km from haulout sites (Fig. 4.3a). Percentage mud content in seabed substrate was the second most important variable (Table 4.3). At the beginning of the time series, preference was strongest for areas of 40 - 60% mud (Fig. 4.3b). However, this declined in the third and fourth months, and at the end of the time series preference was strongest for areas of < 20% mud. Percentage gravel content was also selected in the model but did not change with pup age (Table 4.3). Strongest preference was shown for areas of 0% gravel, and 30 - 50% gravel (Fig. 4.3c). Preference declined with gravel content > 50%, but confidence intervals also increased past 60% due to a relative sparsity of high gravel content areas

(Appendix A4.1). The least important retained variable was water depth (Table 4.3). Male pups showed strongest preference for shallow areas (< 50 m), but also showed a peak in preference at ~110 m (Fig. 4.3d). Preference declined at depths of > 120 m, but 95% confidence intervals also increased due to a relative sparsity of deep areas in the sampling polygon (Appendix A4.1).

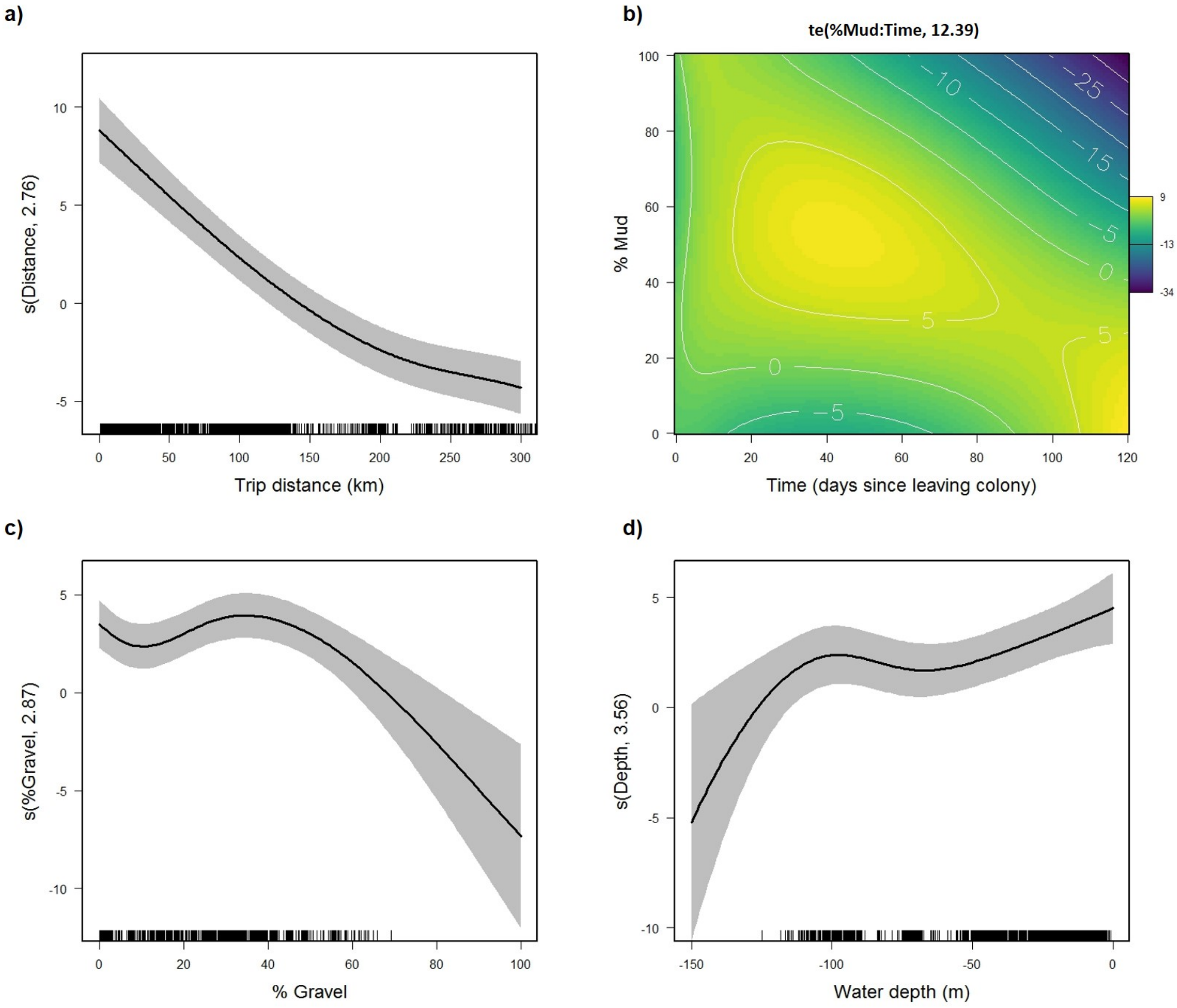

Figure 4.3: Welsh male pup foraging habitat preference. *Plots show population mean effect of modelled covariates on pup foraging habitat preference, on the scale of the link function. 95% confidence intervals around model predictions (a, c-d) are indicated by a shaded area, rugs show the distribution of presence data. Contour plot (b) shows the interaction between % mud and time since leaving colony. Estimates of uncertainty for this plot are presented in Appendix A4.4. Number of effective degrees of freedom for each smooth are shown in parentheses.*

(b) Females

The best model of foraging habitat preference of female pups in W Wales included distance to haulout, water depth and % sand, but did not include slope, % mud or % gravel (Table 4.3). Lagged mean winter SST was collinear with depth (VIF = 4.2) and so was excluded from model selection once depth was selected in the model. Distance to haulout and water depth showed an interaction with *time since leaving colony* (Table 4.3). Percentage gravel was selected in initial model selection, but subsequent cross-validation favoured a more parsimonious model (Appendix 4.3), and so it was dropped from the final model.

Of the candidate predictor variables, distance to haulout was the most important (Table 4.3). Foraging habitat preference declined steeply with increasing distance from haulout > 10 km at the beginning of the time series (Fig. 4.4a). Preference remained strongest for areas close to haulouts throughout the time series but declined after the first month. Female pups showed weak preference for foraging areas up to 75 km from the haulout from the second month onwards (Fig. 4.4a). Water depth was the second most important predictor variable (Table 4.3). Within the first 10 days after leaving the colony, female pups showed strong preference for areas < 40 m deep (Fig. 4.4b). Preference for shallow areas (< 20 m) remained strong throughout the time series, but females also developed preference for areas of 60 – 80 m depth in the second month, which continued to the end of the time series (Fig. 4.4b). Preference declined steeply beyond 90 m water depth. The least important variable was percentage sand content in the sediment (Table 4.3). Strongest preference was shown for areas of 0% sand, and areas of > 80% sand, but 95% confidence intervals remained wide throughout the range of the predictor variable, suggesting a large amount of variability (Fig. 4.4c).

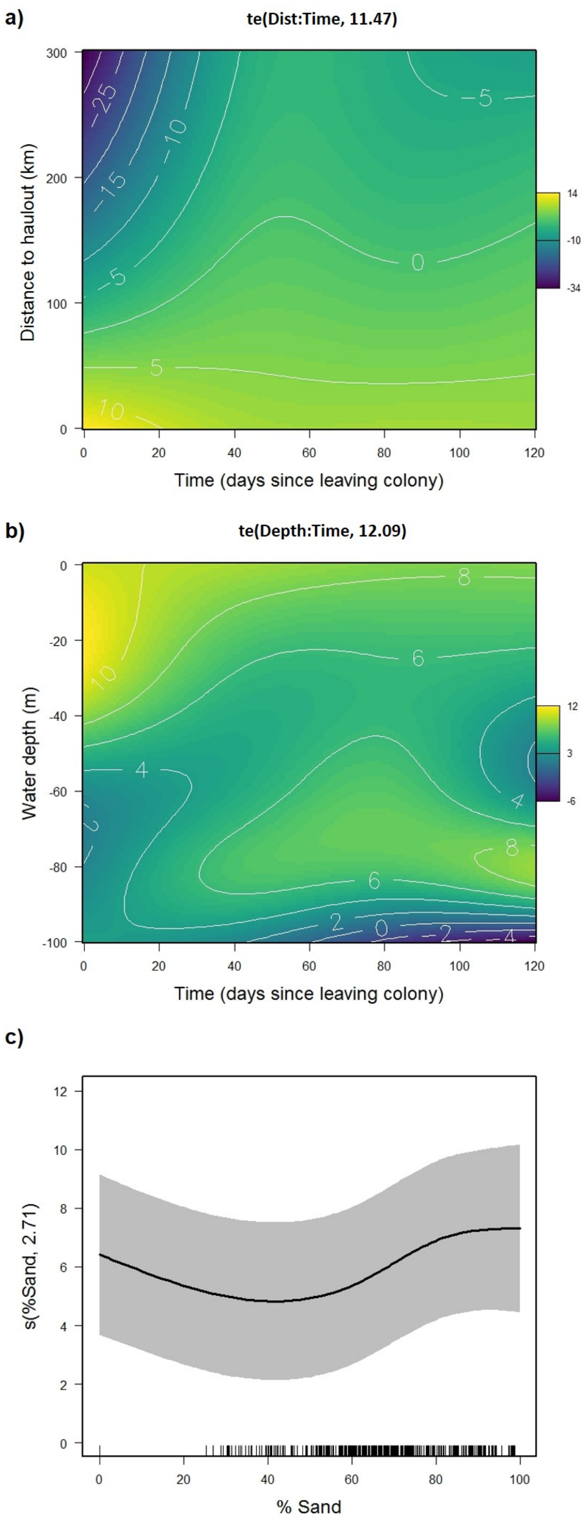

Figure 4.4: Welsh female pup foraging habitat preference. *Plots show the population mean effect of modelled covariates on pup foraging habitat preference, on the scale of the link function. Contour plots (a-b) show the interaction between covariates and time since leaving colony. Estimates of uncertainty for these plots are presented in Appendix A4.4. For % sand (c), 95% confidence intervals around model predictions are indicated by a shaded area, rugs show the distribution of presence data. Number of effective degrees of freedom for each smooth are shown in parentheses.*

For all sex-region groups, the change in AIC score associated with the addition of each predictor variable is shown in Appendix A4.3, along with results of cross-validation. Estimates of uncertainty (95% confidence intervals) surrounding model predictions for temporal interactions are presented in Appendix A4.4. Model residual semivariance and autocorrelation functions (ACFs) were assessed, and no evidence of autocorrelation issues was detected (semivariance < 0.1, ACF < 0.1).

4.4 Discussion

We have presented the first assessment of foraging habitat preference in grey seal pups by combining putative foraging locations from hidden Markov model output with environmental data in a use-availability framework. Pups exhibited clear regional differences in foraging habitat selection during their first four months of nutritional independence at sea. Preference changed over time as pups got older, potentially reflecting ontogenetic changes in experience and physiological development, and seasonal shifts in prey distribution. Individuals in NE Scotland showed highest preference for sandy areas that had low lagged mean winter SST values, consistent with areas of high sandeel abundance. Pups in W Wales displayed different habitat preference to pups in Scotland, and there was clear evidence of sex-specific resource selection; females foraged in shallower areas than males.

4.4.1 Implications for foraging ecology

(a) NE Scotland

The results of habitat preference analysis in NE Scotland presented here suggest that grey seal pups may select foraging areas associated with high abundance of overwintering sandeels. Lesser sandeel recruitment is negatively correlated with winter SST, since climate influences the distribution and abundance of zooplankton, especially calanoid copepods, on which they depend (Fromentin and Planque 1996, Arnott and Ruxton 2002, van Deur et al. 2009). Carroll et al. (2017) showed that lesser sandeel SSB increases with decreasing lagged mean winter SST (previous winter) in the North Sea, with highest SSB in areas that recorded mean temperatures below 6.5^{0}C. Pups preferentially foraged in areas of low (5 – 6.5^{0}C) lagged mean winter SST throughout the first three months after leaving the colony. Adult lesser sandeels overwinter buried in the sediment, but emerge to spawn in mid-December before burrowing back into the sediment, and do not emerge again until spring to feed on the planktonic bloom (Winslade 1974). Pups tagged in NE Scotland departed the natal colony throughout mid- to late-December, coinciding with sandeel spawning and overwintering. Moreover, analysis of lesser sandeel habitat preference has revealed that they primarily burrow in sandy substrate, avoiding finer muddy sediment (Holland et al. 2005). Our results show that grey seals preferentially forage in sandy areas in NE Scotland (Fig. 4.4c), and this was the only seabed sediment variable selected in the final model, consistent with targeting this prey type.

A recent analysis of grey seal faecal samples collected in Scotland found that sandeels accounted for 75 - 97% of the fish consumed by weight in mainland Northeast Scotland, and 18 - 35% in Orkney and the Shetland Islands (Wilson and Hammond 2016). However, faecal samples do not provide information on the age of the seal that produced them. Due to the logistical and practical constraints associated with obtaining faecal or gut content samples from young seals, there has been no assessment of weaned pup diet. However, recent stable isotope analysis of grey seal tooth material deposited throughout juvenile and adult life has suggested that immature seals (< 5 years old) in the North Sea forage on low trophic level benthic prey fish (Hanson et al. 2018). In particular, the study found an ontogenetic shift in the trophic level of seal prey, suggesting that younger animals are more reliant on low trophic level benthic species, such as sandeels, than adults (Hanson et al. 2018). Indeed, 2010 – 2011 was a particularly productive period for sandeels throughout the North Sea, with the highest SSB levels recorded since 1998 (ICES 2013). Our data are therefore consistent with sandeels forming a vital part of the diet of grey seal pups in NE Scotland.

Temporal changes in foraging habitat selection may be related to pups learning the location of productive foraging grounds. Pups showed an increase in preference for foraging areas close to haulouts (< 50 km) in the third month after leaving the colony (Fig. 4.2a), which we attribute to an increase in foraging experience. Previous work has shown that pup foraging trip duration also decreases during this time (Carter et al. 2017; Chapter II), and travelling behaviour becomes faster and more directed (Chapter III). We suggest that such changes are driven by an ontogenetic shift in foraging behaviour as pups progress from exploring their environment to a more optimal search strategy. Hanson et al. (2018) showed that sexually immature grey seals in the North Sea forage on benthic prey, closer to shore than adults. Our results suggest that this inshore foraging behaviour develops in pups within the first four months at sea.

Inter-individual variation in early-life behaviour may also explain some of the patterns of habitat preference. In the first two months after leaving the colony, pups showed two peaks in water depth preference, one in shallower water (< 80 m) and another in deeper water (~150 m). We suggest that this pattern arises as some pups remained closer to shore during their exploratory phase, whilst others performed prolonged offshore exploratory movements into deeper water. In the third and fourth months, preference was focussed on a narrower depth band of 40 to 80 m, with pups avoiding shallow and deep areas (Fig. 4.2d). Previous analysis showed that benthic diving is also concentrated in this depth band from the third month (Carter et al. 2017; Chapter II), which suggests that pups begin to select foraging habitat in which they can maximise their time at the seabed. Such behavioural change may reflect an increase in both their knowledge of foraging grounds and their physiological diving capacity (Chapter III, Noren et al. 2005).

In addition to ontogeny, temporal variation in pup habitat preference may also be related to seasonal phenomena. For example, we found a switch in foraging habitat selection during the fourth month after leaving the colony, whereby pups foraged preferentially in warmer (7.5 - 9^{0}C) lagged mean winter SST areas. This change in foraging habitat preference coincides with the onset of spring. The change in pup behaviour could be driven by the emergence and displacement of sandeels from the sediment, or the appearance of an alternative seasonally-abundant prey resource, such as salmon smolt (Hvidsten et al. 1998).

(b) W Wales

Pups in W Wales displayed evidence of sex differences in the ontogeny of foraging resource selection. Females showed stronger preference for foraging in shallow areas (< 40 m deep) than males. This supports previous findings that female pups in this region dive in shallower water than males (Carter et al. 2017; Chapter II). However, our results also show that females developed a bimodal relationship with water depth in the third month, displaying preference for deeper areas (60 – 90 m) as well as shallow areas. This may be driven by the existence inter-individual variation in dispersal strategies among female pups. Whilst most male pups dispersed from the natal colonies soon after first entering the water, some females remained in shallow coastal areas adjacent to the colony throughout the time series, and others dispersed throughout the Celtic and Irish Seas in the third and fourth months, into deeper water (Carter et al. 2017; Chapter II). This trend is also manifested in the distance from haulout of foraging habitat selection. Females initially selected foraging habitat within 25 km of the haulout, but preference for areas up to 75 km increased at around 40 days after leaving the colony, whilst males showed no temporal relationship. Together, these findings suggest that coastal foraging habitat may be particularly important for some female pups in W Wales, especially during the initial two months after leaving the colony. These sex differences in early-life foraging resource selection provide further evidence that male and female grey seals develop different foraging strategies before the onset of sexual size dimorphism in W Wales. The lack of sex difference in Scottish pups may be related to regional differences in the availability of different depth ranges, habitats and prey types. For example, the Celtic and Irish Seas feature a more complex coastline with many shallow bays and a deep-water channel within 50 km of the coast, offering a greater diversity of habitat types (EMODnet Seabed Habitats Consortium 2016). However, seabed sediment composition and terrain is more homogeneous in the North Sea, and depth generally increases monotonically with distance from shore (Appendix A4.1). The greater diversity of habitat features accessible to pups in the Celtic and Irish Seas may therefore offer more opportunities for sexual segregation in foraging habitat preference.

Preference for specific seabed substrate composition was less obvious in Welsh pups than in the Scottish dataset. This suggests that Welsh pups select a greater diversity of foraging habitats, and may have a broader, more generalist diet, or that their prey is less-associated with a particular sediment type. Again, this may be driven by the greater diversity of accessible habitat types. Moreover, inter-annual variation in resource distribution may impact the foraging habitat preference of pups. Indeed, the fact that the Welsh dataset spans two consecutive cohorts of pups (2009 and 2010), whilst the devices were only deployed in NE Scotland in 2010, could be a factor affecting the regional difference in strength of the habitat preference signal. There were not sufficient data to test for a year effect by separating the dataset. Further deployments of tracking devices are recommended in both regions to investigate inter-annual variation in pup foraging resource selection.

4.4.2 Priorities for future work

Lesser sandeels are an important prey resource for many marine predator species in the North Sea, with established links between low sandeel stocks and the decline of seabird populations (Furness and Tasker 2000, Rindorf et al. 2000, Frederiksen et al. 2004). Stocks fluctuate annually in relation to climatic variation (Arnott and Ruxton 2002), but fishing pressure also has a large influence on the abundance of sandeels, with cascading effects on marine predators (Furness and Tasker 2000, Carroll et al. 2017). Relatively high SSB was recorded during this study timeframe (ICES 2013), therefore the foraging habitat preference of NE Scotland pups presented here may not translate across years. Given the difficulties associated with obtaining dietary information from young seals, habitat preference studies such as this represent the best current option for inference of prey resource selection. However, the application of such analyses is ultimately limited by the availability of telemetry data. Further data collection of pup movements in the North Sea across multiple years is recommended to determine the extent to which pup behaviour may be related to sandeel abundance, and elucidate the consequences of low sandeel SSB, due to climate change or increased fisheries pressure, for pup behaviour and survival probability.

Comparatively little is known about the diet of grey seals in the Celtic and Irish Seas compared to other regions of the UK. This lack of baseline information, coupled with high levels of variation in the data from pups in W Wales, meant that inferring likely prey species was problematic. Studies of grey seal diet in the Welsh population would be extremely helpful to understand the relationship between habitat use and foraging resource selection. Furthermore, there is evidence of high spatial overlap between the foraging areas of grey seals in the Celtic and Irish Seas and passive (net and line) fisheries (Cronin et al. 2016). Dietary analyses would improve our understanding of the extent and consequences of competition between grey seals and fisheries in the region, and aid the design of effective conservation management.

4.4.3 Conclusions

As the footprint of human activity on the marine environment continues to grow, so too will associated negative effects on biodiversity (McCauley et al. 2015). Among the species most immediately and obviously affected by anthropogenic habitat modification are large, highly-mobile marine predators, with cascading effects in underlying tropic systems (Baum and Worm 2009, Estes et al. 2011). Designing effective mitigation will depend upon a sound understanding of the factors affecting predator foraging ecology (Embling et al. 2010, Reisinger et al. 2018). For grey seals, the months following departure from the natal colony represent perhaps the most vulnerable time in their life as they learn to forage (Bennett et al. 2010, Carter et al. 2017; Chapter II), yet few studies have addressed their early-life behaviour at sea. Our work suggests that overwintering sandeels may be a particularly important prey resource for pups in NE Scotland, and that sex-specific foraging habitat requirements are mediated by regional extrinsic factors such as water depth. Our results highlight the importance of considering regional and intrinsic (sex, age) sources of variation in habitat preference, and therefore in conservation management. Furthermore, we have demonstrated how robust statistical inference of behaviour from hidden Markov models can be combined with use-availability habitat models to investigate resource selection in the context of foraging. A natural continuation of this work would be to examine inter-annual variability in foraging habitat preference, which requires further data collection over multiple years in both regions.

Chapter V

Conservation and research priorities for grey seal pups at sea

5.1 Introduction

The UK is a globally important area for grey seals (*Halichoerus grypus*), with approximately 38% of the world population (SCOS 2017). The species is protected under the Conservation of Seals Act 1970 (England and Wales), the Marine (Scotland) Act 2010, and the Wildlife Order 1985 (Northern Ireland). Furthermore, grey seals are listed on Annex II of the European Habitats Directive (92/43/EEC). As such, the UK has an obligation to maintain grey seal populations in favourable conservation status (FCS). Seals are protected on haulout sites and breeding beaches in the UK by the designation of Special Areas of Conservation (SACs). Overall, grey seal numbers have been increasing steadily over the past 60 years since survey effort began, with regional nuances in population trajectories (SCOS 2017). However, in recent years, conservation concerns for grey seals have extended to the offshore environment, as increased fishing activity, offshore construction and habitat degradation mean that human impacts to seal foraging grounds are increasingly likely. There has been growing research interest in the behaviour of seals at sea, and the identification of important offshore habitat to assess and mitigate the impacts of anthropogenic activity (Russell et al. 2013, 2014, Jones et al. 2015, Hastie et al. 2016).

The vast majority of research into grey seal foraging ecology and habitat use offshore has focussed on adults of reproductive age. Therefore, conservation management decisions are frequently based on our understanding of adult behaviour (SCOS 2017). However, grey seal pups are abandoned on the colony after a brief suckling period and must learn to forage alone without the guidance of their parents. The movements and behaviour of naïve pups during the initial months of independence at sea are therefore unlikely to represent those of adults. Important habitat features for pups as they learn to be effective foragers are unknown. First-year survival probability is naturally low, and starvation is a major cause of mortality (Baker et al. 1998). However, ensuring that survival probability remains stable is critical for sustaining grey seal populations in FCS (Harwood and Prime 1978). Identifying and mitigating potential threats to grey seal pups during this vulnerable life stage should therefore be a conservation priority. Given that grey seals are slow to reach sexual maturity (females: 6 years; males: 10 years) (Harwood and Prime 1978), any population consequences of impacts to pups will only be manifested after a considerable time lag. This chapter presents the findings of a detailed study into the at-sea behaviour of grey seal pups born on colonies in two distinct regions of the UK; (1) north & east Scotland and (2) west Wales. In light of the key findings, a number of issues relating to conservation and priorities for future research are raised which should be considered by managers to mitigate impacts on grey seal pups.

5.2 Summary of grey seal tag data

Satellite tracking tags were deployed on 52 recently-weaned pups at six colonies in the UK between 2001 and 2010 (Table 5.1). Two different device types were used; earlier deployments (Isle of May, 2001-2002) were ARGOS Satellite Relay Data Loggers (SRDLs), and all other deployments (2009 - 2010) were GPS-GSM phone tags. Both device types collected and transmitted location and dive data (depth and duration), but technological advances meant that the newer GPS-GSM tags had a much higher transmission frequency (Table 5.1). Data from the SRDL tags were therefore used to characterise grey seal pup trip behaviour, but could not be used for any other analysis. Colonies were grouped into two regions based on the geographical extent of the pups' movements (North Sea and Celtic and Irish Seas). Previous research on young grey seals has shown that the first four months after leaving the natal colony are likely critical for the development of effective behavioural strategies, during which time they are particularly vulnerable to disturbance (Bennett et al. 2010, Breed et al. 2011a). Therefore, data were restricted to the first four months after leaving the colony. Pup tracks are presented in Figure 5.1.

Table 5.1: Device deployment summary information. *Tagged pup sample sizes by deployment site and year. Colonies were assigned to two geographic regions; NS = North Sea, CIS = Celtic and Irish Seas.*

			No. tagged seals			
Deployment site (year)	**Region**	**Device type**	**f**	**m**	**Total**	**Mean no. locations day^{-1} ± SD**
Isle of May (2001)	NS	SRDL	5	6	11	4.5 ± 2.3
Isle of May (2002)	NS	SRDL	5	5	10	5.2 ± 1.7
Bardsey (2009)	CIS	GPS-GSM	2	0	2	35.5 ± 5.4
The Skerries (2009)	CIS	GPS-GSM	1	2	3	33.1 ± 5.7
The Skerries (2010)	CIS	GPS-GSM	4	1	5	57.2 ± 13.8
Ramsey (2010)	CIS	GPS-GSM	3	4	7	37.3 ± 9.7
Muckle Green Holm (2010)	NS	GPS-GSM	4	3	7	22.5 ± 9.6
Stroma (2010)	NS	GPS-GSM	5	2	7	24.4 ± 4
		Total:	**29**	**23**	**52**	

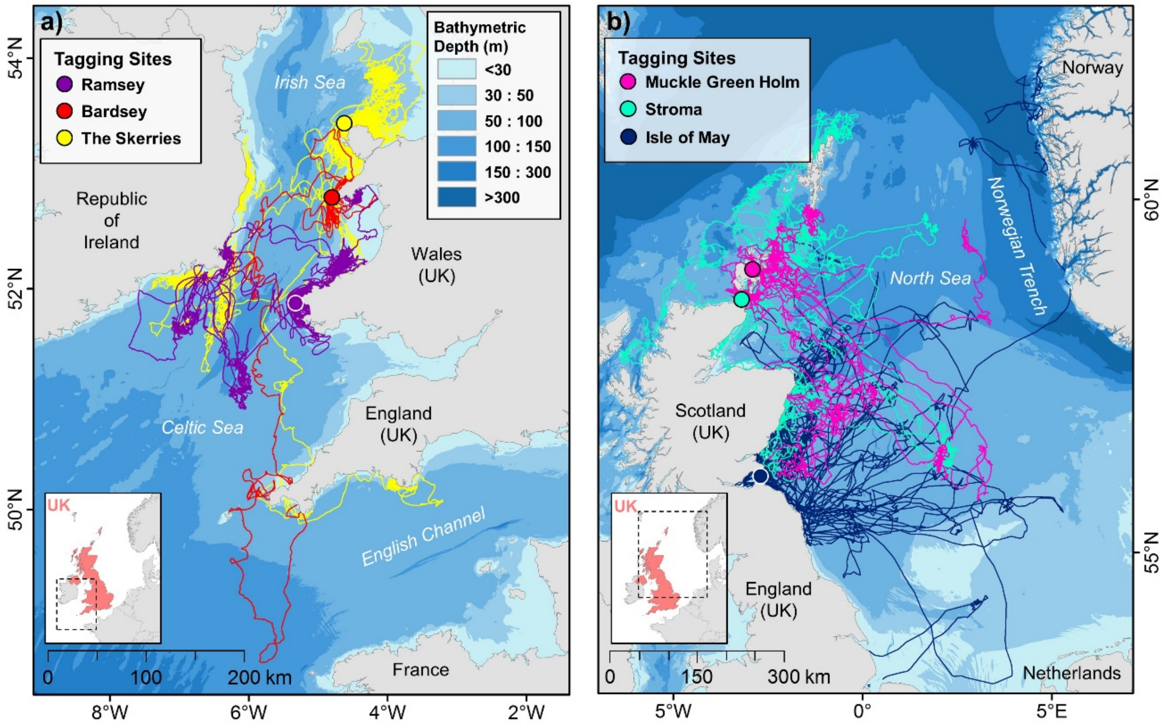

Figure 5.1: Pup tagging sites and trips at sea. *Pups (n=52) were tagged at six colonies in the United Kingdom (UK). Colonies were assigned to one of two geographic regions; (a) Celtic and Irish Seas (CIS), and (b) North Sea (NS). Tracks show pup trips during the initial four months after leaving the colony.*

5.3 Summary of key findings

Early-life movements of pups were generally characterised by an initial exploratory phase, followed by development of adult-like foraging trip behaviour, commuting between favoured haulout sites and known foraging areas (Fig. 5.2). The duration and spatial extent of the exploratory phase varied among individuals. Trip duration was significantly longer for pups tagged in Scotland, with some animals remaining offshore for up to 60 days after leaving the colony without hauling out. Whilst some pups tagged in Wales also performed longer trips immediately after leaving the colony, they generally did not exceed 18 days, and some individuals never travelled more than 30 km from the natal colony throughout the initial four months. In Wales, pups generally dispersed along the west coast of Wales, with some crossing the Irish Sea to the southeast coast of Ireland (Fig. 5.1a). Pups that crossed to Ireland made repeated trips into the Celtic Sea, whilst pups that stayed in Wales generally remained more coastal. Two individuals travelled south to the south coast of England. In Scotland, pups dispersed along the east coast of Scotland and northern England, but many travelled up to 300 km from shore into the centre of the North Sea on their initial exploratory phase (Fig. 5.1b). One pup from the Isle of May crossed the North Sea to Norway.

No significant differences in trip duration were detected between the sexes, but male pups in the Celtic and Irish Seas travelled significantly further on their trips to sea than females (Fig. 5.3a). Behavioural analysis of the tracks revealed that females spent longer in foraging mode than males whilst at sea (Fig. 5.3b). A sex difference was also reflected in the diving behaviour of pups, with males diving deeper, in deeper water. There was no sex difference in dive duration. As females dived to shallower depths, they achieved a larger proportion of the dive duration in the bottom phase (at foraging depth). This suggests that sex-specific foraging strategies emerge as early as nutritional independence in grey seals. It is possible that females target more predictable but lower-yield prey items in shallower water, closer to the coast, and thus have to forage for longer. Males may adopt a riskier foraging strategy, travelling further and diving in deeper water but targeting larger prey items. As a result, males likely have fewer foraging opportunities for higher energetic expenditure, but may have the chance to feed on higher quality prey. This may explain the estimated lower first-year survival probability of males (0.4) compared to females (0.6) (Hall et al. 2001). The absence of such sex differences in the North Sea dataset suggests that regional extrinsic factors likely play a part in mediating the sex-specific behaviour.

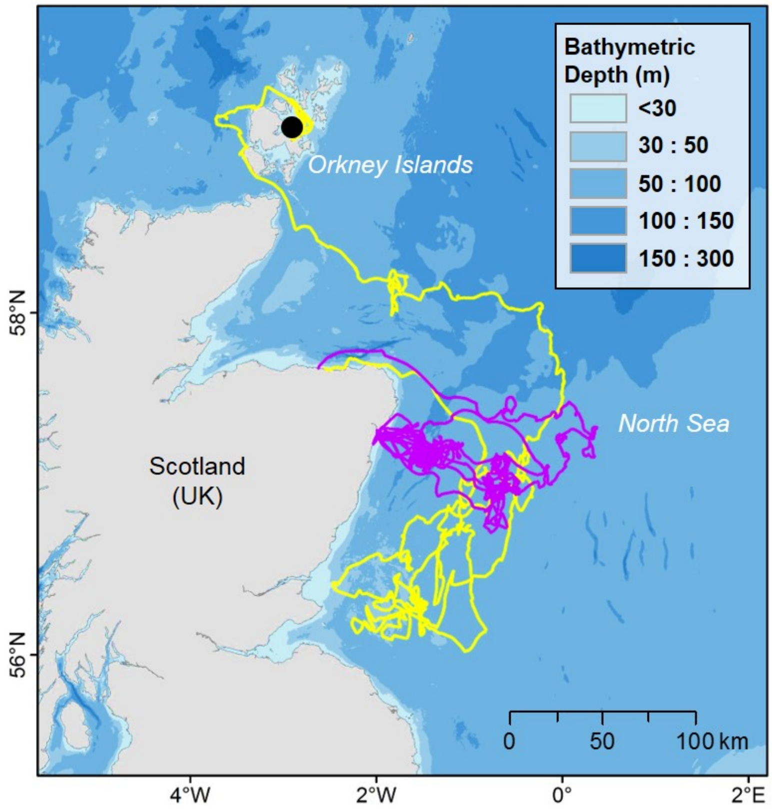

Figure 5.2: Changes in Scottish pup trip behaviour with time since departing the colony. *Initial exploratory trip of a pup from Orkney (black dot), during which it did not haul-out for 64 days (yellow track). During the following 56 days, the pup performed repeated short-duration (5-14 days) foraging trips (purple tracks), travelling between the haulout site and specific putative foraging areas.*

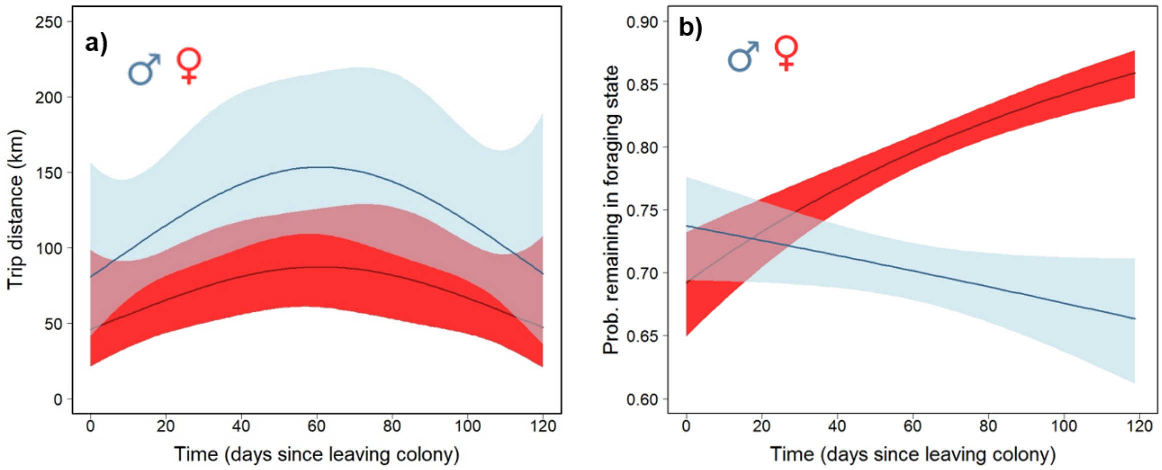

Figure 5.3: Sex differences in Welsh pup behaviour. *Sex differences in behaviour of Welsh pups emerged soon after nutritional independence. (a) Analysis of pup trip behaviour using generalized estimating equations revealed that males (blue) travelled significantly further on foraging trips than females (red). (b) Behavioural analysis of pup tracks using hidden Markov models revealed that females pups had a higher probability of remaining in a foraging state than males, meaning that males were more likely to switch from foraging to resting or travelling, and thus had shorter foraging bouts than females.*

Pup foraging habitat preference was characterised by modelling foraging locations, as identified with a hidden Markov model, in a use-availability analysis with generalized additive mixed models (GAMM). In the North Sea, pup foraging habitat selection was consistent with predation on overwintering lesser sandeels (*Ammodytes marinus*). Pups preferentially foraged in sandy areas that had a low mean winter sea surface temperature (SST; previous winter). Winter SST values in the North Sea are negatively correlated with sandeel spawning stock biomass, suggesting that areas that experienced a low mean winter SST will have high numbers of sandeel the following year (Carroll et al. 2017). In the Celtic and Irish Seas, pup foraging habitat preferences were less clearly-defined, suggesting that pups had a more generalist diet, and more individual variation in foraging habitat selection. Female pups selected shallower foraging habitat than males in the Celtic and Irish Seas, whilst there were no sex differences in the North Sea dataset.

5.4 Conservation and research priorities

5.4.1 Fisheries interactions: bycatch and entanglement

A recent study has shown significant spatial overlap of grey seal at-sea locations with passive fishing activity (nets and lines) in the Celtic and Irish Seas (Cronin et al. 2016). Bycatch is a major cause of mortality for juvenile grey seals (Baker et al. 1998, Bjørge et al. 2002, Northridge et al. 2017). An estimated 610 seals (95% confidence limits 449-1262) were bycaught in UK fisheries in 2016, and the number appears to have been increasing across the last three years (Northridge et al. 2017). Bycatch rates are estimated to be particularly high in gill net fisheries in the Celtic and Irish Seas, and are likely to be unsustainable, resulting in population-level impacts (Northridge et al. 2017). The bycatch of grey seals in the south west appears to be biased towards juvenile males (Northridge et al. 2017). Our study suggests that male pups adopt riskier foraging strategies than females in this region, and the propensity to take risks may imply that they are more likely to interact with fishing gear. Whilst acoustic deterrent devices (ADDs) have been successful in reducing the bycatch of cetaceans in live-capture fisheries, their effectiveness for seals is heavily disputed (Coram et al. 2014). Further research is urgently needed to determine the drivers of increased grey seal bycatch in the Celtic and Irish Seas, and to design effective mitigation.

Our results suggest that pups in the Welsh population occupy a diversity of habitats, and potentially forage on a large diversity of prey species. This may translate to an increased probability of overlap with various fisheries. Cronin et al. (2016) found a particularly high spatial overlap between seals and passive fisheries off the southeast coast of Ireland (south of Waterford) and the west coast of Wales (Cardigan Bay). Pups tracked in this study frequently passed through these areas and likely foraged there too (Fig. 5.1a). Indeed, a male pup from this study tagged on The Skerries in 2009 drowned off southeast Ireland due to entanglement with a creel pot (SCOS 2012). A priority for future research is to quantify the spatiotemporal overlap between pup foraging areas and commercial fishing activity. A key component of this work will be the identification of foraging areas that are of population-level importance. This will likely require further tagging effort, and could be achieved using spatial predictions from models of habitat preference. Such predictive modelling will allow more detailed assessment of the vulnerability of pups to human disturbance on foraging grounds. Our study has shown that habitat preference changes through time as pups learn foraging skills. In light of this, the analytical framework for making such spatial predictions will likely require development through collaborations between ecologists and statisticians.

Entanglement in discarded fishing gear is prevalent in the southwest UK; an area visited by pups from this study. A survey of a haulout site in Cornwall recorded that up to 5% of individuals presented net entanglement injuries or trailing fishing material; the highest recorded entanglement rate for a phocid species in the world (Allen et al. 2012). Whilst the impact of entanglement to the fitness of individual seals and to population success is unknown, entangled seals were significantly less likely to be re-sighted than non-entangled seals (Allen et al. 2012). Nevertheless, entanglement in fishing debris is an issue of welfare concern, and pups may be at increased risk due to their inquisitive nature. Furthermore, the energetic consequences of entanglement are likely to be more severe for pups given their smaller body size, and vulnerability to starvation.

Assessing the population-level consequences of elevated juvenile mortality due to fisheries interactions is especially challenging in the Welsh population, as current population estimates in this region have a high level of uncertainty (Northridge et al. 2017, SCOS 2017). Grey seals often haul-out in sea caves and isolated tidal beaches in the Celtic and Irish Seas (Summers 1973, Anderson 1977), making them difficult to count using standard aerial survey techniques (Stringell et al. 2013). Ground- and boat-based censuses have previously provided an alternative method to population census in this region, but require intensive survey effort, and long-term datasets are lacking (Stringell et al. 2013). Given the evidence of high bycatch rates and overlap with fisheries, we suggest that such surveys should be continued to further resolve population dynamics in this region and evaluate the population-level impacts of human activity, which will require consistent funding for survey effort.

5.4.2 Fisheries interactions: competition

Our analysis of pup habitat preference suggests that lesser sandeels are likely to be a key prey species for pups from colonies in northern Scotland, who forage predominantly in the North Sea. Lesser sandeels are known to be important prey for marine mammals (including adult grey seals) and seabirds in the North Sea, and competition with sandeel fisheries has been linked to the decline of seabird populations (Furness and Tasker 2000). Sandeel stocks are vulnerable to annual climatic variation, but the added pressures of fishing likely have cascading effects on marine predators. Sandeel stocks were reported to be relatively high during the time of this study (ICES 2013), therefore it is not clear how the foraging preferences of pups in this region translate to years of low sandeel abundance. If pups are not able to demonstrate plasticity in foraging preferences, then competition with sandeel fisheries may be a conservation concern. Further deployments of tracking devices are required to build a better picture of inter-annual variation in pup foraging behaviour and assess their vulnerability to fluctuating sandeel stocks. Moreover, in Scotland, there is conflict between grey seals and aquaculture; seals may predate or damage stock fish such as salmon, and are often shot under license (Coram et al. 2014). Whilst none of the pups in this study were reported to have interacted with aquaculture facilities, further research on the development of individual foraging specialities in young grey seals will help to understand the prevalence of such behaviour within the population, and inform sustainable conservation management strategies.

5.4.3 Marine renewable energy installations: collision risk

Marine renewable energy installations (MREIs), such as wind farms, tidal turbines and wave energy devices, are becoming increasingly prevalent in the UK marine environment. There is some concern that MREIs may pose a variety of risks to marine fauna (Inger et al. 2009, Grecian et al. 2010, Witt et al. 2012). Of particular concern for diving predators, such as seals, is the possibility of collision with seabed-mounted tidal turbines, which typically feature spinning horizontal blades (Sparling et al. 2017, Hastie et al. 2018). In many cases, such as Ramsey Sound in Wales (Fig. 5.4a) and the Pentland Firth in northern Scotland, these devices are installed in waters adjacent to seal haulout sites and pupping grounds (Thompson 2012, Evers et al. 2018). Whilst studies have shown that adult harbour seals (*Phoca vitulina*) exhibit signs of avoidance to operational turbines (Sparling et al. 2017, Hastie et al. 2018), the behavioural responses of other age classes and species remain unclear. A recent Scottish Government report investigated the water column usage of grey seal pups diving in an area of high tidal flow in Orkney, where a turbine installation is currently proposed (Evers et al. 2018). The report, using data presented in this thesis, found that the majority of dives in this area were mid-water dives, and that pups were only likely to enter the depth band associated with the turbine during 6.5% of the total dive time (Evers et al. 2018). However, this may still represent a significant collision risk, and the ability of seal pups to detect, and avoid, the spinning blades remains unclear. Given that pups increase their dive depth and the time spent in the bottom phase of the dive throughout early life, the collision risk may be greater for older pups. Many of the pups tagged in Orkney returned to the area throughout the four months that we tracked them. The GPS data from this thesis provide evidence that seals do transit through areas of high tidal flow associated with proposed or operational turbine installations (Fig. 5.4), but higher temporal resolution is likely required to further elucidate the behaviour of pups underwater, and therefore the risk of collision.

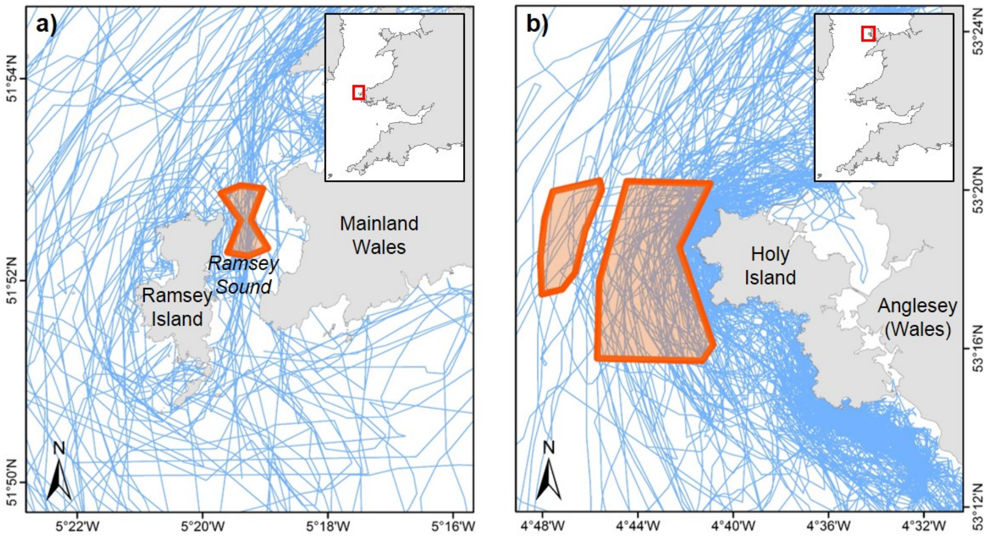

Figure 5.4: Seal pups and marine renewable energy installations. *Maps show pup tracks (blue) and overlaid MREIs in Wales. (a) shows a currently operational tidal energy device (orange polygon) in Ramsey Sound. (b) shows Holyhead Deep tidal device (left; currently in planning) and West Anglesey Tidal Demonstration Zone (in development). The ability of pups to detect and avoid seabed-mounted tidal turbines remains unknown. MREI data from The Crown Estate: https://www.thecrownestate.co.uk/energy-minerals-and-infrastructure/wave-and-tidal/.*

5.4.4 Acoustic disturbance

A growing source of pollution in the marine environment that is of particular concern for marine mammals is anthropogenic noise. Marine mammals, including seals, are sensitive to underwater noise, and may rely on hearing for effective foraging and communication. One source of anthropogenic noise that may be problematic to grey seal pups is offshore construction. For example, wind turbine installation involves impact pile-driving, resulting in intense underwater acoustic pulses (Madsen et al. 2006). There is evidence that pile driving activity can illicit behavioural responses in seals (Edrén et al. 2010, Russell et al. 2016), and has the potential to cause permanent auditory damage (Hastie et al. 2015). Edrén et al. (2010) found that the number of grey seals hauled-out during pile driving was significantly lower than at other times, and Russell et al. (2016) found that harbour seals avoid wind farms during pile driving. However, the implications of such behavioural responses for foraging efficiency and energetics are not known. Analyses in this thesis have shown that seal pups access offshore environments from an early age, diving the full depth of the water column, and so are likely to encounter anthropogenic noise soon after leaving the colony. Seals are at particularly high risk of starvation during their first year of life after weaning (Baker et al. 1998), therefore disturbance to foraging activity or displacement from critical habitat may have important ramifications for survival probability. Further studies are required to determine the energetic consequences for seals of anthropogenic acoustic disturbance.

Besides acute acoustic disturbance, increasing vessel traffic in UK waters will incur chronic noise exposure for marine animals. A recent study showed that harbour seals in the North Sea are exposed to noise from vessel traffic that exceeds levels predicted to cause temporary threshold shift (TTS) (Jones et al. 2017a). However, the implications of this temporary auditory damage for foraging behaviour and energetics remain unclear. Our data show that grey seal pups routinely travel through busy shipping lanes in UK waters, potentially bringing them within audible range of noisy vessels. Advances in sound propagation modelling techniques will likely improve our ability to accurately match seal location and dive data to estimated exposure levels in space and time, and assess immediate and log-term behavioural responses (Chen et al. 2017).

5.5 Conclusions

Our analysis of grey seal pup behaviour during their first four months of nutritional independence at sea has revealed that this time period is likely critical for the development of effective foraging skills. The first two months in particular appear to be important for the development of diving capacity and the ability to locate foraging grounds and haulout sites. Given that pups are at increased risk of starvation during this time, minimising disturbance as pups disperse from colonies and learn to forage effectively should be a conservation priority. Our study has shown that pups do not behave as adults during the initial two months after leaving the colony, often spending prolonged periods offshore without hauling out. Therefore, habitat preferences of pups should be considered as separate to those of adults. Pups travelled through a variety of habitats both nearshore and offshore, and were able to dive the full depth of the water column within days of leaving the colony. This exploratory behaviour likely means that pups are exposed to a wide range of potential anthropogenic threats, including collision with tidal turbines, interactions with fisheries, and acoustic disturbance from offshore construction and vessel traffic. Furthermore, in the Celtic and Irish Seas, males and females displayed contrasting foraging strategies, which likely expose them to different threats, with potential implications for population structure. Females remain in shallower coastal waters and males forage in deeper water further offshore. This may place females at greater risk of disturbance by coastal development and habitat modification than males. Conversely, males seem to be at particular risk of bycatch, and this may be related to the sex differences in foraging strategies.

In conclusion, key conservation concerns for grey seal pups include bycatch (particularly for males in the Celtic and Irish Seas), entanglement in discarded fishing gear, competition with fisheries, collision with tidal turbines, and acoustic disturbance from offshore construction and vessel traffic. These threats may have serious implications for grey seal populations, particularly where the impacts are lethal. Effective mitigation will begin with the incorporation of specific considerations for grey seal pups into management strategies. Methodological developments are required in habitat preference modelling techniques to incorporate the temporal plasticity of pup behaviour into analyses and generate robust population-level predictions of important foraging areas. Further deployments of high resolution tracking devices should also be a priority to investigate how pups behave in proximity to anthropogenic stressors such as seabed-mounted turbines, vessel traffic and offshore construction.

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Appendix I: Supplementary Material for Chapter I

A1.1: Glossary

Aerobic dive limit (ADL): The point during a dive at which lactate begins to accumulate in the blood. This is either classified as ‘observed’ (measured) ADL or ‘calculated’ ADL (estimating oxygen reserves divided by estimated rate of consumption).

Area restricted search (ARS): Foraging pattern characterised by slow movements and high turning rate whereby an animal concentrates its search in a specific small-scale area relative to its overall scale of movement. This may be triggered by a recently encountered prey resource or the presence of other foragers (local enhancement).

Biologging: Use of animal-attached tags to record (and possibly transmit) data relating to that animal’s movement, behaviour, physiology and/or environment.

Biotelemetry: Biologging using devices that autonomously transmit data via satellite or radio telemetry, or mobile phone technology, as opposed to archival loggers.

Conductivity temperature depth (CTD): A multi-sensor logger that can record depth as well as water temperature and salinity. These can be incorporated in satellite relay units. A major advantage is that, when deployed on a diving animal, they can record a vertical temperature and salinity profile for the water column as the animal moves through it.

Displacement: Track metric calculated as the distance travelled between successive location fixes (Fig. 1.4b). Used in conjunction with other metrics such as turning angle to identify area restricted search (ARS) behaviour. Fixes are often regularised to a constant time step before calculating (Fig. 1.4a).

First-passage time (FPT): Track metric calculated as the time taken for an animal to cross a circle of given radius (defined by the maximum peak in FPT relative variance). Used to identify area restricted search (ARS) behaviour (Fig. 1.5b-c).

Hidden Markov model (HMM): Form of state-space model (SSM) often used to classify discrete movement states (from which behaviours such as 'resting', 'foraging' or 'travelling' can be inferred) from movement metrics such as turning angle, displacement, and diving activity (Fig. 1.5d).

Kalman Filter (KF): Form of state-space model (SSM) often used to improve the location accuracy of Argos tracking data.

Optimal dive theory (ODT): Application of optimal foraging theory (OFT) to diving animals, predicting that animals maximise foraging effort within the limitations of oxygen reserves, rarely reaching aerobic dive limit (ADL).

Optimal foraging theory (OFT): Theory of animal foraging that predicts the best strategy for maximising energy gain (and therefore fitness) whilst minimising energetic cost by concentrating effort in areas of successful feeding.

State-space model (SSM): Time series model that predicts the future state of an object given its previous states in a probabilistic manner. Can be used to improve location accuracy for low-resolution data (e.g. Kalman filter; KF) or to determine allocation of behavioural states along a track (e.g. hidden Markov model; HMM).

Stomach temperature telemetry (STT): An animal's stomach temperature can be recorded by STT devices, which are retained in the animal's stomach for several days. Sharp drops in temperature are generally accepted to indicate ingestion of cold prey.

Time allocation at depth (TAD) index: Analytical method for quantifying the allocation of time throughout the time-depth profile of a dive. Index values close to 1 indicate a dive where the individual has spent longer at the bottom phase of the dive than in ascent and descent (i.e U-shaped dive). Values close to 0.5 indicate an equal distribution of time across all depths (i.e. V shaped dive). Higher values are often used to infer foraging.

Time-depth recorder (TDR): Miniaturised sensor recording depth (via pressure) as a function of time. Sensors can be activated by a salt-water switch or pressure/depth threshold.

Turning angle: Track metric calculated as the change in bearing from one location fix to the next (Fig. 1.4b). Often used in conjunction with other metrics to identify area restricted search (ARS) behaviour.

Appendix II: Supplementary Material for Chapter II

A2.1: Tag duration

Transmission duration ranged from 13 to 337 days (mean 177 days ± 81.1 days SD). Tags ceased to transmit in a relatively linear fashion over time (Fig. A2.1). Battery performance will vary between devices depending on tag parametrisation; i.e. higher duty cycles and frequency of transmission attempts require higher battery demand. In this study, GPS-GSM devices recorded and transmitted more data than SRDLs. However, the longevity of the two device types was comparable (Fig. A2.1). This is likely due to an increase in battery efficiency and power demands in the newer GPS-GSM devices. Tag failure due to battery exhaustion is likely to occur from around 120 days after deployment.

Both Argos SRDLs and GPS-GSM devices record location and dive data, however data transmission methods differ. Argos data are relayed via polar-orbiting satellites, whilst GPS-GSM devices transmit data via the mobile phone network once a tagged individual comes into GSM coverage. Therefore, it is possible that some of the GSM devices continued to collect data past the recorded maximum tag duration, but that these data were not transmitted as the seals did not enter GSM range before the battery expired.

A General Linear Model (GLM) was fit to investigate differences in tag duration as a function of sex, region and year of deployment. There was no significant difference in tag duration between the sexes (GLM; $F_{49,50} = 16.26$, $p = 0.961$), between the regions (GLM; $F_{50,51} = 0.93$, $p = 0.341$), or among deployment years (GLM; $F_{48,49} = 0.04$, $p = 0.837$). Although it was not possible to accurately assess pup survival for the above reasons, pup mortality is likely to be a feature of the observed trend in tag duration during the first six months as individuals are at greater risk of starvation and death (Bennett et al. 2010).

Three of the pups tagged in Wales were later re-encountered. One female was found dead ashore 13 days after leaving Bardsey. A necropsy did not reveal any obvious cause of death (SCOS 2012). Another female from Bardsey was found ashore in the south-west of England in an emaciated condition, two months after leaving the colony, and was taken to the National Seal Sanctuary for rehabilitation. A male from The Skerries was by-caught and died off the south-east coast of Ireland around six months after leaving the colony. The fate of all other pups is unknown.

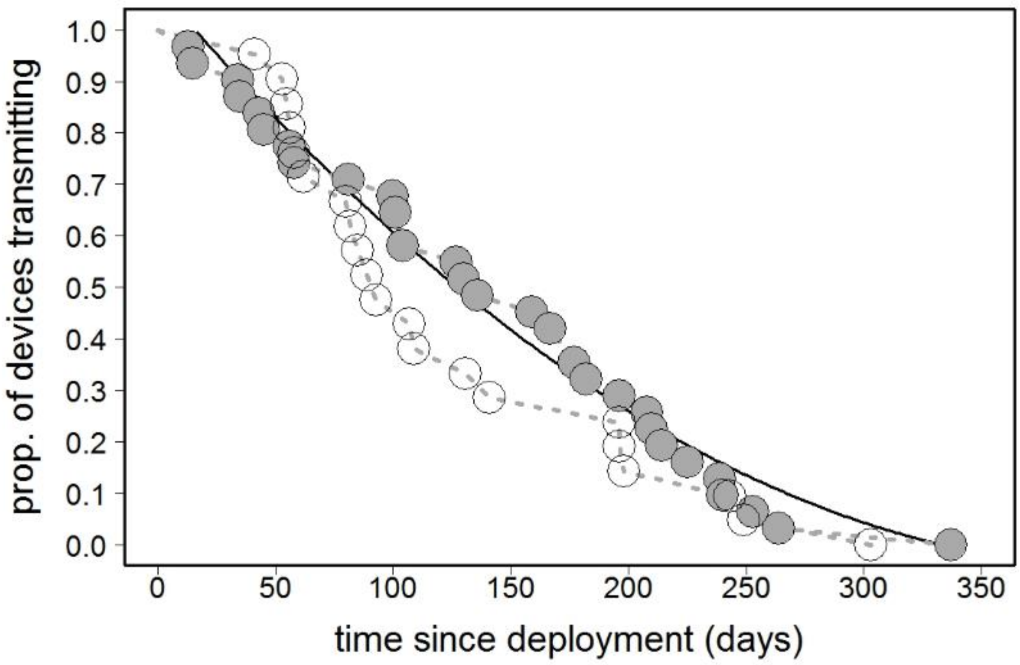


Figure A2.1: Tag duration by device type. *Time-series plot shows the proportion of SRDL (open circles; n=21) and GPS-GSM (filled circles; n=31) devices transmitting as a function of time since deployment. Points indicate when a device stops transmitting. Black line is a second order polynomial regression curve for all deployments (n=52).*

A2.2: Classification of benthic dives

We first calculated the difference, for each dive, between the maximum dive depth and the bathymetric depth of water where that dive occurred (hereafter referred to as "distance from seabed"). Many distance values were negative, indicating that the seal dived deeper than the water column depth. This is likely due to differences in the way that both forms of depth data are recorded. The bathymetric depth data used here are mostly supplied as estimates of water depth at Lowest Astronomical Tide (LAT), whereas dive depths are recorded as depth below the surface regardless of tidal state. Given that seals dive at all states of tide, the resulting dive depth values may exceed the estimated water column depth. Furthermore, dive locations were assigned using interpolation between GPS location fixes (see Chapter II Methods), and this may lead to uncertainty in locations, affecting the accuracy with which dives can be matched to bathymetric data. To overcome this uncertainty, benthic dives may be identified using a mixture distribution model approach (Ramasco et al. 2015).

Following Ramasco et al. (2015), we fit a mixture of normal distributions to the frequency distribution of distances from seabed (Fig. A2.2). We decided on three distributions *a priori* as we expect that the data contain benthic, midwater and surface (transit/travelling) dives. We then took the distribution with mean closest to 0 (-3.69 m) as representing the distribution of distance from seabed for benthic dives (Ramasco et al. 2015). Following Ramasco et al. (2015), the threshold for benthic dives was taken as the upper 95th percentile of this distribution. Benthic dives were therefore determined as any dive with a distance to seabed ≤ 0.31 m (Fig. A2.2).

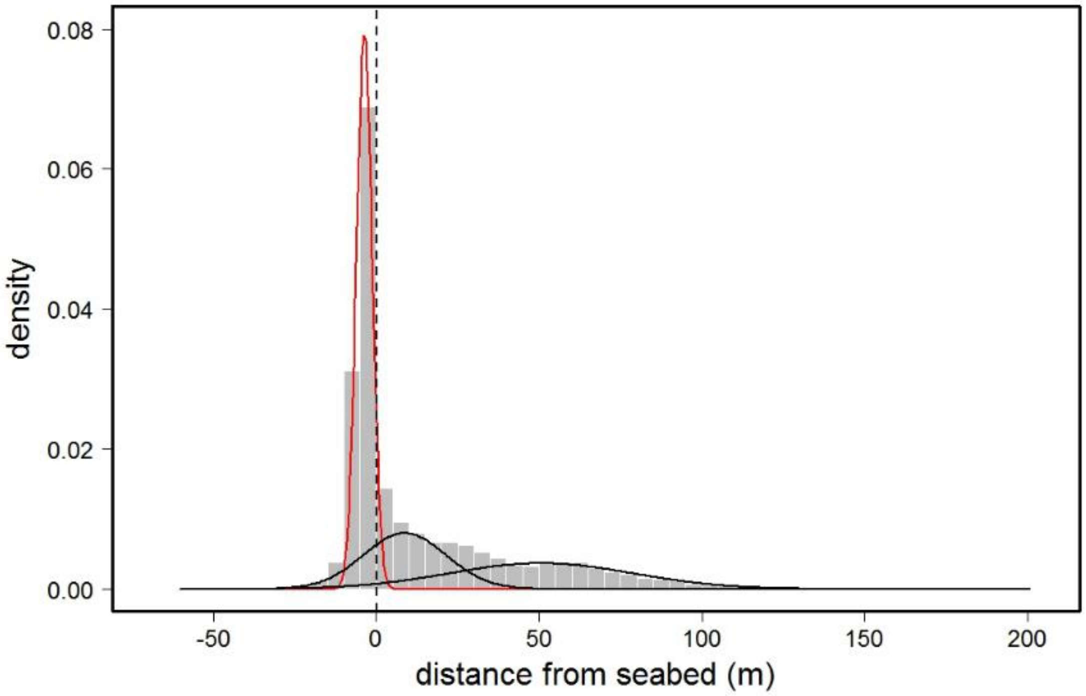


Figure A2.2: Classification of benthic dives. *Histogram shows the density distribution of distance from seabed for all dives. A mixture of three normal distributions was fit to the data (solid lines). The distribution with mean closest to 0 (-3.69 m; shown in red) was taken to be the distribution of distance from seabed for benthic dives. The upper threshold for classification of benthic dives was set at the upper 95th percentile of this distribution (0.31 m; dashed line).*

A2.3 Effects of bathymetric depth on benthic diving

To investigate how the temporal changes in proportion of benthic dives were related to the bathymetric depth of water where those dives occurred, we modelled the daily proportion of dives that were benthic in a GEE-GAM as a function of a four-way interaction between time since departing colony (days; as a smoothed term), bathymetric depth (m; as a smoothed term), region (as a factor) and sex (as a factor). Bathymetric depth was taken as the mean of dive bathymetric depth values per pup per day. Individual was used as the grouping variable to generate a population mean response. Models were weighted by the number of dives in each time (day) – depth (m) category.

The daily proportion of benthic dives was best explained by a three-way interaction between time since departure, sex, and bathymetric depth (Fig. A2.3; $\chi^2_9 = 56.5$, $p < 0.001$) and a three-way interaction between time since departure, region and bathymetric depth (Fig. A2.3; $\chi^2_9 = 49.6$, $p < 0.001$).

All pups increased the depth at which they were able to perform benthic dives over the initial 40 days (Fig. A2.3). Although confidence intervals were wide, due to the model predicting across time and space in which few dives occurred, it is evident that the depth band between 60-80 m becomes important for benthic diving in all pups from 60 days onwards. Shallow waters (<20 m) appear to be important for benthic diving in NS pups during the first 10 days, then again later from 60 days onwards as pups perform shorter distance trips and remain closer to the coast. This supports the findings of Hanson *et al.*[1] that NS juveniles forage on benthic prey in nearshore habitat. CIS females performed a greater proportion of benthic dives in shallower water (<20 m) than CIS males throughout the entire time series. Although results presented in the main article show that the mean water depth of dives for CIS females remained shallow throughout the time series, results presented in Fig. A2.3 show that some individuals likely entered deeper water towards the end of the time series and were able to reach the bottom.

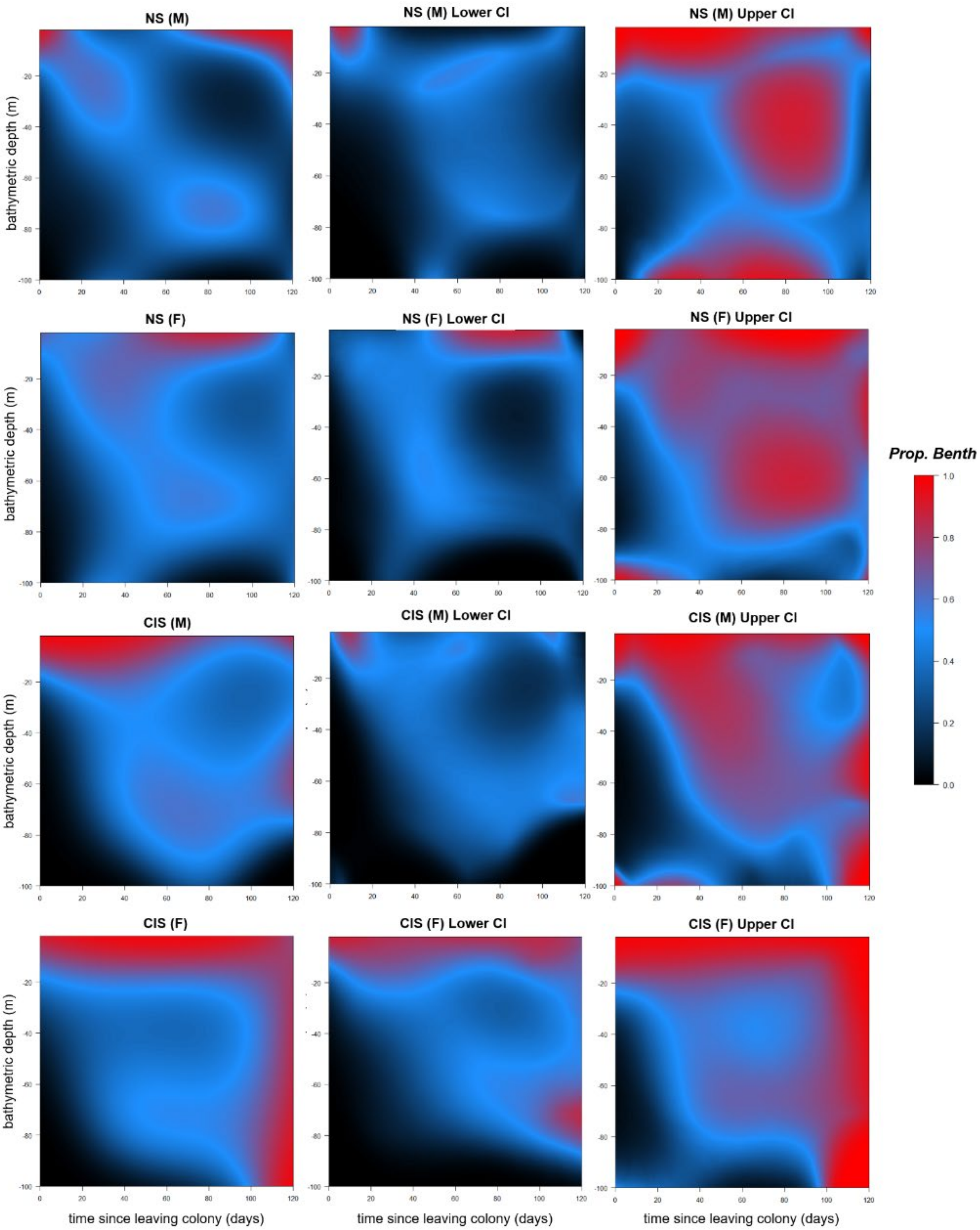


Figure A2.3: Effects of bathymetric depth on benthic diving. *Surface plots show model-predicted population mean estimates for the proportion of dives that were benthic (colour palette) by bathymetric depth (y axis) and time since leaving colony (x axis). Left hand panels show model-predicted population mean estimates, centre panels are GEE-based lower 95% confidence intervals, and right-hand panels are upper 95% confidence intervals.*

A2.4 Colony departure dates

It is possible that pups born later in the breeding season undergo a shorter post-weaning fast on land, and therefore depart the colony at a younger age than those born earlier due to some seasonal effect such as weather patterns. It is also possible that pups that leave later experience different water column characteristics and food availability than those that leave earlier. These factors may have an effect on subsequent behavioural development. For the majority of pups included in this study, natal and weaning dates were not observed, and so calendar age at point of departure from the colony was not known. However, for 17 individuals instrumented on the Isle of May, age at weaning and departure and calendar date of departure are all known. We therefore tested whether natal date had an effect on post-weaning fast duration using a Spearman's Rank correlation test. There was no significant correlation between natal date and post-weaning fast duration (Fig. A2.4; Spearman's Rank Correlation, r = -0.079, n = 17, p = 0.763).

Earliest and latest departure dates are presented for each deployment site in Table A2.1. Calendar date of departure differed by 73 days across the whole study, mostly as a result of the wide spread of departure dates in 2010. There was a mean of 40 and 58.5 day difference in calendar day of earliest and latest departure between NS and CIS colonies respectively, which reflects the shift in timing of the breeding seasons in different parts of the UK. The Isle of May calendar departure days differed by approximately 1 month between the earliest and latest. All departure dates within any of the other deployments were within 16 days of each other, which should minimise any effect of calendar day of departure on behaviours measured.

Table A2.1: Pup departure dates. *Table shows day of the year (DOY) of earliest and latest departure from each of the study sites in each sample year.*

Deployment site (year)	Region	Device type	DOY earliest departure	DOY latest departure	Max. difference (days)	No. individuals
Isle of May (2001)	NS	SRDL	338	366	28	11
Isle of May (2002)	NS	SRDL	333	357	24	10
Bardsey (2009)	CIS	GPS-GSM	296	303	7	2
The Skerries (2009)	CIS	GPS-GSM	295	302	7	3
The Skerries (2010)	CIS	GPS-GSM	300	311	11	5
Ramsey (2010)	CIS	GPS-GSM	293	299	6	7
Muckle Green Holm (2010)	NS	GPS-GSM	346	361	15	7
Stroma (2010)	NS	GPS-GSM	349	365	16	7

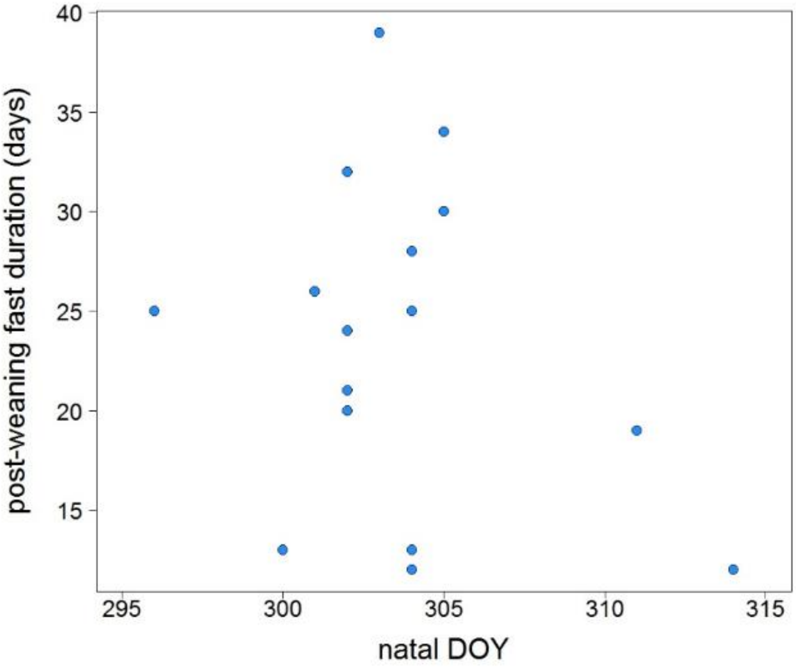


Figure A2.4: Effect of natal date on post-weaning fast duration. *Pups born on a later day of the year (DOY) do not have a shorter post-weaning fast than those born earlier.*

Appendix III: Supplementary Material for Chapter III

A3.1: Implementation of covariate effects in the generalized HMM

Covariate effects on data stream probability distribution parameters

Covariate effects (*time since leaving colony*, *region* and *sex*) were implemented on state-dependent probability distribution parameters in the following way: $\mu_t^{(Z)} = \exp\left(\exp\left(\alpha_\mu^{(Z)}\right) - \exp\left(\boldsymbol{y}_t \boldsymbol{\beta}_\mu^{(Z)}\right)\right)$, where, for each time interval (t), mean step length ($\mu_t^{(Z)}$) depends on the state (Z), the (log-scale) asymptote $\left(\exp\left(\alpha_\mu^{(Z)}\right)\right)$, the row vector of covariates ($\boldsymbol{y}_t$), and the corresponding column vector of coefficients $\left(\boldsymbol{\beta}_\mu^{(Z)}\right)$. The exponential function is used to ensure that $\mu_t^{(Z)} > 0$. Similarly, for directional persistence parameter, $\gamma_t^{(Z)} = \frac{\mathrm{logit}^{-1}\left(\alpha_\gamma^{(Z)}\right)}{1+\exp\left(-\boldsymbol{y}_t \boldsymbol{\beta}_\gamma^{(Z)}\right)}$, where $\mathrm{logit}^{-1}\left(\alpha_\gamma^{(Z)}\right)$ is the asymptote and the inverse-logit transformation is applied to ensure that $0 < \gamma_t^{(Z)} < 1$. The *time since leaving colony* covariate was standardised to zero mean and unit variance for numerical stability. The inclusion of time relaxes the stationarity assumption of the data stream probability distributions, whilst the inclusion of *region* and *sex* covariates serves as a partial-pooling mechanism (Zucchini et al. 2016). This was done because previous analysis of grey seal pup movements has revealed that ontogenetic changes in behaviour are not equal between region and sex sub-groups (Carter et al. 2017; Chapter II). Normal 95% confidence intervals for $\mu_t^{(Z)}$ and $\gamma_t^{(Z)}$ were calculated based on the Delta Method using finite difference approximations of the first derivative (e.g. Casella & Berger (2002)).

Covariate effects on state transition probability matrix

Covariate effects on the state transition probability matrix ($\Gamma^{(t)}$) were implemented with a multinomial logit link function:

$$\Gamma^{(t)} = \begin{pmatrix} \psi_t^{(11)} & \psi_t^{(12)} & \psi_t^{(13)} \\ \psi_t^{(21)} & \psi_t^{(22)} & \psi_t^{(23)} \\ \psi_t^{(31)} & \psi_t^{(32)} & \psi_t^{(33)} \end{pmatrix} = \begin{pmatrix} \frac{1}{1+e^{\eta_t^{(12)}}+e^{\eta_t^{(13)}}} & \frac{e^{\eta_t^{(12)}}}{1+e^{\eta_t^{(12)}}+e^{\eta_t^{(13)}}} & \frac{e^{\eta_t^{(13)}}}{1+e^{\eta_t^{(12)}}+e^{\eta_t^{(13)}}} \\ \frac{e^{\eta_t^{(21)}}}{e^{\eta_t^{(21)}}+1+e^{\eta_t^{(23)}}} & \frac{1}{e^{\eta_t^{(21)}}+1+e^{\eta_t^{(23)}}} & \frac{e^{\eta_t^{(23)}}}{e^{\eta_t^{(21)}}+1+e^{\eta_t^{(23)}}} \\ \frac{e^{\eta_t^{(31)}}}{e^{\eta_t^{(31)}}+e^{\eta_t^{(32)}}+1} & \frac{e^{\eta_t^{(32)}}}{e^{\eta_t^{(31)}}+e^{\eta_t^{(32)}}+1} & \frac{1}{e^{\eta_t^{(31)}}+e^{\eta_t^{(32)}}+1} \end{pmatrix}$$

where, for $i, j \in \{1,2,3\}$ and $i \neq j$, $\eta_t^{(ij)} = \boldsymbol{y}_t \boldsymbol{\beta}^{(ij)}$. The $\eta_t^{(ij)}$ are first exponentiated to obtain positive values, then divided by the row sums to obtain the probability of transitioning from state *i* at time *t-1* to state *j* at time *t* $\left(\psi_t^{(ij)}\right)$.

A3.2 Model validation

Model pseudo-residuals

Model validation was performed by visual inspection of pseudo-residuals. Pseudo-residual plots are presented for the minimal adequate generalized HMM (Fig. A3.1) and the minimal adequate conventional HMM (Fig. A3.2). Pseudo-residuals were close to normally distributed (Fig. A3.1a-d), however the autocorrelation function (ACF) revealed some residual autocorrelation for step length (Fig. A3.1e). This indicates the presence of some underlying exogenous pattern in the step data that is not captured by the model. The residual autocorrelation may suggest the need for more states or covariates to capture all elements of the data. Nevertheless, whilst more states may improve model fit, it would likely impact on our ability to biologically interpret model output. Based on the advice of Pohle et al. (2017), our choice of three states here is informed by careful and pragmatic consideration of grey seal ecology as well as the fundamental constraints of the dataset.

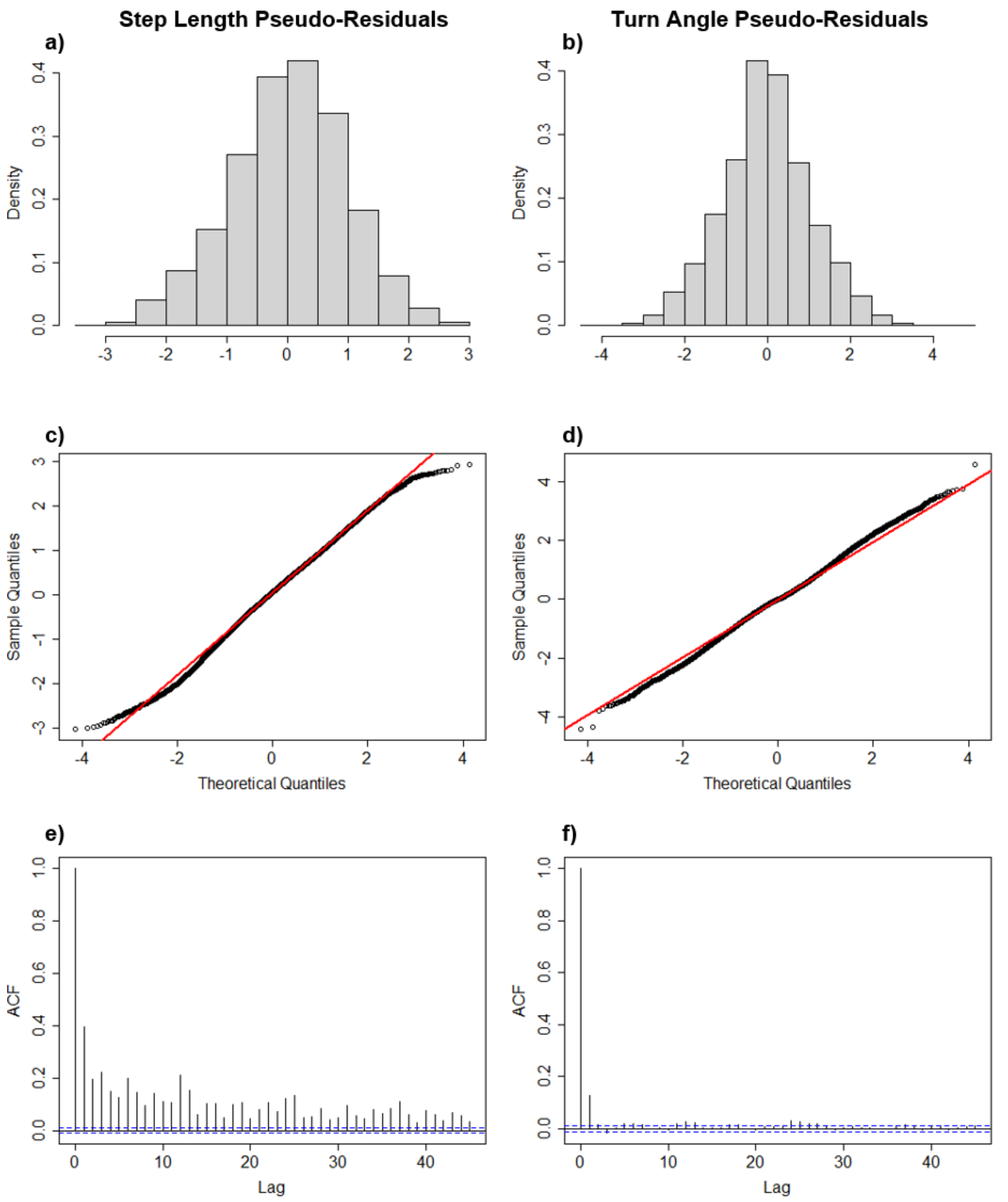


Figure A3.1: Model pseudo-residuals for minimal adequate generalized HMM. *Histograms (a-b) and quantile-quantile plots (c-d) show that model pseudo-residuals are normally distributed. Autocorrelation function for step length (e) reveals some residual autocorrelation not explained by the model.*

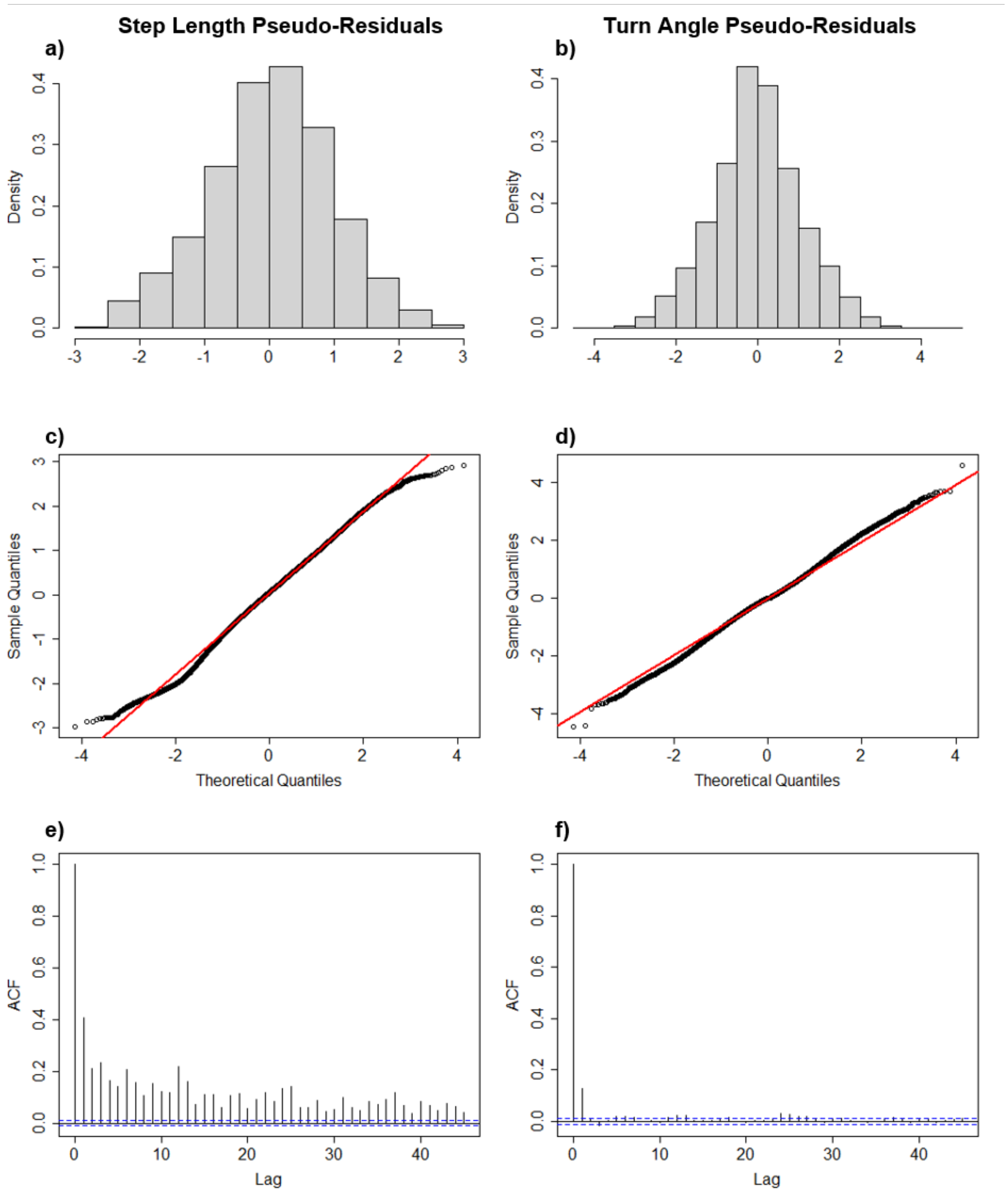


Figure A3.2: Model pseudo-residuals for minimal adequate conventional HMM. *Model pseudo-residuals were almost indistinguishable from those of the minimal adequate generalized HMM (Fig. A3.1).*

Appendix IV: Supplementary Material for Chapter IV

A4.1: Distribution of environmental variables

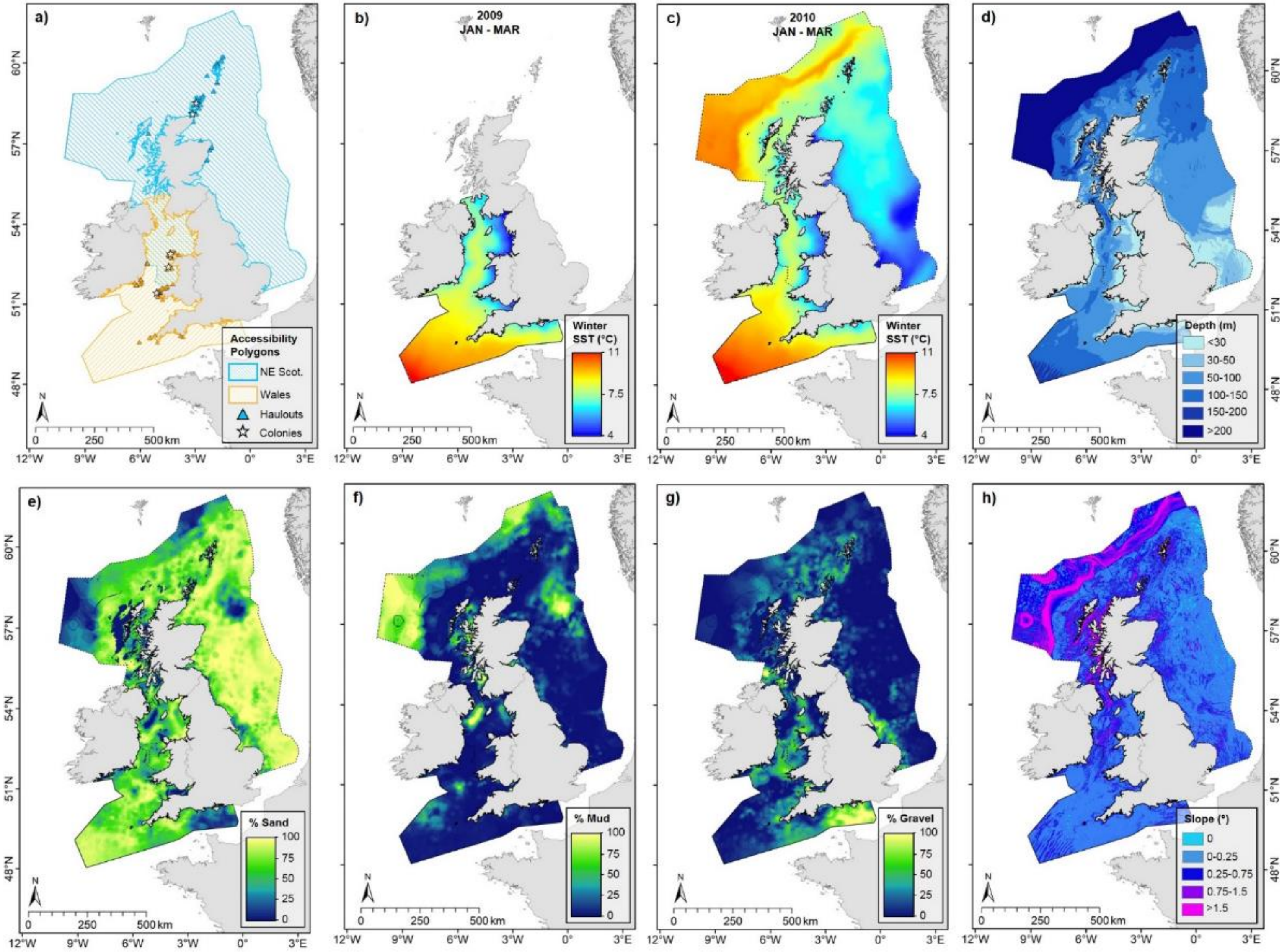
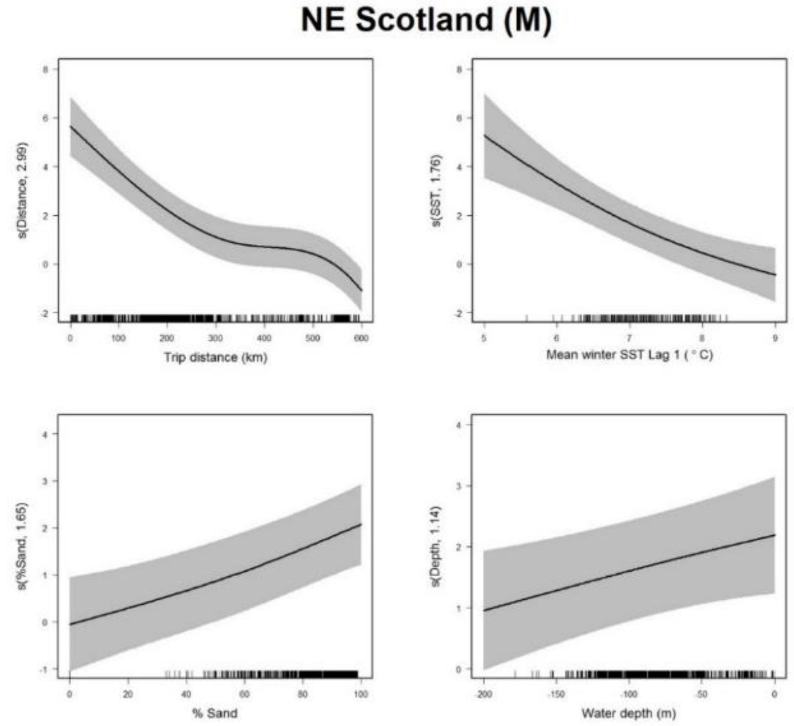


Figure A4.1: Candidate environmental variables. *Map (a) shows the regional accessibility polygons. Maps (b-h) show the distribution of environmental variable values within the polygons. Winter SST (b-c) values are shown as mean values for the winter (January – March) prior to pup tracking data.*

A4.2: Models selection for male and female NE Scotland pups



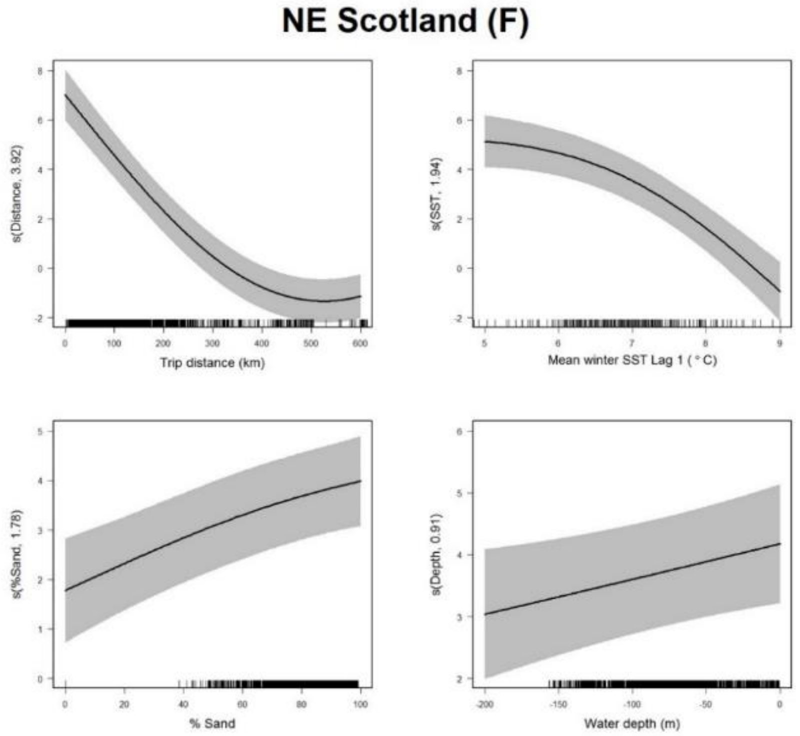


Figure A4.2: Lack of overt sex difference in NE Scotland pup foraging habitat preference. *Average-individual model predictions for male (top) and female (bottom) pups from NE Scotland revealed a lack of substantial sex differences for male and female pups in NE Scotland. In the interest of parsimony, males and females were modelled together in the main study.*

A4.3: Models selection and cross-validation

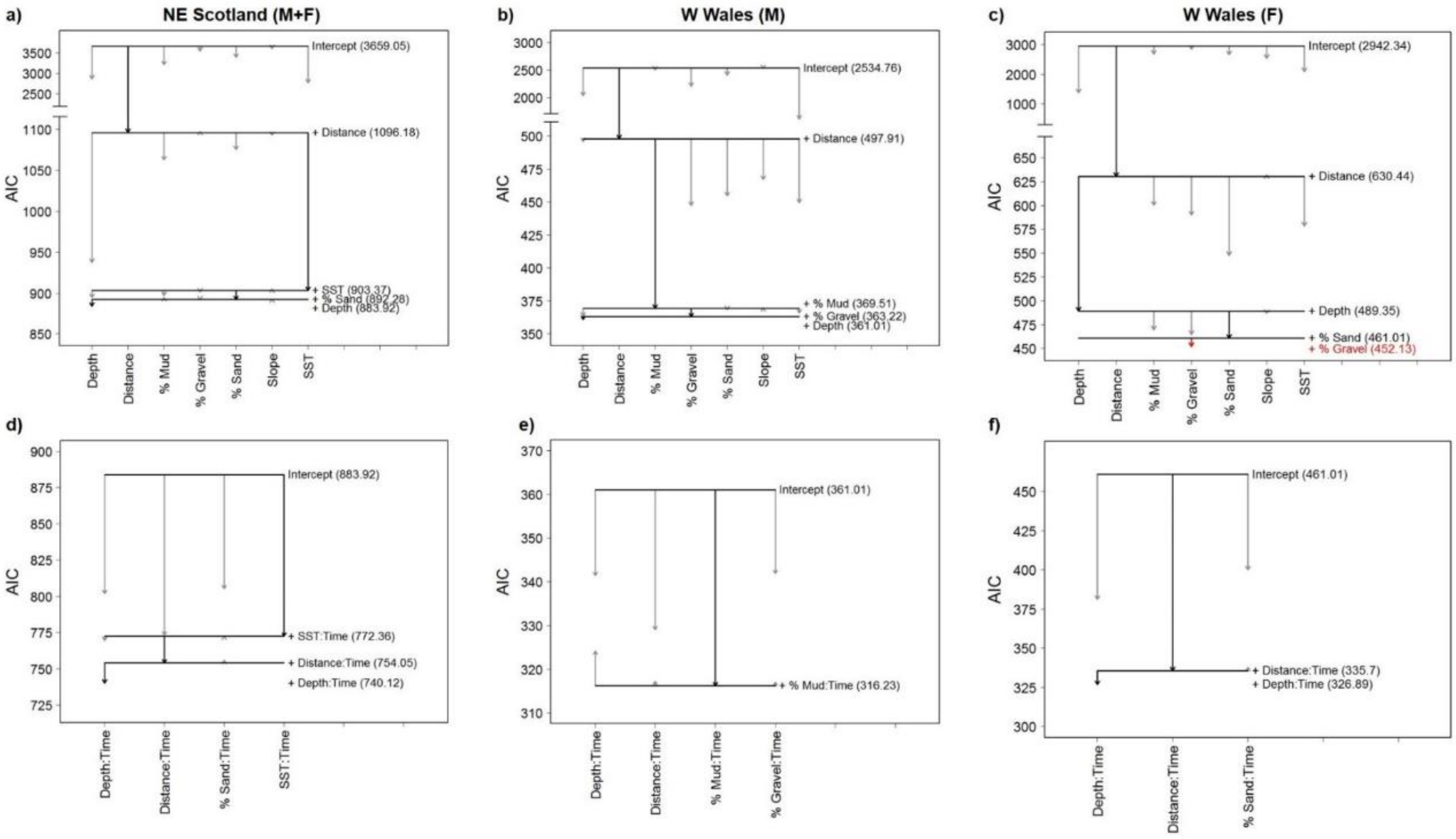


Figure A4.3: Forwards model selection by AIC score. *Arrows show the change in AIC score with the addition of environmental variables, leading to the best model. Candidate predictor variables were first fitted as individual fixed effects (a-c). Those that were retained in the model (black arrows) were then fitted in an interaction (":") with time since leaving colony (d-f).*

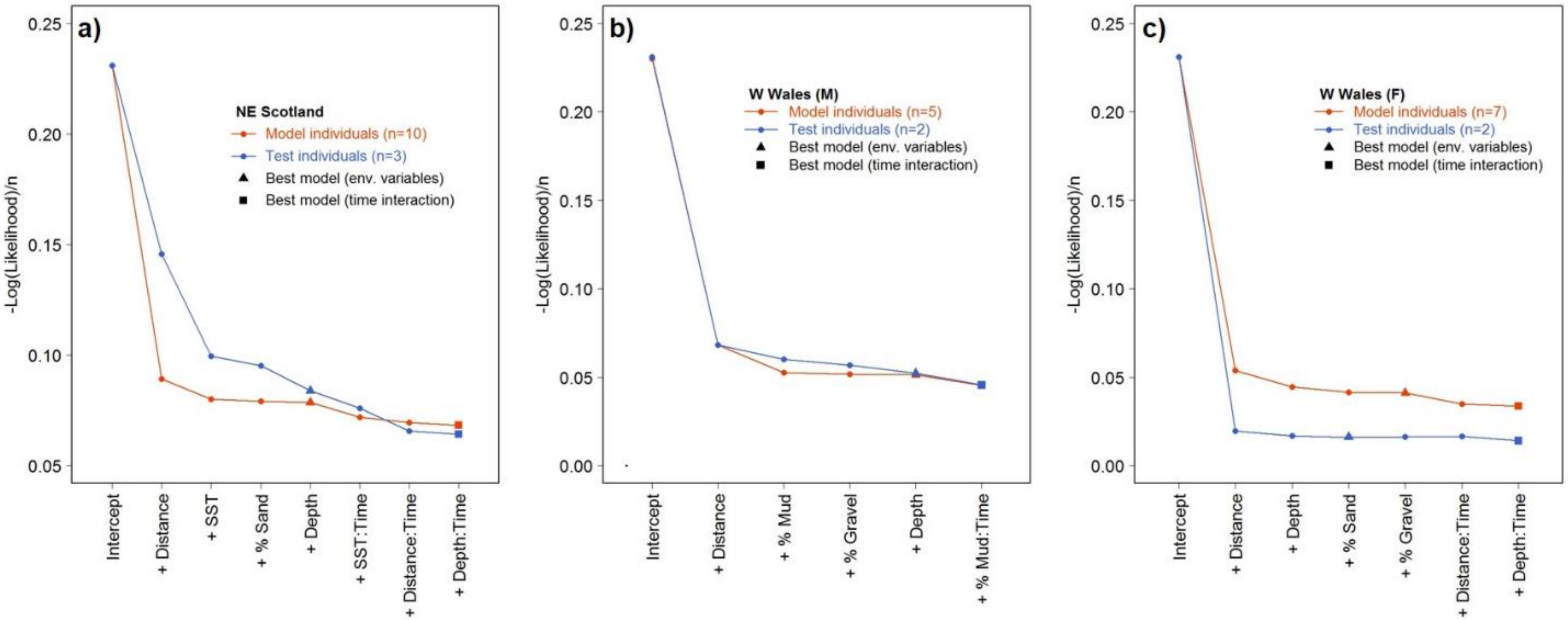


Figure A4.4: Model cross-validation. *Models were cross-validated for each group by first training the model with ~75% of the dataset, then testing the selected models on the remaining individuals in the dataset by comparing the change in negative log likelihood score divided by the number of observations. In (c), this value increased for the test dataset with the addition of % gravel, indicating a poorer fit. Therefore, the most parsimonious model (excluding % gravel) was selected.*

A4.4: Model uncertainty estimation (temporal interactions)

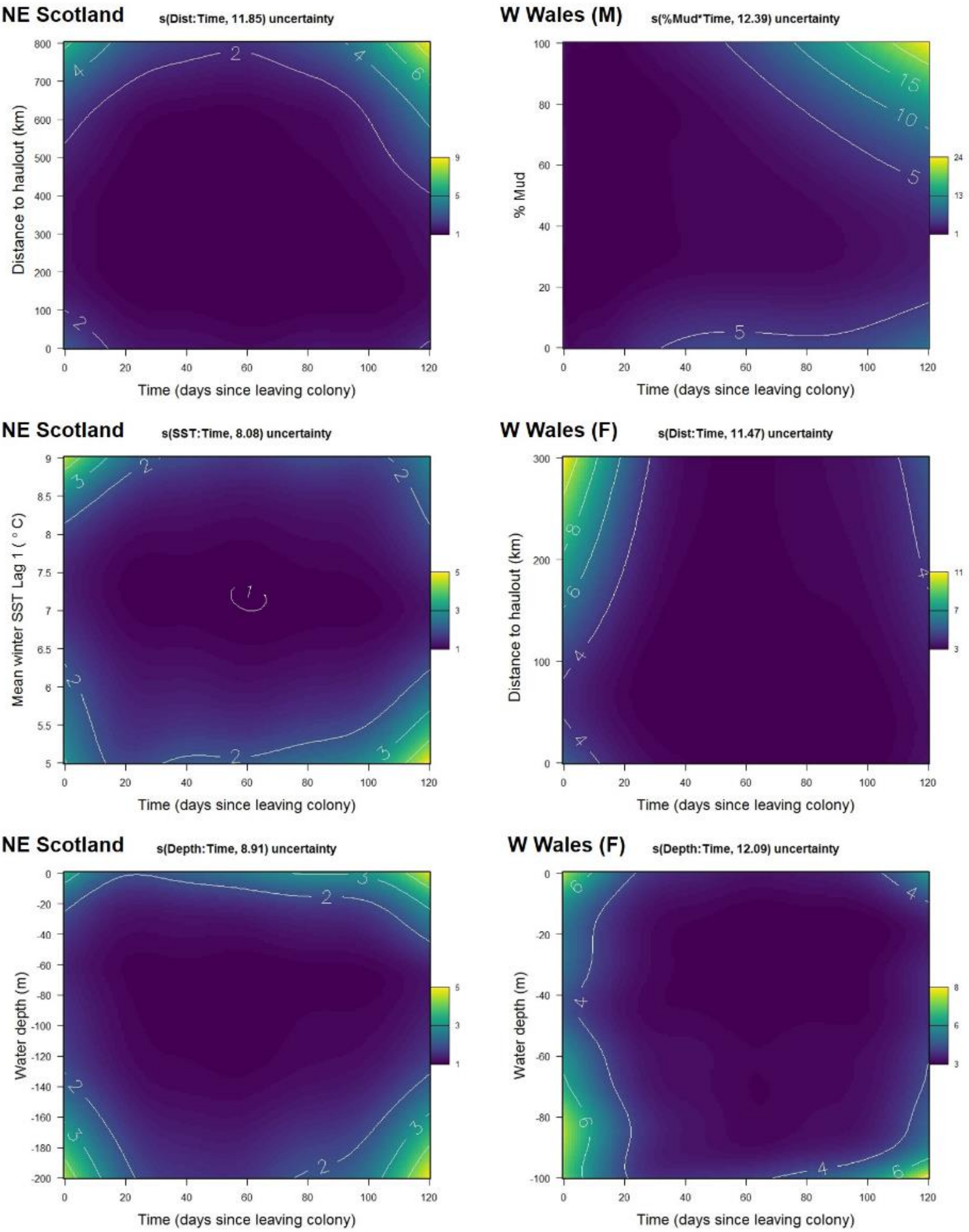


Figure A4.5: Model uncertainty plots. *Plots show 95% confidence limits for average-individual model predictions presented in main study, for all temporal interactions*