

**Odontocete Ecology off Northumberland, UK:
Advancing the Application of Passive Acoustic
Monitoring**

A thesis submitted by

Matthew Sharpe

for the award of Doctor of Philosophy (PhD)



School of Natural and Environmental Sciences, Newcastle University

Newcastle-upon-Tyne, NE1 7RU, UK

September 2022

Abstract

Effective conservation requires robust data on species occurrence, abundance, and area usage. Providing this information for odontocetes is difficult given that they are highly mobile, occupy areas at low density and are visually cryptic. The first chapter presents the result of a structural topic model used to evaluate abstracts representing odontocete research over the last 50 years. The results provide a comprehensive overview, acts as an introduction to the research field and identifies the need for further conservation related research. It further identified Bioacoustics and Communication as important areas of odontocete research. Passive Acoustic Monitoring (PAM) has proven a viable approach to studying odontocetes as all species produce sounds (e.g., echolocation clicks) that can be detected using hydrophones.

To date, PAM studies have mostly focused on occurrence with few studies addressing other research aims. To address this, emerging and novel approaches to analysing PAM data were applied to recordings collected at three sites off the Northumberland coast, UK, a relatively understudied area of growing interest due to increased common bottlenose dolphin (*Tursiops truncatus*) activity in recent years.

The effect of environmental drivers on the occurrence of three sympatric species (common bottlenose dolphin, white-beaked dolphin (*Lagenorhynchus albirostris*) and harbour porpoise (*Phocoena phocoena*)) were identified using GAM-GEE analysis of species-specific click detections, identifying key drivers such as seasonality, location, and diel phase.

Bottlenose dolphin area usage was investigated by incorporating click and whistle detections into a single hidden Markov modelling framework to identify latent “activity states”. Differences in activities interpreted as foraging and socialising were identified across each location, and across diel and tidal phases.

Abundance estimates were produced for bottlenose dolphin from individual specific “signature whistles” using different modelling approaches. These estimates were compared to a separate estimate produced from photo-ID data collected at the same time from boat-based surveys.

Dedication

I dedicate this thesis to Beccy Gregory for all the love and support that she has given over the last four years and for everything she had to put up with.

Acknowledgement

This work would not have been possible without the continued and unwavering support of my primary supervisor Prof. Per Berggren for that I am truly grateful. It was greatly facilitated by the additional perspective and support from my second supervisor Prof. Nick Wright.

Fieldwork and data collection would not have been possible without the expertise, knowledge and generosity of Neil Armstrong and Barry Pearson, who were always there to provide support and to ensure the safety of all the fieldwork conducted during the project.

I would like to thank Team Marine aka Georgia Atkinson, Cameron Trotter, and Kirsten Crane for all the early mornings and heavy lifting/pulling; Prof. Jeff Neasham for his support and advice; and Molly Stockill for her commitment to assisting me during the first summer season.

Additionally, I would like to thank Miguel Angel Miguel Morales Maqueda and the members of the Marine Megafauna Lab for collaboration and assistance. Finally, I am grateful to the Ridley Fellowship for the studentship that provided this opportunity.

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Thesis overview

Background and rationale

Odontocete populations that occupy urbanised coastal waters are subjected to multiple anthropogenic stressors that can lead to population decline and welfare concerns. Direct effects such as fisheries bycatch and vessel strikes can lead to increased mortality and/or injury (Read et al., 2006, Van Waerebeek et al., 2007, Slooten et al., 2013, Brownell Jr et al., 2019) and habitat degradation due to urbanisation (habitat homogenisation and fragmentation, reduction in prey species, and increased noise and chemical pollution) can lead to reduction in fitness and reproductive success (Weilgart, 2007, Pirotta et al., 2013, Huang et al., 2014, Jepson et al., 2016, Nelms et al., 2021). Such threats can often be difficult to quantify and measure (with the exception of bycatch that can be directly observed with appropriate monitoring) and may individually only have small effects across relatively large temporal scales. However, if not identified and managed correctly, these multiple stressors can act synergistically leading to population decline or extirpation (Turvey et al., 2007, Sharpe and Berggren, 2019). Identifying population trends is also difficult for odontocete species as they are difficult to observe due to the logistics of observing highly mobile species at sea, and their population parameter estimates tend to have relatively large errors and provide low statistical power for detecting trends. This has led to the recommendation of using the precautionary principle for managing odontocete species in impacted areas, whereby declining trends are not a prerequisite for conservation action (Thompson et al., 2000). Even under this management paradigm, robust and up-to-date data on species occurrence, abundance and area usage are required to inform policy decisions and safeguard biodiversity.

The coastal waters of Northeast England are highly industrialised with economically important river ports, coastal industrial zones, offshore developments (wind turbine arrays) and a number heavily populated towns and cities along the coast. The coastal waters of Northumberland are also recognised for their conservation importance with the area having three marine protected areas designated, that together cover the whole area (the Berwickshire and North Northumberland SAC, Berwick to St Mary's MCZ and the Coquet to St Mary's MCZ). The Northumberland

coast also provides habitat for three sympatric species of odontocete (common bottlenose dolphin (*Tursiops truncatus*), harbour porpoise (*Phocoena phocoena*) and white-beaked dolphin (*Lagenorhynchus albirostris*). However, information on their ecology is limited and there are no long-term monitoring programs or specific conservation efforts for the species in the area. None of the species are listed as species features in any of the current MPAs. Odontocetes require specific consideration to protect them from threats that may be overlooked by policy makers such as noise pollution, interaction with fisheries, and spatial overlap with recreation activities (e.g., recreational boating, jet skis etc). In recent years there has been an increase in bottlenose dolphin occurrence caused by an increased range shift of the “East Coast” population historically associated with the Moray Firth and Aberdeenshire coast (Wilson et al., 2004, Cheney et al., 2013, Arso Civil et al., 2019). If this trend persists, there may be increased pressure on the species caused by increased public awareness and emerging ecotourism. Increased monitoring of odontocetes off Northumberland is therefore warranted to better inform policy makers, especially in regard to increased occurrence of bottlenose dolphin.

Passive Acoustic Monitoring (PAM) is a well-established methodology for monitoring odontocete species that detects vocalisations and uses them as a proxy for species presence in the monitored area (Mellinger et al., 2007). All odontocetes vocalise, with every species producing echolocation clicks to navigate their environment and to facilitate prey capture (Au, 1993). Many delphinid species also produce whistles that are used in social contexts (Janik, 2009), with some species (including the bottlenose dolphin) producing individually specific whistles (Caldwell and Caldwell, 1968). All these sounds can be detected by deployed hydrophones, but to date most PAM studies use echolocation click detections to investigate occurrence and to infer foraging behaviour from patterns in echolocation clicks (increased repetition rates). There is growing interest in the use of signature whistles as a means of estimating abundance (Longden et al., 2020, Fearey et al., 2022) and there is potential for whistle detections to provide even deeper insights into dolphin activities and area usage.

PAM that detects both click and whistle vocalisations has the potential to greatly improve the ability to monitor odontocete species, increasing its application from providing baseline data on species occurrence to more detailed studies of area

usage and estimating abundance. To facilitate this, further development of PAM methodologies is needed along with novel modelling approaches that can address more detailed research questions (e.g., related to species specific abundance and area usage). Tested and applied off the coast of Northumberland, in-depth analysis of PAM data would provide much needed data on odontocete species, including the bottlenose dolphin that has increased in occurrence in recent years.

Problem statement

Odontocete ecology off the Northumberland Coast is not well studied and there is a lack of specific conservation efforts for the area. Year-round occurrence of bottlenose dolphins in recent years has generated increased attention on the region's biodiversity. A comprehensive study of odontocete ecology including all three sympatric species (bottlenose dolphin, white-beaked dolphin and harbour porpoise) is required to provide managers with up-to-date datasets on species occurrence, abundance, and area usage that can inform future conservation planning.

This thesis aims to address the current data gaps, provide species specific occurrence, and provide deeper insights into bottlenose dolphin abundance and area usage off Northumberland through the development and application of novel analysis methods for passive acoustic monitoring data. The developments presented in the thesis have wider application to the monitoring of odontocete species that can help improve conservation efforts and the status of odontocete species globally.

Chapter 1. The Evolution of Odontocete Research: Topics and Trends

1.1 Introduction

Odontocete research (defined here as scientific research on any of the 34 genera and 77 species of toothed whale) is a relatively new field. Its early development began in the mid-20th century as researchers benefited from the increased availability of captive animals, allowing for detailed studies of their biology and behaviour (McBride and Hebb, 1948, McBride and Kritzler, 1951, Schevill and Lawrence, 1953). Studies of wild populations increased in popularity during the 1970s and 1980s (Leatherwood, 1975, Würsig and Würsig, 1979, Barham et al., 1980, Norris and Dohl, 1980, Irvine et al., 1981, Leatherwood and Reeves, 1983) as techniques such as photo-identification allowed for new insights into population dynamics and social organisation (Saayman and Tayler, 1973, Würsig and Würsig, 1979, Bigg, 1982a, Scott et al., 1990, Smolker et al., 1992). Contemporary odontocete research is now a multidisciplinary and global field that continues to advance scientific knowledge in all aspects of odontocete biology and ecology.

An important goal of odontocete research is to protect biodiversity. Human activities associated with the aquatic environment cause multiple and often simultaneous stressors (e.g., chemical and noise pollution, interaction with vessels, overfishing of prey species, and bycatch in fisheries), which impact survivability and reproductive success (Culik, 2010, Avila et al., 2018, Nelms et al., 2021). As K-selected species (i.e., long lived with low reproductive output), odontocetes populations are sensitive to changes in both reproductive and mortality rates (Martien et al., 1999, Manlik et al., 2016) and if stressors and mortalities are left unmitigated, it can lead to population decline and risk of extirpation (Sharpe and Berggren, 2019). The most significant threat to odontocete populations is bycatch in gillnet fisheries (Read et al., 2006, Nelms et al., 2021). First identified in the late 1960s (Mitchell, 1975) and brought to further attention in the 1990s (Perrin et al., 1994), bycatch is responsible for the likely unsustainable mortalities of many odontocetes globally each year (Read et al., 2006). The situation has become critical for many species and populations (Brownell Jr et al., 2019), however the full extent of the problem requires further attention and assessment (Temple et al., 2021b). To date, one species of

odontocete has become functionally extinct due to anthropogenic activities including bycatch, the Baiji (*Lipotes vexillifer*) (Turvey et al., 2007) and a number of other odontocete species and populations are at high risk of extirpation and/or extinction (Brownell Jr et al., 2019, Jefferson, 2019). According to the IUCN Red List of Threatened Species, of the 76 odontocete species assessed to date, 22% are listed in a threatened category (i.e., Critically Endangered, Endangered or Vulnerable), 12% are listed as Near Threatened, 55% as Least Concern, and 11% are listed as Data Deficient (iucn-csg.org).

Since the late 20th century there has been rapid growth in the volume and availability of digital information. In scientific research, the digitisation of manuscripts now allows easy access to both newly published and archived manuscripts. 'Big data' text mining (Berry, 2004) techniques (where computer algorithms extract information from large quantities of digitised text) provide a relatively new and efficient approach to analysing research publications (Nunez-Mir et al., 2016). One such technique is probabilistic topic modelling (Blei, 2012), which statistically infers latent semantic themes within a corpus without supervision. Resulting themes are interpreted based on keywords outputted by the model and represent topics within the corpus. The approach is objective, and contrasts supervised topic modelling where the researcher would sort texts into predefined topics based on prior knowledge of the subject area. Once topics are identified, further investigation into their prevalence, trend, generality, and correlations can be assessed. Bibliometric analysis of this kind can help identify research priorities of a given field and how they change over time (Neff & Corley 2009). This allows for a deeper understanding of the evolution of research fields that can benefit the research community, funding bodies, and publishers, helping to identify areas for improvement and drive the future direction of the field.

In this study, topic modelling is applied to a corpus of odontocete research abstracts representative of the whole field. The analysis was restricted to odontocetes research rather than including all cetacean species due to the considerable differences between odontocete and mysticete biology, ecology, and conservation and the effect these differences have on the type and volume of research conducted. Resulting topics were identified and grouped with other correlated topics and their prevalence within the corpus was estimated, quantifying the relative research effort

applied in each area. Temporal trends and differences in topic prevalence between genus groups were also investigated. The aim was to provide a synthesis of scientific research on all toothed whale species during the 20th and 21st centuries, presenting the field as a broad network of topics and quantifying research effort in each area. Such an analysis also provides an introduction to the subject taxonomic group of the following chapters of this thesis. Specific attention in the discussion of this chapter is given to passive acoustic monitoring and related topics to further introduce the primary theme of the thesis.

1.2 Methodology

1.2.1 Structural topic models

Structural Topic Models (STM) (Roberts et al., 2014) were the chosen statistical framework for performing the topic modelling procedure. STM are an extension of Latent Dirichlet Allocation (LDA) (Blei et al., 2003), a specific type of probabilistic topic model that models documents (in this case abstracts) as a probabilistic mixture of topics and topics as a probabilistic mixture of words. A brief description of LDA and how STM extends the framework are provided below.

LDA is composed of three components (Figure 1.1): topical prevalence parameters, topical content parameters, and a core language model. These components combined provide the generative process for each document (indexed by $d \in \{1, 2, \dots, D\}$) as follows:

- The number of words N_d in a document is drawn from a Poisson distribution.
- Topic proportions (θ_d) within the document is random variable drawn from a Dirichlet distribution with prior α (these represent the topic prevalence parameters).
- Each of the user specified number of topics (indexed by $k \in \{1, 2, \dots, n\}$) is a probability distribution for all words in the vocabulary, with word proportions specified by β_k , a random variable drawn from a Dirichlet distribution with prior η (these represent the topic content parameters).
- For each word in the document (indexed by $n \in \{1, 2, \dots, N\}$), the topic of the word is represented by $Z_{d,n}$, a random variable drawn from the multinomial distribution θ_d .

- The observed words, $W_{d,n}$ are random variables drawn from another multinomial distribution that define $P(W_{d,n} | Z_{d,n}, \beta_k)$ (these latter two variables make up the core language model).

The resulting θ_d and β_k distributions are the important outputs of the model that can be interpreted as the topic proportions of each document and the words that represent each topic, respectively. A Bayesian approach is then applied to compute the posterior distribution of the latent variables given the text from each document in the corpus (Blei et al., 2003).

STM differs from LDA by allowing topics to co-occur with greater probability than expected by chance, see Correlated Topic Models (Blei and Lafferty, 2007). STM also differs from LDA by incorporating metadata (data about each document) directly into the model. The metadata is used to “structure” the prior distributions of document-topics. With STM, rather than θ being drawn from common Dirichlet distribution (as in LDA), this parameter is a random variable drawn from a Log-normal distribution based on the document covariates (Roberts et al., 2013). Similarly, rather than the parameter β being drawn from a common Dirichlet distribution, it is instead produced from a multinomial logit model, where a word’s prevalence is based on document covariates, topics, and topic-covariate interactions. This model is defined by:

$$\beta_{d,k,v} \propto \exp \exp (m_v + k_v^y + k_v^y + k_v^{k,y})$$

Where:

- v indexes individual words in the relevant vocabulary.
- m_v is the baseline log frequency for word v ,
- k terms represent the adjustments based on the topic and covariate data.

Figure 1.1 shows the plate notation of STM alongside with the notation for the LDA for comparison.

After the STM model is fit, covariables can also be used to model differences in topic prevalence across metadata covariables using the “method of composition” (Tanner, 1993). This method takes the posterior distribution of topic proportions for each document and evaluates the covariables using a linear model analogous with generalised linear models. This method allows uncertainty in topic allocation to be

incorporated in the regression model and is robust to differences in number of abstracts across covariables of interest (e.g., differences in abstracts across publication year).

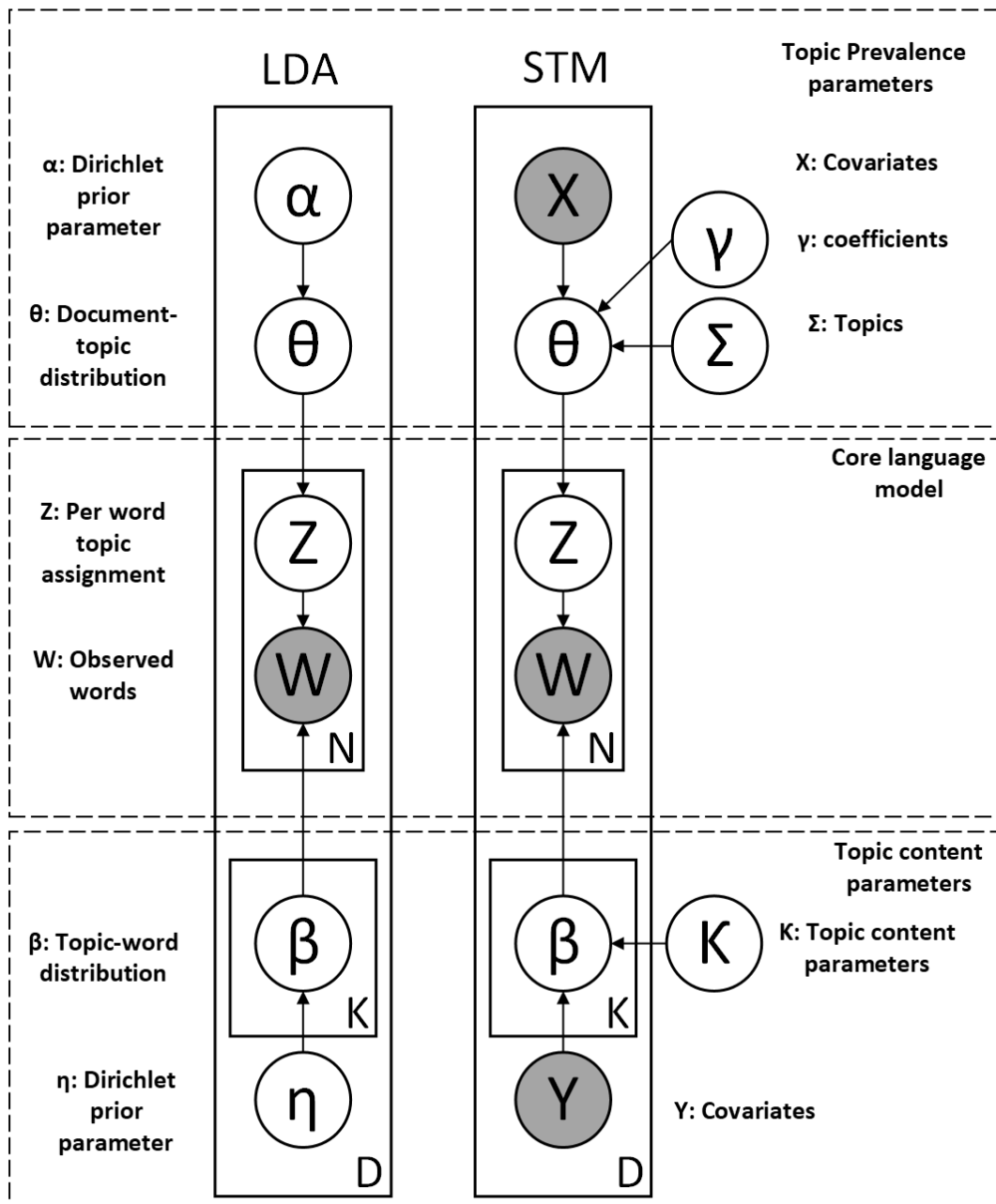


Figure 1.1. Plate notation for LDA and STM. The boxes in solid line represents each plate and denote iteration in the generative process. N represents the iteration through each word within each document; K represents iteration through each topic; and D represents each iteration through each document within the corpus. Dashed boxes represent the three components of the model. Each node represents a parameter within the model, where shaded nodes are directly observed and unshaded nodes are estimated.

R package *stm* (Roberts et al., 2019) was used to apply the STM framework. Metadata included in the analysis were year of publication and genus group for topic prevalence. No covariables were used to model topic content, as this was not required for the research objectives. Year of publication was directly available for each abstract from the Scopus database. Genus group was extracted from the abstracts by using the dictionary function provided by R text mining package *tm* (Meyer et al., 2008). Each of the 34 odontocete genera were searched for in each abstract. A raw count of abstracts for each genus was conducted but the metadata used in the model required each abstract to be labelled by a single factor variable. When only one genus name was found in an abstract, the abstract was labelled as that genus. Abstracts with more than one genus were labelled “mixed” and those with no genus words were labelled “none”.

Package *stm* provides four sets of keywords for interpreting the theme of each topic outputted by the model based on the metrics: *highest probability*, *lift*, *score* and *FREX*. The simplest metric for ranking keywords is *highest probability* that ranks each word based on how frequently it appears in the topic based on the posterior topic-word distribution (β_d). Although this is useful for interpreting themes, more common words may be highly probable in many topics making them less important to theme interpretation; the other metrics account for this. *lift* ranks words based on the word frequency within the topic, divided by the word frequency outside of the topic, effectively boosting the rank of words within the topic that are uncommon outside of the topic (Taddy, 2012). The metric *score* is similar to *lift* but ranks words based on the log frequency of the word within the topic divided by the log frequency of the word outside of the topic (Chang and Chang, 2010). The *FREX* methodology is based on the work of Airoidi and Bischof (2016) and ranks words based on both frequency and exclusivity, with the latter accounting for the prevalence of a word both within and outside of the topic. *FREX* calculates the weighted harmonic mean of the word frequency (derived from the Empirical Cumulative Distribution Function (ECDF) of the word in its topic distribution) and exclusivity (derived from the ECDF of the word within the topic after column normalisation of the beta-matrix) (Roberts et al., 2019). All keywords were considered when interpreting each topic.

1.2.2 Odontocete research corpus and document processing

The corpus used in the analysis was compiled using the online abstract and citation database, Scopus (www.scopus.com). The Scopus database was queried for all odontocete research articles in their final stage of publication via the advanced search feature. A single search string was used which returned all titles and abstracts that included the term odontocet* (* wild card character to return both odontocete and odontoceti) and each of the 34 odontocete genera (e.g., *Tursiops*, *Physeter*, *Orcinus*). The following alterations to this formula were made due to some genus terms having additional usage, therefore returning many unrelated articles: *Sousa* was replaced with "humpback dolphin" and *Delphinus*, *Steno*, *Monodon*, and *Inia* were paired with their respective species names (e.g., "*Monodon monoceros*"). An "AND NOT" term was added to remove articles about the anamorphic fungal genus *Stenella*. The full search string:

```
TITLE-ABS (odontocet* OR cephalorhynchus OR "delphinus delphis" OR "delphinus capensis" OR feresia OR globicephala OR grampus OR lagenodelphis OR lagenorhynchus OR lissodelphis OR orcaella OR orcinus OR peponocephala OR pseudorca OR sotalia OR "humpback dolphin" OR stenella OR "steno gedanensis" OR tursiops OR delphinapterus OR "Monodon monoceros" OR neophocaena OR phocoena OR phocoenoides OR kogia OR berardius OR hyperoodon OR indopacetus OR mesoplodon OR tasmacetus OR ziphius OR "Inia geoffrensis" OR platanista OR lipotes OR pontoporia OR physeter AND NOT Hyphomycetes OR Hyphomycetus OR Mycosphaerellaceae OR Mycosphaerella OR cercospora OR cercosporoid OR adeniae OR Africana OR anthuriicola OR araguata OR aucklandica OR canavaliae OR capparidicola OR "S. constricta" OR deightoniana OR gahniae OR gynoxidicola OR iteae OR lythri OR "novae-zelandiae" OR palmicola OR paullinae OR pittospori OR sinuosogeniculata OR stipae OR subsanguinea OR tristaniae OR uniformis OR vangueriae OR vermiculata) AND ( LIMIT-TO ( DOCTYPE , "ar" ) AND LIMIT-TO ( DOCTYPE , "final" ) )
```

returned 8786 articles on May 15, 2021. The approach to building the corpus would exclude scientific research articles about odontocete species which do not refer to the subject species by binomial name or contain the words odontocete and

odontoceti. The corpus therefore represents a sample of the total body of odontocete research available for the period of interest (20th and 21st centuries).

All abstracts returned by the search were downloaded as .csv files and imported into R (R Core Team, 2013). Further filtering was performed using custom built scripts that removed; duplicated entries, entries with no abstract, or those not in English (Figure 1.2). Finally, abstracts with a publication year before 1970 and after 2020 were removed. This step was taken due to the low number of abstracts available from Scopus from before the 1970s and that some years prior to 1970 had no available abstracts. After filtering, a final corpus of 7941 abstracts representing odontocete research from 1970 to 2020 was accepted for further processing and analysis.

The accepted corpus abstracts were further processed using R package *tm* so that the text of each abstract was in a more appropriate format for topic modelling. The procedure was as follows:

1. All text relating to publisher or copyright information typically found at the end of the abstract was removed.
2. All species names (binomial and common) were removed.
3. All stop words (e.g., and, in, because) were removed. Full list of stop words removed can be found under the English and smart lists available in the *tm* package documentation (<https://rdr.io/rforge/tm/man/stopwords.html>).
4. All non-alphanumeric characters except spaces were removed without replacement. This resulted in hyphenated words (e.g., mark-recapture) becoming one word (e.g., markrecapture).
5. Words shorter than 3 letters long were removed.
6. Numbers were removed.
7. Words were “stemmed”, the process of reducing inflected words to their stem (e.g., climbed, climbing, and climbs become climb).
8. Thresholds for the minimum and maximum documents per word were set at 20 and 1400, respectively.

The text cleaning process did not reduce any abstract to being without any words and resulted in a final dataset of 7941 documents, 2476 vocabulary terms, and 389,236 individual tokens.

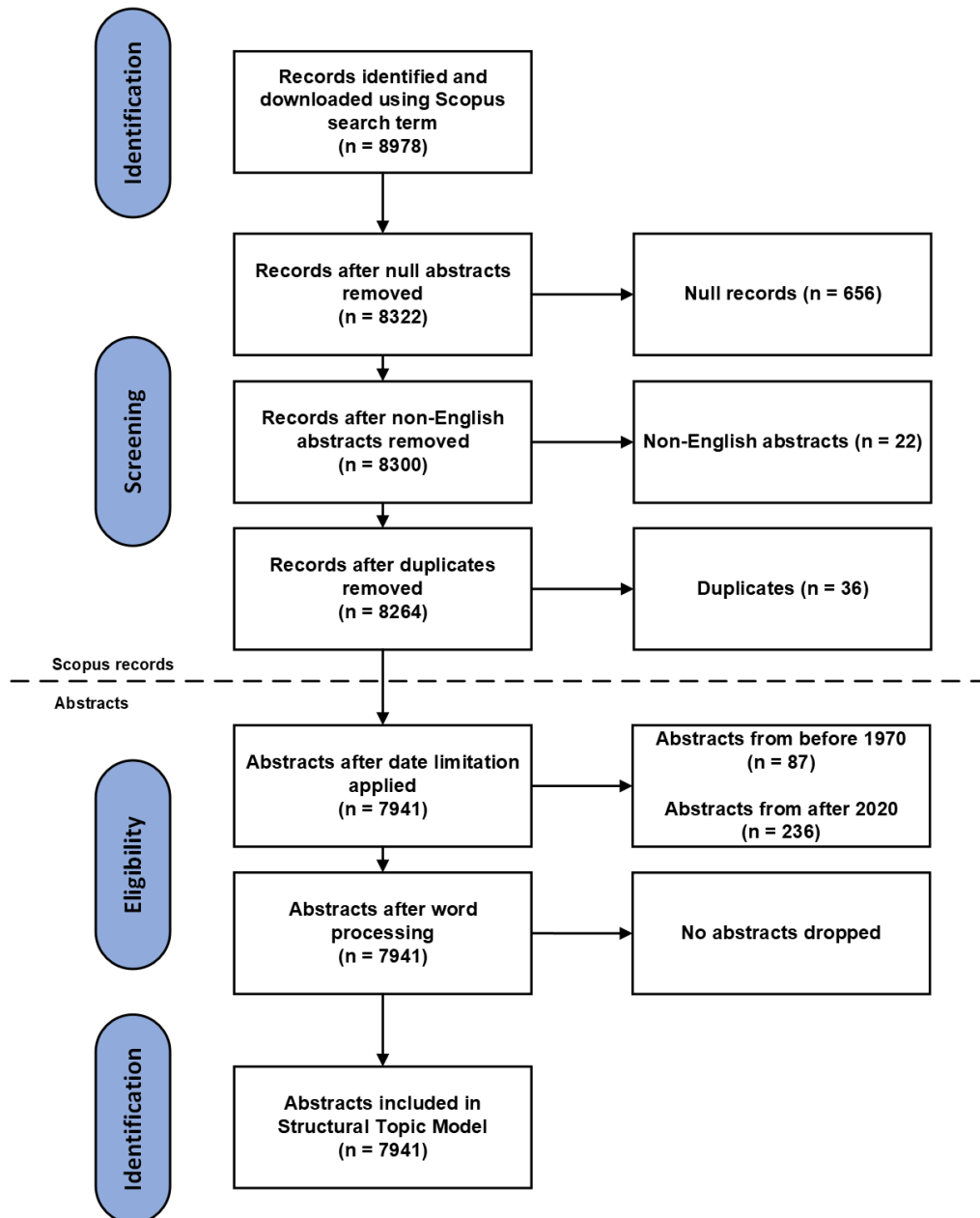


Figure 1.2. Flow diagram showing the process of document search, filtering and processing that resulted in the final corpus used in the structural topic model.

1.2.3 Number of topics

STM, as with most unassisted topic models, require the user to specify the number of latent topics (k). There is no “true” number of topics for any given corpus and an

appropriate value for k depends on the size and variability of the corpus, as well as the requirement of the specific research question the model is attempting to address (Grimmer and Stewart, 2013). As a rough guide, 50-100 topics is considered a sensible range for corpora of academic journal articles (Blei, 2012). *stm* provides a statistical approach to finding candidate values for k which includes held-out likelihood (Wallach et al., 2009), residual analysis (Taddy, 2012), and semantic coherence and exclusivity metrics (Roberts et al., 2014). These tests were applied to an initial set of models with k values ranging from 10 to 100 in multiples of 10. After inspecting the output for support, a second set was tested between 60 to 80 in multiples of 5. It is also recommended that a qualitative assessment of different model outputs is included in determining k (Roberts et al., 2014) and candidate models of 60, 64, 65, 68, 70, 72, 75 and 80 were then individually modelled and the resulting topics were checked for semantic coherence and exclusivity and qualitatively assessed, checking both the key words for each group and the correlations between the topics. The preferred model of 65 was selected as all topics had similar semantic coherence and exclusivity, with no outliers when visually inspected and topic keywords and correlations were easily interpreted.

1.2.4 Further statistical analysis

The relationship between metadata covariates and topic prevalence were modelled using regression analysis performed using the *stm* package. The publication year variable was non-linear transformed using a cubic b-spline (7 degrees of freedom and 4 knots specified at 1980, 1990, 2000 and 2010).

Two additional metrics were calculated to identify topics that were more general and those that were more specific. Specific topics would be expected to have a high assigned probability in documents where it was the most probable but a lower average probability in all other documents compared to general topics. Conversely, a general topic would be expected to have a relatively high probability across all documents but have a lower probability across documents where it was most probable, reflecting its general presence across the corpus. Each abstract in the corpus was therefore assigned to the topic for which it had the highest probability, based on the results of the STM model ($\max \theta_d$). The mean probability was then calculated separately for each topic across abstracts that were assigned to that topic

and from abstracts that were not assigned to that topic. This provided two metrics for each topic to compare generality and specificity, referred to as “mean selected” and “mean unselected” metrics, respectively. A general topic would have lower mean selected and higher mean unselected metrics and specific topics would have the opposite.

Topic correlations were calculated by the Meinshausen and Buhlmann procedure (Meinshausen and Bühlmann, 2006) after non-paranormal transformation of the topic proportions using R package *huge* (Zhao et al., 2012). The resulting graph was then analysed for sub graphs using a label propagation algorithm (Raghavan et al., 2007) performed in package *igraph* (Csardi and Nepusz, 2006). This resulted in clusters of topics which could be interpreted as a higher-level set of research, hereafter referred to as topic groups. Topic group proportion was calculated by combining the topic proportions contained within each group. This allows for differences in topic group prevalence to be investigated for the whole corpus and for each publication year. Trends in topic group prevalence were analysed using Mann-Kendall trend test adapting the procedure in Chen et al. (2020).

1.3 Results

1.3.1 Overview of topics and topic groups

The 65 resulting topics can be viewed in Figure 1.3. Further information including expected corpus proportion, specificity/generality metrics, FREX keywords and exemplar topics can be viewed Appendix A (Table A1). The 5 most prevalent topics across the whole corpus were (expected % proportion in parentheses): 1. *conservation and management* (3.27), 2. *ocean/geographic region* (3.26), 3. *habitat modelling* (2.7), 4. *population assessment* (2.55) and, 5. *population genetics* (2.53). The label propagation algorithm organized the 65 topics into 11 groups (expected % proportion in parentheses): 1. “Population Ecology and Genetics” (29.75), 2. “Conservation and Management” (8.79), 3. “Behaviour” (5.75), 4. “Ecological Niche” (4.83), 5. “Bioacoustics” (8.93), 6. “Biochemistry and Cellular” (12.04), 7. “Health and Disease” (8.4), 8 “Life History and Social Ecology” (8.2), 9. “Communication” (2.72), 10. “Physiology” (7.08) and, 11. “Polar and Subpolar Ecology” (3.52) (Figure 1.3).

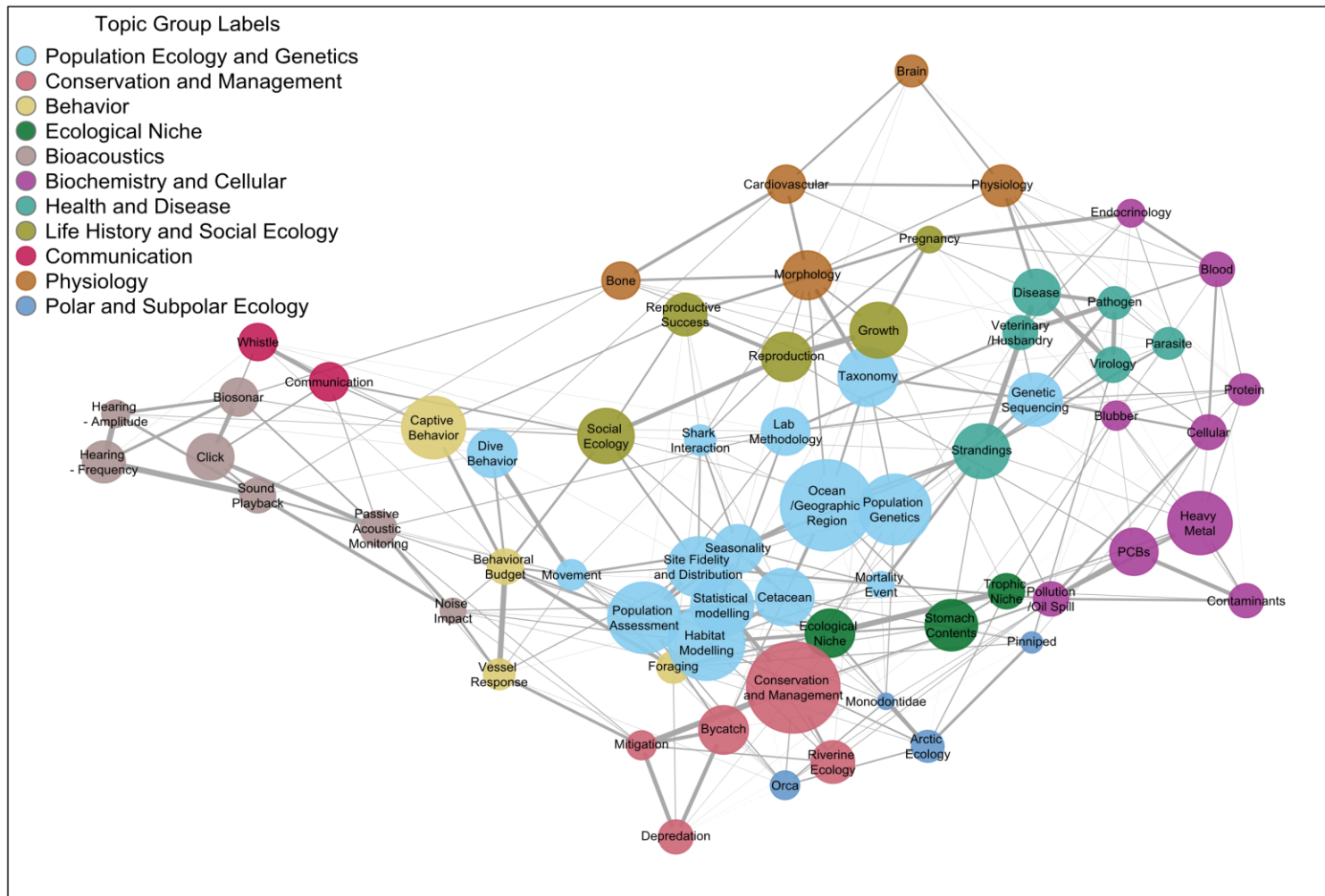


Figure 1.3 Network Diagram of latent topics inferred from a corpus of odontocete research abstracts by the structural topic model. Resulting clusters referred to as topic groups are shown and colour coded. Size of node represents expected proportion of the corpus and width of edge represents correlation between topics. The nodes and edges were arranged using the force-directed layout algorithm by Fruchterman and Reingold (1991).

1.3.2 Topic and topic group trends

The cubic B-splines for all topics and were qualitatively evaluated to assess apparent trends. The topics *ecological niche*, *conservation and management*, *passive acoustic monitoring*, *statistical modelling*, and *habitat modelling and noise impact* had the most apparent upward trends (Figure 1.4). Topics *blubber*, *protein*, *brain*, *growth*, *morphology*, *hearing – frequency* and *blood* had the most apparent downward trends (Figure 1.5). B-splines for all topics can be viewed in Appendix A (Figure A1-65).

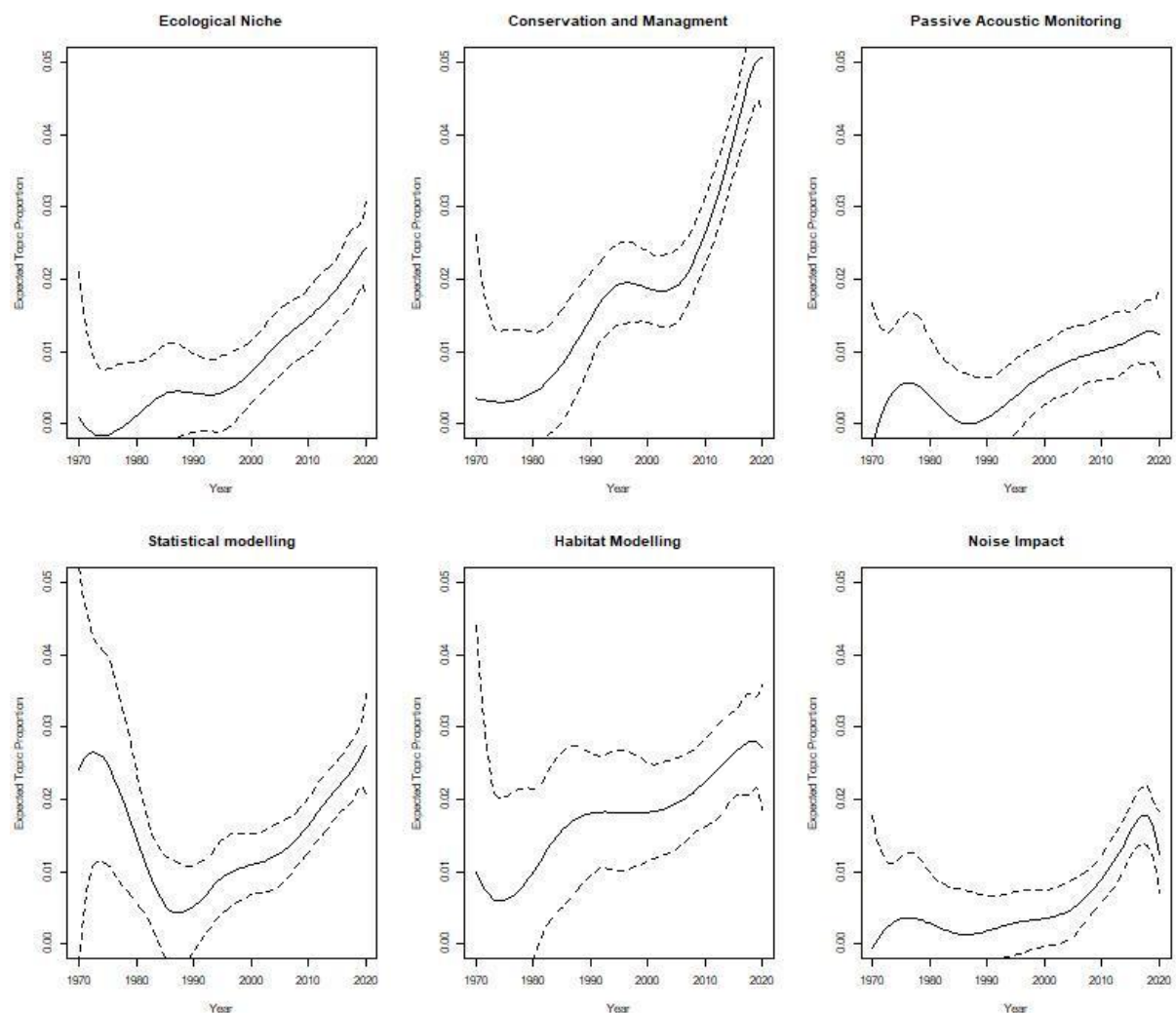


Figure 1.4. Odontocete research topics which show an upward trend in cubic -b-spline of expected topic proportion. 95% confidence intervals represented with dashed line.

Topic groups with a statistically significant upward trend were ‘Population Ecology and Genetics’, ‘Conservation management’, ‘Behaviour’, ‘Ecological Niche’, ‘Health and Disease’, and ‘Communication’. Topic groups with a statistically significant

downward trend were 'Biochemistry and Cellular', and 'Physiology'. Topic groups that showed no trend were 'Bioacoustics', 'Life History and Social Ecology', and 'Polar and Subpolar Ecology' (Figure 1.6).

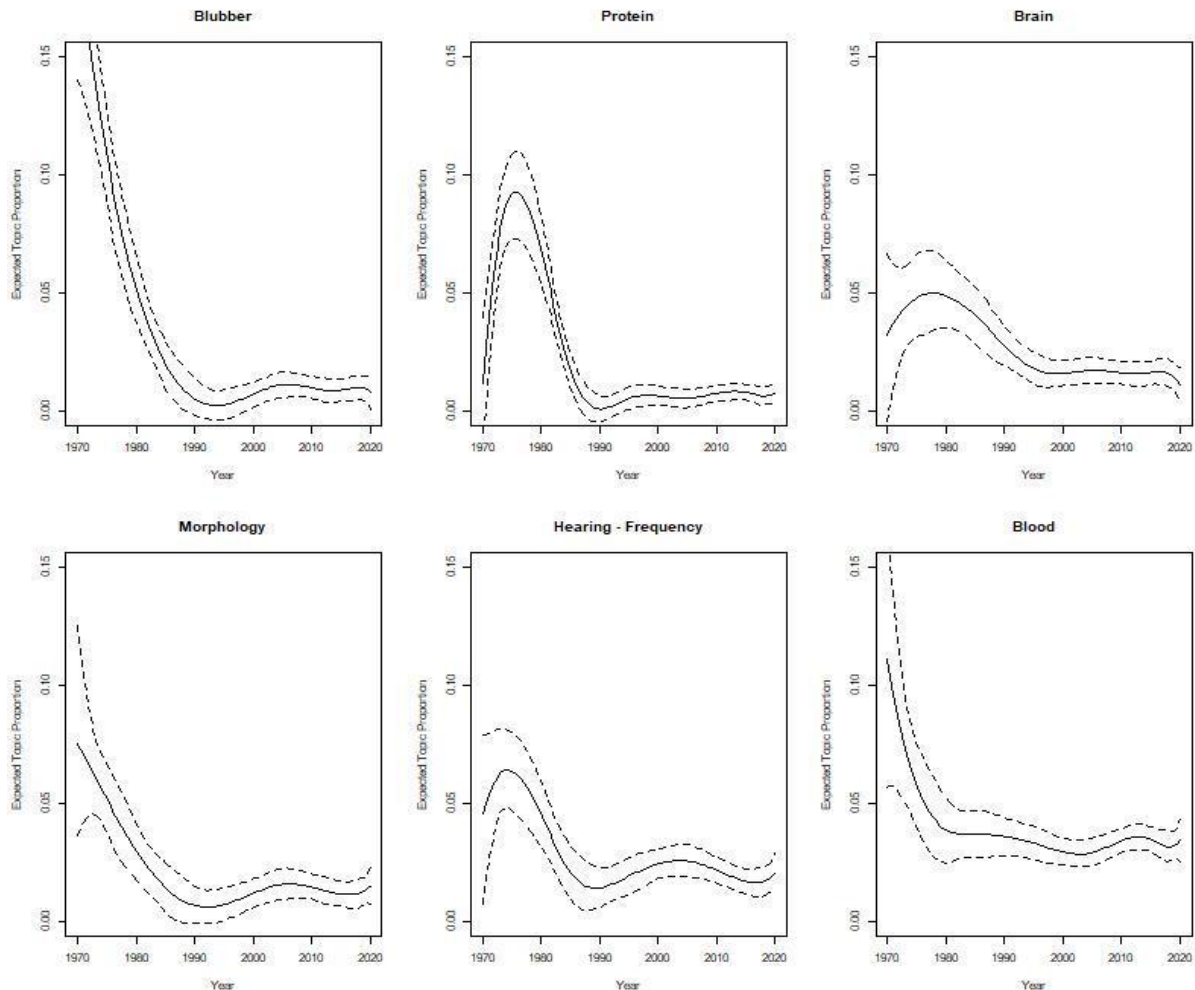


Figure 1.5. Odontocete research topics which show a downward trend in cubic *b*-spline of expected topic proportion. 95% confidence intervals represented with dashed line.

1.3.3 Topic generality

The topics with the highest mean selected metric were: 1. *brain*, 2. *protein*, 3. *blubber*, 4. *biosonar* and, 5. *heavy metal*, representing the most specific topics within the corpus. The topics with the highest mean unselected metric were: 1. *conservation and management*, 2. *ocean/geographic region*, 3. *statistical modelling*, 4. *habitat modelling* and, 5. *population assessment*, representing the most general topics. Figure 1.7 shows the mean selected and mean unselected metric scores for all 65 topics.

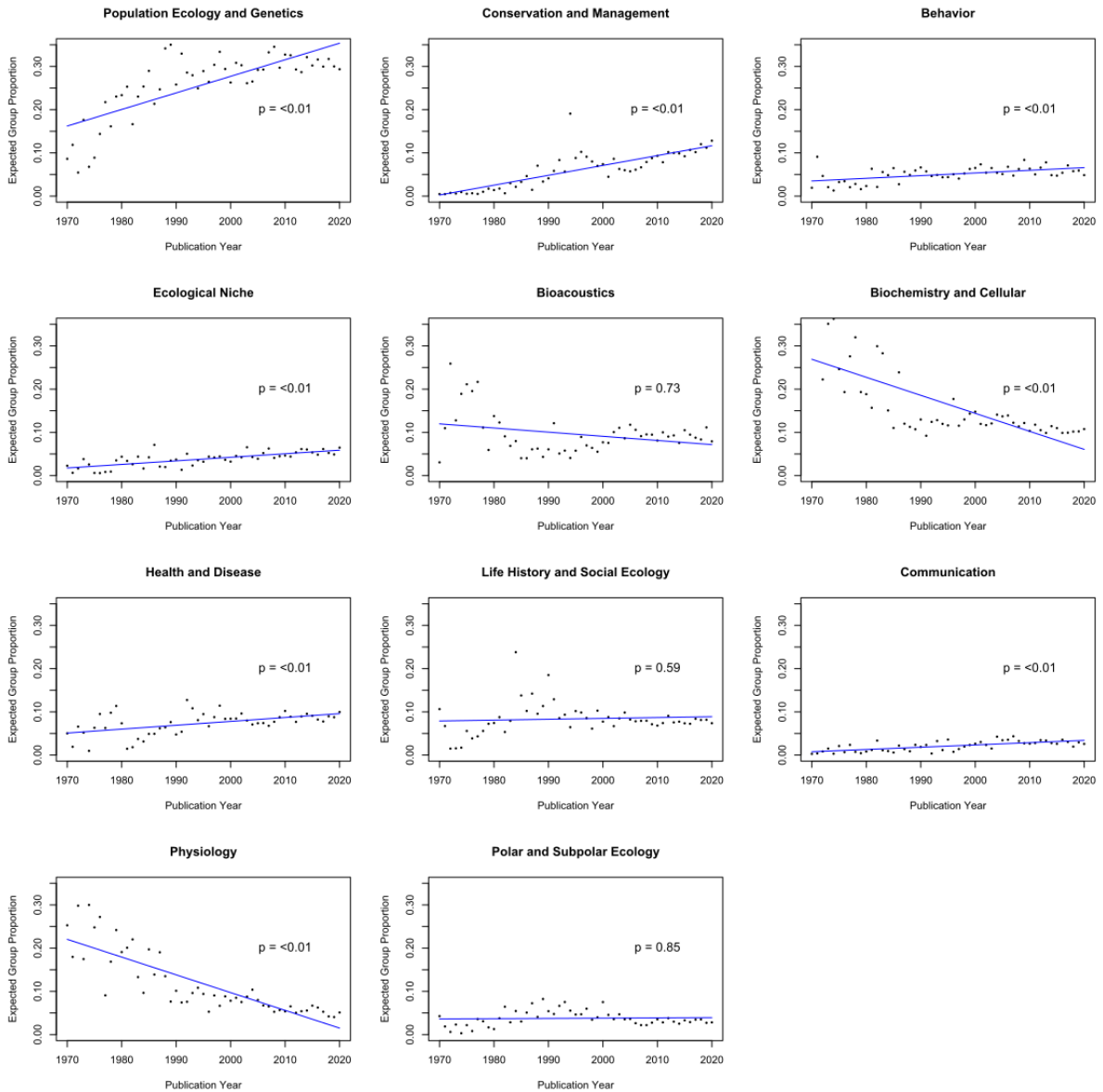


Figure 1.6. Expected corpus proportion over time for each topic group. Significance level of the Mann-Kendall trend test is shown for each topic group. Y axis fixed at 0 to 0.25 to facilitate comparing overall topic group proportion.

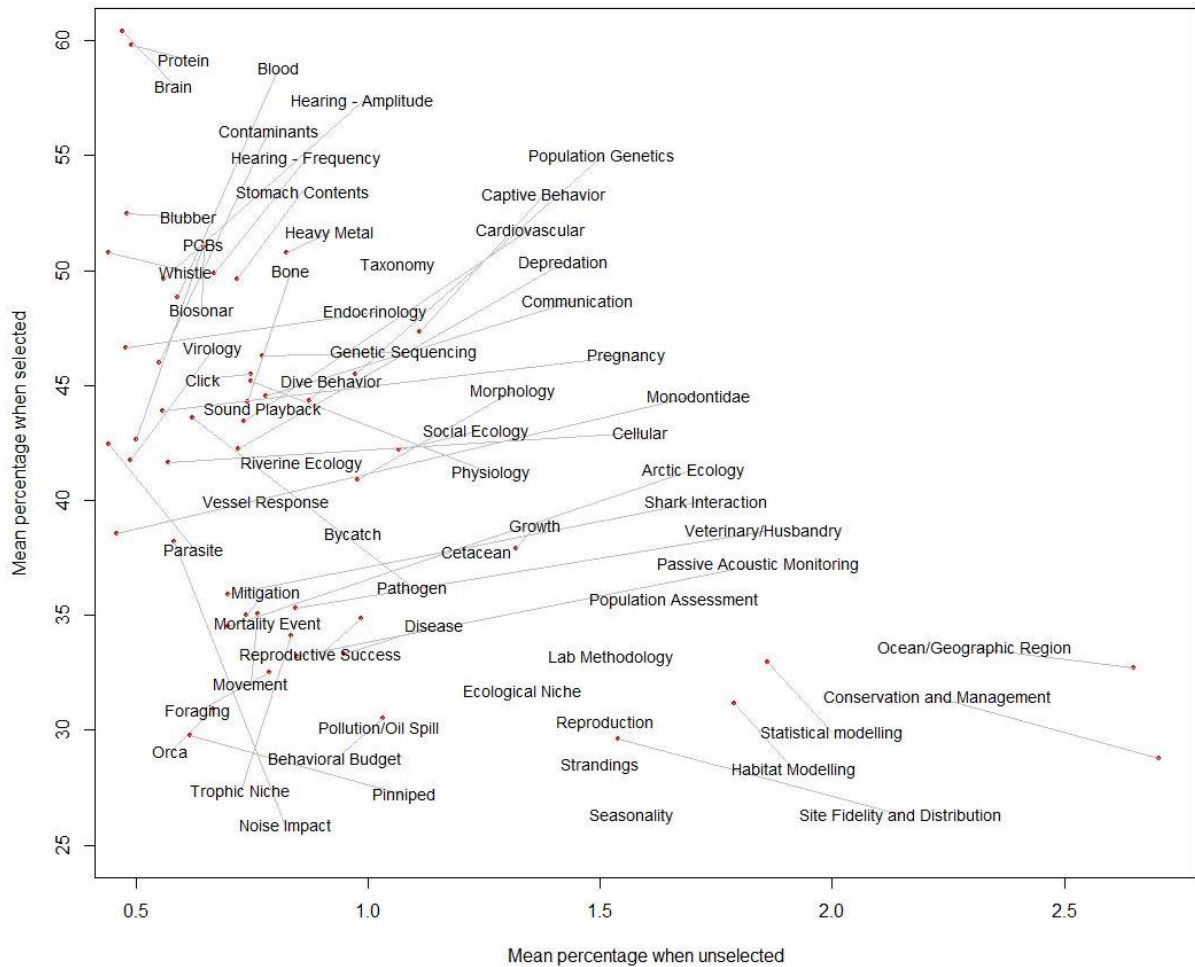


Figure 1.7. Figure showing the generality of topics, the most general topics have a higher mean percentage when unselected positioned to the bottom right of the graph. More specific topics have a lower mean percentage when unselected but a higher mean percentage when selected and are positioned to the top left of the graph.

1.3.4 Genus

The genus with the highest representation in the corpus was *Tursiops* with 2153 abstracts including the genus (27.1% of the corpus) (Figure 1.8).

Genera with the least number of abstracts were: *Tasmacetus* (n = 9, 0.1%), *Indopacetus* (n = 13, 0.2%), *Lissodelphis* (n = 29, 0.4%), *Feresa* (n = 35, 0.4%), *Berardius* (n = 37, 0.5%) and *Lipotes* (n = 45, 0.6%). When abstracts containing none and multiple genera were considered separately (the data available to the topic model), there were 1301 (16.4%) none abstracts and 1294 (16.3%) mixed abstracts. The Genus *Steno* was no longer represented as it was only in mixed genus abstracts. Differences in topic proportion that were significant ($p < 0.05$) for each genus are presented in Table 1.1.

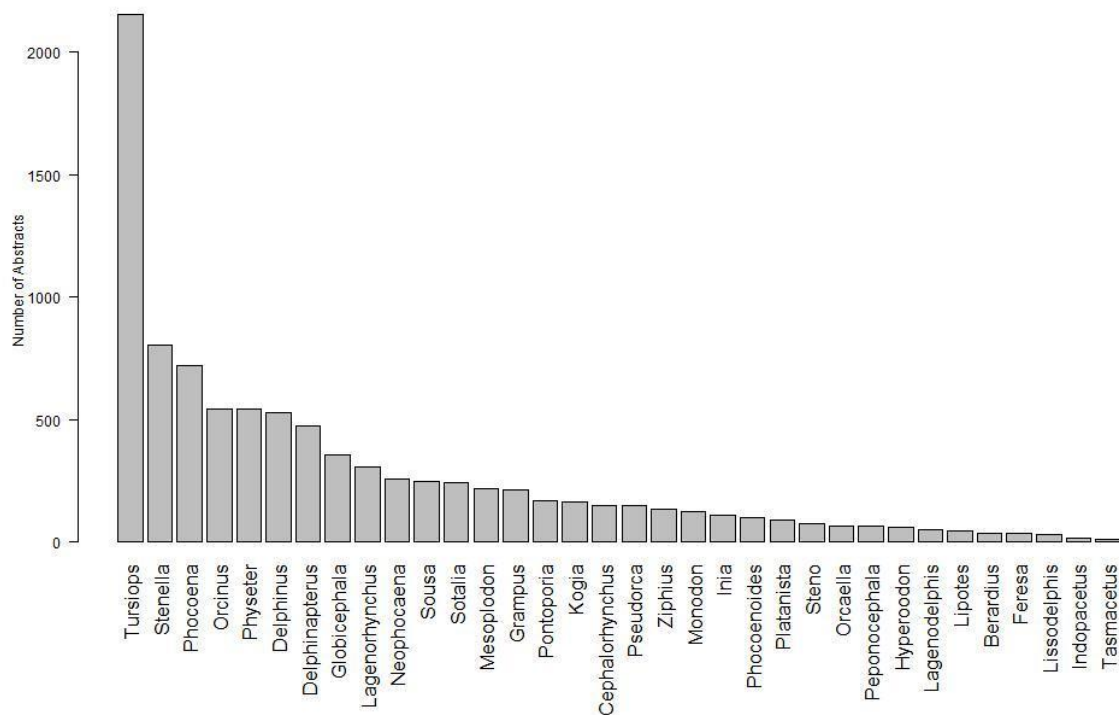


Figure 1.8. Number of abstracts within the corpus which mention the 34 odontocete genera.

Table 1.1. Significant results of regression analysis of topic proportion across genus groups.

Topic	Genus covariate	Regression Coefficient	SD	p-value
Seasonality	<i>Pseudorca</i>	0.052	0.018	0.004
Bycatch	<i>Phocoena</i>	0.044	0.019	0.023
	<i>Pontoporia</i>	0.051	0.022	0.020
Riverine Ecology	<i>Inia</i>	0.112	0.029	<0.001
	<i>Lipotes</i>	0.215	0.036	<0.001
	<i>Neophocaena</i>	0.084	0.019	<0.001
	<i>Orcaella</i>	0.086	0.028	0.002
	<i>Platanista</i>	0.188	0.032	<0.001
	<i>Sousa</i>	0.082	0.032	<0.001
Blubber	<i>Physeter</i>	-0.049	0.024	0.043
	<i>Sotalia</i>	-0.049	0.03025	0.044
Mitigation	<i>Inia</i>	0.042	0.019	0.027

	<i>Orcaella</i>	0.046	0.023	0.043
Protein	<i>Physeter</i>	0.038	0.019	0.048
Dive Behaviour	<i>Delphinus</i>	-0.075	0.037	0.045
	<i>Inia</i>	-0.077	0.038	0.044
	<i>Orcaella</i>	-0.082	0.039	0.036
	<i>Pontoporia</i>	-0.079	0.038	0.037
	<i>Pseudorca</i>	-0.081	0.038	0.035
	<i>Sotalia</i>	-0.079	0.038	0.036
	<i>Sousa</i>	-0.081	0.038	0.032
Whistle	<i>Sotalia</i>	0.052	0.022	0.018
Parasite	<i>Kogia</i>	0.076	0.023	0.001
Heavy Metal	<i>Phocoenoides</i>	0.112	0.038	0.003
Movement	<i>Monodon</i>	0.040	0.020	0.043
Biosonar	<i>Pseudorca</i>	0.104	0.031	<0.001
Conservation and Management	<i>Orcaella</i>	0.069	0.021	<0.001
	<i>Sousa</i>	0.047	0.019	0.011
Pollution/Oil Spill	<i>Sousa</i>	0.036	0.016	0.022
Virology	<i>Stenella</i>	0.036	0.019	0.048
Genetic Sequencing	<i>Lipotes</i>	0.144	0.042	<0.001
Foraging	<i>Lagenorhynchus</i>	0.032	0.016	0.039
	<i>Orcinus</i>	0.029	0.014	0.044
Growth	<i>Pontoporia</i>	0.044	0.022	0.043
Social Ecology	<i>Physeter</i>	0.040	0.021	0.050
Ocean/Geographic Region	<i>Delphinapterus</i>	-0.091	0.034	0.008
	<i>Inia</i>	-0.078	0.035	0.027
	<i>Lipotes</i>	-0.087	0.037	0.018

	<i>Monodon</i>	-0.090	0.035	0.010
	<i>Neophocaena</i>	-0.071	0.035	0.041
	<i>None</i>	-0.072	0.034	0.035
	<i>Phocoena</i>	-0.073	0.034	0.031
	<i>Platanista</i>	-0.075	0.036	0.036
	<i>Tursiops</i>	-0.076	0.034	0.026
Arctic Ecology	<i>Delphinapterus</i>	0.072	0.019	<0.001
	<i>Monodon</i>	0.125	0.026	<0.001
Depredation	<i>Pseudorca</i>	0.049	0.020	0.015
Site Fidelity and Distribution	<i>Cephalorhynchus</i>	0.034	0.017	0.044
	<i>Sotalia</i>	0.056	0.017	<0.001
	<i>Sousa</i>	0.066	0.016	<0.001
Orca	<i>Delphinapterus</i>	0.033	0.014	0.020
	<i>Orcinus</i>	0.073	0.015	<0.001
	<i>Physeter</i>	0.028	0.014	0.046
Pregnancy	<i>Phocoenoides</i>	0.066	0.025	0.009
Monodontidae	<i>Delphinapterus</i>	0.039	0.009	<0.001
	<i>Monodon</i>	0.050	0.013	<0.001

1.4 Discussion

1.4.1 The odontocete research corpus

The corpus was created using a single search string to query the Scopus database. It was designed to retrieve articles which contained genus names. Most scientific articles reference the binomial name in full in the abstract or title and this approach yielded more than 8700 articles. Any scientific research articles about odontocete species which do not refer to the subject species by binomial name or contain the words odontocete and odontoceti would not have been included in this analysis. The

odontocete corpus therefore represents a sample of the total body of odontocete research currently available for the period of interest. The approach taken to build the corpus in this study would likely bias research in odontocete biology and ecology (areas which would reference binomial names), rather than other scientific disciplines which may not. Given the objectives of the study this approach was suitable, and the results provide a meaningful insight into odontocete research. However, it is recognised that different approaches to build the corpus may result in different conclusions regarding topics, their prevalence, and their correlations.

1.4.2 Topic validity

Topic themes were identified by examining the keywords most associated with the topic under four different criteria (most frequent, FREX, lift and score). Furthermore, package *stm* provides exemplar documents for each topic, in this case, abstracts from the corpus which best represent each topic. These were helpful in confirming the topics and the two most exemplar abstracts are available for each Appendix A (Table A1). The correlation between topics was also considered and the resulting clusters after analysis were reasonable and provided a meaningful, higher-level set of research groups for consideration.

Another form of validation was comparing topic proportions across genera for topics that would be expected to have genus differences. The process of removing all odontocete genus and species words from the abstracts during the text cleaning stage meant that topics were not influenced by their presence. Topics *Orca*, *Monodontidae*, *river ecology* and *arctic ecology* were identified as topics where genus differences would be expected. For each of these topics, the model identified a significant increase in topic prevalence for the expected genera. Topic *Orca* was significantly more prevalent in the *Orcinus* abstracts; *Monodontidae* and *arctic ecology* were significantly more prevalent in *Delphinapterus* and *Monodon* abstracts, and *riverine ecology* was significantly more prevalent in *Inia*, *Lipotes*, *Neophocaena*, *Orcaella*, *Platanista* and *Sousa* abstracts, all genera which inhabit fresh and brackish waters.

The resulting topics identified by the model were generally intuitive and easy to determine. However, the separation of both *PCBs* and *contaminants* as well as *biosonar* and *click* were difficult to determine, and in both cases would likely have

been merged in a supervised topic model. Topic correlations and topic groups were also generally intuitive and split the topic themes into sensible research areas. The overall ease of interpretation and intuitive correlations suggest that the resulting topics and the further analysis provides meaningful insight into odontocete research. The chosen model included 65 topics. Using a higher number of topics would reveal odontocete research at a greater granularity, however this would be at the cost of coherence and would result in an increased proportion of topics that are difficult to interpret. Reducing the number of topics may result in more coherent topics (e.g., not split *PCBs* and *contaminants*), however, this would be at the detriment of losing some of the more detailed insights provided by the approach taken. The approach of this study, with 65 topics, provided a reasonable balance between granularity and interpretability.

1.4.3 Trends in odontocete research

The resulting 65 topics and the 11 topic groups highlight the multidisciplinary science and research focuses of odontocete biology and ecology in the 20th and 21st centuries. The highest weighted topic group was 'Population Ecology and Genetics' which had an expected proportion of 29.8%. It consisted of 15 topics including *habitat modelling*, *population assessment*, *population genetics*, *site fidelity and distribution*, and *seasonality*, which are all clustered close together on the network graph (Figure 1.3). These topics were also some of the more general, suggesting that abstracts likely included more than one of these correlated topics. This group also contained other correlated topics such as *genetic sequencing*, *lab methodologies*, *dive behaviour* and *taxonomy* which were less well clustered and had strong correlations with other groups. The 'Population Ecology and Genetics' group showed a significant upward trend, driven by the steep increase in this research in the 1970s and 1980s before plateauing at around 30% of the corpus from the 1990s to 2020.

The second most prevalent topic group is 'Biochemistry and Cellular' with an expected proportion of 12.0%. This topic group saw a significant decreasing trend over the period, which was driven by the large prevalence of topics *blubber*, *protein* and *blood* at the start of the study period, which then dropped off in later years. Despite this stark decrease, the topic group still represents a large proportion of the

corpus in the later years of the study. Topic group 'Physiology' (with 7.0% expected proportion) was the only other topic group which had a significant decrease in prevalence over the study.

Topic group 'Conservation and Management' showed a large increase across the period from the 1970s, when there was very little representation, to the later period where it is now well represented. The topic group contained topics *conservation and management*, *mitigation*, *fisheries bycatch*, *depredation*, and *riverine ecology*. The clustering of *riverine ecology* to this group shows that research on river dolphins and similar species has a strong conservation focus. The topic *conservation and management* was the most prevalent within the whole corpus with an expected proportion of 3.3%. It has increased the most over the whole period and with the greatest increase observed in the last decade (Figure 1.9). It was however the most general with the lowest mean when selected (28.8%) and highest mean when not selected (2.7%). This suggests that although this topic was prevalent in many abstracts it was usually discussed alongside other topics rather than being the core research theme of the abstract. This can be explained by authors of academic papers in many areas of odontocete research framing their results and conclusions with their applicability to conservation and management. Topic *mitigation* was another topic within the 'Conservation and Management' group. This topic represents conservation efforts which directly attempt to improve the conservation outlook for odontocete species. It is notable that although the trend over time does show an increase it does not track alongside the increase of topic *conservation* in the latter half of the study. The prevalence of the topic is also influenced by its correlation with *bycatch* and its variable prevalence across time (Figure 1.9).

Bycatch is considered the most serious threat to odontocete species around the world (Reeves et al., 2005, Read et al., 2006, Nelms et al., 2021). Increase in mortality due to bycatch can cause populations to decline, particularly for small, isolated populations that often overlap with fisheries (Brownell Jr et al., 2019). Such isolated populations of odontocetes are typically associated with coastal areas where fishing pressure may be high (Temple et al., 2021b). The trend in bycatch increased in the mid-1980s but then dropped off before further decrease between 2005 and 2020 (Figure 1.9). When compared to other topics the inconsistent pattern suggests that bycatch does not receive the same level of research attention as many other

areas of population ecology or conservation, despite its high prevalence and potential impact on population viability. Calls for increased research and mitigation efforts for odontocete bycatch have been issued by various authors in recent years (Brownell Jr et al., 2019, Dolman et al., 2021, Rogan et al., 2021) as action needs to be taken to protect odontocete species.

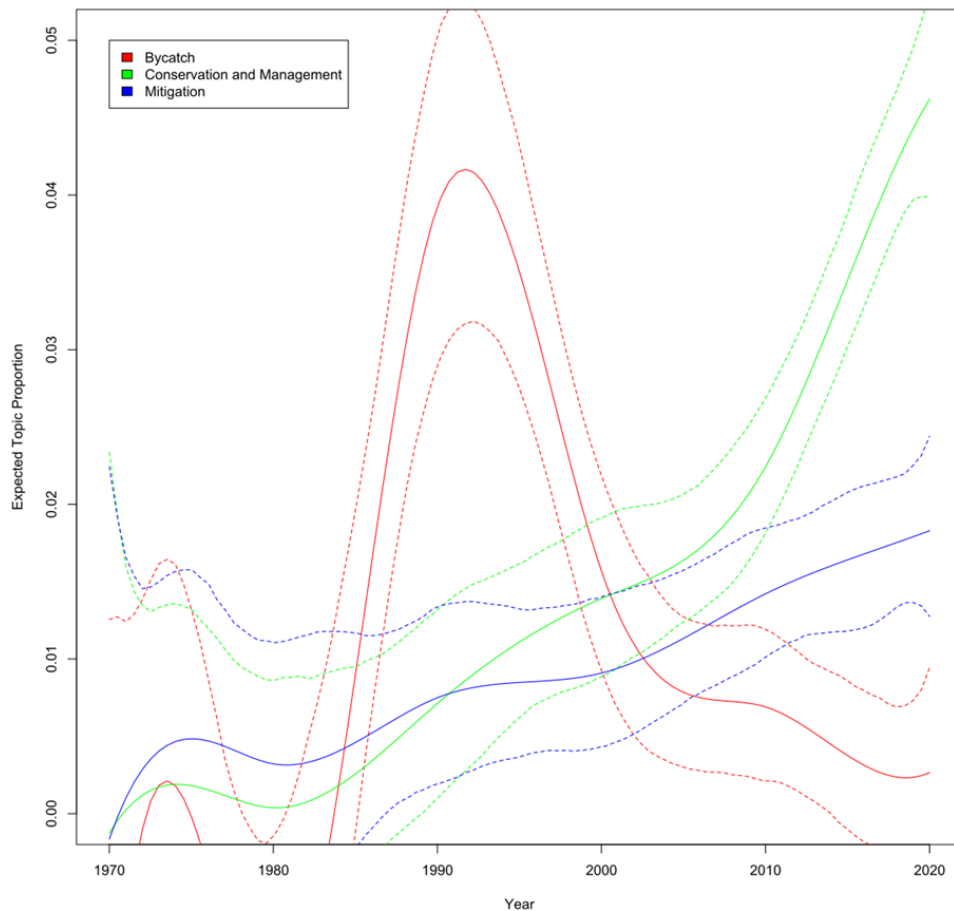


Figure 1.9. Trends in topic proportion over time of topics Conservation and Management, Mitigation and Bycatch

Topic group ‘Health and Disease’ included topics such as *virology*, *pathogen* and *parasites* and is driven by two separate research areas - wild populations and captive animals. Within this group the topic *strandings* is most prevalent, highlighting the importance of studying dead animals that can be sampled or necropsied when they land. Topic *veterinary/husbandry* is also within this group as odontocetes have been kept in captivity since the late 1940s (McBride and Hebb, 1948).

The topic group ‘Life History and Social Ecology’ had an expected proportion of 8.2% and did not show a significant trend. This group contained topics related to growth,

reproductive biology, and social ecology. The other smaller topic groups included 'Behaviour', which consisted of *captive behaviour*, *behavioural budgets*, *foraging and vessel response*, and 'Ecological Niche', which consisted of *stomach contents*, *ecological niche*, and *trophic niche*.

'Polar and Subpolar Ecology' was the only topic group which was not a clearly defined scientific area. This group contained the topics *pinniped*, *Orca*, and *monodontidae* - topics related to specific animal groups and arctic ecology. The emergence of these topics and their correlation suggest that the language used to discuss these topics was different enough to be identified by the STM model. This may be expected given the unique habitat and research challenges associated with working in the polar regions such as strong seasonality, polar winters, and ice cover.

'Bioacoustics' (with expected proportion of 8.9%) and the closely related 'Communication' group (2.7%) are important areas of odontocete research. Odontocetes have evolved to use sound and hearing as their primary sense, with the functionally blind Indus River dolphin representing an extreme case (Herald et al., 1969). Echolocation is used by all odontocete species to navigate, capture prey and investigate objects. Echolocation requires highly specialized tissues (e.g., the phonic lips, melon, and acoustic fat in lower jaw) and hearing capabilities (Brill et al., 1988, Cranford et al., 1996, McKenna et al., 2012, Mooney et al., 2012). Such specialisation has been of interest to the scientific community and is well represented in the corpus. Communication in odontocetes is also well studied, characterised by their use of whistles and other calls (Karlsen et al., 2002, Deecke et al., 2010, King et al., 2019, Courts et al., 2020). For example, bottlenose dolphins (*Tursiops spp.*) have been demonstrated to produce individually specific whistles called signature whistles (Janik and Sayigh, 2013). Killer whales (*Orcinus orca*) have been demonstrated to have distinct dialects between social clans (Ford, 1984) and beluga whales (*Delphinapterus leucas*) have a highly variable vocal repertoire (Maurel et al., 1986). Bioacoustics studies were one of the most prevalent research areas in the 1970s and maintain a high proportion of the corpus across the whole period. The 'Communication' group shows a significant upward trend but has maintained a relatively low proportion overall. The *noise impact* topic has increased in prevalence in recent years reflecting conservation concerns regarding the

increased amount of anthropogenic noise caused by industrial developments, shipping, and other human activities (Duarte et al., 2021).

Passive acoustic monitoring (PAM) (the primary method used in the following chapters of this thesis) has increased in prevalence since the 1990s due to the increasing affordability and accessibility of hydrophones and the advancement of the technology that allows for large amounts of data to be recorded on self-contained systems (e.g., C-POD, www.chelonia.co.uk; SoundTrap, www.oceaninstruments.co.nz). PAM has the potential to collect occurrence and behavioural data on less easily monitored species, such as those occupying deep offshore water where visual surveys are logistically difficult or expensive (Giorli et al., 2016). The topic was grouped into 'Bioacoustics' but it is positioned closer to population ecology and behavioural topics in the network graph, reflecting its application in these fields. A closer inspection of the topics most correlated with *passive acoustic monitoring* identified topics from a range of topic groups, including *population assessment*, *lab methodologies*, *movement*, *vessel response* and *mitigation* (Figure 1.10). Its highest correlation is with topic group *click* reflecting the use of click detections as an often-used detection for PAM studies (Johnson et al., 2006, Soldevilla et al., 2008, Todd et al., 2009, Bailey et al., 2010).

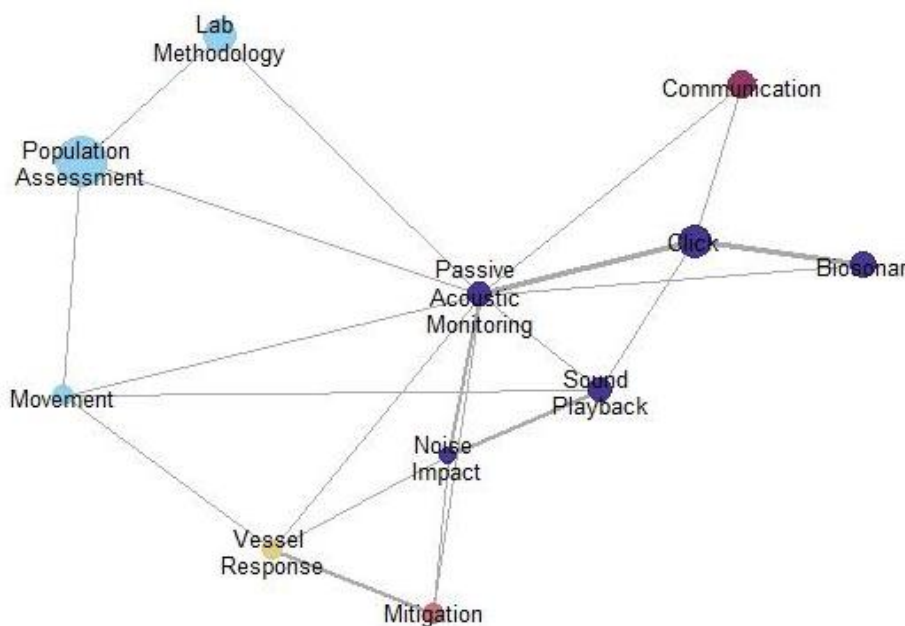


Figure 1.10. Subgraph of the topic network showing the topics correlated to passive acoustic monitoring.

1.4.4 Genus representation

The genus *Tursiops* (i.e., bottlenose dolphins) was by far the most studied group of odontocetes and had the most abstracts in the corpus. Bottlenose dolphins have a cosmopolitan distribution (Wells and Scott, 2018), and many populations inhabit coastal areas and have small home ranges associated with estuaries, bays and inlets (Mazzoil et al., 2005, Balmer et al., 2008, Foley et al., 2010). This allows researchers to have easy and reliable access to these animals and facilitates longitudinal studies such as those conducted in Sarasota Bay, Shark Bay and the Moray Firth (Wilson, 1995, Wells, 2014, Connor and Krützen, 2015). They are also kept as captive animals and are one of the most numerous odontocete species kept in captivity. Genera which had limited representation were *Tasmacetus*, *Indopacetus*, *Lissodelphis*, *Feresa*, *Berardius*, and *Lipotes*. Except for the now functionally extinct Baiji (*Lipotes*) which inhabited the Yangze River, China, these lowest represented genera are oceanic. Animals inhabiting offshore areas are more difficult to study due to the logistics and costs. Animals that occupy large habitats both in terms of area and volume are more difficult to study due to the chances of finding animals to observe or sample.

Difference in topic prevalence was modelled across different genus abstracts and those with mixed or no genus representation. 27 of the 65 topics showed at least one significantly different genus (Table 1.1). Topics which would be expected to have differences were used as model validation as mentioned above. The increased prevalence of *Phocoenoides* in Pregnancy, PCBs and Heavy metals is likely driven by the continued commercial take of this species by Japanese whalers in the North Pacific (Kasuya, 2007).

1.4.5 Conclusion

The Structural Topic Model identified important areas of odontocete research and the trend in research focus over time. At the start of the time period there was a much greater emphasis on morphological and physiological research. The increase in population level studies that started in the 1970s and 1980s is evident in the analysis which also suggests that since the 1990s there remains a consistent research focus in this area. Conservation science has increased as a result of these

studies as the scientific community has become more acutely aware of the risk to long-term survival for many odontocete populations due to human activities.

Conservation research continues to increase in prevalence throughout the study period. However, there is a clear difference in the prevalence of research abstracts that refer to conservation matters, identify threats and highlight potential issues and those that aim to implement change or mitigate threats preventing further risk. This is inferred from the mitigation topic which although increased over time remains at a low expected proportion of the corpus. This is also seen in the variable number of publications on fisheries bycatch across the time period. Fisheries bycatch is one of the greatest threats to population viability as it is a direct cause of increased mortality, impacting all age groups. The next stage of odontocete research needs to have a greater emphasis on facilitating change in human behaviour, through stronger influence of governmental policy, by providing mitigation technologies or strategies, or supporting grassroots change to address the bycatch threat. There also needs to be greater research effort across odontocete species with the corpus currently heavily biased towards bottlenose dolphins. This could be facilitated by research funders providing more support for research on relatively unknown species groups such as oceanic dolphin and beaked whale species.

This study gives a broad overview of the history and current state of odontocete research and highlights in greater detail areas in population assessment and conservation research that can be improved to help protect odontocete species and their viability.

Passive acoustic monitoring is the primary methodology used during the following chapters of this thesis. The topic *passive acoustic monitoring* was identified as an emerging topic over the last 20 years that connects research from the field of bioacoustics to others such as population ecology, behaviour, and conservation. This thesis aims to advance the application of PAM through the use of emerging and novel methodologies, including the use of whistles (an identified topic not correlated to *passive acoustic monitoring*) to investigate dolphin behaviour and abundance.

Chapter 2. Effects of Environmental Drivers on Odontocete Occurrence off the Northumberland Coast, UK

2.1 Introduction

Odontocetes that inhabit urbanised coastal waters are at risk from anthropogenic activities which if not managed correctly can lead to population decline and animal welfare concerns (Brownell Jr et al., 2019, Nicol et al., 2020, Nelms et al., 2021). To protect biodiversity, marine conservation strategies are often based on establishing marine protected areas (MPAs) (Agardy, 1994, Hooker and Gerber, 2004) and MPAs are recommended for the protection of odontocetes species by multiple international frameworks (e.g., ASCOBANS 1991, ACCOBAMS 1992, and EU habitats Directive 1992). In the UK, special areas of conservation (SACs) have been established to protect common bottlenose dolphin (*Tursiops truncatus*) and harbour porpoise (*Phocoena phocoena*) (species listed under annex II of the EU Habitat Directive (92/43/EEC) and remain in place post-Brexit (Fisheries Act 2020)). Designations such as these protect specific areas important for the target species' long-term survival (Bristow and Rees, 2001, Wilson et al., 2004, Embling et al., 2010, Booth et al., 2013), meeting the EU habitat directive's criteria that candidate SACs must be "essential for life and reproduction". Knowledge of species occurrence is therefore essential for identifying new potential and monitoring the effectiveness of already established conservation strategies.

As marine top predators, odontocetes have evolved to exploit highly dynamic ecosystems and exhibit variable patterns of occurrence across different spatial and temporal scales, affected by various biotic and environmental factors that drive resource availability (Barry and Dayton, 1991, Hastie et al., 2003, Bailey et al., 2010, de Boer et al., 2014, Nuuttila et al., 2017, Fernandez-Betelu et al., 2019).

Odontocete are highly mobile and MPAs rarely cover the entire range of the target species (Arso Civil et al., 2019, Charish et al., 2021). Studies conducted across different spatial and temporal scales, both within and outside of established protected areas, are required to identify patterns of occurrence in greater detail to better inform conservation (Arso Civil et al., 2019, Palmer et al., 2019). Studies at smaller spatial scales but with good temporal coverage can identify important areas

that may have high importance for supporting odontocete populations (Pierpoint, 2008, Jones et al., 2014).

One widely applied method for monitoring odontocete occurrence is Passive Acoustic Monitoring (PAM) (Mellinger et al., 2007). Odontocetes produce various vocalisations which can be detected and used as a proxy for species occupancy (Thompson, 2011). Remote, long-term PAM can provide near-continuous monitoring of vocalising odontocetes within their detection radius across temporal scales of weeks to years (depending on sampling protocols), unaffected by diel cycle or seasonal weather patterns (Notarbartolo di Sciara and Gordon, 1997). Long term deployments produce datasets suitable for modelling the effects of temporally variable environmental factors such as diel phase, tidal phase, and seasonal changes as drivers to odontocete occurrence (Thompson et al., 2015).

With the increase in availability of high frequency self-contained recording units (HARP (Wiggins and Hildebrand, 2007); SoundTrap (www.oceaninstruments.co.nz) and specialised click loggers (e.g., T/C/F-POD (www.chelonia.co.uk)), odontocete echolocation clicks have become a viable option for PAM (Mellinger et al., 2004, Verfuß et al., 2007). All odontocete species produce clicks to navigate their environment, investigate objects, and facilitate prey capture (Au, 1993) and they can be identified as transient signals in acoustic recordings (Kandia and Stylianou, 2006, Gillespie and Caillat, 2008). Discriminating between species groups is possible using clicks' spectral and temporal properties: phocoenids and delphinids can be separated from peak frequency, with phocoenids having higher peak and a narrower frequency band (termed narrow band high frequency (NBHF) (Madsen et al., 2005)), with discrimination possible using T/C-PODs (Kamminga, 1996, Bailey et al., 2010); delphinid and sperm whales (*Physeter macrocephalus*) can be separated by frequency with sperm whales producing clicks an order of magnitude lower than delphinids (Goold and Jones, 1995); and delphinids and beaked whales (Ziphiidae) can be separated by spectral properties including frequency sweeps (Zimmer et al., 2005, Johnson et al., 2006). However, separating sympatric delphinid species can be difficult for some species and confound the interpretation of results in areas with higher delphinid diversity (Thompson et al., 2010, Temple et al., 2016, Palmer et al., 2019). One viable method for separating delphinid species is to identify spectral banding in click spectrograms and use this information (i.e., presence and location of

frequency bands) to classify clicks to species level (Soldevilla et al., 2008). Clicks with spectral banding have been identified for Pacific white-sided (*Lagenorhynchus obliquidens*), Risso's (*Grampus griseus*) and white-beaked dolphin (*Lagenorhynchus albirostris*) (Soldevilla et al., 2008, Calderan et al., 2013, Yang et al., 2021) and have been used to identify species for long term monitoring of Risso's and Pacific white-sided dolphin (Soldevilla et al., 2010, Soldevilla et al., 2011). Classifying clicks from delphinid species which do not have spectral banding characteristics remains difficult, but statistical approaches show promise (Yang et al., 2020). Identifying spectral banding requires full spectrum recordings and long-term spectral averaging (LTSA) using the method outlined in Soldevilla et al. (2017), but see Palmer et al. (2019) for approach to differentiating clicks with and without spectral banding from C-POD detection data.

Odontocete occurrence off the Northumberland coast (Northeast England, North Sea) is not well characterised, with information available from only a small number of peer-reviewed publications (VanBressema et al., 2018, Trotter et al., 2019, Yang et al., 2021, Potlock et al., *In Review*), governmental and industry reports (Brereton et al., 2010, Temple and Berggren, 2015, Temple et al., 2019), and from ongoing citizen science projects (e.g., www.seawatchfoundation.org.uk). However, these studies provide consistent evidence of three sympatric odontocete species that exhibit seasonal occupancy of the area: harbour porpoise, white-beaked dolphin, and common bottlenose dolphin. Harbour porpoise and white-beaked dolphin are the most and second most abundant odontocete species in the North Sea, respectively (Hammond et al., 1995, Hammond et al., 2013, Hammond et al., 2017). Harbour porpoises are sighted around the British Isles, but occupancy can vary considerably at small spatial and across different temporal scales (Northridge et al., 1995, Pierpoint, 2008, de Boer et al., 2014, Jones et al., 2014, Nuuttila et al., 2017). White-beaked dolphins are endemic to the North Atlantic Ocean with a preference for colder water (MacLeod et al., 2007, Canning et al., 2008, Kinze, 2009). There is evidence that the species will be impacted by climate change and there has been documented change of distribution with a decrease in the southern North Sea and off the West Coast of Scotland (MacLeod et al., 2005, MacLeod, 2009, Lambert et al., 2014, IJsseldijk et al., 2018). There have been very few studies on white-beaked dolphin at smaller spatial scales, but they are reported to use nearshore waters more

frequently during summer (Weir et al., 2007, Canning et al., 2008). Sightings of bottlenose dolphin off Northumberland have increased in recent years with photographic evidence linking individuals identified in the area from the “East Coast” populations associated with the Moray firth and Aberdeenshire coast (Cheney et al., 2013, Aynsley, 2017). Given the recent distribution change in sighted individuals it is not yet certain what proportion of the population are sighted off Northumberland (see Chapter 4) or whether the distributional shift is long term (Shirakihara et al., 2021).

Most relevant to this study are two PAM studies which used C-POD arrays to investigate odontocete occurrence off Blyth, the first conducted in 2015 was prior to an offshore wind turbine development in the area (Temple and Berggren, 2015) and the second monitored occurrence before, during and after the development between 2016 and 2018) (Potlock et al., *In Review*). The studies presented porpoise and delphinid (bottlenose and white-beaked dolphin) occurrence patterns at a small spatial scale and demonstrated differences in odontocete occurrence across different temporal scales. However, inability to separate delphinid species prevented species specific interpretation and conclusions for bottlenose and white-beaked dolphin.

Northumberland has two overlapping near-shore marine conservation zones, the Coquet to St Marys MCZ (2016) and the Berwick to St Mary’s MCZ (2019) and an SAC, Berwickshire and North Northumberland Coast SAC (2005) (www.gov.uk). The MCZs were designated to protect several subtidal and intertidal habitat types, and to return favourable conservation status of the eider duck (*Somateria mollissima*), respectively. The SAC lists a number of coastal habitat types and grey seal (*Halichoerus grypus*) as primary selection features of the SAC. Neither bottlenose dolphin nor harbour porpoise are listed as a qualifying species despite being listed as annex II species under the EU Habitats Directive for implementing SACs (jncc.gov.uk). There are currently no conservation management strategies in place for odontocete species off Northumberland and no SAC for bottlenose dolphin in England.

This study builds on previous PAM studies conducted in the area (Temple and Berggren, 2015, Potlock et al., *In Review*) by using high frequency broad band hydrophones to collect odontocete click data allowing for a separation of white-

beaked and bottlenose dolphins. The study will investigate the effects of environmental drivers on the occurrence for all the three odontocete species off the Northumberland coast at a larger spatial scale than previously achieved for the area to better inform conservation and management.

2.2 Methodology

2.2.1 Data collection

Acoustic data were collected between July 2019 and October 2021 at three locations along the Northumberland Coast, UK, within the Coquet to St Mary's Marine Conservation Zone. SoundTrap 300HF hydrophones (Ocean Instruments, New Zealand; sensitivity: -171 dB re 1 V/ μ Pa and flat frequency response: $0.4 - 150$ kHz \pm 3 dB) were deployed at Druridge Bay ($55^{\circ} 16.3$ N, $1^{\circ} 31.5$ W; hereafter DB), off Newbiggin-by-the-Sea ($55^{\circ} 11$ N, $1^{\circ} 29$ W; hereafter NB) and off St Mary's Island ($55^{\circ} 04.3$ N, $1^{\circ} 26.3$ W; hereafter SM) (Figure 2.1). The devices were configured to record continuously at a sampling rate of 576 kHz, providing approximately 13 days of continuous data collection for each deployment, due to the limitations of the devices memory capacity. Each hydrophone was deployed 4 m above the seafloor between the 15 and 20 m depth contours (Figure 2.2).

During the data collection period there were a total of 80 successful deployments resulting in a total of $20,845$ number of recorded hours. Figure 2.3 shows data collection at each site across the entire study period. In summary, there was near continuous data collection between July to October 2019 at all three sites; intermittent data collection at NB and SM between October 2019 and March 2020; no data were collected between April and September 2020 (due to the impact of Covid-19 pandemic); and data were consistently collected at all three sites between October 2020 and October 2021 (except for missing data between June to October at SM due to lost devices).

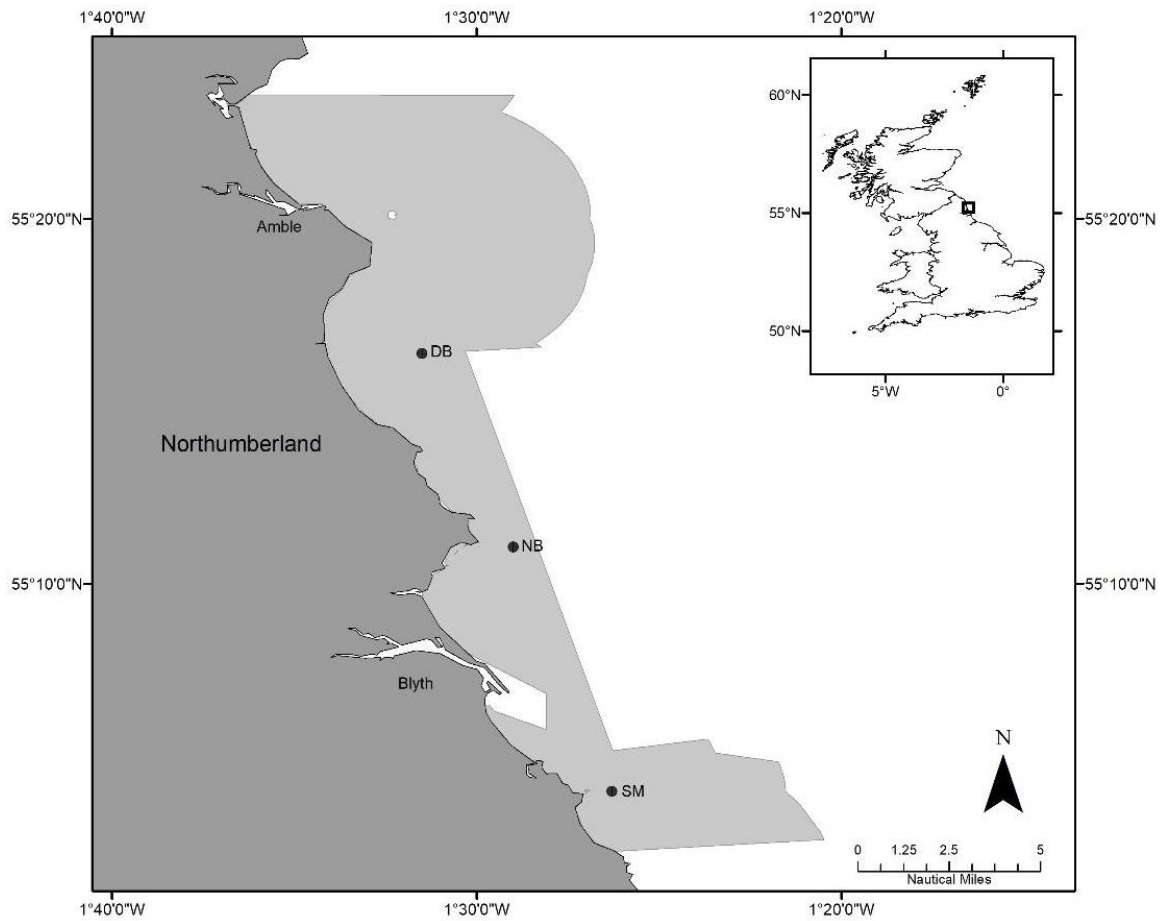


Figure 2.1. Map of study area with the position of each hydrophone deployment identified with a labelled dot (DB = Druridge Bay, NB = Newbiggin and SM = St Mary's). Shaded area identifies the boundary of the Coquet to St Mary's MCZ. Inlaid map of Britain showing location of study area.

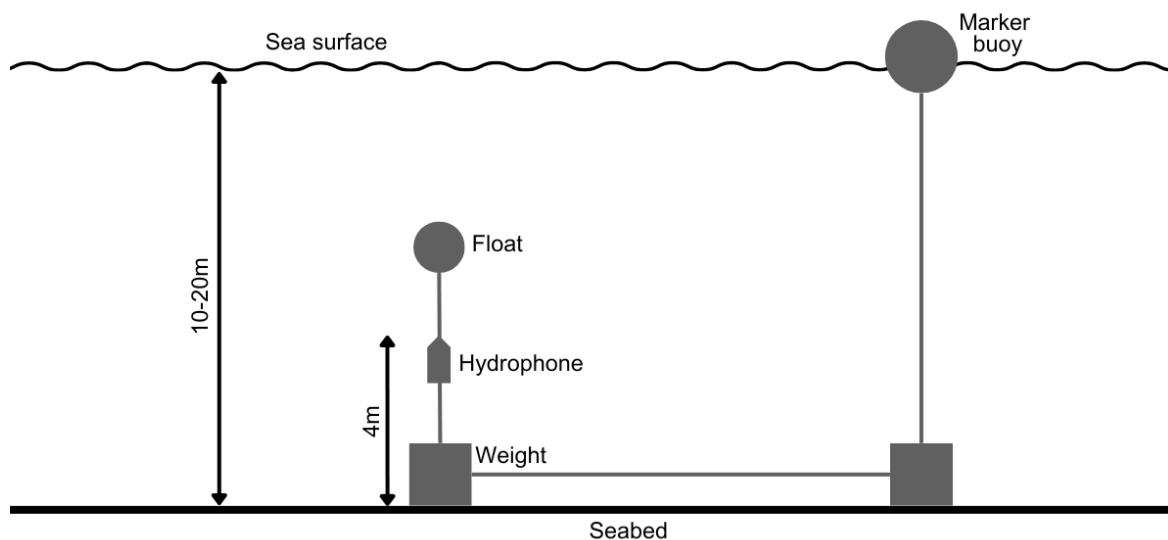


Figure 2.2. Schematic of the hydrophone deployment showing the hydrophone positioned 4 m from the seafloor, between the 10 and 20 m depth contour.

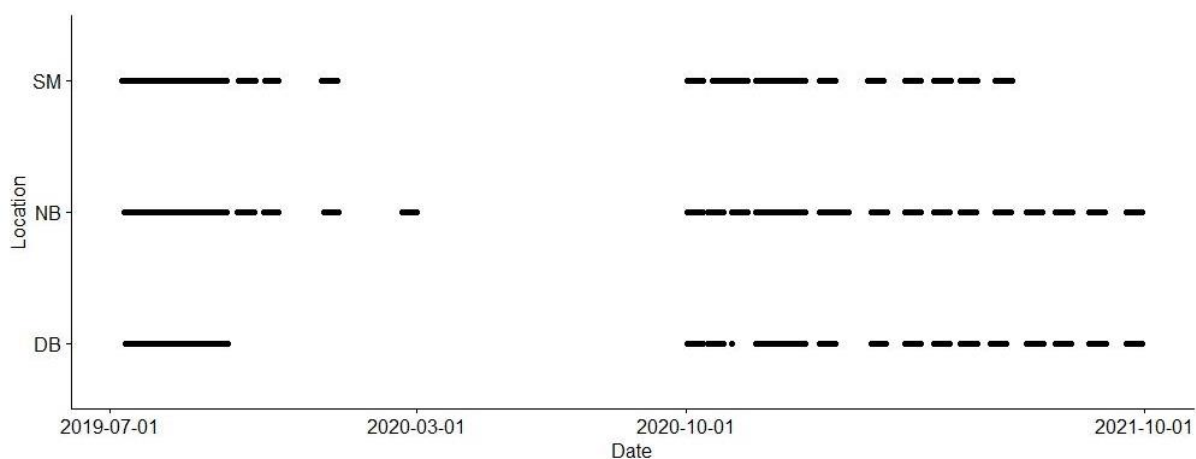


Figure 2.3. Periods of acoustic data collection at each location during the study. Black horizontal lines indicate when the hydrophones were deployed and recording data.

2.2.2 Data processing

A semi-supervised approach was taken to identify odontocete echolocation click trains within the acoustic recordings and to determine species presence/absence for 1-hour time intervals. The approach taken used Pamguard (Gillespie et al., 2008) click detector and click train detector modules to identify possible porpoise or dolphin click trains. Positive detection periods were then evaluated using Pamguard viewer

mode and Long-Term Spectral Averaging (LTSA) to determine true odontocete echolocation click train periods and separate dolphin positive periods to species level (bottlenose or white-beaked dolphin). The flow diagram (Figure 2.4) outlines the data processing and analysis pipeline.

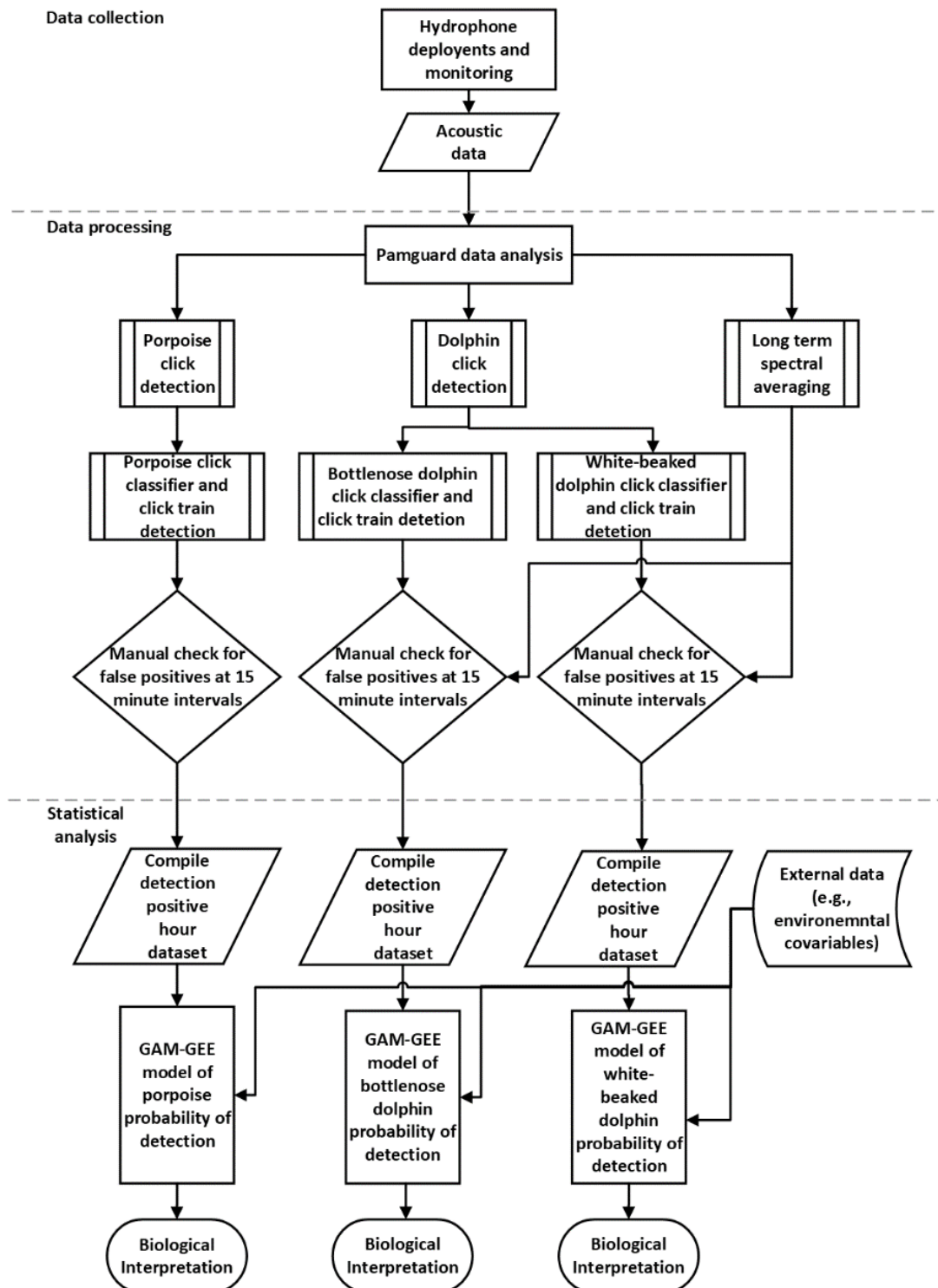


Figure 2.4. Flow diagram of the data collection, processing, and analysis pipeline for the detection and modelling of odontocete occurrence off the Northumberland coast using passive acoustic monitoring.

2.2.3 Click detection

Pamguard's click detector module identifies transient signals (i.e., odontocete clicks) within a raw audio source (in this case, from the SoundTrap recordings). The raw audio passes through a prefilter and trigger filter before entering the trigger component of the click detector which automatically measures background noise and transient signal levels. When the signal level exceeds the noise level by a user specified threshold the trigger is activated, and a click clip is created from the output of the prefilter. The click clip is then passed to the classifier component of the detector. If the click clip meets specific conditions regarding its waveform and spectral components, it passes the classification and is stored and/or displayed.

A single instance of Pamguard was configured which included two separate click detector modules. The first click detector module was configured to detect porpoise clicks and included a 4th order Butterworth 10 kHz high pass prefilter and a 6th order 100 – 150 kHz band pass Chebyshev trigger filter. These settings were based on the standard porpoise detection settings available from the Pamguard website (www.pamguard.org). The signal level threshold was set to 10 dB. A single click classifier was included to determine whether a detected click was produced by porpoise and to remove potential false positives. For a click to pass the porpoise classifier the smoothed waveform required a click length of between 0.07 and 0.1 ms, between 10 and 50 zero-crossings and a zero-crossing frequency sweep between -200 and 200 kHz/ms. A porpoise classified click also had energy within the 110 to 150 kHz range that was at least 12 dB greater than control bands 40 - 90 kHz and 160 - 190 kHz and had a peak frequency between 100 and 150 kHz within an integration range of 20 – 240 kHz (Figure 2.5 A and B).

The second click detector module was configured to detect dolphin clicks and included an 8th order 5 kHz high pass prefilter and a 6th order 20 – 120 kHz band pass Chebyshev trigger filter; trigger threshold was set to 15 dB. These filter settings were based on the frequency domain of both on and off axis dolphin clicks, adapted from filter settings used in Garrod et al. (2018). Detected clicks were passed to the classifier which was configured to have two separate classifiers optimised based on training recordings of bottlenose dolphin (dolphin1) and white beaked dolphin (dolphin2). To pass classifier dolphin1, the smoothed click waveforms had to be less

than 0.16 ms in length and have 2 to 7 zero-crossings. Spectral energy within the test band of 18 – 90 kHz was at least 18 dB greater than control bands 5 - 7 kHz and 150 - 200 kHz and the click peak frequency was between 18-90 kHz within an integration range of 7 – 90 kHz (Figure 2.5 C and D). To pass classifier dolphin2 the smoothed waveform had a click length of less than 0.13 ms and had 7 - 15 zero-crossings. Spectral energy within test band of 35 – 90 kHz was at least 18 dB greater than control band 10 - 18 kHz (Figure 2.5 E and F). Each click clip was first classified by classifier 1 with only failing clips passed to classifier 2.

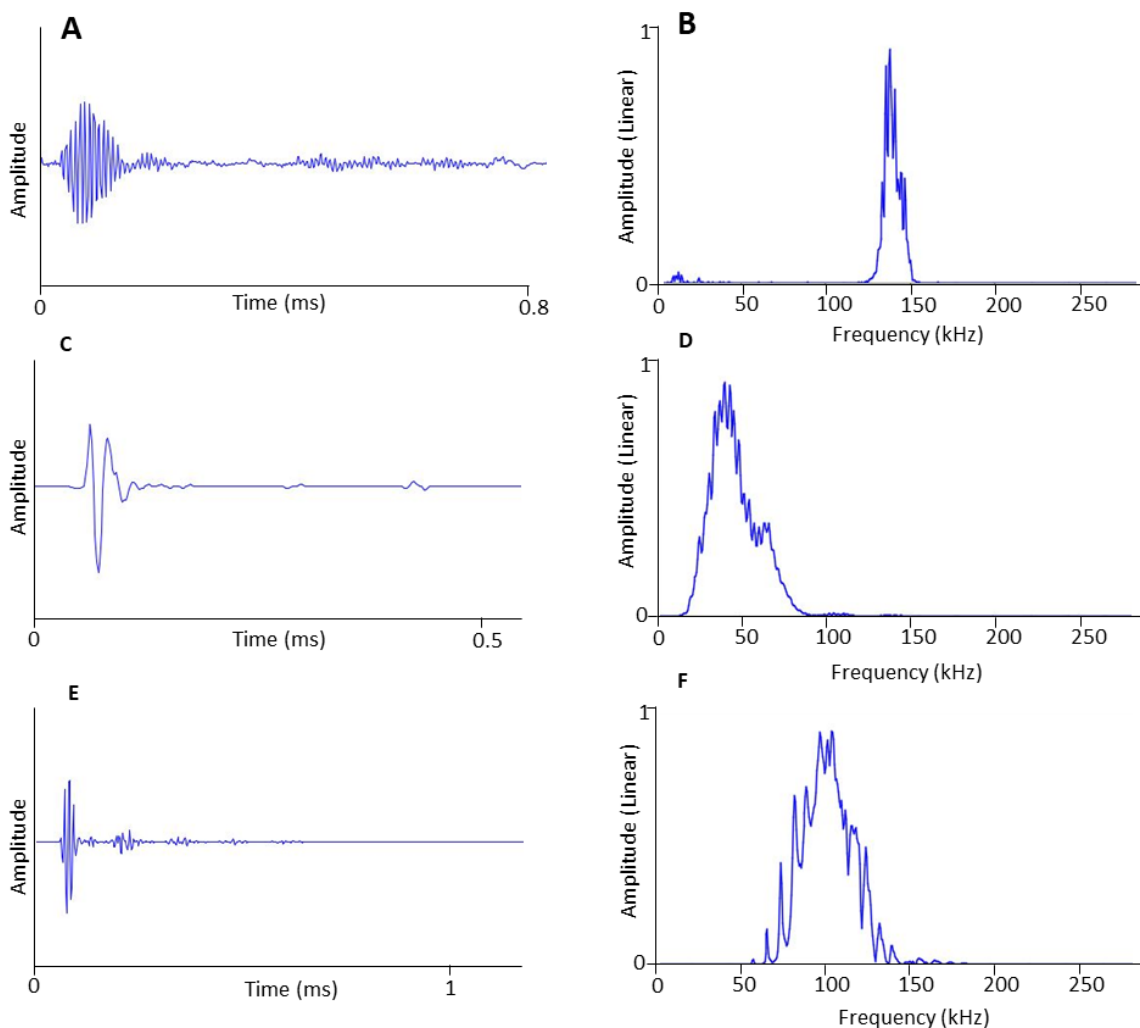


Figure 2.5. The left column shows the waveform, and the right column shows the spectral energy of exemplar porpoise (A and B), bottlenose dolphin (dolphin1; C and D) and white-beaked dolphin (dolphin2; E and F) clicks recorded off Northumberland and identified using Pamguard's click detector.

Using two classifiers with more specific parameters was preferred over a single dolphin classifier with broader parameters as this helped reduce the number of false positive detections. It is important to note that although the two detectors were

configured based on training data from the two species, they were not reliable on their own for species separation as an encounter with either species could result in detections from both classifiers. A second stage of species determination was conducted (see Long Term Spectral Average section below) to confirm species specific detections.

2.2.4 Click train detection

All classified click detections were passed through Pamguard's click train detector module which identifies click train patterns from click detections passed from the click detector. Porpoise, dolphin1 and dolphin2 click detections were analysed separately (i.e., click train patterns were only searched for within click detections from a single classifier). Porpoise detections were passed through the click train detector using both Pamguard's standard porpoise NBHF and porpoise NBHF buzz settings. Both Dolphin1 and Dolphin2 classified clicks were processed using Pamguard's default dolphin click train detector settings.

2.2.5 Long Term Spectral Average

A Long-Term Spectral Average (LTSA) module was also configured to provide an additional visualisation of the acoustic data. LTSA allows for longer periods of spectral data to be visually represented more easily than using spectra data directly from the fast Fourier transform (FFT) by averaging spectral data over a specified interval (Welch, 1967). LTSA settings used were adapted from Soldevilla et al. (2010), making them applicable to Pamguard's parameter settings. Raw audio data were first decimated using the decimator module which outputted 99 kHz low pass filtered audio with a sample rate of 200 kHz. This decimated data were then passed to a FFT module with FFT length of 2048 and hop of 2048, providing spectra data with a frequency resolution of 97.66 Hz and time resolution of 10.24 ms. The spectra data were then passed to the LTSA module that was configured to sample and average the incoming data across a time interval of 5 seconds.

2.2.6 Species level Detection Positive Hour (DPH)

Porpoise click train detections (from both the standard NBHF and buzz click train settings) were summarised into 15-minute positive detection periods. Each of these periods were then manually checked using Pamguard's viewer mode, inspecting the

waveform, spectrum, and amplitude/time displays. Each 15-minute period was determined to be either a true or false positive detection period. Any ambiguous click trains were further checked by viewing raw data in program Raven (Cornell Lab of Ornithology, USA).

All dolphin click train detections (from both dolphin1 and dolphin2 classifiers) were compiled into 15-minute detection positive periods. Each positive period was viewed in Pamguard viewer mode using the available click displays and the LTSA data viewed in a spectrogram display. Each period was determined to be either a false positive with the click trains caused from broad band anthropogenic noise or true dolphin detections. The presence of spectral banding in the LTSA display (Figure 2.6) was considered evidence for the presence of white-beaked dolphin and its absence was indicative of bottlenose dolphin. The resulting dataset had positive detections for either species for each 15-minute period. All other periods were considered as absence for all species and no effort was made to identify false negative periods, the potential biases resulting from this decision are addressed in the discussion. The 15-minute periods were compiled into detection positive hours (DPH) which were used for further statistical analysis.

2.2.7 Statistical analysis

Detection Positive Hours (DPH) (binary response variable; 0 = species absent, 1 = species present) was modelled using a binomial Generalised Additive Modelling (GAM) framework with logit link function and a suite of environmental and biological variables as predictors. GAMs were chosen over Generalised Linear Models (GLM) as the relationships between DPM and predictor variables were not assumed to be linear. All modelling procedures were performed in R (R Core Team, 2013) using various packages identified below.

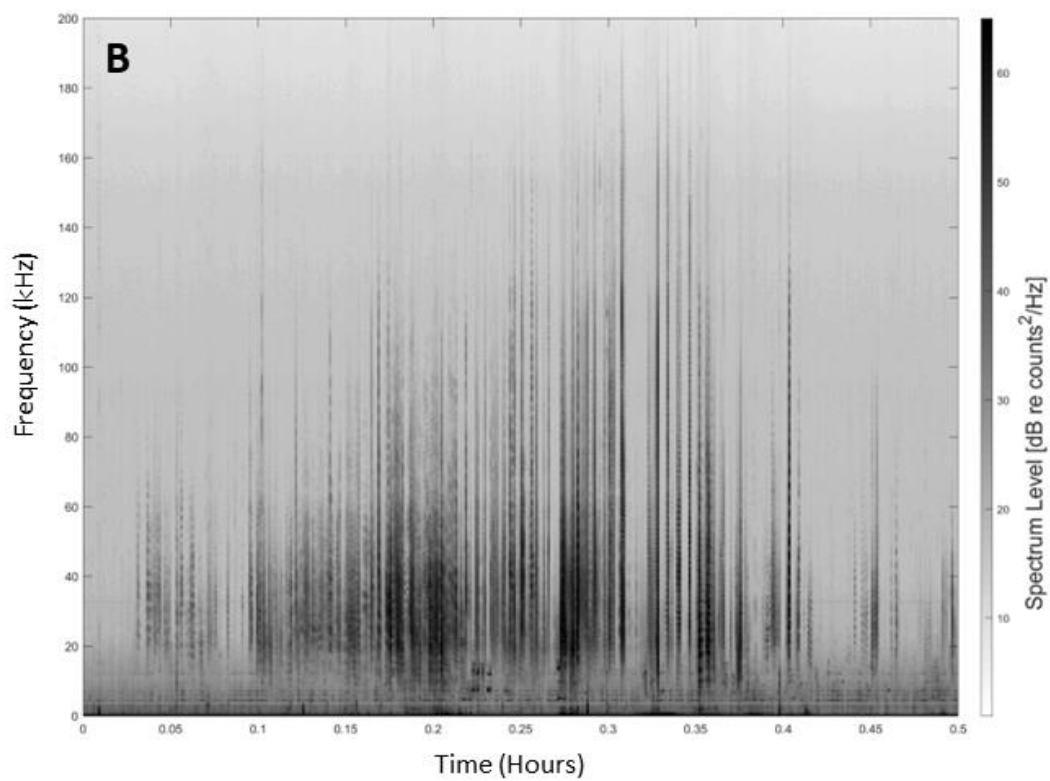
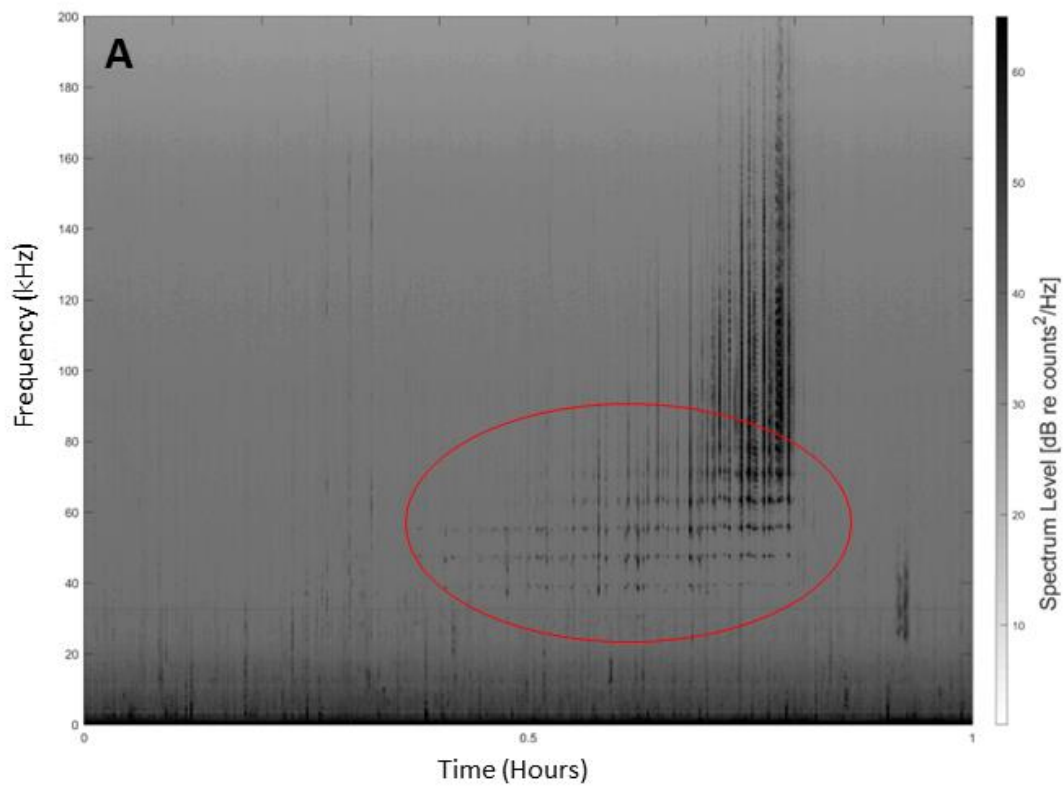


Figure 2.6. Long term spectral average of (A) white-beaked dolphin and (B) bottlenose dolphin clicks recorded off the Northumberland coast. The red oval in spectrogram A highlights the visible spectral banding present in white-beaked dolphin clicks (Yang et al., 2021).

Environmental covariables considered included diel, tide and lunar phases, sea surface temperature, bottom salinity, and day of year. Diel phase was included using a cyclical index (0 to 1) following Risch et al. (2019) whereby 0 and 1 were sunrise and 0.5 was sunset (times of sunrise and sunset were taken from package *maptools* (Lewin-Koh et al., 2012) which calculate times using algorithms provided by the National Oceanic & Atmospheric Administration (NOAA)). Tidal phase was incorporated as a cyclical index from 0 to 1 where 0 and 1 represented low tide and 0.5 represented high tide. Tidal data were retrieved from the program WXTide32 (WXTide32, V2.4) using data from the nearest tidal gauge for the area (North Shields, located on the north shore of the Tyne). Lunar phase was incorporated as an index (0 to 1) where 0 and 1 represented the new moon and 0.5 represented the full moon (taken from package *suncalc* (Thieurmél et al., 2019)). Sea surface temperature (SST) (°C) and bottom salinity (ppt) were also included using data provided by the Copernicus data hub (<https://www.copernicus.eu/en>). To investigate seasonality in species occurrence, day of year was included (ordinal date numbers) for bottlenose dolphin and porpoise models. For white-beaked dolphin models only data collected in July and August were used as there were only two detection hours identified outside of this time and the covariable month was used. Additional factor variables included were year, hydrophone location and for porpoise models the presence/absence of bottlenose dolphin.

Collinear covariates were identified for each species and location by performing an initial generalised linear model (GLM) and comparing variance inflation factor (VIF) (package: *car* (Fox et al., 2012)). Any covariates with $VIF > 2.5$ were dropped from the initial full model. For bottlenose dolphin and porpoise models, temperature and day of year were collinear and day of year was selected.

Once collinear variables were addressed a full GAM model was calculated for each species including all locations (package: *mgcv* (Wood, 2015)). Covariables diel index, tidal index, lunar index, and day of year were modelled as cyclic cubic regression splines. SST and bottom salinity were modelled as cubic regression splines. Year, location, month (white-beaked dolphin models) and bottlenose dolphin presence (porpoise models) were modelled as factors.

Temporal autocorrelation of the model residuals were inspected at each site using autocorrelation function (ACF) and across sites using cross-correlation function (CCF). There was clear indication of autocorrelation at each site for each species and between sites for bottlenose dolphins. A final suite of models were then fit using Generalised Estimating Equations (GEE; Liang and Zeger (1986)) to account for the observed autocorrelation, following Pirodda et al. (2011). GEE directly models the correlation of residuals within defined blocks and assumes independence between blocks. Block size was set based on the ACF and CCF inspection and for porpoise were DB = 63, NB = 32, and SM = 13; for white-beaked dolphin DB = 16, NB = 2, and SM = 2. For bottlenose dolphin, sites were blocked together in 12-hour blocks. The final suite of models combining GAM and GEE frameworks (GAM-GEE) were fitted using package *geepack* (Højsgaard et al., 2006) and *splines2* (Wang and Yan, 2021). These models are defined by the following (Zuur et al., 2009, Wang and Yan, 2021):

1. The systemic component was an additive combination of spline functions to model the non-linear covariables and regression parameters to model linear relationships.

$$\eta = \alpha + \beta_1(\text{LinearCovariable}_{1it}) + \dots + \beta_l(\text{LinearCovariable}_{lit}) + f_1(\text{SmoothedCovariable}_{1it}) + \dots + f_s(\text{SmoothedCovariable}_{sit})$$

Where:

- α is the model intercept,
- β is the regression coefficient for the linear terms (1, ..., l),
- $f()$ represents spline function for the smoothed terms (1, ... , s). Functions included cubic b-splines for non-cyclic smoothed covariables and periodic m-splines (Ramsay, 1988) for cyclic smoothed covariables.
- i indexes the specific block.
- t indexes time.

B-splines are piecewise polynomials that are connected together at a series of breakpoints called knots and where each segment is shaped by a separate basis function. B-splines provide greater flexibility than using single polynomials to model non-linear relationships. For cyclic covariables periodic m-splines were used to directly incorporate periodicity by defining boundary knots at the start and end of the period and ensuring continuity and smoothness between these knots. This approach

differs to the cosinor transformation used in chapter 3 (see section xxx), as it does not assume that the data can be accurately represented as a sum of sinusoidal components. The functions of each spline are in turn a linear combination of parameters that effect the shape of the spline curve at each knot.

$$f_1(\text{SmoothedCovariate}_1) = \sum_{j=1}^p \beta_j x b_j(\text{SmoothedCovariate}_1)$$

Where:

- β_j are the parameters estimated by the model.
- b_j are the basis functions.
- p is the number of basis functions to be fit.

2. The relationship between the conditional mean and the systemic component was defined as:

$$E(Y_{it}|X_{it}) = \frac{e^\eta}{1 - e^\eta}$$

3. The conditional variance structure was defined as:

$$Var(X_{it}) = \Phi X v(\mu_{it})$$

Where:

- Φ is a scaling parameter.
- $v(\mu_{it})$ is a defined as the binomial variance structure $\mu_{it}(1 - \mu_{it}), \mu \in (0,1)$

4. An independent within block association structure was used following recommendation from (Pan, 2001), defined as:

$$Cor(Y_{it'}) = 0, \quad t \neq t'$$

Each non-cyclic covariable was considered as either a linear or smoothed term using Quasi Information Criteria (QIC) (Cui and Qian, 2007) to determine the best fit. QIC was also used to find the best fitting number of knots for each smoothed term, including the cyclical variables. Interaction terms between all covariables and location were included. Interaction terms between temperature, month, and year were also included in the white-beaked dolphin models. Model selection was conducted using backwards stepwise model selection using QIC to identify the most parsimonious model. A full model was first built using all non-collinear covariables and interaction terms. Covariables were removed iteratively until none of the

covariables could be removed without increasing the QIC score. Each remaining covariable was tested for significance using Wald's test. All covariables were retained in the model even if insignificant and are reported in the results.

Goodness-of-fit for each final model was then evaluated using the Area Under Curve (AUC) of the Receiver Operating Characteristics (ROC) (package: *ROCR* (Sing et al., 2005)) and presence-absence confusion matrix. An AUC value of 1 would represent perfect model performance whereas a value of 0.5 would be expected with random classification, therefore a number between 0.5 and 1 can be used to evaluate the model performance (Boyce et al., 2002). The confusion matrices were based on predicted species presence/absence compared to the actual observations for each hour of the study. The threshold for determining whether each observation was predicted as presence was at the point where the distance between the ROC curve and the 45° diagonal was maximal.

Results of the model were visualised using package *ggeffects* (Lüdtke, 2018) to estimate and plot the marginal effects of each of the parameters of interest.

2.3 Results

2.3.1 Detection performance

A total number of 6362, 8033, 6450 hours were recorded at sites DB, NB and SM, respectively. A combined number of dolphin click train detections (from analysing both dolphin1 and dolphin2 classified clicks) was 22,200, which were summarised into 4401 dolphin positive detection 15-minute periods. Of these, 3271 were identified as bottlenose dolphin positive periods and 118 as white-beaked dolphin positive periods based on the absence and presence of spectral banding in the corresponding LTSA image, respectively. There were 7495 porpoise click trains (normal and buzz combined), which were summarised as 1527 15-minute positive periods; of these 1499 were confirmed as true positives based on visual inspection of the Pamguard's click display. The final dataset of bottlenose, white-beaked and porpoise positive hours were 1660, 71, and 1111, respectively.

2.3.2 Effect of environmental and temporal variables

The results of the GAM-GEE analysis for each species modelled for all locations combined and each location separately are available in Table 2.1. The results table

includes model performance (area under ROC curve), confusion matrix of model predictions and Wald's Test for covariable significance.

2.3.3 Bottlenose dolphin

The final model for bottlenose dolphin retained all covariables except tidal index and an interaction between location and day of year after model selection (Table 2.1). All covariables in the final model were significant (Wald's Test, $p < 0.05$) and the covariables with the highest explanatory power were day of year, location, and diel index (Table 2.1). Figure 2.7 shows seasonal change in bottlenose dolphin occurrence which has two peaks, one around day 140 (mid may) and a later peak between day 250 and 300 (early September and mid-October). This trend is similar at all three locations however the first peak is less pronounced at SM and the second is less pronounced at DB. There was also higher probability of bottlenose detections at site DB during non-peak days compared to the other two sites, with SM also having less probability than NB. The effect of each of the other covariables on the presence of bottlenose dolphin in the study area are shown in Figures 2.8 A-D. The effect of diel index shows an increase in bottlenose dolphin detection probability at sun rise (index 0 and 1) and sunset (index 0.5), with daylight hours having the least probability of bottlenose dolphin detection. Lunar phase shows increased detection probability around the new moon (lunar phase 0 and 1). The effect of year shows increased probability with each sequential year, however the difference between 2019 and 2020 is more pronounced than 2020 to 2021. There is also a decreased chance of bottlenose dolphin detection at extremes of the salinity range, which is more pronounced at low salinities.

Table 2.1. Results of binomial GAM-GEE models for common bottlenose dolphin, white-beaked dolphin, and harbour porpoise acoustic presence off the coast of Northumberland between July 2019 and October 2021. Includes Area Under Curve (AUC) as measure of model fit, confusion matrix of predicted vs observed animal presence and the effect of explanatory covariables and significant estimated using Wald's test.

Species	QIC	AUC	Confusion Matrix (observed)		parameter	Walds Test			
			Predicted Presence	Predicted Absence		DF	χ^2	P	
Bottlenose dolphin	10982.0	0.69	Presence	70.24	41.01	Day of Year (smooth)	6	362.21	<0.001
			Absence	29.76	58.98	Salinity (smooth)	4	33.77	<0.001
						Location (factor, 3 levels)	2	63.55	<0.001
						Lunar Index (smooth)	3	34.12	<0.001
						Diel Index (smooth)	3	31.74	<0.001
						Year (factor, 3 levels)	2	11.31	0.003
							Location:Day of Year (interaction)	12	78.18
White- beaked dolphin	653.4	0.84		78.26	18.39	Month (factor, 2 levels)	1	17.83	<0.001
						Year (factor, 2 levels)	1	8.49	0.003
				21.74	81.61	Location (Factor, 3 levels)	2	9.87	0.007
						Diel Index (smooth)	3	14.06	0.002
						Temperature (Linear)	1	14.98	<0.001
						Lunar Index (smooth)	3	1.92	0.590
							Loc:Diel Index (interaction)	6	20.21
Harbour porpoise	7105.0	0.83		79.47	26.28	Day of Year (smooth)	6	96.84	<0.001
				20.52	73.21	Location (factor, 3 levels)	2	514.37	<0.001
						Year (factor, 3 levels)	2	13.66	0.001
						Diel Index (smooth)	4	37.50	<0.001
						Lunar Index (smooth)	4	43.34	<0.001
						salinity (smooth)	3	7.04	0.070
						Bottlenose presence (factor, 2 levels)	1	5.82	0.015
						Tidal Index	3	20.56	<0.001
						Location:Day of Year (interaction)	12	108.63	<0.001
						Location:Diel Index (interaction)	8	33.10	<0.001
						Location:Lunar Index (interaction)	8	14.84	0.062
			Location:Salinity (interaction)	6	14.69	0.023			

2.3.4 White-beaked dolphin

The final model for white-beaked dolphin retained month, year, location, diel index, temperature, lunar index and interactions between location and diel index (Table 2.1). The covariables with the highest explanatory power were diel index, location, and day of year and the interaction between location and diel index. Of the retained covariates, only lunar index was non-significant ($p= 0.59$). Diel index increased detection probability at DB during sunrise and sunset and increased during the night at NB and SM (Figure 2.9). 2021 had a higher probability than 2019, DB had a higher probability of detection than the other two locations and July had higher detection probability than August, but confidence intervals were overlapped (Figure 2.10 A-C). Probability of detection increased linearly with SST but there were large confidence intervals at higher temperatures (Figure 2.10 D).

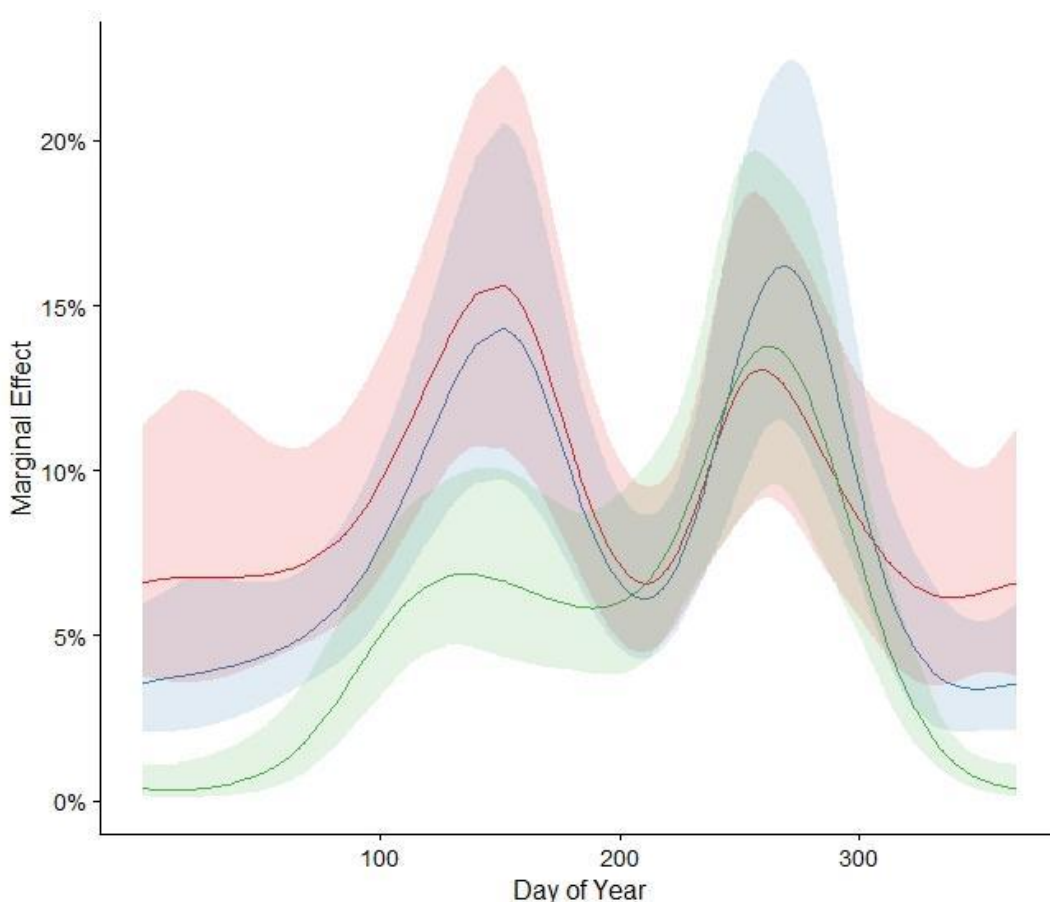


Figure 2.7. Seasonality of common bottlenose dolphin at three sites off the Northumberland coast between 2019 and 2021 based on echolocation click detections. Red line = Druridge Bay, blue = Newbiggin, and green = St Mary's. 95% confidence interval for each marginal effect are represented by the shaded bands.

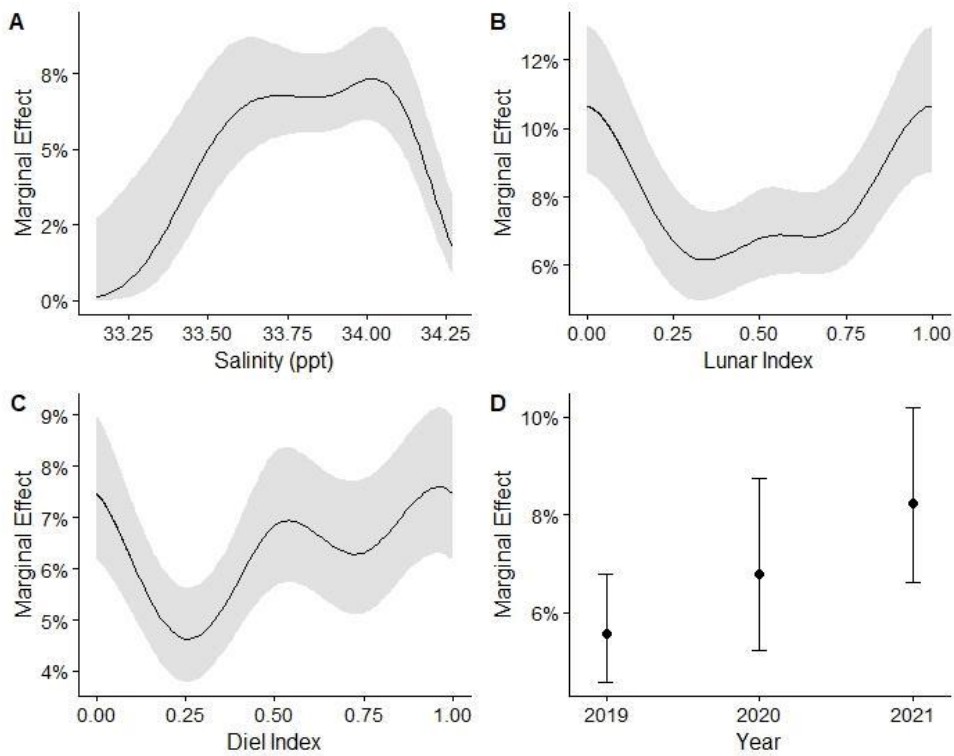


Figure 2.8. Marginal effects of A. salinity, B. lunar index, C. diel index and D. year of study on the probability of detecting common bottlenose dolphin off the coast of Northumberland modelled from acoustic data collected from July 2019 to October 2021. Error bars and shaded bands represent 95% confidence interval for each marginal effect.

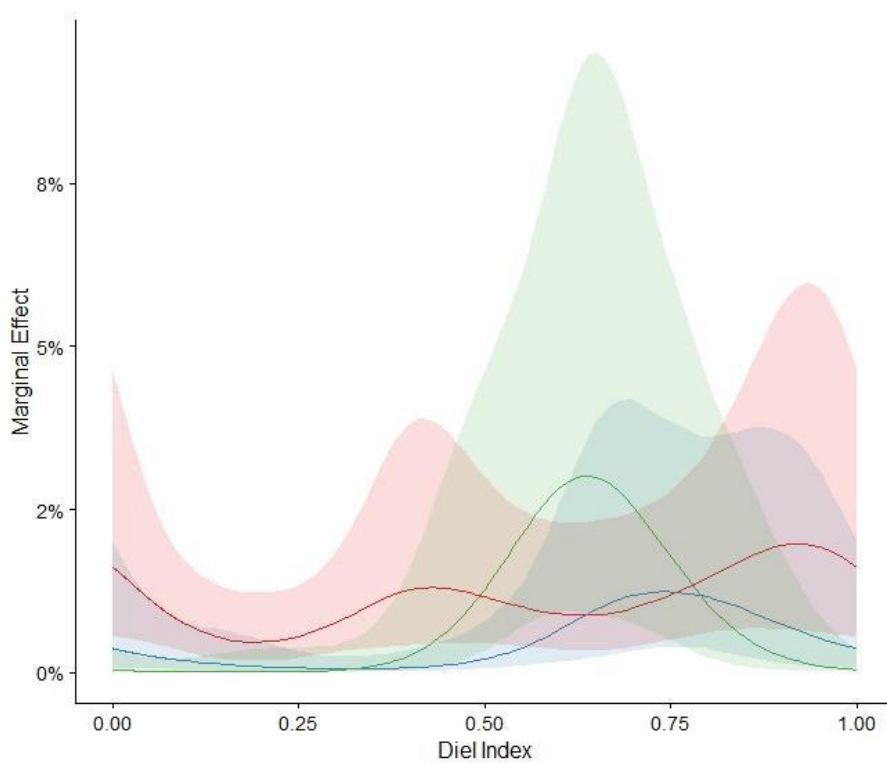


Figure 2.9. Diel patterns of white-beaked dolphin occurrence at three sites off the Northumberland coast between 2019 and 2021 based on echolocation click detections. Red line = Druridge Bay, blue = Newbiggin, and green = St Mary's. 95% confidence interval for each marginal effect are represented by the shaded bands.

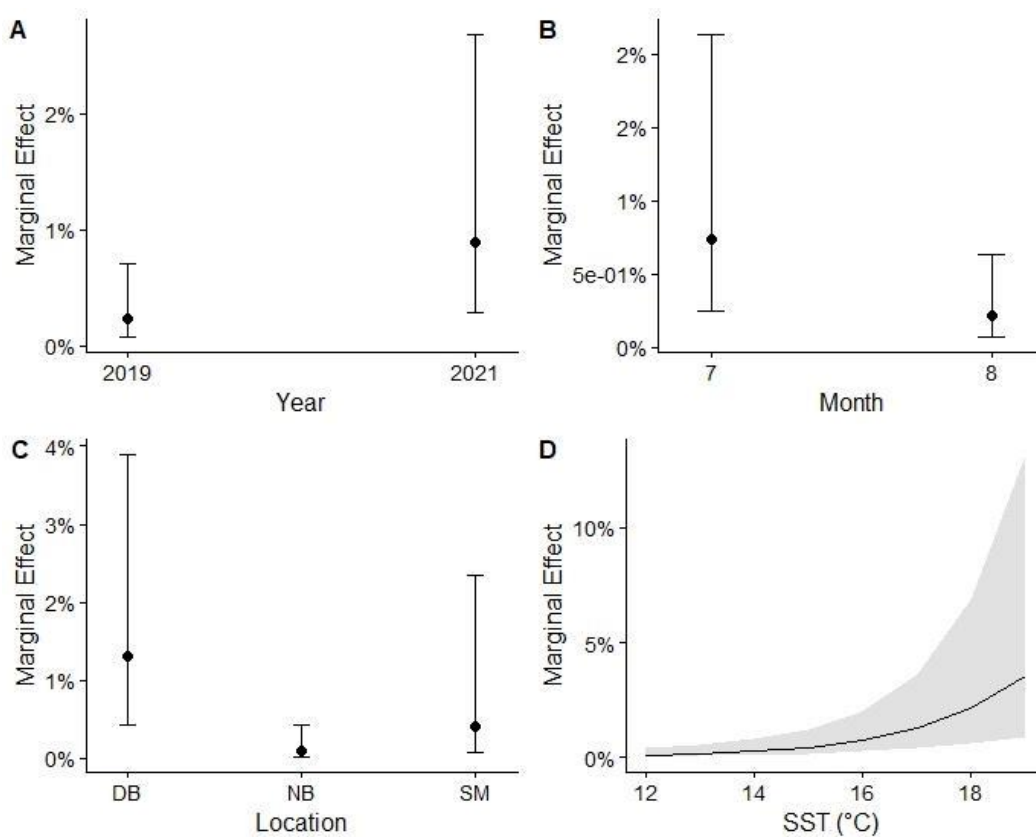


Figure 2.10. Marginal effects of A. year of study, B. month, C. location and D. Sea surface temperature on the probability of detecting white-beaked dolphin off the coast of Northumberland modelled from acoustic data collected during the months of July and August 2019 and 2021. Error bars and shaded bands represent 95% confidence interval for each marginal effect.

2.3.5 Porpoise

The final model for porpoise retained all covariables and interactions between location and diel phase, day of year, lunar index, and salinity (Table 2.1). However, the interaction between location and lunar index was not significant (Wald's test, $p = 0.06$). The covariables with the highest explanatory power for porpoise presence/absence were location, day of year, and lunar index. Salinity was the only covariable which was not significant (Wald's test, $p = 0.07$). Diel index at DB was pronounced with a reduction in detection probability during night-time hours and peak activity at sunrise (diel index 0 and 1) but the effect was not apparent at the other two locations (Figure 2.11 A). Seasonal effects modelled as day of year showed a peak at between day 40 and 60 (mid-February to early March) at all three sites. Location DB had a second peak around day 250 (early September) (Figure

2.11 B). The effect of salinity is also apparent at DB compared to the other two sites with high salinity correlating to an increase in porpoise detection (Figure 2.11 C). Lunar index at DB is more pronounced with increased detection probability at the full moon (moon phase index = 0.5) and at the waxing of the moon before the new moon (moon phase index = 0.8) however, this was not significant (Figure 2.11 D). Location DB had a much higher probability of porpoise detection than the other two locations (Figure 2.12 A). The effect of year shows a reduction in porpoise detections in 2020 compared to 2019 and 2021 (Figure 2.12 B) and bottlenose dolphin presence reduces the probability of porpoise detection (Figure 2.12 C). Tidal current was significant for porpoise with an increase in detection probability at flood and high tide (tidal index between 0.25 and 0.5) (Figure 2.12 D).

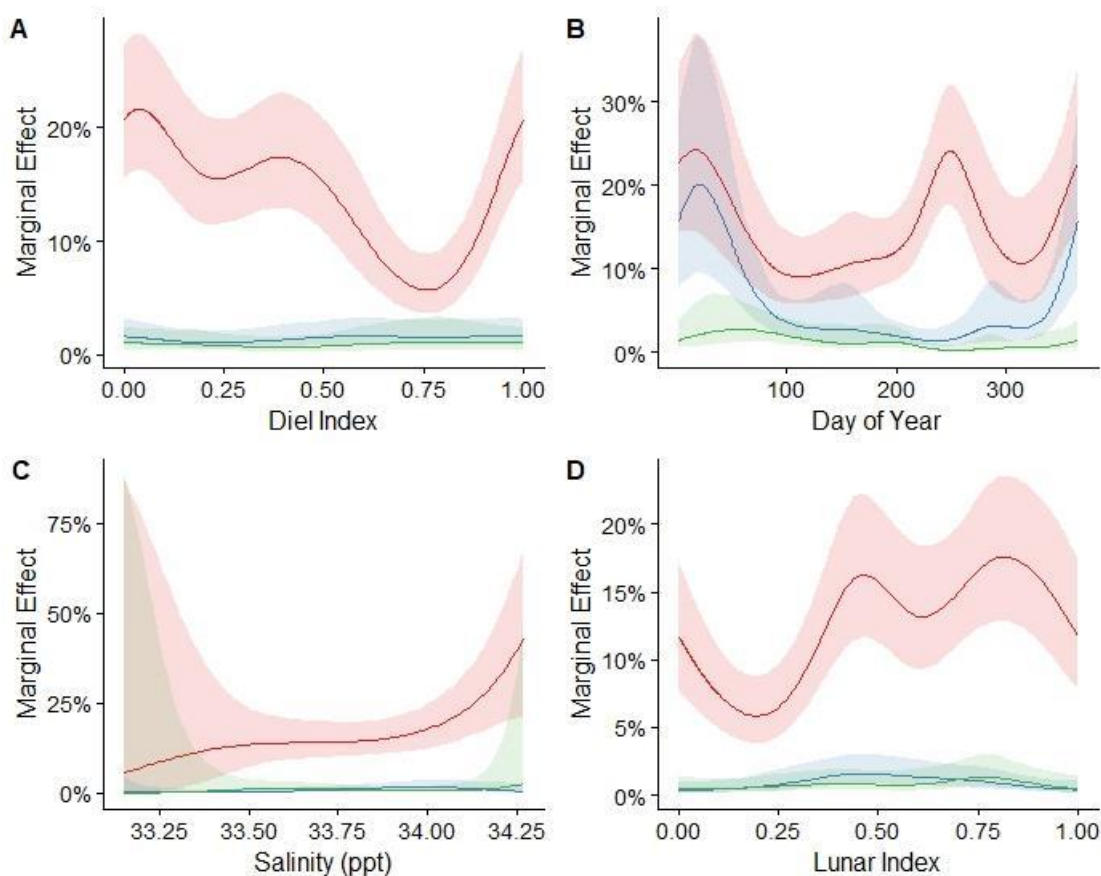


Figure 2.11. Marginal effects of interaction between location and A. diel index, B. day of year, C. salinity and D. lunar index on the probability of detecting harbour porpoise off the coast of Northumberland modelled from acoustic data collected between July 2019 and October 2021. Red line = Druridge Bay, blue = Newbiggin, and green = St Mary's. 95% confidence interval for each marginal effect are represented by the shaded bands.

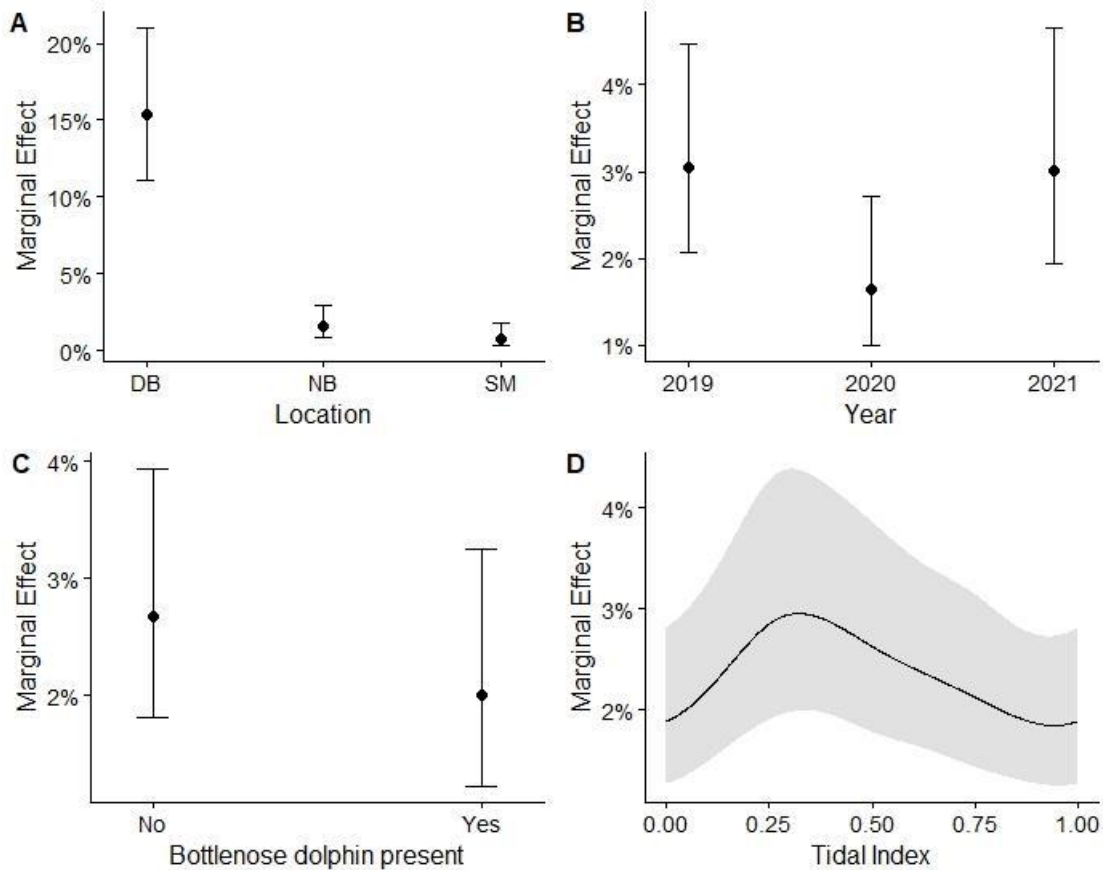


Figure 2.12. Marginal effects of A. location, B. year, C. presence of bottlenose dolphin D. tidal index on the probability of detecting harbour porpoise off the coast of Northumberland modelled from acoustic data collected between July 2019 and October 2021. Error bars and shaded bands represent 95% confidence interval for each marginal effect.

2.4. Discussion

This is the first study to separate white-beaked and common bottlenose dolphin echolocation click detections and identify species specific patterns of occurrence from long-term PAM data. Harbour porpoise occurrence was also identified from NBHF detections (Gillespie and Chappell, 2002) providing a comprehensive assessment of odontocete occurrence off the Northumberland coast. The most significant drivers identified across each species were location and seasonality (Table 1.1). Both harbour porpoise and bottlenose dolphin showed year-round occurrence whereas white-beaked dolphin were predominantly identified during the months of July and August. All three species had higher probability of detection at

Druridge Bay, but this was most pronounced for porpoise. Other important drivers of occurrence were identified for each species and are discussed below.

It is highly probable that all bottlenose dolphin detections recorded during this study were produced by animals of the "East Coast" population historically associated with the Moray Firth (Cheney et al., 2013). This assumption is based on comparisons of photo-identification catalogues from both locations and lack of an alternative source population (Aynsley, 2017). The "East Coast" population's range expansion has been well documented since the 1990's with individuals ranging across approximately 200 km of continuous habitat from the Moray Firth south along the Scottish coast (Wilson et al., 1997, Sini et al., 2005, Stockin et al., 2006, Arso Civil et al., 2019, Palmer et al., 2019). Within this habitat dolphins are known to aggregate in specific areas, with the most southerly hotspot being the Firth of Tay (Arso Civil et al., 2019). This study is the first long-term study of the "East Coast" population's occurrence within English waters and further evidence of an extended range shift for the population.

Species specific PAM detections revealed two seasonal peaks of bottlenose dolphin occurrence in the area with the highest probability of detections in May and towards the end of September. There was an increased probability of detection with each subsequent year of the study suggesting that either an increased number of dolphins visited, or a specific subpopulation spent more time in the area with each subsequent year. There were site specific differences in occupancy across the year, with Druridge Bay (the northernmost site) having a more pronounced first seasonal peak and the Newbiggin and St Mary's sites having larger second peaks. Outside of peak periods the marginal effect did not drop to 0 at Druridge Bay or Newbiggin across the year confirming year-round occupancy of the northern part of the study area. Bottlenose dolphin distribution and habitat selection is driven by foraging opportunities (Hastie et al., 2003, Hastie et al., 2004) and the two seasonal peaks are likely to be driven by increased foraging opportunity. Northumberland's rivers (e.g., Aln, Coquet, and Blyth) and the larger Tyne and Wear rivers to the south are used by Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*). The salmon river fishing season in Northumberland is open between April and October when salmon return to the river systems to reproduce. This period overlaps with both peaks in bottlenose dolphin occurrence and is likely to be an important driver of seasonal

occurrence in Northumberland. Seasonal differences in salmon abundance has also been suggested for increased foraging occurrence at the Moray Firth and the Aberdeenshire coast (Pirodda et al., 2014, Arso Civil et al., 2019). Bottlenose dolphins are also known to feed on *Clupidae* and *Scombridae* ((Hernandez-Milian et al., 2015, Bräger et al., 2016)) and the summer occurrence of Atlantic herring (*Clupea harengus*) and spring/summer occurrence of Atlantic mackerel (*Scomber scombrus*) off Northumberland may also provide important foraging opportunities and drive increased occurrence. Higher year-round occurrence (particularly at Druridge Bay) is also likely to be driven by prey availability with this habitat providing foraging opportunities outside of the salmon run season. Santos et al. (2001) identified gadoid prey items as important for bottlenose dolphin off the Moray Firth and near shore occurrence of cod (*Gadus morhua*), whiting (*Merlangius merlangus*) and pollock (*Pollachius pollachius*) during winter may provide foraging opportunities. However, at this time the specific prey populations and hydrographical aspects of this site that may explain year-round prey requires further research.

At smaller temporal scales both diel index and lunar index were significant explanatory variables in the bottlenose dolphin GAM-GEE model. Diel phase was notable for the pronounced reduction in dolphin detection probability during the day, with lowest probability at 0.25 index halfway between times of sunrise and sunset. Reduced detections of bottlenose dolphin during daylight hours have been reported in previous studies (Temple et al., 2016, Fernandez-Betelu et al., 2019) with the decline in clicks assumed to reflect difference in actual occurrence. Differences in dolphin behaviour may also drive this trend. If dolphins occupying the area during the day are less likely to echolocate due to differences in behaviour, click detection would be reduced despite the area being occupied (Fernandez-Betelu et al., 2019). However, it remains to be determined whether decreased echolocation clicks during the day are caused by diel shifts in dolphin behaviour and this question is specifically addressed in Chapter 3 of this thesis.

Bottlenose dolphin click detection increased during the new moon lunar phase (index 0 and 1). Fish activity has been shown to respond to the lunar phase in tropical mangroves, with increased abundance during the new moon (Ramos et al., 2011). Foraging of common dolphin (*Delphinus delphis*) is also linked with increased availability of mesopelagic prey that surface during dark periods of the night (Simonis

et al., 2017). The effect of lunar phase on prey populations off the Northumberland coast is not known, all areas were relatively shallow (approx. 20 m) and vertical movement of prey would be less impactful on foraging than for odontocetes foraging in deeper water. However, there may have been an increased availability of some prey species during dark nights during the new moon phase, increasing the foraging opportunity for bottlenose dolphins off Northumberland. The other significant explanatory variable in the model was salinity, salinity ranged from 33.3 to 34.3 (parts per thousand) and dolphin detection probability was reduced at both extremes. These values are well within the normal range of salinities for dolphin habitat (Booth and Thomas, 2021). Dolphins have been documented to both avoid (Hornsby et al., 2017) and tolerate (Takeshita et al., 2021) areas of low salinity with the levels of salinity recorded in other studies far lower than recorded in this study. The effect of salinity identified in this study is therefore likely to be indirect, affecting, for example, prey availability or other processes not directly observed such as freshwater output from local rivers. Tide was included in the full model but not retained by the backward selection process. Tide has been shown to be a less important factor driving bottlenose dolphin occurrence in open coastal environments and the results of this study provides further support for that conclusion (Pierpoint, 2008, Fernandez-Betelu et al., 2019).

White-beaked dolphins off the North Sea UK coast are not well studied despite the species being the second most abundant cetacean species in the area (Hammond et al., 2017). The species is known to move inshore during summer months potentially following prey species such as mackerel or to seek more sheltered habitat for calving (Canning et al., 2008). This study only detected white-beaked dolphin in 71 hours during the whole study. These detections predominantly occurred during July and August reflecting known seasonal occurrence, the only DPH outside of these months were two consecutive hours in January 2021, where spectral banding was identified in the Long-Term Spectral Averaging LTSA and attributed to white-beaked dolphin occurrence. Modelling of environmental drivers only used data collected during July and August to identify their predictive power during peak months. White-beaked dolphin occurrence at Druridge Bay was higher during sunrise and sunset but higher at night for Newbiggin and St Mary's. Explanatory covariables month and location

were also significant with higher occurrence of white-beaked dolphin during July and at Druridge Bay.

SST was retained in the final model and showed a significant positive correlation between white-beaked dolphin occurrence and increased temperature. White-beaked dolphins are considered to be a cold-temperate species with a preferred thermal niche of waters below 18°C (MacLeod et al., 2007, Canning et al., 2008, MacLeod et al., 2008) and the observed trend may seem contradictory to this. However, this interpretation would be premature considering the small spatial and temporal scale of the study and the relative marginal effect size of SST in the model. The trend shows a short-term preference for warmer waters during the summer months, close to shore, for white-beaked dolphin occurring at relatively low densities. This does not necessarily contradict larger scale patterns of white-beaked dolphin distribution. The preference for warmer waters observed in this study may be related to the same drivers hypothesised for increased coastal occurrence in summer months. Warmer waters may be beneficial for calf rearing or may correlate with increased prey resources (Ridgway, 1972, Boyd, 1991, Urian et al., 1996).

Climate change is predicted to have a considerable effect on this species (MacLeod, 2009, Lambert et al., 2014) and there is already documented range shrinkage within the North Sea, with distribution retracting northward (IJsseldijk et al., 2018). If SST increases in the area and surpasses the known limit of the species thermal tolerance, then white-beaked dolphins may no longer use the area, being forced northward. At this current time, however, Northumberland waters are an important area for white-beaked dolphins (VanBressem et al., 2018) and further research is required to understand the ecology and determine potential conservation strategies for the protection of the species. Species specific identification using PAM will be a useful tool for future research, but future studies should consider increasing the study size compared to this current study, with emphasis on extending monitoring further from the coast. Given the confirmation of regular seasonal occurrence in nearshore waters off Northumberland, future research should also focus on identifying abundance, community structure and area usage during July and August, when there is potentially greater overlap with anthropogenic activities.

Within the Northeast Atlantic patterns of porpoise occurrence is associated with different environmental factors including bottom topography (Booth et al., 2013, Jones et al., 2014), hydrographic features (Skov and Thomsen, 2008), tidal cycle (Johnston et al., 2005, Marubini et al., 2009, Isojunno et al., 2012), and diel cycle (Todd et al., 2009) with significant variability in the effect of these drivers between sites at different spatial scales (Schaffeld et al., 2016, Zein et al., 2019). Porpoise exhibit ultra-high foraging rates (Booth, 2020) as they need to forage near constantly to meet energetic requirements (Lockyer, 2003). Foraging hotspots are therefore important drivers of porpoise occurrence which limit ranging far from known and reliable patches (Lockyer, 2003, Santos et al., 2004, Jones et al., 2014). Variability in drivers have been linked to habitat type and foraging behaviours (Schaffeld et al., 2016, Williamson et al., 2017, Zein et al., 2019). Some studies show increased foraging at night (Carlström, 2005, Nuuttila et al., 2017, Nuuttila et al., 2018) however more shallow and sandy habitats have been associated with daytime foraging (Schaffeld et al., 2016, Williamson et al., 2017). In this study there was considerable difference between sites, with Druridge Bay having much greater probability of detection. There was a marked decline in porpoise occurrence after sunset at Druridge Bay, followed by a sharp increase towards sunrise (diel index 0 and 1). The location of the hydrophone at Druridge Bay contrasts the other two sites with the former being a relatively shallow sandy bottom bay and the latter two characterised as rocky headlands. The habitat type at Druridge Bay may provide suitable daytime foraging habitat for porpoise in the area similar to sandy sites identified in Schaffeld et al. (2016). In support of this hypothesis is the findings of Potlock et al. (*In Review*) that show different diel patterns from detections made using an array of C-PODs at Blyth approximately 20 km south of Druridge Bay where most hydrophones within the array were positioned in deeper water (40 m). The Potlock et al. (*In Review*) study showed a shift in diel pattern towards night compared to the current study's findings at Druridge Bay. Tide phase was retained by the backward selection process and showed increased detection probability at flood time similarly to other studies, however the effect of the tide was relatively small and did not interact significantly with location.

At all three sites there was an increase in porpoise detections in winter months similar to reports in other studies around the UK and Ireland (Nuuttila et al., 2017,

Todd et al., 2020). However, Druridge Bay was also characterised by a second peak with detections increasing in July and peaking in September. UK porpoises reproduce seasonally mainly in July and August and give birth from May to July (Learmonth et al., 2014). The coast of Northumberland may provide suitable habitat for porpoise when the demand for food is high due to the energetic cost of reproduction (Read and Hohn, 1995, Read, 2001). Further research is needed to better understand the importance of Druridge Bay and other areas of the Northumberland coast that may provide similar habitat for porpoise at different temporal scales such as diurnal and nocturnal foraging and at times of year where these habitats may support reproduction.

All three species analysed in this study showed increased detections at Druridge Bay compared to the other sites providing evidence against spatial segregation of these species in the study area. However, each species showed different seasonal preferences. This is illustrated in Figure 2.13 that shows the marginal effect of day of year at Druridge Bay for bottlenose dolphin and porpoise but normalised to a value between 0 and 1 (see species specific Figures 2.7 and 2.11 B for actual marginal effects and confidence intervals in the results section); white-beaked dolphin peak months of July and August are also shown. There are clear seasonal differences suggesting temporal segregation with high porpoise occurrence in winter, followed by the first peak in bottlenose dolphin occurrence in spring. The seasonal occurrence of white-beaked dolphin is timed between the first and second bottlenose dolphin peak. Interestingly, there is clear overlap between the second peaks of porpoise and bottlenose dolphin (Figure 2.13). This second peak for both species may result in increased lethal interactions between these species (Ross and Wilson, 1996, Jepson and Baker, 1998, Patterson et al., 1998, Williamson et al., 2022). At smaller spatial scales there is considerable overlap with all three species showing preference for the time of sunrise and sunset at Druridge Bay (Figure 2.14). However, both dolphin species show reduced detections during the day, whereas porpoise detections are increased, possibly reflecting differences in area usage across diel phases between delphinids and porpoise, assuming that decreased detections represent an actual reduction in occupancy (see Chapter 3).

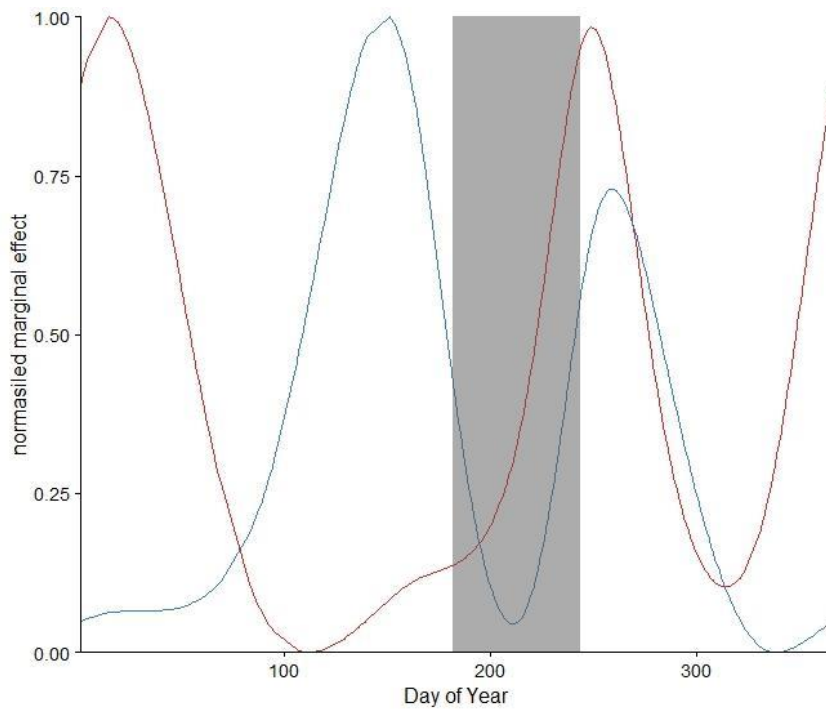


Figure 2.13. Seasonal occurrence of red: harbour porpoise and blue: bottlenose dolphin and shaded area representing peak months of white-beaked dolphin off the coast of Northumberland. Peak times show temporal segregation at the start of the year but with overlap between harbour porpoise and bottlenose dolphin during autumn.

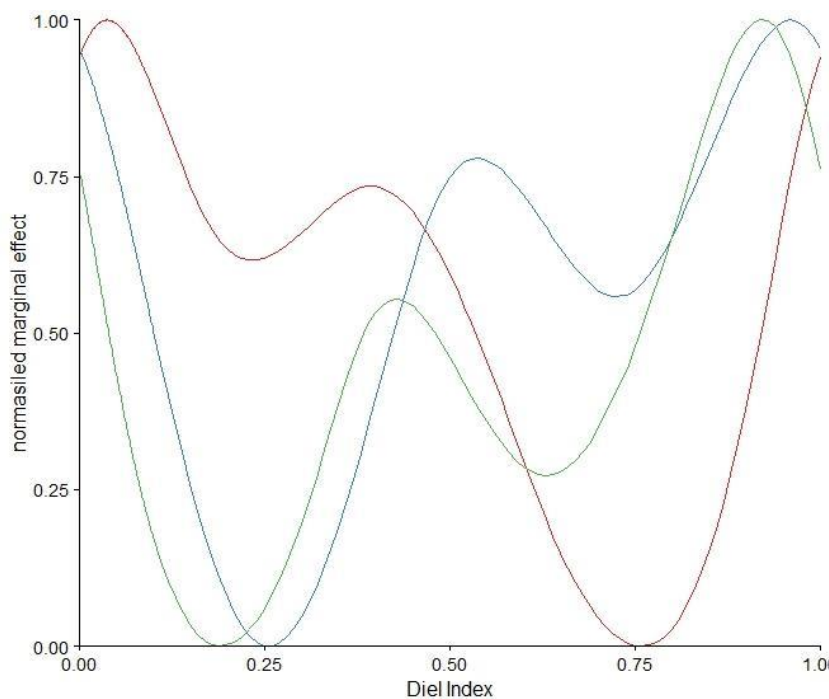


Figure 2.14. Diel occurrence of red: harbour porpoise, blue: bottlenose dolphin and green: white-beaked dolphin at Druridge Bay. All three species show increased detection around sunrise (diel index 0 and 1) and sunset (diel index 0.5). Porpoise detections are increased during the day compared to night, whereas the delphinid species have lowest detections during the day.

The click analysis combined both single click detection and classification, and visual inspection of LTSA spectrograms to confirm species-specific presence and remove false positive periods. The two separate click classifiers were developed to ensure that both dolphin species were detected rather than as the primary method for separating species. This approach was taken in response to the initially developed “dolphin1” classifier performing poorly with white-beaked dolphin training examples. Expanding the classification criteria (to provide a single-classification approach) resulted in many false positives during non-dolphin periods whereas a two-classifier approach provided more acceptable results. There were, however, still regular false positive clicks reflecting both natural and anthropogenic noise at the three sites. To account for this Pamguard’s click train detector was used to identify patterns in clicks which were likely to be true positives, using this module significantly reduced the number of detection periods which needed checking for true dolphin detections. The inspection of LTSA spectrograms to identify the presence of spectral banding is an established approach for identifying certain species (Soldevilla et al., 2008, Soldevilla et al., 2010, Soldevilla et al., 2011) and was applied here to identify white-beaked dolphin, a species known to produce clicks with spectral banding characteristics (Yang et al., 2021). The combination of these approaches gave good confidence in species separation, the resulting dataset, and the subsequent analysis.

LTSA spectrograms and resulting true positive dolphin detections were identified at 15-minute periods as this was the optimum resolution for interpreting the images. Detection data for all species were modelled using detection positive hours (DPH by pooling detection data for each hour. DPH is a widely used unit for dolphin and porpoise PAM studies (Williamson et al., 2017, Todd et al., 2020, Bailey et al., 2021) and was selected based on the time intervals of the covariate data available for modelling. Modelling smaller intervals (e.g., 15- or 30-minute intervals) may have provided greater granularity for interpreting diel and tidal phase, however this would have resulted in large block size for the GEE modelling due to increased temporal autocorrelation in the residuals. Selecting detection positive hours was appropriate granularity for the temporal scale of the data collection and temporal covariables of interest.

No attempt was made to identify false negative detection hours due to the scale of the study and required man-hours required to do so. The study used manually

confirmed odontocete detections as a proxy for occurrence which may cause some biases in the results, where reduced detections are not directly related to species occurrence. False negatives may have been the result of odontocete density (group size) and vocalisation rate, or the result of extrinsic factors which affect the probability of detection (e.g., masking from ambient noise or hydrological features such as thermoclines which effect sound propagation). Interpretation of the result of this study should therefore be considered with these potential biases in mind. However, the results of the study cannot be explained only by extrinsic factors. For example, thermoclines caused by warmer surface waters in summer may have caused a decrease in porpoise detections during summer and may explain the increased detection in winter, however this could not explain the secondary peak in July-September when waters were warmer. Differences in ambient noise and masking may have caused the differences in detections between Druridge Bay and the other sites. However, this would not explain the differences in interaction effects between location and diel phase and seasonality seen across each species groups. These effects are better explained by differences in actual animal occurrence and potential habitat usage as discussed above. Given the high number of true bottlenose dolphin and porpoise detections across the study, false negatives are unlikely to have impacted the results and their interpretation significantly. Conclusions drawn about white-beaked dolphins should be considered more carefully and be more general given the low probability of detection observed.

It is possible that other delphinid species occurred in the area during the study period and were consequently detected by Pamguard's click detector and falsely classified as either bottlenose dolphin or white beaked dolphin. For example, Risso's dolphins have been identified as species which produce clicks with spectral banding (Soldevilla et al., 2008) and occasionally can occur in the North Sea, although very rarely (Jefferson et al., 2014). Likewise common dolphin could have been detected and falsely classified as bottlenose based on the lack of spectral banding (Soldevilla et al., 2008). Common dolphins are considered rare in the North Sea however there have been increased sightings in the Moray Firth over the last two decades (Robinson et al., 2010). The possibility of a small number of false bottlenose dolphin detections caused by transient occurrence of common dolphin in the study area would have had minimal impact on the results given the relatively high frequency of

bottlenose dolphins in the area. The results of the study should therefore be considered robust providing a detailed insight into the odontocete ecology of the Northumberland Coast

2.4.1 Conclusion

The identification of year-round occurrence of two annex II (EU habitat Directive) species, the harbour porpoise and bottlenose dolphin, has clear implications for the management of these species in UK waters. There is currently only one SAC designated for harbour porpoise on the east coast of the UK, the Southern North Sea (www.gov.uk). This SAC is the largest designated in the UK (36,951 km²) and covers nearshore waters to the south but only offshore waters to the north. The findings of this study, including the year-round and diurnal patterns of occurrence at Druridge Bay suggest importance of nearshore waters not covered by this SAC. The “East Coast” population of bottlenose dolphins is currently protected by the Moray Firth SAC. The population’s range expansion since the 1990s has called into question the effectiveness of this original designation (Wilson et al., 2004, Arso Civil et al., 2019). The increase in bottlenose dolphin activity in English waters could provide the impetus for additional designations for the population at the southern extent of its range. This could include a new designation off Northumberland, which would represent the first SAC for bottlenose dolphins within English waters. White-beaked dolphins are not listed under annex II of the habitat directive. However, the species is a conservation concern (Ijsseldijk et al., 2018, VanBresseem et al., 2018) and further work is required to identify the most appropriate strategy to protect the species. PAM studies such as this, that can identify species specific detections will be valuable in future efforts to delineate important white-beaked dolphin habitats, informing conservation strategies.

Chapter 3. Decoding Activity States of Free Ranging Bottlenose Dolphin from Passive Acoustic Data using Hidden Markov Models

3.1 Introduction

Behavioural observations are required to quantify area usage and elucidate the underlying functional mechanisms that drive cetacean distribution (Hastie et al., 2004). Identifying spatial and temporal patterns in habitat usage can delineate areas and/or time periods critical for population fitness (e.g., habitats used for reproduction, feeding, resting, and socialising) (Karczmarski et al., 2000, Lusseau and Higham, 2004, Tyne et al., 2017). This information can aid conservation planning by identifying areas or periods where anthropogenic activity should be minimised (referred to as “refuges”) to safeguard population health (Ashe et al., 2010, Parsons, 2012, Guerra and Dawson, 2016).

Both visual and acoustic observations can be used to investigate area usage of small coastal odontocetes (e.g., bottlenose dolphin, *Tursiops sp.*). Visual studies typically link directly observable surface behaviours (e.g., swim speed, dive types, breaching, physical aggressions, sexual contact) to broader behaviour categories (e.g., foraging, resting, travelling, and socialising) and spatially aggregate group observations to identify differences in habitat selection and usage (Shane, 1990, Ballance, 1992, Bräger, 1993, Fertl, 1994, Allen et al., 2001, Lusseau, 2006, Torres and Read, 2009). Above water observations are limited to daytime and miss a large proportion of behaviours as dolphins spend most of the time below the surface. Acoustic data collection is not subject to these same limitations. However, acoustic studies to date, have been more restricted in scope, typically using echolocation click detections as a proxy for occurrence (see chapter 1) and the presence of inter-click-intervals (ICI) of <10 ms (termed buzzes) used to indicate foraging behaviour (Todd et al., 2009, Leeney et al., 2011, Wahlberg et al., 2011, Nuuttila et al., 2013, Yang et al., 2021). Such studies usually aggregate buzz and regular click detection minutes into relatively large temporal bins (e.g., 1 hour) and use the proportion of buzz clicks to regular clicks as a measure of relative foraging activity at different hydrophone locations and across time (Pirodda et al., 2014, Temple et al., 2016, Charish et al., 2021, Trabue et al., 2022). Analysing data of this type prevents differentiation between foraging behaviours that may be important in understanding habitat

selection. Bottlenose dolphins exhibit plasticity in foraging behaviour and prey selection at both species and population level (Krützen et al., 2005, Sargeant et al., 2007, Sargeant and Mann, 2009, Rossman et al., 2015). These can include habitat specific adaptations and differences in response to prey type (e.g., cooperative behaviour when foraging on schooling prey) (Wells, 2019). Furthermore, differences in foraging behaviour drives habitat selection at fine spatial scales and is important to consider when investigating area usage (Ingram and Rogan, 2002).

In addition to echolocation clicks, bottlenose dolphins have evolved many different call types related to different aspects of their behavioural ecology (Jones et al., 2020). The most prevalent and well-studied of these are whistles that serve multiple social functions, including identifying individuals within social groups (termed signature whistles (Janik and Sayigh, 2013); see chapter 4 for more detail) and the signalling of foraging or feeding opportunities (where dolphins produce specific whistle types which are often matched and overlapped) (King and Janik, 2015). Other less well studied sounds include burst pulses of high frequency clicks used in social contexts (Overstrom, 1983), lower frequency “pop” sounds associated with courtship (Smolker and Connor, 1996) and sounds that manipulate the movements of prey species (termed bray calls) (Janik, 2000a). Despite this variation in sound types and understanding of their behavioural context, few studies have used the presence of vocalisations other than foraging buzzes from Passive Acoustic Monitoring (PAM) data to identify behavioural differences linked to area usage.

One problem with identifying different behaviours from remote sensing such as PAM is that true behavioural states cannot be observed directly and must be inferred from acoustic detections (i.e., inferring foraging behaviour from patterns of click ICIs). Hidden Markov Models (HMM) are a class of statistical models that accounts for changes in unobservable states (Schuster-Böckler and Bateman, 2007, Zucchini et al., 2016). HMM achieve this by modelling two time series simultaneously, a hidden underlying state (modelled as a Markov process) and the observation process (which can be modelled using different distributions). HMM were first developed for speech processing (Juang and Rabiner, 1991) but have been used in many other scientific fields, including ecology where it has been used to infer hidden ecological or behavioural states (McClintock et al., 2020). Within animal research they have been used primarily for analysing animal movement and behaviour (Patterson et al., 2009,

Langrock et al., 2012), including movement and behaviours of marine mammals (DeRuiter et al., 2017, Leos-Barajas et al., 2017, Quick et al., 2017, Ngô et al., 2019, Tennessen et al., 2019). They have also been applied for the classification of baleen whale calls (Brown and Smaragdis, 2009, Putland et al., 2018, Trawicki, 2021).

The aim of this study was to identify activity states of common bottlenose dolphin (*Tursiops truncatus*) from analyses of click and whistle acoustic time series data at three locations off the coast of Northumberland, UK using HMMs. This was achieved in a multi-step modelling process that first identified dolphin presence and absence using a 2-state model. Dolphin present data was then modelled using a n-state activity HMM that statistically inferred the number of states in a data driven modelling procedure. Click and whistle detections data were modelled based on ICI and temporal overlap, respectively, and resulting activity states were interpreted under the assumptions that clicks with low ICIs were used mostly for foraging but potentially also for social burst pulses and that high occurrence of whistles were indicative of social and foraging behaviour (where overlapping whistles were stereotyped (King and Janik, 2015)). Inferred activity states were further modelled to investigate patterns of state occurrence across environmental covariables (location, tide, and diel cycle). The study offers a novel approach to analysing and interpreting PAM time series data of bottlenose dolphin or any other vocalising species for which behavioural specific calls are known.

3.2 Methodology

3.2.1 Modelling approach

The first step of the modelling approach was to identify dolphin presence and absence using a 2-state HMM. In this model the observation process (Z, \dots, Z_T) was the presence and absence of dolphin clicks and whistles during each sampled minute ($t = 1, \dots, T$) of the acoustic recordings and the distribution of these observations were dependent on the underlying state process ($S_t \in \{1,2\}$), that represented dolphin presence and absence. The second model was a n-state HMM used to identify latent dolphin activity states from presence only sampled minutes, as determined by the first HMM. This was done so that inferred states in the second model could be better attributed to actual dolphin activity states. In this model the observation process was categorical data where each sampled minute was assigned

a category based on the click and whistle types observed (see section 3.2.4). The distribution of the categorical data were dependent on N activity states ($S_t \in \{1, \dots, N\}$), where N was statistically inferred in a data driven process selecting the number of states based on Akaike Information Criterion (AIC). Starting values for this model were also determined in a data driven process. Both HMM modelled click and whistle data under the assumption that these observations were conditionally independent. The final n-state model was developed from a simple single location model to a complex multi-location model with covariable effects on both the observation process and state switching probabilities (see section 3.2.6).

For both models a first order Markov chain was used to model the underlying state process where the probability of the state at time t is determined by the state at $t-1$ and the progression of states across time is modelled by the probabilities of single state to state transitions represented by the transition probability matrix (TPM).

$$\gamma_{i,j}^t = Pr(S_{t+1} = j | S_t = i) \text{ for } i, j = 1, \dots, N$$

All HHMs were fitted using R package *momentuHMM* (McClintock and Michelot, 2017) that performs the numerical optimization of the likelihood based on the forward algorithm (Zucchini et al., 2016).

$$L = \delta^{(0)} \Gamma^{(1)} P(z_1) \Gamma^{(2)} P(z_2) \Gamma^{(3)} \dots \Gamma^{T-1} P(z_{T-1}) \Gamma^{(T)} P(z_T) 1^N$$

Where:

- $\delta^{(0)}$ is the initial distribution.
- $\Gamma^{(T)} = \gamma_{i,j}^t$ is the TPM.
- $P(z_T) = \text{diag}(p_1(z_T), \dots, p_N(z_T))$, $p_s(z_T)$ is the conditional probability density of Z_t given $S_t = s$
- 1^N is a N -vector of ones.

Package *momentuHMM* was developed for the analysis of animal movement data by HMM and related statistical models, however it can be used to model data from other sources under the HMM framework. The observations at each time interval are included in the *momentuHMM* framework as data streams and there is no limit to the number of data streams that can be used. The probability distribution for each data stream can be from different distributions (e.g., gamma, binomial, categorical etc.) and covariables can be easily included as functions of any of the parameters of the

selected distributions using link functions. Furthermore, covariables can be included as functions of the state transition probabilities by the multinomial logit link (Michelot et al., 2016).

The final state sequence for both HMMs were decoded using the Viterbi algorithm (Forney, 1973). The Viterbi algorithm is a dynamical programming algorithm that computes the most probable state sequence given the parameters of the trained HMM (i.e., the initial probability distribution, transition probability matrix and probability distributions of the data streams) and the sequence of observations.

$$S_{0:T}^* = \operatorname{argmax}_{S_{0:T}} P(S_{0:T}, Z_{0:T})$$

The most probable sequence is identified by recursively computing the probabilities of reaching each state at each time step. The following equations describe the recursive process for finding the maximal probability (μ) for each state at each time period.

$$\mu_t(S_t) = \max_{S_{t-1}} P(Z_t, S_t)P(S_{t-1})\mu_{t-1}(S_{t-1}) \text{ for } t = 2, \dots, N$$

and

$$\mu_1(S_1) = P(S_1)P(S_1, Z_1)$$

The final step in the modelling process was to investigate the occurrence of activity states across different locations and environmental covariables using both a GAM and GEE framework (full details in section 3.2.9). An overview to the multi-step modelling approach used in this study is presented as a flow diagram in Figure 3.1.

No visual (shore or boat based) observations were made concurrently with the acoustic recordings and the activity states are derived statistically and interpreted as biologically meaningful dolphin activity states based on known dolphin sound use and behavioural ecology.

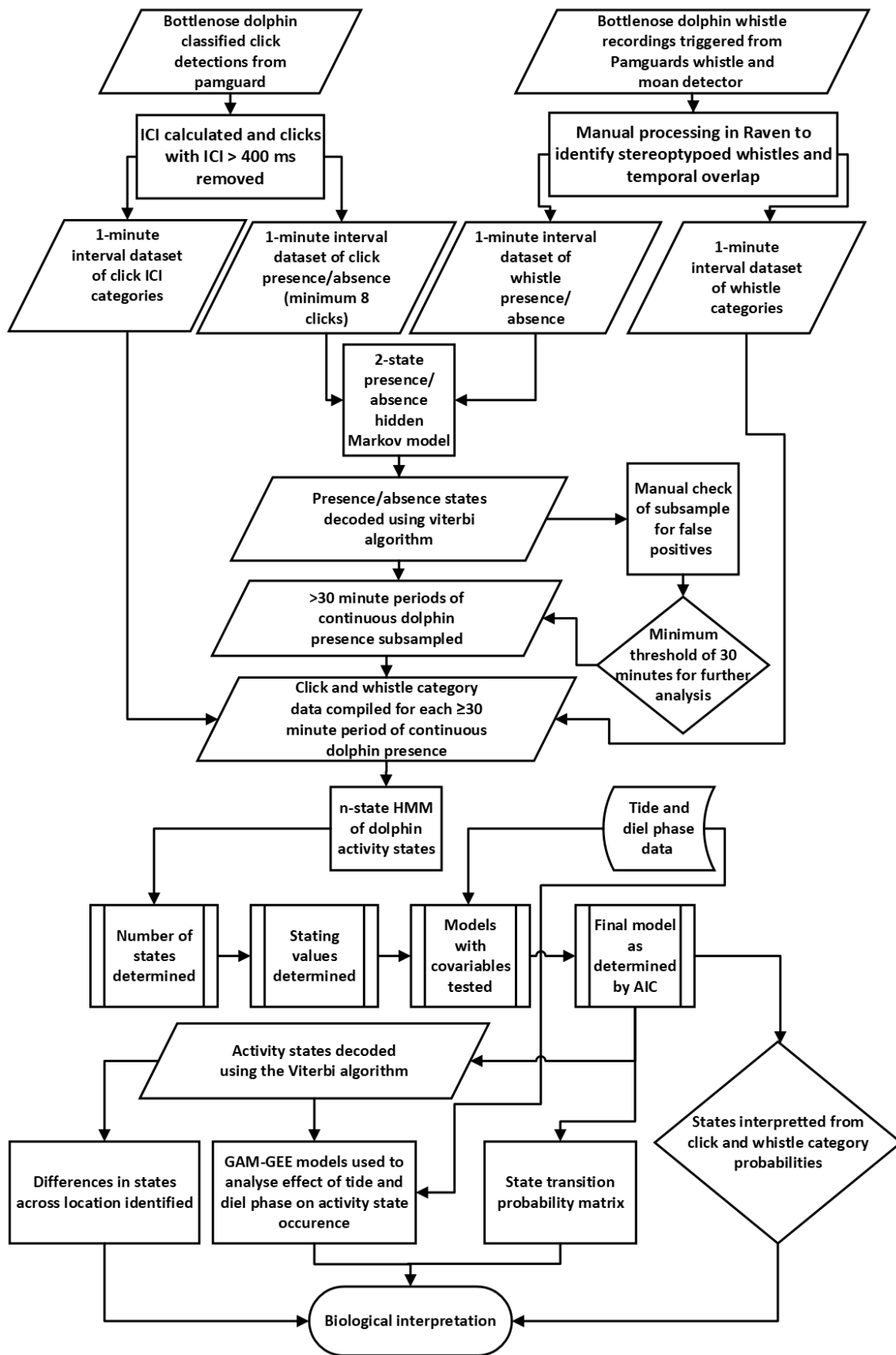


Figure 3.1. Flow diagram outlining the multi-step analysis pipeline for decoding activity states of bottlenose dolphin from acoustic recordings using hidden Markov models.

3.2.2 Data Collection

A full description of the acoustic data collection is outlined in Chapter 2 section 2.2.1 and data collected from Druridge Bay (DB), Newbiggin-by-the-Sea (NB) and St Mary's lighthouse (SM) between July 2019 and October 2019 were used. As this study focuses on bottlenose dolphin vocalisation activity any periods which contained white-beaked dolphin (*Lagenorhynchus albirostris*) clicks were removed from the dataset.

3.2.3 Data Processing

Clicks were identified in the acoustic recordings using Pamguard click detector and click classifier configured to classify dolphin clicks based on training recordings from bottlenose dolphin (classifier 'dolphin1'), described in detail in Chapter 2 section 2.2.3. All 'dolphin1' classified click detections (stored as Pamguard binary files) were imported into R for analysis using package PAMpal (<https://github.com/TaikiSan21>). The inter-click-interval (ICI) for each click was calculated using PAMpal's native functions, whereby each click was assigned an ICI value based on the time interval between it and the preceding click. Clicks were then categorised based on the ICI values: ICI less than 10 ms were categorised as buzz clicks; ICI greater than 10 ms and less than 400 ms were categorised as regular clicks; and clicks with ICI greater than 400 ms were categorised as noise and removed from analysis.

Pamguard's whistle and moan detector was used to identify tonal signals in the acoustic recordings within the frequency band of 3 and 35 kHz. The audio data were first passed through Pamguard's decimator module which reduced the sampling rate to 96 kHz and applied a (38 kHz, 6th order Chebychev) low pass filter. Each time the whistle and moan detector was triggered a sample of the decimated audio was taken including 1 second before the trigger signal and 15 seconds after. Any additional signals that occurred during the 15-second period extended the recording by an additional 15 seconds, therefore a sequence of whistles with intervals of <15 seconds were included in the same recording.

Each whistle and moan triggered recording was viewed in Raven (Cornell Lab of Ornithology, USA) using the spectrogram display, loading 10 seconds at a time. Viewing the sound files in Raven allowed for the visual identification of each true dolphin whistle or group of overlapping whistles and for recordings triggered by false

detections to be discarded. Raven's 'selection table' function was used to annotate the start and end time for each true whistle or whistle group and to label each selection as either a single whistle, a group of overlapping whistles where at least two whistle contours matched, or a group of overlapping whistles where none of the whistles contours matched based on King and Janik (2015). Whistles were considered overlapping if the start of the first whistle overlapped temporally with the proceeding whistle by any amount of time (King and Janik, 2015). Categorising each whistle as single or each group as either different or matched was done on a whistle-by-whistle basis while visually evaluating the recording, and whistles were used in the analysis if they could be adequately identified in the spectrogram. Processing the data this way resulted in a dataset which contained the start time and the duration of each whistle or overlapping group of whistles and included a label relating to each selection's temporal overlap: "single", "overlap match", and "overlap no match" (Figure 3.2)

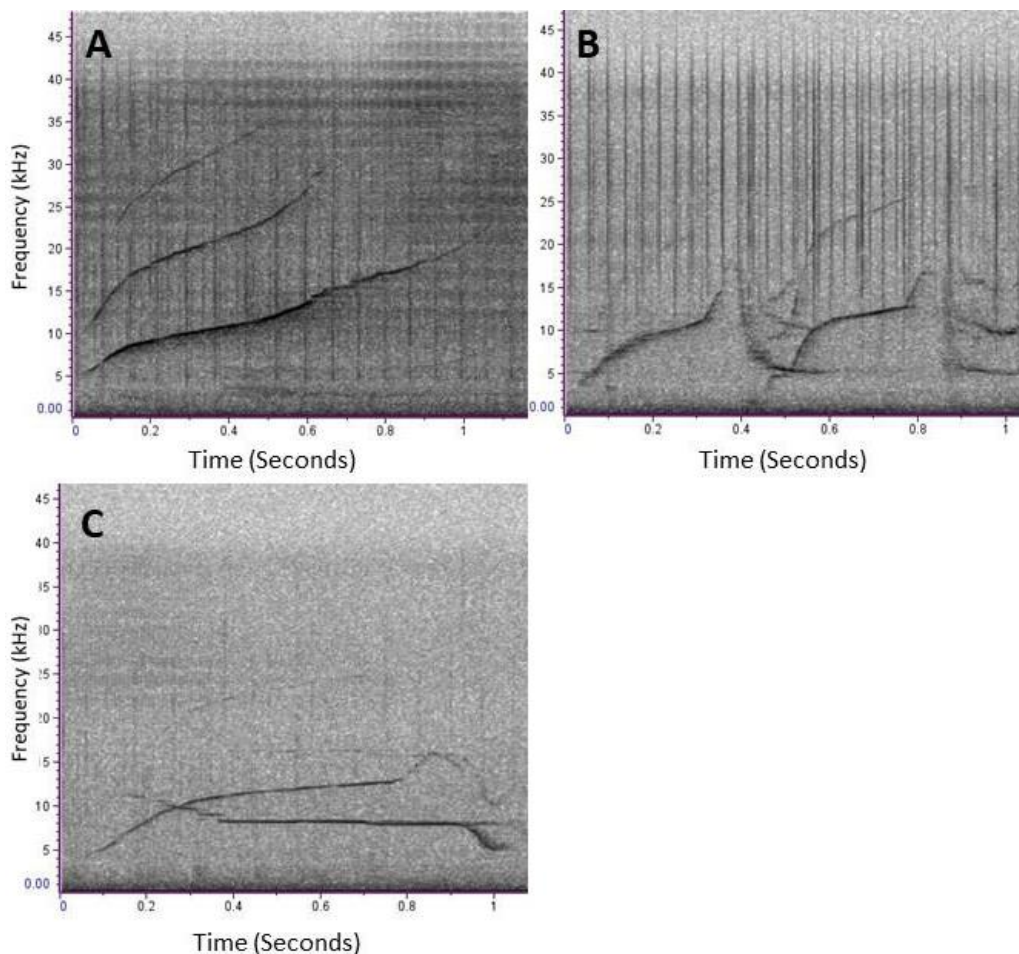


Figure 3.2. Example spectrograms for each bottlenose dolphin whistle category based on temporal overlap: A "single whistle, B "overlap match" and C "overlap no match".

A persistent feature of the acoustic recordings and resulting whistle and click detections was noise and false positive detections due to both natural and anthropogenic noise sources producing tonal signals which triggered the whistle and moan detector and transient signals which both triggered the click detector and passed the click classifier (see chapter 1). To account for this, all whistle recordings were visually inspected and only true whistles were highlighted and used in the analysis. For clicks, all detections with ICIs > 400 ms were removed from the analysis. Furthermore, when assigning click categories, for a minute to be considered as click positive (2-state model) or as regular/buzz click (n-state model) a threshold number of clicks needed to be met (2-state model all clicks = 8; for the n-state model regular clicks = 8, buzz clicks = 4). These thresholds were determined based on inspection of the relative frequency of click counts per minute across periods where whistles were both present and absent. Although this process would have removed many false clicks from the data used for the analysis, high intensity anthropogenic noise which causes large numbers of false click detections (with low ICI) would still be included. To account for this, only sections of the recording that included at least 30 minutes of continuous dolphin detection (2-state model) were included in the n-state model, effectively removing transient noise sources such as passing vessels. This would also have removed short periods of dolphin detection. Therefore, the n-state dolphin activity analysis should be considered as an investigation of area usage when dolphins are active in the area for an extended period. As extended period of anthropogenic noise (e.g., stationary vessels with engines running or potting vessels operating machinery) or periods where there was of both dolphin and anthropogenic noise could still have been included in the analysis “activity states” resulting from the n-state model were considered under the possibility of there being false positive click detections.

3.2.4 Data Streams

For the 2-state presence/absence HMM the click and whistle data streams used included the presence/absence of at least 8 clicks (excluding those identified as “noise”) and presence/absence of any whistle, respectively. Whistle presence was assigned to each minute which had a whole or partial whistle as recorded in the Raven selection tables. Whistle selections which started in one minute and ended in the next minute were counted as present in both minutes. The distributions of both

data streams were modelled using the binomial distribution including a single probability of success parameter.

The two data streams used in the n-state model were based on click and whistle categories with the click data stream including three click categories and whistle data stream including four. Click category 1 (hereafter BC; Buzz Click) was allocated to any 1-minute period that included at least four buzz clicks; click category 2 (RC; Regular Click) was allocated to one-minute periods that included at least eight regular clicks but less than four buzz clicks; and click category 3 (NC; No Click) was for one-minute periods which did not include at least eight regular or four buzz clicks. Whistle category 1 (WOM; Whistle Overlap Match) was allocated to any period which contained an overlapping whistle of the same type; whistle category 2 (WNM; Whistle overlap No Match) was allocated to any minute period which contained an overlapping whistle but not an overlapping whistle of the same type; whistle category 3 (SW; Single Whistle) was for minute periods which contained a whistle but with no overlap; and whistle category 4 (NW; No Whistle) was allocated to minute periods which did not contain a whistle whether it was single or overlapping. The distribution for each observation was modelled using a categorical data distribution that included n-1 probability parameters where n is the number of categories.

3.2.5 Dolphin Presence and Absence – 2-state model

The starting values used for the click presence and whistle presence distributions were set at 0.9 and 0.8 for the dolphin present state and 0.01 and 0.001 for the dolphin absent state, respectively. Furthermore, the probability of whistle presence was fixed to zero for the dolphin absent state, this effectively forced the model to identify the state as dolphin present if there was a whistle detected during that minute. This was appropriate given the manual inspection of each whistle and the inclusion of only true positive detections. To prevent the model from erroneously calculating transition probabilities from non-consecutively recorded minutes, each continuous recording was identified and labelled by a recording number and included in the analysis as an "ID". Within the *momentuHMM* modelling framework a new "ID" causes the Markov chain to reset. Two models were fitted, one that included the covariable location on both click and whistle probabilities and one that didn't include any covariables. No covariables were included on the transition probabilities.

To select the minimum length of recording section with consecutive dolphin presence for further analysis, the rate of false positives was manually checked from a randomly selected number of sub samples of dolphin present sections across a range of section lengths (number of minutes). A total of 208 randomly drawn sections were viewed in Pamguard, inspecting both click display and Long-Term Spectral Averaging (LTSA) with whistle contours overlaid (see chapter 1 for the LTSA settings). The outcome (true/false dolphin presence) was then modelled using a binomial GLM with both length and location used as predictor variables. The length of section where the probability of true detection was predicted to be approximately 1 for all locations was used as the minimum length of section analysed by the second model.

3.2.6 Model 2 – N-state model of dolphin activity

Sections of the time series which had continuous dolphin presence (as identified by the 2-state HMM) for a minimum of 30 minutes were extracted from the initial dataset for further analysis using an n-state HMM, with each continuous period assigned a unique “ID” and with the 1-minute interval retained.

The total number of states and starting values of the n-state model were not assumed a priori and were statistically inferred by running multiple models with differing states and random starting values. Running different starting values was essential to avoid selecting starting values which would result in the algorithm converging on local rather than global likelihood maximums. An initial set of models were performed on data from only one location (DB) and included running 6 iterations of models with 3 to 14 states. Model AIC was used to determine the number of states which produced the most parsimonious models. Had the models with the lowest AIC been 14 states the modelling procedure would have continued with additional states (15, 16, etc).

Multiple iterations ($n = 100$) were then run with random starting values and with the number of states identified by the first run of models. This was to identify the most appropriate starting values for use in all subsequent models.

The next step in the modelling process was to use the number of states and starting values as identified in the previous step to fit a HMM on data from all locations. At this stage, models were fitted that considered the effect of location as a function of

the observation distribution parameters. This was to allow the parameters flexibility when determining states at each location as the initial parameters were selected using DB only data. The most parsimonious model was identified using AIC.

The model selected from the above step was then used as the base model from which to investigate the effects of environmental covariables on the transition probability matrix. These included diel phase and tide which were both modelled as an index from 0 to 1 where 0 and 1 represented sunrise and low tide and 0.5 represented sunset and high tide, respectively. Both cyclical indices were incorporated into the model using cosinor transformation (Barnett and Dobson, 2010), with period = 1. The cosinor function creates two covariates:

$\cos(2\pi * index\ value)$ and $\sin(2\pi * index\ value)$,

that are both incorporated into the fitted model. This method was used in this part of the analysis over the use of periodic m-splines as used in chapter 2 due to numerical problems fitting these splines in the HMM.

Location was also included as a factor covariable with three levels representing each of the hydrophone deployment locations. Interactions between location and tide, and location and diel phase were also included.

3.2.7 Decoding states and interpretation

The most parsimonious model for the above modelling procedure was used to identify the latent activity states, the click and whistle category probabilities and to assign each minute of the data set to a state using the Viterbi algorithm.

Each state was interpreted from the probabilities of each of the click and whistle categories and the transition probabilities. States which were attributed to foraging behaviour were identified by high probability of the BC and the WOM categories. States attributed to possible social behaviour were identified by high levels of whistle activity (WNM and SW) but with low probability of BC and WOM. States that fit neither of these broad assumptions were considered separately based on click and whistle category probabilities. A full consideration for the interpretation of each state is presented in the discussion.

3.2.8 Model Diagnostics

Pseudo-residuals (Zucchini et al., 2016) for each data stream were calculated using a continuity adjustment (Harte, 2017) as both data streams were discrete distributions. Temporal autocorrelation of pseudo-residuals were inspected using autocorrelation function (ACF) and their distribution was plotted with a Q-Q plot to identify whether they fit the normal distribution. However, it is noted that when using continuity adjustment, for observations that are close to the boundary of the domain, pseudo-residuals will provide a poor indication of goodness-of-fit (Harte, 2017).

3.2.9 Effect of location, diel phase, and tidal phase on state occurrence

For each location the proportion of time allocated to each state was calculated to investigate the relative occurrence of each state across each location. In addition, the presence and absence of each state was identified for each minute of the “dolphin present” time series and were modelled using a binomial GAM-GEE (GEE was used due to temporal autocorrelation between consecutive minutes; for detailed description of the GAM-GEE modelling framework see section 2.2.7). Each recording section (“ID”) used as the blocking variable and with tide cycle, diel cycle and location fitted as predictor covariables. For each model the full starting model used included an interaction between tide and location, and location and diel phase. Cyclic covariables tide and diel phase were fitted as m-splines using package *splines2*. A backward model selection process was implemented that used the drop1 function from package *geeasy* (<https://github.com/annennenne/geeeasy>).

3.3 Results

3.3.1 Dolphin Presence/Absence Hidden Markov Model

The 2-state model to identify dolphin presence and absence that included location as a covariable was selected. The probability of detecting at least 8 clicks was 0.001 for the dolphin absent state and 0.621 for the dolphin present state. The probability of detecting a whistle was 0 (fixed in the model formulation) for the dolphin absent state and 0.541 for the dolphin present state. A total of 329,947 minutes were decoded as the dolphin absent state and 17,004 for the dolphin present state.

The probability of a section of the recording identified as dolphin present being a true positive approached 1 when greater than approximately 30 minutes (Figure 3.3) and

this length was selected as the minimum length of recording used in the next stage. The binomial GLM identified length as significant (z value = 4.913, $p < 0.001$) and the effect of location near significant for NB and insignificant for SM (NB z value = -1.943, $p = 0.052$; NB = -1.095, $p = 0.274$). There were a total of 167 sections of ≥ 30 minutes of consecutive dolphin present minutes, totalling 13,931 minutes. This subsample of the data was used in the next modelling stage.

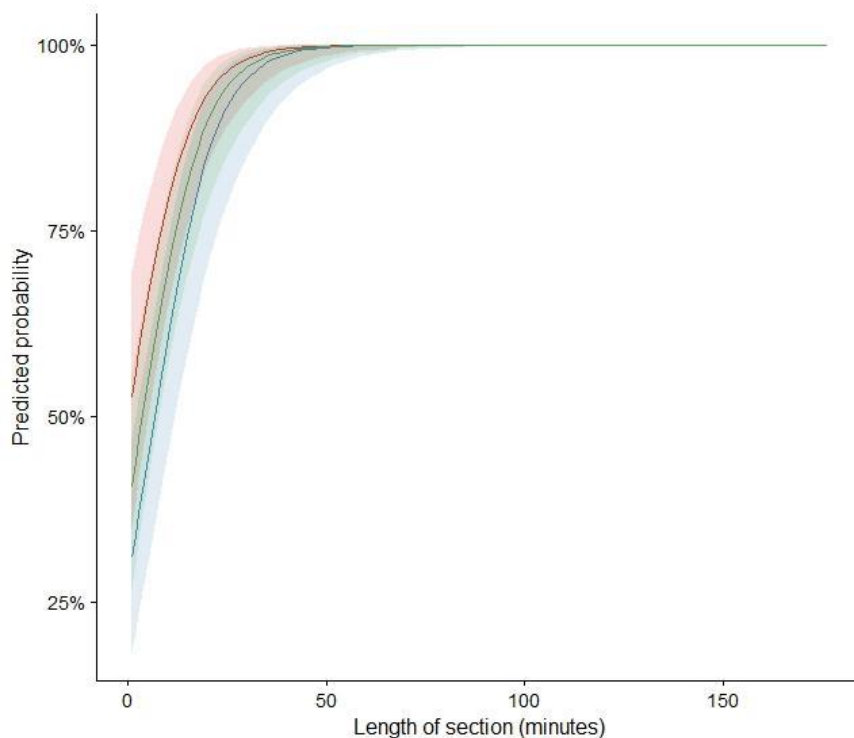


Figure 3.3. Predicted probability of a recording section being a true positive dolphin detection as a function of recording length. Shorter recording sections were more likely to be false positives. Each line represents location with Druridge Bay (red) having the least false detections and Newbiggin (blue) having most; St Mary's is represented by the green line.

3.3.2 Activity states Hidden Markov Model

The model with the lowest AIC from the first batch of models (including 6 iterations of states 3 to 14 with random starting parameters) included seven activity states (Figure 3.4). AIC steadily increased with each additional state up to seven states, and the AIC scores for models greater than seven states remained low, indicating similar support for models with greater than seven states. Given the difficulty in interpreting overly complex models the decision was made to proceed with models that had seven hidden states (Pohle et al., 2017).

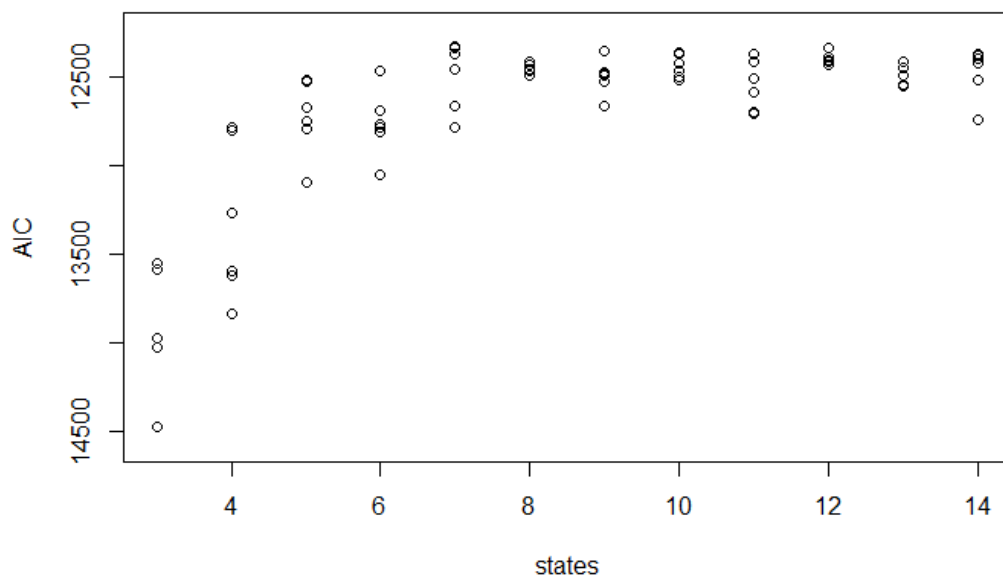


Figure 3.4. Model AIC for each iteration ($n=6$) for each potential number of states (3-14). Models were run with random starting values to determine the most appropriate number of states for the dolphin activity HMM.

After 100 iterations of 7-state models with random starting values the model with the lowest AIC (12302.48) was selected to provide the starting values of all subsequent models; these starting values presented on the working scale (logit) are shown in Table 3.1.

The 7-state model which allowed for the probabilities of each category to vary with location and diel phase was favoured by the AIC (Table 3.2). This was therefore used to model the effect of tidal phase, location, and diel phase on the TPM. The most parsimonious model from this final set of models was the model that included an effect of diel phase on the TPM (Table 3.2).

Table 3.1. Starting values for each parameter of all subsequent 7-state HMM of bottlenose dolphin activity on the working (logit) scale.

Parameter	State						
	1	2	3	4	5	6	7
Click category 1 (BC)	1.63	-1.56	-4.39	4.87	1.45	14.19	-1.95
Click category 2 (RC)	-0.38	17.08	-13.91	2.85	1.18	-1.90	3.30
Whistle category 1 (WOM)	2.89	3.66	-2.48	-6.99	-3.82	0.20	1.50
Whistle category 2 (WNM)	-3.57	-0.46	3.19	3.97	-1.26	-2.89	-0.43
Whistle category 3 (SW)	-5.65	-5.02	-1.71	0.78	3.24	3.69	0.46

Table 3.2. Model selection table showing AIC and maximum log-likelihood of all 7-state HMM.

Models with covariable effects on DM only		
Model	AIC	Maximum log-likelihood
~ Location	42297.3	-20995.8
~ No covariate	42443.2	-21138.6
Model DM ~ Location + Diel with following covariable effects on TPS		
Model	AIC	Maximum log-likelihood
~ Location + Diel + Tide	42094.2	-20747.1
~ Location + Diel	42120.0	-20844.0
~ Location	42126.8	-20931.43
~ Location * Tide + Diel	41923.8	-20602.9
~No covariate	42143.1	-21023.6
~Location + Tide	42145.6	-20856.8
~Diel	42195.4	-20947.7
~ Location * Diel + Tide	42178.3	-20621.2
~ Diel + Tide	42182.4	-20875.2
~ Location * Tide + Location * Diel	42182.4	-20455.2
~ Location * Diel	42220.6	-20726.3
~ Tide	42226.0	-20981.0
~Location * Tide	42238.4	-20735.2

The click and whistle category probabilities averaged across location for each state are shown in Table 3.3 and were used for state interpretation. The effect of location on each parameter is shown in Appendix B (Figures B1-B5). Of the seven states identified, two (states 4 and 7) were interpreted as “high intensity foraging” based on these states having greater than 80% probability of buzz clicks. State 4 also had a high probability of WOM whistles that are known to be associated with foraging. States 1 and 2 were interpreted as “low intensity foraging” due to the probability of buzz clicks being greater than 10%, state 1 also had higher probability of WOM whistles. All other states were considered as non-foraging. State 3 was interpreted as “low whistle activity” due to the generally high click probability and low whistle probability. State 5 was considered most likely to represent social activity due to the high probability of whistles and was labelled “possible socialising”. State 6 was characterised by having generally low detection probability for both clicks and whistles and was labelled “low acoustic activity”. An overview of each state’s

interpretation is shown in Table 3.4. There were differences in the amount of time allocated to each state at each location providing evidence of differences in area usage (Table 3.5). General trends included more minutes allocated to “high intensity foraging” at Druridge Bay and more minutes allocated to non-foraging states at St Mary’s, with Newbiggin being intermediate - having more allocated minutes to non-foraging states than Druridge Bay and more minutes allocated to “high intensity foraging” than St Mary’s. The average probability of each state transition is shown in Table 3.6 with figures showing the effect of location, diel phase, and tidal phase available in the Appendix B (Figures B6 – B11).

Table 3.3. Probabilities for each click and whistle category for each state of the final bottlenose dolphin activity state HMM.

State	BC	RC	WOM	WNM	SW	Total click	Total whistle
1	0.24	0.72	0.26	0.37	0.36	0.96	0.99
2	0.13	0.7	0.01	0.07	0.51	0.83	0.59
3	0.05	0.74	0	0	0.07	0.79	0.07
4	0.97	0.03	0.31	0.4	0.28	1	0.99
5	0.01	0.13	0.07	0.25	0.58	0.14	0.9
6	0	0.14	0	0	0.34	0.14	0.34
7	0.84	0.15	0.03	0.11	0.55	0.99	0.69

Table 3.4. Interpretation of each state from the final HMM model including a brief justification of each decision.

State	Interpretation	Justification
1	“Lower intensity foraging”	High probability of BC and WOM but with higher probability of RC
2	“Lower intensity foraging”	High probability of BC but with higher probability of RC
3	“Low whistle activity”	High click probability suggesting high dolphin presence but with lowest whistle probability
4	“Higher intensity foraging”	Very high probability of BC and WOM.
5	“Possible socialising”	Very high total whistle probability but with low total click probability
6	“Low acoustic activity”	Low click and whistle probability
7	“Higher intensity foraging”	Very high probability of BC.

Table 3.5. The proportion of time (as a percentage) allocated to each bottlenose dolphin activity state at each location, decoded from the activity state HMM using the Viterbi algorithm.

Location	State 1	State 2	State 3	State 4	State 5	State 6	State 7
DB	9 %	16 %	21 %	16 %	9 %	19 %	11 %
NB	9 %	11 %	26 %	7 %	13 %	24 %	9 %
SM	8 %	14 %	11 %	3 %	23 %	37 %	4 %

Table 3.6. Average transition probabilities between each state of the bottlenose dolphin activity state HMM. To be read as row state transitioning to column state (i.e., rows sum to 1).

State	1	2	3	4	5	6	7
1	0.92	0.02	0	0.03	0.03	0	0
2	0	0.8	0	0	0.03	0.09	0.08
3	0.02	0.06	0.9	0	0	0	0.02
4	0.03	0	0	0.95	0	0	0.02
5	0.04	0.02	0	0	0.76	0.18	0
6	0	0.02	0.04	0	0.09	0.86	0
7	0	0.13	0.01	0.01	0	0	0.84

3.3.3 Model Diagnostics

Model diagnostics are shown in Figure 3.5. ACF of pseudo-residuals of both data streams (click and whistle categories) showed good fit of data suggesting that the model explained the temporal patterns of activity states well. QQ plots of the whistle pseudo-residuals were a close fit to the normal distribution but did deviate suggesting improvements to the model could be made. The QQ plot of the click data stream did not fit the normal distribution with the pseudo-residuals having heavy tails, highlighting potential problems with the model. Heavy tailed residuals suggest that the model may be underestimating the variability in the data or may be due to lack of flexibility in the modelling process (Zucchini et al., 2016). More generally, poor model diagnostics suggest there may be unmodeled dependencies in the data and that parameter estimation using maximum likelihood estimation may be biased. Potential improvements to the HMM model and the handling of the click data stream is addressed in the discussion.

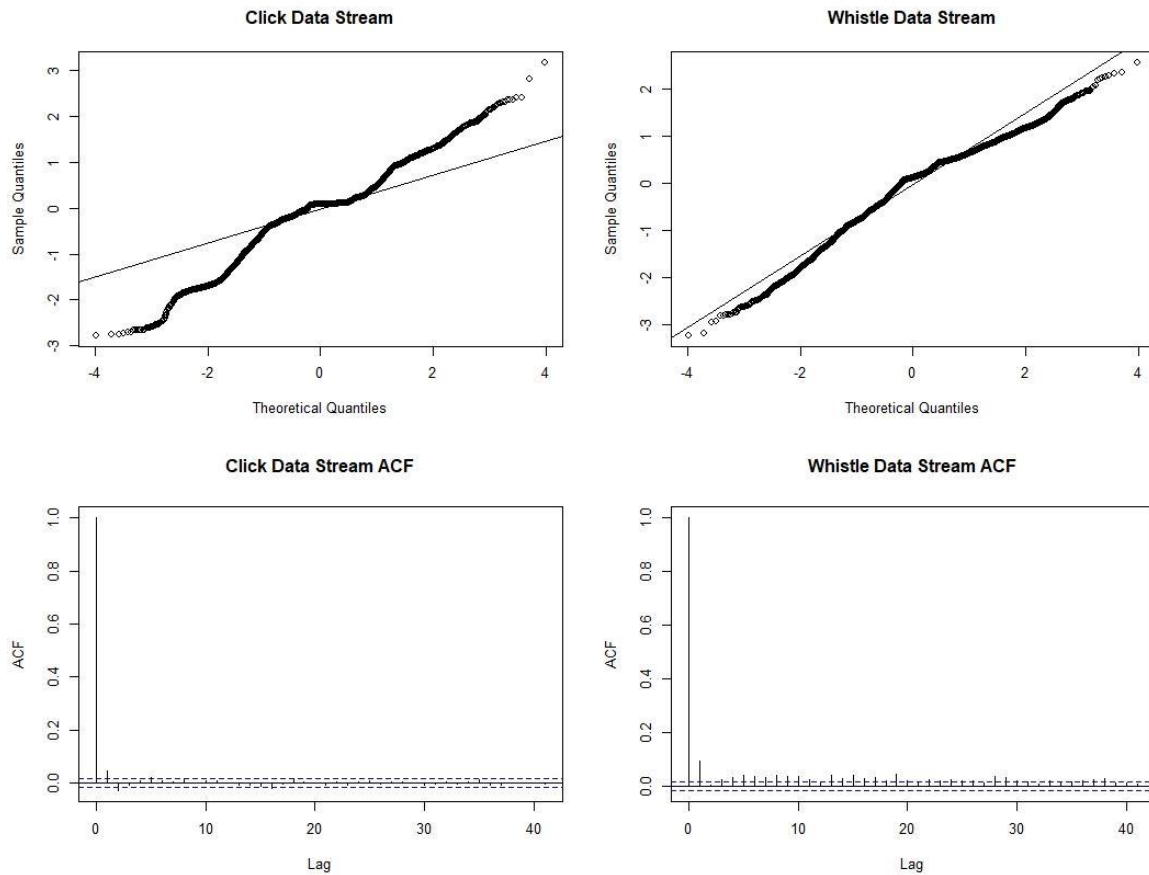


Figure 3.5. Model diagnostics of click and whistle data streams from the bottlenose dolphin activity state HMM showing QQ plot and autocorrelation function (ACF).

3.3.4 Effect of location and environmental covariables on state occurrence

The results of the binomial GAM-GEE for each state are available in Table 3.7 and show differences in the effects of location, diel phase, and tidal phase on the occurrence of activity states. The results show that all three variables have some effect on state occurrence but the covariables and interactions with location that are significant differ across states. The predicted effect of each significant covariable can be seen in Figures 3.6 and 3.7. There was a general pattern for increased occurrence of foraging states around sunset (diel index 0.5) although there were differences in secondary peaks across locations (Figure 3.6 B, D, F). Tide was generally less important across states except for state 4 (Figure 3.6, E) where an interaction with location identified strong tidal influence at Druridge Bay (where this state was more frequently identified) and state 5 (Figure 3.7 A) where an interaction with location identified a peak during ebb tide at St Mary's, low tide at Newbiggin and two peaks during flood and high tide at Druridge Bay.

Table 3.7. Result table of each binomial GAM-GEE for each state (1-7) of the bottlenose dolphin activity state HMM, covariates retained for backward selection are shown with the result of the Wald's test.

Model		Wald's Test		
State	Parameter	DF	χ^2	P value
1 - "Lower intensity foraging"	Tide	6	3.08	0.799
	Location	2	0.50	0.779
	Diel	6	23.24	<0.001
	Tide:Location	12	25.49	0.013
2 - "Lower intensity foraging"	Tide	6	11.82	0.066
	Diel	6	21.67	0.001
	Location	2	2.76	0.252
	Diel:Location	12	22.53	0.032
3 - "Low whistle activity"	Diel	6	20.40	0.002
	Location	2	25.38	<0.001
4 - "Higher intensity foraging"	Tide	6	9.80	0.133
	Location	2	23.08	<0.001
	Tide:Location	12	32.48	0.001
5 - "Possible socialising"	Tide	6	7.00	0.321
	Location	2	26.16	<0.001
	Diel	6	19.23	0.004
	Tide:Location	12	49.32	<0.001
6 - "Low acoustic activity"	Location	2	34.69	<0.001
7 - "Higher intensity foraging"	Tide	6	10.26	0.114
	Diel	6	7.32	0.292
	Location	2	18.42	0.001
	Diel:Location	12	21.97	0.038

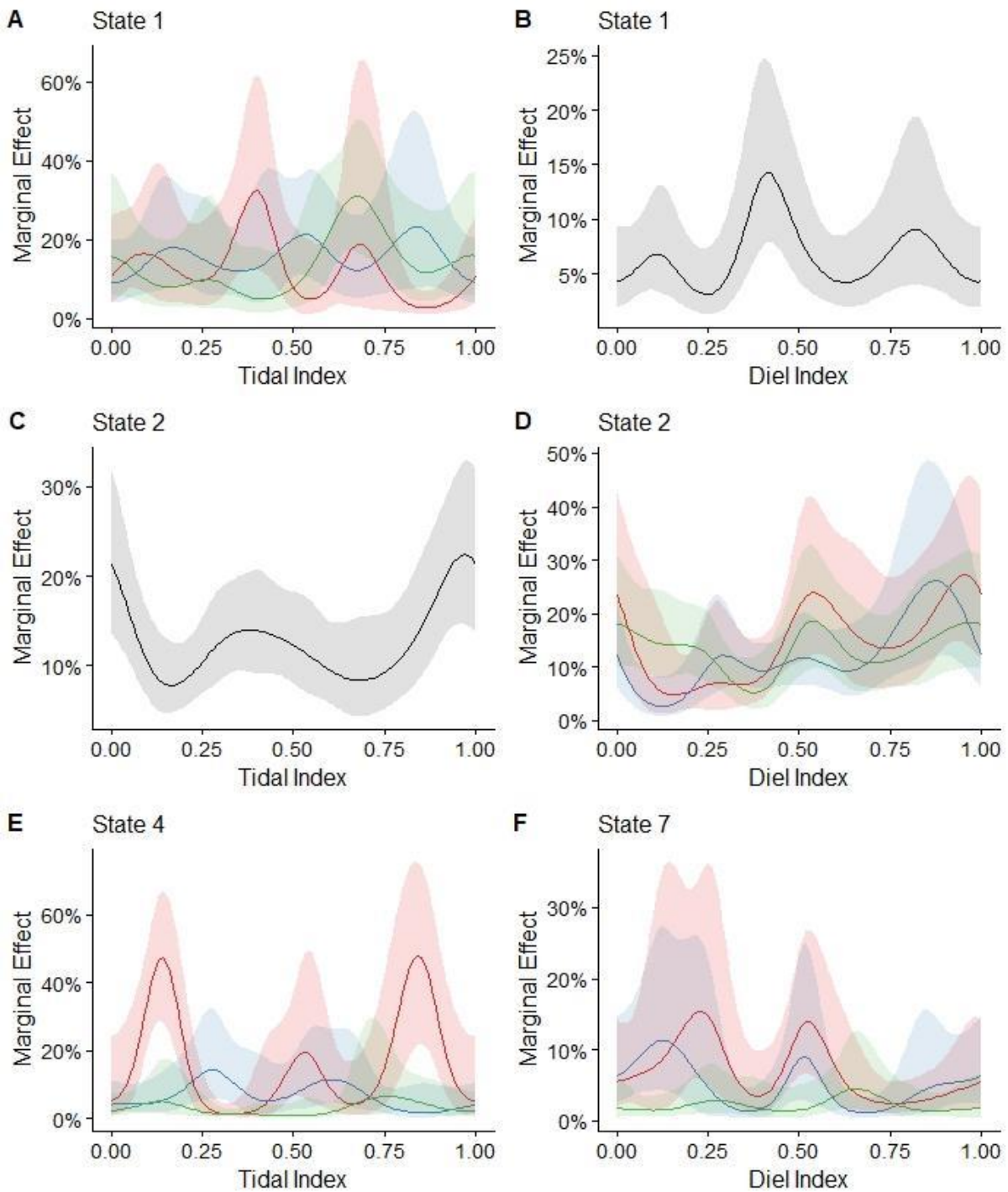


Figure 3.6. Effect of tidal phase, diel phase, and location of foraging states. State 1 (A and B) and state 2 (C and D) were interpreted as “lower intensity foraging”; state 4 (E) and state 7 (F) were interpreted as “higher intensity foraging”. Effect of tidal phase is shown in the left column and diel phase is shown on the right column. Where the interaction effect between tidal or diel phase and location is significant, each location is represented as a separate line: red = Druridge Bay, blue = Newbiggin, and green = St Mary’s.

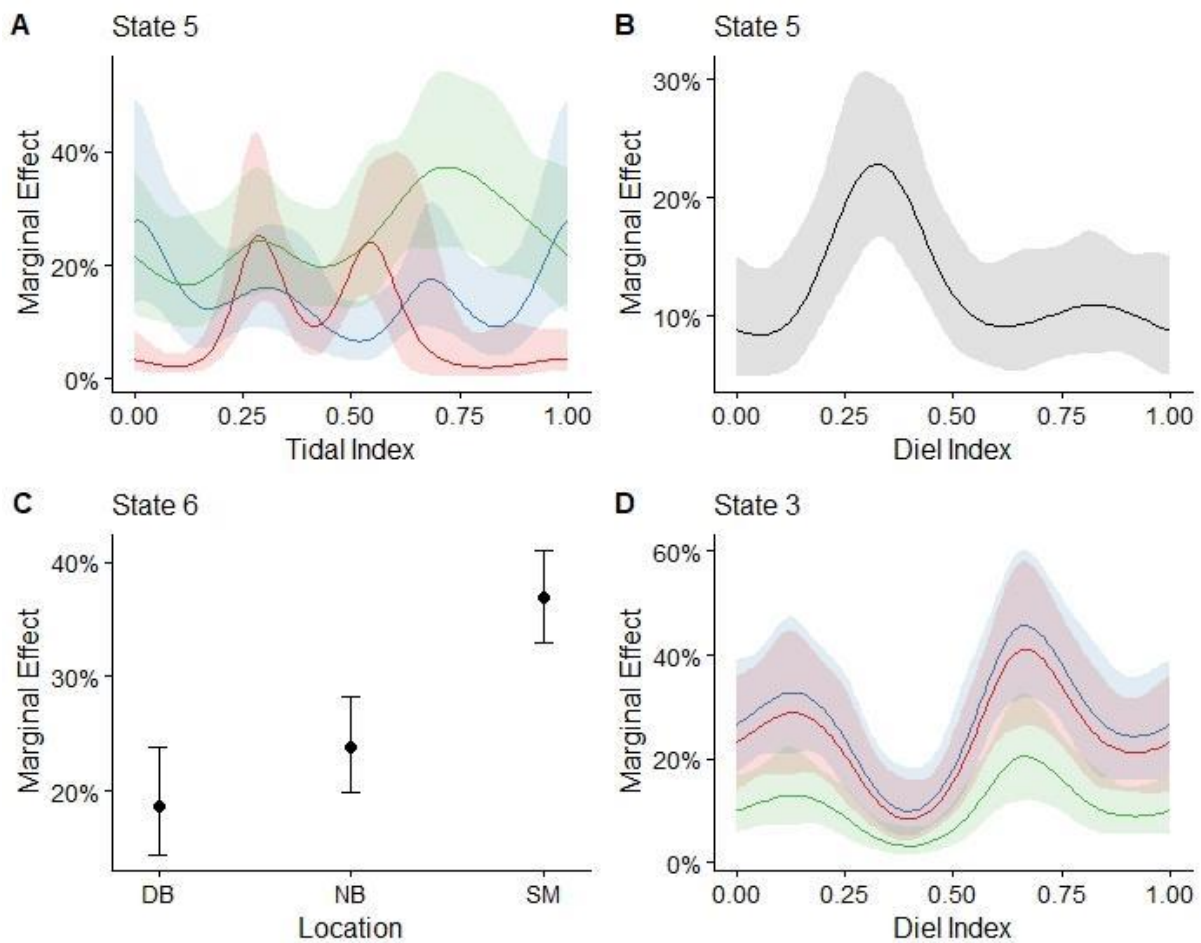


Figure 3.7. Effect of covariables tidal phase, diel phase, and location on non-foraging states. State 5 (A and B) was interpreted as “possible socialising”, state 6 (D) was interpreted as “Low acoustic activity”, and State 3 (C) was interpreted as “low whistle activity”. In figures A and D each location is represented by a separate line: red = Druridge Bay, blue = Newbiggin, and green = St Mary’s.

3.4 Discussion

Behavioural observations of odontocetes cannot be made directly using passive acoustics and must be inferred from detectable acoustic emissions. To date, studies have been limited to using the proportion of buzz click detections to regular click detections as a coarse quantification of site-specific foraging behaviour. This study presents a novel approach to investigating area usage of dolphins from acoustic emissions by identifying “activity states” from echolocation click and whistle data. A total of seven activity states were statistically inferred from the acoustic time series and interpreted as “higher intensity foraging” (states 4 and 7), “lower intensity foraging” (state 1 and 2), “low whistle activity” (state 3), “possible socialising” (state 5), and “low acoustic activity” (state 6). The proportion of the recording minutes allocated to each state was different across locations, providing evidence of differences in area usage across the study area. The starkest difference was

between Druridge Bay (which had a higher proportion in states 4 and 7, both foraging states) and St Mary's (which had higher proportion in states 5 and 6, both states characterised by low click probability) (Table 3.5). Modelling the probability of state transition (within the hidden Markov models (HMM) framework) and state occurrence (using GAM-GEEs) identified differences in the effects of diel and tidal cycles on the probability of each activity state, providing evidence that bottlenose dolphin group activity and spatial use is modulated by these environmental factors (Table 3.7, Figures: B7, B8, B10, B11), as also reported by other studies (Harzen, 1998, Allen et al., 2001, Bailey and Thompson, 2010, Fury and Harrison, 2011). The results of this study provide a more detailed differentiation of site-specific behaviours than previously achieved using long-term acoustic data. These include, identifying multiple foraging states that would not be identifiable from using the presence of buzz clicks alone (e.g., states 4 and 7 both had >80% buzz click probability) and identifying periods of high dolphin activity from whistles when click detections were low and therefore would have been missed by click detection only studies (e.g., state 5).

The objectives of the study were achieved by integrating click and whistle detections into a single modelling framework using HMM. HMM were used to simultaneously model both a hidden state process (representing the unobservable group behaviour occurring within detection radius of the hydrophone) and a (state-dependent) observation process (the temporal pattern of dolphin acoustic emissions that were directly detected from the hydrophone data).

HMM model the underlying state process as a Markov chain, whereby future states are dependent only on previous states. Markov chains have been used to model dolphin behaviour dynamics in other studies (Lusseau, 2003, Christiansen et al., 2010). In these studies, group behaviour was directly observed and represented by discrete behavioural categories (e.g., resting, foraging, socialising, and travelling), whereas in this study behaviour was not observed directly but statistically inferred from the observation process. Another contrast is that group behaviour was sampled by vessel-based focal follows where observations were mostly unaffected by the focal group's movements as sampling was done while following the dolphin groups. In this study sampling was limited to point sampling with activity states representing area specific behaviours occurring within the hydrophone's detection radius.

However, the principle that behavioural states evolve over time as a Markov chain is consistent between the approach of this study and other studies using Markov chains to analyse group behaviour based on visual observations.

The observation process was modelled using click and whistle categories, whereby each minute was assigned a category based on the presence of buzz clicks and the presence of temporally overlapping whistles. These categories were selected based on the known use of sound by bottlenose dolphins that would allow for interpretation of the resulting states. The observation process resulted in different distributions of these categories reflecting their relative importance of each vocalisation category for each state. Aside from subjectively choosing these click and whistle categories, the modelling process (e.g., selecting the final number of states and the resulting click and whistle category distributions) were implemented in an unsupervised and data driven approach. As such, the interpretation of the states in terms of representing biologically meaningful dolphin behaviour was restricted to broad categories referred to as “activity states” to avoid over-interpretation. States which had overall high probability of detection of clicks and whistles allowed for more confidence in the interpretation. However, confounding factors (such as orientation both in terms of distance and angle from the hydrophone) limited the interpretation of states that were characterised by low detection probabilities. This was because low detection probabilities could be caused by extrinsic factors resulting in false negative detections. Angle of the vocalising dolphin would affect the relative detections as clicks are directional beams and thus more impacted by angle than whistles that are non-directional (Au et al., 1978, Janik, 2000b, Au et al., 2012). A potentially greater confounding factor was distance to the hydrophone which could not be measured using a single hydrophone deployment in this study. Larger distances may have impacted the ratio of clicks to whistles when dolphins were further from the hydrophone as lower frequency whistles have a higher potential propagation distance than higher frequency clicks. Studies of click detections using C-POD reported a maximum click detection distance of between 1343-1779 m, with a median of between 462-729 m (Nuutila et al., 2013). Whistles however have higher reported maximum distances with extremes of 25 km under certain conditions (e.g., sea state 0) (Janik, 2000b). Under normal environmental conditions this maximum range may be quite rare and vary depending on environmental factors (Quintana-

Rizzo et al., 2006). Jensen et al. (2012) investigated active space of dolphin whistles and reported that 95% of whistles were detectable at 220 m, with a median detection range of 740 m and maximum detection range for whistles with highest source level of 5740 m. When investigating whistle detection probabilities, Fearey et al. (2022) assumed a detection distance of 1500 m of signature whistles, within the maximum detection range of clicks for C-PODs. Despite higher maximum distances for whistles, median detection distances reported by Nuutila et al. (2013) and Jensen et al. (2012) were similar and activity states were interpreted based on the assumption that click and whistle probabilities represented true dolphin emission rates. However, this is with the caveat that states characterised by low rates of click detection may be significantly impacted by the extrinsic factors outlined above and this should be considered when drawing conclusions about area usage and recommending improvements to the methodology.

Despite the limitations identified above, five of the seven states had a combined click category probability of more than 79% (Table 3.3). Of these, states 4 and 7 had very high buzz click probability which gave good confidence in interpreting these states as “higher intensity foraging”. The main difference between these two states was the probability of different whistle categories with state 4 having the highest probability of the WOM whistle category. Overlapping whistles of the same type have been shown to be associated with foraging, potentially signalling foraging opportunity to the conspecifics and the probability of this category was expected to be high during periods of with high probability of buzz clicks (King and Janik, 2015). In contrast however, King and Janik (2015) demonstrated that overlapping whistles of different type (WNM, in this study) were less likely to be detected during foraging behaviours. In contrast, state 4 showed similar probabilities for both overlapping whistle types (WOM = 0.31 and WNM = 0.40). State 7 had a lower probability of whistles with mainly non-overlapping (SW) whistles detected during this state. There are also differences in the state transition probabilities between these two states with state 4 more likely to proceed into state 4 again and with a higher number of states for which the probability was zero (Table 3.6). State 7 however had a higher probability of transitioning into other states with a relatively high probability of transitioning to state 2 (low intensity foraging) (Table 3.6). When the occurrence of these states was modelled using GAM-GEE, there were differences in the significant explanatory

covariables for the states. State 4 was significantly affected by the interaction between tidal phase and location. With large marginal effects (shown in Figure 3.4 E) at Druridge Bay, characterised by having three peaks across the tidal cycle. State 7 however showed the interaction between diel phase and location as more significant (Table 3.7). Both states accounted for a higher proportion of time at Druridge Bay and Newbiggin than at St Marys, with state 4 accounting for an even greater proportion of time at Druridge Bay (Table 3.5). These findings suggest that Druridge Bay and to a lesser extent Newbiggin are more important habitats for foraging. Differences in diel and tidal drivers at these sites suggest that they affect area usages at relatively small spatial scales.

Potential drivers between the differences shown in the “higher intensity foraging” states could be driven by foraging techniques in response to prey type or habitat features. Higher probability of whistles including overlapping categories could be indicative of increased cooperation in affecting the movements of prey species. King and Janik (2015) reported that WOM whistles were more likely to be detected in close temporal proximity to “bray calls”, a call that has been linked to manipulating salmonids (Janik, 2000a). Foraging bouts without the need for these calls (i.e., non-salmonid prey types) may have resulted in periods with high probability of buzz clicks and single whistles (i.e., state 7).

States 1 and 2 had high overall click detections but with a lower proportion of buzz clicks and were interpreted as “lower intensity foraging”. The reduced buzz click detections may be due to a true reduction in buzz click production by animals during this state caused either by a general reduction across all animals or as a result of there being few animals within the detection radius. Group size is another factor which confounds interpretation of the states. A further possibility is that the reduced number of buzz clicks was due to foraging buzzes not propagating as far as regular clicks due to a decrease in source amplitude. Similarly, to “higher intensity foraging” states 4 and 7, states 1 and 2 show similar differences in whistle categories suggesting that they may reflect the same group behaviour only affected by one of the above explanations to reduced buzz click detections. If distance to the hydrophone was the only factor causing the reduction in buzz click detections, then one would expect to find similar patterns in state occurrence between state 1 and 4 and 2 and 7 from the GAM-GEE models. This however is not apparent, with the

marginal effect of tide showing different patterns between states 1 and 4 and with marginal effects showing different patterns in diel phase. There is also a difference in the proportion of each state at each location with state 1 being consistent across all three locations and state 2 having a more even representation across each site than state 7. These considerations suggest that these states may represent more than just the effect of distance to hydrophone when compared to states 4 and 7, and that they may represent less intense foraging activity either as a result of smaller group size, a reduced proportion of the group foraging, or by lower density of prey items available, reducing the number of buzz clicks detected. Similar to the high intensity states, differences between these states may reflect differences in foraging technique, with greater whistle production signifying cooperative foraging or other difference in foraging behaviour.

State 3 was characterised by a relatively high probability of clicks with a greater proportion of regular clicks and a relatively low probability of whistles and was given the less informative “Low whistle activity”. Despite there being some buzz clicks detected, given their low probability during the state it was not interpreted as foraging. Behavioural interpretation of this activity state is less intuitive, however, unlike states with reduced clicks, the reduced whistles were only considered as a reduction in actual whistle emissions. This state may represent periods of relatively low activity without foraging or social interactions. The state was more likely to occur just after sunset based on the GAM-GEE, it was also less likely to transition into states 4 and 5 which were characterised by high intensity foraging and potential social activities.

State 5 (categorised as “possible socialising”) included relatively low click probability and high whistle probabilities. This, as previously discussed, is more difficult to interpret with the possibly confounding factors relating to click detection. Given relatively high probability of WOM whistles and a non-zero probability of buzz clicks this state could possibly be indicative of foraging behaviour similar to state 1 but further from the hydrophone limiting click detection. However, based on the decision to interpret states based on the assumption that clicks and whistles were indicative of actual emissions this state was interpreted as social behaviour. Under this assumption non-zero buzz click probability could be caused by social burst pulses (Overstrom, 1983). This state showed differences across tidal phase and location,

and diel phase (without interaction with location) with a pronounced increase during the day and during ebb tide at St Mary's. St Mary's is positioned between two river estuaries which are hotspots of foraging activity (personal observation). If this state is indicative of socialising, then it may be driven by its proximity to good foraging habitats whilst also providing resting and socialising areas used between foraging bouts.

State 6 was the state with lowest detection generally and given the limitations to interpreting states based on reductions in emissions the state was categorised as "low acoustic activity/detection". If this state represented true dolphin emissions a deeper interpretation could be that it reflects rest or periods of inactivity between other states, however there were too many variables that could have produced the result so biological interpretation was avoided.

To identify the activity states outlined above, a 2-step modelling procedure was implemented. The first process was to identify sections of the recordings where there was extended periods of dolphin acoustic activity. For this, a 2-state HMM was performed using the presence and absence of click and whistles as the data streams with the resulting states identified as either dolphin present or dolphin absent, depending on the distribution of the click and whistle detections. The model resulted in two states which clearly represented presence and absence of dolphin detections (dolphin present: click probability = 0.6 whistle probability = 0.5; dolphin absent: click probability = 0.001, whistle probability was fixed to 0). However, a subsample of the resulting dolphin positive periods was manually checked for the presence of true positives and revealed that false positive click detections caused some periods to be assigned as dolphin present when there were no dolphins. Modelling the result of this manual checking showed that as the length of the recording section (defined as consecutive dolphin present minutes) increased the probability of true detection approached 1 with detections greater than 30 minutes. This informed the decision to include only periods with greater than 30 minutes of consecutive dolphin presence to be used in the next stage of the modelling process (the activity state HMM as detailed above). This had the effect of making all conclusions about area usage relevant to periods of dolphin presence where dolphins were in the detection distance of the hydrophone for at least 30 minutes. This was however congruous to the aims of the study as extended periods of occupancy were more relevant to

understanding spatially specific area usage, whereas transient detections (omitted by this process) such as a group of dolphins travelling through the area were less important. Transient behaviours such as travelling were, therefore, avoided when interpreting the resulting states.

The click and whistle data streams used in the second HMM expanded the number of categories from two (present and absent) to three and four for click and whistles, respectively. The additional click category separated buzz clicks from regular clicks, whereas the additional whistle categories differentiated whistle presence based on the temporal overlap and matching contours of overlapping whistles. The motivation for choosing these click and whistle categories was to provide an adequate representation of the raw detections to identify both foraging behaviour and periods of high acoustic activity that were unlikely to be indicative of foraging. These non-foraging periods were considered socialising if there was a high occurrence of whistles. It is well documented that buzz clicks are used by odontocetes during foraging activities as they approach and catch prey items (Todd et al., 2009, Leeney et al., 2011, Wahlberg et al., 2011, Nuuttila et al., 2013, Yang et al., 2021). Furthermore, King and Janik (2015) identified that overlapping whistles of the same type are associated with foraging behaviour for bottlenose dolphins on the east coast of the UK. Whistles have been shown to increase with social behaviours in multiple studies but also during foraging (Acevedo-Gutiérrez and Stienessen, 2004, Quick and Janik, 2008). Therefore, high numbers of whistles were only considered indicative of social behaviour in the absence of foraging vocalisations (buzz clicks and overlapping matched whistles).

Categorical representation was a natural choice for the whistle data stream given that each whistle identified in the spectrogram was described as a distinct and unordered type. Using categories for the click data stream may seem less intuitive than using a measure of click counts and ICIs. The decision to use categories was based on the ability to represent both the presence of clicks and to separate out important differences in ICI (i.e., buzz clicks) within one data stream. Modelling click counts and average ICI for example would have taken two separate data streams that could not have been considered conditionally independent, violating one of the model assumptions. Using click categories also avoided the use of counts which was deemed favourable given that click counts per minute would have been highly

dependent on the number of echolocating animals within the detection distance from the hydrophone. Aggregating click counts and ICIs into representative categories made the representation of the raw data less impacted by group size. Separate data streams for click and whistle categories were considered independent under the assumption that a group of dolphins within recording distance of the hydrophone were producing clicks and whistles independently from each other.

The number of states for the activity states HMM were determined by running multiple iterations with a varying number of states and starting values. Model AIC showed support for models with seven or more states. Models with higher numbers of states, although providing better model fit can often lead to difficulties in interpreting the results. It was therefore decided to continue the modelling process using models with seven hidden states. The final model selection included models with covariate effects of location on the data stream distribution. The underlying differences between location in click and whistle probabilities for each state likely represent multiple factors that were not directly observed such as group size, location from hydrophone, position of dolphins in relation to the hydrophone, increased human activities and noise, and increased noise due to environmental factors. The effect on the click and whistle category probabilities can be viewed in the Appendix B (Figures B1-B5). For most of the parameters the effect was low, and the general trend was for increased BC and WOM probability at Druridge Bay across different states, suggesting that there was more foraging behaviour at this site (reflecting the general patterns observed between location and states). Overall, the effect of location on the parameters did not impact their interpretation, with the average probabilities (shown in Table 3.3) used to determine the biological relevance of each state.

Model fit was investigated by calculating pseudo-residuals (Figure 3.3).

Autocorrelation Function (ACF) showed that the temporal patterns in dolphin activity states was well represented by the model. The distribution of the pseudo-residuals however showed considerable deviation from normal distribution. Improvements in how the acoustic emissions are represented is something that could be improved in future studies, especially for echolocation clicks which showed the largest deviation from normal distribution. One area to consider is the temporal groupings of clicks. Whereas the whistles were indicative of group behaviour (i.e., at least two dolphins

were required to produce an overlapping whistle), buzz clicks, and regular clicks are individual and may be better represented by smaller divisions of time. This could be achieved using hierarchical hidden Markov models (Leos-Barajas et al., 2017) which would allow flexibility in modelling each acoustic emission. Improving the click detectors to remove false positives or using click trains rather than single clicks may also improve the modelling of the click data stream.

Additional improvements to the methodology should also focus on the confounding factors which may affect detection probability of clicks and whistles (e.g., distance from hydrophone and group size). Estimating the distance of emissions from the hydrophone could be modelled as a covariate affecting the data stream distributions and may improve activity state modelling and interpretation. Furthermore, it could also provide an insight into area usage of large groups of dolphins and how it influences activity states. Quick and Janik (2012) localised dolphin emissions from a towed hydrophone array and a similar methodology could be adapted for static deployments for future attempts to identify activity states. Estimating group size would also provide greater insight into area usage and improve activity state modelling. For example, Quick and Janik (2008) showed that whistle rate decreased with group size which would impact identifying activity states. Future studies attempting to estimate the number of dolphins from PAM recordings could consider signature whistles (see chapter 4), and other statistical approaches to click analysis (Hamilton et al., 2021).

The methodology presented in this chapter could also be improved by addressing some of the practical elements of the approach. As presented, the methodology required considerable effort in data collection, processing, and analysis; both in terms of manual effort and computer processing power. The analysis requires constant recording of broad band acoustic data to allow for the HMM analysis of both whistles and clicks, resulting in terabytes of acoustic data collected across the sampling period. These data were initially processed in Pamguard, and the resulting whistle detections were manually inspected to determine whistle categories. Furthermore, the HMM analysis included multiple runs to establish the final model with each requiring several hours of processing time. There was also manual inspection of the resulting states of the 2-state model to determine false positives and establish the subsampling for the n-state model. The following improvements

could be considered to streamline the methodology. The first would be to simplify the modelling process to only include the n-state model. Appropriate periods of dolphin activity could be identified using other methods such as long-term spectral averaging (see Chapter 2, section 2.2.5) or by directly assessing the outputs of Pamguard. Secondly, data collection could be improved by reducing the amount of unused data that is collected. This could be achieved using the SoundTrap click detector (www.oceaninstruments.co.nz) to initiate broad band data collection only when dolphin clicks are detected and maintaining a lower sampling rate recording during times when clicks are not detected. For species that do not whistle (e.g., Phocoenidae and *Cephalorhynchus* species) click detectors such as C-PODs and F-PODs could be used to detect clicks or click trains, reducing the amount of data collected and reducing processing time. At this time there are no available “whistle detectors”, where whistles can be detected and stored onboard a device (as with C/F-PODs), and archival recorders are necessary to study whistles. Processing time of recordings could be greatly improved with automated methods to facilitate whistle categorisation such as using trained neural networks or signal processing, with such approaches becoming available to researchers (Jiang et al., 2019, Shkury et al., 2019, Li et al., 2020). Automating this part of the methodology would greatly reduce the hours required to incorporate whistle detections into the analysis.

The approach taken in this chapter (after consideration of the above improvements) could be applied to other species where researchers are interested in inferring area specific group activity states from the sounds produced by the animals. A prerequisite would be that a minimum of one vocalisation or sound emission is both detectable and related to a known behaviour or activity. Following the methodology here, the vocalisations would be categorised for incorporation into the model, however other options of quantifying the levels of the sound emissions would be possible (e.g., counts of vocalisations). The approach could be applied to address more specific questions of odontocete ecology including quantifying the impact from human disturbance on group activities (Scarpaci et al., 2000, Lusseau, 2003, Marley et al., 2017, Perez-Ortega et al., 2021, Antichi et al., 2022). Applied to other taxon (including terrestrial species) different activity states could represent states of alertness driven by the presence of predators or anthropogenic activity (Papworth et al., 2013, Marley et al., 2017). The methodology could also be applied to determine

states within a community of vocalising animals where differences in soundscapes (Pavan, 2017) could be modelled to reveal hidden states and state changes at relatively granular temporal scales.

3.4.1 Conclusion

Latent “activity states” identified by HMM revealed new insights into area usage of bottlenose dolphin off the coast of Northumberland, UK. Druridge Bay to the north of the study area was more important to “high intensity foraging” states. At Druridge Bay state 4 (identified with high probability of buzz clicks and WOM whistle categories) was linked to tidal phase with three peaks identified during the tidal cycle. Tidal phase was also shown to be important to other states with differences in patterns across locations (Figure 3.4 and 3.5).

Newbiggin had intermediate proportions allocated to foraging and non-foraging states and may represent a habitat that is important to both foraging and non-foraging behaviours. There were differences in the effect of tidal and diel phase on foraging states between Druridge Bay and Newbiggin demonstrating that environmental drivers have differing effects at relatively small spatial scales.

St Mary’s to the south of the study area had considerably less time allocated to foraging activity states (Table 3.5) and may be an area more important to socialising (state 5) and other non-foraging behaviours. This may be driven by its proximity to two large estuaries which may provide better foraging habitat. The location of the hydrophone between these sites may have been used during periods when estuarine foraging was less preferable and could explain the increase in this activity during ebbing tide phase (Figure 3.5B). Diel phase was a significant variable in the occurrence of state 5 (which was characterised by low click detections) with an increase in this state during daytime hours. This is a significant finding for the interpretation of dolphin occurrence during the day using click detections, as reduced clicks due to increased social behaviour may drive patterns misinterpreted as decreased occupancy (Fernandez-Betelu et al., 2019).

Future work should focus on improving how dolphin emissions are represented in the model (particularly the click data stream), addressing the confounding factors that limit state interpretation and streamlining the approach. Combined visual and acoustic studies can provide valuable datasets for improving state interpretation,

these should include both shore-based observation and focal follows. With these improvements, the approach identified in this study has the potential to greatly increase the scope of passive acoustic monitoring of odontocetes to provide detailed behaviour specific habitat selection or be applied to other species or habitats. The approach provides a valuable tool for conservation efforts by identifying critical habitats for specific foraging and social behaviour which can be protected from unsustainable anthropogenic disturbance.

Chapter 4: Seasonal Abundance of Common Bottlenose Dolphins off the Northumberland Coast, UK: A Comparison of Estimates Based on Photo-ID and Signature Whistles

4.1 Introduction

Abundance of a species (i.e., the number of individuals in a defined area) is a fundamental parameter to investigate species ecology and conservation (Krebs, 1972, Cardinale et al., 2020). Abundance estimates are necessary for modelling population dynamics, estimating extinction risk, and quantifying the impact of anthropogenic disturbance (Boyce, 1992, Hastings, 2013, Sharpe and Berggren, 2019). Its importance to conservation efforts is exemplified by the IUCN Red List, with abundance being required to inform 3 of 5 assessment criteria (A. Population size reduction; C. Small population size and decline; D. Very small or restricted population) (IUCN, 2012). Estimating abundance for cetaceans is, however, logistically difficult due to their biological and behavioural characteristics (i.e., they occupy aquatic habitats where they spend most of their time submerged, often at low densities and range across large distances). Despite their apparent elusiveness, cetaceans are at high risk from anthropogenic disturbance, overlapping with multiple human activities that increase mortality or reduce reproductive fitness (Nelms et al., 2021, Temple et al., 2021a). A high proportion (24%) of the identified 90 cetacean species are currently listed as threatened (Critically Endangered, Endangered or Vulnerable) by the IUCN Red List (Thomas et al., 2016, Brownell Jr et al., 2019) with an additional 10 species listed as Near Threatened and 9 species as Data Deficient (www.iucn-csg.org). Providing robust estimates of population parameters and identifying population trends in a timely manner and with economic efficiency, are important goals for conservation research. Emerging methods with the potential to facilitate this aim need to be considered, field-tested, and where appropriate, utilised.

The two primary methodologies for estimating abundance of cetaceans are transect sampling and capture-recapture (see Hammond et al. (2021) for a review). The former typically uses vessel or aerial surveys to sample animals along predefined transect lines to estimate animal density for the sampled area with abundance extrapolated from the density estimate (Buckland et al., 2001). Capture-recapture requires individual identification and estimates population size based on the

probability of detecting a single individual across multiple capture occasions (Williams et al., 2002). For cetacean studies, individual recognition usually relies on photographic identification (photo-ID) of natural markings such as nicks on the dorsal fin (e.g., odontocete species) (Saayman and Tayler, 1973, Würsig and Würsig, 1979, Bigg, 1982b), pigmentation patterns on tail fluke (e.g., humpback whale) (Cheeseman et al., 2021) and facial recognition (Genov et al., 2018) (see also Hammond et al. (1990) for a review of this methodology on marine mammals).

Data collected from vessel and aerial platforms have been successfully used to estimate abundance for many years but they both rely on costly surveys aboard vessels and data collection is limited to good environmental conditions (typically excluding harsher seasons) (Evans and Hammond, 2004, Braulik et al., 2018). This bias in data collection has led to data gaps at certain times of year, in less economically developed areas, and in areas that are difficult to access, disproportionately affecting species that only inhabit these areas (such as pelagic species) (Kaschner et al., 2012, Mannocci et al., 2018, Ashe et al., 2021). As discussed in previous chapters of this thesis passive acoustic monitoring has the potential to overcome these limitations.

Passive acoustic data have been used to estimate density and abundance within line transect and point sampling frameworks (Barlow and Taylor, 2005, Marques et al., 2012), used as both the primary data source (Lewis et al., 2018) and as supplementary data to visual observations (Rankin et al., 2020). More recently the application of PAM to estimate abundance within a capture-recapture framework has been explored using signature whistles of common bottlenose dolphins (*Tursiops truncatus*) as a means of identifying individuals (Longden et al., 2020, Fearey et al., 2022).

Bottlenose dolphins produce three main types of vocalisations; echolocation clicks, burst pulses, and narrow band tonal signals termed whistles (Sayigh, 2014). Within a dolphin's whistle repertoire there are two main categories; signature whistles and variant whistles (Caldwell and Caldwell, 1968, Sayigh et al., 2017). Signature whistles are stereotyped emissions that often occur in bouts (Janik and Sayigh, 2013) and function as a means of broadcasting the identity of the whistling dolphin, facilitating group cohesion, and assisting with mother and calf reunion (Smolker et

al., 1993, Janik and Slater, 1998, King et al., 2016). They are individually unique, developed over the first year of life and remain stable for at least 18 years but probably for the individual's lifetime (Caldwell and Caldwell, 1979, Sayigh et al., 1990, Santos et al., 2005), although coalition males (Connor et al., 2001) may converge on a similar shared whistle whilst still retaining individual aspects (Smolker and Pepper, 1999, Watwood et al., 2004). Signature whistles account for between 38 – 70% of the whistles produced by wild free-swimming dolphins, however this depends considerably on social and behavioural contexts (Buckstaff, 2004, Cook et al., 2004).

Recordings of dolphin whistles when displayed as a spectrogram appear as narrow band signals that frequency modulate over time, producing a unique pattern (Figure 4.1). These patterns can be identified and catalogued. Signature whistles were first identified in captivity and with temporarily restrained wild animals (Caldwell and Caldwell, 1968, Sayigh et al., 1990). Under these unnatural conditions signature whistles make up the majority of vocalisations of dolphins that have been restrained and can be easily allocated to the individual (Janik and Slater, 1998, Sayigh et al., 2007). Early studies of signature whistles of wild populations required a precompiled catalogue to identify which whistles were signatures (Buckstaff, 2004). However, Janik et al. (2013), presented the SIGnature IDentification (SIGID) method for identifying signature whistles from acoustic recording based on their inter-whistle-intervals (IWI) that requires no other information or concurrent visual observations. Signature whistles are identified if the 75% of IWIs of the stereotyped whistle within the bout are between 1 and 10 seconds. This has increased the application of using signature whistles for capture-recapture or other analyses of individuals (Longden et al., 2020, Bailey et al., 2021) and allows signature whistles to be identified and analysed from recordings in areas (or for populations) that have had no prior research attention.

Applying the same capture-recapture modelling frameworks used with photo-ID data requires whistle data to be aggregated across time and (if more than one hydrophone is deployed) space which introduces subjectivity and loss of information (Borchers et al., 2014). However, if multiple hydrophones are used to collect data, density and abundance can be estimated using spatially explicit capture-recapture (SECR) models, which explicitly model the spatial arrangement of the hydrophones

(Borchers and Efford, 2008). The primary objective of SECR is to calculate density in a defined area but it can also be used to calculate abundance (the number of animals in a pre-defined area), having an advantage over non-spatial methods as they overcome the edge effect (i.e., temporary immigration/emigration) (Efford and Fewster, 2013). The approach can be seen as the combination of both distance sampling and

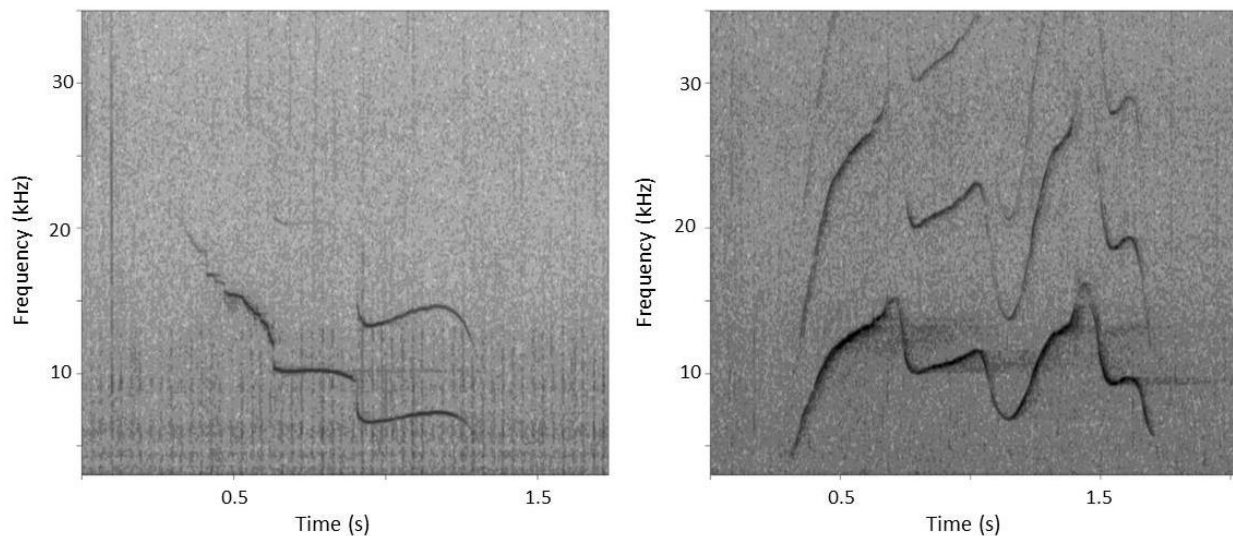


Figure 4.1. Examples of whistle contours of bottlenose dolphin recorded off Northumberland during the study period (July – September 2019).

capture-recapture (Borchers, 2012). SECR was first developed for trapping data where the movement of a trapped animal is restricted (Borchers and Efford, 2008) but was developed further, introducing the concept of “proximity” detectors which record the presence of an individual without the restriction of movement (e.g., camera traps and passive DNA sampling) (Efford et al., 2009). SECR has been applied to acoustic data to calculate density and applied to minke whale (*Balaenoptera acutorostrata*) “boing” sounds (Marques et al., 2012), however in that study individual identification was not possible and resulted in estimation of relative “boing” density. Applied to signature whistles of bottlenose dolphins using the proximity detector approach, SECR is a viable way of calculating abundance of bottlenose dolphins using PAM and requires further consideration.

The aims of this study were to estimate the abundance of bottlenose dolphins off the Northumberland coast from signature whistle and photo-ID data collected during the

same sampling period, and to compare the results of the two data sources. Closed capture-recapture models were used for each data source, but different modelling approaches including SECR were considered for the signature whistle data that accounted for the data collection process. Estimates, measures of precision and resulting parameter values were used to compare models.

4.2 Methods

4.2.1 Data collection and processing

Photo-ID

Opportunistic dolphin photo-ID surveys were conducted off the southern Northumberland coast between 12th July and 10th October 2019 (Figure 4.2) using a 5.6 m rigid-hulled inflatable boat powered with a 50hp 4-stroke outboard engine. The survey area included the Coquet to St Mary's Marine Conservation Zone (MCZ) (www.gov.uk) and overlapped the deployment location of three hydrophones used for passive acoustic monitoring. The northern boundary of the MCZ represented the northern limit of the survey area although a number of surveys were conducted beyond the southern boundary of the MCZ with the most southerly surveys reaching the mouth of the Wear, Sunderland. Within the survey area effort was made to survey across a range of depths, however adverse weather conditions made surveying further offshore difficult on some days and resulted in more survey effort conducted near shore.

When at sea the position of the boat was recorded every minute using a GPS (Garmin GPSMAP 64x). Start and end times of dedicated observer effort were recorded and when "on effort" environmental conditions (weather, Beaufort Sea state) were recorded every 10 minutes or if conditions changed. All surveys were conducted in Beaufort Sea state ≤ 3 and in fair weather. If weather conditions deteriorated during a survey, effort was paused, if adverse weather conditions persisted then the survey was terminated.

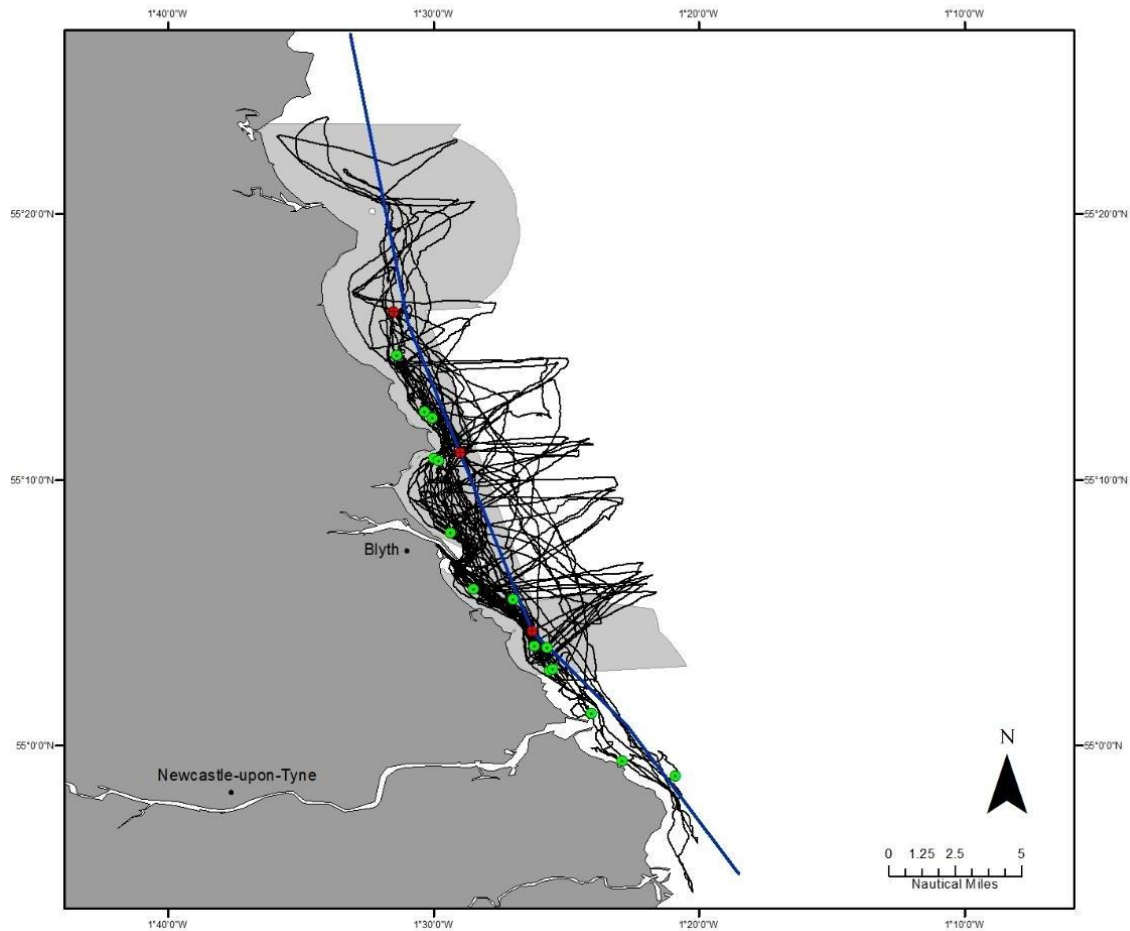


Figure 4.2. Map of study area with the location of each hydrophone as a red circle (north to south = DB, NB and SM); common bottlenose group sightings where photo-ID data were collected in green circle; vessel track lines (sampled each minute) for all surveys in black line; Coquet to St Mary's MCZ shaded in grey and; represented as a blue line is the linear habitat mask used in SECR model to estimate density and abundance.

When “on effort” the boat motored at a steady speed of between 8 – 12 knots and at least two dedicated observers continuously searched for dolphin groups. Dolphin groups were identified from visual cues such as fins above the surface, splashes, associated seabirds, and leaps. When a dolphin group was encountered, observer effort switched to group sighting data collection. A dolphin group was defined as a group of dolphins with all members within 100 m of each other (Irvine et al 1981). During each encounter data were recorded on dolphin species, group size and composition, time, location, environmental conditions, and photo-identification data were collected using a digital SLR camera (Canon EOS 550D digital SLR camera with a Canon 70-200 mm zoom lens).

When taking photographs for photo-ID, effort was made to randomly sample the group and not bias data collection to dolphins that were more approachable. When

an encounter consisted of more than one subgroup of dolphins, observers tracked the location of subgroups, and each subgroup was approached to minimise the number of dolphins missed during data collection.

All images collected during the photo-ID surveys were initially processed to remove any image that failed to capture a dolphin and images with multiple dolphins were copied and cropped to contain only one fin. All images that contained a single dolphin were then given a quality rating based on criteria outlined in Urian et al. (2015). The quality ratings were defined as, Q4 = Well lit, in focus, dolphin close to camera and angle approximately perpendicular to the side of the fin.; Q3 = some deviation from the perfect angle, lighting or focus but overall good image; Q2 = out of focus, taken at a considerable angle or the dolphin is far from the camera, other obstructions such as splashes and glare also present; Q1 = Very poor focus, at an angle and totally backlit. Only high-quality images (Q4 and Q3) were retained and used to compile the photo-ID catalogue. The photo-ID catalogue was created by matching fins based on notches in the forward and trailing edge of the fin, prominent scars, rake marks, and pigmentation patterns visible on the fin or body (Figure 4.3). Fins were first matched within each encounter and organised into left and right sides before matching between sides.

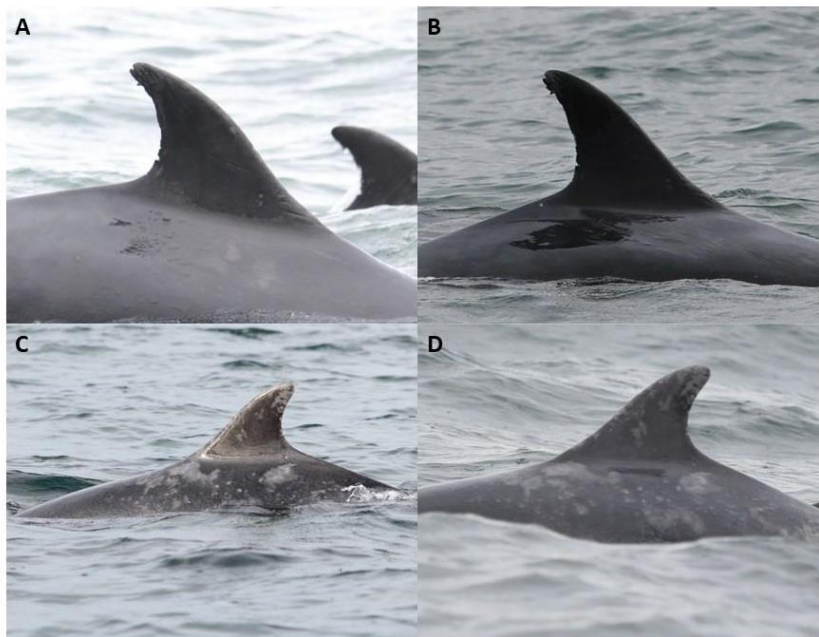


Figure 4.3. Examples of Q1 fins of two individual bottlenose dolphins photographed during vessel-based surveys off the Northumberland coast. Images A and B show a D1 individual captured on two separate survey days. Images C and D show a D2 individual captured on two separate survey days.

Each fin was given a distinctiveness score, D1 = highly distinctive with several large and clearly visible notches in the forward or trailing edge, also include rakes and pigmentation; D2 = at least one large or several smaller notches in the trailing edge and some other pigmentation or marks; D3 = no visible notches on either forward or trailing edge of the fin, difficult to reliably match between left and right sides, some pigmentation or marks that allow for matching a single side. Calves were identified during each encounter by the size, colouration, association with the mother and swimming position. All calves were omitted from the analysis as they cannot be considered independent from the mother. The final catalogue was compiled by matching D1 and D2 images between encounters with resightings of individuals between surveys providing the basis for the encounter history table for capture-recapture analysis.

As only D1 and D2 fins were used to compile the encounter table the resulting abundance and error estimates from capture-recapture analysis represent only the distinctive proportion of the population. To estimate total population size, the distinctive population size was divided by the proportion of distinctive fins in the population (theta; $\hat{\theta}$).

$$\hat{N}_{total} = \frac{\hat{N}_{dist}}{\hat{\theta}}$$

Where:

- \hat{N}_{total} = the total population size estimate
- \hat{N}_{dist} = the estimated population size of the distinctive population
- $\hat{\theta}$ = the estimated proportion of distinctive individuals in the population, estimated using the approach outlined in Nicholson et al. (2012)

Standard error for the total population was estimated using the formula for the standard error of a ratio using the delta method (Williams et al., 2002).

$$SE(\hat{N}_{total}) = \sqrt{(\hat{N}_{total})^2 \left(\frac{SE(\hat{N}_{dist})^2}{(\hat{N}_{dist})^2} + \frac{1 - \hat{\theta}}{n\hat{\theta}} \right)}$$

To calculate 95% confidence intervals for the total population the procedure from Burnham (1987) was applied.

$$C = \exp \left(-1.96 \sqrt{\ln \left(1 + \left(\frac{SE(\hat{N}_{total})}{\hat{N}_{total}} \right)^2 \right)} \right)$$

With the upper limit calculated as $\hat{N}_{total} * C$ and the lower limit as \hat{N}_{total} / C .

Passive Acoustic Monitoring

Acoustic data collection is outlined in full in Chapter 2 (section 2.2.1). For this study, data from July 2019 – September 2019 (the time period overlapping the photo-ID data collection) from all three hydrophones (Druridge Bay (DB), Newbiggin (NB) and St Mary’s (SM)) were used. Any periods where white-beaked dolphin clicks were identified (see Chapter 1) were removed to ensure that only recordings with bottlenose dolphin whistles were included in the analysis.

Whistles were identified and extracted from the acoustic recordings using Pamguard’s (Gillespie et al., 2008) whistle and moan detector. The full configuration for the detector is outlined in Chapter 3 (section 3.2.3). In summary, Pamguard’s whistle and moan detector identified tonal signals in the raw acoustic recordings. When a tonal sound was detected, a recording module would trigger producing shorter “whistle recordings”, recorded at a sample rate of 96 kHz. These whistle recordings were date and time stamped so that the start time of each recording was known and labelled according to the deployment location (DB, NB, and SM).

Whistle identification

Each whistle recording was visually inspected using the spectrogram function in program Raven (Cornell Lab of Ornithology, USA; 1024 window length, page size 10-second). Each occasion of a single or overlapping group of whistles was identified and highlighted using Raven’s “selection table” function, ensuring that the start and end time of the whistles were accurately recorded; for overlapping whistles, the start of the first whistle and end of the last whistle was used. By adding the start time of the whistle (seconds) to the start time of the recording (date and time; UTC), the true date and time of each whistle could be calculated. The selection table was configured to include an annotation column and each whistle selection was given a quality rating from 0 – 3. A score of 0 was given to any selection with 2 or more

overlapping whistles which made identifying the contour difficult (irrespective of signal to noise ratio). The approach here differed to Chapter 3 where overlapping whistles were defined only by their temporal overlap and whistles with only marginal overlap were considered as overlapping. Whistles were quality rated 0 if there was considerable temporal and frequency overlap of whistles which masked or obscured contour recognition. Whistles with only minor temporal overlap were considered as separate. Quality rating for single whistles was derived following Kriesell et al. (2014) and defined as: Quality rating 1 was given to poor quality whistles defined by having low signal to noise ratio, partially visible contours and unclear start and end times. Quality rating 2, was given to good quality whistles, where the signal to noise ratio was good and the start and end times were identifiable. Quality score 3 was for high quality whistles, reserved for contours which had very strong signal to noise ratio and very clear contour definition.

Concurrently during the whistle identification process bouts of stereotyped whistles (Table 4.2) were also identified. These are defined as repeated sequences of the same whistle contour (Janik et al., 2013). An additional selection table was created per bout to mark the exact start and finish times of each whistle within the bout as well as marking the exact start and finish time of the inter whistle interval (IWI). All quality whistles were considered when identifying bouts and calculating IWI (Fearey et al., 2019), however at least one whistle in the bout had to be quality 2 or 3 for it to be matched between encounter periods. Whistle bouts were then determined to be signature whistles using the SIGID method (Janik et al., 2013). The SIGID method defines signature whistle bouts as having IWIs between 1 and 10 seconds and that at least 75% of IWIs within a bout must meet this criterion. Therefore, a minimum bout of 5 whistles was needed (equating to four IWIs) to be considered for the SIGID method. Whistle bouts which passed the SIGID criteria were recorded as signature whistle type (SWT).

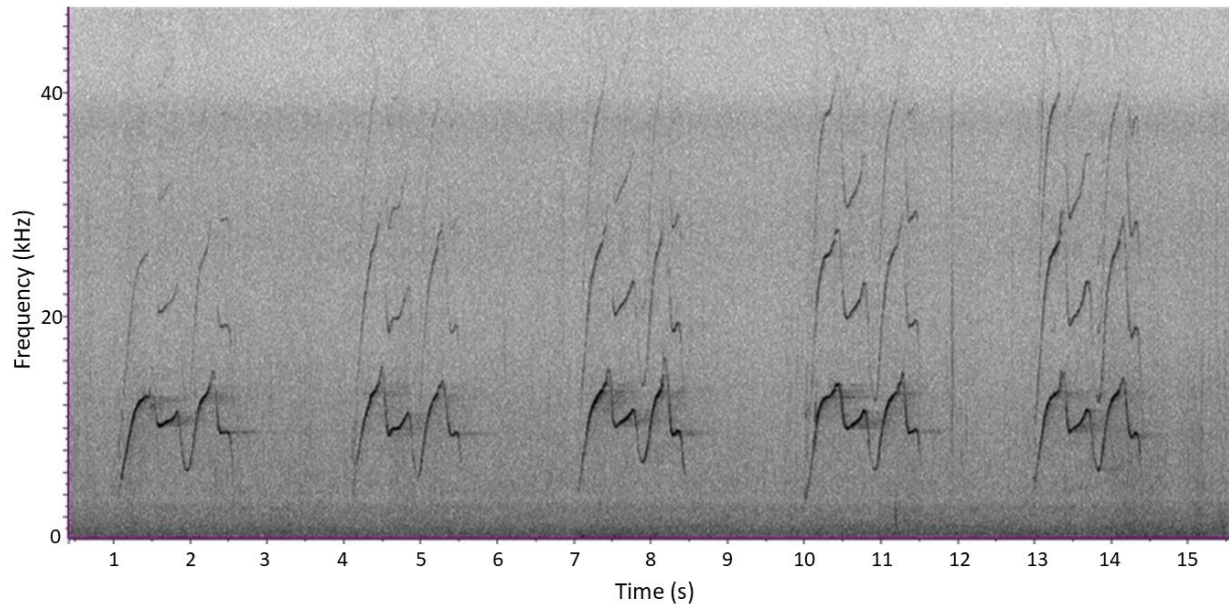


Figure 4.4. Example of a stereotyped whistle where each inter-whistle-interval within the bout is between 1 and 10 seconds, therefore passing the SIGID criteria for a signature whistle.

Table 4.1. Glossary of whistle terms.

Term	Definition
Whistle contour	The visual representation of a dolphin whistle displayed as a spectrogram.
Stereotyped whistle	A specific whistle contour shape which is determined to be the same.
Whistle type	A stereotyped whistle which has been catalogued and can be reidentified.
Signature whistle type (SWT)	A whistle type which has been identified within a "SIGID bout" and has been determined to be a signature whistle which represents an individual dolphin.
Whistle bout	A repeated sequence of a specific whistle type identified in the acoustic recordings
SIGID bout	A whistle bout that meets the criteria of the SIGID method (Janik et al., 2013)
Whistle selection	A whistle that has been identified in the acoustic recordings and recorded within a Raven selection table. All whistle selections are quality graded.

Signature whistle catalogue

Selection tables were used to produce spectrogram images using R package *WarbleR* (Araya-Salas and Smith-Vidaurre, 2017). Firstly, all whistle selections identified within SIGID bouts were produced which allowed for matching between SIGID bouts, identifying which SIGID bouts contained the same SWT. Each unique SWT was catalogued and formed the basis for individual recognition of bottlenose dolphins within the acoustic recordings. Secondly, spectrograms of all whistle selections of quality grades 2 and 3 were produced. These spectrograms were organised into batches based on the location of the recording (DB, NB, SM) and the week of recording (each Monday to Sunday period from the first week of study to the last, numbered in chronological order). Each unique SWT from the SWT catalogue was then matched against all whistle selections in each batch. Each matching whistle selection was recorded and provided the basis for compiling the encounter history tables for signature whistles (see section 4.2.3).

4.2.2 Abundance estimates

Non-spatial capture-recapture analysis of photo-ID and whistle data were performed in *RMark* (Laake, 2013) using a suite of closed models (Otis et al., 1978). Closed SECR models were performed in R package *secr* (version 4.5.6) (Efford, 2022).

Closed models were considered appropriate given the relatively short period of the study relative to the lifespan of the species making demographic closure likely. However, as with most cetacean capture-recapture studies, edge effect was likely. Applying non-spatial closed models when there is edge effect would result in the estimation of a superpopulation, defined as the total population of individuals which visited the area during the study period (Schwarz and Arnason, 1996, Brown et al., 2016) and this would apply to both photo-ID and signature whistle abundance estimates. Other assumptions for closed capture-recapture analysis, the validation of these assumptions for this study, and the potential biases to the estimates if these assumptions are violated are available in Table 4.2.

Table 4.2. Model assumptions of closed capture-recapture analysis.

Assumption	Photo-ID validation	Whistle Validation
Population is closed	Demographic closure likely due to length of study period relative to bottlenose dolphin. Unlikely to be closed from temporary immigration and emigration (edge effect). Non-spatial models can be considered to estimate a super population.	Same as Photo-ID surveys. The use of SECR models on whistle data has the advantage of not being affected by edge effect.
Marks or not lost or misidentified	Only distinctive individuals used in analysis to prevent misidentification. Dolphin nicks and scars can change over time but given the relatively short period of the study, this was not considered a concern.	Signature whistles are unique to the individual and are well conserved (Sayigh et al., 1990). SIGID method identifies signature whistles with very low probability of false positive identification (Janik et al., 2013).
Sampling is instantaneous	Each survey was considered as an encounter period and photo-ID sampling was done in the shortest time possible. Violation of this assumption would lead to an upward bias in abundance estimate.	Sampling with hydrophones is not instantaneous. Both pooled data where this assumption is violated and a duty-cycle which accounts for this assumption were considered in the analysis of whistles.
Captures are independent	Given the fission fusion nature of bottlenose dolphin groups individuals were likely to be independently sampled however there are preferred associates (e.g., long term male bonds) which may violate this assumption (Smolker et al., 1992, Connor et al., 2001). Calves were removed as they cannot be considered independent to the mother.	Not possible to remove SWTs from calves in the dataset. Violation of this assumption would lead to reduction in precision but not bias the estimate in a direction.

4.2.3 Whistle encounter histories

There is added complexity when capturing signature whistles compared to photo-ID data that needs to be considered when analysing capture-recapture methods. The first consideration is that to identify a signature whistle from the recordings there needs to be at least one occurrence of the SWT within a SIGID bout (Table 4.1) as determined by the SIGID method. Once a SWT is identified in a SIGID bout and catalogued it can then be identified again either within a SIGID bout or as a single whistle (that is, the whistle can be identified again whether it is in SIGID bout or not) (Longden et al., 2020). For an individual dolphin to be available for capture-recapture analysis, it needs to have at least one occurrence of its SWT available within a SIGID bout. Any dolphin, regardless of its presence in the area during the study period which does not have a recording as a SIGID bout is unavailable for capture. Put another way, there are effectively two probabilities required for a capture, first is the probability of being detected in a SIGID bout and catalogued throughout the data collection period, and the second is the probability of capture by detection of any occurrence of the whistle during each capture period. This is different to photo-ID data collection or other types of capture-recapture data and needs to be considered when choosing an appropriate modelling framework or treatment of the data.

When considering modelling approaches for signature whistle data one available option is to use the Huggins formulation (Huggins, 1989) of capture-recapture which conditions the likelihood on the probability of being captured at least once in the study. This approach was used in Longden et al. (2020), the only other study to apply closed capture-recapture methods to signature whistle data. To apply this approach in the current study an encounter table was generated that included all captures of an SWT regardless of whether it was in a SIGID bout or not (Table 4.3).

Alternatively, only SWTs identified within a SIGID bout can count as captures and recaptures, whereby the probability of capture is the probability of a SIGID bout detection during each capture occasion. This has the benefit that the model estimates abundance based on a single probability of capture and are not confounded by having different capture types. However, it is less probable to identify a SIGID bout than a single whistle which may impact the resulting abundance estimate as it removes potentially useful information. For this approach an additional

encounter table was produced that included only signature whistles identified within SIGID bouts (Table 4.3).

Another available approach is to model the difference in probability within the (spatial and non-spatial) capture-recapture analysis by using different parameters for first and subsequent recaptures. This approach is well established within the field of capture-recapture and is primarily used to model behavioural responses to being captured (Otis et al., 1978). To make the encounter history table fit this approach, all SWT selections that were identified before the SWTs first SIGID bout were removed, and this was applied across all locations (Table 4.3). This resulted in the first capture of any given SWT within the encounter history table being the first time the SWT was identified in a SIGID bout and catalogued as a signature whistle. By using the model formulation which accounts for difference in first and subsequent capture probabilities (M_b), the difference between having to first identify a SWT within a SIGID bout and subsequent captures can be modelled directly.

A second consideration to be made when handling whistle data for capture-recapture is that for closed models one of the assumptions (see Table 4.2) is that capture occasions must be instantaneous. Given that the hydrophones were recording constantly with detections pooled into weekly sampling periods after data collection, this assumption is violated and would cause an upwardly biased abundance estimate. To account for this, a duty cycle could be used that allows data to be collected for a set period before closing to allow for the population to mix before sampling again, thus meeting the assumption of instantaneous capture. To test this, the acoustic dataset was subsampled based on an artificial duty cycle (Fearey et al., 2022), that simulated the process. The artificial duty-cycle allowed for 6 hours of continuous recording then was closed for 24 hours, before repeating the cycle. Having a 30-hour duty-cycle allowed for the on-cycle to sample across different times of day and tidal phases. In this context, sampling for 6 hours can be considered instantaneous and is the approximate duration of each Photo-ID survey. A set of encounter histories were created from the subsampled data for each of the three non-spatial modelling approaches above (Table 4.3). Any 6-hour periods that did not detect a single whistle or SIGID bout were dropped from the analysis.

The third consideration is that of edge effect. To account for edge effect, SECR models were also fitted to the whistle data. A SECR framework requires a different capture history table which retains location information for each detection (Table 4.3). These data were pooled across week and used the SIGID bout only data as used with the non-spatial data to avoid potentially confounding effects of SWT detection types. SECR also allows for multiple detections of an individual during a single capture period (Borchers, 2012). In this study for an individual to be counted an additional time, required a gap of at least 12 hours, to avoid inflating the count data for whistles occurring at the same time (e.g., in bouts). A 12-hour period was selected based on the result of the cross-correlation function of bottlenose dolphin clicks, see Chapter 2.

Table 4.3. Encounter histories used for modelling signature whistles using (spatial and non-spatial) capture-recapture. Model abbreviations: 0 = constant probability, t = time varying, b = different probability between first and subsequent captures, h2 = heterogeneity in probability modelled as a mixture of two, h3 = heterogeneity in probability modelled as a mixture of three. For non-spatial models these are applied to the probability of capture (p), for SECR models these were applied to detection probability at the centre of the individual's home range (λ_0) and the scaling with distance parameter (σ).

Encounter history	Model formulation	Specific models considered
Pooled weekly, all whistles	Huggins formulation of closed models	M0, Mt, Mh2 Mth2
30 hr duty cycle, all whistles	Huggins formulation of closed models	M0, Mt, Mh2 Mth2
Pooled weekly, SIGID bout only	Full likelihood formulation of closed models	M0, Mt, Mh2 Mth2
30 hr duty cycle, SIGID bout only	Full likelihood formulation of closed models	M0, Mt, Mh2 Mth2
Pooled weekly, SIGID first capture – single whistle for recapture	Full likelihood formulation of closed models	Mb, Mbt, Mbh2 Mbth2
30 hr duty cycle, SIGID first capture – single whistle for recapture	Full likelihood formulation of closed models	Mb, Mbt, Mbh2 Mbth2
Pooled weekly, SIGID bout only, SECR	Spatially explicit capture-recapture models: λ_0 (detection parameter) σ (animal movement parameter)	λ_0 (combinations of 0, t, h2, h3) Sigma (combinations 0, t, h2, h3)

4.2.4 Non-spatial capture-recapture

Photo-ID data

For the photo-ID data, full likelihood closed capture models were used (Otis et al 1978). These models parameterise the probability of capture (p), the probability of recapture (c) and the number of unseen individuals (f_0). No models accounting for a behavioural response (where probability of first capture is different to probability of recapture; $p \neq c$) were considered. This is due to the chance of data collection having an impact on future data collection (subsequent captures) was very low given the non-invasive nature of photo-ID studies. Models included were constant capture probability (M_0), time varying capture probability (M_t), heterogeneity in capture probability (M_{h2}) and a time varying and heterogeneity in capture probability additive model (M_{th2}).

Whistle data

The Huggins formulation of capture-recapture analysis (Huggins, 1989) was applied to the weekly pooled and duty-cycle encounter histories which included all whistles regardless of whether they were a SIGID bout or not. These models also parameterise the probability of capture (p) and recapture (c), however they do not parameterise the number of animals not seen (f_0). Models considered for each encounter history table were constant capture probability M_0 , time varying capture probability M_t , heterogeneity in capture probability M_{h2} , and a time varying and heterogeneity in capture probability model M_{th2} .

The full likelihood formulation of capture-recapture analysis was applied to the weekly pooled and duty-cycle encounter histories which included only SIGID bout captures. Non-spatial models considered for each encounter history table were M_0 , M_t , M_{h2} and M_{th2} .

For the whistle data where all whistles that occurred before the first SIGID bout were removed for each SWT, only behavioural models (where $p \neq c$; denoted at M_b) were considered and applied using the full likelihood formulation of the capture-recapture analysis. To reiterate, this was not due to a behavioural response to capture but rather to account for the difference in probability of detecting a signature bout (required for the first capture of an individual) and the probability of detecting the

whistle again (when the whistle can be identified within a qualifying bout or not). Models fitted included behaviour model with constant probability of capture and recapture (Mb), time varying probability of capture and recapture (Mbt), heterogeneity in probability of capture and recapture (Mbh2) and time varying and heterogeneity on capture and recapture probability (Mbth2).

4.2.5 SECR

SECR models were fitted to the signature whistle data. To estimate density and abundance SECR combine two models, a state model that describes the unobservable home range of each individual within a habitat and an observation model that parameterises the probability of detecting an individual at a given detector based on the distance of the detector to the individuals home range centre (Borchers, 2012). The individual home ranges are modelled as a point process, usually a homogeneous Poisson process with a single parameter, intensity (representing the density of home ranges). If the density of home ranges is considered to vary across space, then an inhomogeneous Poisson process can be used. The state model estimates the density of individuals over a defined area (usually estimating individuals per hectare), however a linear, one-dimensional habitat can also be used (that estimates individuals per km) (Efford, 2017). In practice, the habitat (area or linear) is represented in the models by a habitat mask that is spatially related to the position of the detectors using a coordinate system (Efford, 2022).

The observational process is modelled by a detection function, (e.g., half-normal (HN), hazard half-normal (HHN) and exponential). The detection function includes two parameters, one to control the probability of detecting an individual at the centre of the individuals home range (g_0 for HN, λ_0 for HHN and exponential) and the other to control the effect of distance from home range centre on the probability of detection (σ for all detection functions). Similar to the parameterisation of capture probabilities in Otis et al. (1978), parameters g_0 (or λ_0) and σ can be parameterised using covariates including time, behaviour or heterogeneity (with mixtures of two (h2) and three (h3) available in package *secr* (Efford, 2022).

In this study, a linear habitat mask was used that represented the 20-metre depth across the surveyed area and was incorporated into the model using the package

seclinear (Efford, 2017). The density of bottlenose dolphin home ranges therefore represented the number of individuals along the Northumberland coast. Each hydrophone was considered as an independent “detector” with each recording of an identified signature whistle within a SIGID bout considered as an individual capture. A HHN detection function was used due to its suitability for count data and combinations of time varying and heterogeneity mixtures were modelled for the λ_0 and σ parameters. The abundance estimate reported from the SECR model for bottlenose dolphin whistles was the realised estimate generated from the state process density (Johnson et al., 2010). The state process was not parameterised to vary across the extent of the habitat mask and was therefore modelled as a homogeneous Poisson process.

For all models (spatial/non-spatial, photo-id and whistle) Akaike Information Criterion (AIC) was used to select the most parsimonious model from each group (Table 4.4). The abundance estimates and 95% confidence intervals for the selected model for each group are compared in the results.

4.3 Results

4.3.1 Photo-ID survey

A total of 26 surveys were conducted between July and October 2019. Bottlenose dolphins were encountered on 12 of these days with a total number of group encounters of 14. The photo identification catalogue included 43 individual non-calf bottlenose dolphins and the proportion of distinctive individuals ($\hat{\theta}$) was estimated to be 0.77.

4.3.2 Whistle detections

A total number of 239 signature whistle bouts were identified which met the SIGID criteria. Of these 45 were unique whistles contours and formed the SWT catalogue. A total number of 12,598 additional high-quality whistles were identified from the recordings of which 4,134 were matched with the signature whistle catalogue.

4.3.3 Abundance estimates

For the photo-ID data the most parsimonious model was Mt (see Table 4.4). The abundance estimate for the distinctive population was 49 individuals (standard error (SE) = 3.76). The total population size when accounting for non-distinctive

individuals was 63 (SE = 7.1; 95% confidence interval (CI) was 51 to 78) (Figure 4.5).

Results of model selection for signature whistle models can be seen in Table 4.4 with each model selecting for both heterogeneity and time dependence in capture probability. The resulting abundance estimates and errors, however, vary considerably as can be seen in Figure 4.5. The Huggins models (using all whistle detections whether within a SIGID bout or not) estimated abundance as 45 (SE = 0.80, 95% CI 45 -50) when data was pooled across each week and 27 (SE = 0.42, 95% CI 27 - 29) when using the duty-cycle (Figure 4.5). Both of these estimates equal the number SWTs used in each model with a very small estimate of error and a subsequent small upper 95% confidence interval, providing little confidence in the validity of these results.

For the full likelihood models that included only SIGID bout detections, the most parsimonious model when using the pooled weekly data was Mth2 estimating abundance as 71 (SE = 18.37; 95% CI 53 – 135). When using the duty cycle data, the most parsimonious model was mth2 however the model did not successfully estimate abundance producing a standard error of 0 and an estimate of 27, equal to the number of signature whistles identified during the duty cycle on time. This approach provides a more realistic estimate when data is pooled weekly, although the error is greater than the photo-ID estimate. The failure of the duty-cycle model can be attributed to the low detection probability of SIGID bouts.

For the full likelihood models that included the first SIGID bout as the first capture for a given SWT, the most parsimonious model was Mbth2 when pooled across weeks estimating abundance at 108 (SE = 52.46, 95% CI 60 – 306) and Mbt when using the duty cycle dataset estimating abundance at 34 (SE = 10.26; 95% CI 28 – 84) (Figure 4.5). The large error of these estimates suggest that they should not be considered.

Table 4.4. Model selection table for non-spatial capture-recapture models of both photo-ID and signature whistles data.

Dataset	Model	AICc	Δ AICc	AICc weight	No. of parameter	Deviance
Photo-ID	Mt	215.1	0.0	0.5	14	152.6
	M0	216.2	1.1	0.3	3	176.5
	Mth2	217.2	2.1	0.1	15	152.6
	Mh2	218.3	3.1	0.1	4	176.5
Whistle: pooled by week - Huggins	Mth2	581.3	0.0	1.0	15	487.6
	Mt	647.7	66.4	0.0	14	556.2
	Mh2	765.0	183.7	0.0	3	696.1
Whistle: Duty cycle - Huggins	M0	802.6	221.3	0.0	2	735.7
	Mth2	541.3	0.0	1.0	22	449.3
	Mt	556.5	15.2	0.0	21	466.6
Whistle: Pooled weekly, SIGID bout only	Mh2	662.5	121.2	0.0	3	610.4
	M0	667.1	125.7	0.0	2	617.0
	Mth2	172.6	0.0	1.0	14	129.7
Whistle: Duty cycle, SIGID bout only	Mt	204.4	31.7	0.0	13	163.6
	Mh2	250.4	77.8	0.0	4	228.4
	M0	271.3	98.7	0.0	3	251.3
	Mth2	292.1	0.0	1.0	21	208.6
Whistle: pooled by week - Full likelihood	Mt	303.4	11.3	0.0	20	222.1
	M0	401.6	109.5	0.0	3	356.1
	Mh2	403.7	111.6	0.0	4	356.1
	Mbth2	195.5	0.0	1.0	17	134.6
Whistle: Duty cycle - Full likelihood	Mbt	214.7	19.2	0.0	16	156.0
	Mbh2	364.1	168.6	0.0	5	328.2
	Mb	372.1	176.6	0.0	4	338.2
Whistle: Duty cycle - Full likelihood	Mbt	279.4	0.0	0.8	21	195.9
	Mbth2	281.6	2.2	0.3	22	195.9
	Mb	336.6	57.2	0.0	4	289.0
	Mbh2	338.6	59.2	0.0	5	289.0

Table 4.5 shows the resulting probability of capture (and recapture) values for each of the most parsimonious models of the weekly pooled signature whistle data. Included are probabilities for each mixture and for each week of the study. The results show consistency in the mixture parameter for the full likelihood models, but these are considerably different compared to the Huggins models. The Huggins

model also estimates the probability of capture to be much higher than the other two models, including the recapture parameter for the SIGID as first capture model. The p values of the SIGID bout only model were still relatively high despite the specific conditions needed to identify the whistle bouts.

The most parsimonious SECR model for the SIGID bout only data was lambda0: h2, sigma: 1 (Table 4.6) and the estimate for abundance was 66 (SE = 11.93, 95% CI 56 - 104) (Figure 4.5). This model provided a lower error than the non-spatial full likelihood models that used pooled weekly data. The parameters estimated by the model are shown in Table 4.7. Similar to the non-spatial full likelihood models the h2 mixture identifies a smaller proportion of high probability individuals and a large proportion of low probability individuals ($pmix1 = 0.28$, $lambda01 = 0.19$; $pmix2 = 0.72$, $lambda02 = 0.02$). The very large sigma estimate is likely due to inadequate spacing of the hydrophones relative to the ranging distance of the animals, with the model unable to estimate this parameter accurately.

Table 4.5. Resulting capture (P) and recapture (C) probabilities for each of the most parsimonious models of the pooled weekly signature whistle data. As each model include heterogeneity in capture probability the proportion of the population for each set of capture probabilities is provided. As each model includes time varying capture probability there is a different probability for each week of the study, where SIGID bout only data were modelled, weeks without a single SIGID bout are dropped. For the model that included different probabilities for first capture and recapture p and c values are presented.

	Huggins (All whistles): Mth2		Full likelihood (SIGID bout only): Mth2		Full likelihood (SIGID as first capture): Mbth2			
	pi (SE)	1-pi	pi (SE)	1-pi	pi (SE)	1-pi	pi (SE)	1-pi
	0.15 (0.06)	0.85	0.24 (0.07)	0.76	0.27 (0.11)	0.73	0.27 (0.11)	0.73
Week	p (SE)	p (SE)	p (SE)	p (SE)	p (SE)	p (SE)	c (SE)	c (SE)
1	0.03 (0.02)	0.51 (0.08)	0.23 (0.09)	0.02 (0.01)	0.15 (0.07)	0.01 (0.01)	Recapture not available	
2	0.02 (0.01)	0.38 (0.08)	Dropped, no detections		0.02 (0.02)	0 (0)	0.31 (0.18)	0.02 (0.02)
3	0.09 (0.06)	0.78 (0.06)	0.23 (0.09)	0.02 (0.01)	0.09 (0.05)	0 (0)	0.71 (0.13)	0.09 (0.07)
4	0.08 (0.06)	0.76 (0.07)	0.40 (0.11)	0.04 (0.02)	0.18 (0.09)	0.01 (0.01)	0.85 (0.07)	0.18 (0.12)
5	0.03 (0.02)	0.49 (0.08)	0.10 (0.06)	0.01 (0.01)	0.07 (0.04)	0 (0)	0.63 (0.12)	0.06 (0.05)
6	0.04 (0.03)	0.59 (0.08)	0.10 (0.06)	0.01 (0.01)	0.05 (0.03)	0 (0)	0.54 (0.13)	0.05 (0.03)
7	0.12 (0.08)	0.83 (0.06)	0.32 (0.1)	0.03 (0.02)	0.29 (0.12)	0.02 (0.01)	0.91 (0.04)	0.29 (0.15)
8	0.83 (0.16)	0.99 (0.01)	0.81 (0.06)	0.20 (0.10)	0.72 (0.15)	0.09 (0.08)	0.98 (0.01)	0.72 (0.13)
9	0.24 (0.13)	0.91 (0.04)	0.69 (0.09)	0.11 (0.06)	0.46 (0.22)	0.03 (0.03)	0.95 (0.03)	0.46 (0.16)
10	0.14 (0.09)	0.85 (0.05)	0.61 (0.10)	0.08 (0.05)	0.35 (0.21)	0.02 (0.02)	0.93 (0.04)	0.35 (0.15)
11	0.24 (0.13)	0.91 (0.04)	0.75 (0.08)	0.15 (0.07)	0.49 (0.23)	0.04 (0.03)	0.96 (0.02)	0.49 (0.15)
12	0.01 (0.01)	0.23 (0.07)	0.1 (0.06)	0.01 (0.01)	0.01 (0.01)	0 (0)	0.27 (0.09)	0.01 (0.01)
13	0 (0)	0.08 (0.04)	Dropped, no detections		0 (0)	0 (0)	0.10 (0.06)	0 (0)

Table 4.6. Model selection table for spatial explicit capture-recapture (showing only top 6 models).

Dataset	Model	AICc	Δ AICc	AICc weight	No. of parameter
Whistle: Only	Lambda0 h2 / sigma 1	151.5	0	0.8	5
SIGID bout, SECR	Lambda0 h2 / sigma h2	154.2	2.7	0.2	6
	Lambda0 h3 / sigma 1	157.0	5.5	0.0	7
	Lambda0 h3 / sigma h3	163.1	11.6	0.0	3
	Lambda0 1 / sigma h2	169.2	17.7	0.0	5
	Lambda0 1 / sigma h3	171.3	19.8	0.0	9

Table 4.7. Real parameters for the most parsimonious SECR model of bottlenose dolphin density and abundance off the Northumberland Coast between July and September 2019.

Model	Density	Lambda0:1 b0	Lambda0:2 b0	Sigma b0	Pmix:1	Pmix:2
Only SIGID bout:	1.10	0.19 (0.02)	0.02 (0.01)	75362093.68	0.28	0.72
Lambda0 h2 / sigma 1	(0.24)			(1.12)	(0.07)	(0.07)

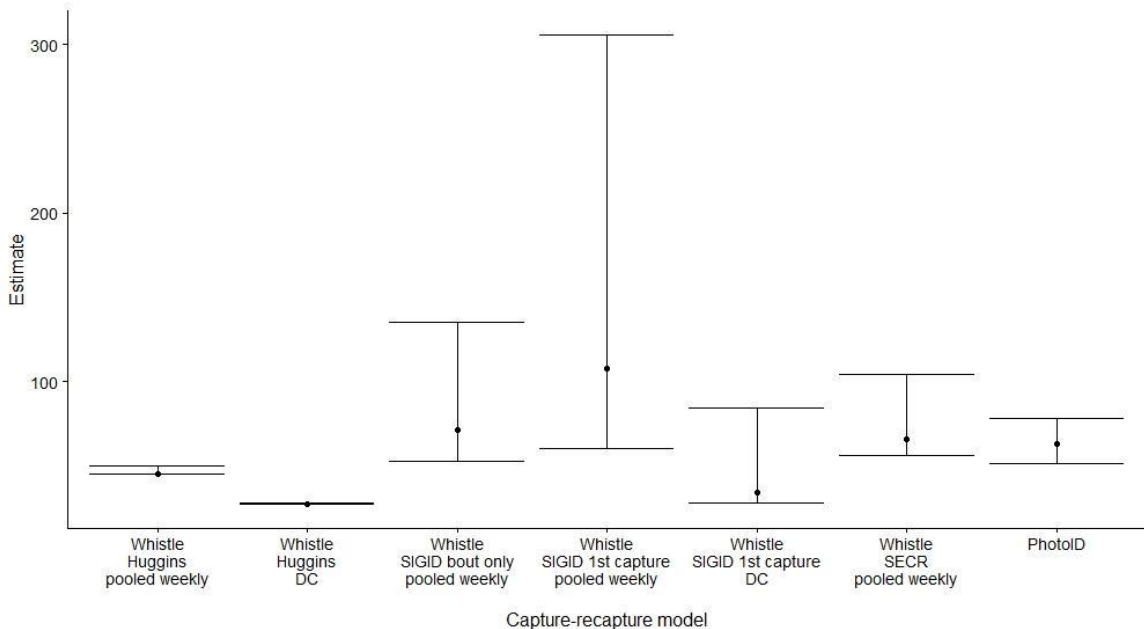


Figure 4.5. Resulting estimates and standard error (SE) of bottlenose dolphin abundance from different (spatial and non-spatial) capture-recapture models of whistle and photo-ID data. All data used in these analyses were collected between July and September 2019 from Northumberland UK.

4.4 Discussion

Reliable identification of individuals is required to estimate abundance from capture-recapture analysis. In cetacean studies, the primary approach is to use photo-identification to identify individuals from unique markings. This approach has been used across multiple species and locations over the last five decades (Saayman and Tayler, 1973, Würsig and Würsig, 1979, Bigg, 1982b, Hammond et al., 1990, Elliser et al., 2022). More recently, the use of signature whistles of bottlenose dolphins has gained research interest as a potential alternative, using PAM recordings (Longden et al., 2020, Fearey et al., 2022). Signature whistles are unique to the individual, remain stable for many years, and can be identified from acoustic recordings using bout analysis (SIGID), supporting their applicability in capture-recapture methods (Janik et al., 2013, Janik and Sayigh, 2013). Fully developed methodologies for applying capture-recapture methods to signature whistle data would provide many of the benefits associated with PAM data collection (e.g., data collection not being seasonally restricted or increased accessibility to offshore populations) to estimating abundance and survival of (signature whistle producing) delphinid species. To date, one published study has used signature whistles from long-term PAM deployments to successfully estimate abundance of bottlenose dolphins in one geographical area (Longden et al., 2020). The study produced a comparable estimate to previously reported estimates for the same area using photo-ID, validating the methodology. Given this success, further attention is warranted to test, improve, and provide more evidence of its applicability. In this study, both photo-ID and signature whistle data were collected during the same period from the Northumberland coast to estimate seasonal abundance of bottlenose dolphin from both photo-ID and acoustic data. Multiple approaches to modelling signature whistle data were explored within the closed capture-recapture framework, expanding on the work of Longden et al. (2020).

The final abundance estimate from the photo-ID data was 63 (95% CI 51 - 78) non-calf individuals. Signature whistles were extracted from the acoustic data and modelled using different approaches. The resulting abundance estimates varied considerably depending on how the data were modelled, ranging from extremes of 27 (95% CI 27 - 29) to 108 (95% CI 60 - 306). The different approaches to modelling the signature whistle data were based on different aspects of the data collection

process that were considered likely to impact the resulting estimate. Individual signature whistles which represented an individual bottlenose dolphin is referred to as a signature whistle type (SWT). The first consideration was how to include SWT data in the model, unlike photo-ID a SWT must first be identified as a signature whistle from SIGID bout analysis. This has the effect of making the pool of SWTs available for capture conditional on at least one successful SIGID bout identified during the whole study. If the probability of detecting a SIGID bout is low, this may have a significant effect on the final estimate. This was not explicitly addressed in Longden et al. (2020), but the authors used the Huggins formulation of closed capture-recapture analysis which conditions the likelihood on the probability of being identified at least once. The same approach was taken in the current study, analysing an encounter history created using all detections of each SWT whether identified as a single whistle or within a SIGID bout, which was then modelled using the Huggins formulation of closed capture-recapture models. In addition to this, encounter tables were compiled using only SWT detections when they were captured within a SIGID bout. This had the effect of drastically reducing the number of available detections from 4134 to 239 with the implication that any animal in the area during the capture period had the same probability of capture (assuming each individual broadcasts its signature whistle with the same probability). Another consideration was to include SWT detections that were identified as a SIGID bout and as a single whistle but removing all single SWT detections that occurred before the first SIGID. This approach more accurately represented the SWT identification process. The model used different parameters to model first capture and subsequent recapture (the behaviour effect model in Otis et al. (1978)) to model the difference in probability between the initial identification of an SWT that must be a SIGID bout and subsequent recaptures that could be either a single whistle or SIGID bout.

The Huggins formulation estimate was 45 (95% CI 45 - 50) which did not estimate abundance greater than the total number of SWTs identified during the whole period. The estimate from the full likelihood of SIGID bout detections was 71 (95% CI 53 - 135), providing a more reasonable estimate of error. The best fitting model (based on AIC) for both datasets was time varying with individual heterogeneity (Mth2), reflecting both the potential difference in signature bout production between individuals and the difference in detectability during each week of the study.

Inspection of the resulting probability of capture estimated by these approaches reveals differences that explain the differences in abundance estimate (Table 4.5). Both models included a mixture, representing differences in capture probability between groups that included a group with high probability and a group which had lower probability during each capture occasion. However, inspecting the difference in p_i values between models reveals that the Huggins model allocated a larger proportion (85%) to the high probability group than the low probability group, whereas the full likelihood models allocated a larger proportion of the population (~75%) to the low probability group. Furthermore, the probability of capture was generally higher for the Huggins model than the full likelihood model, reflecting the difference in capture probability using the different whistle types. Despite the large reduction in available SWT detections when using SIGID bout only data, this approach still provided relatively large p values (as high as 0.81 during week 8) and produced a reasonable estimate. The Huggins formulation in this study did not perform well and contrasts Longden et al. (2020), where the modelling formulation produced estimates more similar to photo-ID based estimates from the same area, although some numerical issues were reported for some models.

The approach that modelled two probabilities using the “behavioural effect” referred to as “SIGID as first capture” estimated abundance as 108 (95% CI 60 – 306). The total number of animals in the whole “East Coast” population is estimated to be between 189 – 230 based on photo-ID data collected in 2015 (Arso Civil et al., 2019). The upper limit of the “SIGID as first capture” model is therefore too high to be considered reasonable, evidence of considerable problems with this modelling approach. Inspection of the model’s real values shows a similar p_i value to the full likelihood model using only SIGID bout captures, with 27% allocated to the high probability group and 73% allocated to the low probability group. As expected, the recapture probabilities (parameter c ; Table 4.5) are greater reflecting the increased probability of detecting SWTs as single whistles. This increased probability did not have the desired effect of improving the estimate. Compared to the full likelihood model the first capture estimates were low, reducing to 0 during some weeks which may have reduced the accuracy of this approach. All models had higher probability estimates during weeks 7 to 11 (corresponding to the end of August to the end of September), indicative that there were increased bottlenose dolphin activity during

these weeks. This would be expected given the findings of Chapter 2 of this thesis (see section 2.3.3).

High estimates of abundance from the two full likelihood estimates compared to the photo-ID study may have been driven by the violation of the assumption of instantaneous capture (Table 4.2). To address this each of the above approaches were run with data that was filtered by an artificial duty cycle that retained data within 6-hour intervals in every 30 hours (20% “on” time). This was selected to provide a 6-hour window before closing for 24 hours to allow for the population to mix before a new 6-hour sampling period. The results on the estimates reduced the abundance estimates for all models. The Huggins approach (similarly to the estimate produced from the whole data set) provided an estimate that was equal to the number of SWTs available. The full likelihood approach using only SIGID bout captures failed to estimate abundance, returning the total number of SIGID bouts identified during the duty cycle with an error of 0. The model that accounted for probability of first capture and recapture estimated abundance of and 34 (95% CI 28 - 84), providing an estimate and confidence interval that was lower than the total number of identified dolphins during the study and therefore cannot be considered valid. Overall, the results from the duty cycle datasets were poor and did not improve the estimates. A large duty cycle was implemented to try and better meet the assumption of instantaneous capture by simulating a data collection protocol that was comparable to photo-ID surveys (i.e., approximating the length of time a survey is conducted for). Duty cycles with large durations have been shown to reduce accuracy of estimates for cetacean studies and were not recommended for signature whistle studies (Thomisch et al., 2015, Fearey et al., 2022). Duty cycles with much smaller redundancy cycles were recommended as potential way of increasing battery life of autonomous recorders and should be considered when planning data collection using long-term acoustic recorders (Thomisch et al., 2015). However, the results of this study provide more evidence against using duty cycles with large durations and with high proportion of “off” time, even when the approach is justified from model assumptions.

Another violation of closed capture-recapture analysis is edge effect or the movement of individuals out of the study area, thus becoming unavailable for capture during a sampling occasion. Pooling across weeks may have accounted for some of

the daily variation in individual movement but given the ranging patterns of bottlenose dolphin and the total distance of available habitat, temporary emigration of greater than a week was highly likely. This was also confirmed by inspecting the probability of captures across each week. Using time varying capture probability would have accounted for some of the variation but it may have still impacted the resulting estimate. To avoid the confounding effects of edge effect, spatially explicit capture-recapture (SECR) models were fitted. SECR models do not have the same problem with edge effect as non-spatial methods as animal movement is included in the model formulation. SECR also does not have the same issue with instantaneous sampling providing flexibility when modelling the detection process. The “proximity” detector type was used when modelling the signature whistle data as it best represented the data collection process.

SECR models require a habitat mask to estimate density over, which can be an area, or a linear habitat represented in one dimension. In this study a linear habitat was selected, representing the 20 m depth contour along the total study area visually surveyed. Although dolphins are not restricted to this depth, a linear habitat mask was selected as it best represented the spatial movement of the species that range up and down the coast with limited movements offshore. The hydrophones were deployed at approximately this depth, and it was assumed that increasing the spatial arrangement of hydrophones to cover habitat further offshore would not have increased the number of individuals detected. However, this assumption needs to be tested. The use of a linear habitat mask allowed density to be across the length of coastline, best reflecting the animal movements and spatial arrangement of the hydrophones. One limitation to the current study is the relatively low number of hydrophones used ($n=3$) and approximate distance between hydrophones (10 km) relative to the home range size of “East Coast” population of bottlenose dolphin (>500 km). This must therefore be considered when interpreting the parameters of the final models. The most parsimonious model of the SIGID bout only data included a two-mixture heterogeneity effect on the λ_0 parameter indicating differences within the population of detection at the centre of the home range. Similar to the non-spatial heterogeneity models, the mixture included a high and low probability group, with 28% allocated to the high detection group and 72% allocated to the low probability group. The estimate for σ was very high and reflects the inadequate

spacing of the hydrophones relative to the ranging distance of the species. Density for the study area was estimated as 1.10 (0.24) animals per km and the resulting abundance estimate was 66 (95% CI 56 – 104).

Of all the modelling approaches considered for signature whistles, the datasets that included only SIGID bout detections provided the most appropriate results and relatively consistent estimates between non-spatial and spatially explicit (SECR) modelling frameworks, and between these estimates and the photo-ID estimate (Table 4.8). The non-spatial estimate was larger with larger error, potentially reflecting biases caused by non-instantaneous sampling and edge effect, therefore the SECR estimate should be considered the most appropriate signature whistle-based approach used in this study. The SECR estimate was larger than the photo-ID estimate, possibly due to the inclusion of calves. However, whistles develop over the first year of the calf's life and may not be easily detected from the acoustic data. Further research is required to understand the whistle detection rates of young calves to better understand the effect on abundance estimates using signature whistles. SECR in this study was limited by the number and spatial arrangement of the hydrophones but the resulting estimate showed promise for using this approach for estimating abundance using signature whistles. SECR allows greater flexibility for modelling multiple detections within capture periods and better reflects the data collection using hydrophones. Further research is required to identify the most optimal spacing of hydrophones, but this is likely to be highly dependent on the ranging characteristics of the focal population and the area they inhabit.

Use of SIGID bout only detections greatly reduced the number of detections available for modelling, however they still produced robust estimates. If SIGID bout only detections have similar probability of detections in other studies, it may be more appropriate to only use this type of detection as it would significantly reduce the amount of data processing a SWT cataloguing needed providing a more efficient data processing protocol. However, a statistical framework for specifically modelling the difference in probability for SIGID bout whistles and single SWT detections may be warranted to increase the detectability of individuals and improve the ability to model abundance from signature whistle data.

Table 4.8. “Best” estimates of abundance of bottlenose dolphin off the Northumberland coast between July and September 2019 produced from photo id and signature whistle data.

Model	N	SE	CI
Photo-ID – Mh2	63	7.1	51 - 78
Non-Spatial – Mth2	71	18.4	53 - 135
SECR – Lambda h2, Sigma 1	67	11.9	53 - 104

The practical advantages of PAM over visual surveys have been discussed previously in this thesis. However, there are other specific advantages and disadvantages to the using PAM and whistle detections for abundance estimates using capture recapture over photo-ID surveys. Compared to photo-ID surveys, PAM has the advantages of increasing the temporal scale of studies due to the ability to collect data continuously over extended periods of time. Furthermore, with the appropriate number of devices, spatial scale can also be greatly increased compared to vessel-based studies. However, with this increase in sampling effort the amount of time required to process data and to identify stereotyped and signature whistles time becomes a bottleneck. One potential solution to this problem is the use of artificial intelligence (AI) to automate the process of identifying and cataloguing stereotyped whistles (Shkury et al., 2019, Frasier, 2021). Automating each step of the whistle cataloguing process would greatly improve the efficiency of the methodology outlined in this chapter. AI is also being applied to fin recognition for photo-ID studies improving the ability of researchers to process more data and have less bias in fin matching (Maglietta et al., 2022, Trotter et al., 2022).

One disadvantage of using whistles is that the difference in individual signature whistle emission rates within a population is not well understood (Janik and Sayigh, 2013) and may be problematic for reliably estimating abundance. Heterogeneity in capture probability is also present in photo-ID studies, but this can generally be accounted for with good study design and field protocols (e.g., ensuring that all individuals of a group are captured) (Urian et al., 2015). With PAM there is no option for correcting for this as the data collection is unsupervised. This issue will be more limiting to open population models such as Cormack-Jolly-Seber (CJS) (Cormack,

1964, Jolly, 1965, Seber, 1965), where homogeneity in capture probabilities is an important assumption of the model and heterogeneity cannot be incorporated into the model, as with closed models (Otis et al., 1978).

A further advantage of PAM is that it is non-invasive compared to vessel-based surveying. Some species show stress responses in the presence of vessels which has led to different data collection protocols being implemented (e.g., drones) (Ryan et al., 2022). At this time however, use of signature whistles for abundance estimates has only been demonstrated for bottlenose dolphins and further research is needed to identify which species have signature whistles (van Parijs and Corkeron, 2001, Fearey et al., 2019, Cones et al., 2022) before the methodology can be used as a minimally invasive approach to monitoring sensitive species.

The range shift of the "East Coast" population of bottlenose dolphin out of the Moray Firth has been well documented since the 1990s with a large proportion of the population now inhabiting areas outside of the Moray Firth such as St Andrews Bay and the Tay estuary (Wilson et al., 2004, Arso Civil et al., 2019). Abundance estimates for these areas show that approximately 50% of the total population use the St Andrews Bay and the Tay estuary with limited annual spatial mixing between the areas and the Moray Firth, suggesting that the area is equally important to the population as the Moray Firth. Increased occupancy of bottlenose dolphins in Northumberland suggests that the range of the population has expanded even further south. The photo-ID estimate (provided using similar methodology to previous studies of the "East Coast" population) is the first for the area and suggests approximately 30% of the total "East Coast" population were present off Northumberland during the study period (compared to the most recent (2015) total population size estimate of 209 (95% CI 189–230) (Arso Civil et al., 2019). This is a significant proportion of the population using habitats at the southern extent of its range with numbers comparable (albeit smaller) to the estimates of abundance for the St Andrews Bay to the Tay estuary area. The estimate only represents a snapshot of bottlenose dolphin occurrence off Northumberland, and it is not possible to infer inter-annual variation or to estimate rates of spatial mixing between Northumberland and other hotspot areas along the Scottish east coast.

Future research should consider the use of PAM and signature whistle detection to integrate information about individuals across the population's home range and different seasons. This could include SECR to generate population estimates and identify high density areas within the population's range and how this is affected by season. Large scale acoustic monitoring could also provide data to investigate inter-annual trends to better understand the changing distribution of bottlenose dolphin occupying the east coast of Scotland and England.

4.4.1 Conclusion

The findings of this study identify a significant proportion of the "East Coast" population using the Northumberland coast during the summer months of 2019, with potential implications for the long-term monitoring and conservation of the population. Estimates produced from photo-ID and signature whistle detections produced similar results. The best approach for modelling signature whistles was with SECR, a modelling framework that does not have the same issues with edge effect as non-spatial models. However, the SECR estimate still had a larger error and higher upper confidence interval than the photo-ID estimate. Other approaches to modelling whistles such as use of a duty cycle and attempts to model difference in capture probability between single whistle detection and bout detections did not improve the estimates. However, one technical finding was the suitability of using only SIGID bout detections despite their lower probability of detection. The results show further evidence for the applicability for using signature whistles to estimate abundance of bottlenose dolphins.

Chapter 5. Conclusion

5.1 Odontocete ecology off the Northumberland Coast

Coastal odontocetes are impacted by anthropogenic activities that can reduce survival and reproductive rates (Culik, 2004, Avila et al., 2018, Nelms et al., 2021). A large proportion of odontocete species are identified as at risk by the IUCN Red List and conservation efforts are needed globally to protect biodiversity and ecosystem function (www.iucn-csg.org). Conservation efforts must be supported by robust data that identify population trends and delineate critical habitats that provide the resources needed for species survival (Evans and Hammond, 2004). In areas where data are deficient an important first step is to provide baseline data on species level occurrence, abundance, and area usage, that can support initial conservation planning (Lusseau and Higham, 2004, Cañadas et al., 2005, Hammond et al., 2013).

The importance of population ecology and conservation within the field of odontocete research is evident from the topic modelling analysis of Chapter 1. The topic group “Population Ecology and Genetics” contained some of the most prevalent individual topics of the corpus (e.g., *population assessment*, *habitat modelling* and *statistical modelling*). The group had a relatively high and consistent prevalence (approximately 30% of the corpus) since the 1990s after a steady increase during the 1970s and 1980s. Closely positioned within the network graph of topic correlations was the topic *conservation and management*. This topic showed the most pronounced increase in prevalence across all topics in recent years (increasing in corpus proportion from approximately 2% in the 2000s to 5% by 2020). This increase was driven by its high generality and inclusion in abstracts alongside other topics.

In contrast to these broad trends in odontocete research, odontocete ecology off the Northumberland coast is relatively understudied, with a paucity of peer-reviewed publications, long-term monitoring efforts and specific conservation strategies for the area (Brereton et al., 2010, Temple and Berggren, 2015, VanBressem et al., 2018, Temple et al., 2019, Trotter et al., 2019, Yang et al., 2021, Potlock et al., *In Review*). This is despite the area being used by three sympatric odontocete species (harbour porpoise (*Phocoena phocoena*), white-beaked dolphin (*Lagenorhynchus albirostris*), and common bottlenose dolphin (*Tursiops truncatus*)) and the potentially high levels

of risk associated with industrialised coastal areas. This thesis aimed to address this lack of knowledge by providing robust baseline data for all three odontocete species and a more detailed investigation of bottlenose dolphin behaviour and abundance. The aim was achieved through passive acoustic monitoring; using broad band archival recorders to record click and whistle detections to identify species specific spatio-temporal patterns of occurrence and for bottlenose dolphin, abundance, and area usage.

In Chapter 2, Occurrence for all three species was investigated by detecting species specific clicks that were used as a proxy for occupancy. Modelling the effect of environmental drivers on click detections identified significant factors affecting occupancy for all three species. The most prevalent temporal patterns were driven by the effects of season and diel phase. Porpoise seasonality was characterised by increased occurrence in winter months, identified across all three locations, but with a second peak identified during early autumn at the Druridge Bay site. White-beaked dolphins were detected mainly in July and August, with only two (consecutive) hour detections identified outside of these months. Bottlenose dolphins however, showed year-round presence in the area but with two peak periods corresponding to spring (May) and early autumn (September).

Detections of all three species were increased during sunrise and sunset, but porpoises showed increased detections during daytime hours compared to night. In contrast, delphinid species had increased detections during night-time hours. Diel phase was also an important driver of bottlenose dolphin activity and area usage identified in Chapter 3. The selected Hidden Markov Model (HMM) included diel phase as a factor affecting the transition between states and for the individual state occurrence GAM-GEE models. The activity state 5 “possible socialising” was characterised by having low probability of clicks and high probability of whistles and was more prevalent during daylight hours. This finding suggested that behaviours that produced less clicks were more likely to occur during the day. This may play a role in the low click detections during the day possibly leading to false interpretations about daytime occurrence. Other states showed differences in occurrence between diel phase and location suggesting a complex relationship between diel phase, habitat choice and behavioural activities for bottlenose dolphin.

Tidal phase was only retained by model selection for the porpoise occurrence model, showing an increase in detection during flood tide, identified across all sites.

However, tidal phase was retained in the HMM model of dolphin activity states as a covariate effect on the transition probability matrix (TPS) and retained in a number of the state specific GAM-GEE models. The effect of tide was particularly pronounced from state 4 (the “high foraging activity” state that had a high occurrence of overlapping whistles of the same type) at Druridge bay, characterised by three peaks in activity during the tidal cycle. This suggests that tide has an important role in modulating dolphin activity (including foraging activity), even in open coastal habitats where tide has been found to be less important in previous cetacean studies (Pierpoint, 2008, Fernandez-Betelu et al., 2019).

The study was conducted at a relatively small spatial scale with the three hydrophones deployed at locations approximately 10 km apart. Despite this, there were significant differences in species occupancy identified across the three sites, with all three species having a higher level of occupancy at Druridge Bay. The most pronounced difference was in porpoise occurrence, where environmental drivers also had a greater effect on porpoise detection. The increase in Druridge Bay occurrence for bottlenose dolphins was driven by a higher occupancy rate throughout the year. However, Druridge Bay had a lower second seasonal peak compared to the other two locations. White-beaked dolphins showed a less pronounced preference for Druridge Bay, but this was still significant and retained in the model.

Odontocete distribution is primarily driven by foraging opportunities and predator avoidance (Heithaus and Dill, 2002). For delphinid species, the risk of predation can be considered minimal within the near shore coastal waters of Northumberland, as possible predators such as killer whales (*Orcinus orca*) are rare. The role of bottlenose dolphin and grey seal (*Halichoerus grypus*) may be important in driving the distribution of harbour porpoise as both species are known to attack and kill porpoise (Ross and Wilson, 1996, Leopold et al., 2015). The GAM-GEE model of porpoise occurrence did identify a significant reduction in porpoise detections during periods when bottlenose dolphin was also present, but the effect was low relative to other environmental covariables. Spatio-temporal trends of each species did suggest that overlap of these species would occur, with no clear segregation across temporal

scales. Both species had increased probability of detection at Druridge Bay, at sunrise and sunset, and an overlapping seasonal peak in autumn. These findings would suggest that porpoise may be subject to higher risk from bottlenose dolphin attacks during these times. The effect of grey seals on porpoise occurrence was not possible to identify during this study.

The broader spatio-temporal trends in porpoise and bottlenose dolphin occurrence are likely to be driven by foraging opportunity. Higher diurnal detections of porpoise have been attributed to preference for sandy substrate habitats used for benthic foraging (Schaffeld et al., 2016). This is hypothesised to be the main driver for the patterns observed at Druridge Bay. Bottlenose dolphin seasonal peak times coincide with an increase in salmonid prey in the area. However, year-round bottlenose dolphin presence suggests that the Northumberland coast provides foraging habitat and abundance of prey species across all seasons and not just during periods of increased salmonid abundance. Druridge Bay was identified as the location most important to high intensity foraging behaviour during summer months from the activity state HHM, suggesting that occurrence in this area was directly driven by foraging opportunity. In contrast, occurrence at the St Mary's site is likely driven by non-foraging area usage based on the higher frequency of non-foraging activity states identified there. However, this could also be explained by the indirect effect of foraging on habitat selection. St Mary's is an area situated between two large estuaries (the Blyth and the Tyne). Estuaries are known foraging hotspots of bottlenose dolphin and the species have been observed foraging in these areas within the study area (personal observation). The location of St Mary's may provide a habitat away from these core feeding areas that can be used between foraging activities (e.g., for rest or social behaviours).

White-beaked dolphin clicks were predominantly detected during July and August reflecting seasonal trends in near shore occurrence for the species both off Northumberland and for other areas of the North Sea (Canning et al., 2008). There were, however, very few white-beaked dolphin detections compared to the other two species. The lack of detections may reflect a low density of white-beaked dolphin even during the peak periods or sub-optimal placement of the deployed hydrophones. It is possible that white-beaked dolphin prefers deeper habitat even

during periods of increased coastal occurrence and deploying hydrophones in deeper areas may improve detections in future studies.

Abundance of bottlenose dolphins was estimated to be 63 (51-78) non-calf individuals during the summer season of 2019 based on photo-ID from dedicated boat-based surveys, and 67 (53-104) from spatially explicit capture recapture using signature whistles. These data were collected during the period of increased bottlenose dolphin activity and may represent a peak abundance estimate for the year. However, analysis of click detections identified increased occurrence of bottlenose dolphin with each year of the study (2019 to 2021). It is therefore possible that the abundance of bottlenose dolphins off Northumberland has increased since the period in 2019 that the photo-ID abundance was estimated. The presented abundance estimate from Chapter 4 may therefore represent a minimum proportion of the “East Coast” population that now uses the Northumberland during summer months. The increase in detections identified during the whole study period may, however, not be due to increased abundance of bottlenose dolphins but instead caused by increased occupancy of the same number of dolphins. With individuals remaining in the area for a longer duration or moving into the area more frequently. The abundance estimated provided from the single summer season in 2019 represents a large proportion of the “East Coast” population of bottlenose dolphin, comparable to other hotspot areas along the Scottish east coast (Arso Civil et al., 2019) and is the first quantitative evidence of the increased range shift of the population in English waters.

5.2 Advancing the application of passive acoustic monitoring

The ecological findings presented in this thesis were achieved by developing and using novel approaches to analysing acoustic data that integrated both click and whistle detections from broad band archival recorders. This included for the first time the identification of “activity states” used to investigate area usage and estimating abundance from signature whistles.

In Chapter 3 HMMs were used to identify latent activity states of bottlenose dolphin from passive acoustic data. The resulting states provided a more detailed assessment of area usage than achieved to date, as it included activity states defined by increased whistle activity and reduced click activity. The HMM statistical

framework used in this chapter to identify activity states could be used to address other research questions using PAM. The HMM modelled two time series, an unobserved state process and a dependent observation process (Zucchini et al., 2016). This framework fits PAM data as it accounts for temporal dependence in observations and for the limitation that acoustic data do not directly observe the species of interest. PAM detections only represent a proxy for animal presence and behaviour. There is potential of HMM to be used to identify other “hidden” states in odontocete acoustic time series (e.g., species separation and interspecific interactions).

In Chapter 4 signature whistles were used to estimate abundance of bottlenose dolphin building on recent work in this area and providing further validation of the approach (Longden et al., 2020, Fearey et al., 2022). The chapter also considered SECR (Borchers, 2012), a modelling framework with the advantage of overcoming edge effect and better modelling the detection process (Efford and Fewster, 2013). The SECR model did have a reduced error compared to non-spatial models analysing the same data and shows promise for future applications. The SECR estimate was comparable to the photo-ID estimate produced during the same time despite the sub-optimal spacing of the hydrophones relative to the ranging patterns of the focal species. The results also showed that using only signature whistle detections that were identified as SIGID (Janik et al., 2013) bouts (at least 5 consecutive whistles spaced between 1 and 10s) produced good estimates. This has the benefit of significantly reducing the amount of manual data processing, cataloguing, and matching needed to produce a data set capable of producing robust abundance estimates for bottlenose dolphin.

5.3 Recommendations for future research

Future research should aim to test the hypothesis that shallow open bays provide day-time foraging habitat for harbour porpoise off Northumberland. Future studies should expand passive acoustic monitoring to include additional near-shore areas along the Northumberland Coast of similar habitat type to Druridge Bay and deeper water areas which may be used for night-time foraging. Analysis of click detections could also consider differences in porpoise foraging buzzes between sites and environmental cycles. However, Schaffeld et al. (2016) reported that foraging buzzes

were not detected as often at shallow sandy habitats, potentially due to benthic foraging clicks being less detectable as the acoustic beam is directed into the substrate. This should be taken into consideration when investigating differences in foraging patterns between different habitats. Offshore areas of high porpoise occurrences could be identified by random point sampling using static hydrophone deployments or by using acoustic transects. The latter could be achieved using WaveGlider technology, as deploying hydrophones to these devices has shown success in detecting cetacean species (Bingham et al., 2012, Davis et al., 2016, Bittencourt et al., 2018), including a pilot study conducted in Northumberland (Berggren et al., unpublished data). Such an approach would allow for night-time transects that may be difficult to achieve using manned vessels.

The effect of bottlenose dolphin occurrence on porpoise habitat selection should also be investigated further to better understand the effect of the increased bottlenose dolphin occurrence in the area. If there is significant avoidance behaviour, bottlenose dolphins will displace porpoise from important daytime foraging habitat or have increased impact during autumn months which may be of importance to porpoise calf survival (Williamson et al., 2022). Understanding porpoise habitat selection and the interspecific effects should then be considered when managing anthropogenic activities, as human disturbance could potentially displace porpoise from less risky habitats (Wisniewska et al., 2016). Larger PAM arrays (as suggested above) could be used to better understand the impacts of bottlenose dolphin on porpoise occurrence across different spatial and temporal scales.

Increased research attention is needed for white-beaked dolphins off the coast of Northumberland and PAM can be a valuable method for identifying the species given the development of a species-specific detection pipeline outlined in Chapter 2. The low detection rates achieved in Chapter 2 should be addressed by including additional hydrophones further from shore. As suggested for porpoise, a pilot study could be implemented that uses random point sampling or acoustic line transect surveys to identify the most suitable depth contours to maximise white-beaked dolphin detections using PAM. Increased white-beaked dolphin detections would allow for more detailed analysis including approaches similar to those used on bottlenose dolphin data in this thesis. Chapter 1 identified the disparity in publications between bottlenose dolphin and other odontocete species, with

research on the latter accounting for a much greater proportion of the published abstracts. Future research efforts should attempt to reduce this disparity and apply research techniques and ideas developed for bottlenose dolphin studies on other more elusive species. Off Northumberland this could be achieved by using the advanced application of PAM developed using bottlenose dolphin data and applying it to white-beak dolphin recordings. One limitation to this approach is that the patterns and acoustic behaviours of white-beaked dolphins are not as well described compared to bottlenose dolphins (Rasmussen and Miller, 2002, Rasmussen et al., 2006, Yang et al., 2021). An important first step would be to identify acoustic emissions related to behavioural activities and to identify whether white-beaked dolphins use signature whistles. This could be achieved by applying the SIGID methodology (Janik et al., 2013) to white-beaked dolphin whistle recordings and identifying acoustic behaviours via vessel based focal follows.

The increase in bottlenose dolphin occurrence and estimation of a significant proportion of the “East Coast” population using the Northumberland coast requires further research. This should include long-term monitoring across the population’s southern range. This should include passive acoustic monitoring, with a monitoring program that includes the full extent of animal movements along Northeast England. Research could be coordinated with long-term research efforts off Scotland to fully understand the population dynamics of the “East Coast” population. PAM could be a highly valuable method for collecting data over this large area, including the use of whistle detections to identify individuals. SECR could be used to estimate differences in dolphin density and abundance across different temporal scales (e.g., summer and winter). Spatial mixing could also be identified without the limitation of relying on only summer visual surveys (Arso Civil et al., 2019).

5.4 Recommendations for conservation and management

This study provides data on the occurrence of three odontocete species, two of which (harbour porpoise and bottlenose dolphin) are annex II species under the EU habitat directive (92/43/EEC) which was transposed in UK law post-Brexit (Fisheries Act 2020). Under this conservation framework authorities are to provide annex II species Special Areas of Conservation (SACs) to be implemented to maintain or restore their favourable condition. There are currently six SACs designated for

harbour porpoise in the UK, with five these on the west coast and one on the east coast (Southern North Sea) (www.gov.uk). There are two SACs for bottlenose dolphins (Moray Firth and the Cardigan Bay), the former providing protected habitat for the same population of bottlenose dolphins identified off the Northumberland coast. The findings of this study suggest that providing an additional SAC may be justified for protecting both species in English North Sea waters. The area has been identified as an important year-round habitat for both species that provides important foraging opportunities. Future work will likely identify further evidence that the area is “essential to life and reproduction” as determined by the Habitat directive, for both harbour porpoise and bottlenose dolphin.

The Northumberland coast is already a protected area under the Marine Conservation Zone (MCZ) and SAC frameworks. The area has two overlapping MCZs: the Coquet to St Mary’s MCZ (protecting inter- and subtidal habitats) and Berwick to St Mary’s MCZ (designated to protect the eider duck). There is also a SAC that covers the North of Northumberland (Berwickshire and North Northumberland Coast) that is designated to protect a number of habitat types and the grey seal. Odontocete species, however, are currently lacking protection. Increased protection could be provided by increasing the designation of MCZs already present or by extending the Berwickshire to North Northumberland Coast SAC, southward to include the habitat in south Northumberland. Increased protection for odontocete species in the area would provide the framework for continued monitoring and help to ensure that the UK’s conservation goals are met (e.g., include ensuring good environmental status (GES) under the UK Marine Strategy and protecting key species (e.g., predator populations) under the 25 Year Environmental Strategy).

5.6 Conclusion

The work presented in this thesis provides much needed information on three species of odontocete off the Northumberland coast. The novel developments in analysing and modelling PAM data have provided an example of the potential for acoustic studies to investigate abundance and behaviour, that can be applied to better inform conservation and management for odontocete species globally.

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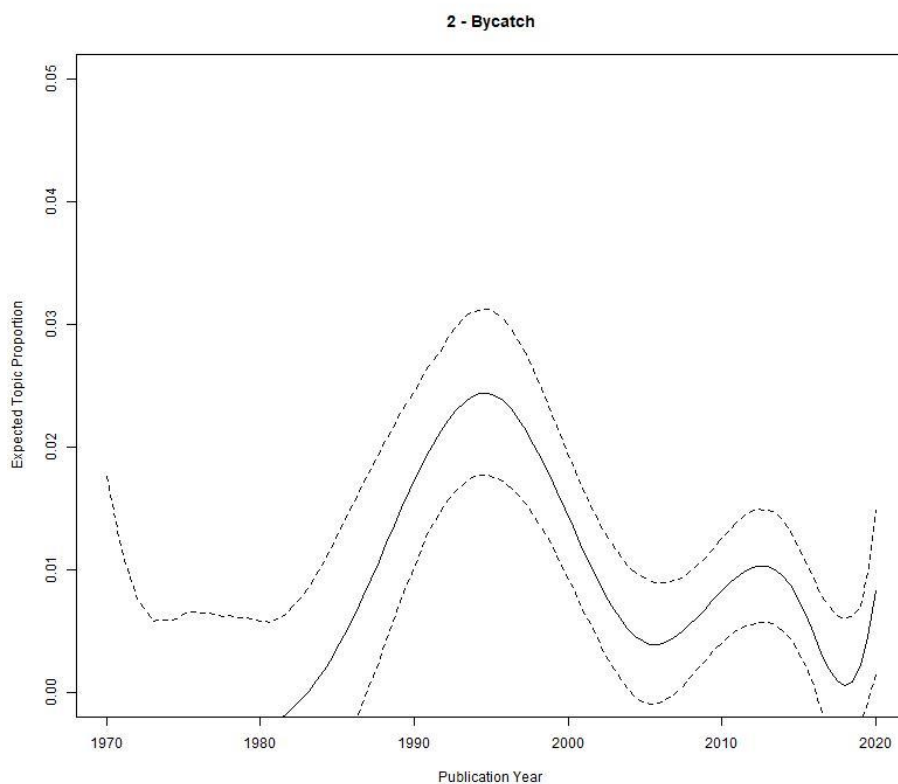
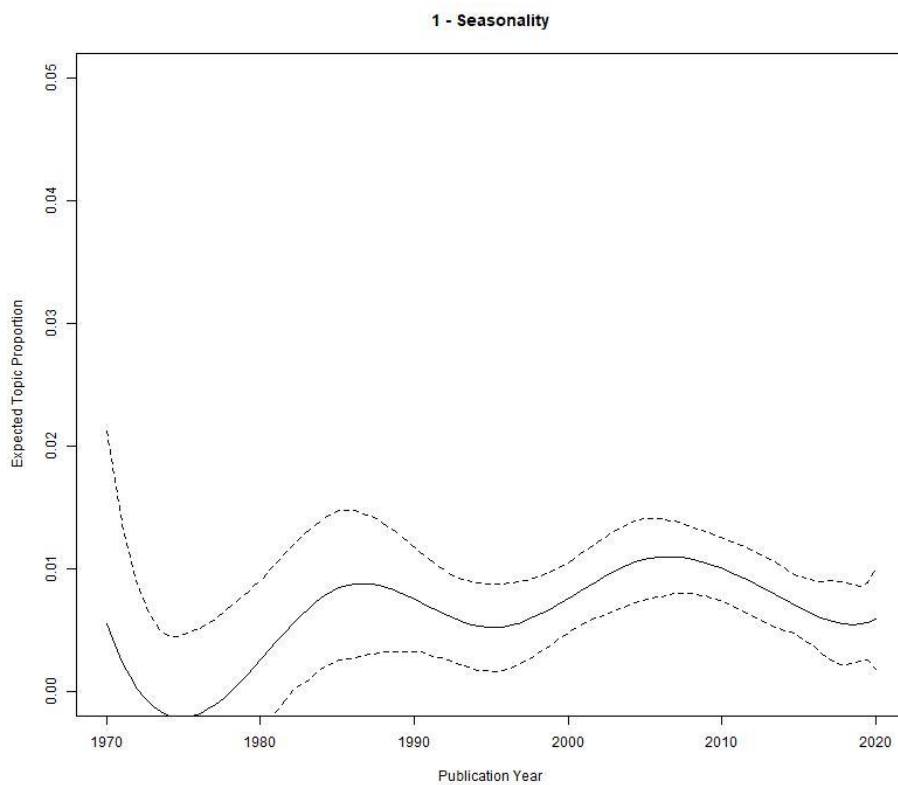
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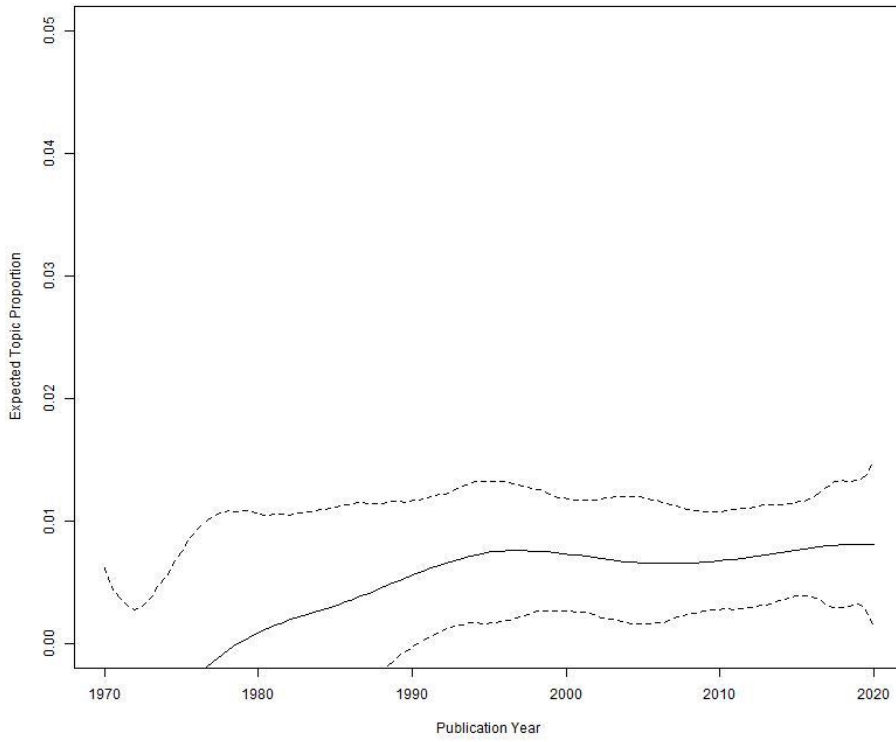
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Appendix A – Model results of Structural Topic Models

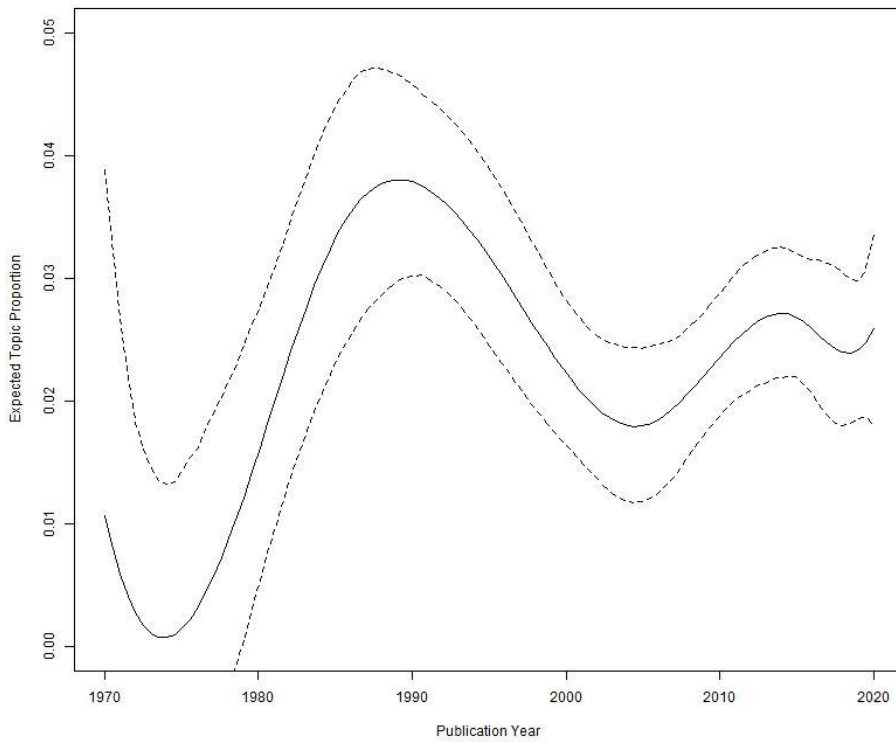
Figure A1-65 showing trend over time for each of the resulting topics from the odontocete research corpus.



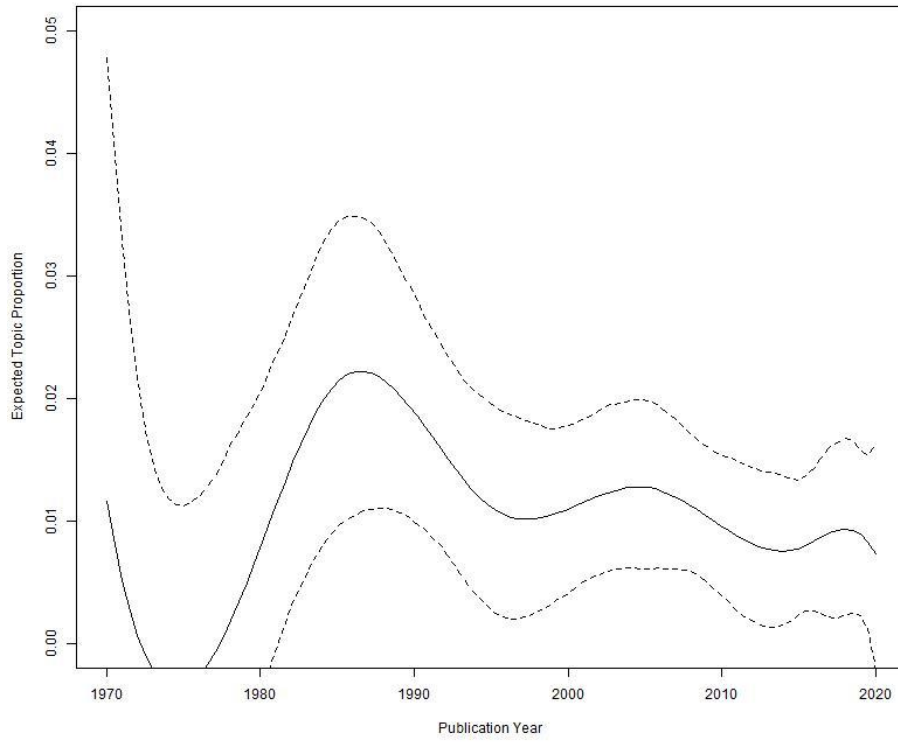
3 - Riverine Ecology



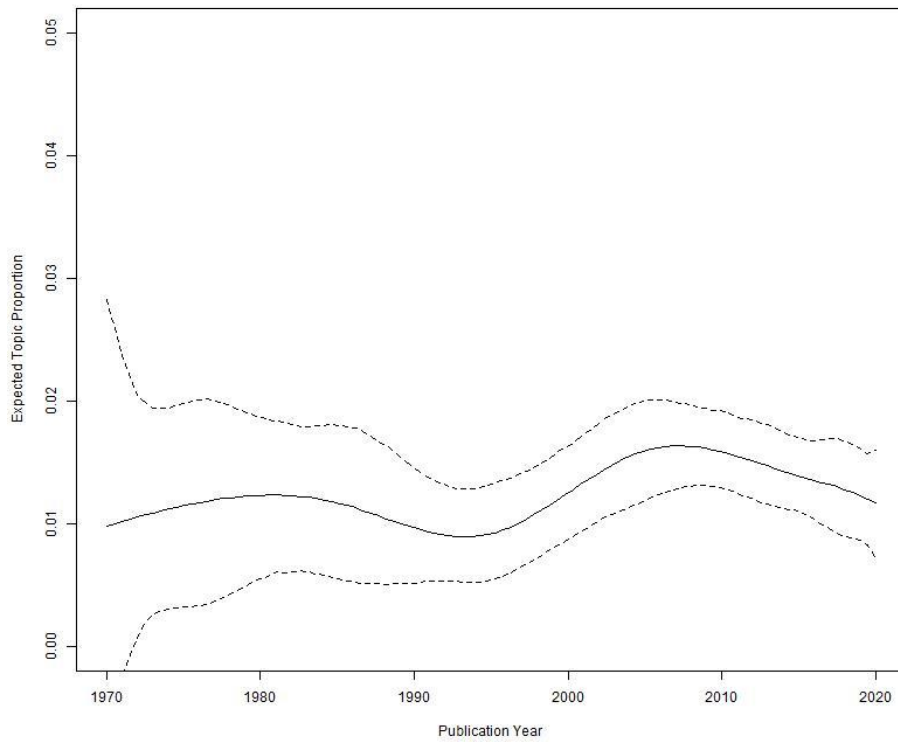
4 - Population Assessment



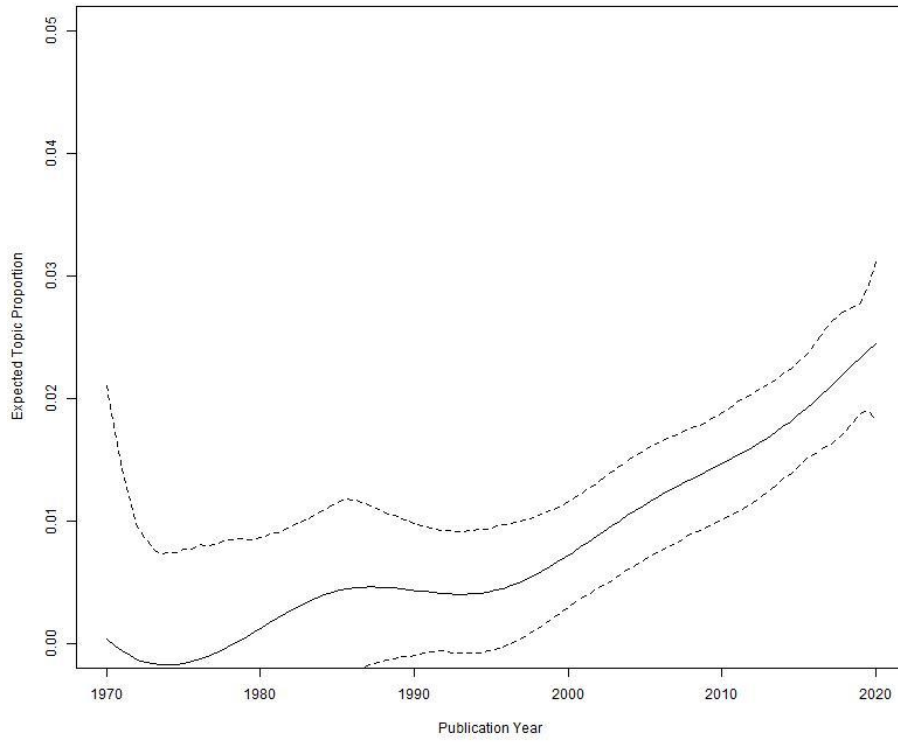
5 - Taxonomy



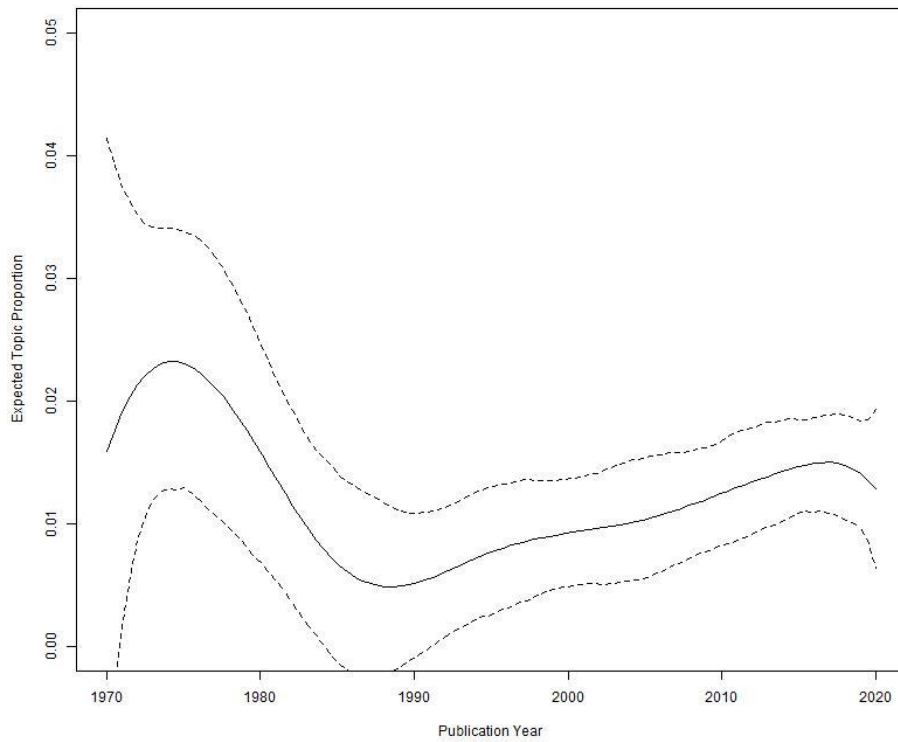
6 - Vessel Response



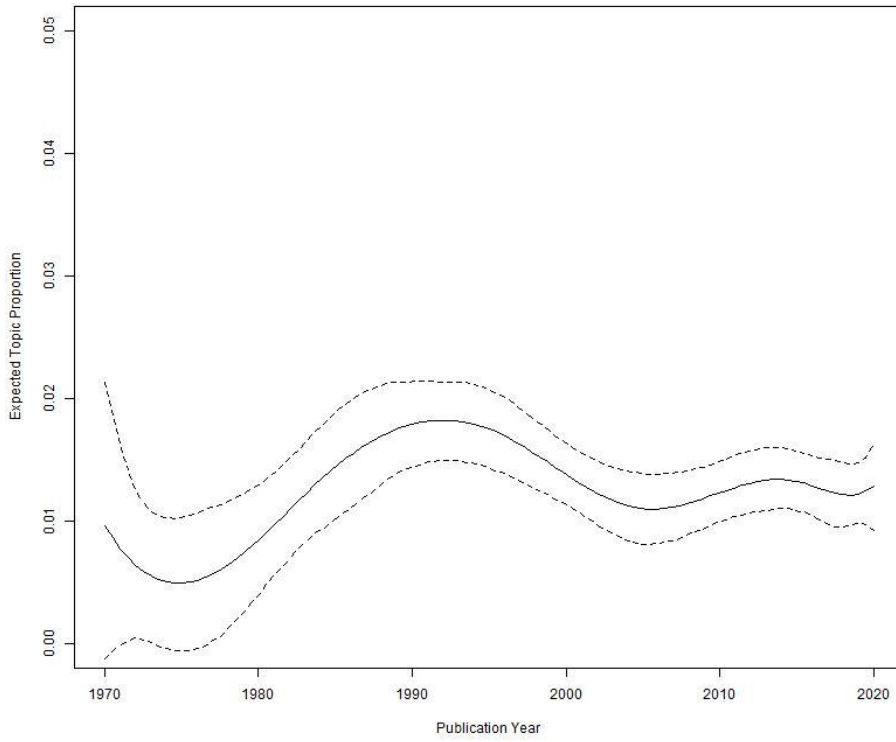
7 - Ecological Niche



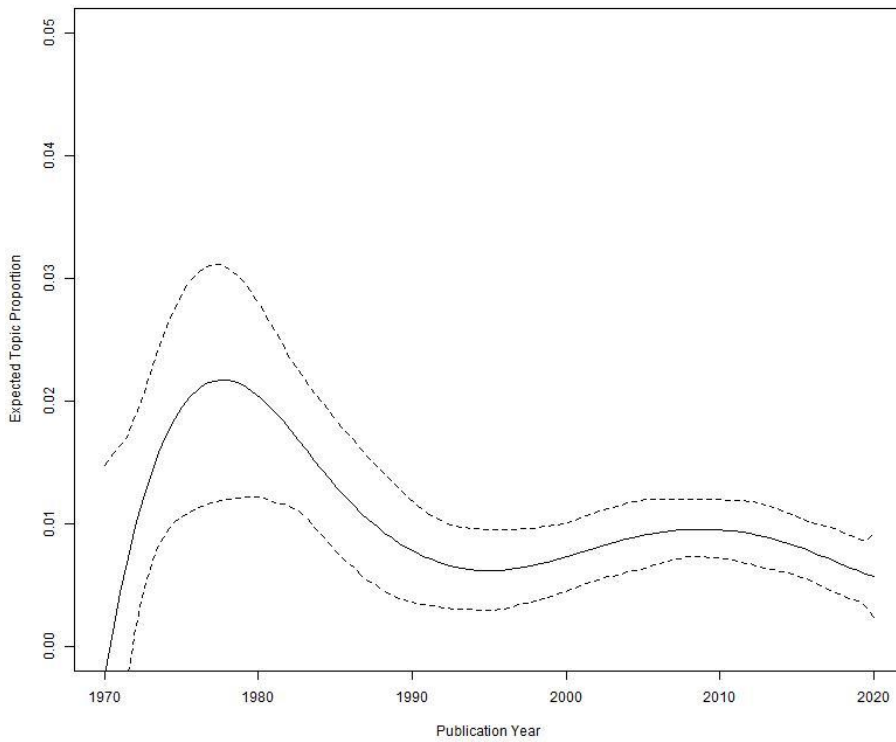
8 - Sound Playback



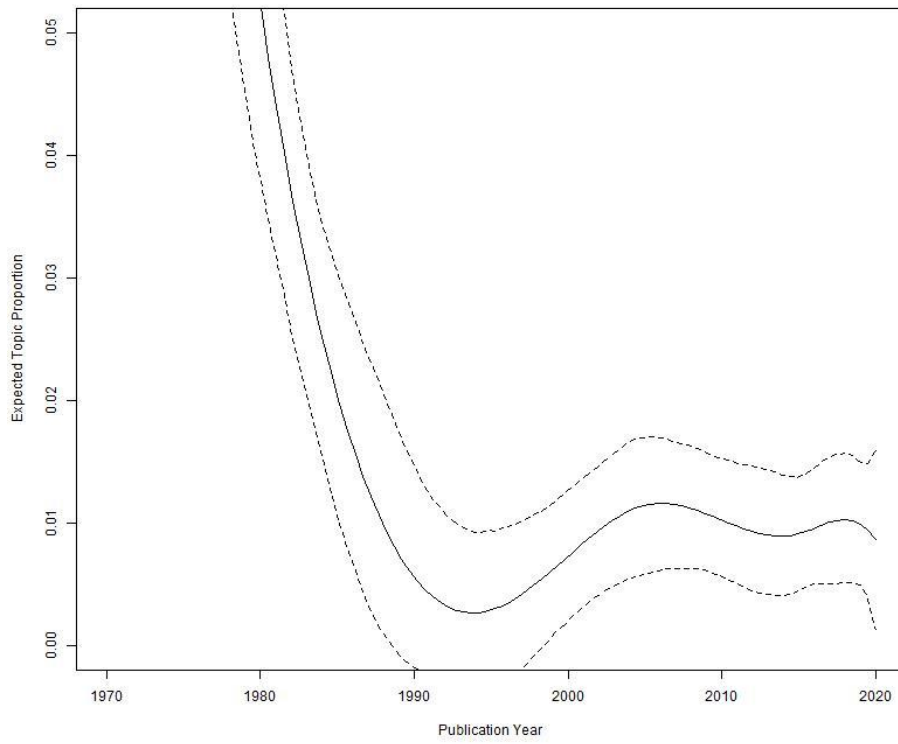
9 - Mortality Event



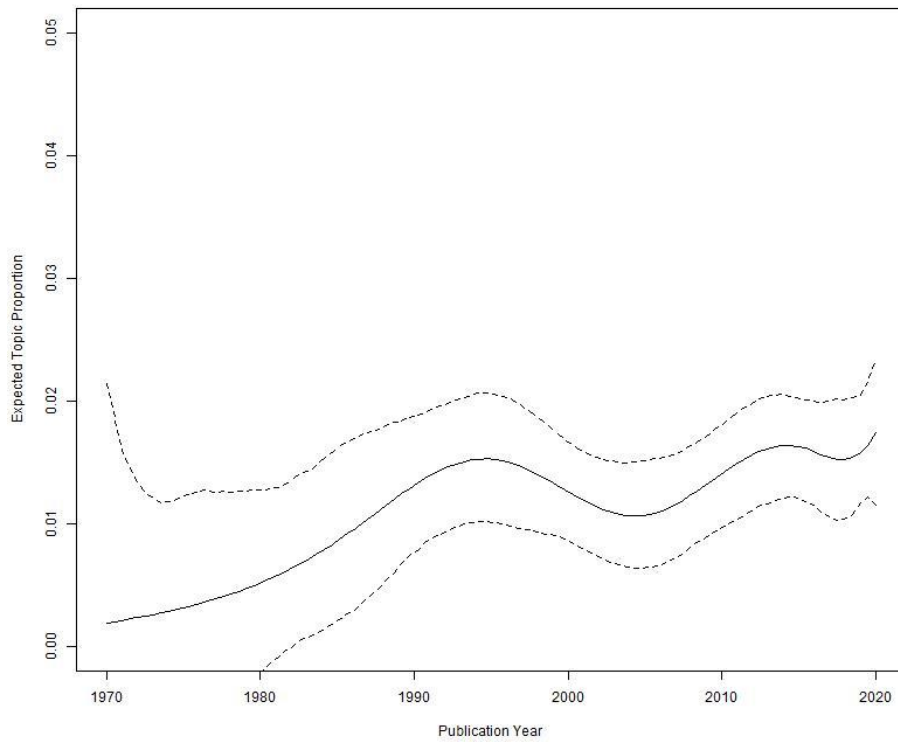
10 - Lab Methodology



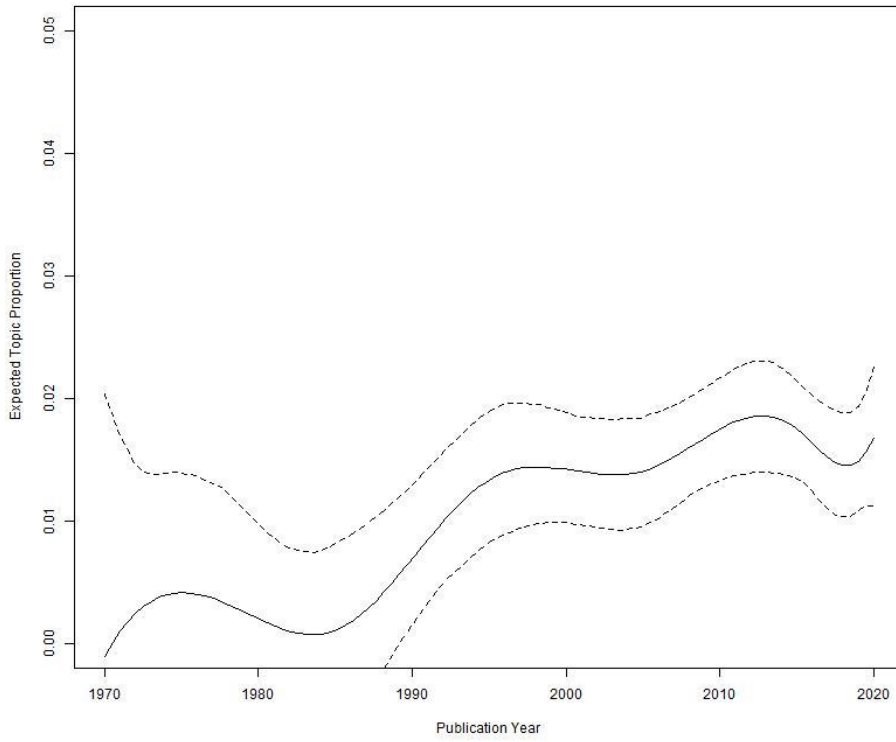
11 - Blubber



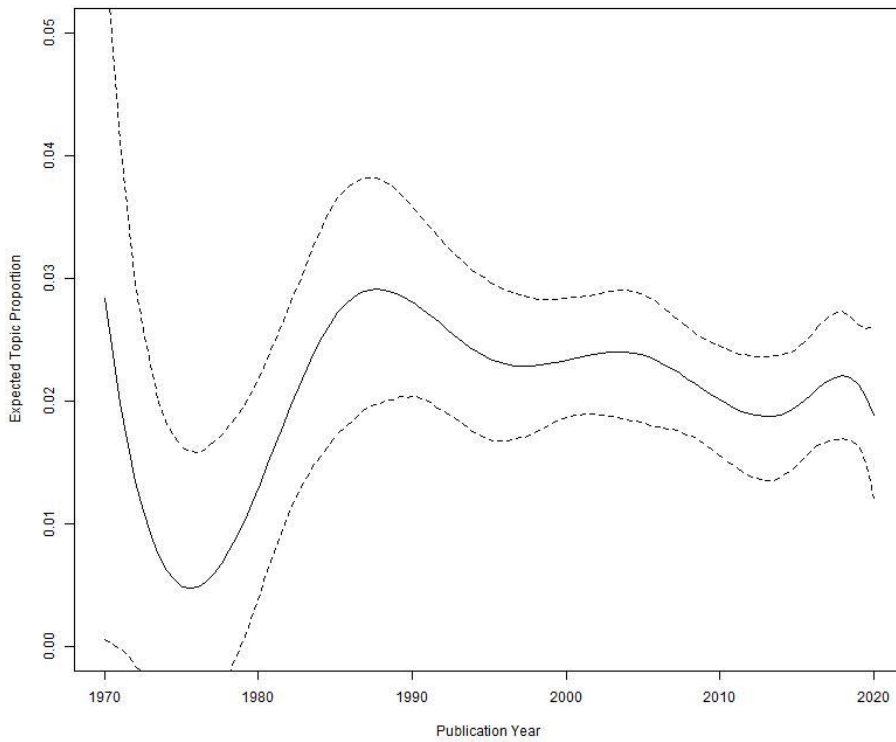
12 - Mitigation



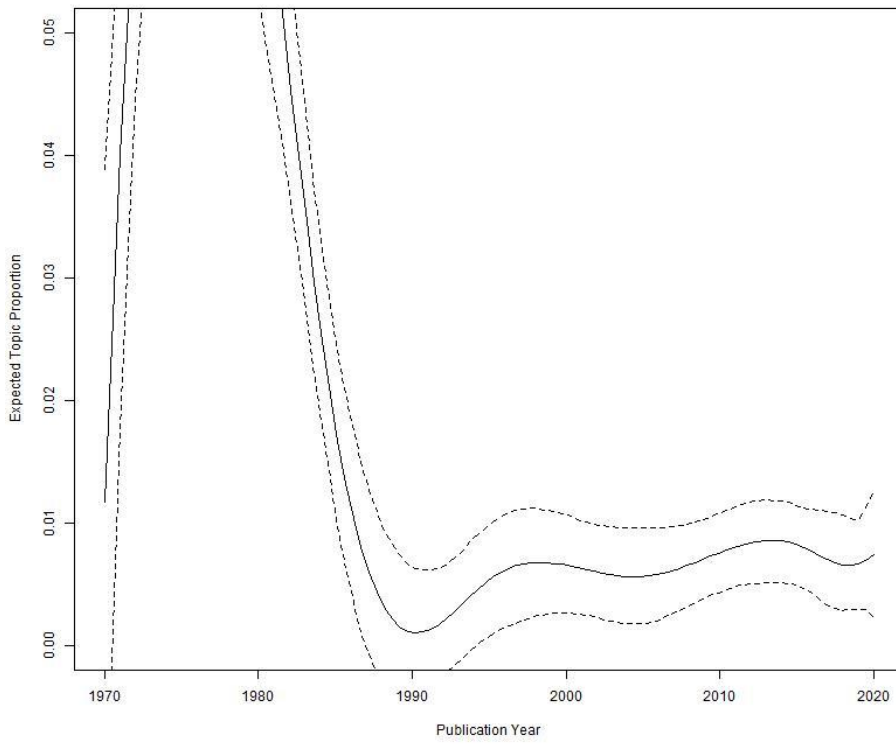
13 - Strandings



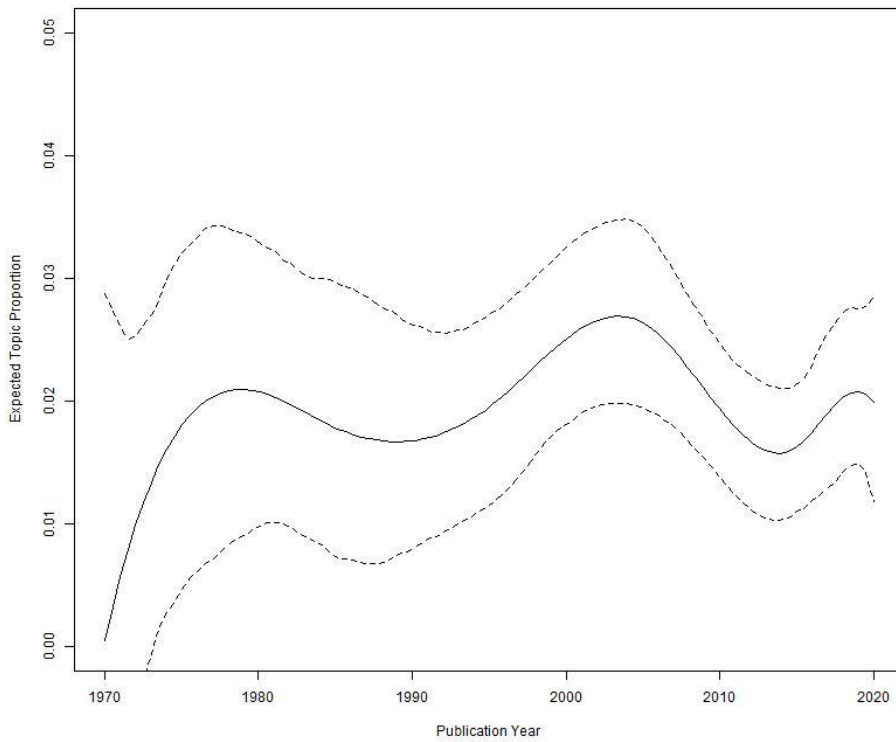
14 - Reproduction



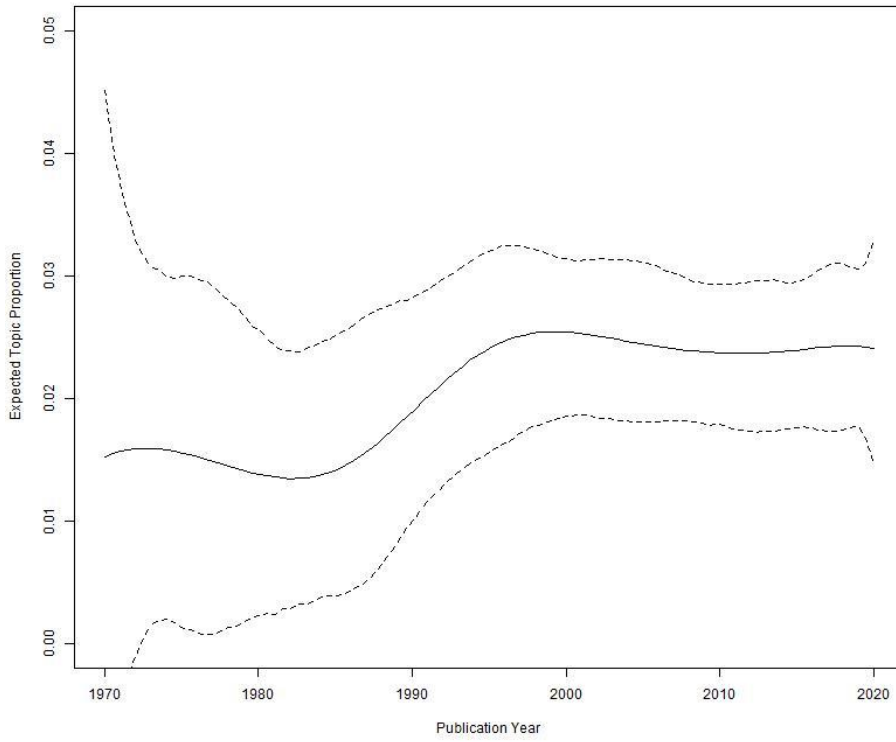
15 - Protein



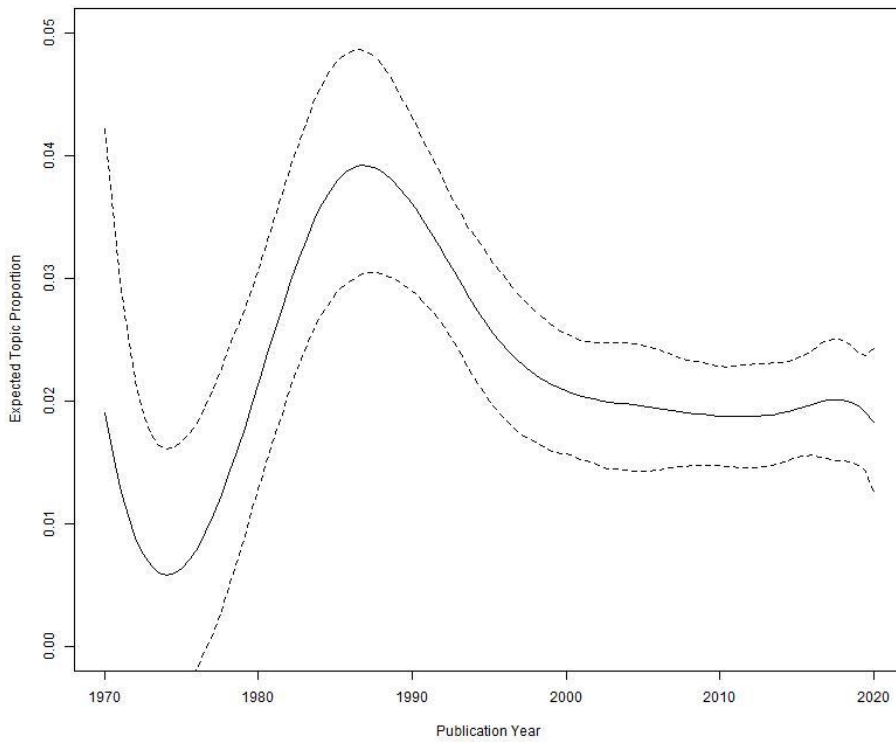
16 - Dive Behavior



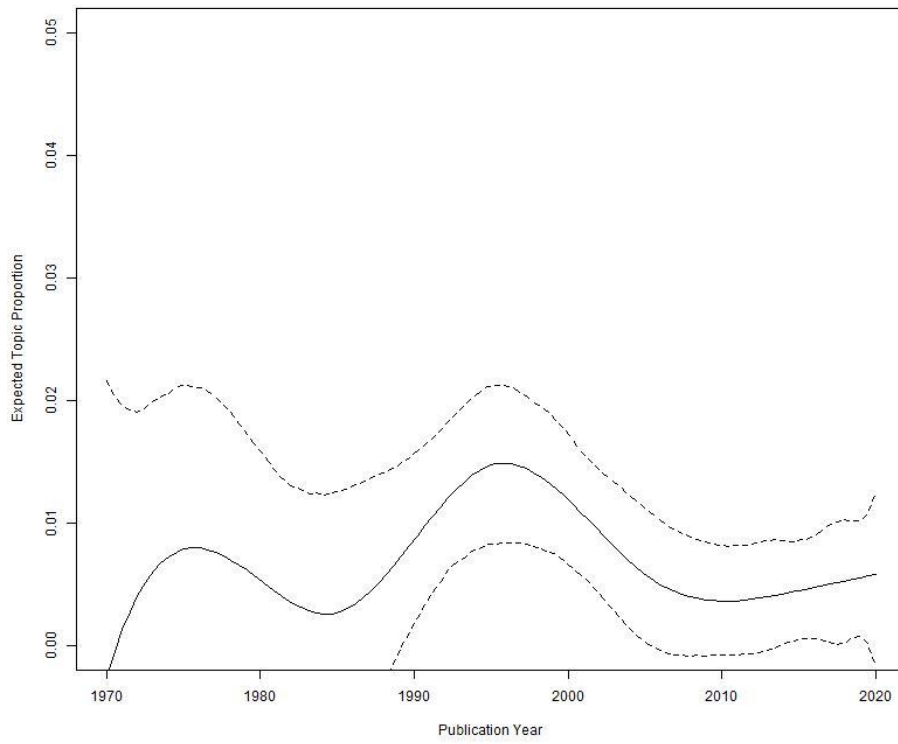
17 - Whistle



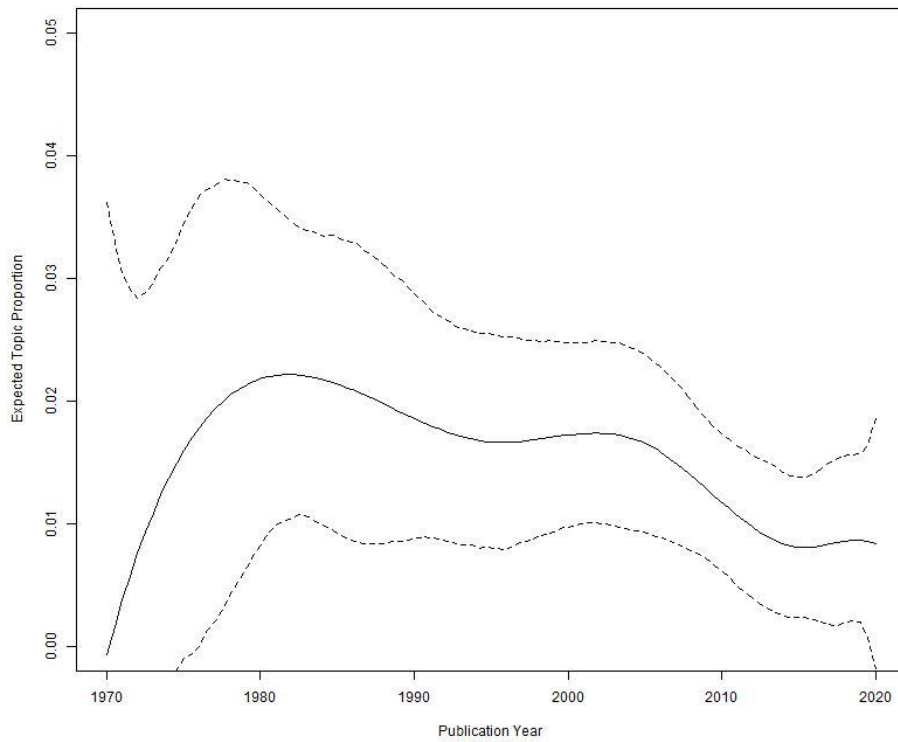
18 - Reproductive Success



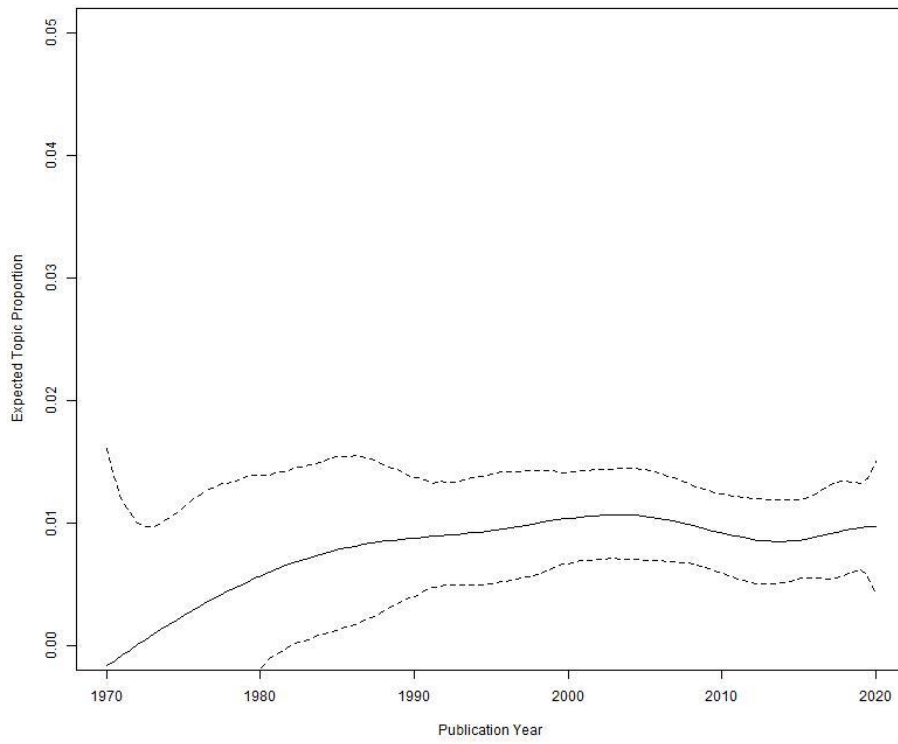
19 - Parasite



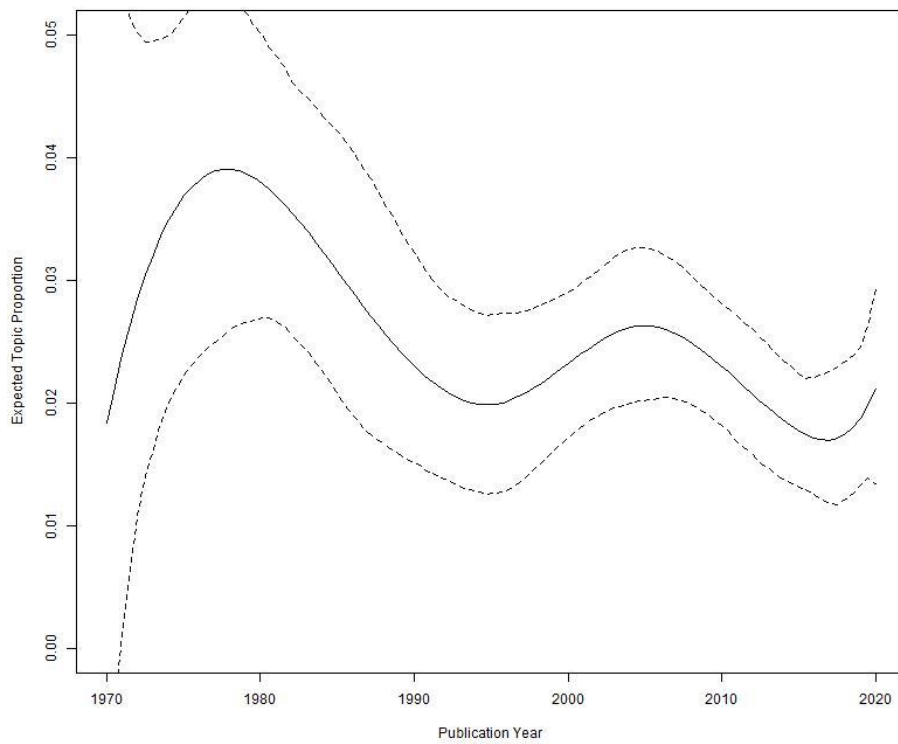
20 - Heavy Metal



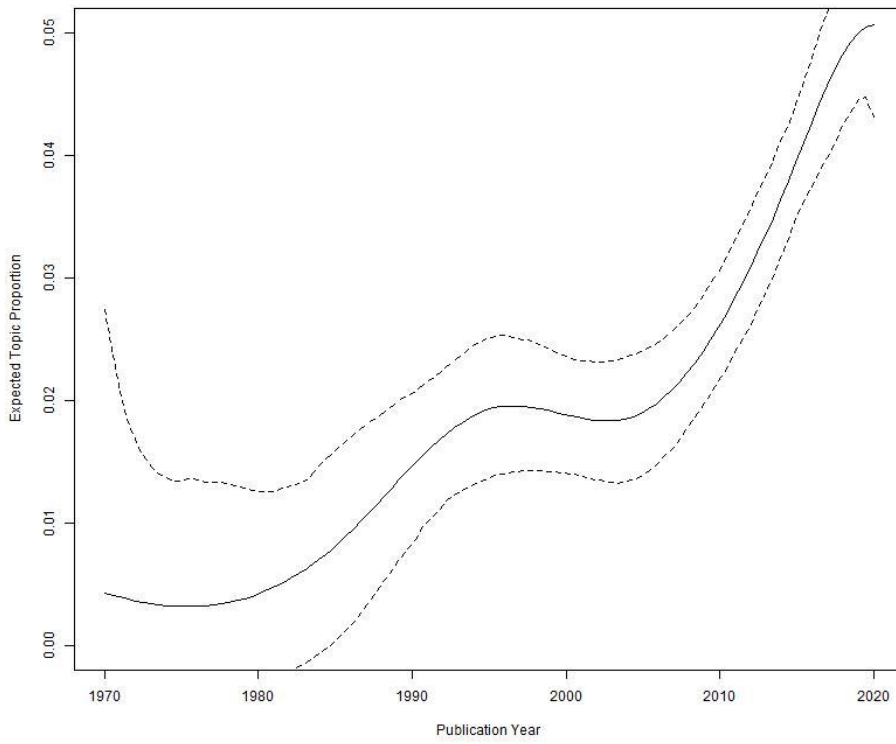
21 - Movement



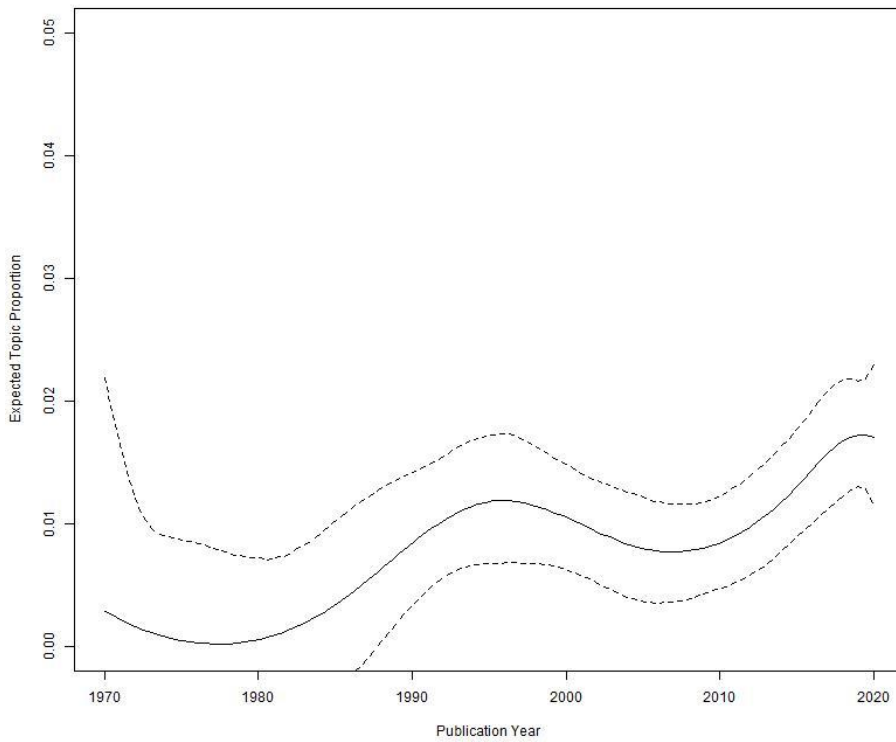
22 - Biosonar



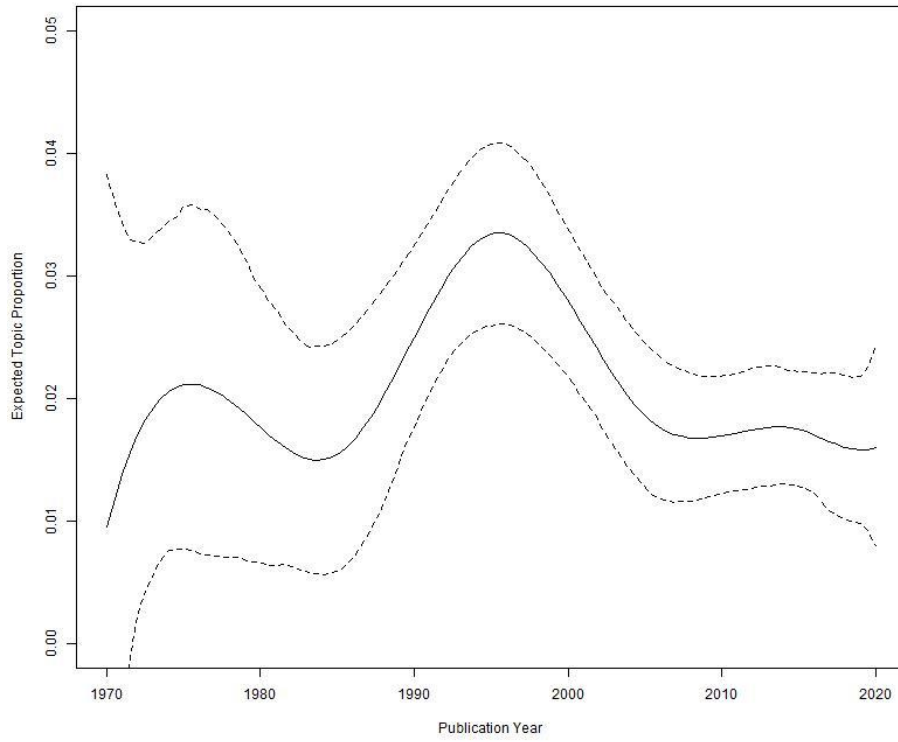
23 - Conservation and Management



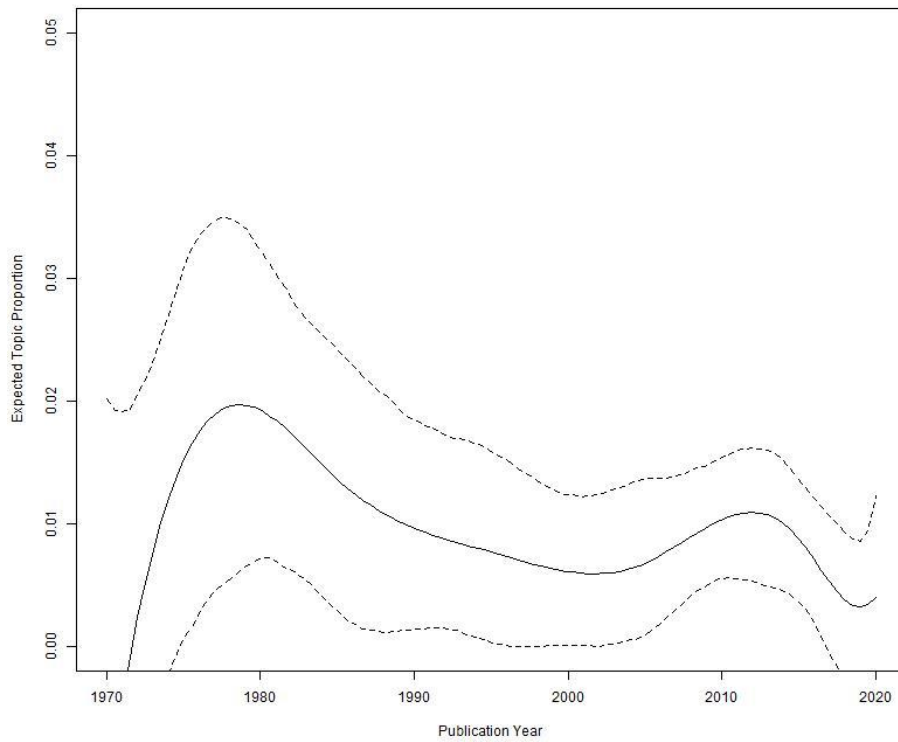
24 - Pollution/Oil Spill



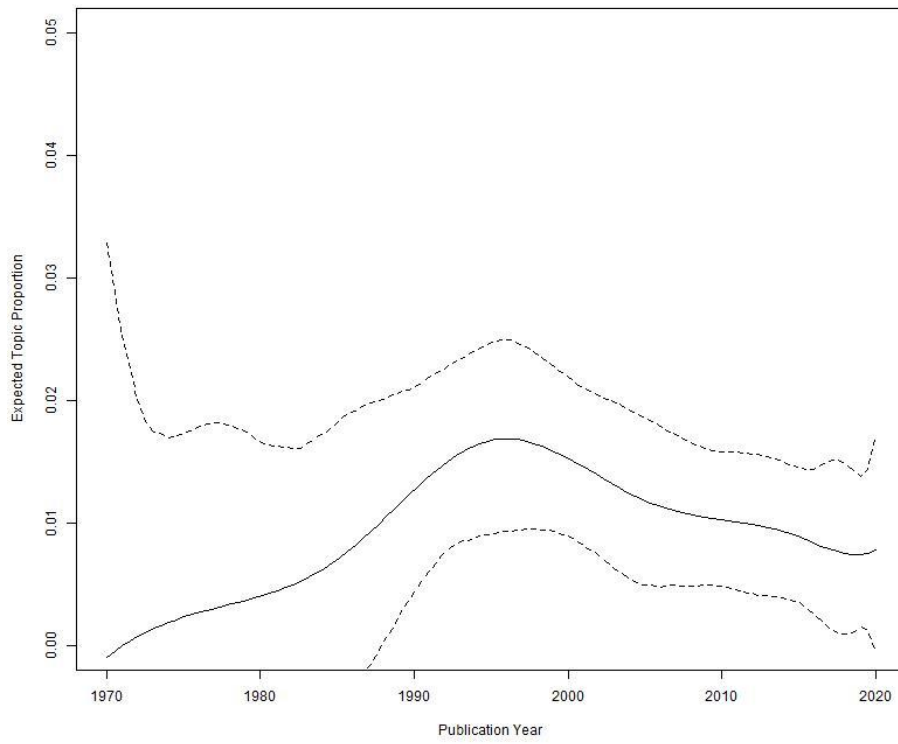
25 - Virology



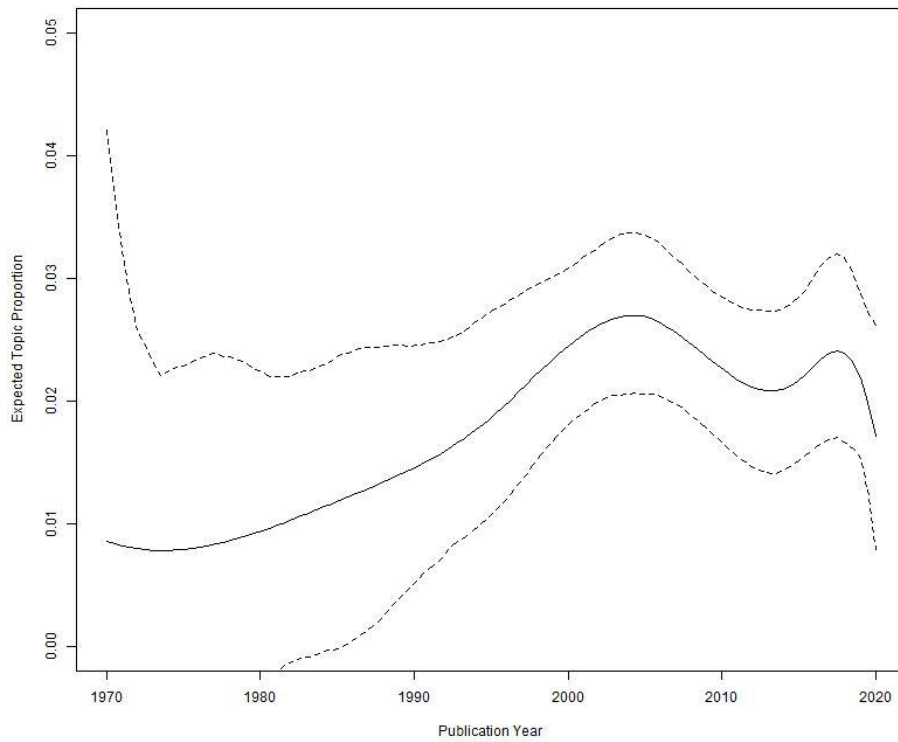
26 - Cetacean



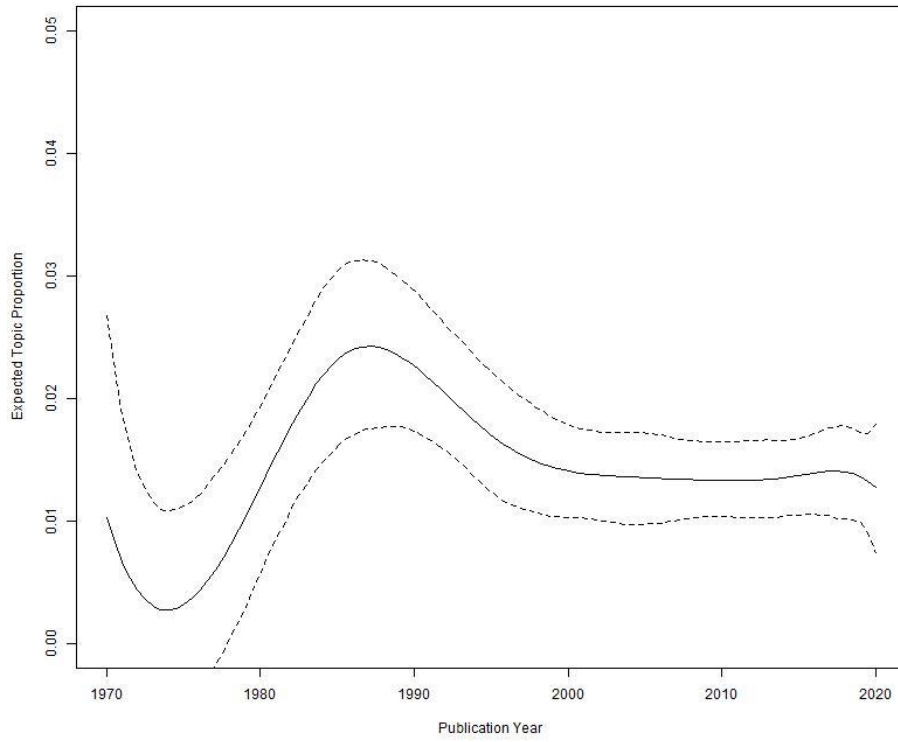
27 - Stomach Contents



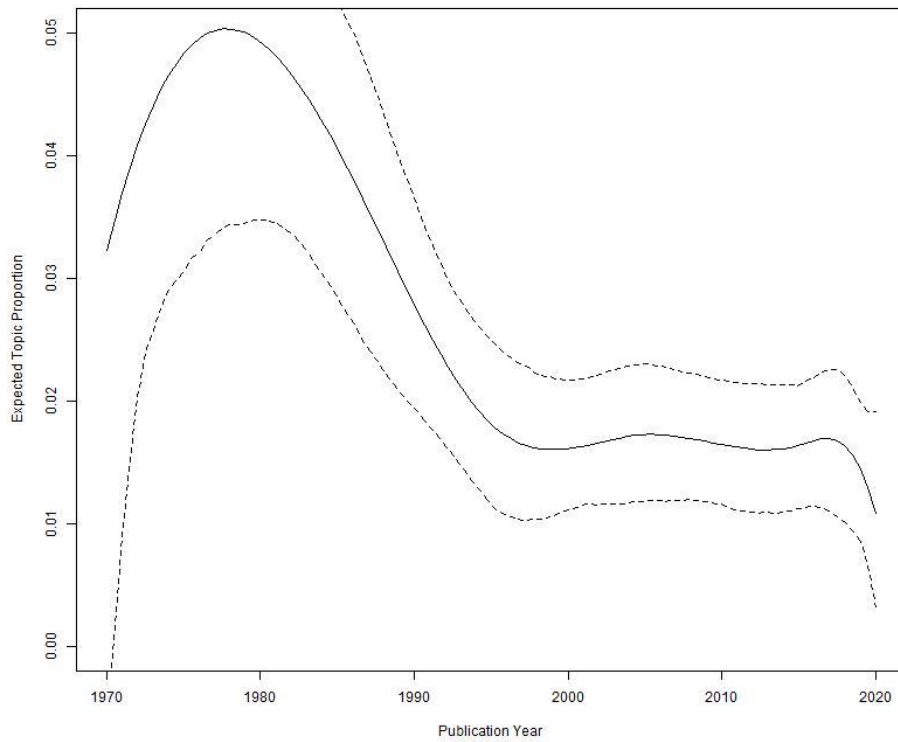
28 - Genetic Sequencing



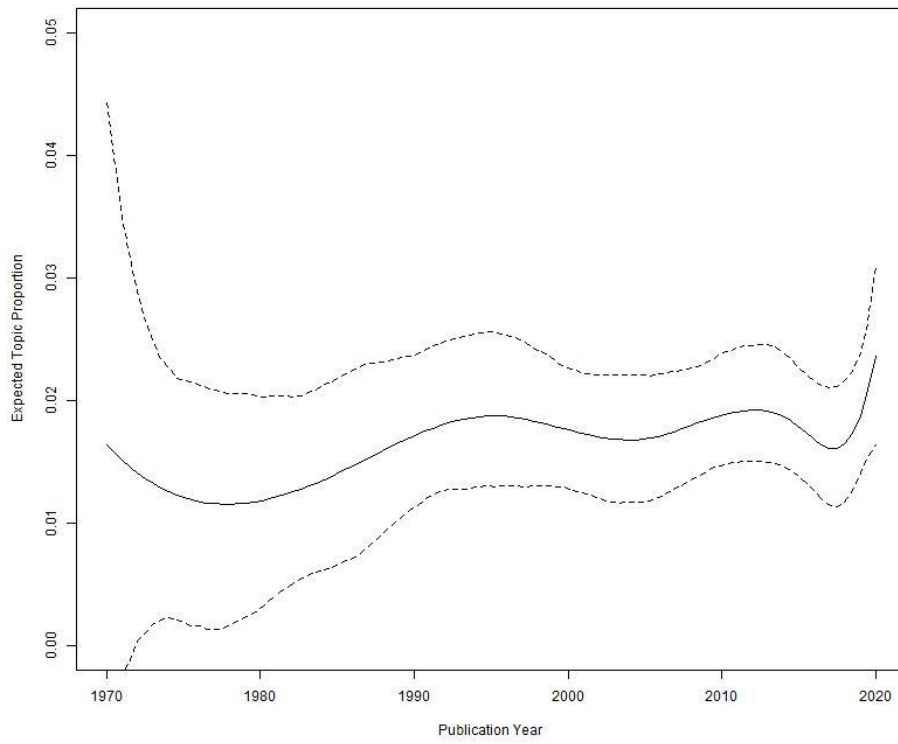
29 - Behavioral Budget



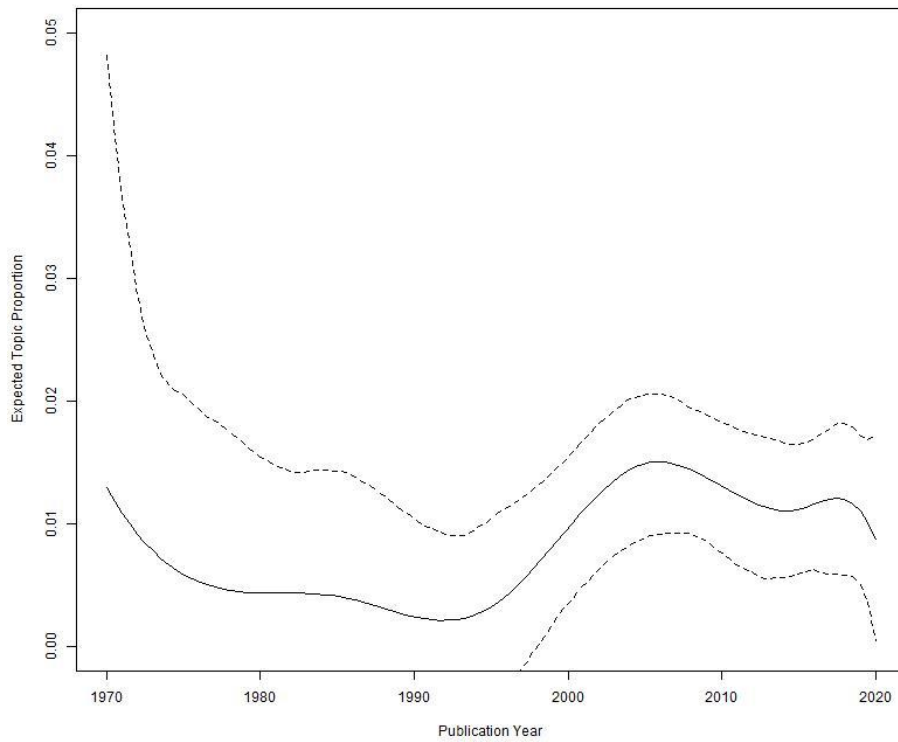
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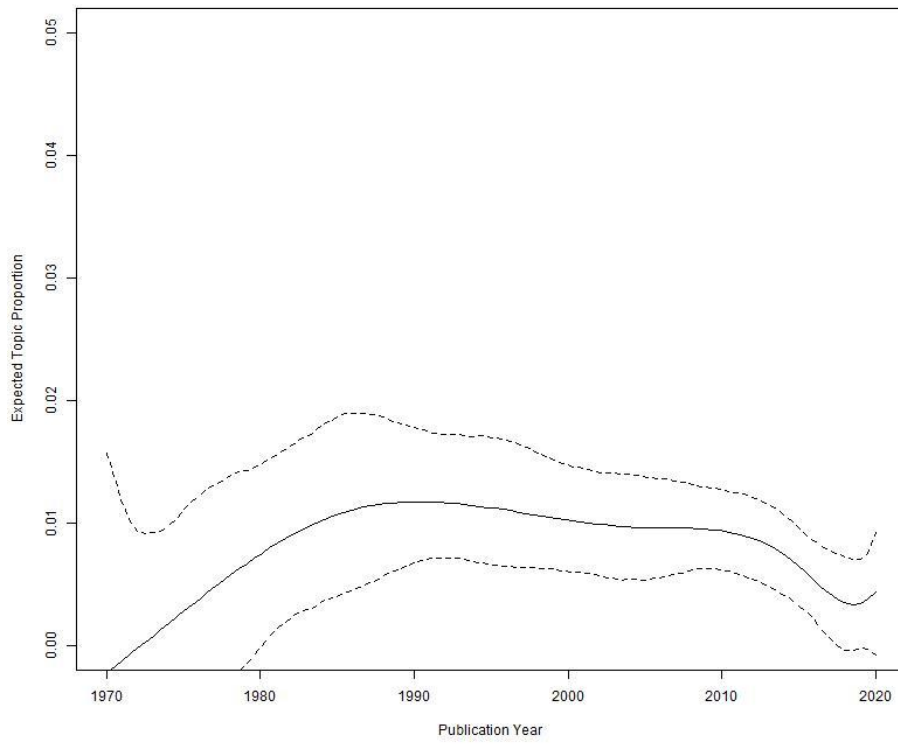
31 - Disease



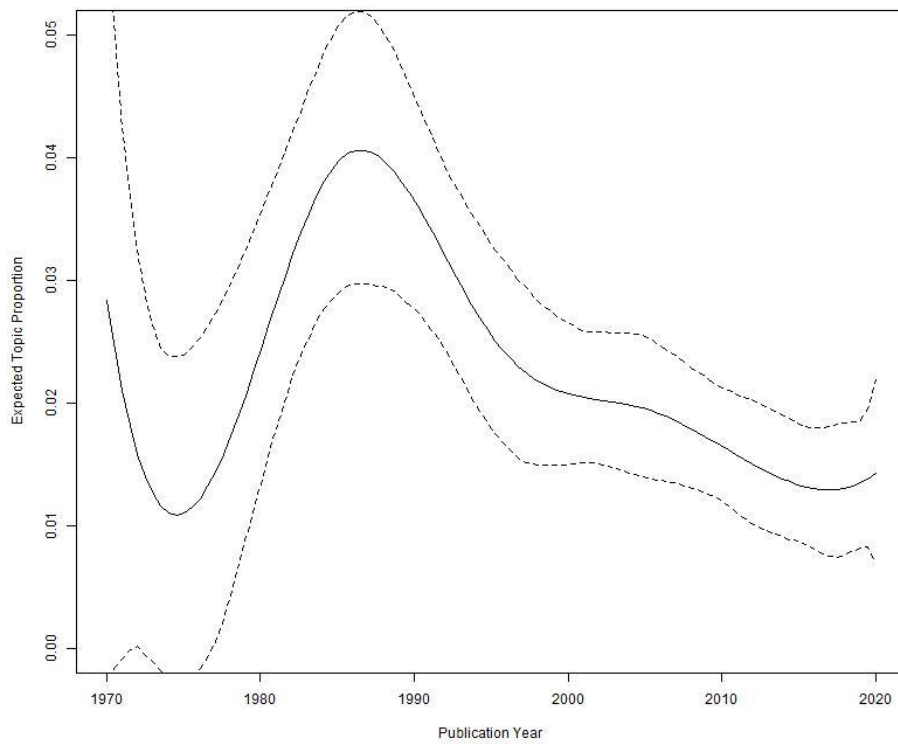
32 - Click



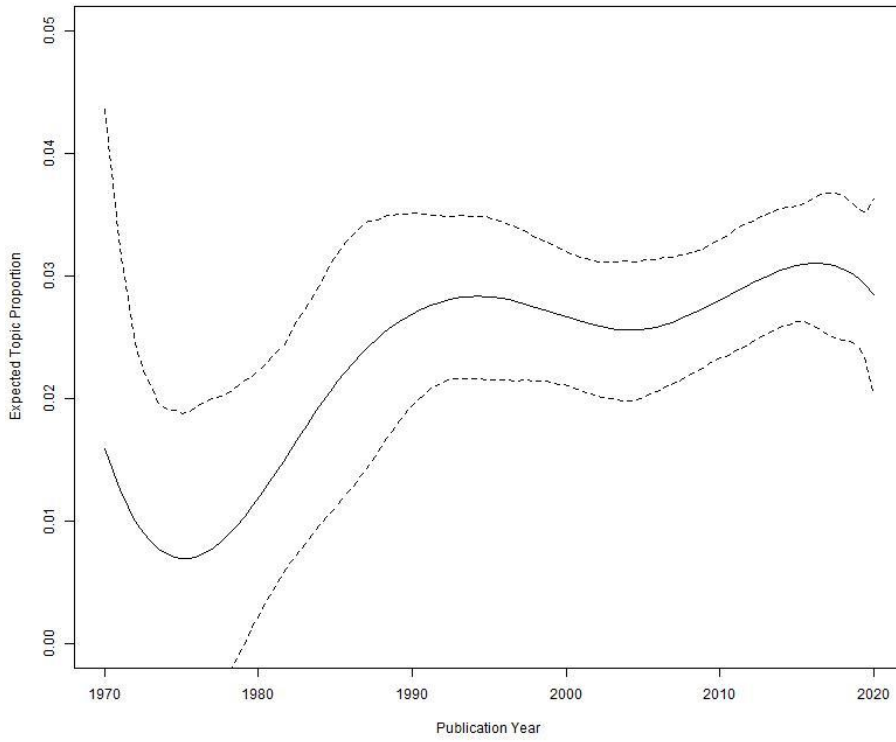
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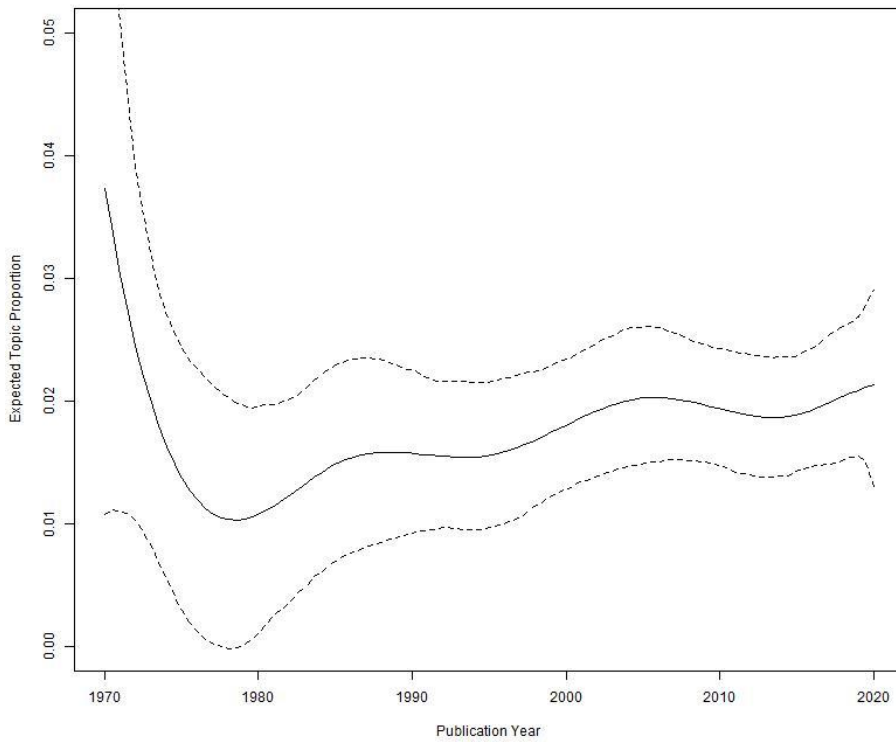
34 - Growth



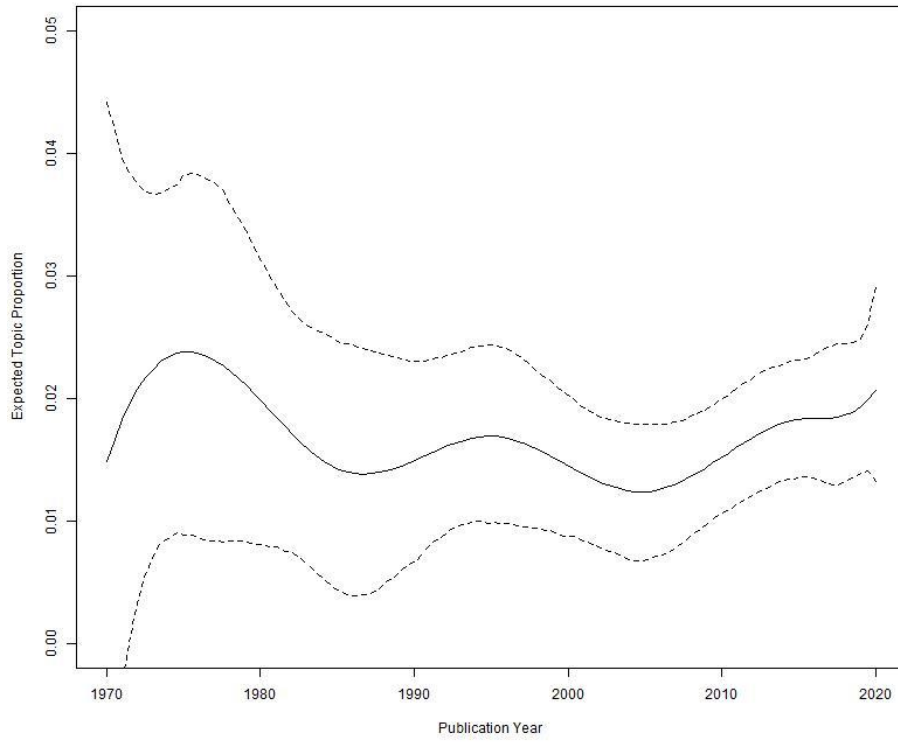
35 - Social Ecology



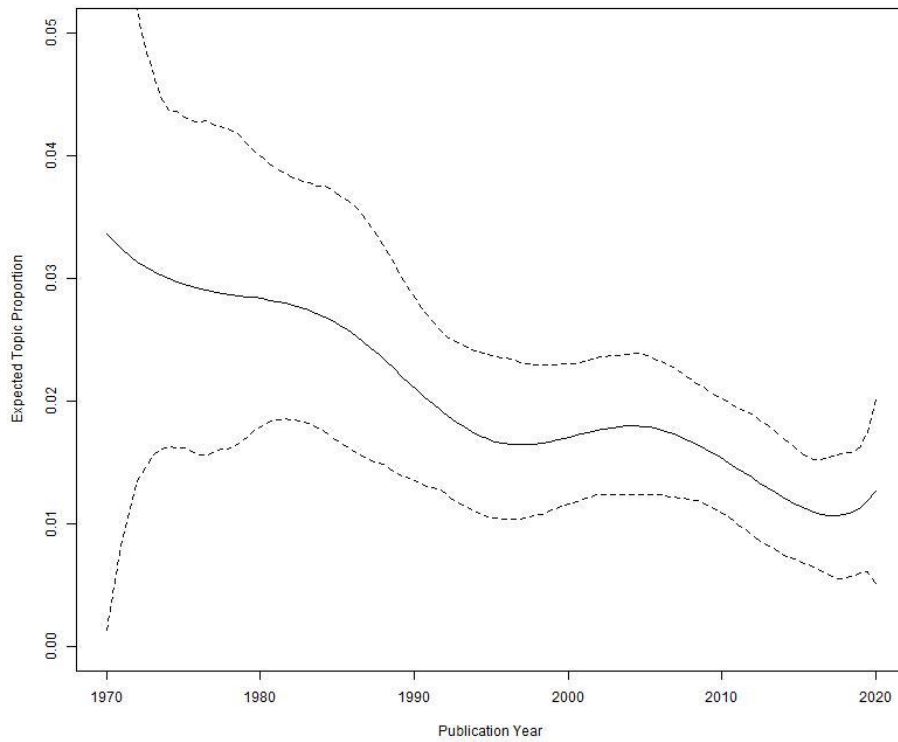
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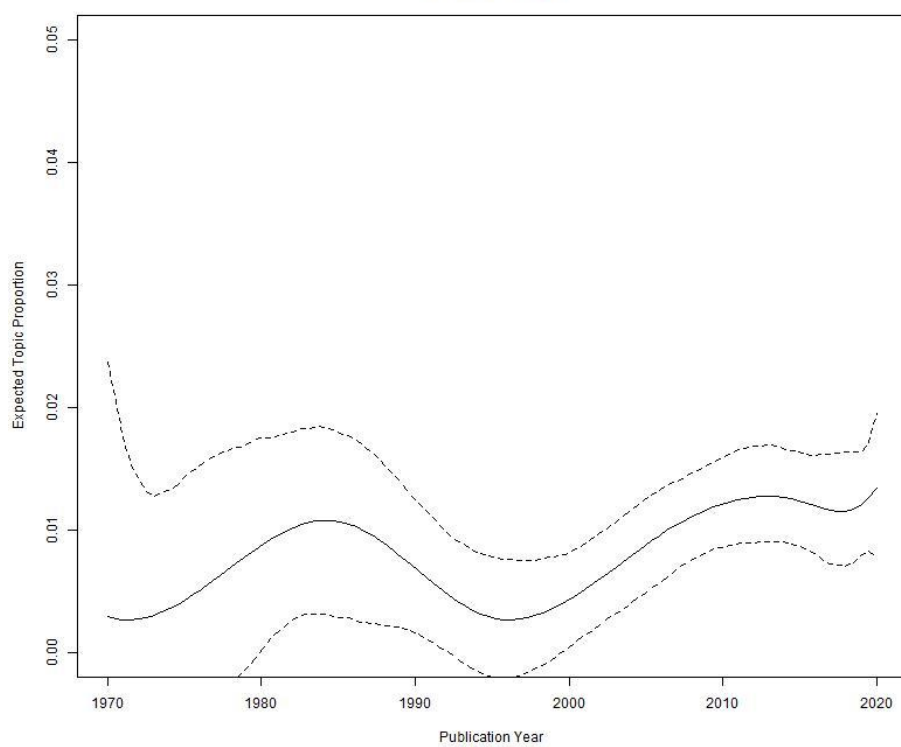
37 - Pathogen



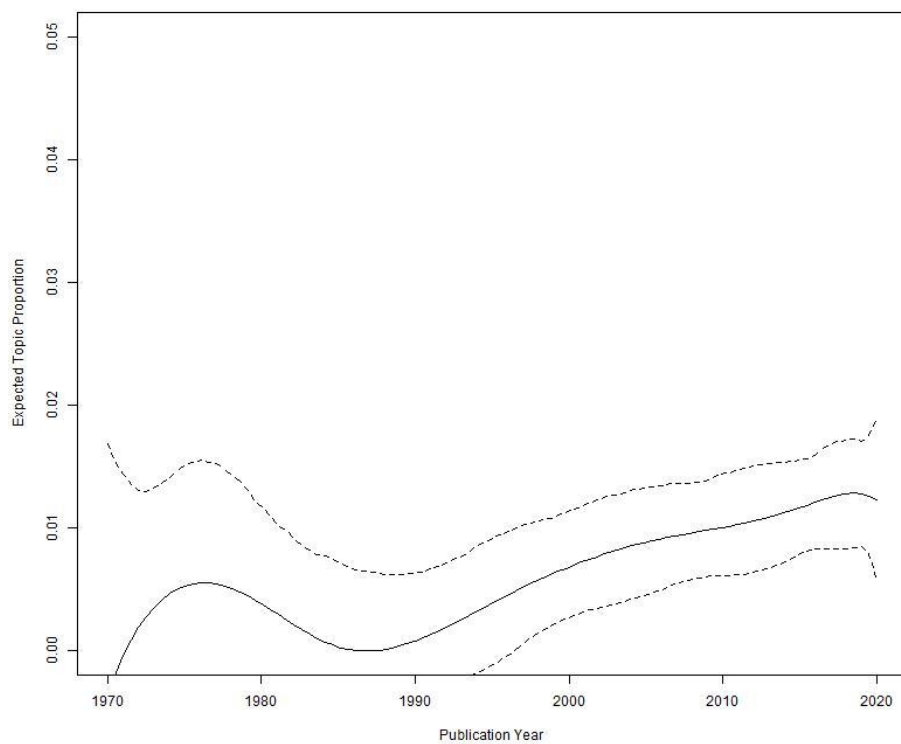
38 - Physiology



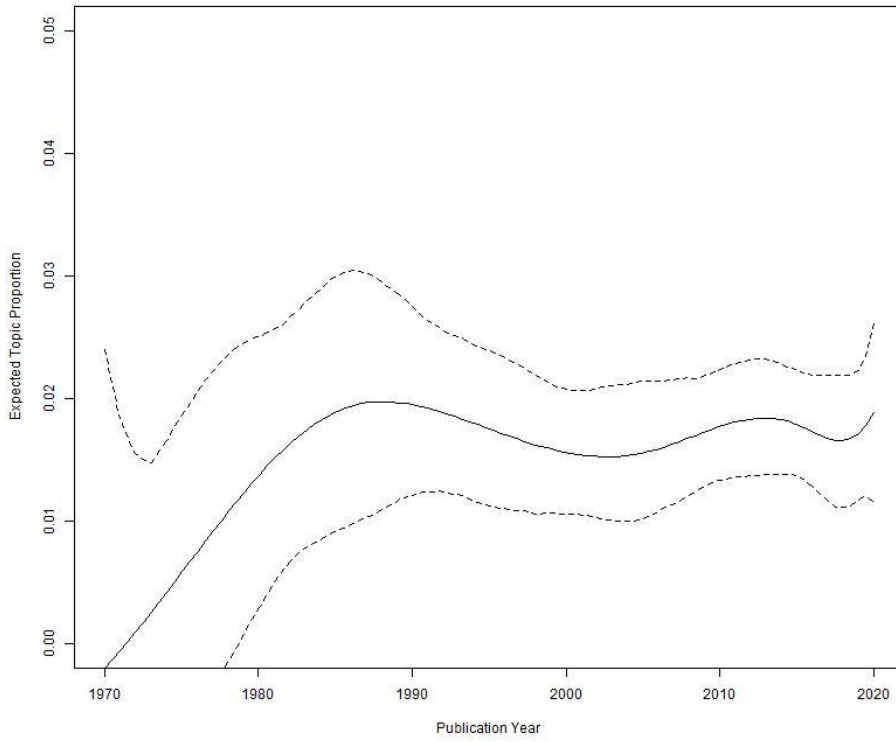
39 - Trophic Niche



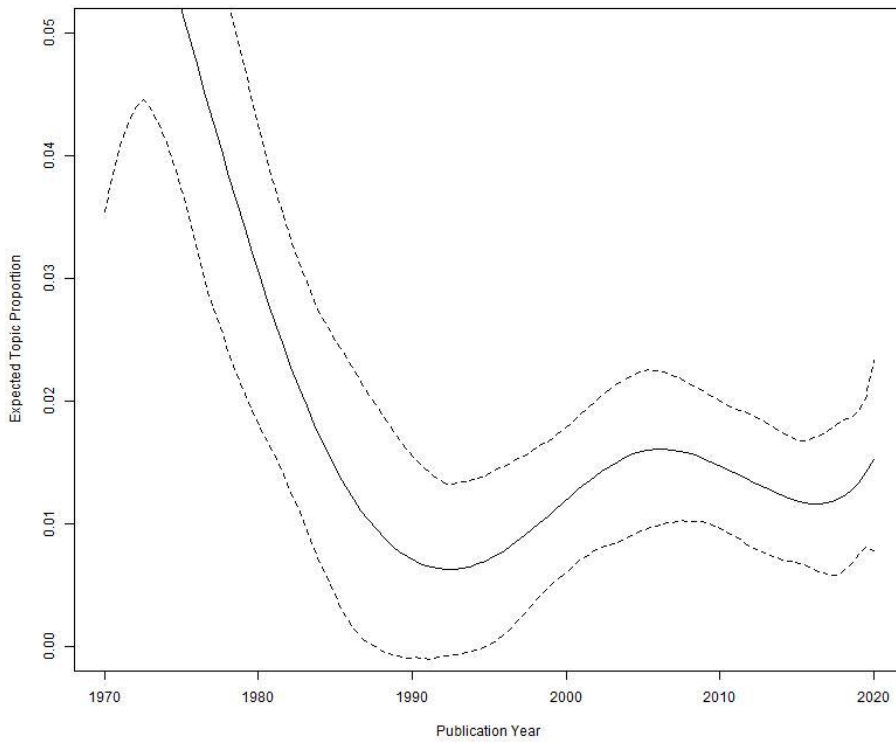
40 - Passive Acoustic Monitoring



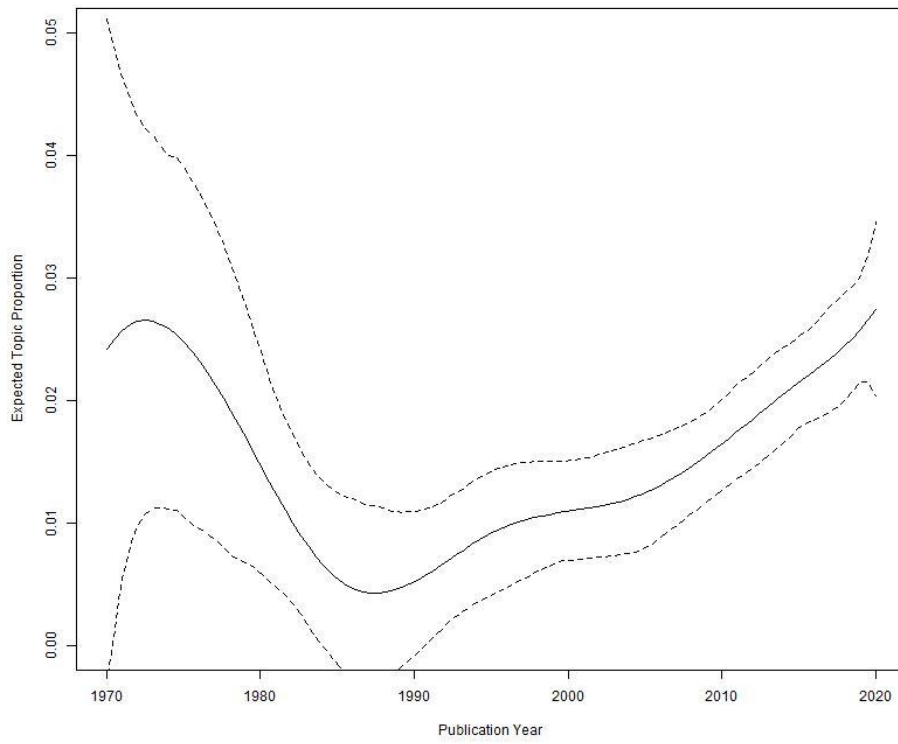
41 - Ocean/Geographic Region



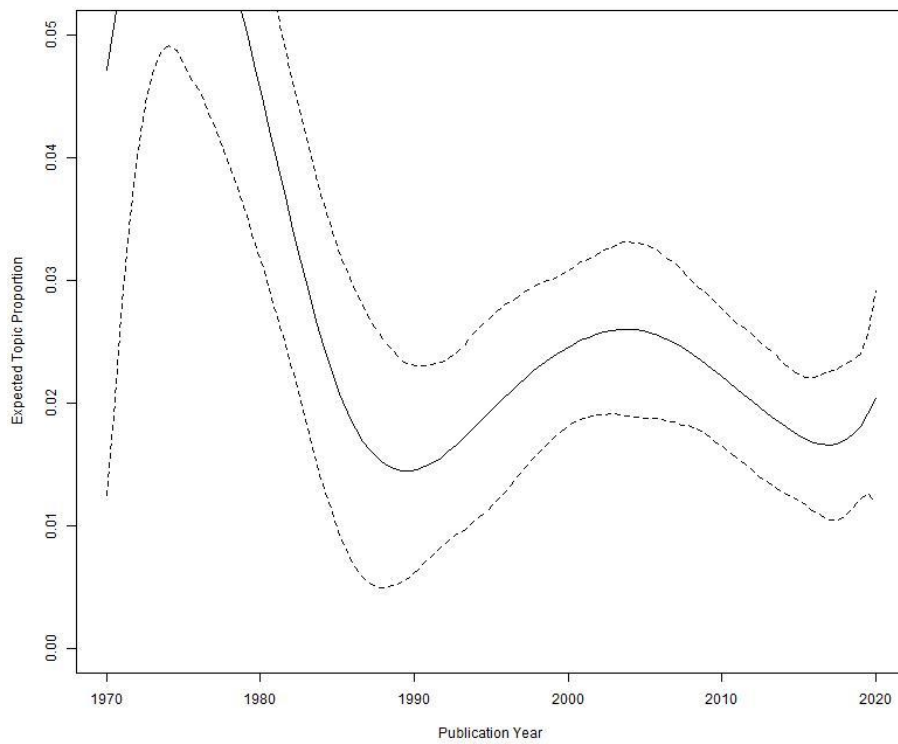
42 - Morphology



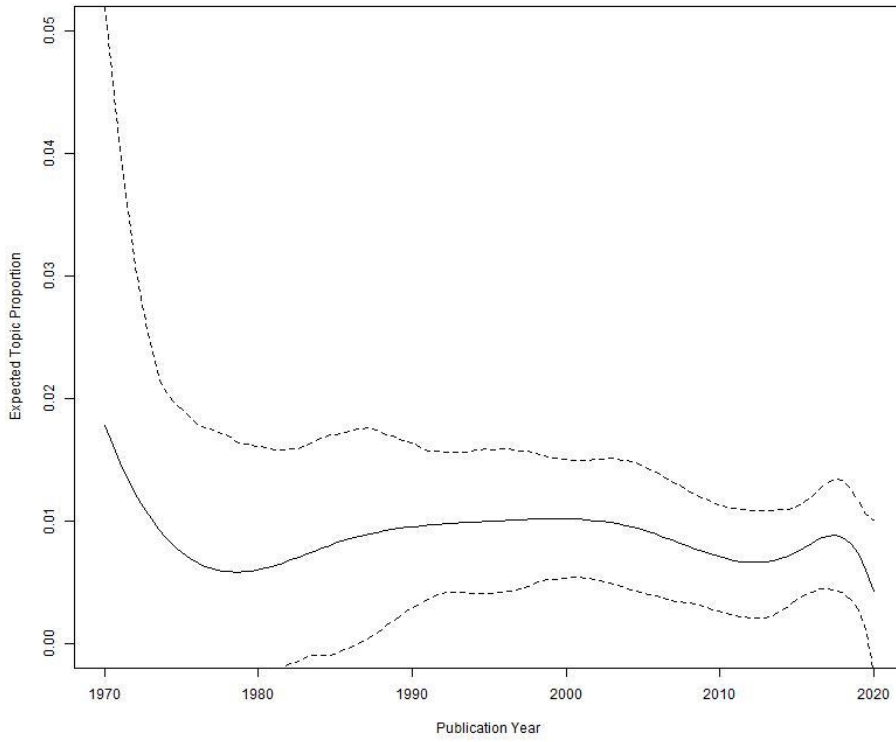
43 - Statistical modelling



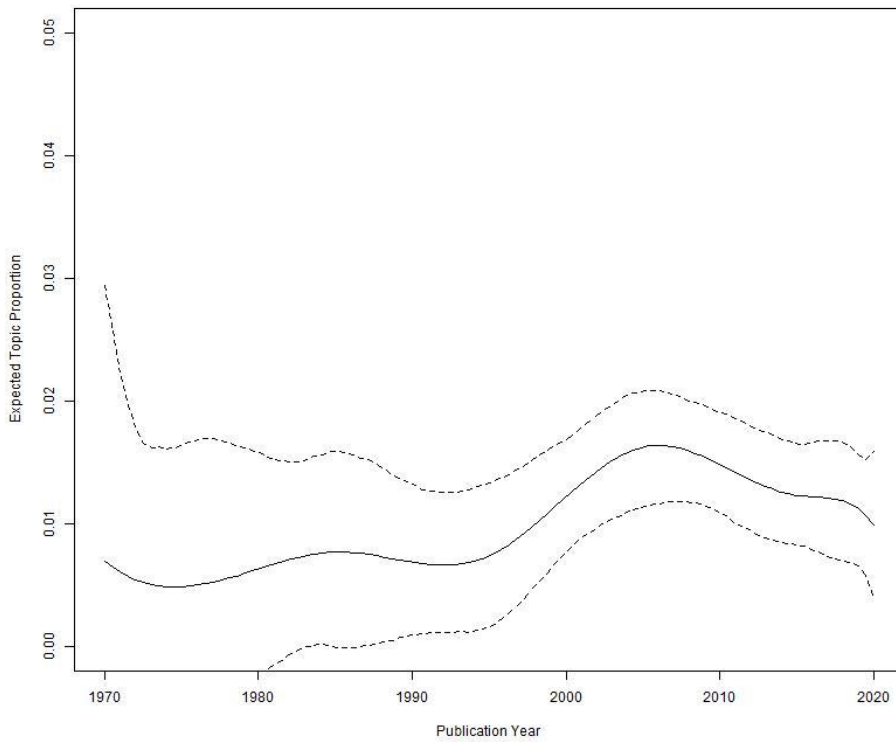
44 - Hearing - Frequency



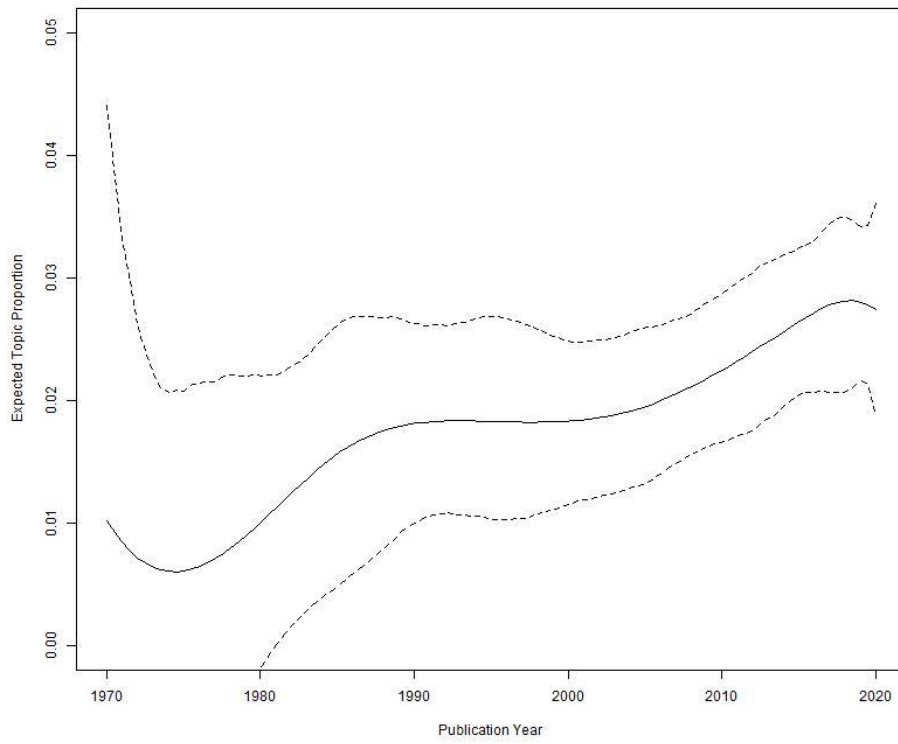
45 - Bone



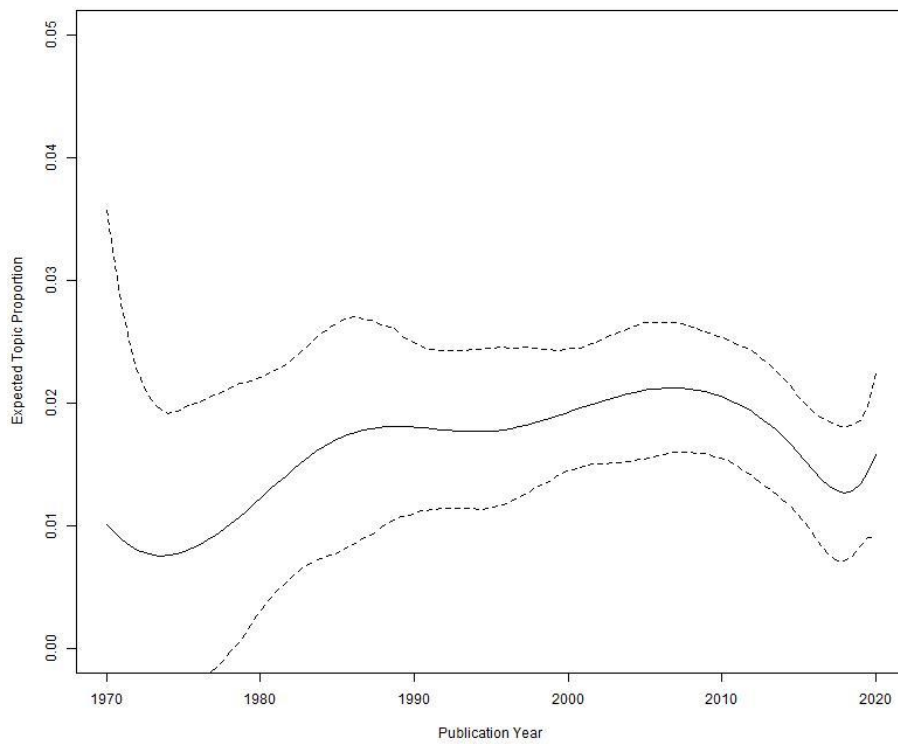
46 - Communication



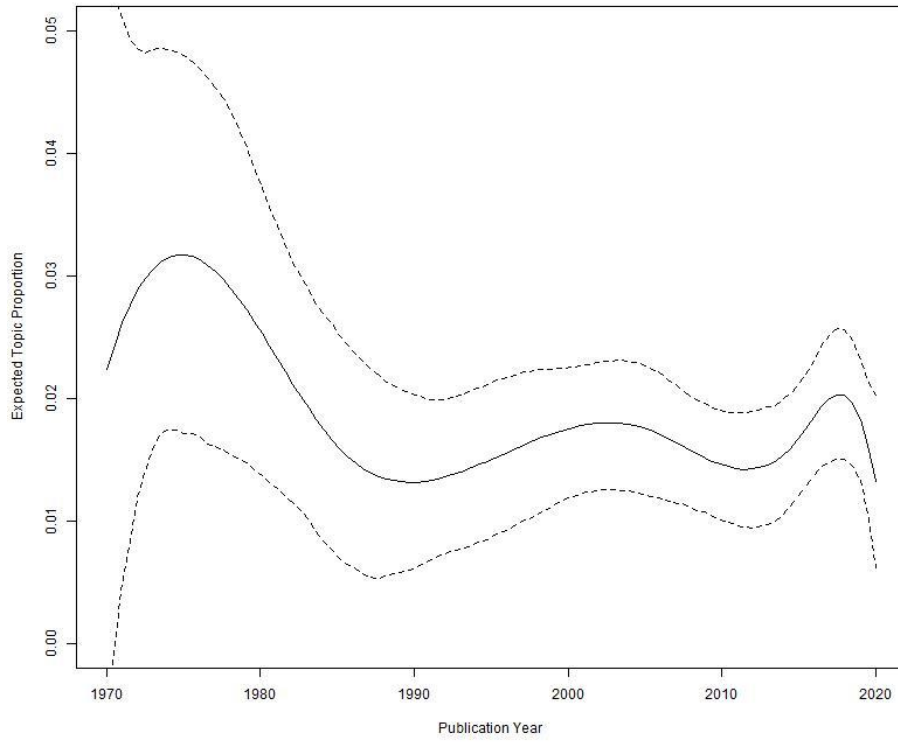
47 - Habitat Modelling



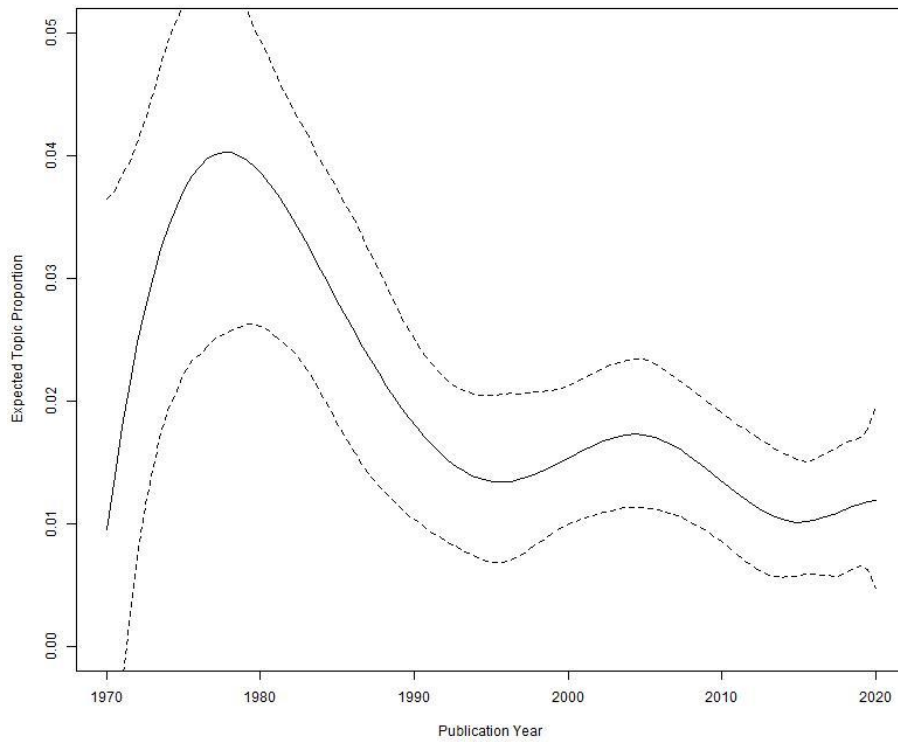
48 - Contaminants



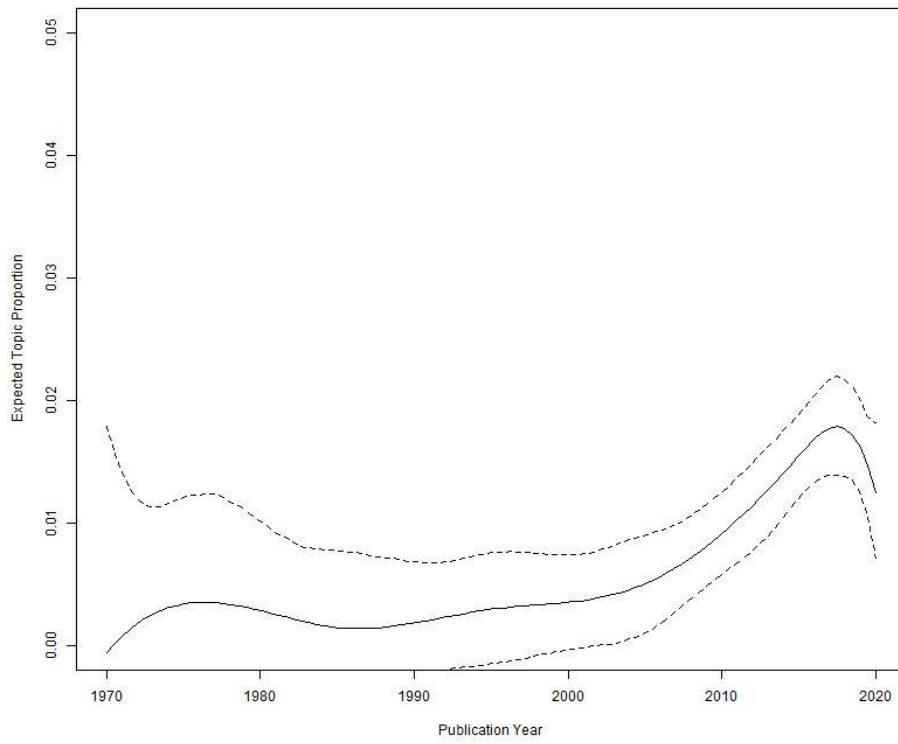
49 - Hearing - Amplitude



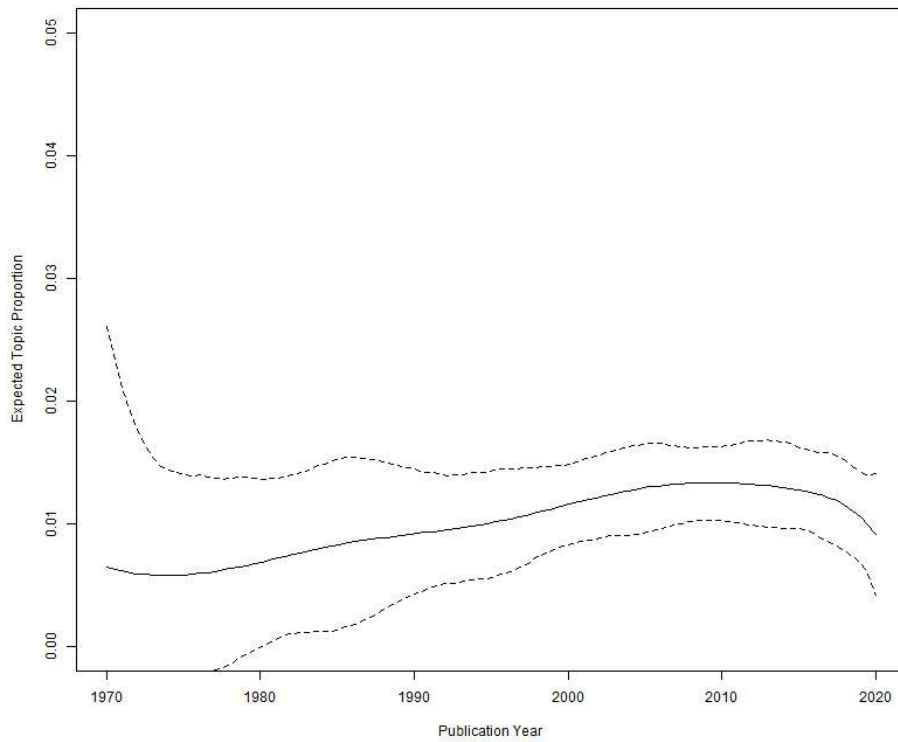
50 - Cardiovascular



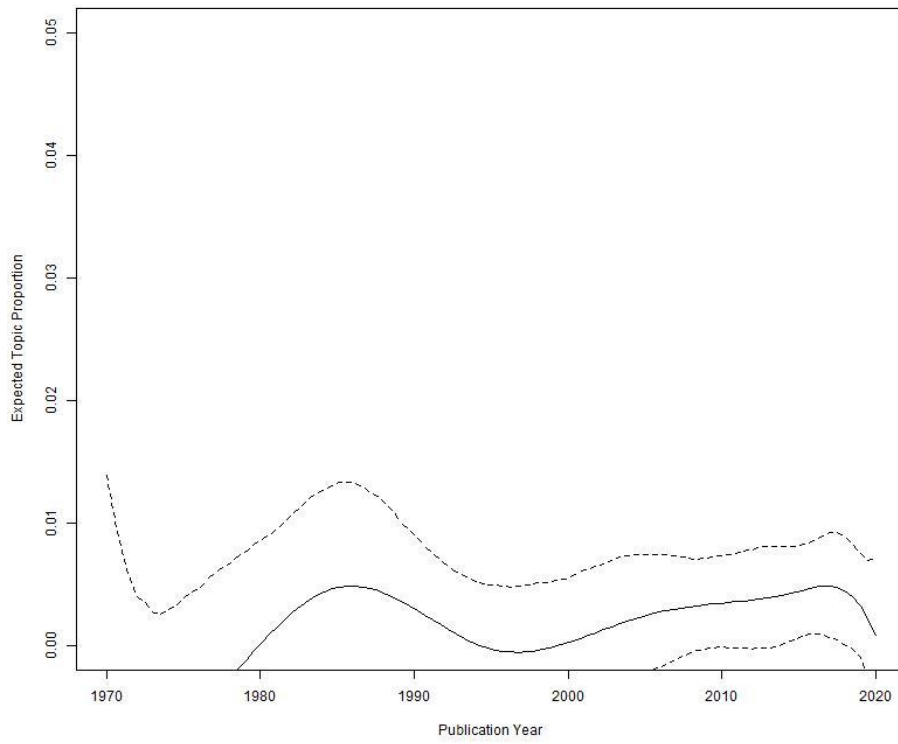
51 - Noise Impact



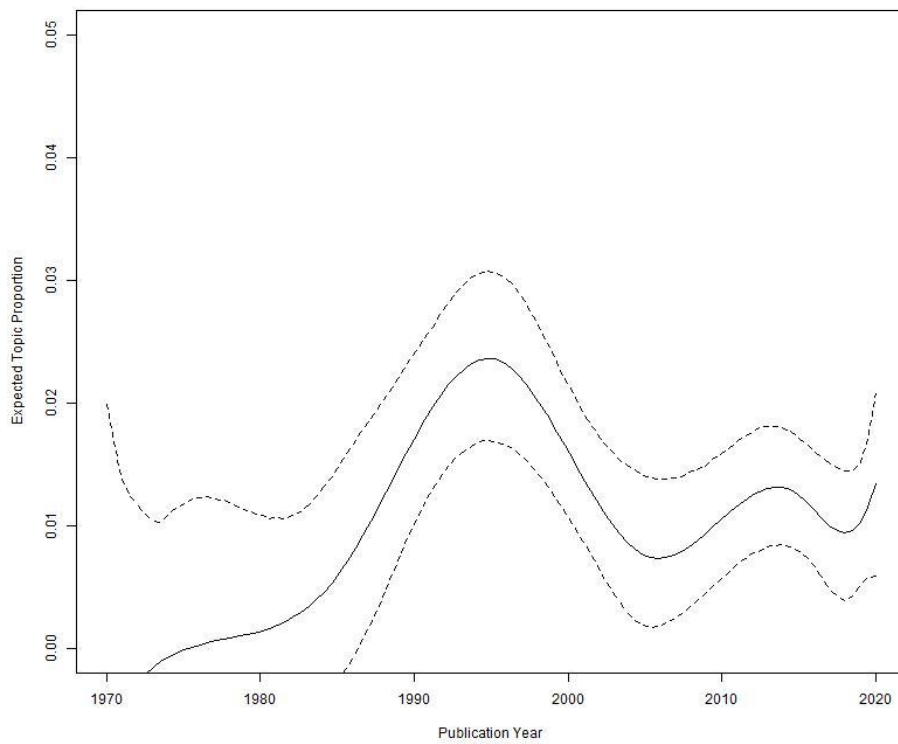
52 - Shark Interaction



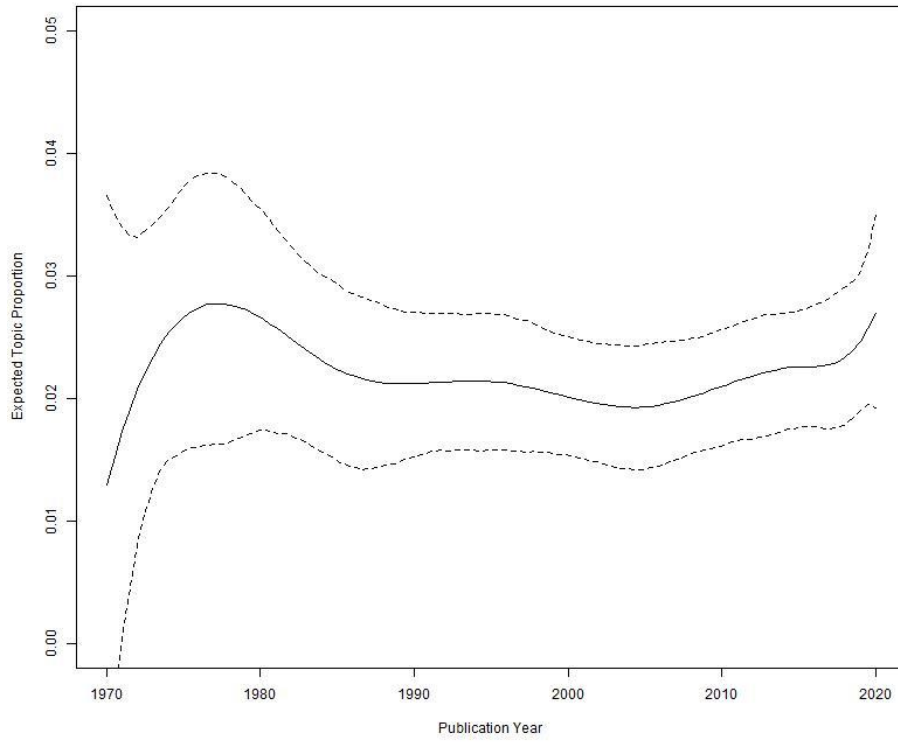
53 - Arctic Ecology



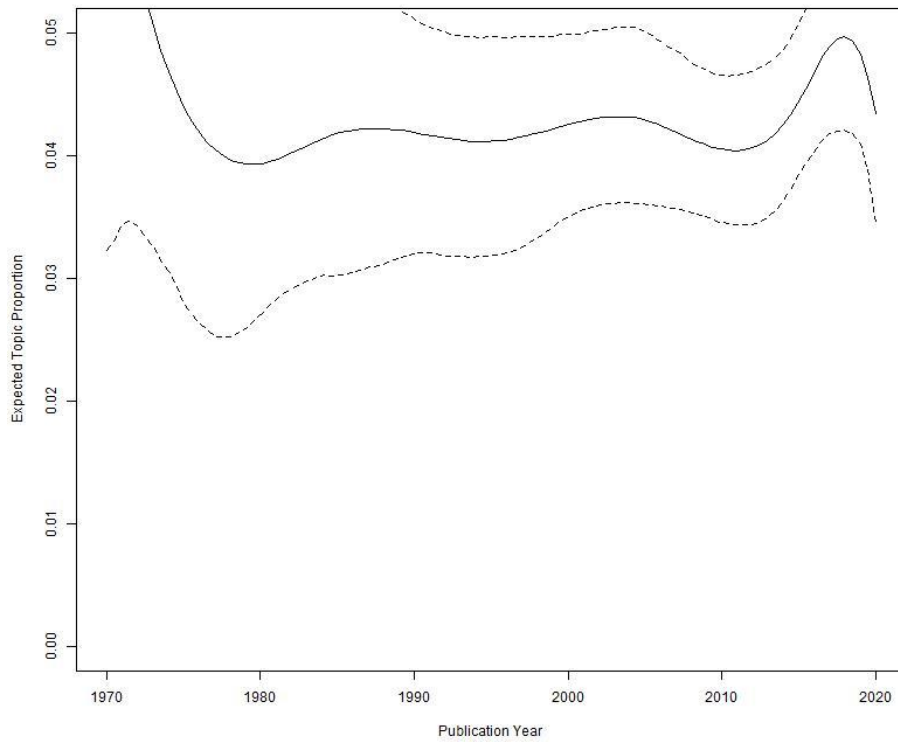
54 - Depredation



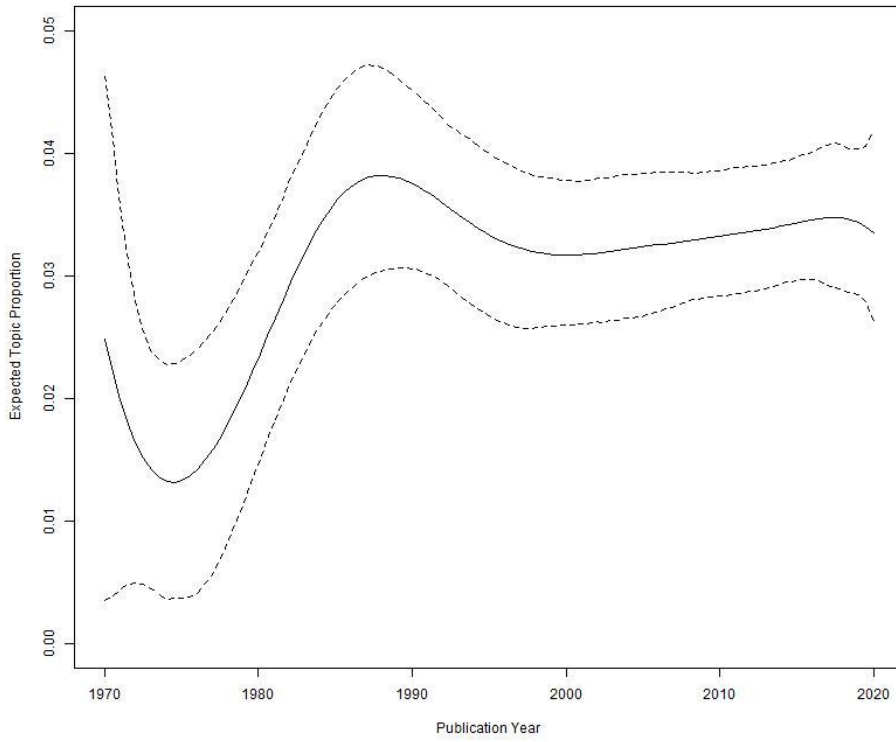
55 - Veterinary/Husbandry



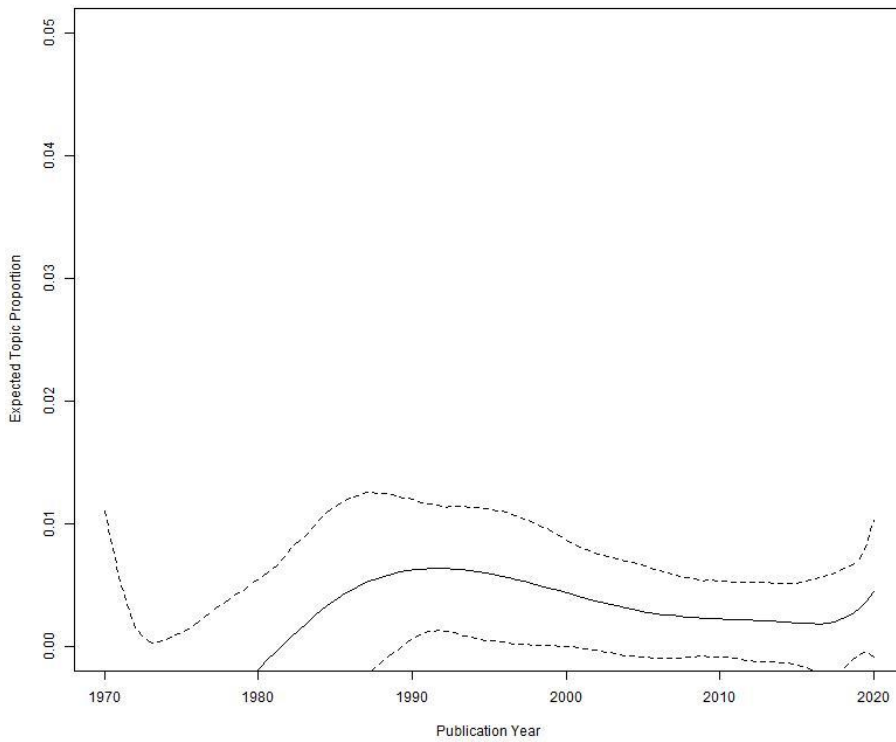
56 - Captive Behavior



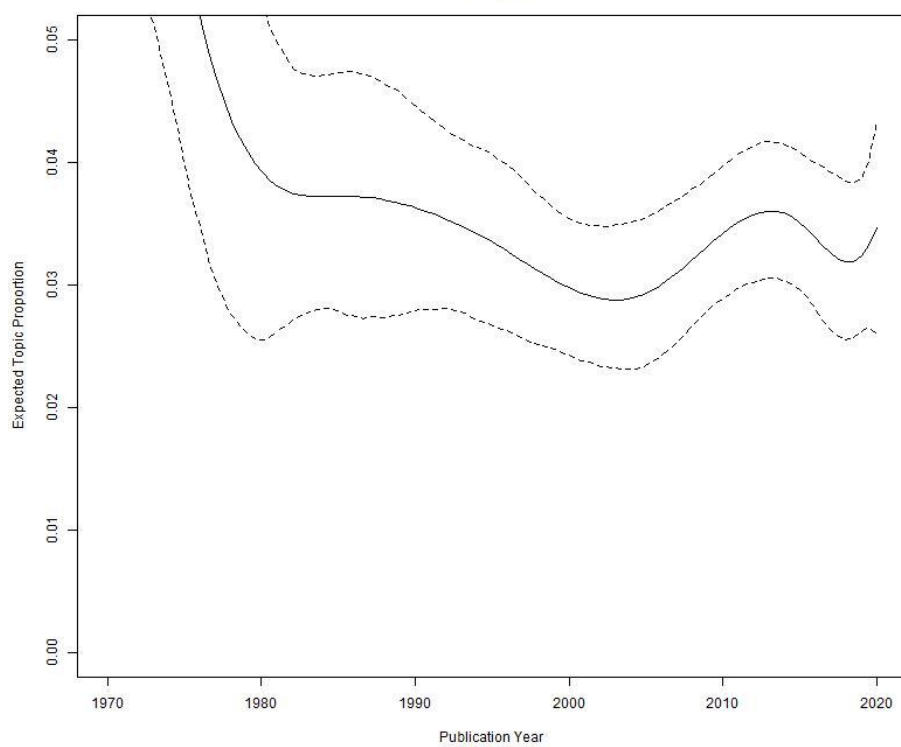
57 - Site Fidelity and Distribution



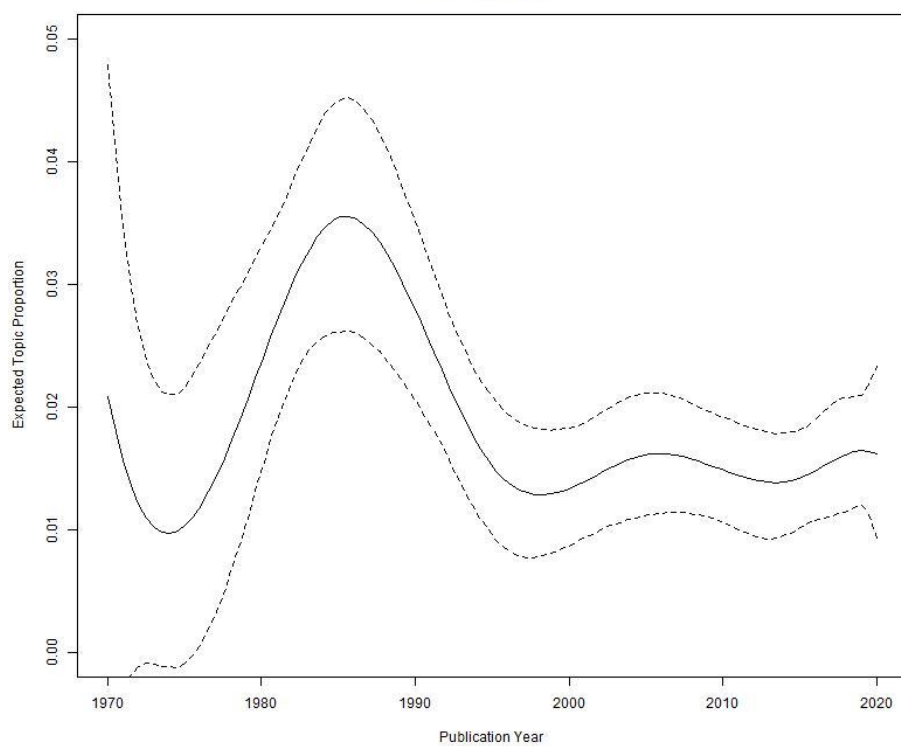
58 - Orca



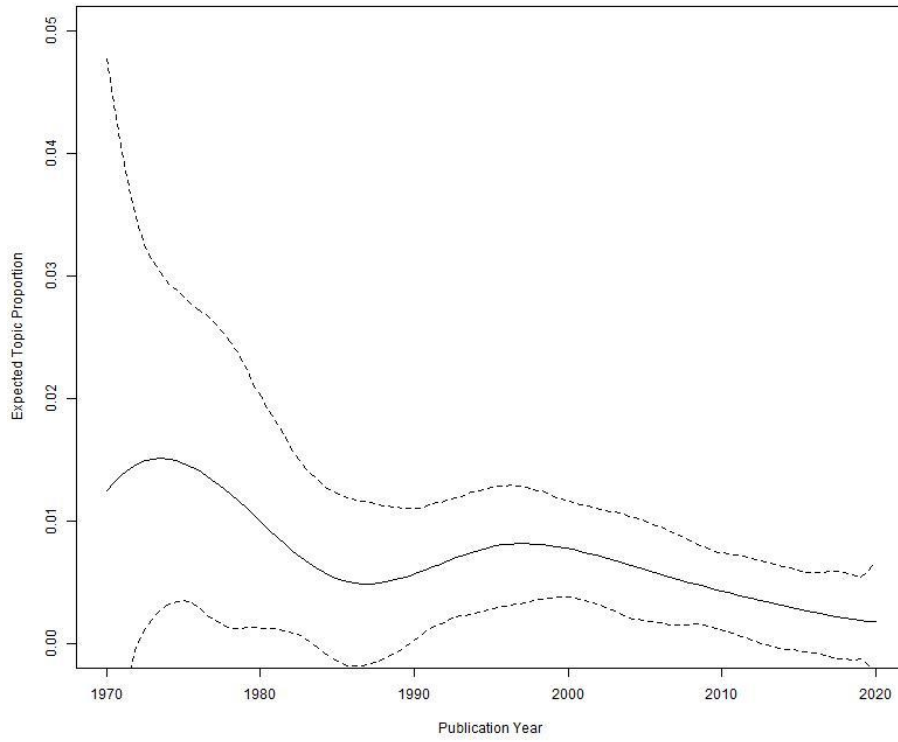
59 - Blood



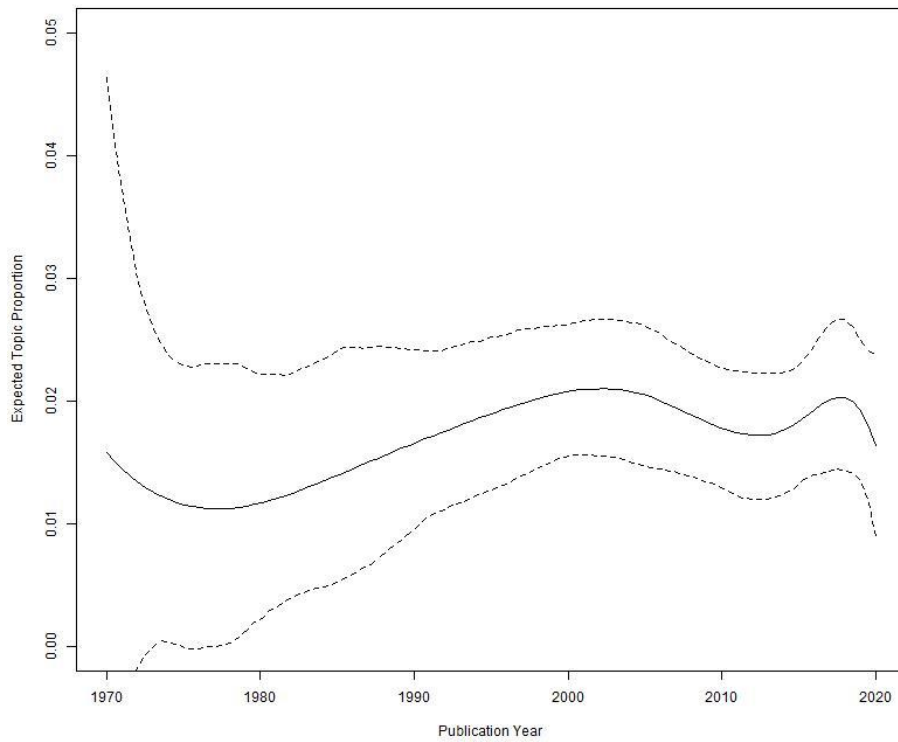
60 - Pregnancy



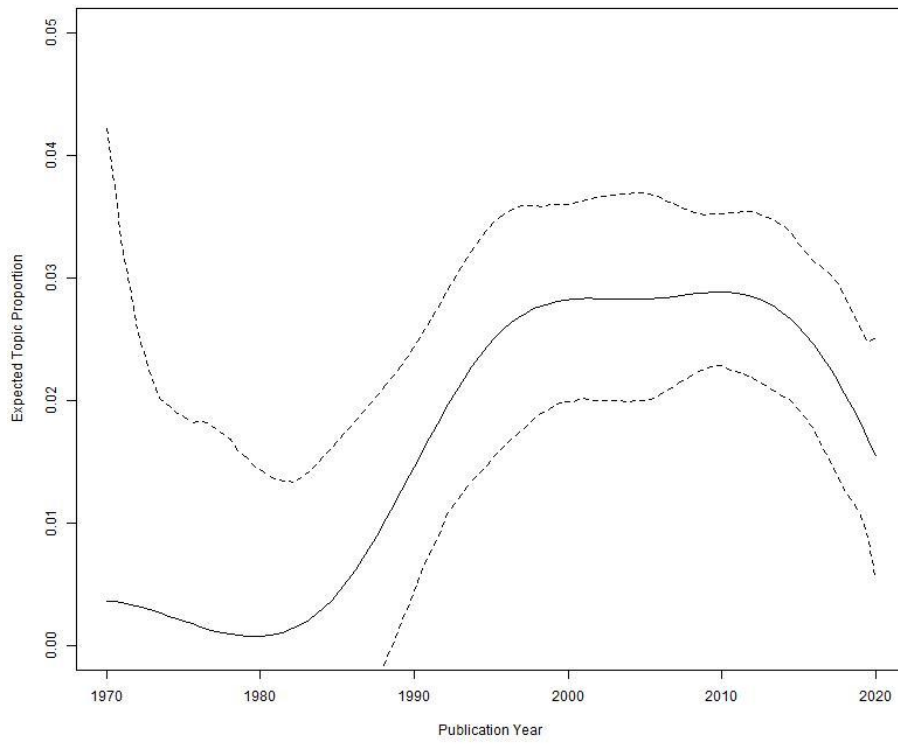
61 - Pinniped



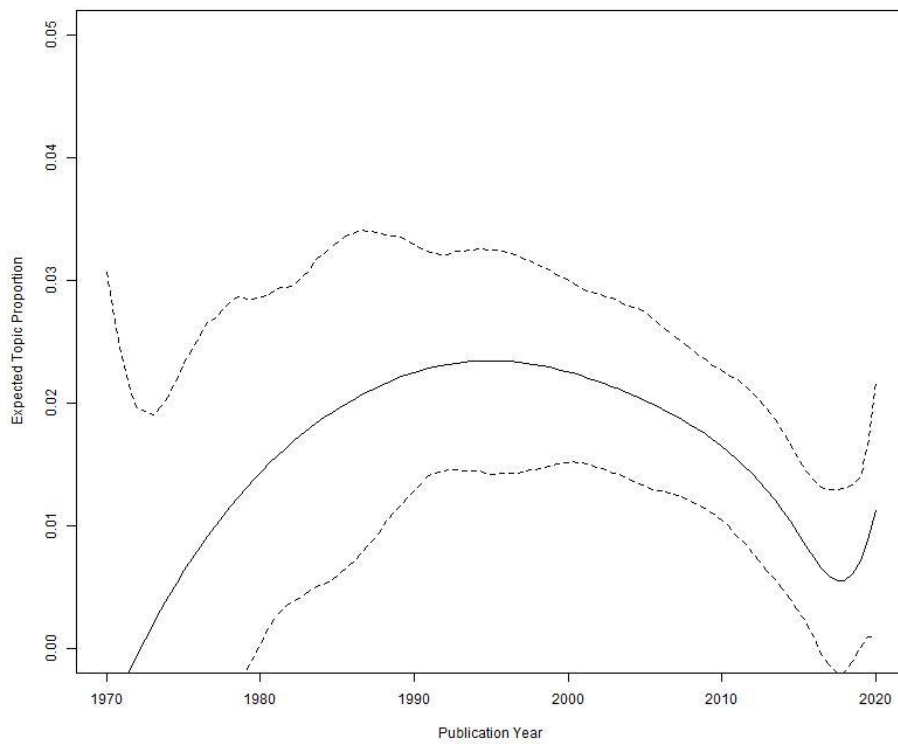
62 - Cellular



63 - Population Genetics



64 - PCBs



65 - Monodontidae

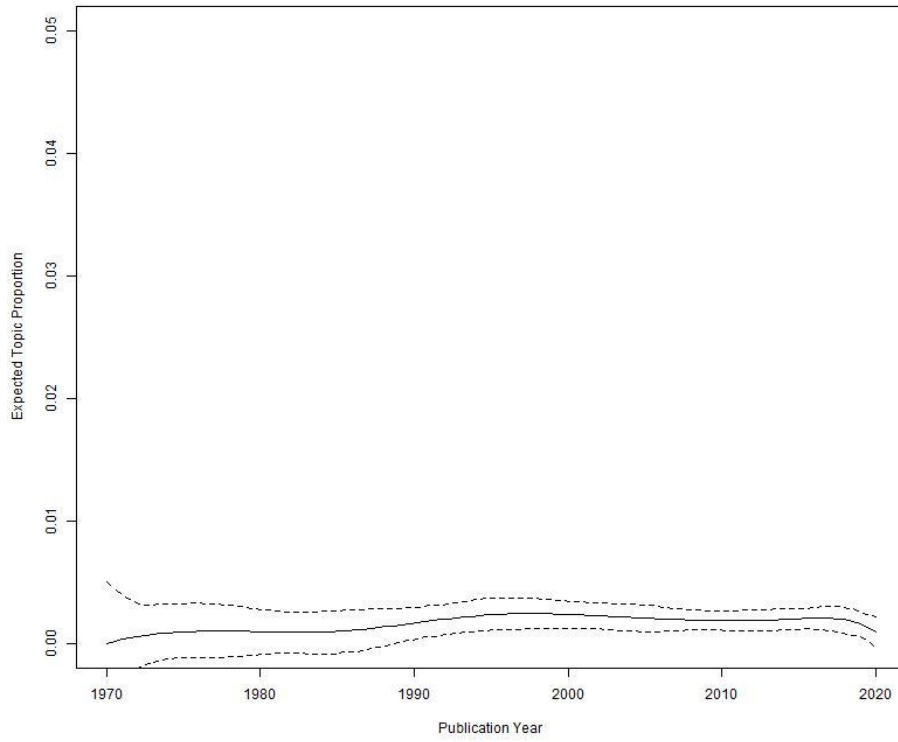


Table A19. Results of structural topic model of odontocete research abstracts, showing the 65 emergent topics, their expected proportion, mean selected and mean unselected weight, FREX keywords and exemplar abstracts. Topics are ordered by topic group and expected proportion, topic groups are ordered by expected group proportion.

Topic Group	Expected Group Proportion	Topic Theme	Keywords (FREX)	Expected Topic Proportion	Mean proportion when selected	Mean proportion when unselected	Exemplar Abstracts
Population Ecology and Genetics	29.75	Ocean/Geographic Region	ocean, south, tropic, brazil, north, pacif, africa	3.26	32.7	2.65	(Moreno et al. 2005, Paro et al. 2014)
		Habitat Modelling	season, spatial, habitat, canyon, oceanograph, slope, tidal	2.7	31.15	1.79	(Baumgartner et al. 2001, Di Tullio et al. 2016)
		Population Assessment	estim, abund, transect, densiti, aerial, survey, bias	2.55	35.7	1.66	(Barlow et al. 1988, Viquerat et al. 2014)
		Population Genetics	genet, haplotyp, mtdna, microsatellit, differenti, mitochondri, loci	2.53	45.49	0.97	(Gaspari et al. 2015, Ju et al. 2012)
		Statistical modelling	model, predict, variabl, appli, dynam, dataset, predictor	2.21	32.96	1.86	(Freitas et al. 2008, Isojunno et al. 2012)
		Site Fidelity and Distribution	coastal, fidel, site, inshor, home, bay, estuarin	2.15	29.62	1.54	(Bertulli et al. 2015, Rossi-Santos et al. 2007)
		Taxonomy	fossil, miocen, genus, delphinida, extant, phylogenet, clade	2.1	50.24	1.07	(Nelson & Uhen 2020, Perrin et al. 2013)

		Cetacean	balaenoptera, physalus, novaeanglia, megaptera, sight, mink, acutorostrata	2.06	37.8	1.23	(Di Sciara et al. 1993, Kiszka et al. 2007)
		Genetic Sequencing	genom, gene, sequenc, mhc, clone, amino, amplifi	1.9	46.28	0.77	(Inoue et al. 2000, Inoue et al. 1999)
		Seasonality	juli, island, june, august, septemb, april, octob	1.74	26.29	1.57	(Baird et al. 2013, Frost et al. 1993)
		Dive Behaviour	dive, swim, depth, speed, breath, min, deep	1.74	44.33	0.87	(Martin & Smith 1999, Skrovan et al. 1999)
		Lab Methodology	method, techniqu, hybrid, number, standard, repeat, accur	1.7	33.16	1.52	(O'Brien & Robeck 2010, Robeck et al. 2011)
		Movement	tag, movement, satellit, track, move, releas, transmitt	1.09	35.06	0.76	(Stone et al. 1998, Whitehead 2016)
		Shark Interaction	photograph, mark, scar, fin, shark, bite, pigment	1.09	35.91	0.7	(Dwyer & Visser 2011, Wcisel et al. 2010)
		Mortality Event	mexico, gulf, event, bloom, florida, mississippi, usa	0.93	34.64	0.79	(Fire et al. 2015, Fire et al. 2011)
Biochemistry and Cellular	12.04	Heavy Metal	mercuri, liver, kidney, metal, selenium, element, trace	2.26	50.77	0.82	(Paludan-Müller et al. 1993, Yang et al. 2007)
		PCBs	pcbs, pcb, ddt, pop, polychlorin, organochlorin, biphenyl	1.69	42.65	0.5	(Stockin et al. 2010, Tanabe et al. 1982)
		Cellular	immun, express, cypa, vitro, cell, induc, transcript	1.25	41.63	0.57	(Garrick et al. 2006, Miller et al. 2000)
		Pollution/Oil Spill	risk, pollut, oil, health, spill, pah, pre	1.23	30.08	1.02	(Lundin et al. 2018, Wise Jr et al. 2018)

		Blood	blood, plasma, hematolog, hemoglobin, serum, urin, healthi	1.23	48.82	0.59	(Cornell 1983, Koopman et al. 1999)
		Contaminants	irl, ngg, pfos, wet, pbde, lagoon, compound	1.22	45.97	0.55	(Houde et al. 2009, Moon et al. 2010)
		Protein	myoglobin, peptid, residu, fraction, bind, protein, enzym	1.13	59.83	0.49	(Jones et al. 1978, Jones et al. 1979)
		Blubber	fatti, acid, fat, lipid, blubber, ester, composit	1.04	52.47	0.48	(Bagge et al. 2012, Varanasi & Malins 1971)
		Endocrinology	hormon, stress, cortisol, ngml, testosteron, temperatur, serum	0.99	46.64	0.48	(Schmitt et al. 2010, Suzuki et al. 1998)
Bioacoustics	8.93	Click	click, puls, echoloc, train, buzz, interclick, signal	1.65	45.51	0.75	(Li et al. 2007, Wahlberg et al. 2011)
		Hearing - Frequency	hear, threshold, khz, sensit, mask, audiogram, frequenc	1.5	49.86	0.67	(Kastelein et al. 2003, Lemonds et al. 2012)
		Biosonar	echo, beam, target, aep, horizont, vertic, plane	1.37	51.03	0.65	(Au & Turl 1983, Turl et al. 1991)
		Passive Acoustic Monitoring	passiv, acoust, alarm, deploy, hydrophon, monitor, detect	1.28	33.2	0.85	(Freitag & Tyack 1993, Garrod et al. 2018)
		Sound Playback	sound, tts, receiv, pressur, sonar, exposur, playback	1.25	43.96	0.77	(Kastelein et al. 2016, Kastelein et al. 2013)
		Hearing - Amplitude	abr, stimuli, amplitud, evok, auditori, modul, wave	0.98	49.62	0.56	(Dolphin 1996, Popov et al. 2018)
		Noise Impact	disturb, farm, nois, pile, drive, ship, anthropogen	0.9	38.21	0.58	(Brandt et al. 2011, Paiva et al. 2015)

Conservation and Management	8.79	Conservation and Management	conserv, manag, protect, inform, knowledg, futur, critic	3.27	28.77	2.7	(Alessi et al. 2019, IJsseldijk et al. 2018)
		Bycatch	bycatch, gillnet, incident, net, baltic, fisheri, catch	1.74	38.53	0.97	(Lowry & Teilmann 1994, Reyes & Van Waerebeek 1995)
		Riverine Ecology	yangtz, lake, freshwat, river, china, amazon, reserv	1.52	41.62	0.86	(Xia 1994, XIANG et al. 2006)
		Depredation	depred, longlin, fish, fishermen, gear, hook, interact	1.22	42.22	0.72	(Peterson et al. 2014, Rabearisoa et al. 2012)
		Mitigation	pinger, fisher, econom, regul, implement, scenario, govern	1.04	35	0.74	(Omeyer et al. 2020, Smith et al. 2008)
Health and Disease	8.4	Strandings	strand, death, carcass, dead, beach, report, die	1.96	28.47	1.5	(IJsseldijk et al. 2015, Jeyabaskaran et al. 2018)
		Disease	lesion, patholog, thyroid, diseas, pulmonari, chronic, pneumonia	1.66	33.3	0.95	(Jepson et al. 2000, Turnbull & Cowan 1999)
		Virology	morbillivirus, virus, gondii, antibodi, herpesvirus, antigen, epizoot	1.27	41.72	0.49	(Alekseev et al. 2009, Van Bressemer et al. 1998)
		Veterinary/Husbandry	resist, respiratori, captiv, wild, diagnost, aquarium, antibiot	1.21	35.32	0.84	(McLaughlin et al. 2013, Zamuruyev et al. 2016)
		Pathogen	brucella, pathogen, isol, strain, fungal, spp, ceti	1.16	43.61	0.62	(Davison et al. 2013, Garofolo et al. 2014)
		Parasite	anisaki, nematod, parasit, simplex, helminth, host, intestin	1.14	42.46	0.44	(Fernández et al. 2004, Herreras et al. 1997)

Life History and Social Ecology	8.2	Growth	matur, age, length, growth, sexual, bodi, year	2	37.92	1.32	(Calzada et al. 1997, Santos et al. 2003)
		Social Ecology	social, associ, clan, network, communiti, cluster, unit	1.97	42.18	1.07	(Elliser & Herzing 2012, Gero et al. 2015)
		Reproduction	male, femal, allianc, juvenil, mate, sex, adult	1.76	30.41	1.52	(Connor et al. 1992, Wallen et al. 2016)
		Reproductive Success	calv, calf, mother, surviv, birth, neonat, infant	1.52	34.87	0.99	(Karniski et al. 2018, Teixeira et al. 2018)
		Pregnancy	pregnanc, pregnant, progesteron, reproduct, lactat, gestat, cycl	0.95	43.89	0.56	(Robeck et al. 2018, Robeck et al. 2016)
Physiology	7.08	Morphology	skull, charact, cranial, shape, morpholog, morphometr, flipper	1.75	40.89	0.98	(Guidarelli et al. 2014, Mikkelsen & Lund 1994)
		Phsyiology	gland, fiber, microscopi, electron, nerv, microscop, optic	1.49	45.21	0.75	(Ortiz et al. 2009, Tarpley et al. 1994)
		Cardiovascular	arteri, anatom, anatomi, heart, imag, thorac, fold	1.36	43.44	0.73	(Perez & Lima 2006, Vogl & Fisher 1981)
		Bone	bone, nasal, teeth, miner, melon, head, rostrum	1.34	44.29	0.74	(Currey et al. 2001, Zioupos et al. 1997)
		Brain	neuron, brain, cortex, cortic, layer, lobe, later	1.14	60.39	0.47	(Glezer et al. 1993, Morgane et al. 1980)
Behaviour	5.75	Captive Behaviour	behavior, object, welfar, contact, eye, aggress, play	2.24	47.32	1.11	(Ikeda et al. 2018, Yamamoto et al. 2019)

		Behavioural Budget	behaviour, rest, budget, night, travel, forag, diel	1.26	30.51	1.03	(Degradi et al. 2008, Filby et al. 2013)
		Foraging	school, seabird, herring, attack, feed, aggreg, norwegian	1.14	32.5	0.79	(Oliveira et al. 2013, Vaughn-Hirshorn et al. 2013)
		Vessel Response	boat, watch, vessel, traffic, tourism, reaction, approach	1.11	40.31	0.68	(Hashim & Jaaman 2011, Nowacek et al. 2001)
Ecological Niche	4.83	Stomach Contents	cephalopod, squid, stomach, beak, diet, item, content	1.84	49.61	0.72	(Clarke & Goodall 1994, Clarke & Young 1998)
		Ecological Niche	predat, resourc, nich, ecolg, top, ecosystem, forag	1.73	31.66	1.33	(Giménez et al. 2018, Young et al. 2017)
		Trophic Niche	isotop, trophic, valu, stabl, food, carbon, milk	1.26	34.09	0.84	(Furuyama et al. 2020, Rossman et al. 2013)
Polar and subpolar ecology	3.52	Arctic Ecology	greenland, ice, bowhead, polar, arctic, climat, bear	1.15	34.51	0.7	(Laidre et al. 2012, Westdal et al. 2017)
		Orca	salmon, inlet, cook, whale, transient, chinook, british	1.03	30.9	0.67	(Matkin et al. 2014, Shields et al. 2018)
		Pinniped	lion, phoca, seal, vitulina, california, fur, pinnip	0.76	29.78	0.62	(Johnson et al. 2003, Schumacher et al. 1993)
		Monodontidae	stock, lawrenc, hudson, canada, summer, bay, estuari	0.58	38.55	0.46	(De March & Postma 2003, Heide-Jørgensen et al. 2013)

Communication	2.72	Communication	call, vocal, type, repertoire, communic, learn, share	1.38	44.55	0.78	(Mishima et al. 2019, Weiß et al. 2011)
		Whistle	whistl, signatur, contour, frequenc, paramet, classif, durat	1.34	50.76	0.44	(Azevedo & Van Sluys 2005, Dong et al. 2019)

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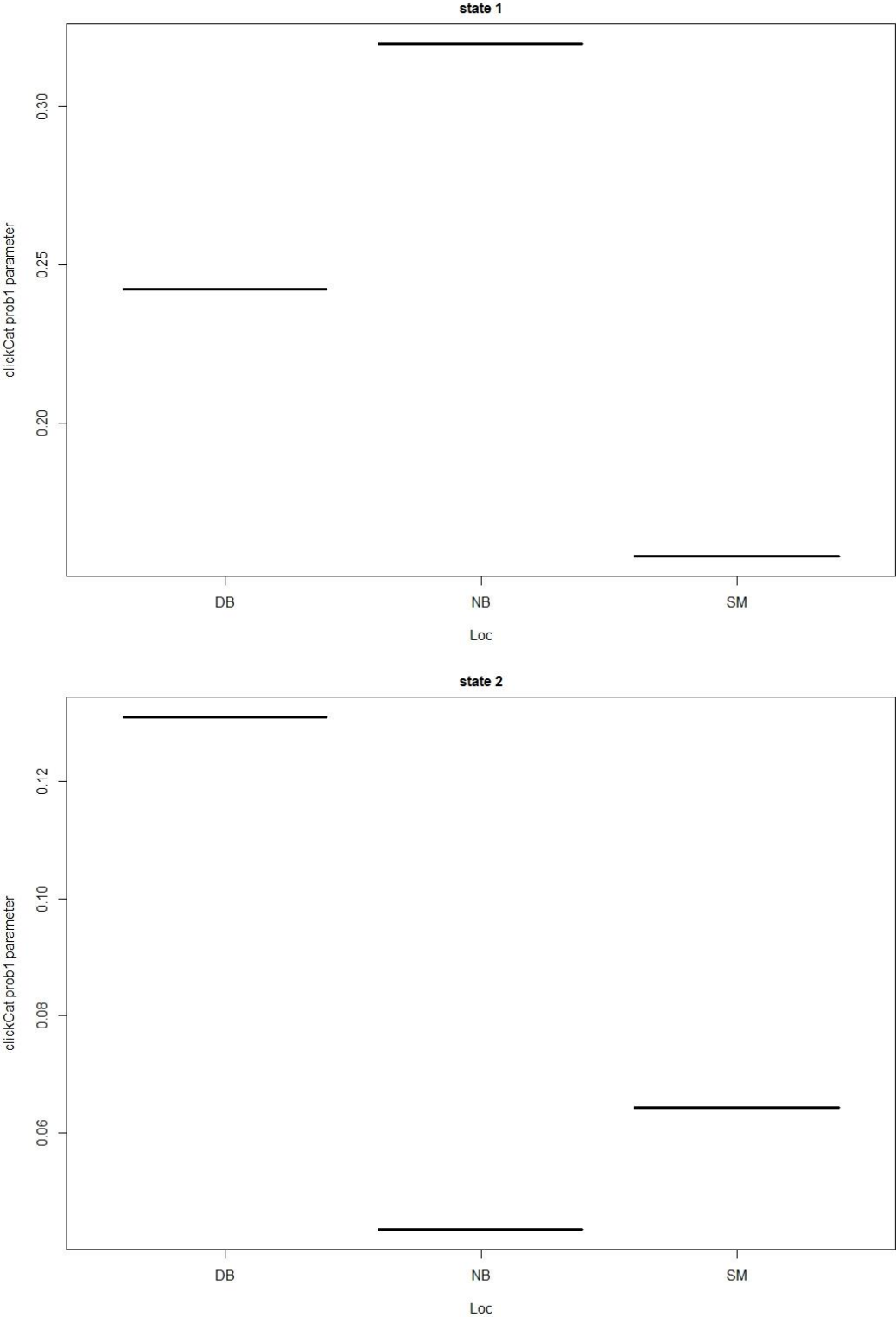
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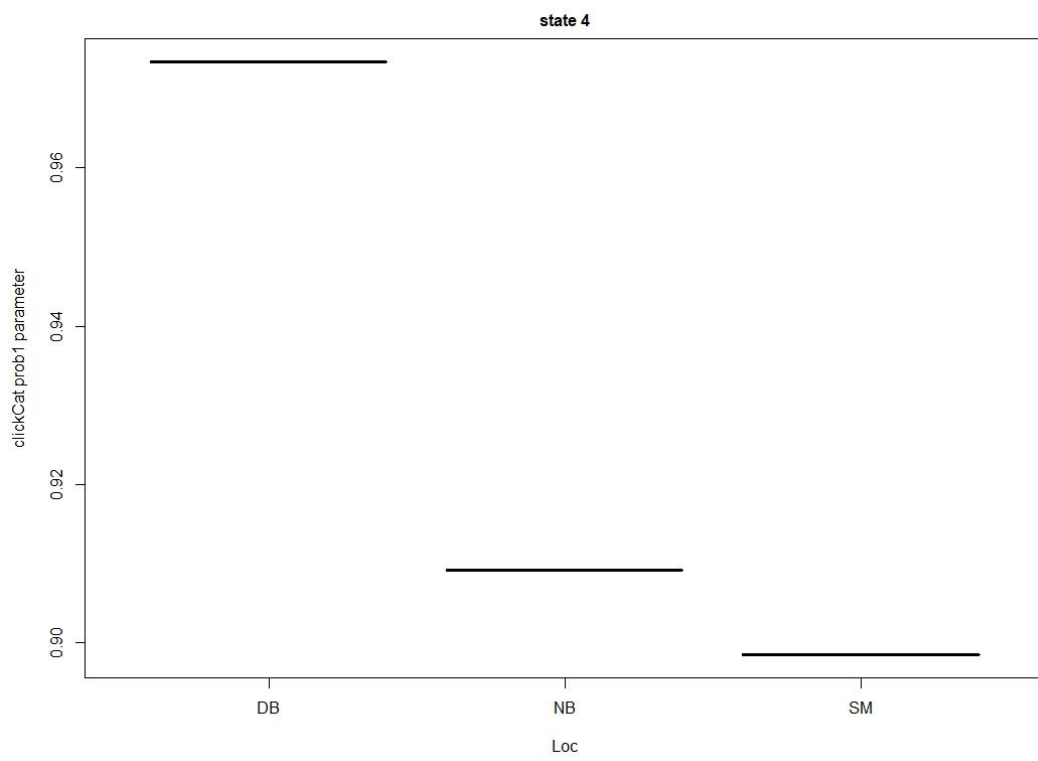
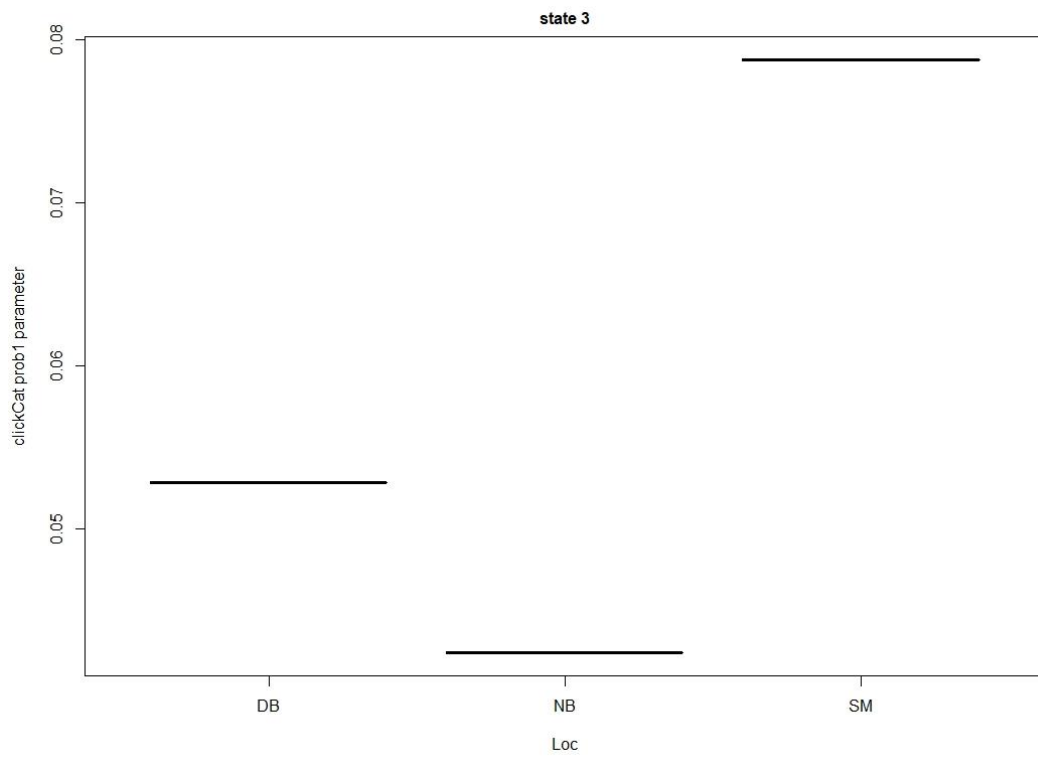
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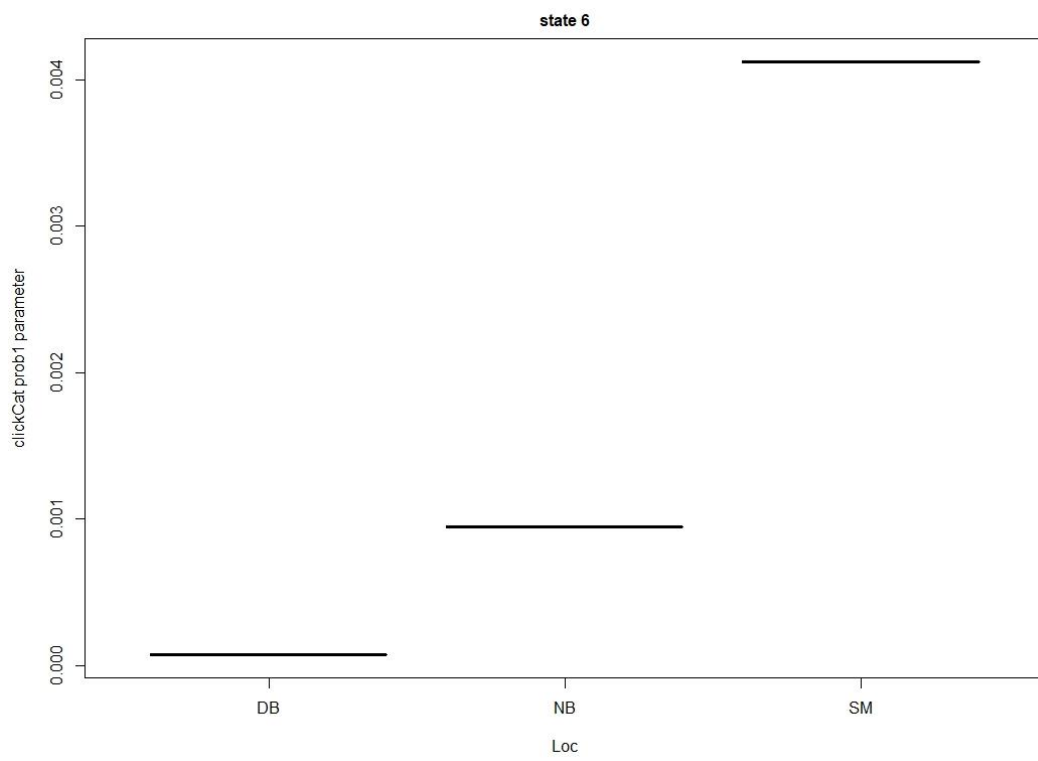
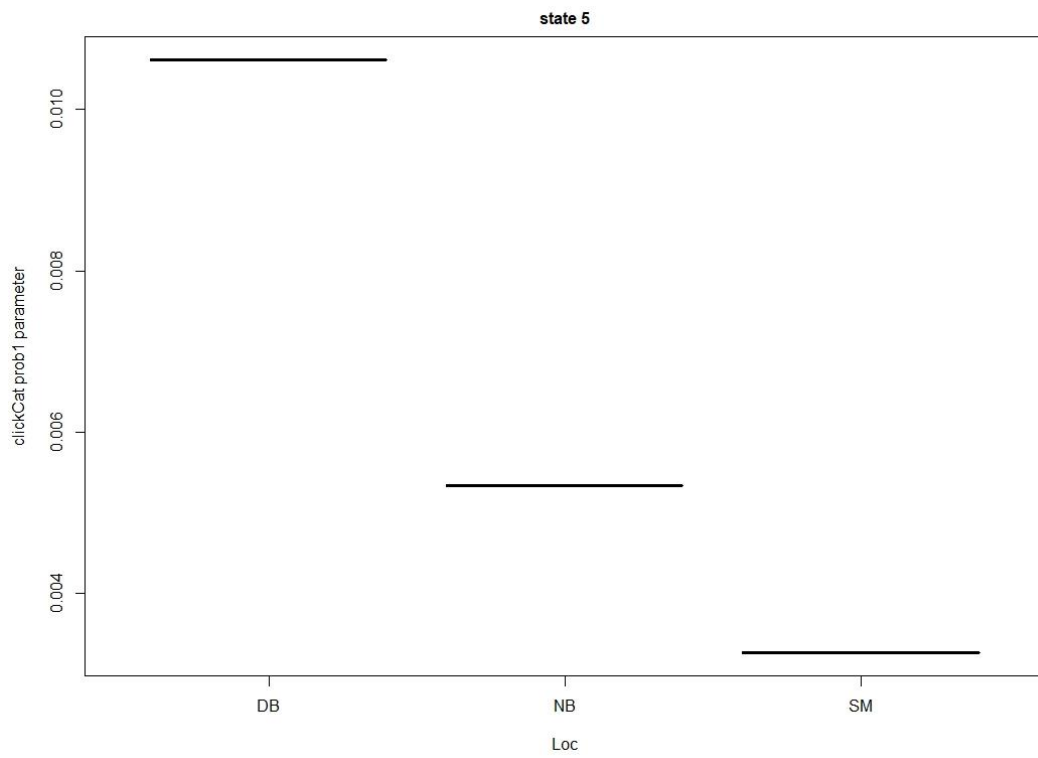
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Appendix B – Model Results of Activity State Hidden Markov Model

Figure B1 A - G. Effect of location on click parameter 1 (buzz click category) for each state of the 7-state HMM of bottlenose dolphin activity.







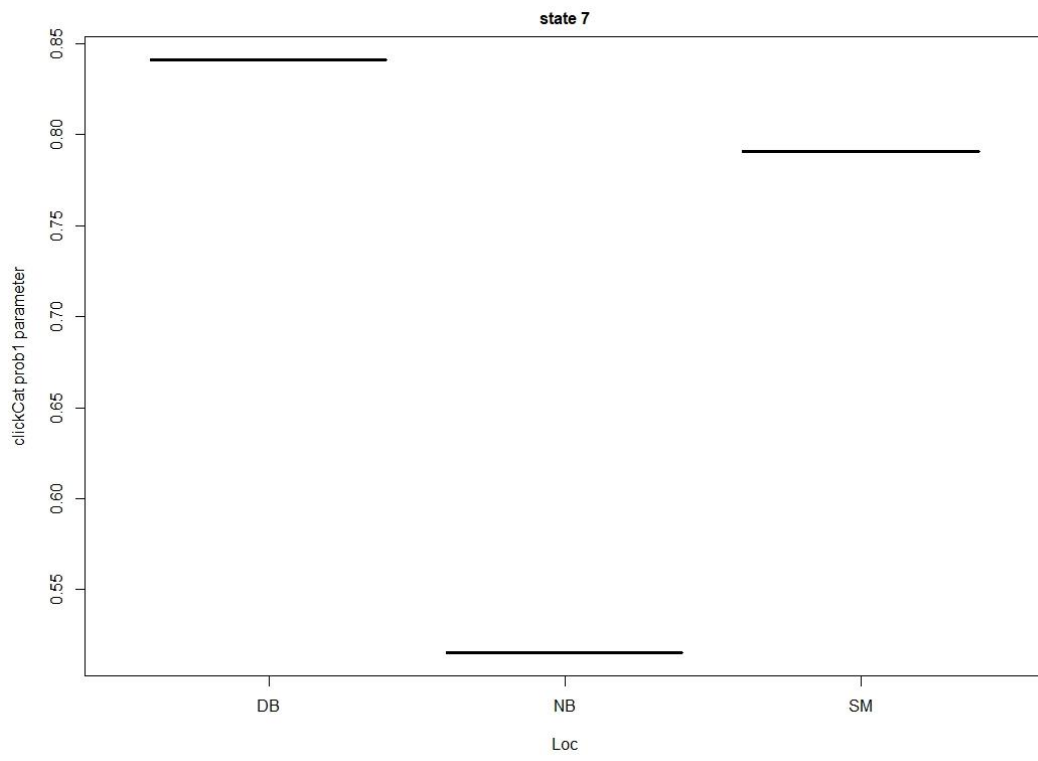
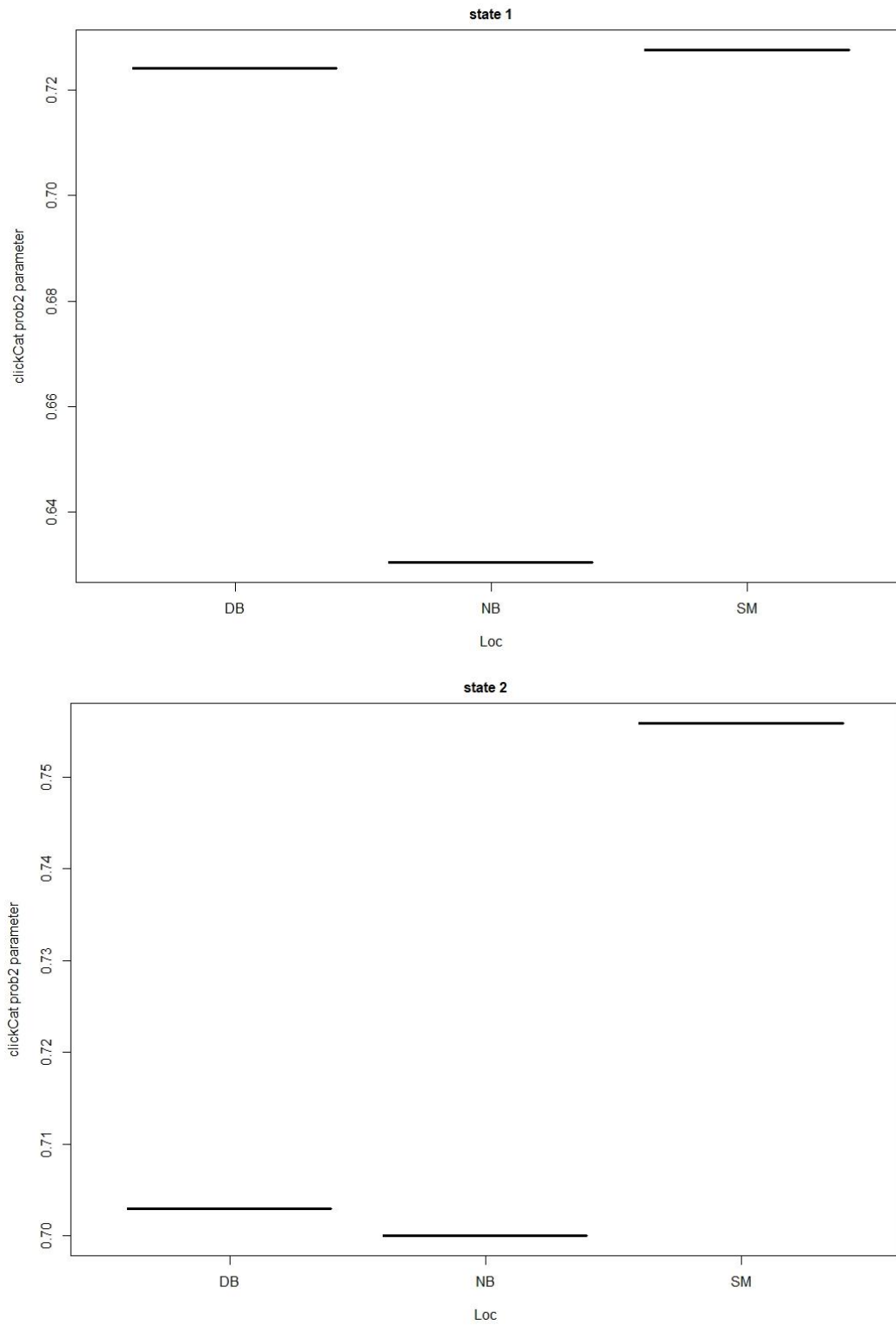
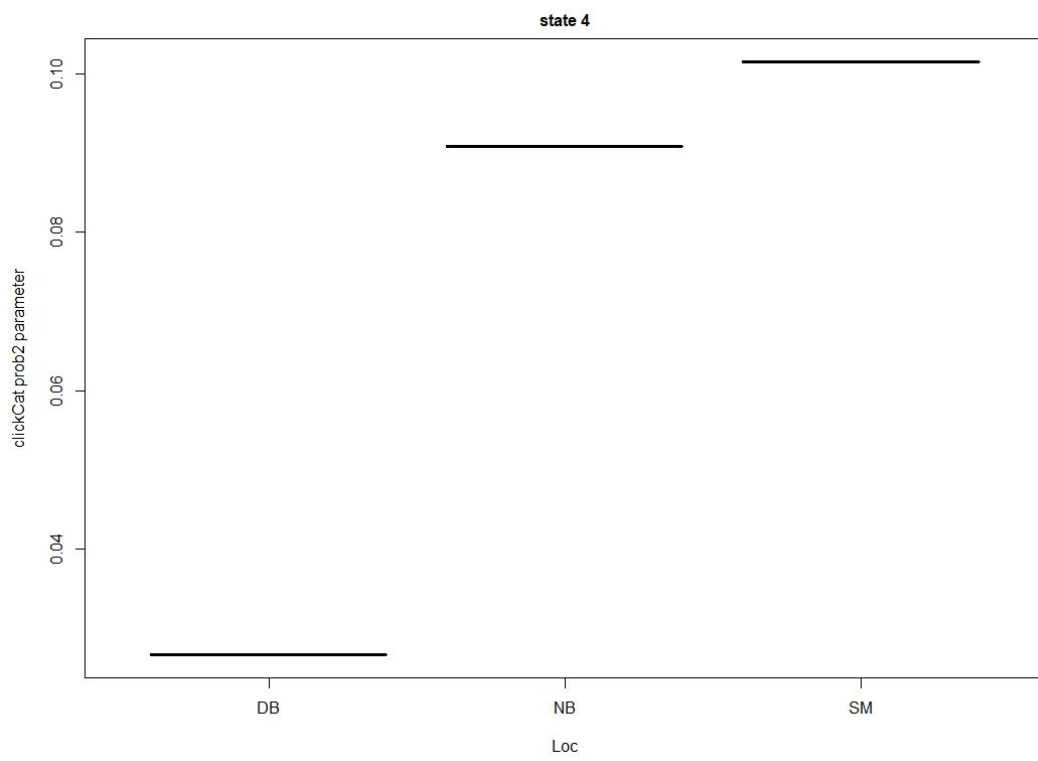
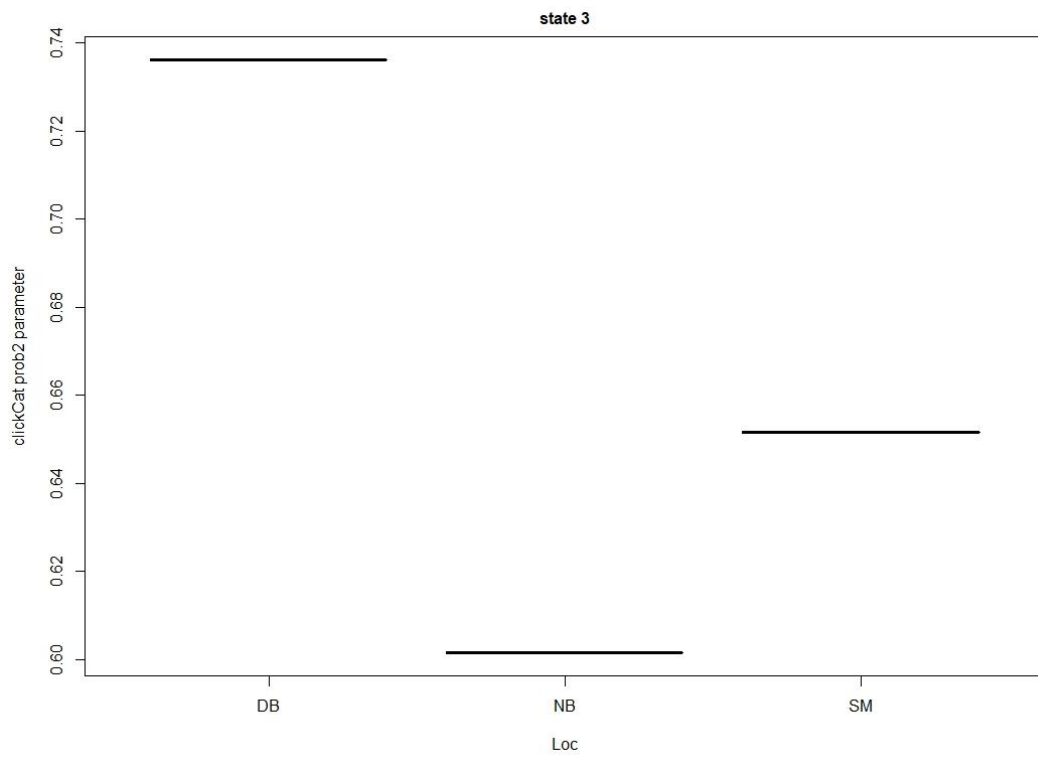
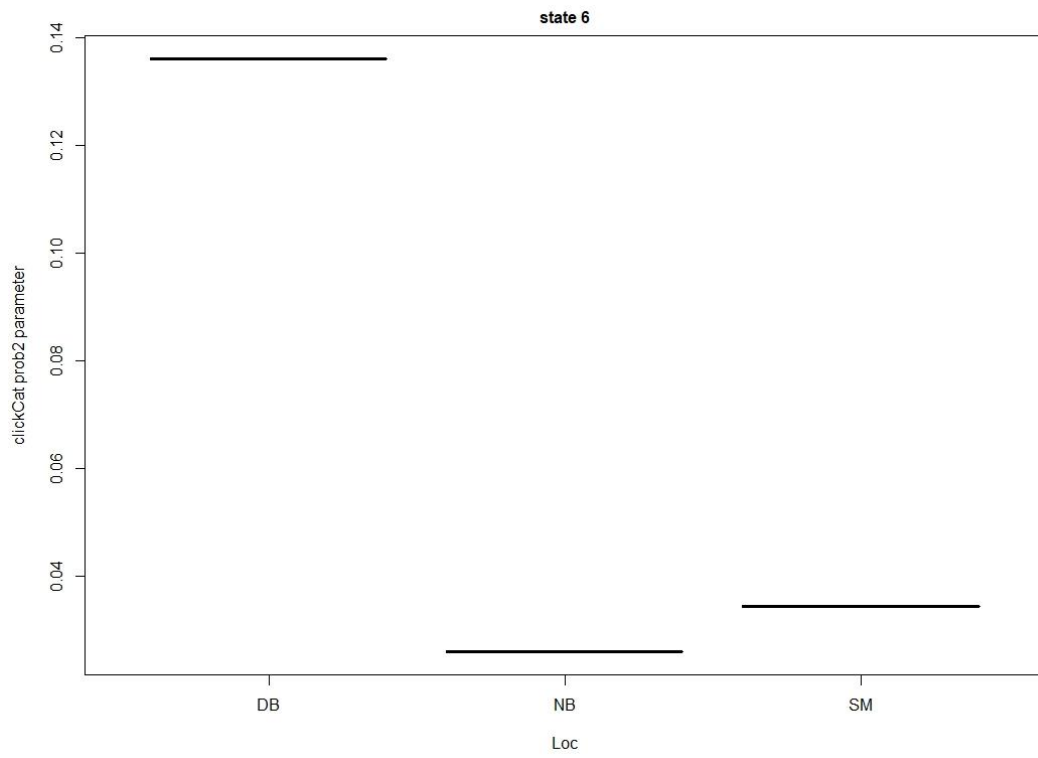
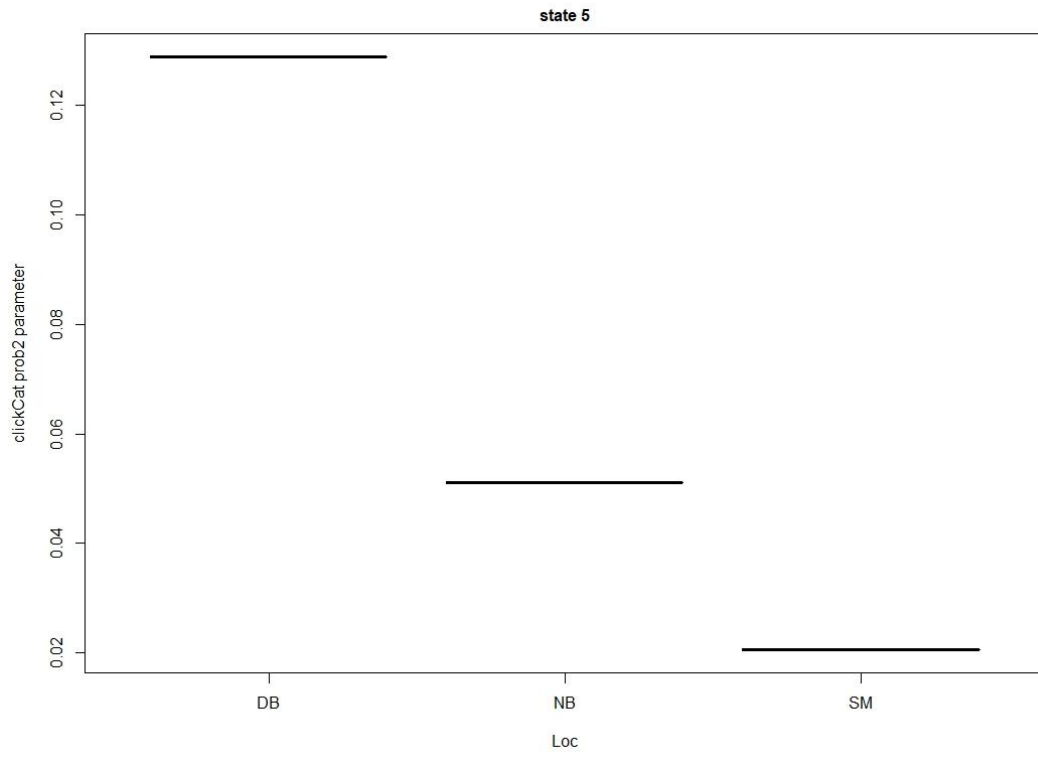


Figure B2 A-G. Effect of location on click parameter 2 (regular click category) for each state of the 7-state HMM of bottlenose dolphin activity.







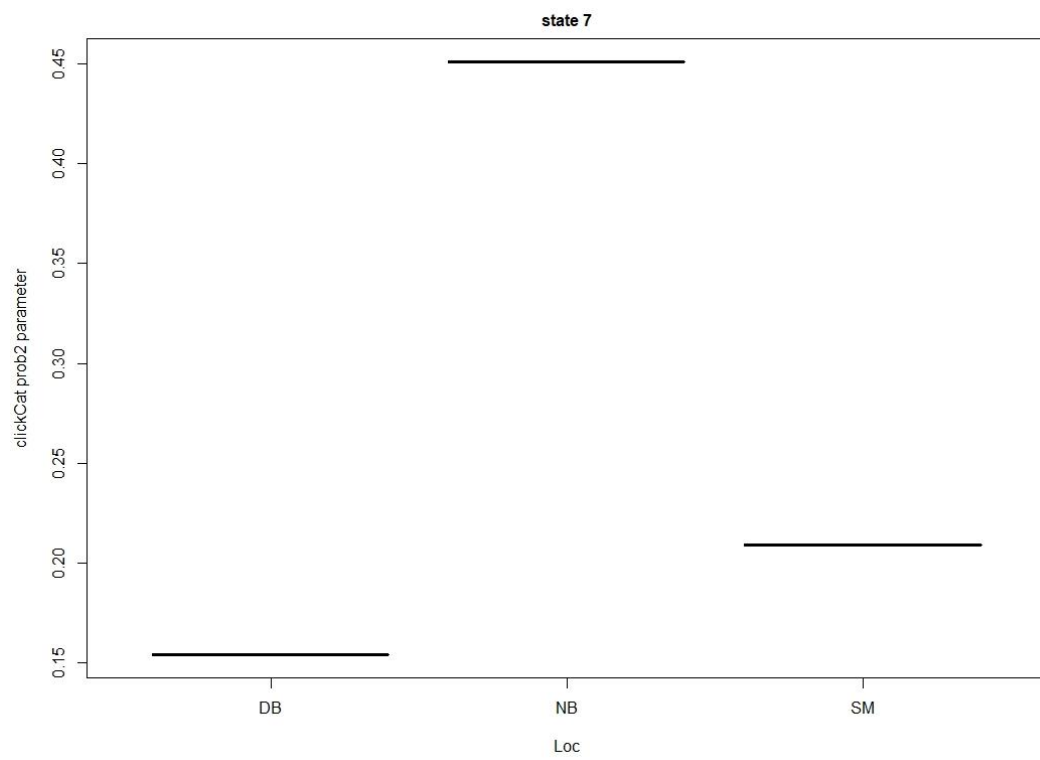
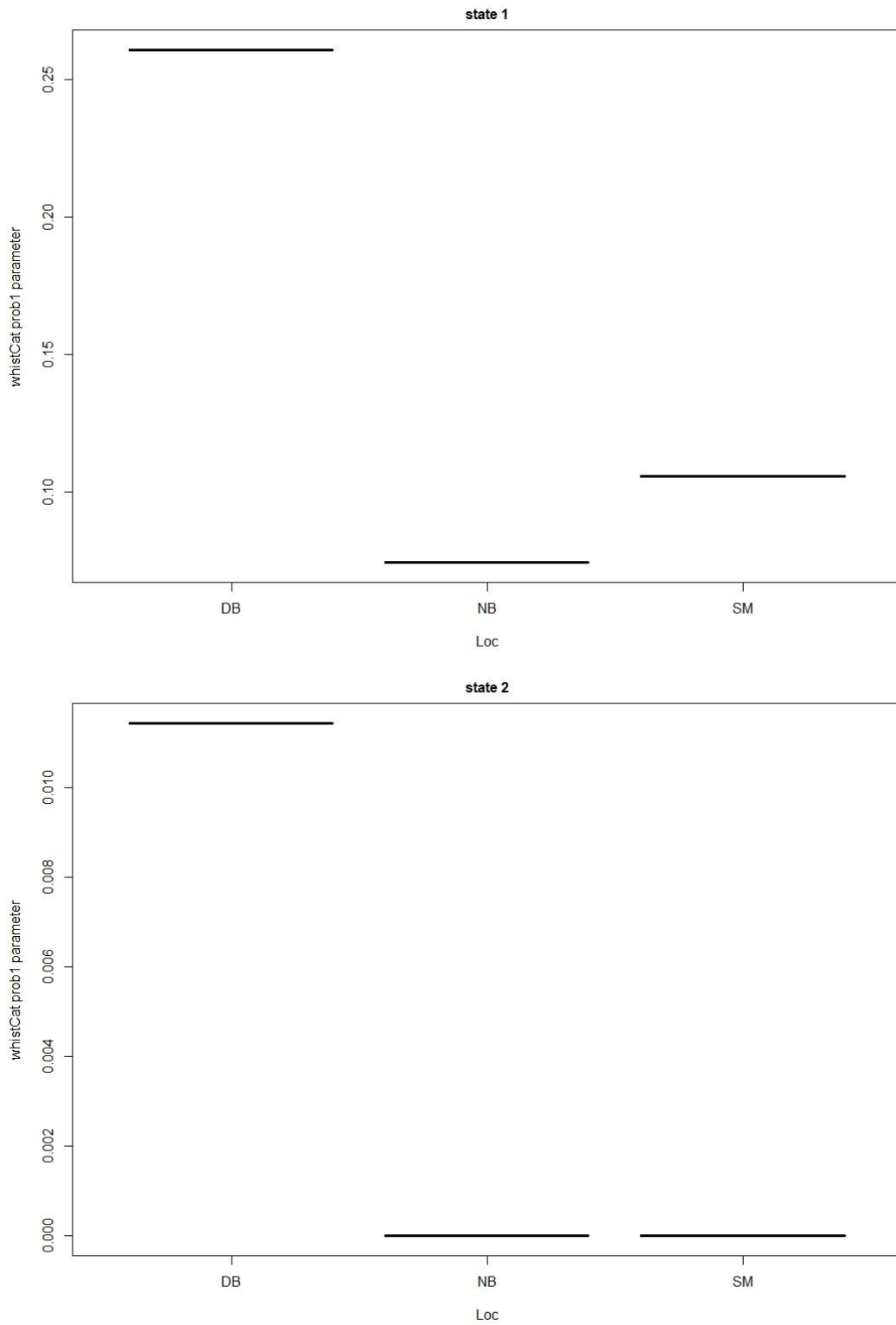
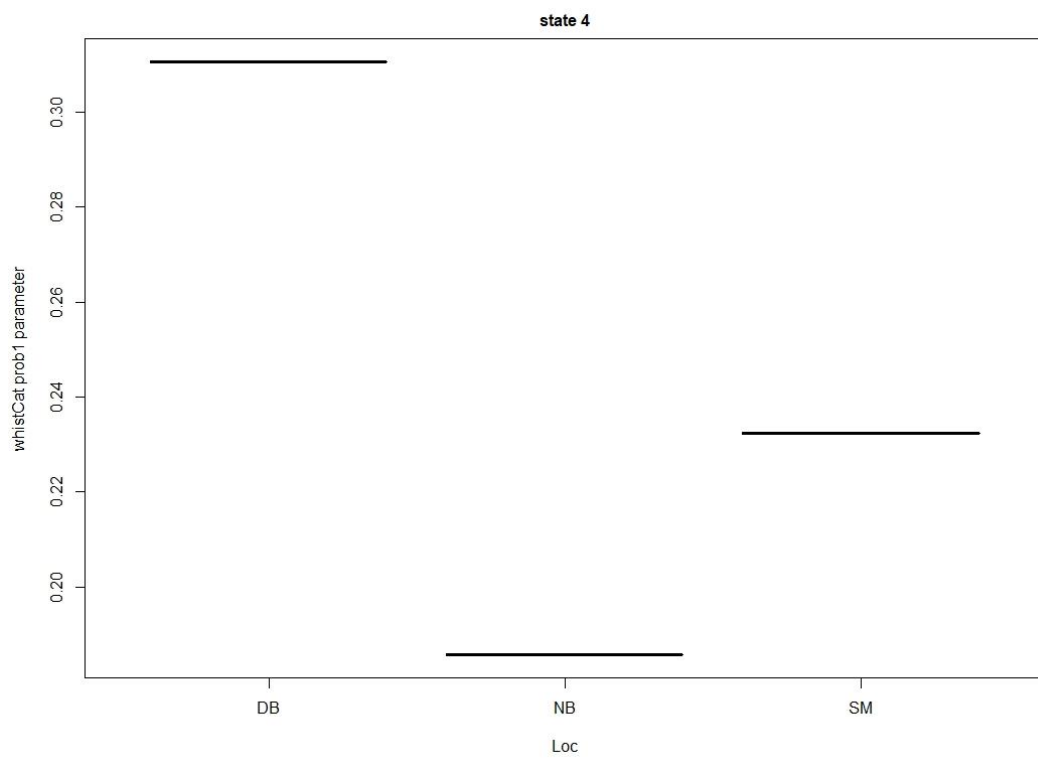
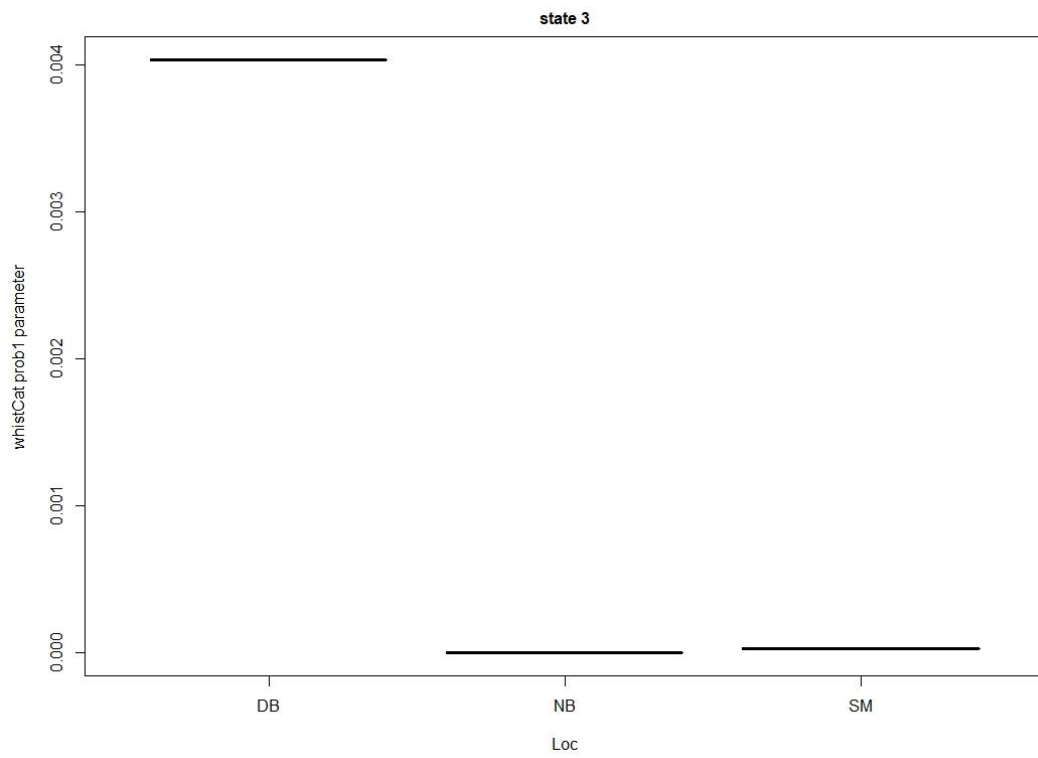
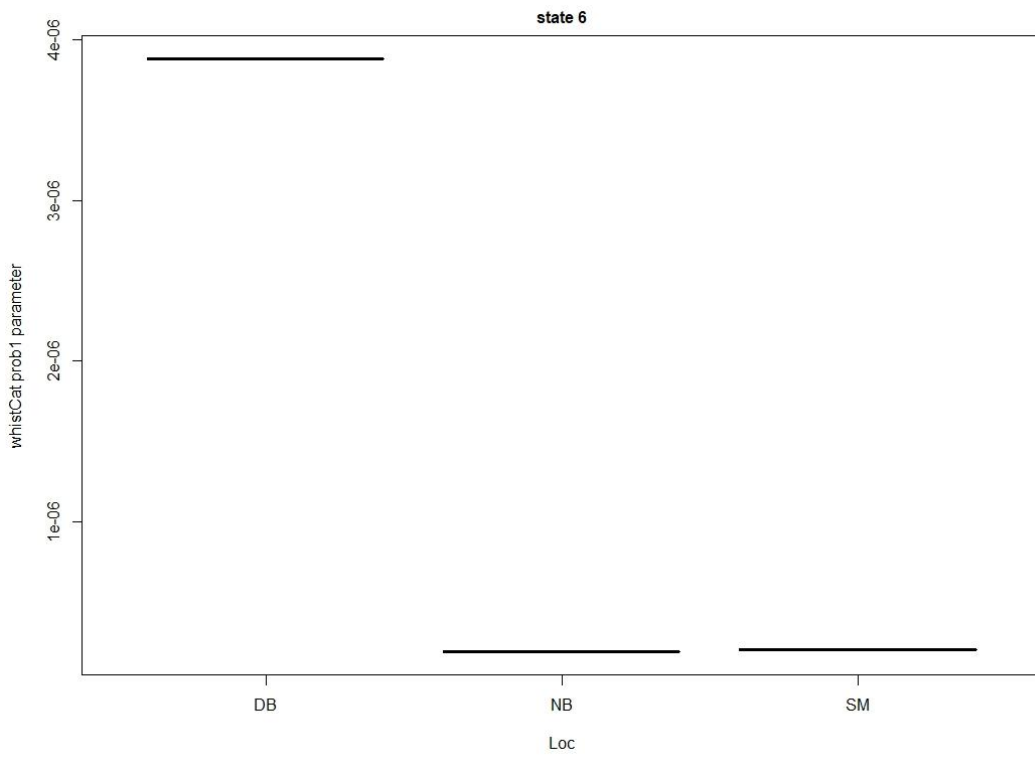
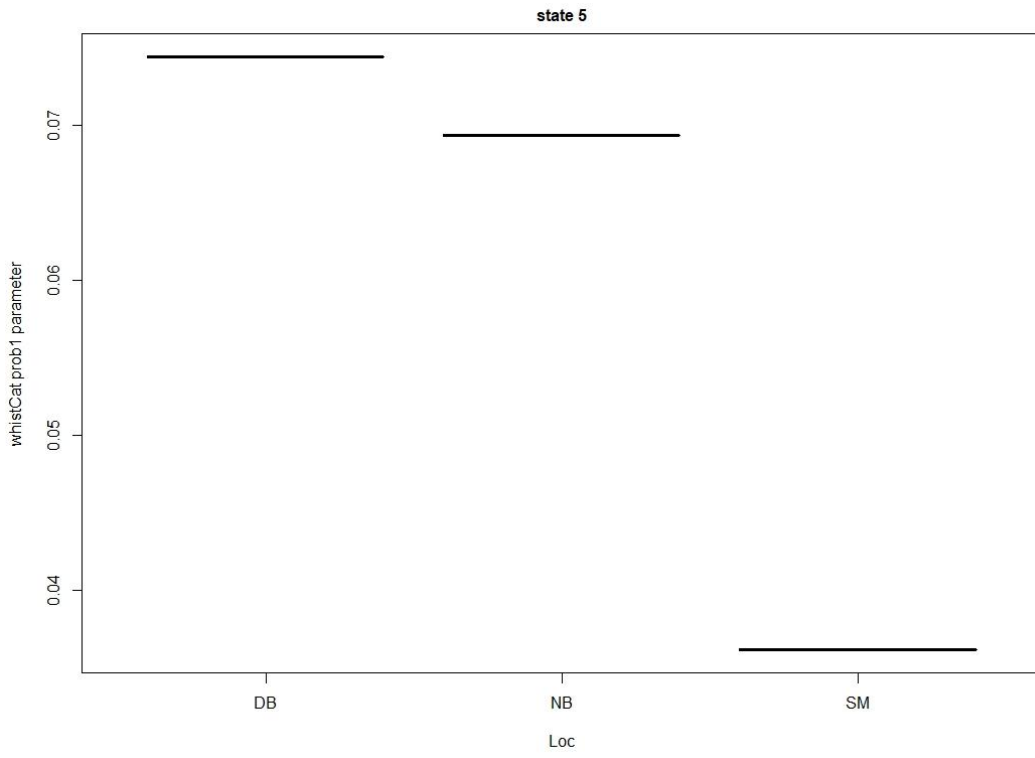


Figure B3 A - G. Effect of location on whistle parameter 1 (WOM category) for each state of the 7-state HMM of bottlenose dolphin activity.







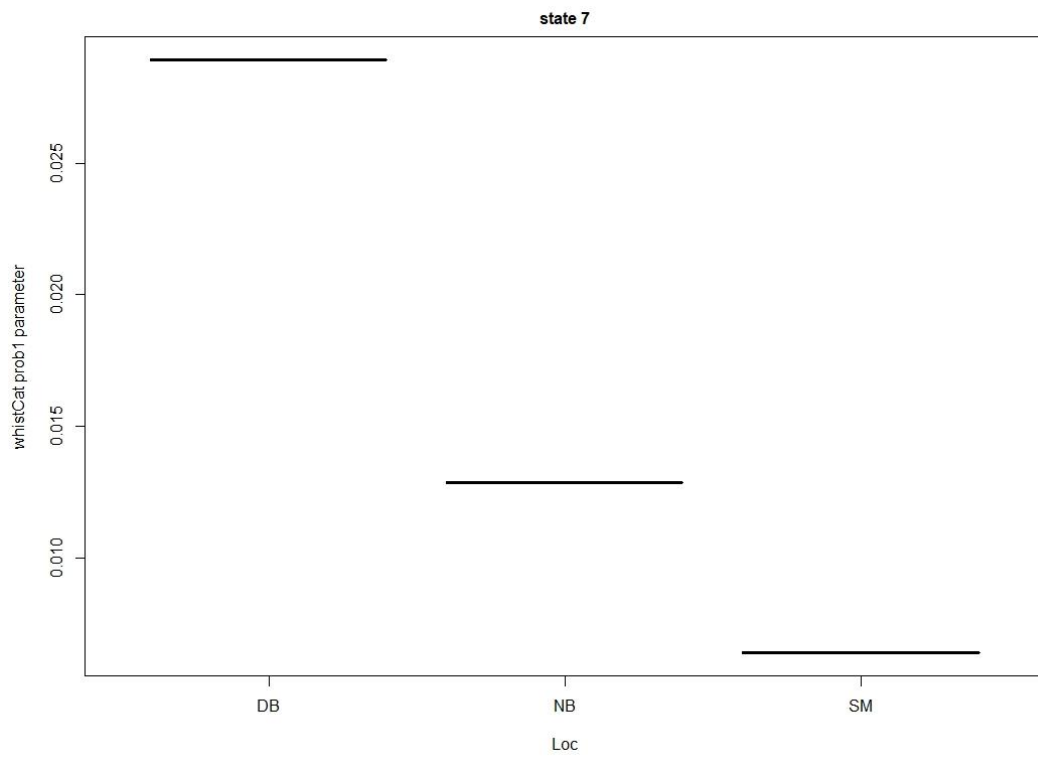
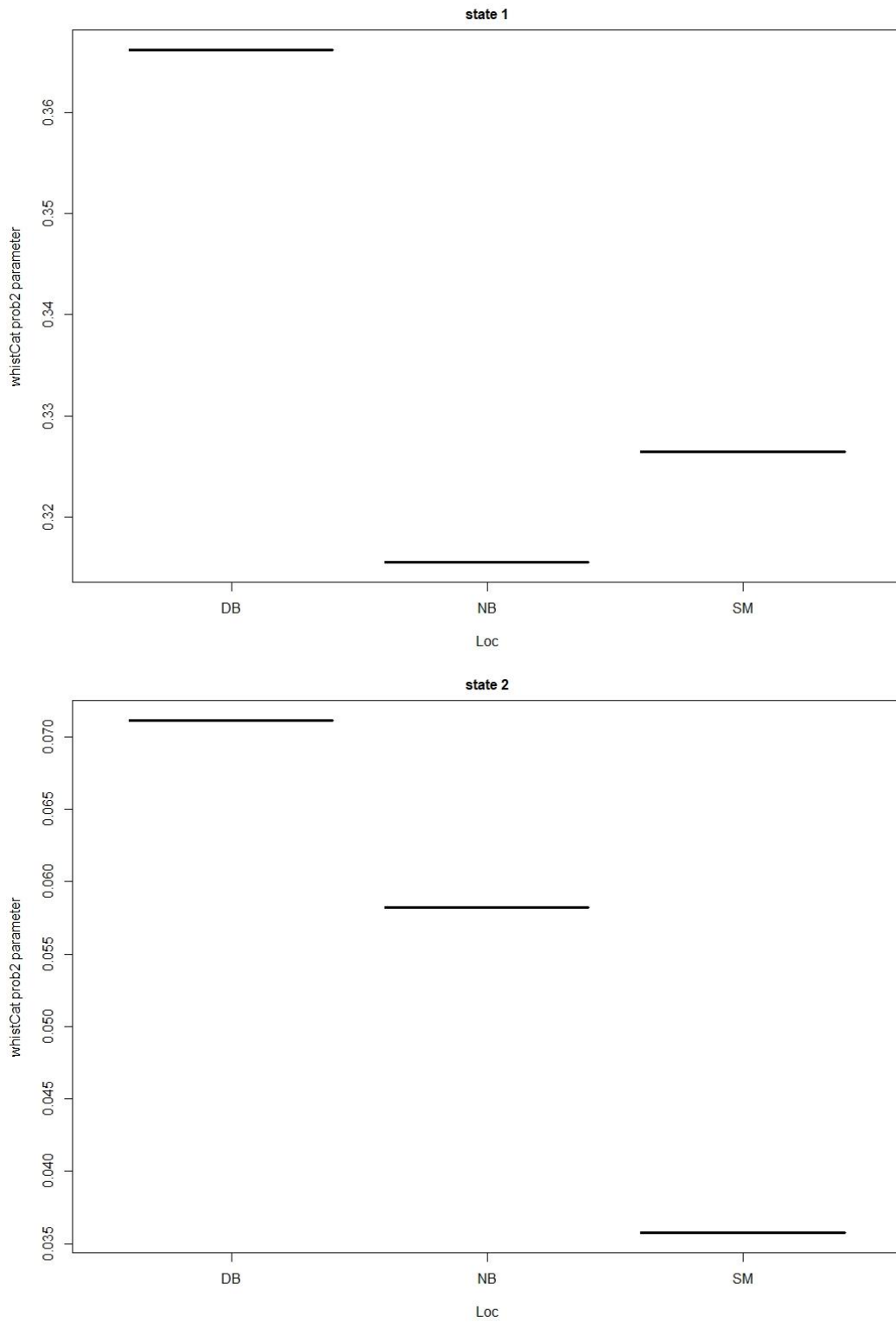
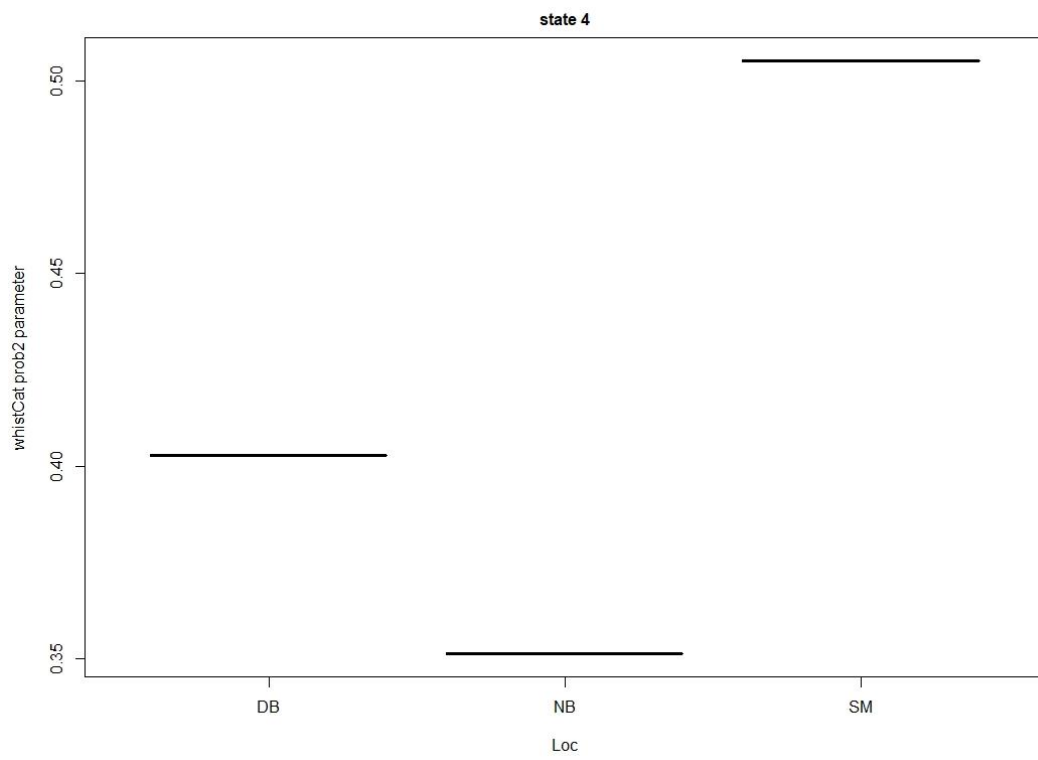
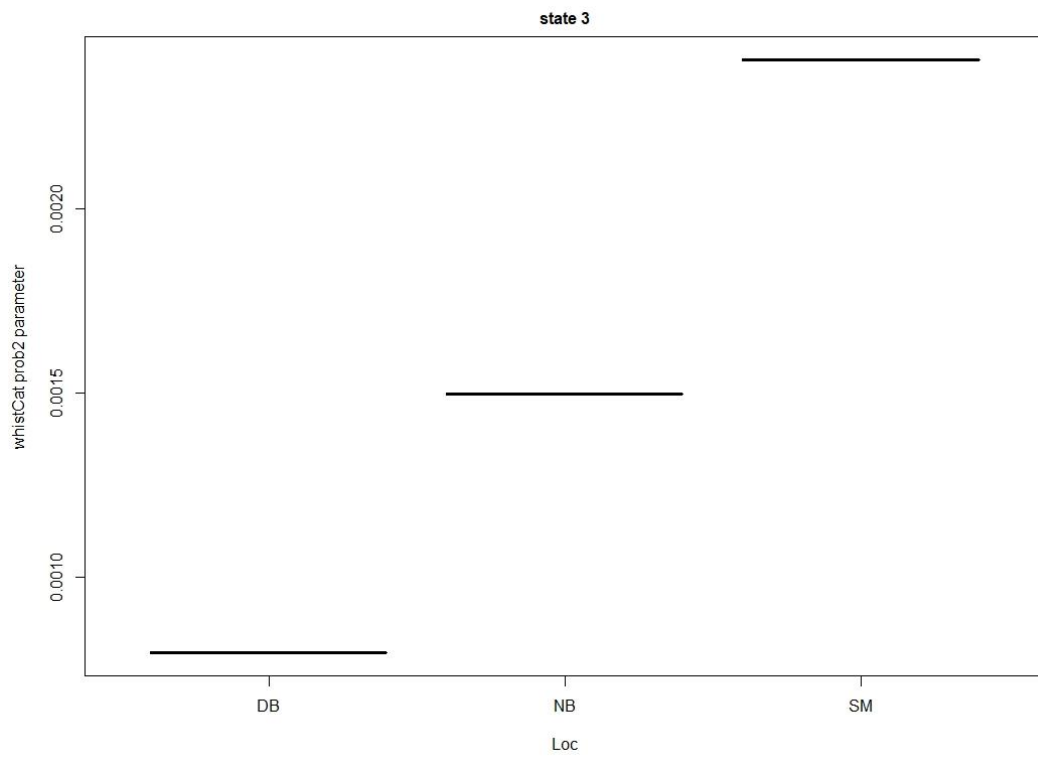
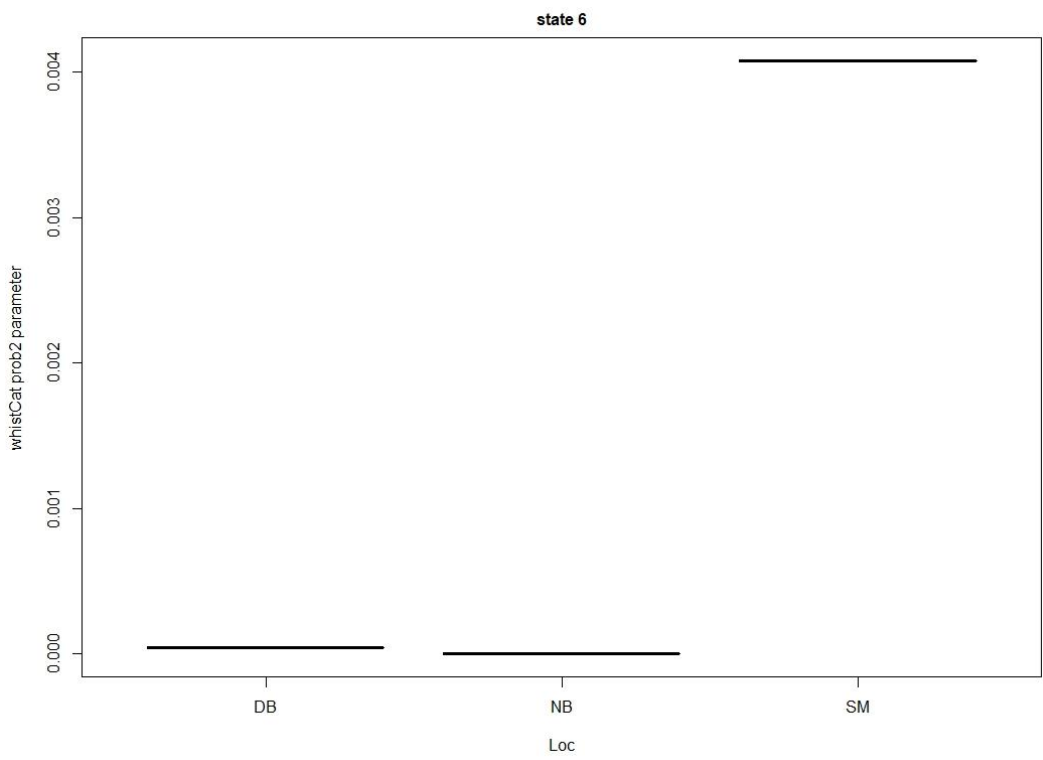
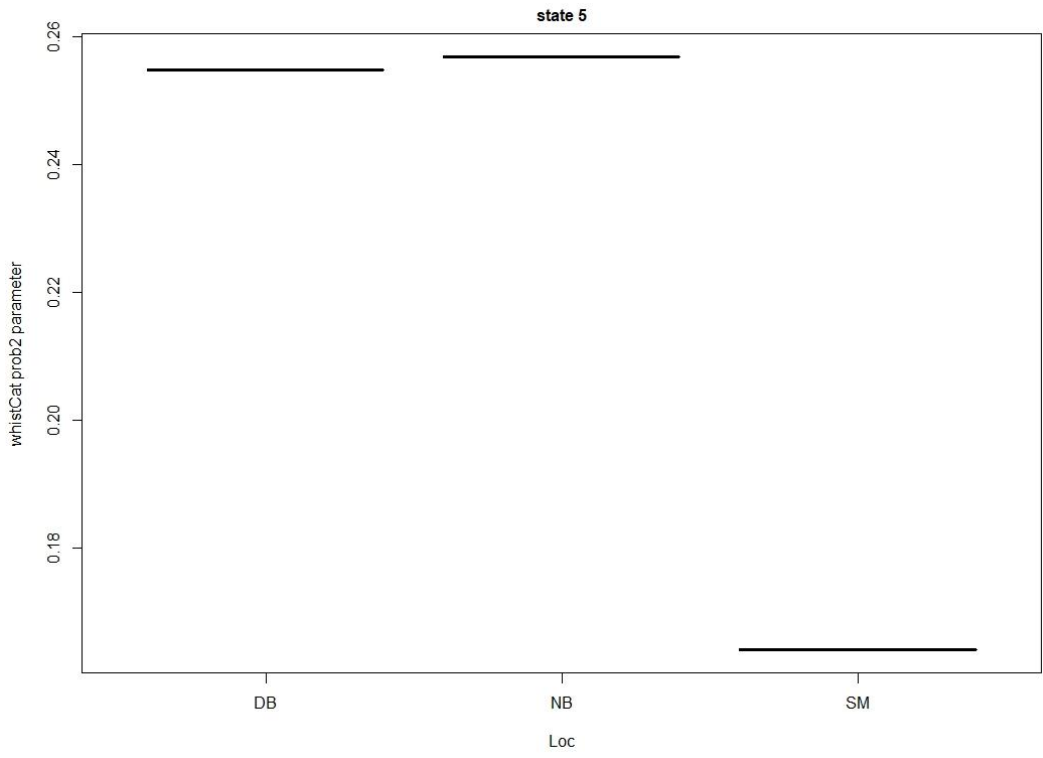


Figure B4 A-G. Effect of location on whistle parameter 2 (WNM category) for each state of the 7-state HMM of bottlenose dolphin activity.







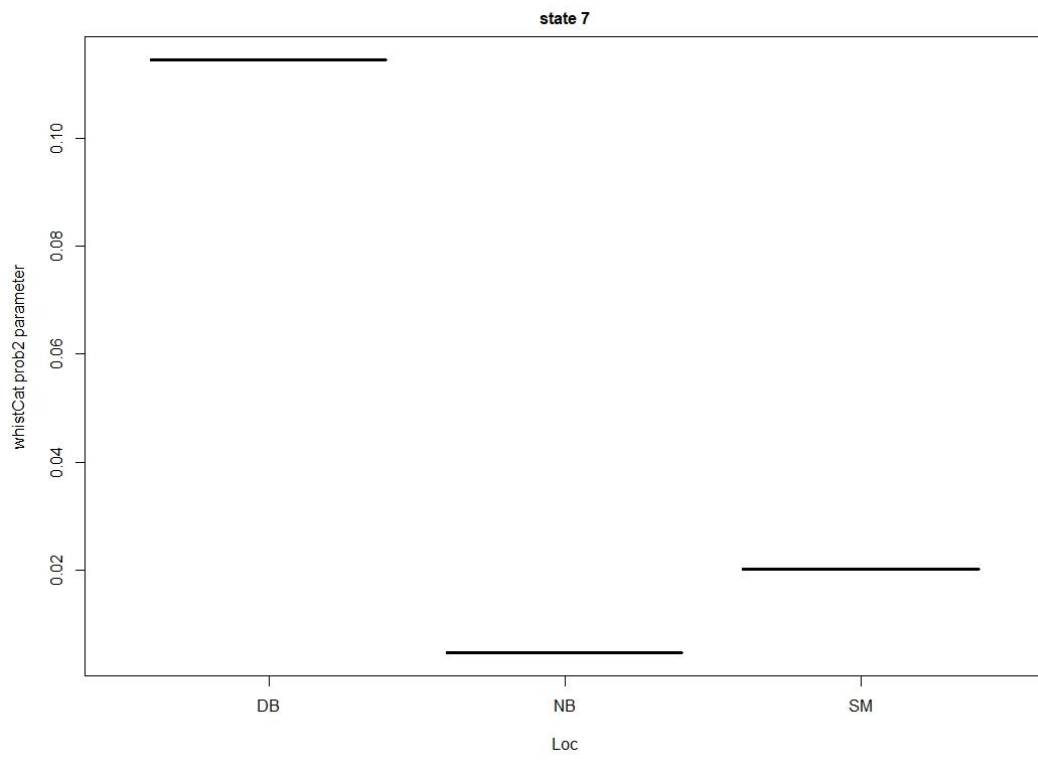
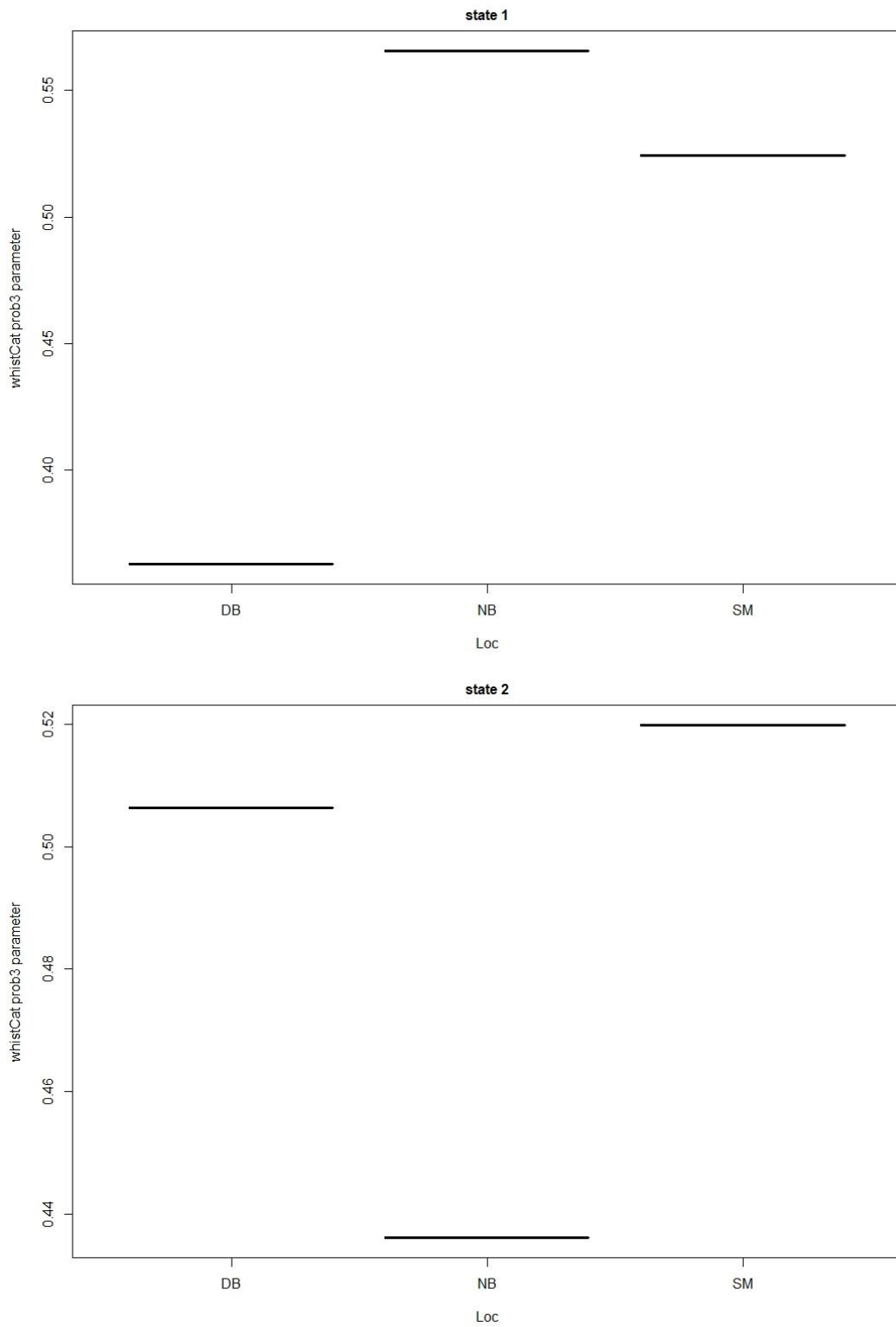
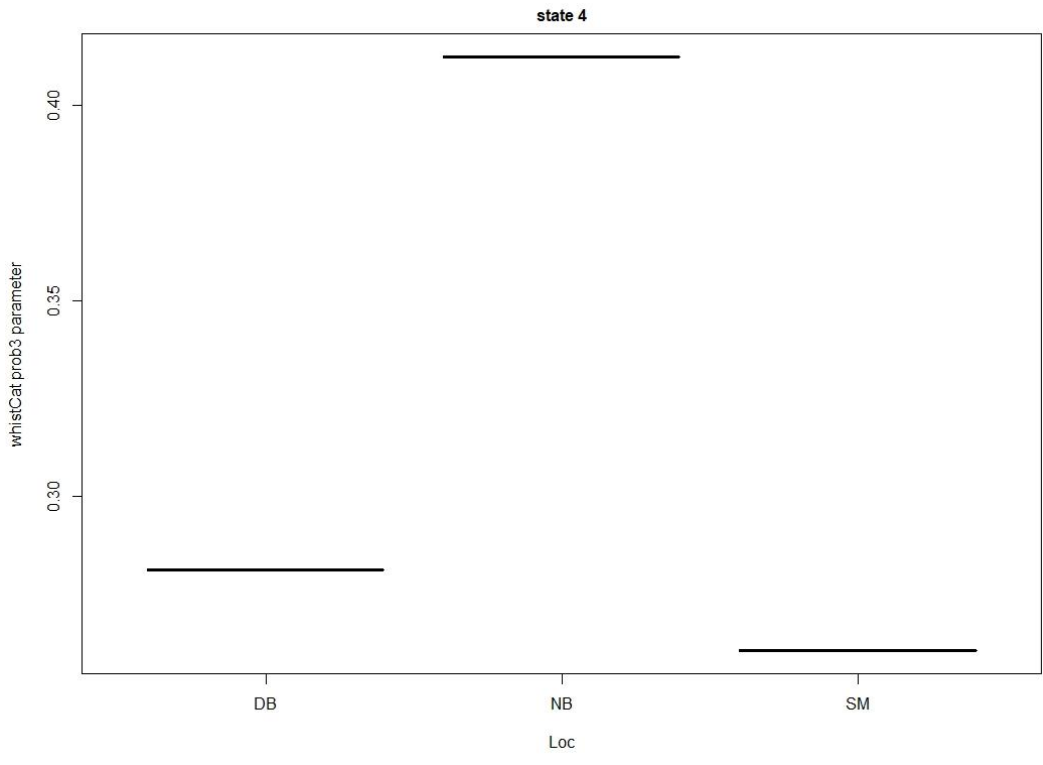
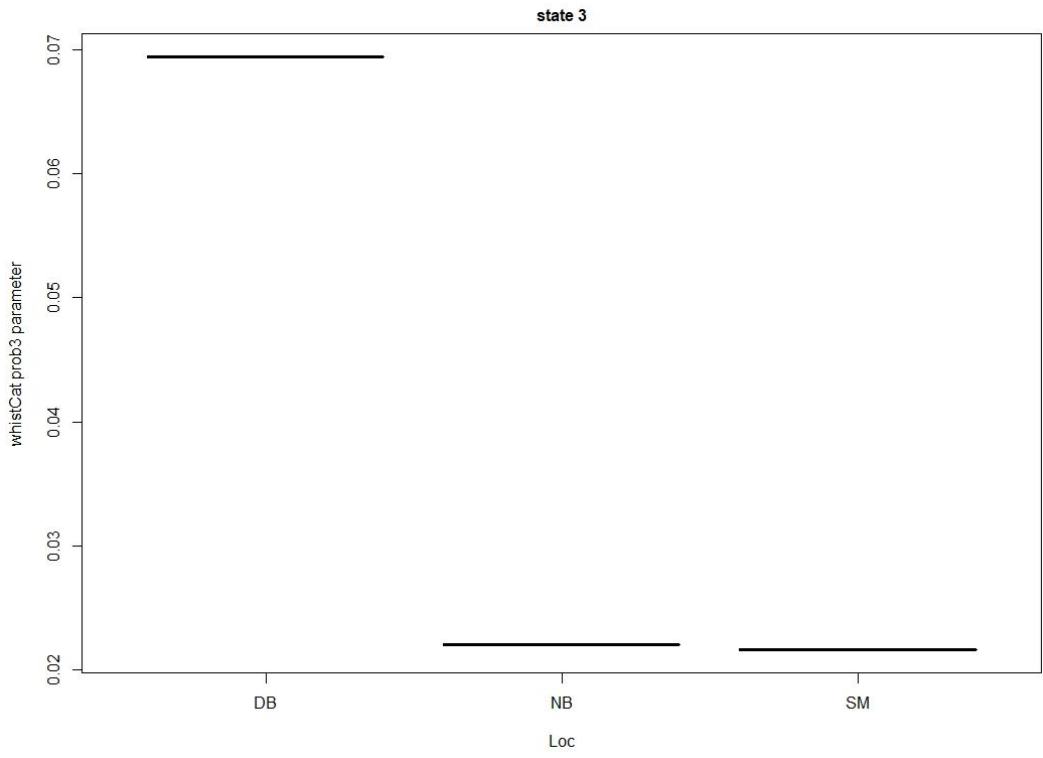
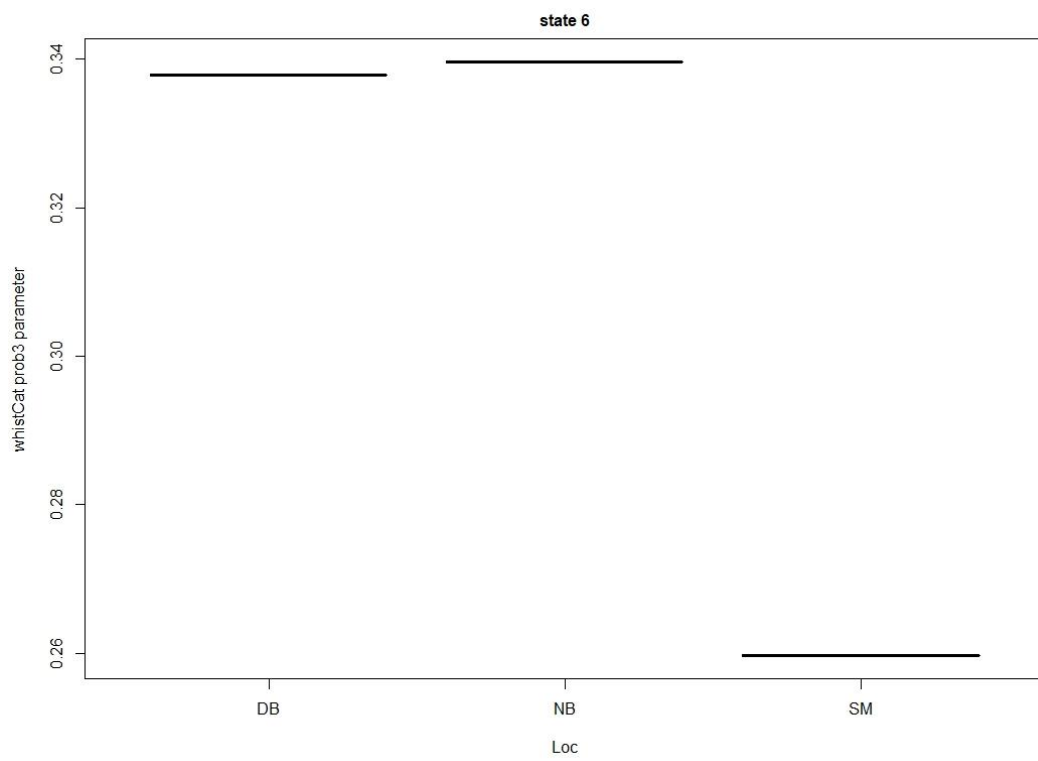
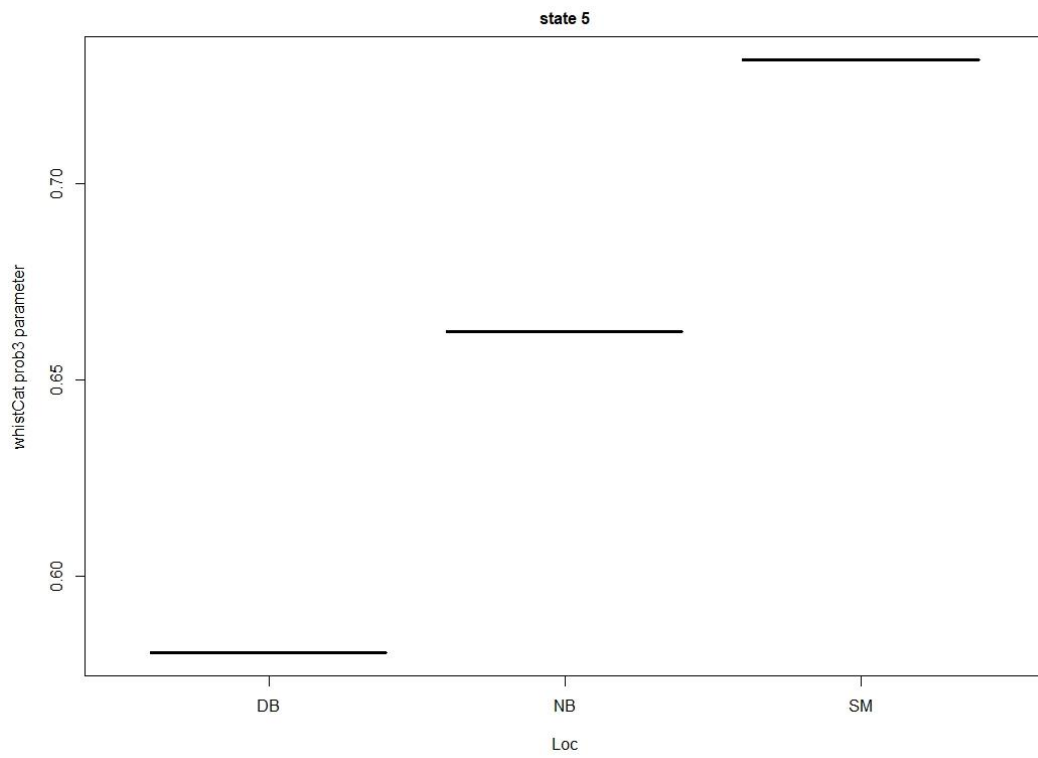


Figure B5 A-G. Effect of location on whistle parameter 3 (SW category) for each state of the 7-state HMM of bottlenose dolphin activity.







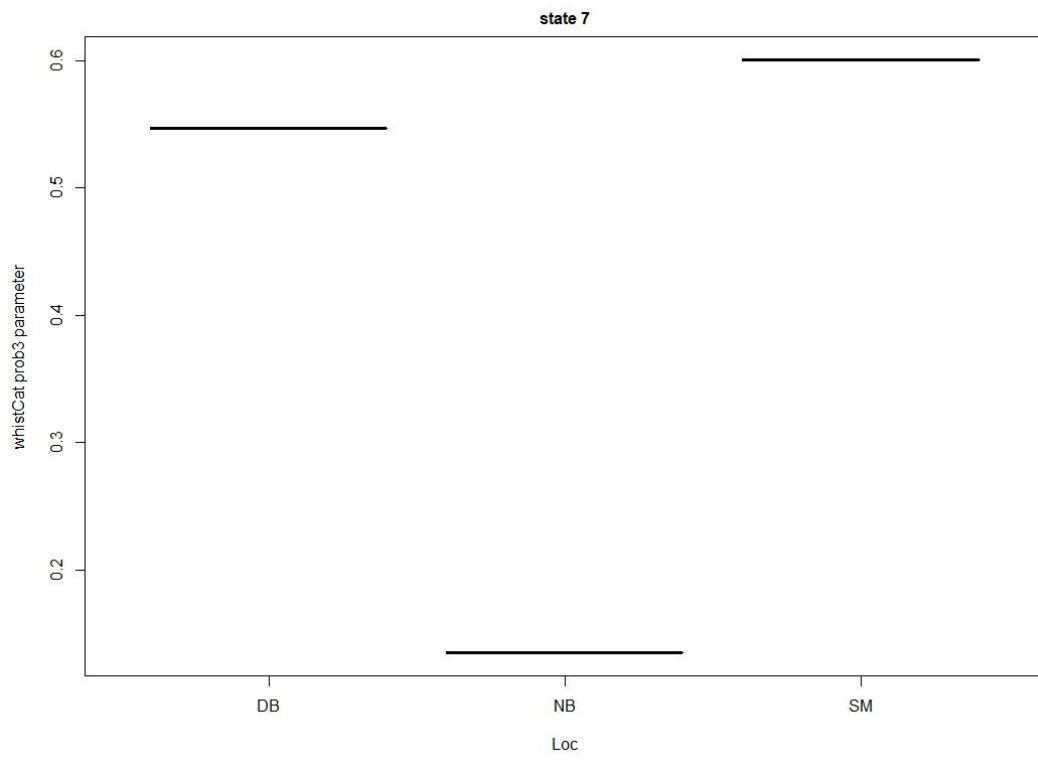


Figure B6. Figures showing effect of location on each transition probability of the transition probability matrix.

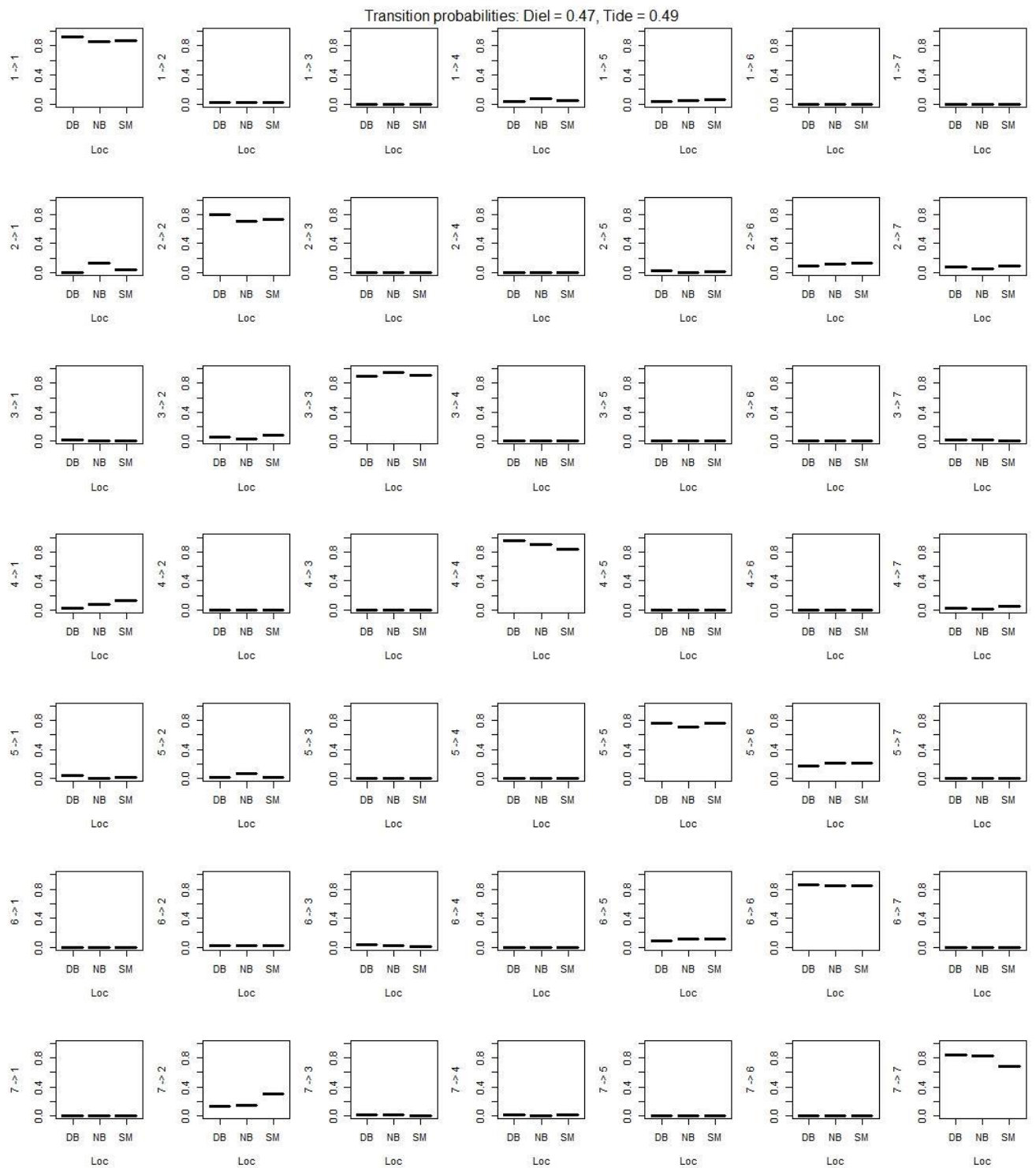


Figure B7 - Figures showing effect of diel phase on each transition probability of the transition probability matrix.

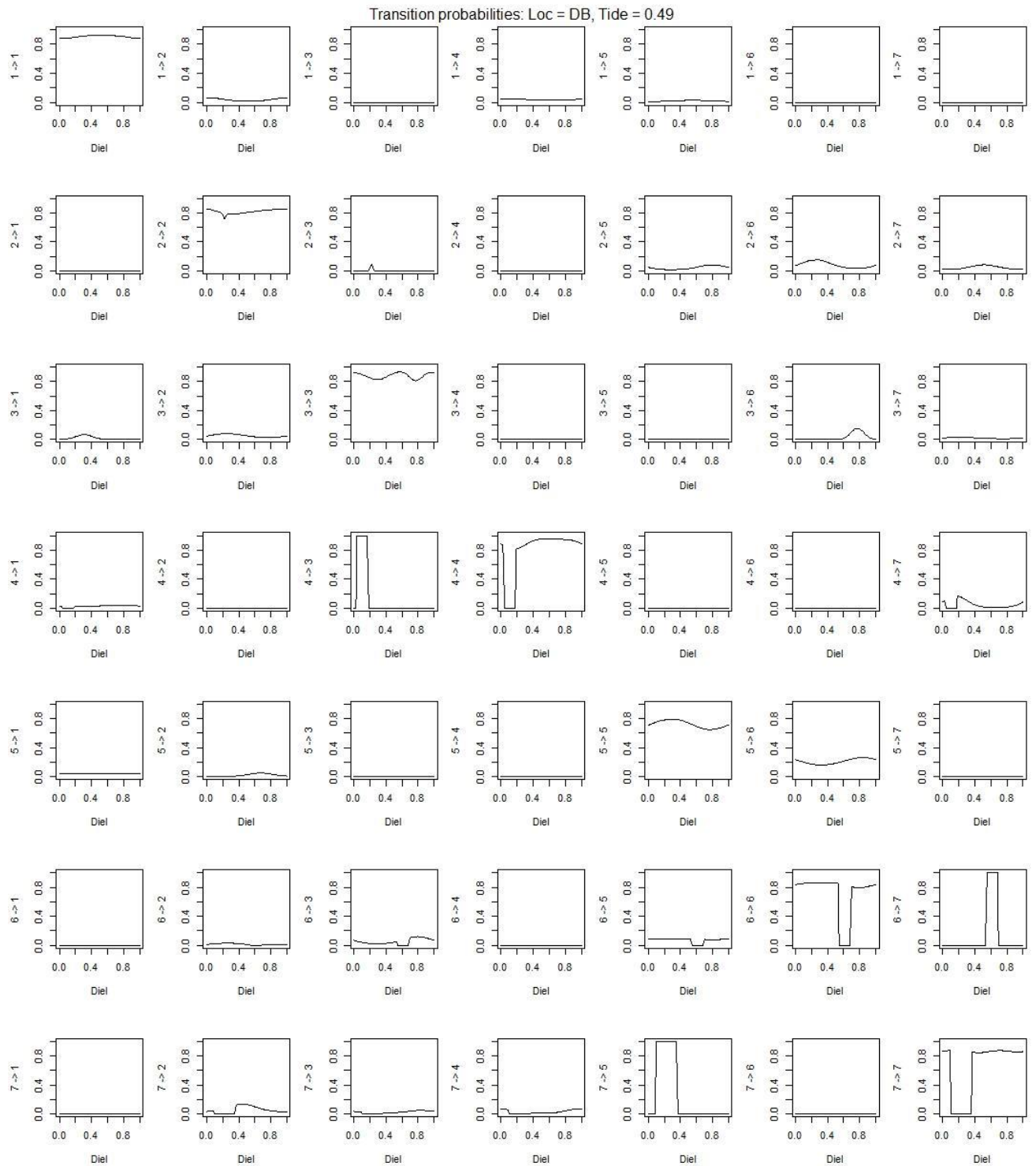
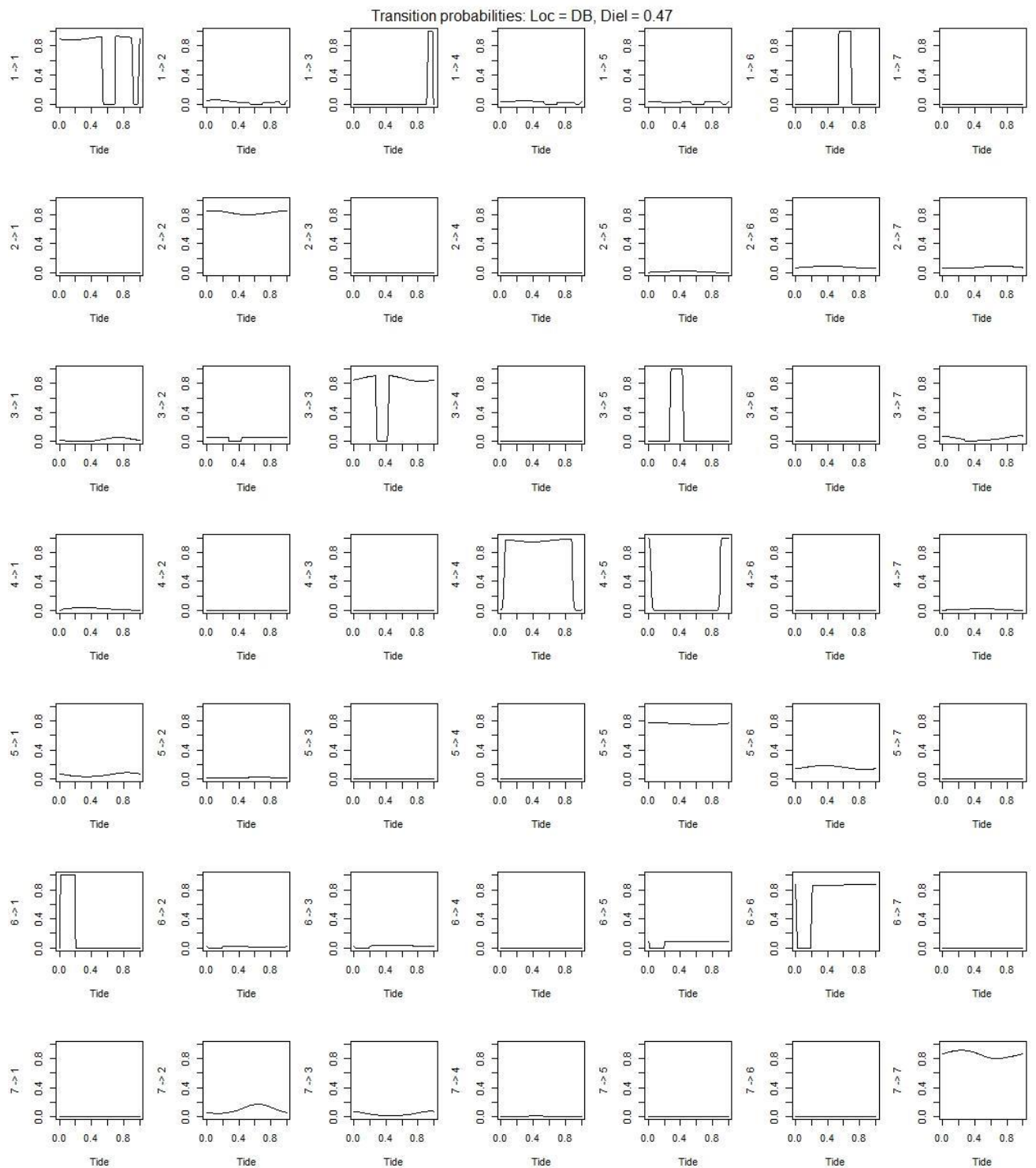


Figure B8 - Figures showing effect of tidal phase on each transition probability of the transition probability matrix.



Stationary state probabilities: Diel = 0.47, Tide = 0.49

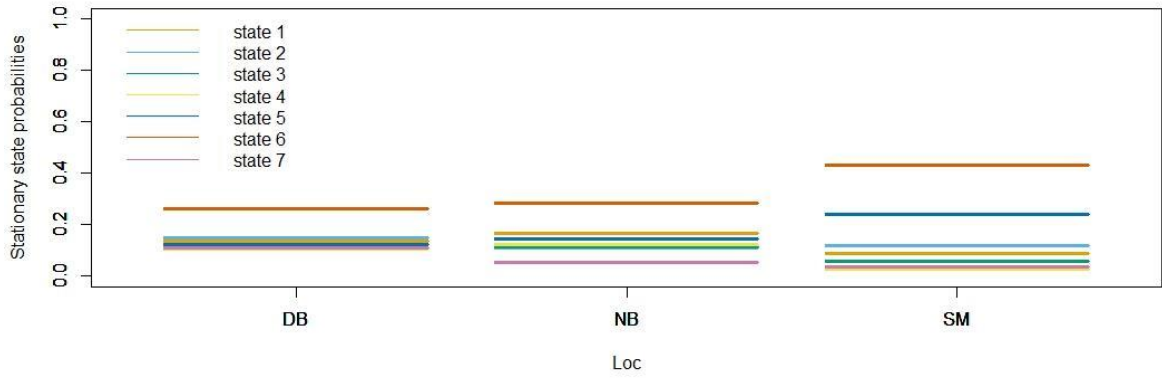


Figure B9. Stationary probability of each state at each location

Stationary state probabilities: Loc = DB, Diel = 0.47

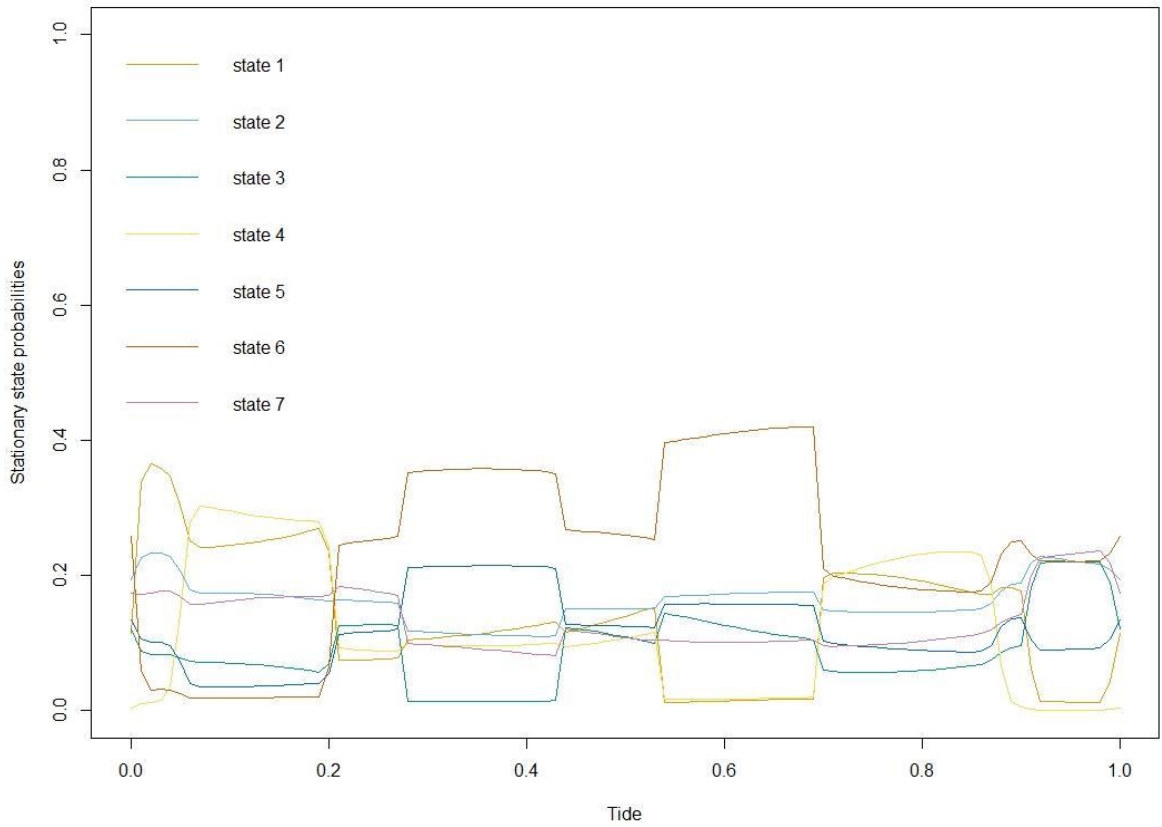


Figure B10. Stationary probability of each state across diel phase

Stationary state probabilities: Loc = DB, Tide = 0.49

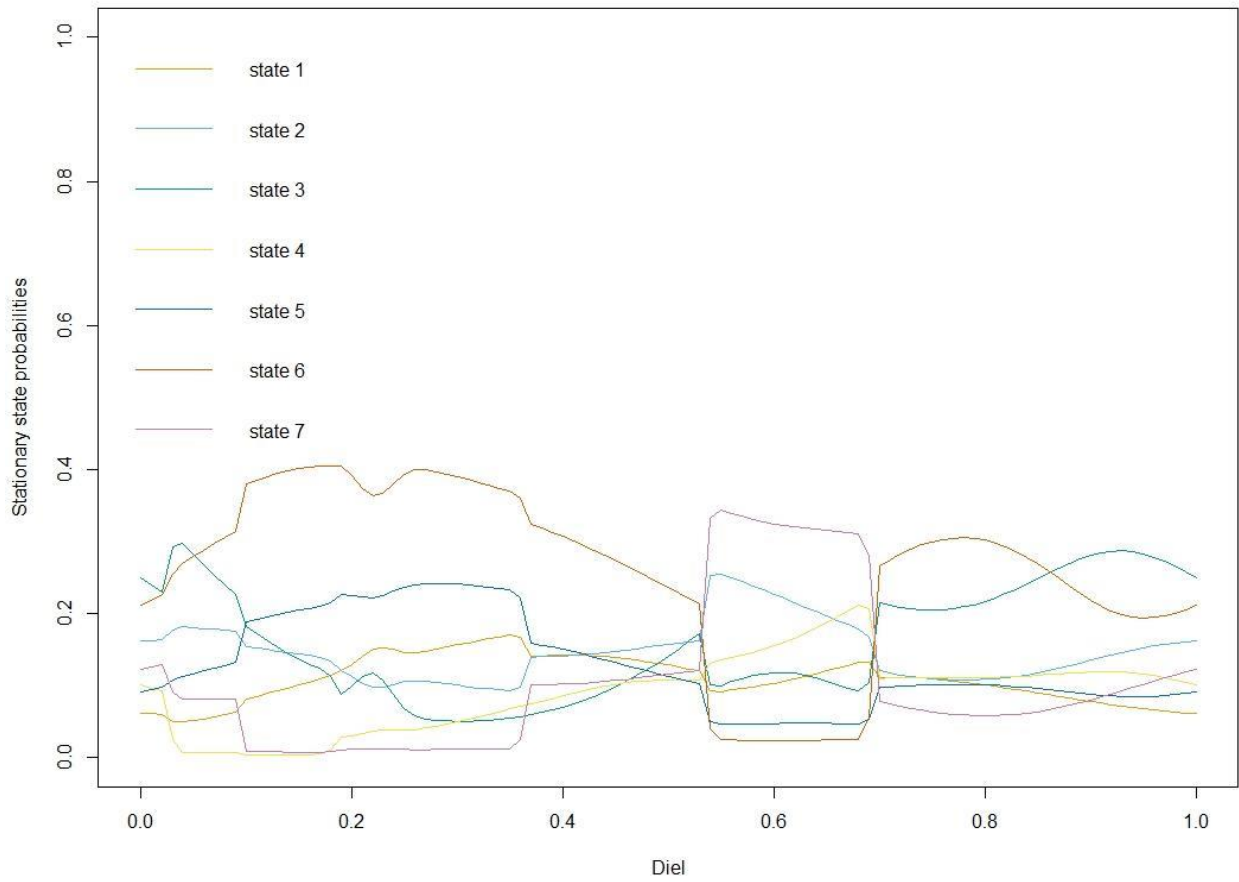


Figure B11. Stationary probability of each state across tidal phase