Large-scale and long-term passive acoustic monitoring of coastal bottlenose dolphins

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Abstract

Bottlenose dolphins in eastern Scotland are a protected and wide-ranging population exposed to a variety of stressors throughout their available habitat. Previously, most studies have focused effort on areas where animals are known to congregate. These areas are easily accessible and cost-effective for visual surveys. However, there is a need to understand the behaviour and habitat use of the population throughout its habitat. In response to this need, the Scottish Government initiated the East Coast Marine Mammal Acoustic Study consisting of 40 passive acoustic monitoring devices deployed along the coastline. While acoustic loggers are a cost-effective way of collecting longitudinal information, the returned data are subject to fluctuating detection probability and species misclassification. Subsequently there are two aims in this thesis. First, I seek to validate the use of autonomous detectors in large-scale and long-term studies where multiple species are present. This includes building a classifier to discriminate between groups of acoustically dissimilar species and investigating how transmission loss and ambient noise could bias occupancy results. Second, occupancy data from the array are analysed in order to understand spatial and temporal trends in habitat use and behaviour. The outputs of this thesis include an acoustic classification system capable of increasing the taxonomic resolution achievable in autonomous logger outputs and a framework for investigating detection probability in a complex acoustic system. The resulting habitat models were consistent with previous surveys showing that that depth and distance to the coast were important predictors for bottlenose dolphin presence. Finally, I found differing patterns in diel activity between a known foraging location and habitat not associated with foraging. Results from this thesis will provide tools for future researchers seeking to use passive acoustic monitoring techniques as well as baseline information about bottlenose dolphin habitat use and behaviour across the Scottish coastline.

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Collaboration and Publication Statement

The work (analysis, writing) used in Chapters 2 and 4 were published in a peer-reviewed journals:

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In both these papers, the candidate was responsible for conceiving both studies, processing the acoustic data, designing and implementing the analysis procedure, and drafting the document.

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Chapter 1

General Introduction

1.1. Overview

Many animals require a variety of habitats to meet their biological needs and these requirements vary with space and time. The temporal scale of any given species' habitat use can vary with life stage, season, or even circadian rhythms (Meyer et al., 2000, Heithaus and Dill, 2002, Barlow and Taylor, 2005, Nowacek, 2005, Moe et al., 2007, Wang et al., 2010, Onorato et al., 2011, Benjamins et al., 2017). Similarly, animal activity cycles vary over a variety of spatial and temporal scales. Most vertebrates follow circadian rhythms and many undergo seasonal migrations; shifting behaviour cycles and energy budgets throughout a migratory cycle (Egevang et al., 2010, Stevick et al., 2010, Stevick et al., 2016).

Understanding the ecological needs of animals as they shift between behavioural states and move within their habitat is paramount to conservation efforts (Sutherland, 1998, Anthony and Blumstein, 2000). Currently, the predominant methodology for enacting marine conservation measures is through the implementation of marine protected areas (MPAs). Within MPAs, activities that have the potential to negatively impact the conservation status of species may be regulated. MPAs usually have fixed boundaries, which means that only a part of the population of a wide-ranging highly mobile species will be present within the boundary at any one time. Networks of MPAs can help in such cases, but their effectiveness will depend crucially on accurately understanding the movements of animals across the population's range. Thus, complex spatial and temporal movements pose a challenge for efforts aiming to main critical habitat integrity and minimise negative interactions.

The focus of this thesis is on a small population of coastal bottlenose dolphins (*Tursiops truncatus*) that reside in the waters off eastern Scotland. Over the last several decades, this population has been extensively monitored. However, much of the work has focused on either areas of high foraging activity or the Special Area of Conservation (SAC) established for the population under the Natura 2000 network of the European Habitats Directive (Hastie et al., 2003a, Hastie et al., 2004a, Bailey and Thompson, 2006, New et al., 2013, Cheney et al., 2014, Merchant et al., 2014a, Pirotta et al., 2015a). These habitats, though ecologically important, represent only a small proportion of the habitat available to the population and through which they are known to transit. It is within these underserved areas that large offshore windfarms are planned. Thus, there is a need to understand if and how areas outside of the SAC are used by this population.

Gaining a basic understanding of the movement and behaviour patterns of cetaceans is extremely challenging. The entirety of their lifecycle takes place in the ocean and most animals are observable from the surface for only brief periods. This makes visual surveys and behaviour studies challenging. Fortunately, most produce acoustic signals (calls) that can be detected metres to kilometres away. Thus, for many species, it is often easier to detect them acoustically than it is to observe them visually. For this reason, bioacoustic studies have been implemented to address numerous biological and ecological questions.

Acoustic surveys are not without their challenges. Principal among these are detecting calls, discriminating between different acoustically active species, and deriving density and abundance estimates, accounting for environmental covariates that result in varying detection probabilities (Caillat, 2013, Frasier et al., 2016). Fixed acoustic recorders are often deployed for weeks and months at a time. Typically, this results in long periods without any animal detections punctuated by short bouts of acoustic activity. Finding these bouts of activity can involve a variety of different detection algorithms all with their own true positive, false positive, true negative and false negative rates. In the North Sea there are several species of dolphin, all of which produce echolocation clicks (Hammond et al., 2002a, Weir et al., 2007, Anderwald et al., 2010). Species misclassification can introduce bias into habitat use models if the non-target species are not accounted for. Similarly, the area monitored by acoustic instruments is dependent on the instrument settings and sensitivity, local bathymetry, water depth, and ambient noise levels (Kyhn et al., 2008, Kyhn et al., 2012, Nuuttila et al., 2013a, Sostres Alonso and Nuuttila, 2014). For example, acoustic instruments deployed near shorelines may monitor a smaller area than instruments deployed in deeper water where the instrument is surrounded by available habitat. These issues must be accounted for prior to attempting to address habitat use by any species using passive acoustic methods (Helble et al., 2013).

The overall aim of this thesis is to add to the existing body of knowledge concerning the habitat use and behaviour of bottlenose dolphins across the eastern Scottish coast. Data for this thesis rely exclusively on the passive acoustic detections produced by a long-term and large-scale passive acoustic study off the eastern Scottish coast. In Chapter 2 I build an acoustic classification system to reduce the influence of number of detections from non-target dolphin species on the occupancy models used in chapters 4 and 5. In Chapter 3 I address the potential bias caused by site-specific changes in detection probability using the sonar equations – a series of equations relating detection probability to the acoustic environment. After addressing these methodological issues, Chapters 4 and 5 investigate distribution and site-specific behaviour of dolphins, respectively. The remainder of this chapter discusses bottlenose dolphin ecology, passive acoustic surveys in general and lastly provides details of the acoustic array used in this study.

1.2. Conservation

The goals of conservation biology include maintaining biological diversity and ensuring continued community survival over time (Callicott et al., 1999, Trombulak et al., 2004). At the most basic level, for any given species, successful conservation efforts mean that mortality does not exceed fecundity over biologically relevant timescales. Typically, management and conservation plans focus on reducing the number of plants or animals killed through anthropogenic activities. Biological removal from a population may be either acute, resulting in immediate mortality (e.g. hunting, fishing, deforestation) or chronic where the reproduction rate is depressed through chronic exposure to a negative stimuli or deprivation (La Marca et al., 2005).Thus, for endangered populations managers must both mitigate acute mortality as well as maintain proper habitat integrity to avoid, or offset, chronic stressors.

Maintaining habitat integrity is arguably the larger task and is challenging particularly for highly mobile species. Migratory or far-ranging animals are exposed to a variety of different threats throughout their habitat. For example, in the Southern Ocean, the Tristan albatross (*Diomedea dabbenena*) populations have plummeted due to anthropogenic mortality in both land and sea. Mature albatrosses are routinely killed in long-line fishing gear (Cuthbert et al., 2005). Meanwhile, eggs and chicks are subject to predation from mice introduced to the nesting islands (Wanless et al., 2007). Furthermore, far ranging animals often cross human boundaries where protections may differ between regions. For instance, grey wolves (*Canus lupus*) are protected within Yellowstone National Park, USA, but face considerable hunting pressure outside the park boundaries (Naughton-Treves et al., 2003).

The order Cetartiodactyla includes a variety of species that are wide-ranging and or migratory. Throughout their habitat, all cetaceans are exposed to chronic and/or acute anthropogenic impact induced by ship-strike, entanglement, bycatch, hunting, chemical contamination, and anthropogenic noise (Lewison et al., 2004, Merrick and Cole, 2007, Wright et al., 2007, Jepson et al., 2016, Clapham, 2017). Therefore, understanding the biological needs of the animals throughout their habitat as well as the threats present is critical for conservation efforts to succeed.

Failure to understand habitat use can produce catastrophic consequences. For instance, in the summer of 2017 the foraging habitat of the North Atlantic right whales (*Eubalaena glacialis*) shifted from the Bay of Fundy where numerous measures were in place to reduce ship strike and entanglement to the Gulf of St Lawrence where no such measures existed. This resulted in the death of at least 17 individuals (Taylor and Walker, 2017). Over the last two decades habitat shift has been observed in bottlenose dolphins on the eastern Scottish Coast (Wilson et al., 2004). In the late 1990s a Special Area of Conservation (SAC) was proposed in the inner Moray Firth, the area believed at that time to contain the main area of concentration of the population(Cheney et al., 2018). However, in the years following the proposal of the MPA, the population’s range expanded and it has since been suggested that the SAC may thence afford less protection for the population than was initially intended (Wilson et al., 1997b, Wilson et al., 1999, Wilson et al., 2004, Thompson et al., 2013a).

1.3. Bottlenose Dolphins

1.3.1. Conservation Status and Populations

Bottlenose dolphins are a cosmopolitan species with populations found in tropical and temperate waters worldwide. While some populations may be decreasing in abundance (Currey et al., 2007, Bejder et al., 2006), the International Union for Conservation of Nature lists the species as a whole under the status of ‘least concern’, indicating a low risk of extinction (IUCN 2018). However, bottlenose dolphins are listed under Appendix 2 of the Convention on the Conservation of Migratory Species of Wild Animals (CMS) indicating they are in need of or would benefit from international co-operation on conservation efforts. They are also listed under Appendix II of the Convention on International Trade in

Endangered Species (CITES) which lists species for which trade must be controlled, as well as Annex IV of the European Habitats Directive which necessitates strict protection be applied across the whole of the species range within the EU.

Several ecotypes have been identified or proposed in different areas of the world. For example, in the Northwest Atlantic on and offshore ecotypes have been identified as distinct stocks with overlapping distributions (Torres et al., 2003). Similar near/offshore distinctions have been made throughout their range (Duffield et al., 1983, Hoelzel et al., 1998). Within the nearshore ecotypes, some populations are thought to be 'resident' and display annual or inter-annual site-fidelity while others undergo seasonal and/or annual migrations (Bearzi, 2005, Genov et al., 2008). Accordingly, home range sizes vary considerably between populations. In Sarasota, FL, USA the population is considered 'resident' and animals are infrequently sighted more than 20km from their 'core range'(Blair and Kaufmann, 1981). However, in eastern Scotland bottlenose dolphins frequently travel hundreds of kilometres between foraging locations.(Wilson et al., 1997a, Hastie et al., 2004b, Arso Civil et al., 2019).

1.3.2. East Scotland population

The bottlenose dolphin population in eastern Scottish waters is the only known 'resident' population of bottlenose dolphins in the North Sea and is protected by a variety of UK and EU legislation. Within the UK this includes the Wildlife and Countryside Act (1981), the Countryside and Rights of Way Act (2000). Additionally, bottlenose dolphins are listed as protected species under Annex IV (species of community interest in need of strict protection) of the EU Habitats Directive. The population is listed as 'recovered' at approximately 189 individuals with a credible interval of 155-216 individuals (Cheney et al., 2018). Since the 1990s, research on this population has provided invaluable information about the abundance, distribution, movements, fecundity and mortality rates of bottlenose dolphins as well as documented a range expansion (Hammond and Thompson, 1991, Wilson et al., 1997b, Wilson et al., 1999, Hastie et al., 2004b, Wilson et al., 2004, Bailey and Thompson, 2006, Cheney et al., 2013, Quick et al., 2014). However, these studies were largely undertaken within the bounds of the SAC reflecting the originally studied 'core' habitat of the population and highest density of animals. Since the late 1990s, research has focused increasingly in additional areas where animals are also concentrated, particularly the St Andrews Bay and Tay estuary area (Arso Civil et al., 2019). Several studies have elucidated factors likely to influence foraging activity as well as habitat selection and fine-scale such as tidal direction, bathymetry gradient and timing relative to the migratory cycle of salmonid fishes (Hastie et al., 2004b, Bailey and Thompson, 2006, Pirotta et al., 2014b, Arso Civil et al., 2019).

The lack of dedicated survey effort in offshore and more remote areas means that the overall distribution of the animals along the coast is not well documented. The most recent assessment of condition of the SAC and the status of the population is that since 2000 the number of dolphins using the SAC has remained stable but the proportion of the population using the SAC has declined by about 7% per year. The likely explanation is that the Scottish east coast population as a whole has increased. The condition status of the SAC is currently assessed as “Favourable (recovered)” (Cheney et al., 2018).

Presently, the population is known to utilise several estuaries outside of the Moray Firth, including Aberdeen (Dee estuary), Montrose Basin, the firth of Forth and the Firth of Tay (Culloch and Robinson, 2008). Approximately 52% of the population uses the St Andrews Bay and Tay Estuary during the summer (Arso Civil et al., 2019, Quick et al., 2014). These are considerably greater proportions than were initially thought to reside partially or primarily outside of the Moray Firth (Curran et al., 1996).

The drop in the proportion of animals using the SAC and the increase in the population have coincided with increased development of offshore renewable energy. Presently, two large offshore windfarms are planned for eastern Scottish waters. The Inch Cape wind farm will consist of 72 turbines placed 15km from the Angus coast, just north of the Firth of Tay. The Neart na Gaoithe wind farm consisting of 64 to 125 turbines is similarly planned for the waters off Fife. This raises the potential for negative interactions between the bottlenose dolphin population and anthropogenic activities resulting from the construction, operation and decommissioning of the turbines, and reinforces the importance of previous and current monitoring in areas outside the Moray Firth where animals are concentrated (Arso Civil et al., 2019, Quick et al., 2014).

1.3.3. Vocal Behaviour

Bottlenose dolphins are capable of producing a wide variety of acoustic signals including whistles, clicks, pops and brays (Au et al., 1978, Connor and Smolker, 1996, Janik, 2000a, Boisseau, 2005). These signals may be divided into three general categories; whistles, broadband clicks, and burst pulse sounds (Caldwell and Caldwell, 1965, Connor and Smolker, 1996, Janik and Slater, 1998, Perrin et al., 2009). Broadband clicks are the most frequently produced vocalizations and are used primarily for echolocation. Whistles are frequency modulated tones that are thought to function primarily in mediating social interactions (Tyack, 1997, Janik and Slater, 1998, Smolker and Pepper, 1999). Signature whistles, a subset of an animal's whistle repertoire, are used to broadcast the individual identity of the caller (Janik and Slater, 1998, King et al., 2014). Finally, burst-pulses consist of a series of broadband clicks with peak frequencies in the ultrasonic range with very short inter-click intervals. While burst-pulses are closer to clicks in structure than whistles, they are thought to be associated with socialising rather than foraging. (Overstrom, 1983, Ridgway et al., 1991, Herzing, 1996). Echolocation clicks, burst pulses, and whistles all contain species-specific characteristics that may help differentiate them from other species (Rendell et al., 1999, Rankin et al., 2017). Moreover, signature whistles may be used to track individual bottlenose dolphins and thereby help inform movement estimates (Caldwell and Caldwell, 1965, King et al., 2014).

1.3.4. Study Methodologies

Coastal bottlenose dolphins have been, and continue to be, some of the best studied cetacean populations. The relative ease of access to wild populations in addition to their robustness to disturbance (e.g. temporary restraint and/or captivity), have allowed researchers to learn more about this species than, arguably, any other cetacean species. Moreover, captive studies of this species have provide invaluable biological insights into the behaviour of both captive and wild animals including the cultural transmission of acoustic signals, development of acoustic signatures between cow/calf pairs, and the existence of behaviour-specific sound production (Overstrom, 1983, McCowan and Reiss, 1995a, McCowan and Reiss, Krutzen et al., 2005). Captive studies have also allowed for detailed physiological investigations into, among other things, caloric intake, growth rate, and husbandry (Peddemors et al., 1992, Kastelein et al., 2002, Wells, 2009).

However, field studies are still required to understand habitat selection, demographics, and the population-specific behaviour of wild populations. Survey methods for wild populations include focal follows with or without acoustic surveys, affixing temporary or permanent tags, and transect surveys (Blair and Kaufmann, 1981, Janik, 2000a, Hastie et al., 2004b, Quick and Janik, 2008, Thompson et al., 2011b). Depending on the research aims, field studies may use any combination of visual, acoustic, and tagging methods. Such studies have been integral in understanding habitat use and movement of bottlenose dolphins in general and the eastern Scottish population specifically (Wilson et al., 1999, Cox et al., 2004, Wilson et al., 2004, Currey et al., 2007, Cheney et al., 2013, Hammond et al., 2013).

Tagging studies involving GPS or satellite linked instruments have similarly provided information regarding swimming speed, dive duration, movement patterns, and survivorship of rehabilitated animals (Mate et al., 1995, Wells et al., 1999, Mazzoil et al., 2008, Balmer et al., 2010). However, tagging studies are generally invasive and provide detailed information on the targeted individual(s) only.

Focal follows provide detailed information on the behaviour of one or a few animals at a time. The method is often preferred when there is need to discriminate the behaviours of the target animals from those of nearby conspecifics. Focal follows typically involve either visual observations or combined visual observations with acoustic recording. Studies using visual only follows have been extremely successful in monitoring habitat selection by several bottlenose dolphin populations including those in both Scotland and Florida, USA (Allen, 2000, Arso Civil et al., 2019). Visual focal follows have also investigated the behaviour of animals in relation to anthropogenic activities such as tourism. Buckstaff (Buckstaff) showed a negative relationship between the amount of time animals spent resting and the number of tourism boats following the animals.

By incorporating visual observations with towed arrays, researchers can ascribe acoustic signals to specific animals or small groups of animals (Buckstaff, 2004, Fripp et al., 2005). This combined visual/acoustic methodology has been integral in the investigation into sound production under various environmental or behavioural conditions. For example, Quick and Janik (Quick and Janik) found that whistle rates of individual bottlenose dolphins decrease with increasing group size and increase when animals are socialising. However, the area of research that has likely benefitted most from combined visual/acoustic focal follows is signature whistle production in wild animals. Discoveries including signature whistle convergence among male ‘alliances’, signature whistle production during reunion events at sea, and signal whistle ontogeny, have all relied on focal follow methodology (Smolker and Pepper, 1999, Cook et al., 2004, Fripp et al., 2005, Quick and Janik, 2012). However, focal follows are necessarily limited in their sample population and may introduce artefacts into the analysis if animals react to the survey vessel.

Transect surveys are primarily used for density and abundance estimation. These surveys typically involve covering a defined area of the animals’ range with visual and/or acoustic observations. Transect surveys may include boat-based visual observations, visual observations from aircraft and/or towed array acoustic arrays. Transect surveys have been used in the Mediterranean, European Atlantic, western Indian, and the Gulf of Mexico (Blaylock and Hoggard, 1994, Forcada et al., 2004, Fazioli et al., 2006, Nicholson et al., 2012, Hammond et al., 2013).

All the methods discussed above have been instrumental in formulating understanding of bottlenose dolphin behaviour, demographics, and conservation. However, except for tagging studies and towed acoustic arrays, these methods all rely on visual observation of animals at the surface and are subsequently limited to periods of good visibility. This precludes or complicates research into diel trends, habitat use during periods of foul weather and/or when survey vessels are not available. As most acoustic studies are not strictly dependent on visual observations, they are able to collect valuable information by monitoring acoustic signals and behaviour of the animals while underwater.

1.4. Passive Acoustic Surveys

1.4.1. Bioacoustic Monitoring

The sounds of marine mammals were first noted during World War II when sonar operators noticed ‘biologic’ sounds when listening for enemy signals. Since then, interest in classification, detection and location of biological sounds in the ocean has increased exponentially. The field has evolved from focusing on military applications (e.g. was that a whale or a submarine?) to wider interest in the behaviour of the animals producing the sounds (Fish, 1956). For marine mammals, much of the early literature was dominated by captive studies of small odontocetes. These studies provide evidence of the first ‘biosonar’ or echolocation in cetaceans (Kellogg et al., 1953, Norris et al., 1961). Following these discoveries, researchers began investigating sound production by cetaceans in the wild. Early field studies led to the publication of numerous influential works including the existence of humpback whale ‘song’, species-specific contact calls, echolocation in porpoise, and early whistle repertoire descriptions (Payne and McVay, 1971, Mohl and Andersen, 1973, Taruski, 1979, Thompson et al., 1979, Clark and Clark, 1980). Acoustic studies are increasingly being used by researchers to monitor marine mammals and gain insights into their behaviour (Rendell and Whitehead, 2003). Though a variety of methods involving acoustics has been devised over the decades, acoustic survey methods can broadly be described as fixed, towed, focal follows, or hybrid methods.

Fixed bioacoustic studies involve holding recording instruments in place for the duration of the study. Because fixed acoustic studies are necessarily limited in the amount of habitat they survey, these surveys are often used for site-specific environmental mitigation and monitoring where offshore developments may be planned, or to monitor critical habitat (Thompson et al., 2013b, Merchant et al., 2014b). Long-term passive acoustic arrays have been integral to understanding of behaviour and habitat use of dolphins and porpoise in European waters (Thompson et al., 2010b, Simon et al., 2010, Sveegaard et al., 2011, Koblitz et al., 2014, Williamson et al., 2016). Long-term recording from fixed arrays has also led to the discovery of previously undescribed marine mammal sounds and behaviours including sei whale (*Balaenoptera borealis*) vocalisations and the continuation of humpback whale winter ‘song’ into the non-breeding season (Clark and Clapham, 2004, Baumgartner et al., 2008). In several areas passive acoustic arrays are being used to provide population monitoring for endangered or protected marine mammals (Jaramillo-Legorreta et al., 2017, Benke et al., 2014).

Towed surveys involve attaching one or several hydrophones to the back of a vessel travelling in a pre-determined pattern. Adding acoustic components to large-scale density and abundance surveys represents little added cost and can increase data coverage for cryptic species and/or when visual observations are untenable. Acoustic surveys have subsequently been the preferred study mythology for species in the Ziphiidae family (Rankin and Barlow, 2007, Baumann-Pickering et al., 2013). Towed surveys of various have allowed for the discovery of previously unknown habitats (Yack et al., 2013). For some species, towed arrays can provide insight into diving behaviour without the need for attaching recording instruments to the animals. However, as both the individuals and the vessel move throughout the environment, accurately assessing the number of animals that are present can be a challenge and is an ongoing area of research.(Marques and Buckland, 2003, Marques et al., 2013)

Focal studies include methods that aim to capture the vocalisations from a single animal or group of animals. This generally involves placing hydrophone(s) near or even on identified individuals or groups. Focal follows have been key in describing cetacean acoustic behaviour. Notable contributions from research involving focal follows include the existence of cultural ‘clans’ in sperm whales (Rendell and Whitehead, 2003) . Additionally, focal follows of wild animals are useful in gaining an understanding of the transmission characteristics of acoustic signals (Rasmussen et al., 2006, Janik, 2000b) which may be incorporated into applied studies (Kusel et al., 2011, Kyhn et al., 2012, Marques et al., 2012, Kusel et al., 2016).

Finally, hybrid surveys may involve acoustic instruments that shift in space and/or time. These surveys may include drifting sensors, such as DASBARs (Griffiths and Barlow, 2016), drifting sensors capable of determining range and bearing to signals (Sirovic et al., 2014), or drifting recorders or powered gliders (Klinck et al., 2012). The latter has shown potential in bridging the gap between towed and fixed sensors.

Like all survey methods, acoustic surveys are subject to limitation. Fixed acoustic surveys provide excellent temporal coverage but limited spatial coverage. Additionally, determining the detection range for calling animals is a challenge as multiple sensors are needed to localise acoustic signals. Conversely, towed surveys provide improved spatial coverage but limited temporal coverage. Accounting for the general movement of animals, avoidance or attraction to the survey vessel, and the movement of the survey vessel itself are challenging. Last, while focal follows provide in-depth information about the behaviour of a small proportion they cannot presently provide long-term monitoring or easily extrapolate findings to a larger population.

1.4.2. Detection and Classification

Over the past several decades, acoustic surveys have become an increasingly important component of marine ecological studies. As instrumentation and data storage costs have decreased, the amount of acoustic data collected has increased exponentially. This is especially true for fixed acoustic surveys which collect data 24hrs a day. A typical fixed acoustic array, involving only a few instruments deployed for three months, collects thousands of hours of continuous data. Processing these data for the presence and absence of animal calls has therefore become a primary challenge for long-term studies using fixed acoustic arrays. Consequently, automatic detection and classification algorithms for various species and call types have become developing at an increasing rate in both academic and commercial fields.

For dolphins, the disparity between the acoustic characteristics of tonal (e.g., whistles) and impulsive sounds (e.g. clicks) has led to the development of independent detection algorithms for each class of call. Early detection systems for impulsive sounds included simple energy detectors and matched filters for tonal sounds including whistles and large whale calls (Stafford et al., 1998, Mellinger and Clark, 2000, Gillespie and Chappell, 2002). However, in the decades following, approaches to detection and classification have diversified. For tonal sounds, classification algorithms include automatic edge detection and contour extraction as well as variety of statistics and modelling procedures (Roch et al., 2007, Moretti et al., 2008, Blumstein et al., 2011, Mellinger, 2012a, Denes et al., 2014, Mellinger, 2012b). Artificial intelligence and 'deep learning' have provided valuable steps forward in the automatic detection and classification of bioacoustic sounds of all types (Bahoura and Simard, 2010).

In addition to detection, ascribing bioacoustic signals to species has also been challenging. This is especially true for many small odontocetes, many of which produce similar clicks that are hard to differentiate. Even so, several authors have shown that echolocation clicks and/or click trains may contain species-specific information (Soldevilla et al., 2008, Baumann-Pickering et al., 2013). However, for single clicks, species classification is often confounded by the directionality of the clicks (Au et al., 1995, Au et al., 1999, Au et al., 2006, Wahlberg et al., 2011, Au et al., 2012b, Au et al., 2012a). When dealing with echolocation clicks alone, some authors have advocated grouping the echolocation click trains of acoustically similar species (e.g. common and bottlenose dolphins) together rather than attempt to classify individual species (Caillat, 2013). For example, in the Southern California Bight, the echolocation clicks of Risso's dolphins have proven difficult to distinguish from those of white-sided dolphin (Roch et al., 2008, Roch et al., 2011a). However, the clicks from both species differed considerably from those of common and white-beaked dolphins. Thus, where single species classification is not possible, studies may divide clicks into groups consisting of many similar species. Even so, significant progress has been made in classifying echolocation clicks and click trains to species. Both Klinck and Mellinger (2011) and Roch et al. (2011a) developed species classifiers for different geographic areas that consider echolocation click detections only. Still other systems incorporate information from both echolocation clicks and whistles (Oswald et al., 2003, Rankin et al., 2017) to increase classification accuracy.

In addition to the acoustic data, classification systems may also incorporate information from ancillary sources such as *a priori* knowledge of animal distribution or concurrent visual surveys. In the outer Moray Firth, Scotland, several species of dolphins are known to co-occur. One acoustic study in the area integrated previously documented species presence with acoustic detections to ascribe a proportion of the detections to non-bottlenose dolphin species (Thompson et al., 2015).

1.4.3. Detection Probability

Ecological surveys seeking to estimate species density, abundance or even occupancy must account for the survey effort (Buckland et al., 2005, Royle and Kéry, 2007). Depending on the survey design, survey effort is the combination of the total time spent looking, or listening, for the animals and/or the total area searched. In both visual and acoustic surveys, the total time spent looking or listening for animals is easily measured. However, calculating the effective area surveyed is more complicated. The area monitored is dependent on how far the animal may be detected from the survey point or transect. The detection function describes the relationship between the probability of observing an animal as a function of its range from the transect point or line. The integration of the detection function over the maximum detection range is referred to as the unconditional probability of detection (Buckland et al., 2005) and is key to most density, abundance, or habitat use survey. Failure to account for environmental effects that impact the detection function have the potential to seriously bias survey efforts and must be addressed in ecological modelling procedures (Helble et al., 2013, Marques et al., 2013).

Such variation in detection conditions are inherent to all field studies (Gonzalez et al., 2017, Hammond et al., 2013). Observational studies are affected by visual masking caused by low light levels or obstructions (e.g., vegetation, glare, or choppy ocean surface) and acoustic studies are similarly affected by noise masking and sound propagation conditions (e.g. acoustic shadowing, shipping noise). In both visual and acoustic surveys, fully accounting for the probability of detection is not always possible or practical. Thus, researchers have devised several methods capable of accounting for changes in detection probability. One method involves measuring environmental conditions on a broad or relative scale. Boat-based surveys often include weather and/or sea state measured on the Beaufort scale as categorical detection covariates (Marques and Buckland, 2003). In passive acoustic studies some authors have opted to either exclude periods of high ambient noise (Roberts and Read, 2014) or include noise level as categorical (low, medium, or high) detection covariate (Marques et al., 2011). However, such methods do not account for periods during which no animals were detected. This raises the question, were there no detections because animals (or their calls) were not present, or because they were masked by the environmental conditions? Thus, a more thorough approach involves including environmental covariates throughout the whole survey period (Royle and Kéry, 2007, Kéry, 2010).

In acoustics, the sonar equations have been used to describe the relationship between the probability of detecting an animal vocalisation, the environmental conditions, and the detection system (Urick). Authors have approached detection probability in acoustic studies by either using simulations of vocally active animals or *in situ* studies where the distance between animals and the sensors is measured by a visual observer. Simulation studies include those by Kusel et al. (2011), Helble et al. (2013), and Frasier et al. (2016). These researchers all used Monte-Carlo simulations to estimate the probability of detection and, ultimately, density of vocally active cetaceans. Alternatively, using visual observations from nearby cliffs, Kyhn et al. (2012) and Nuuttila et al. (2013b) measured the distance between animals and echolocation click loggers to empirically measure the detection probability under a variety of behavioural conditions.

When using commercial echolocation detectors such as C-PODs (www.chelonia.co.uk), observational approaches to detection probability are required as the manufacturer does not release or measure the performance characteristics (relationship between the probability of detecting a click and the amplitude at which it arrives) of the system. Even so, observational studies carry the additional benefit of being able to measure both how environmental conditions impact the probability of detection as well as measure the influence of behavioural state on the detection probability. Nuuttila et al. (2013b) found that the likelihood of detecting an echolocating bottlenose dolphin was highly dependent on the animals' behaviour; single dolphins, groups of dolphins, foraging, and travelling all resulted in different detection probabilities. Unfortunately, neither Nuuttila et al. (2013b) nor Kyhn et al. (2012) measured ambient noise levels or estimated local propagation conditions. Thus, while these studies investigated the behavioural aspects of detection probability, they did not account for the physics of sound transmission and the masking effect of ambient noise.

Accurately accounting for the detection probability at multiple instruments deployed in a variety of marine habitats is one of the primary methodological challenges of this thesis (Gregory and Rowden, 2001, Gannon et al., 2005, Bailey and Thompson, 2006).

1.5. The East Coast Marine Mammal Acoustic Study

1.5.1. Study Area

Previous visual studies using photo-identification have provided a solid starting point for cetacean habitat use outside of the SAC in areas where animals are concentrated. Monitoring areas of lower occurrence has not been a priority. In this study I use data from the ECoMMAS to fill this knowledge gap (Marine Scotland Science, 2013). The acoustic instruments of the ECoMMAS were, and continue to be, deployed in areas where visual survey coverage is lacking. Notably, this includes habitats up to 17 km from the coastline and areas exceeding the northern and southern extents of most visual surveys (e.g. Latheron and St Abbs). The first three years of the study alone resulted in over 9000 days of continuous data collection.

The ECoMMAS array consists of 30 C-PODs and ten continuous recorders (SM2Ms or SM3Ms, www.wildlifeacoustics.com, hereafter SMs) deployed along ~400km of the eastern Scottish coast (Figure 1-1). Deployment locations were chosen to maximize spatial coverage and minimize the likelihood of being displaced by storms or fishing activity. The array covers a variety of bottlenose dolphin habitats along the coast. Each deployment group is arranged approximately perpendicular from the coastline. In doing so, instruments in the array cover areas of known occupancy, such as the nearshore units in Spey Bay and Cromarty, as well as areas not thought represent key bottlenose dolphin habitats such as the offshore deployment locations.

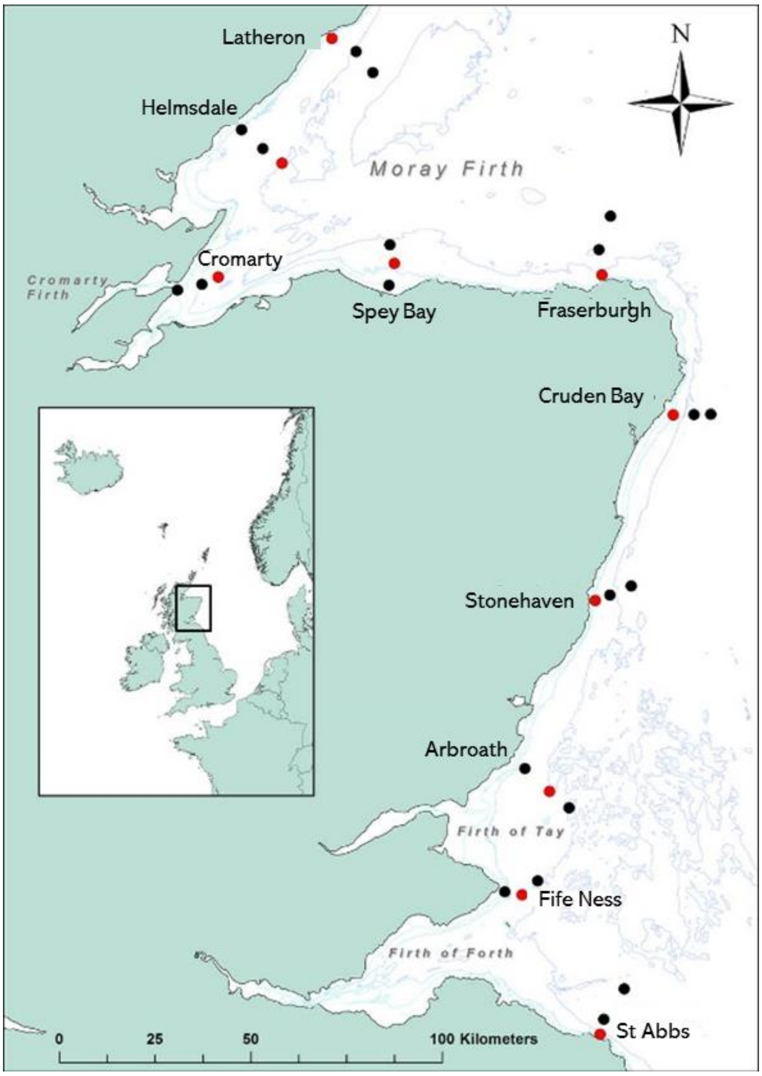


Figure 1-1 Survey locations for the ECOMMAS project C-POD (black) and joint C-POD/SM deployment sites (red). Deployment sites indicated by nearest large town: Latheron (Lat), Helmsdale (Hel), Cromarty (Cro), Spey Bay (Spe), Fraserburgh (Fra), Cruden Bay (Cru), Stonehaven (Sto), Arbroath (Abr), Fife Ness (FiN), St Abbs (Stb). All units were placed at approximately 5, 10, or 15km from the coast.

All units were moored to the seafloor using 100kg chain weights. Some deployments were furnished with surface markers, while others had acoustic releases to facilitate recovery. The choice of mooring type was based upon vessel traffic in the deployment location. C-PODs were deployed in ten groups of three, with moorings within the group deployed approximately 5, 10 and 15 km from the coast. Mooring locations are hereafter referred to as 5, 10, and 15 to indicate that distances from shore were approximate values only. One SM was co-deployed with one of the C-PODs at each deployment group. The SM was attached to the same mooring line as the C-POD and the units were separated by more than one metre.

The full ECoMMAS array was deployed in the spring of each year (2013-2015) and recovered in the autumn of the same year. In 2015 there were two deployments with the array first being deployed in early spring and subsequently being recovered and re-deployed in July. The second deployment in 2015 was then recovered in autumn of the same year. Of the 30 C-PODs in each deployment an average of 6.5 C-PODs per deployment were either lost or failed to collect data. Data from 2013 were used in chapters 2 and 3 while data from 2013-2015 were used in chapters 4 and 5

1.5.2. Instrumentation

Echolocation Click Loggers (C-PODs)

C-PODs (http://www.chelonia.co.uk) and their predecessor TPODs are low-cost echolocation click loggers. The instruments represent a class of detector called zero-crossing recorders. C-PODs are low cost in comparison to most consumer acoustic recorders and simple processing procedures make them attractive for large-scale surveys (Carstensen et al., 2006a, Thompson et al., 2010a, Kyhn et al., 2012, Brookes et al., 2013, Jaramillo-Legorreta et al., 2017).They are different from continuous recording systems that measure sound pressure a specified number of times per second (the sampling frequency) by the electrical output of a piezoelectric sensor. Instead, C-PODs work by recording the time of every Nth oscillation of the piezoelectric element that crosses the neutral position (zero crossing). Thus, in the absence of any signal, the C-POD collects no data as the piezoelectric element is not moving. Similarly, high frequency sounds consisting of short periods will produce more data than low frequency sounds with longer periods between subsequent oscillation. Unlike most commercial recorders that allow users to select the sample frequency, in C-PODs ‘N’ is set by the manufacturer and not disclosed. The data collected by C-PODs are processed for the presence of echolocation click trains using proprietary classifiers that require validation by outside user groups.

The click features (referred to as “details” in the accompanying software) logged by C-PODs are non-standard in the acoustics field and so require careful interpretation. Specifics of the click features are proprietary and defined by the manufacturer as the time of the click, measured with 5μs resolution, dominant zero-crossing frequency (fZC, which should not be confused with peak frequency), end zero-crossing frequency (derived from the last zero-crossing interval), bandwidth measured on an "arbitrary scale" (manufacturers description), and click duration measured as the number of cycles at the dominant frequency (NCycles). C-PODs also document a metric of amplitude which, though reported as sound pressure level, is not corrected for hydrophone frequency response (Dahne et al., 2013).

Laboratory studies have investigated the detection thresholds, and directivity pattern of the C-POD instrument, and field studies have measured the detection radius of the system (C-POD plus KERNO classifier) and made direct comparisons with adjacently deployed continuous recorders (Dahne et al., 2013, Nuuttila et al., 2013b, Verfuß et al., 2013, Roberts and Read, 2014, Sostres Alonso and Nuuttila, 2014). Laboratory validation found that C-PODs minimum detection thresholds were generally consistent between instruments and sensitivities were roughly uniform (Dahne et al., 2013). *In situ* studies reported very low false positive detections rates for the system but found that the detection radius varied considerably depending on the deployment depth and the behaviour of the animals around the system (Nuuttila et al., 2013b, Roberts and Read, 2014, Sostres Alonso and Nuuttila, 2014).

Both C-PODs and T-PODs have been used extensively to monitor dolphin and porpoise habitat use in the Moray Firth. Results from these studies have provided insight into the relative density of animals, winter habitat use, effects of ambient noise, and foraging behaviour of both species (Thompson et al., 2011a, Brookes et al., 2013, Thompson et al., 2013a, Thompson et al., 2013b, Bailey et al., 2014a, Pirotta et al., 2014a, Williamson et al., 2017). However, one of the major challenges in passive acoustic monitoring in general and with C-PODs in particular is discriminating between different odontocetes. While C-PODs reliable discriminate between porpoises and dolphins they cannot so easily discriminate between multiple dolphin species.

In the Inner Moray firth, bottlenose dolphins are the most frequently sighted odontocete and passive acoustic studies routinely assume that all detections represent bottlenose dolphins. However, the same assumption does not hold outside of the Moray Firth where multiple delphinids are known to inhabit the same area (Weir et al., 2007, Anderwald et al., 2010). Recent studies have begun to address this issue by using visual surveys to predict the probability that a given echolocation click train was produced by bottlenose dolphins (Thompson et al., 2015). However, this methodology relies on the presence of both types of surveys in the area and provides little temporal resolution. As such, similar studies for the entire coastline are not practical for the ECoMMAS and there is subsequently a need to develop a classification system for C-POD detections.

Continuous Recorders (SMs)

Acoustic recorders sample the pressure on the hydrophone at a given rate, accurately recording the acoustic environment between the minimum response frequency of the hydrophone and the Nyquist frequency. Numerous marine recording systems are commercially available and vary considerably in cost and deployment specifications. The ECoMMAS used SM2Ms and SM3Ms (www.wildlifeacoustics.com, hereafter SMs). In 2013 the duty-cycle was set to a 10 min 50/50 on/off sequence. In subsequent deployments the duty-cycle was set to 10 min on 20 min off in order to increase data coverage period. Post-processing the acoustic data for the presence of echolocation clicks (Chapter 2) and ambient noise levels (Chapter 3) was done using freely-available PAMGuard software (Gillespie et al., 2009).

1.6. Thesis Structure

In this thesis my primary aim is to add to the existing knowledge of bottlenose dolphin habitat use and behaviour by investigating large scale trends in acoustic occupancy. However, because of the complexities in using C-POD detectors, the first two chapters of this thesis aim to validate the available data to ensure that the occupancy values are primarily based on detections of the species of interest and are robust to changes in detection probability. Building on the first two chapters, the following chapters add to the existing knowledge of the habitat use and behaviour of the eastern Scottish bottlenose dolphin population.

In Chapter 2, I compare groups of echolocation clicks recorded by the SMs to the echolocation features documented by the C-PODs. I build a classification system that is capable, with considerable variation, of discriminating between the echolocation clicks to two groups of dolphins white-beaked and Risso’s (*Lagenorhynchus albirostris, Grampus griseus*) vs. short-beaked common (*Delphinus delphis*) and bottlenose dolphins.

In Chapter 3, I investigate whether site-specific transmission loss and continuously varying ambient noise levels measured across the ECoMMAS array have the potential to bias the relative occupancy rates produced by the C-PODs. In this Chapter I use the sonar equations to estimate how much changes in detection probability may influence the occupancy rates reported by the C-PODs. Because C-PODs are black-box detection systems I was not able to account for the detector performance. Because of the lack of detector performance metrics, here I focus on the implications of bias in the detection probability rather than the exact calculation of the detection probability.

In Chapter 4, I use the results of Chapters 2 and 3 to investigate dolphin acoustic occupancy rates produced by the ECoMMAS array where acoustic occupancy is defined as the binary presence/absence acoustic signals of the species of interest. The chapter reports the proportion of days where dolphin click trains were detected (acoustic occupancy rate) at the 30 deployment sites across the first three years of the study and uses generalised estimating equations (GEEs) to model temporal trends in detections at each of the deployment groups. Finally, generalised additive mixed models (GAMMs) are used to model and map bottlenose dolphin acoustic occupancy across the entire eastern Scottish coastline.

In Chapter 5, I look for trends in detections on an hourly scale. As with Chapter 4, this chapter uses the results of Chapter 2 to discriminate between the echolocation click trains of different species present in the array. I use GAMMs to model the probability of detecting an echolocation click train at different locations in the array as a function of diel and tidal phases.

In Chapter 6, I synthesise ecological implications from Chapters 4 and 5 into the wide body of knowledge currently available for this population of bottlenose dolphins. I also discuss where passive acoustic monitoring studies fit in the overall conservation aims for this population and how data from the ECoMMAS array specifically can contribute to those aims. Finally, I also investigate whether large-scale passive acoustic monitoring surveys for this population of bottlenose dolphins are, in fact, as cost effective as touted (Van Parijs et al., 2009).

Chapter 2

Increasing the Taxonomic Resolution of Echolocation Click Loggers

2.1. Introduction

Passive acoustic monitoring is an established method of studying the movement, distribution and behavior of acoustically active species (Fenton, 1982, Van Parijs et al., 2009, Brookes et al., 2013, Kalan et al., 2015, Kloepper et al., 2016). The field of cetacean ecology has especially benefited from advances in acoustic monitoring as these animals are largely visually inaccessible to researchers for the majority of their lives. Moreover, cetaceans produce acoustic signals that can be detected by acoustic recorders and data loggers. Accordingly, passive acoustic monitoring has provided invaluable insights into the habitat use (Mellinger et al., 2007, Van Parijs et al., 2009), communication (Parks et al., 2009), population size (Jaramillo-Legorreta et al., 2017, Harris et al., 2013), and behavior (Buckstaff, 2004, Koschinski et al., 2008, Nuuttila et al., 2013b, Pirotta et al., 2014b) of multiple genera. Moreover, passive acoustic monitoring is directly involved in both long-term and real-time conservation efforts for protected cetacean species (Clark et al., 2005, Van Parijs et al., 2009, Jaramillo-Legorreta et al., 2017, Klinck et al., 2012).

Taxonomic classification of the echolocation clicks of odontocetes is an ongoing problem in passive acoustic surveys. The received characteristics of any given click depend on the animal’s behavior as well as the filtering effects of the cranial anatomy, the propagation environment and the parameters of the recording system (Au et al., 1985, Au et al., 1995, Carlström, 2005, Johnson et al., 2006, Deruiter et al., 2009, Au et al., 2012a, Roch et al., 2015). Since echolocation signals are highly directional, the received amplitude and spectral characteristics of echolocation clicks further depends on the orientation of the vocalizing animal with respect to the receiver (Rasmussen et al., 2004, Wahlberg et al., 2011, Au et al., 2012c). Together, these filtering effects render it virtually impossible to classify individual echolocation clicks to species.

Researchers have addressed the classification task by averaging echolocation click characteristics across multiple clicks, click trains, and/or acoustic encounters. In doing so, group and species-specific features in echolocation clicks have been discovered. For example, Baumann-Pickering (Baumann-Pickering et al., 2013) compared the location of satellite tagged animals to passive acoustic recordings and was able to describe species-specific characteristics of false killer whale (*Pseudorca crassidens*) and short finned pilot whale (*Globicephala macrorhynchus*) echolocation clicks. Similarly, distributions of peak frequency, center frequency, click duration, inter-click interval (ICI) and bandwidth have been useful in discriminating between the echolocation clicks of melon-headed whales (*Peponocephala electra*), Gray's spinner dolphins (*Stenella longirostris longirostris*) and to a lesser extent, bottlenose dolphins (*Tursiops truncatus*) (Baumann-Pickering et al., 2010). In other studies, the structure of the frequency spectrum has proven useful in classifying click trains. In the Pacific, the echolocation clicks of white-sided dolphins *(Lagenorhynchus obliquidens)* and Risso's dolphins (*Grampus griseus*) have been shown to display consistent peaks and notches in spectral energy below 48 kHz (Roch et al., 2007). Risso's dolphins click trains contained peaks in energy at 22.4, 25.5, 30.5 and 38.7 kHz and at 22.2, 26.6, 33.7 and 37.3 kHz for white-sided dolphins. The spectral location was sufficient to discriminate between the two species but site and instrument-specific anomalies reduced the confidence of the classifications (Roch et al., 2007). In the same habitat, bottlenose dolphin and common dolphin (*Delphinus delphis*) echolocation clicks were found to have a more uniform energy distribution between 40 and 80 kHz (Soldevilla et al., 2008). Echolocation clicks from these species were nearly indistinguishable but easily discriminated from the peak and notch structure of Risso's and white-sided dolphins, especially when site and instrument specific parameters were accounted for (Roch et al., 2011b, Roch et al., 2015). Uniform energy between 40-120 kHz was recorded for on-axis clicks of bottlenose dolphins in the Indian Ocean, and held for off axis angles up to ~13°, beyond which peaks and notches in energy were observed but were dependent on the angle between the animal and the recording system (Wahlberg et al., 2011). Similarly, in the North Atlantic Calderan et al. (2013) investigated whether the peaks and notches in spectral energy observed in Pacific animals were also present in clicks produced by Risso's and white-beaked dolphin (*Lagenorhynchus albirostris*), the latter having morphologically similar cranial structure to Pacific white-sided dolphins. A towed arrays in western Scottish waters suggested that a similar peak-and-notch structure was present in both species (Booth et al., 2011). Taken together, these studies suggest that the presence of stable peak-and-notches in spectral energy may be useful for increasing taxonomic resolution from acoustic recordings.

While significant progress has been made in classifying echolocation clicks in continuous recordings, little effort has been directed toward classifying echolocation clicks in click logging devices. C-PODs (Chelonia, Ltd.) are commercially available click logging devices popular in marine studies. The C-POD system returns a series of summary parameters related to detected clicks but does not save the waveform of the clicks themselves. Consequently, the volume of data collected by these systems is drastically less, while some of the click frequency/time information is preserved. Such systems are efficient, have low false positive detection rates, and produce generally consistent output between units (Dahne et al., 2013, Roberts and Read, 2014). For these reasons, C-PODs are a popular tool used to study odontocete behavior and ecology worldwide (Carstensen et al., 2006b, Koschinski et al., 2008, Bailey et al., 2010, Pirotta et al., 2014a, Jaramillo-Legorreta et al., 2017). For species with mid- to high-frequency echolocation clicks, long-term and full spectrum (*fs* >200 kHz) continuous recordings are often impractical due to the high up-front cost of continuous recorders, high data volumes, time-consuming post-processing to extract echolocation clicks, and limited recording duration compared to click loggers.

Data collected by the C-POD data are generally processed to detect the presence of odontocete echolocation click trains with the accompanying KERNO classifier. The KERNO software is capable of discerning between dolphin and porpoise clicks based on the frequency and bandwidth of the detections. However, C-PODs currently lack the ability to discriminate between most dolphin species. Thus, where users can be relatively confident that only the target dolphin species is present, the use of C-PODs has proven to be both cost and time effective (Simon et al., 2010, Pirotta et al., 2015a). However, where the scientific and/or regulatory concern focuses on a single species within a large habitat, the ability to discriminate between target and non-target species becomes a critical aspect of the research methodology.

The motivation for this study is the need to efficiently monitor the resident population of bottlenose dolphins found on the eastern coast of Scotland. This population is protected by a variety of UK and EU regulations including the designation of a Special Area of Conservation (SAC) in the Moray Firth. However, the population expanded its range in the 1990s (Wilson et al., 2004, Cheney et al., 2014) and the proportion of the population using the SAC is decreasing (Cheney et al., 2018). Additionally, the construction of large offshore wind farms is planned off Eastern Scotland for the coming years. Determining what effect, if any, the construction, operation, and decommissioning of these structures will have on these animals is important for long term conservation goals. Thus, a better understanding of how the population uses the entire Eastern Scottish coast habitat is needed.

One of the primary challenges to meet this objective using passive acoustic monitoring techniques lies in discriminating between target (bottlenose dolphin) and non-target species known to occur in the area. These include common dolphin, Risso’s dolphin and white beaked dolphin (*Lagenorhynchus albirostris*) (Weir et al., 2007, Quick et al., 2014). Thompson et al. (2013a) addressed the multi-species concern by integrating visual observations of various dolphin species and echolocation click detections from C-PODs. In their study, effort-controlled visual survey data from 1980 through 2010 were combined with up to three seasons worth of C-POD detections from the Moray Firth. Results from their study strongly suggested that bottlenose dolphins primarily occupy the nearshore areas (<10 km from the coast) within the inner Moray Firth while a greater diversity of dolphin species were found in the offshore waters.

Discriminating between any dolphin species in C-POD data would represent a major step forward in the application of such systems in multi-species contexts. This challenge of species discrimination has been recognized and approached by researchers working with a similar group of species in Irish waters (Robbins et al., 2016). In that study the authors used multi-dimensional scaling techniques to try and discriminate between visually-confirmed Risso’s, common and bottlenose dolphin detections in C-POD data. The authors found that the limited metrics produced by the C-POD system in combination with their own post-processing metrics were insufficient to classify detections to species. This result is unsurprising given the difficulty in discriminating between common and bottlenose dolphin clicks even with continuous, full-spectrum recordings (Soldevilla et al., 2008, Roch et al., 2011b).

In the present study I investigated the potential for discriminating between echolocation clicks with distinct peaks and notches, hereafter termed “frequency banded” and those that, when averaged across encounters, lack distinct peaks and troughs in spectral energy below 48 kHz, referred to hereafter as “broadband”. I denote this task as “categorization” rather than classification as I am not seeking to identify the exact species producing the click-types. I used data from acoustic recorders deployed alongside C-PODs to build a model that discriminated between broadband and frequency-banded clicks in C-POD data, and then used this model to classify data from a larger set of C-PODs for which there was no co-deployed recorder.

2.2. Methods

2.2.1. Data Collection

Acoustic recordings and C-POD logs from the first year of the ECoMMAS study (2013) were used in the analysis of this chapter. Because ten of the C-PODs were deployed on the same moorings as the SM2Ms, I was able to compare the continuous recordings from the SM2Ms, from which I could identify broadband and frequency banded echolocation click trains, to the C-POD detection logs. The C-PODs logged continuously from the deployment date, while SM2Ms were programmed to commence recording on August 13^{th}, 2013 with a 10 minute on/off duty cycle and sampling rate of 96 kHz and 12 dB gain. All units recorded until their battery capacity was exhausted and were recovered between October and November of the same year, as weather allowed (Table 2-1). For units displaced during the deployment, the C-POD outputs related to temperature, angle of the device and sonar detection were examined to determine the date on which the device was moved out of position. All data from midnight of that day onwards were removed from the analysis.

Table 2-1 Locations, dates and number of days for which usable data were obtained for all deployed devices (SM suffix indicates SM2M units, all others are C-PODs). For C-PODs, the number of click trains logged, the number of acoustic encounters, and the number of broadband or frequency banded click trains contributed to the training dataset, along with – in parentheses – the number of unique days represented by that contribution, are also given All dates are dd/mm in 2013. Five C-POD deployments that returned no usable data are omitted – Spey Bay 15, Fraserburgh 10 and 15, Cruden Bay 10, and Stonehaven 10.

Location name (SM=SM2M unit)	Data From	Data To	# Days	# Click Trains	# Encounters	Training Data: Broadband	Training Data: Frequency-banded
Latheron 05	31/07	23/10	84	480	26		337 (9)
Latheron 05 SM	10/08	14/10	65				
Latheron 10	20/06	09/10	111	71	3		
Latheron 15	20/06	07/10	109	36	4		
Helmsdale 10	20/06	10/10	112	144	6		
Helmsdale 05	01/08	22/10	82	0	0		
Helmsdale 15	20/06	06/10	108	5	1		
Helmsdale 15 SM	10/08	25/09	46				
Cromarty 05	01/08	21/10	81	3680	199		
Cromarty 10	01/08	25/08	24	105	9		
Cromarty 15	01/08	23/10	83	23	4	22 (2)	
Cromarty 15 SM	10/08	15/10	66				
Spey Bay 05	24/07	22/10	90	330	24		
Spey Bay 10	20/06	06/10	108	0	0		
Spey Bay 10 SM	10/08	12/10	63				
Spey Bay 15	-	-	-				
Fraserburgh 05	25/07	24/10	91	859	21		303 (8)
Fraserburgh 05 SM	10/08	07/10	58				
Fraserburgh 10	-	-	-				
Fraserburgh 15	-	-	-				
Cruden Bay 05	26/07	26/11	123	910	29		
Cruden Bay 05 SM	10/08	12/10	63				
Cruden Bay 10	-	-	-				
Cruden Bay 15	19/06	26/11	160	541	31		
Stonehaven 05	26/07	26/11	123	955	34	226 (7)	32 (2)

Stonehaven 05 SM	10/08	03/10	54			
Stonehaven 10	-	-	-			
Stonehaven 15	19/06	26/11	160	1047	77	
Arbroath 05	27/07	26/10	91	224	16	
Arbroath 10	27/07	25/10	90	20	2	
Arbroath 10 SM	10/08	11/10	62			
Arbroath 15	21/06	27/11	159	887	44	
Fife Ness 05	27/07	28/10	93	183	22	
Fife Ness10	27/07	28/10	93	0	0	
Fife Ness 10 SM	10/08	18/10	69			
Fife Ness 15	21/06	10/10	111	55	3	
St Abbs 05	27/07	27/11	123	55	6	5 (1)
St Abbs 05 SM	10/08	03/10	54			
St Abbs 10	27/07	25/10	90	71	4	
St Abbs 15	20/06	27/11	160	72	8	

2.2.2. C-POD Click Detection and Feature Extraction

C-POD data were downloaded and processed for echolocation click detections using the manufacturer's software and accompanying KERNO classifier (v2.042). The KERNO software classifies impulsive detections into one of the following four groups: "Sonar", "NBHF" (narrowband high-frequency click trains often indicative of porpoise species), "Other Cet" (wideband clicks indicative of most dolphin species) and "Unk" (representing unclassified/unknown clicks). The C-POD software and KERNO classifier group "NBHF" and "Other Cet" signals into short "click trains" based on temporal proximity and assign a "click train ID" to each such group. The manufacturer states that this detection and classification system allows multiple clicking animals to be differentiated from each other. The KERNO classifier also assigns a quality class to each detection (high, moderate, or low) indicating the probability that the click train was correctly discriminated from other "non-train" sources such as snapping shrimp or rain (Tregenza, 2016).

For this analysis, all "high" or "moderate" quality "Other Cet" detections were selected, and the accompanying click features, referred to as "click details" by the manufacturer, were exported to a text file. For each click train (i.e. all clicks with the same "click train ID"), I also calculated the median inter-click-interval, mean dominant zero-crossing frequency, mean bandwidth and mean click duration (NCycles).

2.2.3. C-POD Data Quality

Initial data exploration was undertaken to identify collinearity between click train features documented by the C-POD. The distributions of all train features were visually inspected, and I excluded all click trains for which there were insufficient data to produce reliable models (i.e. the tails of the distributions). Thus, all click trains with median inter-click-intervals greater than or equal to 0.4 seconds, mean click durations greater than or equal to 11 cycles (NCycles), mean bandwidths greater than or equal to 7 (manufacturers arbitrary units), or dominant frequencies less than 30 kHz were excluded from the categorization portion of the analysis (resulting in the removal of ~1% of all logged click trains).

I then grouped C-POD click trains into “acoustic encounters,” consisting of all click trains on the same C-POD occurring within 30 minutes of another click train (Thompson et al., 2011a). In this process I assumed that each encounter was produced by the same animal or group of animals and that groups of acoustically dissimilar species (e.g., Risso’s and bottlenose dolphins) were not represented in the data. This is consistent with visual observations indicating that mixed odontocete groups, especially any containing bottlenose dolphins, are extremely rare in Scottish coastal waters (Ross and Wilson, 1996, Hammond et al., 2002b).

2.2.4. Identifying Broadband and Frequency Banded Click Trains in the C-POD Detections

The few click features documented by the C-POD system are not sufficient to allow users to visually discriminate between click trains matching the broadband and frequency banded categories described above. Thus, I used continuous recordings to identify time periods with clearly identifiable bouts of broadband or frequency banded click trains. These periods were compared to the click log produced by the C-POD at the same mooring. Where echolocation click trains were present on both instruments at the same time, I assumed that the echolocation click trains had originated from the same animal or group of animals.

Data from the SM devices were downloaded, converted to spectrograms (1024 point fast-Fourier transform, 10.67 ms window, and 50% overlap) and processed for echolocation clicks using PAMGuard click detecting software (Gillespie et al., 2009). Click detection trigger was set to 10 dB and click detections were manually scanned for the presence of high signal-to-noise echolocation click encounters and annotated as such. Echolocation clicks from high SNR encounters containing at least 500 clicks were extracted and the average spectrum was inspected for the presence of either distinct peaks or notches in energy indicative of white-beaked or Risso's dolphins or unimodal energy between 20 and 40 kHz suggestive of bottlenose and/or common dolphins. While visually inspecting the continuous recordings for high SNR frequency banded click trains, I did not seek an exact match the location of the spectral energies as reported by Calderan *et al.* (2013) or Soldevilla et al. (2008). Both environment and recording equipment impart site and equipment-specific filter effects on the received signals (Roch et al., 2015), so I expected some variation in the received characteristics of echolocation clicks. Neither did I attempt to differentiate between species within the two click encounter types (e.g. common vs bottlenose dolphin). Instead encounters where the average spectrum contained at least two peaks in energy between 35 and 43 kHz and with >3 dB peak-to-peak difference between successive peaks and notches were annotated as "frequency banded". Click encounters for which there was a unimodal peak in energy between 20 and 30 kHz were annotated as broadband (Figure 2-1).

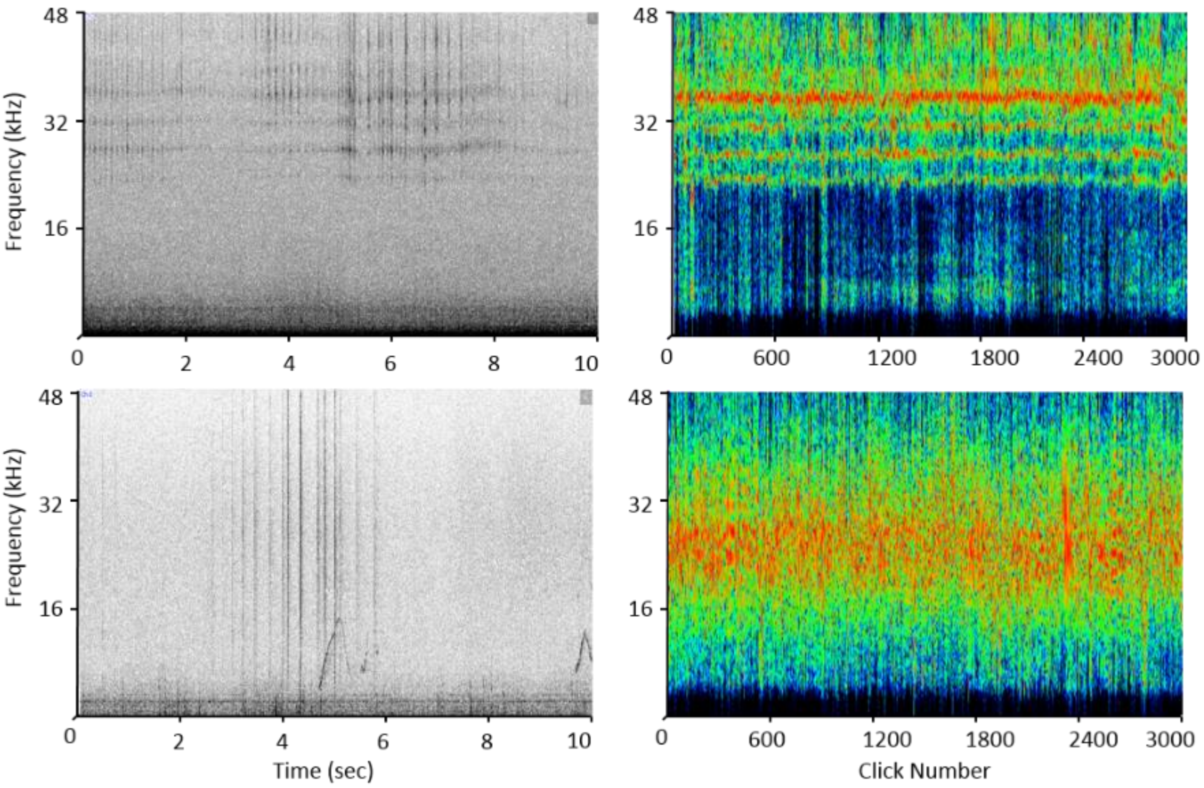


Figure 2-1 Spectrograms (left; fs 96 kHz,, 10.67 ms Hann window, 50% overlap) and concatenated click spectrums (right) of echolocation clicks within from frequency banded (top) and broadband (bottom) acoustic encounters. Top row: 10 seconds of recordings from a frequency banded encounter consistent with white beaked and/or Risso's dolphins and 3000 concatenated echolocation clicks from the frequency banded encounter. Bottom row: 10 seconds of recordings from a broadband encounter containing whistles and echolocation clicks consistent with bottlenose and/or common dolphins.

The times of acoustic encounters documented by the C-PODs were compared with the times of broadband and frequency banded click trains observed in the continuous SM2M recordings. The train features from "high" or "moderate" quality "other cetacean" trains coinciding with visually confirmed broadband and frequency banded encounters in the continuous recordings were used to build and train categorization models.

To increase the volume of C-POD click trains from broadband encounters, click train features from the Cromarty 05 C-POD, for which there was no adjacent SM2M recorder, were randomly selected for inclusion in the broadband training dataset. Despite the lack of concurrent acoustic recordings, I am confident that the vast majority of the click trains logged by the C-POD at this location were produced by bottlenose dolphins and as such represented my broadband category. The area in and around the Cromarty and inner Moray Firths has been continuously surveyed for the last 25 years and is a well-known bottlenose dolphin habitat (Hammond and Thompson, 1991, Wilson et al., 2004, Cheney et al., 2013, Thompson et al., 2015, Pirotta et al., 2015b). These studies strongly suggest that no dolphin species besides bottlenose regularly occupy the area. To further reduce the probability of including frequency banded click trains in the broadband training data, only click trains from the month of August, coinciding with timings from the majority of visual surveys, were added to the training dataset.

Obtaining a representative sample of echolocation click behaviors is important in order to produce an accurate categorization system. Of the 1195 C-POD click trains that could be linked to trains in the adjacent SM recordings only 270 (22%) were broadband. I added only as many click trains from the Cromarty 05 site as needed to provide an equal number of broadband and frequency banded click trains for the categorization task. I could have reasonably included all of the data from the Cromarty 05 C-POD based on the overwhelming evidence showing that the area is primarily occupied by bottlenose dolphins. However, I chose to limit the number of auxiliary click trains included from this C-POD for two reasons. First, the Cromarty 05 unit contained almost as many “OtherCet” click trains as the other 25 recovered C-PODs combined. Therefore, I sought to reduce potential bias introduced by site-specific behavior present in the data from that unit. Second, the Cromarty Firth is a known “hotspot” for bottlenose dolphin foraging (Hastie et al., 2004b, Hastie et al., 2006, Pirotta et al., 2014b). Thus, I would expect to document more clicks with shorter inter-click-interval (reflecting the production terminal buzzes characteristic of prey capture attempts) near that location (Pirotta et al., 2014b). Including an excessive number of buzzes in the training data would introduce bias towards low ICI’s within the broadband category.

2.2.5. Model-based Prediction and Categorization

The above procedures generated a set of C-POD click trains, with measured features, for which I was reasonably confident of the species group producing the clicks. I used these acoustically verified click trains to build and characterize a binomial family generalized additive model (GAM) that output the predicted probability that each click train consisted of broadband clicks. The covariates for this model included: median inter-click-interval, mean zero-crossing frequency, mean click bandwidth and mean click duration. The GAM categorization model was created in R version 3.2.4 revised (R Core Team, 2016) with the MGCV package version 1.8-12 (Wood, 2006).

Here, my goal was to build and select the GAM model best able to discriminate between the two echolocation click train encounters documented on the eastern Scottish coast. Thus, a *k*-fold cross validation approach was used to characterize candidate GAM models and provide parameters for final model selection.

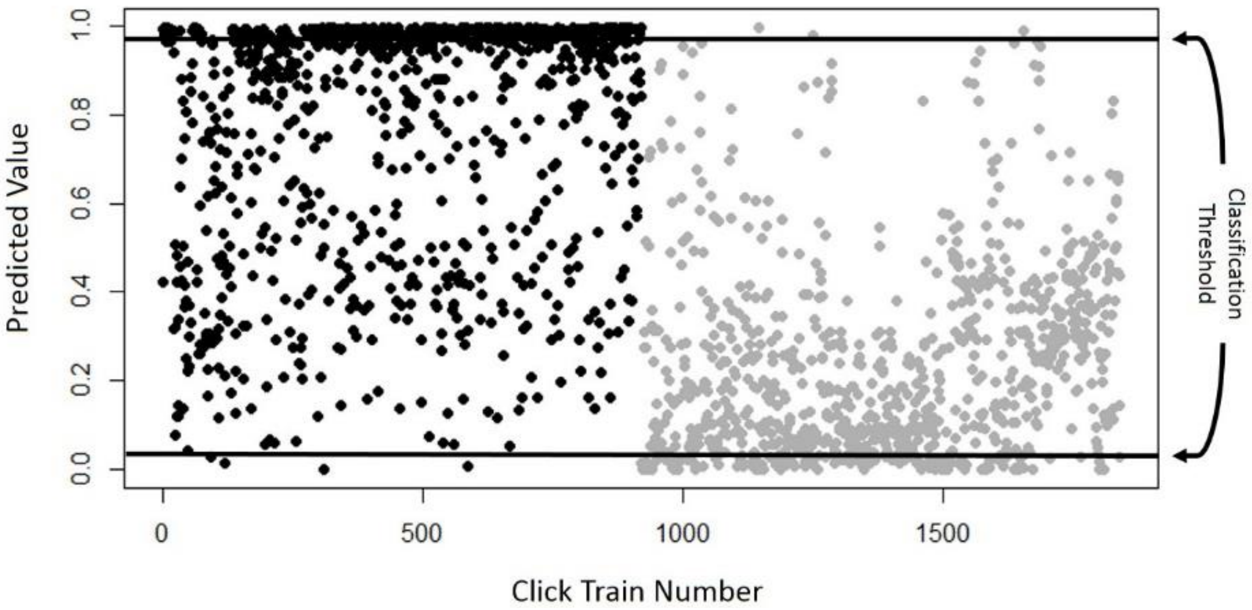


Figure 2-2 Predicted probability of a C-POD echolocation click train being associated with broadband encounter from the adjacent recordings (*P*, Equation 2-1). Points represent C-POD click trains associated with broadband (black) and frequency banded (grey) click encounters in the adjacent SM2M recordings. Horizontal lines represent the minimum classification threshold (*Tt*, Equation 2-2) above and below which click trains were classified as broadband and frequency banded, respectively. Click trains failing to meet the threshold (i.e. between the lines) were deemed too ambiguous to classify and left uncategorized.

For model comparison, all candidate GAMs were assessed using 200 iterations of a 5-fold cross-validation procedure and train categorization threshold of 0.425 (T_t; Equation 2-1). Thus, all click trains with predicted *P* exceeding 0.925 were categorized as broadband and those less than 0.075 were categorized as frequency banded (Figure 2-2). Click trains with predicted probabilities between 0.075 and 0.925 were considered too ambiguous to categorize and were therefore denoted as “unclassified”.

$$Train\ Classification(P) = \begin{cases} P \geq 0.5 + T_t \ \rightarrow Broadband \\ P \leq 0.5 - T_t \rightarrow Frequency\ banded \\ 0.5 - T_t < P < 0.5 + T_t \rightarrow Unclassified \end{cases} \qquad \text{Equation 2-1}$$

For each model iteration 1/5th of the verified C-POD click trains were randomly selected and used as the validation set. The remaining 4/5ths of the verified C-POD click trains were used to build the GAM models. In this portion of the analysis acoustic encounters were not considered and all verified click trains were treated as independent. For each iteration, I calculated the following metrics: proportion of broadband and frequency banded click trains that met either categorization threshold (proportion classified), the proportion of correctly categorized click trains (correct categorization rate), and the proportion of incorrectly categorized click trains (incorrect categorization rate). Performance values for each GAM were calculated using the same train threshold for all models (T_t, Equation 2-1). I then calculated the mean and standard deviation of all performance metrics across the 200 iterations and used these values to select the model meeting my selection criteria.

Model selection focused on reducing the proportion of frequency banded click trains incorrectly categorized as broadband, and thereby minimize the chances of artificially inflating the bottlenose dolphin acoustic occupancy rates throughout the survey area. I also sought to categorize the highest proportion of click trains possible, regardless of type. Thus, my model selection criterion (SC; Equation 2-3) was defined as

$$SC = 3FP_f + U \qquad \text{Equation 2-2}$$

where FP_f was the false positive rate for frequency banded click trains and U was the proportion of uncategorized click trains. I introduce a scalar value of three representing my qualitative decision to penalize frequency banded click trains incorrectly categorized as broadband over click trains left uncategorized. The selection criterion was calculated for all candidate models and the GAM with the lowest criterion score was used to predict the probability that each click train was comprised of broadband clicks.

2.2.6. Encounter Likelihood

By itself, the GAM model could not account for the fact that click trains recorded in close succession were most likely produced by the same individual or group of animals. To incorporate this information and increase the proportion of categorized click trains, I calculated the joint likelihood of each acoustic encounter by taking the product of all GAM predictions within the acoustic encounter. I then calculated the joint likelihood that all click trains comprising each encounter were either broadband or frequency banded. The two likelihoods were then combined into a likelihood ratio (LR; Equation 2-3) calculated as

$$LR = \frac{\prod_{i=1}^{n} P_i}{\prod_{i=1}^{n}(1-P_i)} \qquad \text{Equation 2-3}$$

where P_i is the predicted probability from the GAM categorization model that the i^{th} of n click trains in the acoustic encounter was broadband. Since the model was binary, the likelihood that an encounter was comprised of frequency banded click trains was calculated by simply replacing P_i with $(1 - P_i)$ to give the denominator of Equation 2-3. As with the click train analysis, a minimum likelihood encounter threshold (T_e; Equation 2-4) was chosen above and below which all trains within acoustic encounters were categorized as broadband or frequency banded:

$$Encounter\ Classification = \begin{cases} Broadband, & LR \geq T_e \\ Frequency\ Banded, & LR \leq 1/T_e \\ Unclassified, \frac{1}{T_e} < LR < T_e \end{cases} \qquad \text{Equation 2-4}$$

In this portion of the analysis I therefore needed to choose a minimum likelihood threshold (T_e) that balanced the risk of incorrectly classifying encounters against the risk of failing to classify most encounters. I compared the encounter categorization produced by the likelihood ratios to the validated training data to determine the correct and incorrect encounter classification rates. Through a process of trial and error I found that T_e=5, so that the evidence had to be five times as strong for one option than the other for a positive classification to be made, produced the optimal balance of maximizing classification rates while minimizing classification errors. Thus, all encounters with likelihood ratios above 5 were classified as broadband and encounters with likelihood ratios below 1/5 were classified as frequency banded. All click trains from encounters with likelihood ratios (*LR*) between 1/5 and 5 were deemed too ambiguous for categorization and were left unclassified. Finally, the GAM and the encounter analysis were applied to the full C-POD data set for which simultaneous acoustic recordings were not available.

2.3. Results

2.3.1. Echolocation Click Encounters in C-PODs and Continuous Recordings

All SM2M units were successfully recovered in late 2013, but four C-PODs were not recovered, while four others were on moorings that had been displaced, or had stopped recording early, and subsequently excluded from the analysis (Table 2-1). The number of usable recording days varied considerably between units based on battery life and/or displacement during the survey period. The median number of usable days for the C-PODs was 108 (range 24-160). Due to the increased power and storage requirements, the SM2M units recorded for fewer days than the C-PODs, with a median number of recording days of 62.5 (range 46 -69; Table 2-1).

Together the C-PODs identified 10,753 high or moderate quality "Other Cet" click trains, representing undetermined delphinid species (Table 2-1). The number of "Other Cet" click trains logged by each C-POD varied from zero (recorded by the Helmsdale 10, Spey Bay 10 and Fife Ness 10 units; Figure 2-1) to a maximum of 3662 (recorded by the Cromarty 05 unit). Of these, 1% represented click trains from the tails of the click feature distributions and were therefore excluded from the analysis. Data exploration indicated that dominant frequency and end frequency were collinear and so the latter was excluded from the categorization analysis.

2.3.2. C-POD Echolocation Click Features

Five of the 10 C-PODs deployed with adjacent SM2Ms registered click trains that were also identifiable in the full spectrum SM2M recordings (Table 2-1). The lack of concurrent detections in the other five C-POD/SM2M pairs could partly be attributed to the very few echolocation click detections by either the SM2M or the C-POD at those locations (e.g., Spey Bay and Fife Ness 10). In other cases, such as Cruden Bay 05, the failure to detect clicks on the adjacent SM2M likely arose from the duty cycle of the SM2M units which precluded visual categorization of the echolocation clicks. Last, differences in detection probability between the C-PODs and SM2M units may result in fewer click trains overall being recorded by the C-PODs.

In total, 925 click trains detected by the KERNO classifier occurred concurrently with visually confirmed broadband (n=253) or frequency banded (n=672) click train encounters in the continuous recordings. The vast majority of verifiable broadband click trains (89%) were extracted from the Stonehaven 05 deployment. This distribution was therefore not representative of either the spatial or temporal scale of the survey. To obtain a more representative sample of broadband click features, 419 click trains were randomly selected from the Cromarty 05 C-POD, where long term sighting records confirm the overwhelming presence of bottlenose dolphins and added to the broadband training. Four hundred and nineteen were used to include an equal number of frequency banded and broadband click trains with which I built the GAM for categorization (see Methods).

2.3.3. Categorization Model Performance

The model with the best categorization score was a tensor product smooth with mean zero-crossing frequency, mean bandwidth and median inter-click interval. Tensor smooths are multi-variate functions that allow for interactions between inputs with different units (e.g. frequency in kHz, and Number of Cycles). Five-fold cross validation resulted in a mean false categorization rate of 1.4% for verified frequency banded click trains and, on average, categorized 40% of the training data (Figure 2-3, Table 2-1).

Table 2-2 Mean and standard deviation for the true classification rate (TCR), false classification rate (FCR), and proportion of unclassified click trains for each model as estimated by the k-fold cross validation. Mean and standard deviation of the GAM classification model performance metrics for the top 15 models using a classification threshold (Tt, Equation 2-2) of ±0.425.

	Broadband Click Trains		Frequency Banded Click Trains			
Formula	TCR	FCR	TCR	FCR	Unclassified	Selection Criterion
Speciesid~te(MedICI, MeanNCycles, Meanzfc)	0.49 ± 0.02	0.02 ± 0.01	0.29 ± 0.02	0.01 ± 0.01	0.60 ± 0.01	0.638
Speciesid~te(MedICI, MeanNCycles, Meanzfc)+s(MeanBW)	0.49 ± 0.02	0.02 ± 0.01	0.29 ± 0.02	0.02 ± 0.01	0.59 ± 0.01	0.640
Speciesid~te(MedICI, MeanNCycles, MeanBW)+s(Meanzfc)	0.48 ± 0.03	0.03 ± 0.01	0.28 ± 0.04	0.02 ± 0.01	0.60 ± 0.03	0.644
Speciesid~te(MedICI, MeanNCycles, MeanBW, Meanzfc)	0.47 ± 0.03	0.03 ± 0.01	0.27 ± 0.03	0.02 ± 0.01	0.61 ± 0.02	0.658
Speciesid~te(MedICI, MeanNCycles, MeanBW)	0.47 ± 0.03	0.03 ± 0.01	0.27 ± 0.03	0.02 ± 0.01	0.61 ± 0.02	0.659
Speciesid~te(MedICI, MeanBW, Meanzfc)+s(MeanNCycles)	0.52 ± 0.03	0.02 ± 0.02	0.20 ± 0.05	0.02 ± 0.01	0.62 ± 0.05	0.681
Speciesid~te(MedICI,MeanNCycles)+s(MeanBW)+s(Meanzfc)	0.48 ± 0.03	0.02 ± 0.01	0.19 ± 0.03	0.02 ± 0.01	0.65 ± 0.02	0.693
Speciesid~s(MedICI)+te(MeanNCycles, MeanBW, Meanzfc)	0.48 ± 0.03	0.01 ± 0.01	0.21 ± 0.03	0.02 ± 0.01	0.64 ± 0.03	0.693
Speciesid~te(MedICI, MeanNCycles)+s(Meanzfc)	0.49 ± 0.03	0.02 ± 0.01	0.19 ± 0.03	0.02 ± 0.01	0.65 ± 0.02	0.698
Speciesid~te(MedICI, MeanNCycles)+s(MeanBW)	0.48 ± 0.03	0.02 ± 0.01	0.18 ± 0.02	0.02 ± 0.01	0.65 ± 0.02	0.704
Speciesid~s(MedICI)+te(MeanNCycles, Meanzfc)+s(MeanBW)	0.48 ± 0.03	0.01 ± 0.01	0.18 ± 0.02	0.02 ± 0.01	0.66 ± 0.02	0.717
Speciesid~te(MeanNCycles, Meanzfc)+s(MedICI)	0.47 ± 0.03	0.01 ± 0	0.16 ± 0.02	0.02 ± 0.01	0.67 ± 0.02	0.728
Speciesid~te(MedICI, Meanzfc)+s(MeanNCycles)+s(MeanBW)	0.47 ± 0.02	0.01 ± 0.01	0.14 ± 0.02	0.02 ± 0.01	0.68 ± 0.02	0.729
Speciesid~s(MedICI)+te(MeanNCycles, MeanBW)+s(Meanzfc)	0.47 ± 0.03	0.01 ± 0.01	0.14 ± 0.03	0.02 ± 0.01	0.68 ± 0.02	0.734
Speciesid~s(MedICI)+s(MeanNCycles)+te(Meanzfc, MeanBW)	0.46 ± 0.03	0.01 ± 0.01	0.15 ± 0.03	0.02 ± 0.01	0.68 ± 0.02	0.735

Table 2-3 Results of the binomial GAM used to analyze click type (ClickTrain) using a tensor smooth of median inter-click interval (MedICI), mean number of cycles in clicks (MeanNCycles) and mean zero crossing frequency (meanzfc).

Parametric Coefficients

Formula: ClickTrain~te(*MedICI*, *MeanNCycles*, *Meanzfc*,
family=*Binomial*, link=*logit*)

Intercept Estimate	Standard Error	z-value	Pr(>|z|)
-0.3500	0.1254	-2.791	0.00525

Approximate Significance of Smooth Terms

Est. df	Reference df	Chi squared	P-value
69.28	79.31	612	<.001

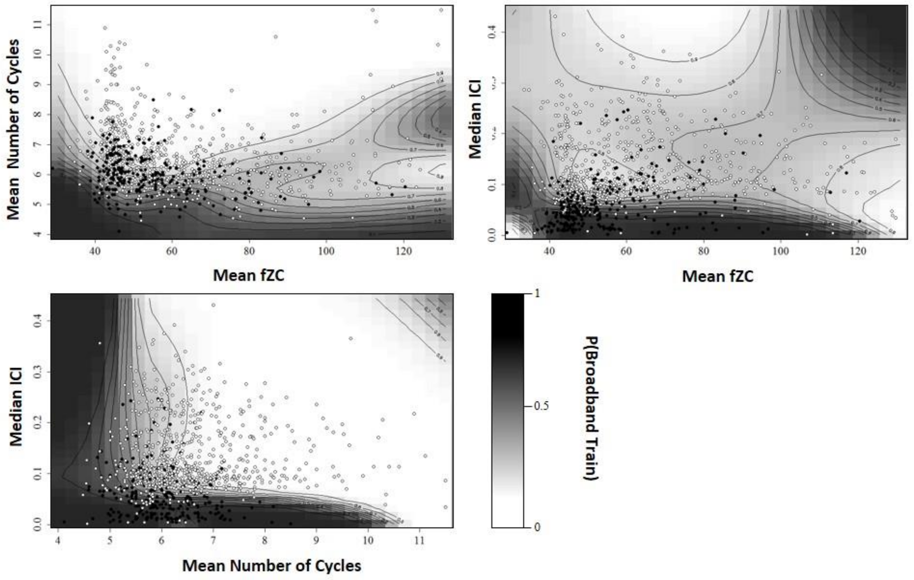


Figure 2-3 Two dimensional representations of the four-dimensional tensor-smooth binomial classification GAM. Shade indicates the probability that a given click train was broadband (black) or frequency banded (white) based on the mean inter-click-interval (Median ICI), mean number of cycles (e.g. duration) of the clicks, and mean zero-crossing frequency (Mean fZC) of the click trains. Points represent training data for broadband (black) and frequency banded (light gray) click trains.

When applied to the full C-POD dataset (minus the training data), the model categorized a total of 3968 (37%) of the click trains, of which 2737 were identified as broadband and 1231 frequency banded. The remaining 63% of the click trains failed to meet either categorization threshold (T_t). As expected, the proportion of click train types varied across the deployment sites. C-PODs near the inner Moray Firth (Cromarty and Spey Bay) contained primarily broadband click trains and units to the north and south (Helmsdale and Fraserburgh) contained primarily frequency banded click trains. Uncategorized click trains were present on all units and, with the exception of the Cromarty locations, generally represented the majority of the click trains detected at each deployment site (Figure 2-4).

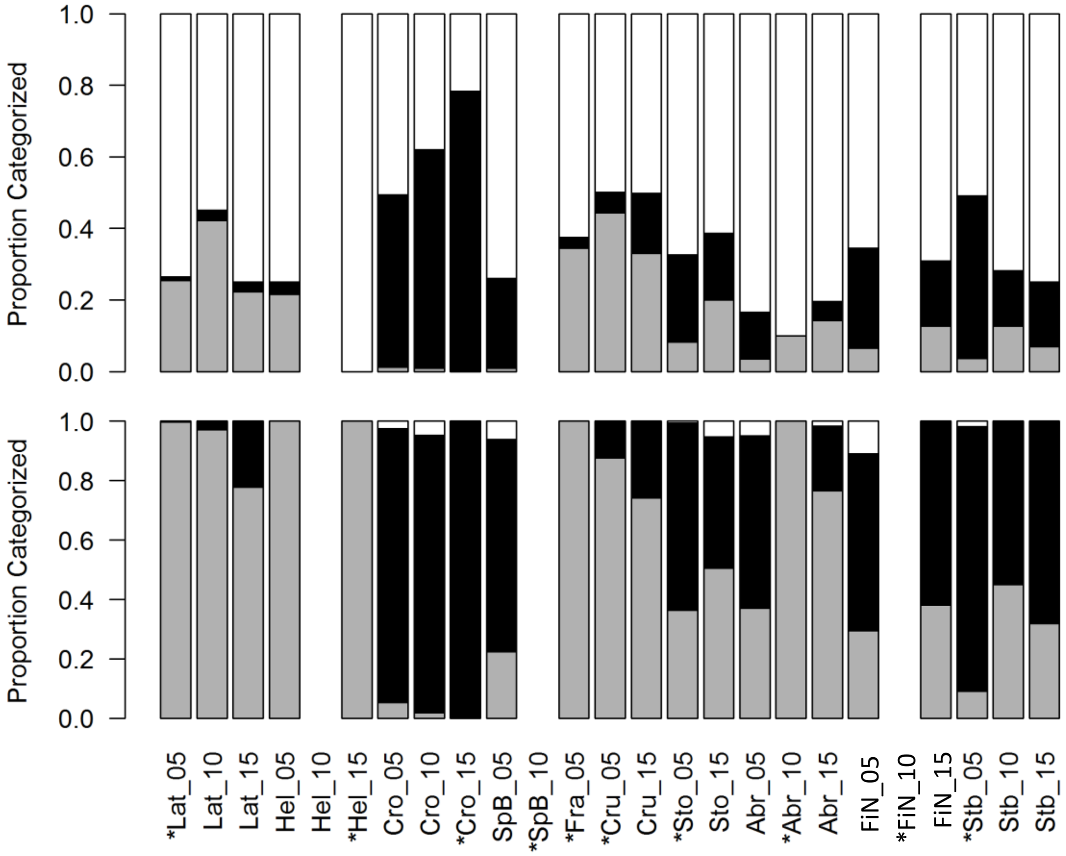


Figure 2-4 Upper Panel: The proportion of click trains classified as broadband (black), frequency banded (gray) or unknown (white) by the GAM classification model with a minimum classification threshold of ±0.425(Tt Equation 2-2). Lower Panel: The proportion of click trains classified as broadband, frequency banded or unknown by the combination of the GAM click-train classification and the encounter likelihood ratio. Asterisks indicate joint C-POD/SM2M deployment locations from which training data were derived. Displaced units (SpB 05, Fra 10, Fra 15, Cru 10, Sto 10) not shown.

2.3.4. Encounter Likelihood

The 10,753 click trains documented by the 26 recovered C-PODs represented 573 encounters. Twelve encounters coincided with visually verified broadband trains recorded by the adjacent SM2M recordings and 27 encounters coincided with visually verified frequency-banded click trains in the SM2M recordings (Table 2-1). Using a minimum likelihood ratio of five ($T_e = 5$), 10 of the verified broadband click-train encounters were correctly categorized, two were incorrectly categorized as frequency banded encounters and none were left unclassified, while 24 of the 27 verified frequency banded encounters were correctly categorized, none were incorrectly categorized and three were left unclassified. When the likelihood model was applied to the remaining data, 264 (43%) total encounters were categorized as broadband, 273 (45%) as frequency banded and the remaining 75 (12%) were left unclassified (

The highest daily acoustic occupancy rates were observed at the Cromarty 05 deployment location, with other peaks around the Latheron, Fraserburgh, Arbroath and Fife Ness sites (Figure 2-5). No encounters of either type were documented by the Helmsdale 10, Spey Bay 10 and Fife Ness 10 units. The daily acoustic occupancy rates of broadband and frequency banded click encounters differed between locations. Deployments near the inner Moray Firth showed higher daily acoustic occupancy rates for broadband click encounters than frequency banded click encounters while the converse was true for the Latheron, Fraserburgh and Cruden Bay sites. These results are consistent with long-term studies in the area that have shown regular bottlenose dolphin presence in and around the SAC (Hammond and Thompson, 1991, Wilson et al., 1997b, Quick et al., 2014). Interestingly, encounters in

Stonehaven and Arbroath showed similar rates of detection positive days for both broadband and frequency-banded click types, indicating the presence of multiple species.

2.4. Discussion

The categorization results reported here for C-POD detections are consistent with the visual surveys available for areas outside of the Moray Firth. This study identified primarily broadband encounters in the data from all three Cromarty C-PODs. This finding is unsurprising given that a portion of the broadband training detections were derived from the Cromarty 05 unit. However, the prevalence of broadband click trains at the other two Cromarty deployment sites is consistent with previous studies in the area. Based on the long history of visual observations in the area, it is reasonable to assume that the click trains classified as frequency banded at the site represented misclassifications. Similarly, broadband encounters were more prevalent than frequency banded click trains in the C-POD detections at the Fife Ness and St Abbs sites, where bottlenose dolphins are the most frequently sighted species (Cheney et al., 2013). Approximately equal numbers of broadband and frequency banded detections occurred through the Grampian region (Cruden Bay, Stonehaven and Arbroath), which agrees well with reported sighting rates for bottlenose and white-beaked dolphins between Cruden Bay and Stonehaven (Anderwald et al., 2010). Similarly, Weir et al. (2007) report multiple sightings of white-beaked dolphins in and around the Aberdeen area (between Cruden Bay and Stonehaven).

Daily acoustic occupancy rates from the C-POD data suggest a degree of spatial partitioning between species producing broadband and frequency-banded clicks. Broadband click encounters comprised the majority of the detection positive days logged by the C-PODs deployed in the inner Moray Firth (Cromarty). Contrary to my expectations, the acoustic encounters on the Helmsdale C-PODs, which were located within the Moray Firth SAC, were dominated by frequency banded click trains. This suggests that, over the 2013 deployment period, bottlenose dolphins were not the most common species using this portion of the SAC.

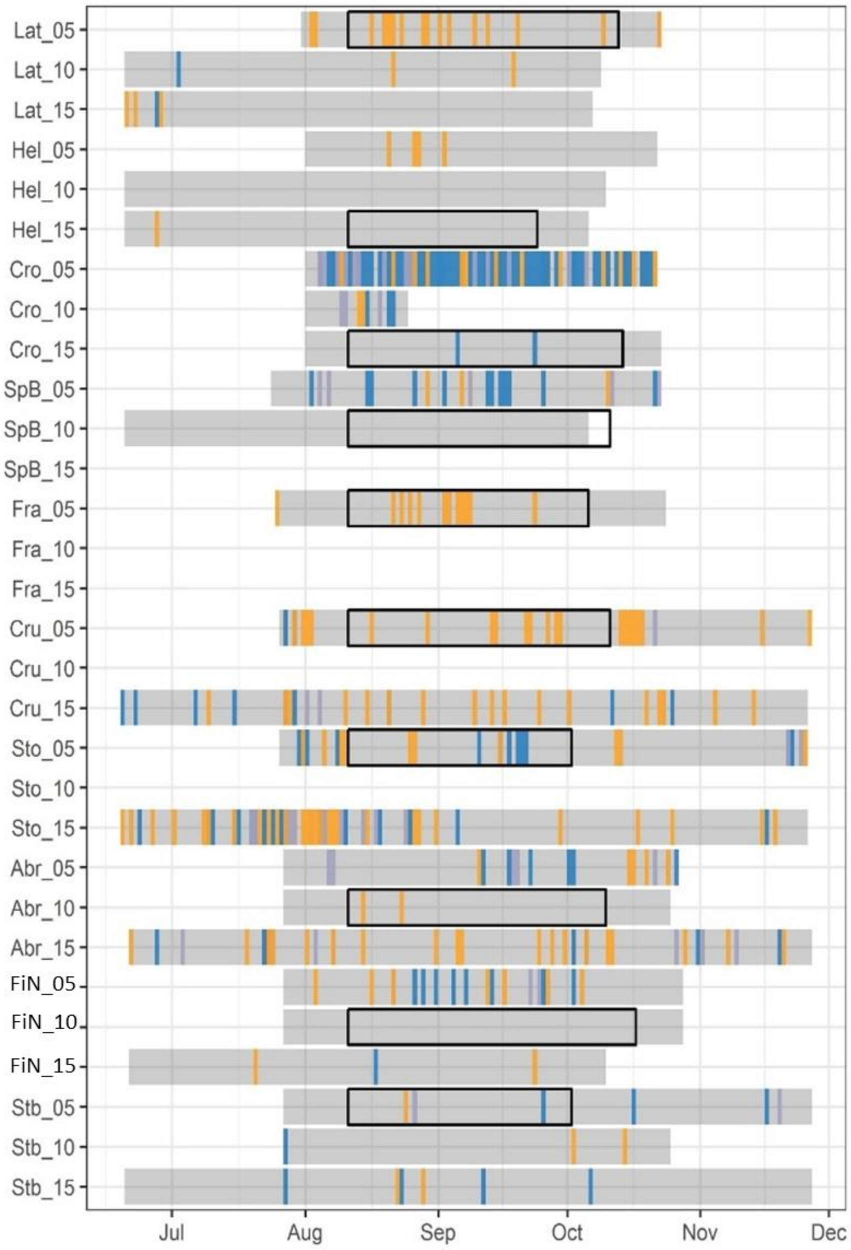


Figure 2-5 Daily occupancy of broadband echolocation click encounters (blue), frequency banded echolocation click encounters (yellow) and uncategorized echolocation click train encounters (dark gray). Gray blocks indicate times when the C-PODs were recording and black rectangles indicate periods for which there were simultaneous SM2M recordings.

Outside of the SAC, both broadband and frequency banded click encounters were frequently observed. However, for each deployment group (e.g., Fife Ness, Arbroath etc.) broadband click trains were more common in the nearshore (~5 km) than the offshore deployment sites (~10 and 15 km). This is consistent with previous studies that suggest bottlenose dolphins preferentially use nearshore areas (Quick et al., 2014) . The Stonehaven C-PODs contained a mix of broadband and frequency banded encounters, matching visual surveys indicating that both bottlenose and white beaked dolphins are commonly sighted in that area (Weir et al., 2007, Anderwald et al., 2010). These results hint at the possibility of areas along the eastern Scottish coast having different ecological importance for the two groups. This has been confirmed for bottlenose dolphins in the inner Moray Firth where foraging buzzes are more frequently documented near known “hotspots” (Hastie et al., 2004b, Pirotta et al., 2014b). However, fewer data are available for the other species present in the area and/or outside of the Moray Firth.

The similarity between my results and previously published sightings data indicates that the C-POD encounter categorization system presented here works well for eastern Scottish waters. However, it would be inappropriate to directly apply this categorization tool to C-POD detections collected from other regions. Recent classification studies on similar species groups using full spectrum recording (*fs* = 200 kHz) have shown that deployment location and instrument type can adversely affect the performance of click train classifiers (Roch *et al.*, 2015). It is unclear whether this might be the case with C-POD data for which fewer click features are collected. While it is possible that the zero-crossing method combined with the limited click parameters are more robust to site and/or instrument specific variations, it could just as easily be the case that the limited click features recorded by the C-PODs are *more* susceptible to such variations. Thus, future studies seeking to use this classifier or these methods must not omit a validation process. Ideally this would involve comparing C-POD detections with concurrent visual sightings (e.g., Roberts and Read 2014, Robbins *et al.*, 2015, Nuutilia *et al.* 2013). However, where visual observations are not possible or practical, pairing C-PODs with continuous recorders is an alternative method.

The use of C-POD data processed only with the KERNO classifier is justified in surveys where the researchers can be confident that the majority of detections represent single dolphin and/or porpoise species. This is the case for the dolphin detections within the inner Moray Firth where bottlenose dolphins represent the principle dolphin species. Similarly, throughout the North Sea, harbor porpoise (*Phocoena phocoena*) represent the only resident cetacean capable of producing “NBHF” clicks and are, therefore, unlikely to be confused with other species. In such contexts, C-PODs and similar devices can directly inform studies of cetacean abundance and behavior (Jaramillo-Legorreta and Rojas-Bracho, 2011, Kyhn et al., 2012, Brookes et al., 2013, Wilson et al., 2013, Pirotta et al., 2014b, Williamson et al., 2016). However, where multiple odontocete species with similar click features are present, additional methods are needed to increase taxonomic resolution. This study highlights the benefits of developing methods to increase taxonomic precision in detections from low-cost click loggers when full acoustic audits are impossible or impractical. This is especially pertinent given that C-PODs and their predecessor T-PODs are widely used for monitoring and mitigation associated with offshore industrial activities (Carstensen et al., 2006b, Scheidat et al., 2011).

In this work I relied on several assumptions, but a key one was that all click trains detected by the C-PODs were produced by one of the four most common species seen in the area. C-PODs are capable of recording echolocation clicks from all odontocetes with the exception of sperm whales (*Physeter macrocephalus*) for which the energy is below the sensitivity of the instruments (Dahne et al., 2013). This includes clicks from species that, while infrequent, are known to visit the eastern Scottish coast including killer whales (*Orcinus orca*), long-finned pilot whales (*Globicephala melas*), and Atlantic white sided dolphins (*Lagenorhynchus acutus*). Based on published click characteristics (Deecke et al., 2005, Eskesen et al., 2011), click trains from these species would likely be classified as broadband click encounters by this categorization system. Thus, it is possible that some of the “Other Cet” click trains detected by the C-PODs represented one or more of these species. However, previous visual surveys indicate that such species are infrequent visitors to the eastern Scottish coast and could therefore contribute only a trivial amount of noise to the encounter rates presented here. Regardless, the ambiguity in dolphin detections reiterates the need to inform acoustic-only methods with other sources of information about the study system.

The interpretation of these results assumed that stable frequency banding, or the lack thereof, in echolocation clicks was diagnostic of the species-group producing them. This assumption is debated in the literature, with several authors providing evidence of species discrimination based on the spectral location of peaks and notches (Houser et al., 1999, Soldevilla et al., 2008, Calderan et al., 2013), while others have postulated that spectral banding cannot be diagnostic of species (Wahlberg et al., 2011). While an in-depth analysis of this debate is outside of the scope of this study, careful consideration is prudent to understand the validity of the categorization analysis presented here. Currently two hypotheses exist regarding how frequency banding might be produced. Wahlberg et al. (2011) and Rasmussen et al. (2004) measured on-axis clicks from free-ranging bottlenose and white sided dolphins, respectively. Both studies fitted a baffled piston model to the received clicks, and Wahlberg et al. (2011) suggested that the banding found in other species was attributed to the off-axis banding effects dictated by the piston aperture size. However, these studies primarily analyzed clicks from on-axis angles and may therefore have missed the filter effects caused by the cranial anatomy. If this is the case then it does not preclude the independent documentation of stable spectral peaks and notches in the spectra of clicks recorded off-axis from a number of species with similar cranial morphology (Soldevilla et al., 2008, Au et al., 2012c).

The off-axis spectral characteristics of echolcoation clicks have been measured for bottlenose dolphins. Au et al. (2012c) measured the entire biosonar field around captive bottlenose dolphins and found that, off-axis, echolocation clicks degraded into discrete pulses most likely produced by the phonic lips and internal reflections from within the animal’s head (Au et al., 2012c). Multiple pulses, when processed with an FFT or DFT algorithm, result in “ripples” in the spectrum consistent with the peaks and notches described by Soldevilla et al. (2008). However, as with sperm whales, the inter-pulse-interval in bottlenose dolphin echolocation clicks is highly sensitive to the off-axis angle (Goold, 1996). Therefore, when energy is averaged across multiple clicks collected from a variety of angles relative to the animal, the peaks and notches in spectral energy from this species become less distinct.

Unfortunately, detailed studies of off-axis clicks from “frequency banded” species including Risso’s, white-beaked and white-sided dolphins are lacking. However, it is possible that differences in cranial morphology between the species groups could account for differences in the stability of spectral peaks and notches. For example, assuming the multi-pulse model of echolocation click propagation, more uniform path lengths between the phonic lips and melon for frequency banded species would result in consistent inter-pulse-intervals. This would subsequently lead to less variation in the spectral location in peak and notch energy for off-axis clicks in these species. Additional studies are needed to determine whether or not this is the case.

Assuming the presence of stable spectral peaks and notches is diagnostic of species group, on-axis clicks will necessarily confound my ability to discriminate between broadband and frequency banded click trains in both the SM2M recordings and the C-POD encounter categorization model (Au et al., 1974, Au et al., 1999, Rasmussen and Miller, 2002, Rasmussen et al., 2004, Wahlberg et al., 2011, Au et al., 2012a). Moreover, if a disproportionately large selection of on-axis click trains were included in the training data, this would add considerable noise to the final categorization task. I limited this outcome by restricting the selection of C-POD click trains used to build the GAM to periods during which more than 500 high SNR click trains could be identified in the adjacent SM2M recordings. This conservative selection criterion reduced the probability of creating a biased sample of clicks from any particular beam angle and thereby increased my confidence in the accuracy of the categorization task.

Our categorization model included ICI as a predictor, yet it is known that odontocetes modify their inter-click-interval depending on their behavioral state (Johnson et al., 2006, Pirotta et al., 2014b, Janik, 2000b). This has the potential to introduce two confounding factors into the analysis presented here. First, there is question of whether ICI can be used to discriminate between different species (or groups) of dolphins. Additionally, there is the potential that the categorization task is describing behavior (e.g. foraging vs. travel) rather than species group.

In addressing whether ICI can be used for species discrimination I note that the GAM model selected here used a tensor smooth across all three click train features recorded by the C-POD. Thus, ICI itself did not predict the click-train category. Instead, prediction was based on the relationship between median ICI, mean zero-crossing frequency and mean bandwidth. Accordingly, while ICI itself has not been widely used to discriminate between species, Johnson et al. (2006) note that in Blainsville’s beaked whales (*Mesoplodon densirostris*) there is a species-specific relationship between ICI, peak frequency and bandwidth of the individual clicks. For this species, as the animal approaches a prey target decreasing ICIs are linked with decreasing click durations and increasing click bandwidths and peak frequencies. Thus, while inter click interval, bandwidth or peak frequency alone would be inadequate to categorize echolocation clicks, the relationship between these variables may be sufficiently different in some species to allow for categorization and/or classification.

Concerning whether my sample of echolocation clicks represented a biased distribution of clicking behaviors (e.g. primarily click trains associated with foraging or travelling), I note that the training data were obtained from multiple times and locations throughout the survey. Therefore, click trains associated with foraging, travelling and socializing activities should all be represented in the training data for both echolocation click types (Pirotta et al., 2014b). *K*-fold cross validation involved subsetting trains from multiple acoustic encounters. This methodology was necessary as very few acoustic encounters could be correlated with the adjacent SM2M recordings (10 broadband and 17 frequency banded encounters; Table 2-1). This also meant I was forced to train and test my model on the same data - with more verified acoustic encounters I could have better characterized in vs. out of sample model performance, and this should still be the aim for future studies.

Because there were so few verified encounters, I was not able to explore variance in classification accuracy. However, in the years following this initial study the C-PODs and SM units returned more data. While there were still insufficient encounters to run an entire k-fold analysis, I was able to look at the proportion of encounters that were correctly and incorrectly identified by the classifier. Through this process I produced a confusion matrix used in Chapters 4 and 5 (see Appendix -2 for details).

As with any acoustic classifier, the one I have developed is not immune to miscategorisation. There are several ways in which future studies may account for this misclassification error. First, the performance of this categorization system should be tailored to the research objectives by modifying encounter thresholds based on cost functions derived from study objectives. For example, in this study a single encounter threshold was set above and below which encounters were categorized as broadband or frequency banded. However, studies for which there is a high cost to false negative detections may wish to take a more conservative approach. In such cases, the likelihood categorization threshold (T_e) could be either decreased or excluded altogether; opting instead to include all click trains with a GAM prediction score above a given threshold (Boyer et al., 2013) in the final analysis. Alternatively, future studies may seek to incorporate misclassification error directly into the analysis. Bayesian occupancy models, in particular, offer sufficient flexibility to allow for the incorporation of correct and incorrect classification rates across all categories (Miller et al., 2011).

Provided the above considerations are kept in mind, it would be worthwhile to investigate whether this categorization system might perform comparably to C-POD detections collected from other habitats. Similar dolphin species compositions have been observed in western Scotland (MacLeod et al., 2005), Ireland (Robbins et al., 2016), California (Soldevilla et al., 2008), and in the Mediterranean Sea (Frantzis and Herzing, 2002). If the C-POD categorization system derived here performs comparably in other habitats, it suggests a wider application of these GAM/likelihood methods may be possible.

2.5. Conclusions

This study indicates that it is possible to increase the taxonomic resolution of low-cost click loggers by using statistical methods to discriminate between acoustically similar species groups. By comparing continuous recordings to logged C-POD detections I was able to identify and discriminate between the broadband and frequency banded click trains produced by the two pairs of dolphin species most commonly encountered in Eastern Scottish coastal waters.

Chapter 3

Ambient Noise and Transmission Loss Bias Acoustic Occupancy Rate Estimates

3.1. Introduction

Over the past three decades, several survey methodologies have been developed to estimate the density, abundance and distribution patterns of plants and animals. Notable among these are distance sampling techniques (Harris et al., 2013), and occupancy analysis (Bailey et al., 2007, Bailey et al., 2014b). In distance sampling, the range (distance) between the survey point or transect line and the survey targets (e.g. plants or animals) is measured and used to estimate the proportion of animals ‘missed’ by the survey as a function of range. This relationship is referred to as the detection function. Using this function, researchers can extrapolate the estimated organismal density or abundance over the survey area, assuming the survey data are a representative sample of the area. Distance sampling techniques are particularly well suited for visual transect surveys that provide excellent spatial coverage and the ability to measure or estimate the distance between the transect and the survey target (Thomisch et al., 2016, Gonzalez et al., 2017, Vacquié-Garcia et al., 2017). Occupancy surveys report only organismal presence or absence (but more appropriately detection or non-detection) time and location and thus produce information on the proportion of time a site was occupied. Unlike distance sampling, occupancy studies do not incorporate explicit knowledge of the range between the target and the observer used to calculate the detection function. Instead, researchers collect covariate information and use this to estimate either the absolute survey effort or the relative survey effort between different locations/survey periods. As a result, occupancy studies often have less inferential power because the detection function is not part of the analysis; researchers need only know whether or not the species of interest was present. In contrast, when detection functions are available the precision of the analysis improves as the detection range of each instrument or observer can be accounted for. Detection functions as found in distance sampling and spatially explicit capture-recapture (SECR) are critical for density and abundance studies where the primary goal is to determine the number of animals present in a given area during the survey period. Occupancy studies can provide habitat use information but cannot make the inferential step between presence to abundance when the area monitored is unknown.

The relative ease of collecting occupancy information lends well to longitudinal studies which may modify survey methodology throughout the lifespan of the project. Finally, spatially explicit capture-recapture (Dawson and Efford, 2009) incorporates occupancy measures across multiple sensors to estimate detection functions. By determining the survey locations at which organisms were and were not detected, the maximum range over which the organism is likely to be detected ('home range') can be estimated. While SECR includes many of the positive attributes of both distance and occupancy analysis, detectors must be closely spaced such that each organism or cue is detected by multiple instruments (ideally half of the survey locations). For acoustic surveys of baleen whales, where propagation distances often exceed tens of kilometres, SECR sensors can similarly be spaced several kilometres apart (Marques et al., 2011). However, for small odontocete SECR surveys, the sensors must be densely spaced to accurately estimate the propagation distance. Thus, for a limited instrumentation budget SECR methods may cover smaller areas than studies designed using occupancy analysis.

Regardless of the methodology chosen, at least some knowledge of the probability of detecting the survey target is required to produce accurate estimates of density, abundance, and/or distribution. In distance and SECR methodologies, the unconditional probability of detecting the target species is the integral of the detection function over the maximum detection range (Buckland et al., 2005, Borchers and Efford, 2008, Efford et al., 2009). Occupancy analysis incorporates detection probability by modelling the observed occupancy as the product of the true occupancy (whether or not the organism was there) and the observation process (whether or not the observer detected the organism). The detection probability for occupancy studies is the inverse logit of the observation process (Royle and Kéry, 2007).

In British waters, long-term acoustics studies have been used to investigate the spatial and temporal distribution of harbour porpoise and bottlenose dolphins, as well as model the potential impacts of anthropogenic activities (Simon et al., 2010, Brookes et al., 2013, Williamson et al., 2016, Harris et al., 2017) . In these studies, the presence of an acoustic signal of the animal (e.g., click or whistle) is used as a proxy for true occupancy. Here I use the term 'acoustic occupancy' to indicate the presence of an animal based on the detection of this call. This term differs from true occupancy in that animals may be present but not detected because they either do not produce acoustic signals or their signals are not detected by the instruments.

Despite the influential nature of such studies, none have explicitly considered differences in detection probability between monitoring sites and have implicitly assumed no such differences exist. Differences in propagation conditions, varying ambient noise and animal behaviour are all known to influence the maximum detection range and subsequently the probability of detecting a calling animal (Kusel et al., 2011, Nuuttila et al., 2013b). These changes have the potential to bias survey results by under or overestimating the area monitored through various acoustic means including continuous recorders and C-PODs thereby biasing the extrapolation calculations in their density or abundance estimates.

The issue of detection probability in long-term acoustic surveys has been noted by several authors who estimated detection functions for C-PODs by comparing the range between animals visible at the surface to the presence or absence of echolocation click detections in the C-POD record (Simon et al., 2010, Kyhn et al., 2012, Roberts and Read, 2014). This methodology is highly accurate and provides site-specific detection probability information. However, relying on visual surveys to determine detection ranges is highly labour intensive and not feasible in offshore or large-scale acoustic studies such as the East Coast Marine Mammal Acoustic Study (Marine Scotland Science). Where measuring the range between the calling animal and the sensor is not possible, acoustic models based on the sonar equations represent an alternative methodology for estimating maximum detection ranges and detection probabilities (Kusel et al., 2011, Frasier et al., 2016, Kusel et al., 2016). Acoustic modelling techniques lack the empirical validation used in visual studies, but they are flexible and applicable to survey conditions that preclude direct range estimates to detected individuals.

In this chapter, I use acoustic modelling and simulation techniques to estimate the maximum detection range of the C-PODs as a function of deployment location and ambient noise level. These values are combined with acoustic occupancy records from the C-PODs to estimate whether fluctuating detection probabilities have, if not accounted for, the potential to bias estimated bottlenose dolphin acoustic occupancy rates reported by the array. Due to low acoustic occupancy rates in this chapter I assume all detections are produced by bottlenose dolphins.

3.2. Methods

3.2.1. Overview

In this chapter I use a Bayesian framework to assess whether transmission loss and ambient noise levels measured across the survey area are likely to bias the relative acoustic occupancy rates reported by the C-PODs in the ECoMMAS array. Here I use the sonar equations to estimate the relationship between the area monitored for bottlenose dolphins by the C-PODs at 10 of the 30 survey locations as a function of ambient noise level. My methods follow previous simulation studies that estimate the effects of transmission loss and ambient noise levels on the area monitored by passive acoustic devices (Kusel et al., 2011, Frasier et al., 2016). However, because performance metrics for the KERNO classifier have not been released by the manufacturer, I was unable to produce accurate detection probability estimates. Instead, I assumed three potential performance scenarios for the C-POD and determined which, if any, resulted in significant bias in the *relative* acoustic occupancy levels reported by the systems.

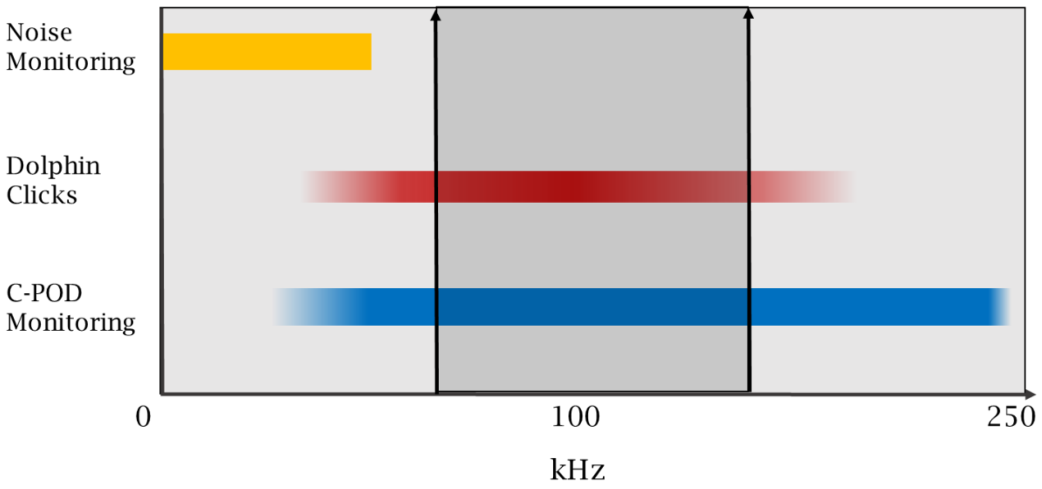


Figure 3-1 Illustration of the available bandwidth of the noise monitoring system, the approximate bandwidth of bottlenose dolphin echolocation click trains and the estimated bandwidth of the C-POD monitoring system. Arrows and grey box indicate bandwidth over which the SONAR equations are integrated to establish detection range. Note noise monitoring does not overlap with the main energy band of either the dolphin clicks or the C-POD monitoring system.

A key aspect of this work concerns relating ambient noise level measurements to the source levels of bottlenose dolphins, propagation conditions around each C-POD, and the sensitivity of the C-POD click train detector. C-PODs “listen” for echolocation clicks in frequencies up to 250 kHz while the continuous recorders in the ECoMMAS sampled at 96 kHz (48 kHz Nyquist frequency). Therefore, the bandwidth of the available ambient noise level recordings did not cover the same bandwidth of either the animals’ echolocation clicks nor of the click detector (Figure 3-1).

To address the incongruity of the acoustic recording systems and the paucity of information about the KERNO classifier, I used simulations to estimate the maximum area monitored by the C-PODs as a function of ambient noise level and deployment location. Accordingly, my work relies on various simplifying assumptions. Where assumptions are necessary, I estimate parameters such that both the variation in area monitored and subsequently detection probability at each deployment location are moderately overestimated. When faced with uncertainty in these assumptions, decisions were made always to maximise the likelihood of site characteristics and ambient noise biasing the acoustic occupancy estimates. Therefore, if the relative acoustic occupancy at each site is unchanged between the naïve analysis (where changes in detection area are ignored) and models where detection area is accounted for, I can be somewhat confident that transmission loss and noise levels are not biasing the relative acoustic occupancy results.

In this analysis, I estimated the maximum area monitored at each C-POD deployment location as a function of ambient noise level. I then related the area monitored by the C-POD to a detection probability by logit-transforming the data. This procedure converts the response variable to a scale limited between 0 and 1 and is common in all binomial models. Detection probability was then integrated into a Bayesian hierarchical acoustic occupancy model to determine whether site-specific and noise-dependent detection probabilities could bias understanding of bottlenose dolphin habitat use. The Bayesian approach provides a flexible platform to investigate these issues as well as establishing a framework which may be easily updated if and/or when C-POD performance parameters become available.

In sections 3.2.3 to 3.2.5 I describe how each component of the sonar equation is calculated or estimated to estimate the maximum area monitored by each C-POD as a function of deployment location and ambient noise level. In Section 3.2.8 I describe the Bayesian hierarchical models used to incorporate the observed acoustic occupancy rates from the C-PODs with the detection area monitored by each C-POD via the detection probability metric.

Unless otherwise specified in this work, all reported sound levels are referenced to 1µPa.

3.2.2. Data Quality

In this chapter I used data from C-PODs that were co-deployed with SM units (Figure 1-1) from the 2013 ECoMMAS deployments. I further restricted C-POD data to include only periods that coincided with the availability of ambient noise levels from the co-deployed SMs. C-POD data were downloaded and processed using the accompanying KERNO classifier for the presence of “high” and “moderate” quality echolocation clicks. This resulted in very few ‘other cetacean’ echolocation click trains and subsequently very low hourly acoustic occupancy rates (Figure 2-5). I therefore chose not to pre-process the echolocation click trains to remove frequency banded click trains (Chapter 2). Doing so would result in so few click trains being included that the acoustic occupancy rate would approach zero, regardless of the propagation conditions and ambient noise levels.

All available noise levels and click detections from the 2013 deployment were included in the noise level analysis.

3.2.3. Area Monitored

The area monitored by an acoustic detector is dependent on the detection thresholds of the instrumentation system and the signal to noise ratio (SNR) at which the sounds of interest (here echolocation clicks) are received (Equation 3-1). The SNR of a click measure at a sensor is determined by the source level (SL) at which the click was produced, the directivity index (DI) of the click, the transmission loss (TL) between the animal and the sensor, and the ambient noise level (NL) at the sensor. Both source level and directivity index are determined by the animal’s behaviour and, for the purposes of this study, are considered constant. Transmission loss is dependent on the range (r) between the animal and the sensor and, in coastal regions with complex bathymetry, the angle (θ) between the source and receiver. Finally, ambient noise levels (NL) vary over time (t) as a function of local conditions including storm and anthropogenic activity. Critically, the sonar equations assume that all sound levels are measured over the same bandwidth.

$$SNR(r,\theta,t) = SL - DI - TL(r,\theta) - NL(t)$$ Equation 3-1

For an ideal acoustic detection system, the maximum range at which an echolocation click can be detected (r_{max}) is defined by the range beyond which the signal to noise ratio of the click at the receiver falls below the detection threshold (TH) of the receiving system (Equation 3-2).

$$TH - SNR(r_{max},\theta,t) = 0$$ Equation 3-2

The area monitored by a sensor at time *t* is approximated by Equation 3-3 where n is the number of angles (θ) as which the maximum detection range (r_{max}) is measured.

$$A(t) \approx \frac{\pi}{n}\sum_{1}^{n} r_{\max}^{2}(\theta)$$ Equation 3-3

Equations 3-2 and 3-3 represent simplified solutions for a continuous source. However, for impulsive sounds including sonar pings and echolocation clicks, the SNR value is dependent on the integration window over which the signal is averaged. Increasing the integration window results in a lower SNR as the power of the impulse is averaged over a longer duration. The energy flux density, *E*, for a pulsed sonar with a peak-to-peak amplitude denoted by *SL'*, as measured at the source, is then defined by Equation 3-4.

$$10log_{10}(E) = SL' + 10log_{10}(\tau_0)$$ Equation 3-4

where τ_0 is the duration of the emitted pulse in seconds. By substitution and the introduction of the integration time (τ_e) the SNR equation may be re-written as an Energy to Noise ratio defined as Equation 3-5.

$$SNR(r,\theta,t) = SL' + 10log_{10}\left(\frac{\tau_0}{\tau_e}\right) - NL(t) - TL(r,\theta) \qquad \text{Equation 3-5}$$

For full details on this method see Kusel (2016).

3.2.4. Noise Levels

Within the context of this study, I refer to ambient noise as continuous noise that has the potential to mask biological signals, reduce the signal-to-noise ratio of such signals when received by the sensors (Kusel et al., 2016). In the shallow waters of the North Sea, such masking noise is largely attributable to local shipping and storm activity (Urick, 1983). Unlike continuous recorders, C-PODs do not monitor ambient noise caused by wind, wave or shipping activity but report “sediment transport noise” that the manufacturer refers to only as “noise”. Sediment transport noise is caused by particles suspended in the water column colliding with the instrument housing. The quality of sediment transport noise is similar to the clicks and pops produced by biological sources (e.g. echolocation clicks and snapping shrimp). As such, sediment transport is more likely to impact the performance of the KERNO classifier rather than masking echolocation clicks from the sensor. Thus, I refer to sediment transport as “interference” and use “noise” to refer only to continuous noise that acts to mask the echolocation clicks from the sensor.

In the sonar equations, ambient noise (NL) is the RMS of the noise integrated over the bandwidth of the detector and reported in dB referenced to 1µPa (for ocean environments). C-PODs record time with 0.2µs resolution which corresponds to a sample frequency of 500kHz. Monitoring ambient noise over the entire frequency band of the C-POD detector is prohibitively expensive in terms of processing power, storage, and deployment duration. The SM units sampled at 96kHz, which precluded measuring noise levels above the Nyquist frequency of 48kHz.

Third octave noise levels were calculated using PAMGuard software with 1 kHz as the reference frequency and the highest third octave centre at 40.3 kHz, although only the upper bands were used in subsequent analysis as they were closest to the frequencies of the signals of interest. This is considerably lower than the peak frequency of bottlenose dolphin echolocation clicks and well below the upper end of the C-POD detection band. Therefore, to simplify estimation of the ambient noise levels within the bandwidth of the echolocation clicks and the C-POD sensor, I assumed that the average energy in each spectrum (dB/Hz) in the 40.3 kHz band was the same as the average energy in the next 1/3 octave bands that cover the frequency range of the echolocation clicks. This is consistent with recent studies that have measured noise in bands up to 150kHz (Hermannsen et al., 2014). I used the spectral characteristics of bottlenose dolphin echolocation clicks reported by Wahlberg et al. (2011), and assume that most of the click energy is between 20 and 120 kHz. The median hourly noise level (NL_{est}) was then estimated using Equation 3-6 where NL is the median hourly noise level in the 1/3rd octave band centred on 40.3kHz; 1_3BW is the bandwidth of the selected 1/3rd octave band (here 9.28 kHz) and D_BW is the theoretical bandwidth of the detector, here 100 kHz .

$$NL_{est} = NL - 10 * log10(1_{3\mathrm{BW}}) + 10 * log10(\mathrm{D}_{\mathrm{BW}}) \quad \text{Equation 3-6}$$

My principal objective was understanding whether site specific trends in in ambient noise levels could bias acoustic occupancy results. For example, acoustic sensors placed near an active vessel port may experience diel trends in ambient noise levels from local fishing activity, lowering detection probabilities during periods of high activity and thereby skewing the acoustic occupancy results for those sensors. Conversely, storm systems that cover most, if not all, of the ECoMMAS area would not be expected to introduce substantial bias into the results of any given sensor compared to others but could potentially give misleading results in temporal analyses.

I measured the distribution of median hourly noise levels from all the SM units to determine whether any sites experienced large (>2dB) variations in noise levels relative to the rest of the array. I also calculated pairwise Pearson correlations for all hourly noise levels across all sensors to produce a correlation matrix for all ten instruments. Large correlation coefficients between distantly spaced SM units are suggestive of acoustic sources affecting large spatial scales (e.g. storm systems) and acting to increase the ambient noise level across the entire array. However, higher correlations between adjacent SM's compared to distant ones may be attributable to localised sources such as fishing activity, construction or permanent shipping lanes.

Only noise levels from 2013, between August 10th and September 24th, inclusive, were included in this part of the analysis, those being the dates for which ambient noise levels were available for all 10 SM units.

3.2.5. Transmission Loss

The AcTUP Bellhop ray tracing model (Porter, 2011) was used to estimate the propagation conditions in and around each deployment location. Ray tracing models were selected over other commonly used propagation models such as parabolic equations or multipath expansions due to their applicability to high frequency sounds in shallow water environments. Furthermore, a recent study indicated that ray-tracing algorithms produce the most accurate transmission loss estimates within a complex range-dependent environment (Farcas et al., 2016).

The Bellhop model creates a two-dimensional grid representing the transmission loss as a function of range and depth from a source. Bellhop parameters include the frequency of the source, source depth, sound speed profile at the source location, bathymetry profile, and sediment characteristics including density, sound speed and attenuation (dB/wavelength). Bathymetry and sound speed profiles with 1 arc second resolution (~30m) were obtained for each deployment location from the EDINA Marine Digimap service (http://digimap.edina.ac.uk) and NOAA World Ocean Atlas (http://www.nodc.noaa.gov/OC5/woa13) respectively. Detailed sediment surveys at each of the ECOMASS deployment locations have not been carried out. However, sediment modelling studies in the North Sea have indicated high sand and mud content throughout the ECOMASS survey area (Stephens and Diesing, 2015). Thus, I assumed a silt bottom with a sound speed of 1575m/s, density of 2400 kg/m^3 and 0.01 dB/λ attenuation for all locations. This assumption would be inappropriate for low frequency sounds such as baleen whale calls for which transmission through the seafloor sediment contributes significantly to the sound field (Weirathmueller et al., 2014). However, at higher frequencies (>10kHz), sound absorption by the medium becomes a major contributor to transmission loss. At 35khz, the transmission loss due to absorption alone is ~7dB/km (Fisher and Simmons, 1977). Therefore, the assumption of homogenous sediments throughout the survey area is unlikely to result in major discrepancies when considering *relative* detection ranges.

Twenty transmission loss grids were created at 18° intervals centred at each deployment.

Similar to previous studies (Helble et al., 2013, Frasier et al., 2016), I employed the acoustic reciprocity principle (Rayleigh, 1876) which allows the source and receiver locations to be switched within the environment. Thus, I simulated an omni-directional source (rather than receiver) at each C-POD deployment location. This assumption allowed me to efficiently calculate the transmission loss between the deployment site and all range-depth values encompassed by the transmission loss grids (Figure 3-2). Propagation models were run on MATLAB (2014) using the AcTUP package (v2.2).

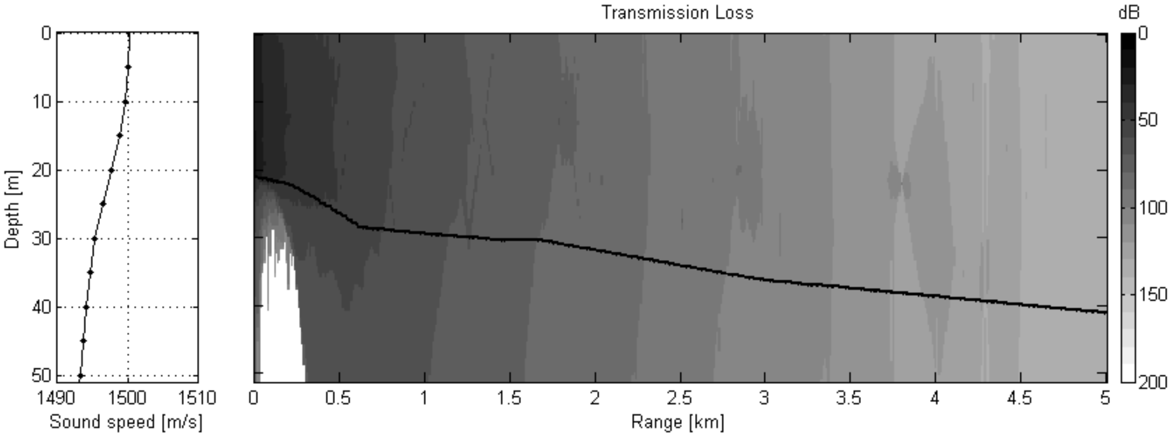


Figure 3-2 Example of a Bellhop transmission loss grid created for Stonehaven 5km deployment site and 35kHz. Vertical axis represents water depth, horizontal axis is range from the receiver (white circle), solid black line is the ocean bed, and grayscale represents the transmission loss between source and receiver.

Bellhop models for each deployment site were created using source frequencies of 30, 40, and 45 kHz. These frequencies correspond to the frequencies incorporated in the 38 kHz 1/3rd octave noise bands (~35 – 48 kHz) and, as such, are an appropriate comparison. Higher frequencies were not included for two reasons. First, they were greater than the upper limit of the noise monitoring instruments. Second, propagation models become less reliable with both increasing frequency, and decreasing water depth as is the case on the eastern Scottish coast (Urick, 1983). The propagation models for all frequencies were then averaged for each angle (θ) such that the average transmission loss at each angle could be calculated as a function of range and depth between the sensor and receiver. Finally, transmission loss values were again averaged over the water depth extending to the sediment in order to calculate transmission loss as a function of range and angle only ($TL(r, \theta)$; Equation 3-5).

While the acoustic reciprocity principle is mathematically sound, transmission loss models such as the ray-tracing algorithms use simplifying assumptions for computational efficiency. As such, switching source (animal) and receiver (C-POD) may result in different transmission loss values and is in violation of the assumptions used here. To test the extent of this violation I measured the maximum range at which animals could be heard at each deployment site for all of the angles tested I then set the sound source at the maximum detection range and estimated the maximum detection range in the opposite direction (i.e. switching source and receiver locations). Through this process I estimated a new maximum area monitored for each survey location. The proportional difference in area monitored between the original transmission loss model and the validation model was incorporated into the Bayesian occupancy analysis as an additional variance on the total area monitored. See Appendix 1- Bellhop Error for details.

3.2.6. Source Level and Pulse Duration

Cetacean echolocation clicks are a complex acoustic signal for which the received characteristics are not easily predicted. Echolocation clicks are generally thought to be produced by using air pressure to separate the phonic lips which then produce an impulsive sound when they slap back together. The impulse is propagated through the animal's head and into the environment via a complex process involving multiple reflections off both internal and external structures (Goold, 1996, Soldevilla et al., 2010b, Au et al., 2012c). The received spectral characteristics of the echolocation clicks are therefore dependent on, among other things, the receiver characteristics, the animal's aspect relative to the receiver, and the behaviour of the animal at the time the click was produced (Au and Benoit-Bird, 2003; Roch *et al.*, 2015). Further complicating the issue, source levels of echolocation clicks are most often collected from on-axis angles and reported as peak-to-peak values (Rasmussen et al., 2004, Clausen et al., 2011). On-axis measurements represent only a small portion of the echolocation clicks that will be documented by any moored passive acoustic system, and peak-to-peak values represent the maximum energy over a limited frequency range. Therefore, selecting a representative source level value or values over which to estimate the probability of detection is a challenge.

My approach to this problem considers that on-axis clicks will result in the largest detection range for each C-POD. Here I assume the peak-to-peak source level was 220 dB_{pp} re 1µPa and the source signal duration was 15µs (SL', $\tau_{0;}$ Equation 3-5). These values represent the upper end of the reported maximum source levels for free-ranging bottlenose dolphins (Wahlberg et al., 2011).

3.2.7. Detector Characterization

All acoustic detection systems contain both a minimum detection threshold, the pressure at which a signal must be received in order for the signal to be registered by the recorder, and an SNR threshold, the level above the ambient noise a signal must exceed in order to be detected. In a simple energy detector, the SNR threshold is triggered if a peak in pressure exceeding the detection threshold (TH, Equation 3-2) occurs within the integration window of the system (τ_e, Equation 3-5). A constant SNR threshold results in false alarm probabilities (i.e. false detections) varying as a function of ambient noise (Urick, 1983, Urazghildiiev et al., 2009). Alternative detection methods use adaptive thresholds that shift in response to ambient noise levels. In doing so, adaptive thresholds maintain a constant false alarm rate despite changes in ambient noise conditions (Gillespie, 1997, Gillespie and Caillat, 2008). For C-PODs, Dahne (2013) report the minimum detection threshold of ~120 dB_{pp} narrowband signals at 60 kHz. The SNR threshold, however, has not been characterised nor is it known whether the C-PODs detection system approximates a constant or adaptive threshold. The C-POD manufacturer describes the behaviour of the detection threshold as follows:

> *If noise* [i.e. interference] *levels are high enough to push the detection threshold up, the average SPL of the weakest clicks in the multipath clusters in trains should be louder. The multipath minima have been used as there are relatively few direct-path clicks in any train that are close to the detection threshold. Including the echo replicates in the multipath clusters increases the useful data volume. The 'Noise levels' export option gives values for the number of all clicks, the number of multipath minima and their mean value (' Nclx, nMMM, MMM'). This approach needs investigation and validation.*

The statement above suggests that the system may employ adaptive SNR thresholds. However, how the system behaves in response to either ambient noise or sediment interference is ill-defined and, as the manufacturer states, un-validated. Moreover, the manufacturer conflates detector interference with ambient noise levels, further confounding any understanding of his system. This means researchers must either make assumptions regarding thresholding behaviour or undertake extensive testing on behalf of the manufacturer. As tank calibrations in the 20-120 kHz range were impractical, I used simulations based on third party publications and reasonable approximations where no data exist. My approach assumes a constant rather than an adaptive SNR threshold. As with noise levels and transmission loss, this assumption leads to greater fluctuation in area monitored by the sensors than would be expected were I to assume an adaptive SNR threshold (for details see Zimmer 2011 pp 116) and is therefore a conservative approach with respect to my research questions. For the reasons stated above, I do not attempt to simulate any adaptive thresholding performed by the C-PODs.

For the simulations, I assumed that all received clicks must both exceed $120dB_{pp}$ as well as the SNR threshold of the system. To account for the lack of knowledge regarding detector performance, I investigated three potential SNR threshold values (TH; Equation 3-2) including 1, 10, and 15dB above ambient noise.

The integration period (τ_e) and detector threshold (TH) have opposite effects on the area monitored by a C-POD. As integration time increases, the detection threshold must decrease in order to maintain consistent detector performance. This reduces the maximum detection range of the C-POD. Conversely, for shorter integration periods, the maximum area monitored increases as signals more easily exceed the threshold. However, in the latter scenario, false positive detections also increase. Since the manufacturer provides no information on this subject, I investigated three potential integration times 1500, 5000, and 8000 µs. These values were paired with SNR thresholds of 1, 10, and 15dB. Without knowledge of the detector performance, the choice of integration times and SNR thresholds was somewhat arbitrary and was limited by processing time. However, in selecting these values I sought to include a broad range of potential detection ranges and probabilities. The lower limit of the integration period was set to be larger than the average click duration for bottlenose dolphins. The upper limit of the integration time was set to be less than previously reported inter-click intervals for bottlenose dolphin buzzes and click trains (Luís et al., 2016, Noren et al., 2017).

3.2.8. Acoustic Occupancy Models

Bayesian occupancy models based on Royle and Kéry (2007) were created to estimate acoustic occupancy rates at each of the 10 sites. In both models, the presence or absence of acoustic detections was described by the effective detection probability (*effp*). The effective detection probability considers both the true occupancy (*true.occ*) and the observation process. True occupancy is the ecologically meaningful portion of the metric that describes the proportion of time that echolocating animals were present within the maximum detection radius of the system. The observation process relates to the detection probability which represents some proportion of the maximum detection area that occurs under low ambient noise conditions and no acoustic shadowing. Because explicit knowledge of the detection function is not known, here ψ was modelled as the relative area monitored by each site. Through this procedure, detections were normalized by the spatial effort represented by the area monitored.

The first model estimated the probability (*Occ*) that each survey location (*j*) was acoustically occupied during each hour (*i*) of the deployment using a Bernoulli distribution (Equation 3-7). By analysing on an hourly scale, this model incorporated both spatial (site-specific transmission loss) and temporal (ambient noise level) aspects of the detection probability.

$$P\left(Occ_{i.j}\right) \sim dbern\left(effp_{i,j}\right) \qquad \text{Equation 3-7}$$

The effective detection probability was defined as the product of the true occupancy (*true.occ*) at each site and the observation process (ψ, Equation 3-8).

$$eff.p_{i,j} = true.occ_j * \psi_{i,j} \qquad \text{Equation 3-8}$$

The true acoustic occupancy rate at each of the sites was represented by the logistical transform of a linear model (Equation 3-9) where α is the site-specific acoustic occupancy rate. *Intercept* and α priors were minimally informative normal distributions with mean of 0 and standard deviation of 10^4.

$$logit\left(true.occ_j\right) = intercept + \alpha\left(Site_j\right) \qquad \text{Equation 3-9}$$

I then scaled the area monitored by each instrument and deployment location in order to relate the area monitored to the observation process. Scaling was done by centring and transforming the data. For each threshold model, I centred the data by subtracting the median area monitored for all sites and all times from the area monitored at each site and time. I then divided each centred area by the standard deviation of the area monitored values at each deployment location. The observation process (ψ) was defined as the inverse logistical transform of the scaled area monitored (*scaledArea*) by each sensor (*j*) at each hour (*i;* Equation 3-10). Variability introduced by errors in the Bellhop transmission estimation was incorporated by assuming that the area monitored by each site and each hour was drawn from a normal distribution with the mean centred on the estimate of the area monitored and the standard deviation described by the estimate of the Bellhop model error (Appendix 1).

$$logit(\psi_{i,j}) = dnorm\ (\ scaledArea_{i,j}\ , \sigma_{i,j}) \qquad \text{Equation 3-10}$$

Results from the models considering the area monitored were compared to a “null” model that did not include the observation process. The null model represents a uniform detection probability across all sites and times and is the standard method for analysing C-POD data (Jaramillo-Legorreta et al., 2017, Jaramillo-Legorreta and Rojas-Bracho, 2011, Roberts and Read, 2014)

The transmission loss simulations indicated larger variation *between* deployment locations than within a survey period for each deployment. This finding suggests that local bathymetry and transmission loss likely had a greater influence on detection probability than did changing noise levels. Thus, the second model aggregated the data and considered only the spatial aspects of the detection function. In this model the effective occupancy rate (*effp*) at each deployment location (*j*) was modelled as a binomial distribution of the number of detections (*Det*) and the number of monitored hours (*N*) at each deployment location (Equation 3-11; Table 3-3).

$$Det_j \sim binom(effp_j, N_j) \qquad \text{Equation 3-11}$$

As with the Bernoulli model, the effective detection probability at each site (j) was defined as the product of the true occupancy (*true.occc*) and the detection probability (ψ) at each deployment location (Equation 3-11). True occupancy and detection probability followed Equations 3-9 and 3-10 excluding the hourly covariate. Non-informative priors for α were used to limit model bias. Intercept and α priors were set to normal distribution with mean of 0 and standard deviation of 10^4. Bayesian models were created and run in R v.3.3.2 (R Core Team, 2016) using the runjags package (Denwood, 2008).

3.3. Results

3.3.1. Acoustic Detections and Continuous Recordings

Dolphin positive hours for deployment times and locations with both C-POD and SM coverage were generally low. With the exception of the Fraserburgh 05 unit, hourly acoustic occupancy rates for all locations during the period of SM coverage were less than 1%. At the Fraserburgh 05 site, 1.09% of the hours contained at least one dolphin detection (Table 3-1).

Table 3-1 Deployment summary for combined SM2M/C-POD moorings. Dolphin positive hours indicate total number of hours with both C-POD and SM2M coverage for which there was at least one click train detected by the KERNO Classifier. Observed proportion of acoustically occupied hours is the proportion of combined monitoring hours containing echolocation click trains

Deployment Location	Dolphin Positive Hours (total)	Observed Proportion of Acoustically Occupied Hours
Lat_05	23	0.77
Hel_15	1	0.04
Cro_15	4	0.13
SpB_10	0	0.00
Fra_05	22	1.09
Cru_05	17	0.74
Sto_05	12	0.93
Abr_10	2	0.10
FiN_10	1	0.04
Stb_05	6	0.21

3.3.2. Noise Levels

Median hourly noise levels in the 40.3 kHz 1/3rd octave band ranged from ~90 to ~109 dB for all units. The noise level distributions were similar across all deployment locations with minimum, 25th, 50th and 75th quartiles all within 1 dB (Table 3-2) for all sites. Maximum noise levels varied by >10 dB but such high levels represented outliers in the data.

Table 3-2 Summary statistics for the median hourly noise levels in the 40.3 kHz 3rd octave band.

	Min	25th Quartile	50th Quartile	75th Quartile	Max
Lat_05	90.5	90.7	91	91.6	108.9
Hel_15	90.4	90.5	90.8	91.2	97.1
Cro_15	90.6	90.9	91.3	91.8	99.3
SpB_10	90.6	90.8	91.2	91.8	103.7
Fra_05	90.5	90.6	91	91.5	98.2
Cru_05	90.4	90.8	91.2	91.6	97.9
Sto_05	90.5	90.6	90.9	91.2	97
Arb_10	90.5	90.6	90.9	91.2	100.5
FiN_10	90.6	91	91.2	91.6	99.1
Stb_05	90.4	90.6	90.9	91.7	102.2

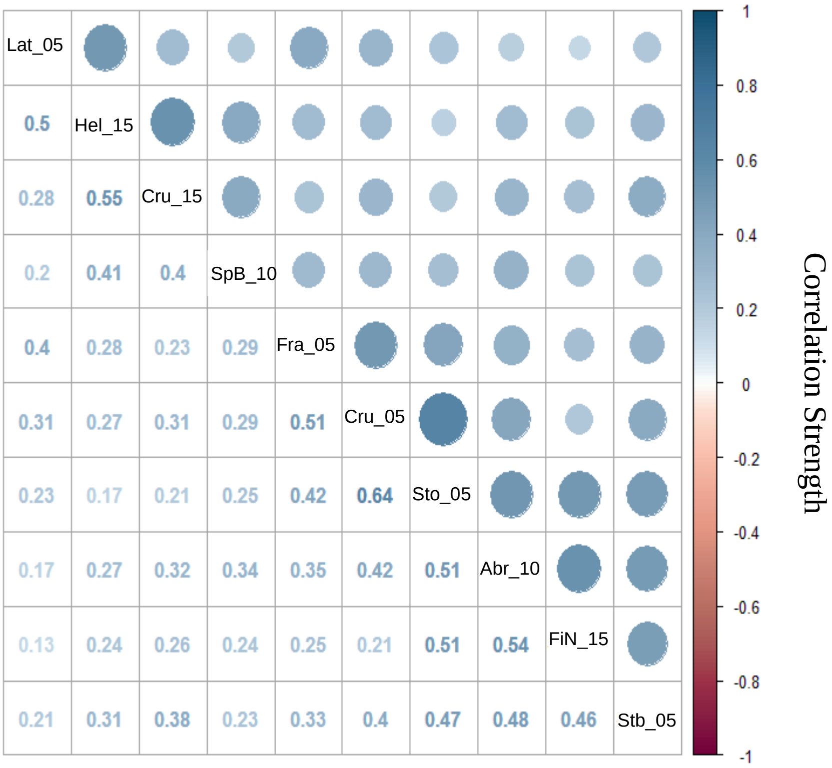


Figure 3-3 Pearson’s pairwise correlation scores (lower) for the 40.3kHz third octave band for the ten deployment locations during periods of SM coverage. Size of the coloured dots represent strength of the correlation (correlation values in corresponding lower panel) and colours indicate direction of the correlation from strongly negative (red) through natural (white) and strongly positive (blue)

All Pearson’s correlation scores were positive (Figure 3-3) and the median score between noise levels across pairs of units was 0.31 (25th and 75th percentile 0.22 and 0.46). The highest levels of correlation were observed between the Cruden Bay and Stonehaven units (*r* = 0.66) and the lowest between Latheron and Fife Ness (*r* = 0.13). Uniformly positive correlation scores across the extent of the deployment suggest that the underlying factors influencing ambient noise levels across the array were related. Higher correlation scores were observed in adjacent SM units than between units spaced further apart indicating that noise levels from units closer together share more similarity than to those from more distantly spaced units (Figure 3-4).

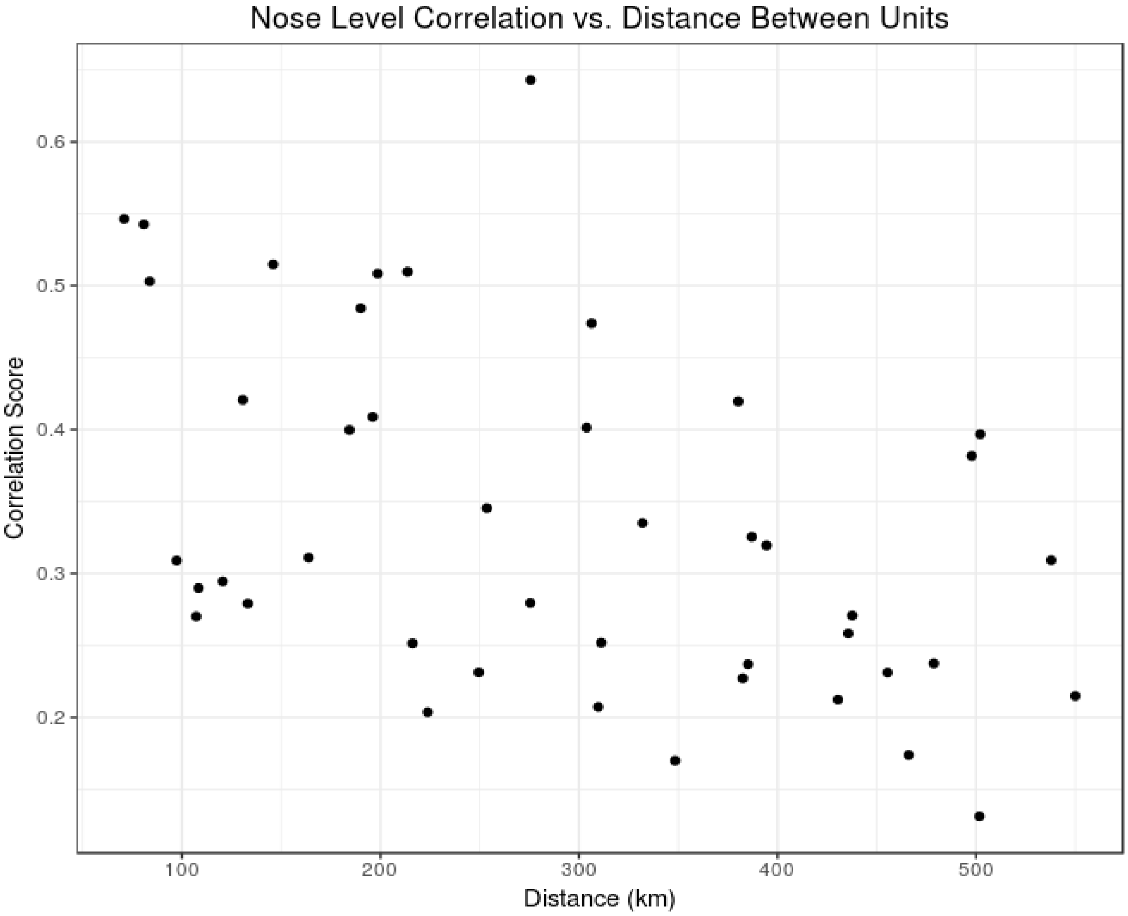


Figure 3-4 Pearson’s correlation score plotted against distance between SM units. While some correlation can be explained by the proximity between units, much of the correlation is left unexplained.

3.3.3. Area Monitored

As expected, the 05 units monitored less area than the mid or offshore units-regardless of the threshold model selected (Table 3-3, Figure 3-5). Models using threshold 2 (τ_e = 8000 µs, TH=10 dB) produced the largest estimate of the area monitored by the C-PODs throughout the deployment, with median values exceeding 25 km^2 for all deployment locations. This threshold also produced the lowest variation in area monitored throughout the deployment period with a median coefficient of variation of 1.72 as opposed to 3.0 and 3.2 for threshold models 1 and 3.

Table 3-3 Modelling variables for the binomial occupancy model. Median Area Monitored is the median area monitored by C-PODs at each of the deployment locations under the three modelled conditions. Model 1: τ_e = 1500 μs and SNR =1 dB, Model 2: τ_e = 5000 μs and SNR =10 dB, Model 3: τ_e = 8000 μs and SNR = 15 dB. Equivalent Detection Radius represents the median detection radius at each of the monitored sites and scaled Area Monitored is median the area monitored by each C-POD relative to the mean area monitored at all C-POD deployment locations.

Deployment Location	Median Area Monitored (km^2)			Equivalent Detection Radius (km)			Scaled Area Monitored		
	Model 1	Model 2	Model 3	Model 1	Model 2	Model 3	Model 1	Model 2	Model 3
Lat_05	10.14	29.58	6.49	1.01	1.73	0.81	-1.03	-0.94	-0.57
Hel_15	13.64	46.69	7.53	1.18	2.18	0.87	0.91	0.98	0.59
Cro_15	13.05	43.32	7.58	1.15	2.10	0.88	0.58	0.6	0.65
SpB_10	13.58	42.97	7.94	1.17	2.09	0.90	0.88	0.56	1.06
Fra_05	10.11	27.79	6.39	1.01	1.68	0.81	-1.05	-1.15	-0.68
Cru_05	11.75	43.49	6.21	1.09	2.10	0.79	-0.14	0.62	-0.89
Sto_05	11.7	27.95	7.51	1.09	1.68	0.87	-0.16	-1.13	0.58
Abr_10	13.86	46.41	7.65	1.19	2.17	0.88	1.03	0.95	0.73
FiN_10	13.37	45.66	7.52	1.16	2.15	0.87	0.76	0.86	0.59
Stb_05	8.76	25.89	5.16	0.94	1.62	0.72	-1.79	-1.36	-2.07

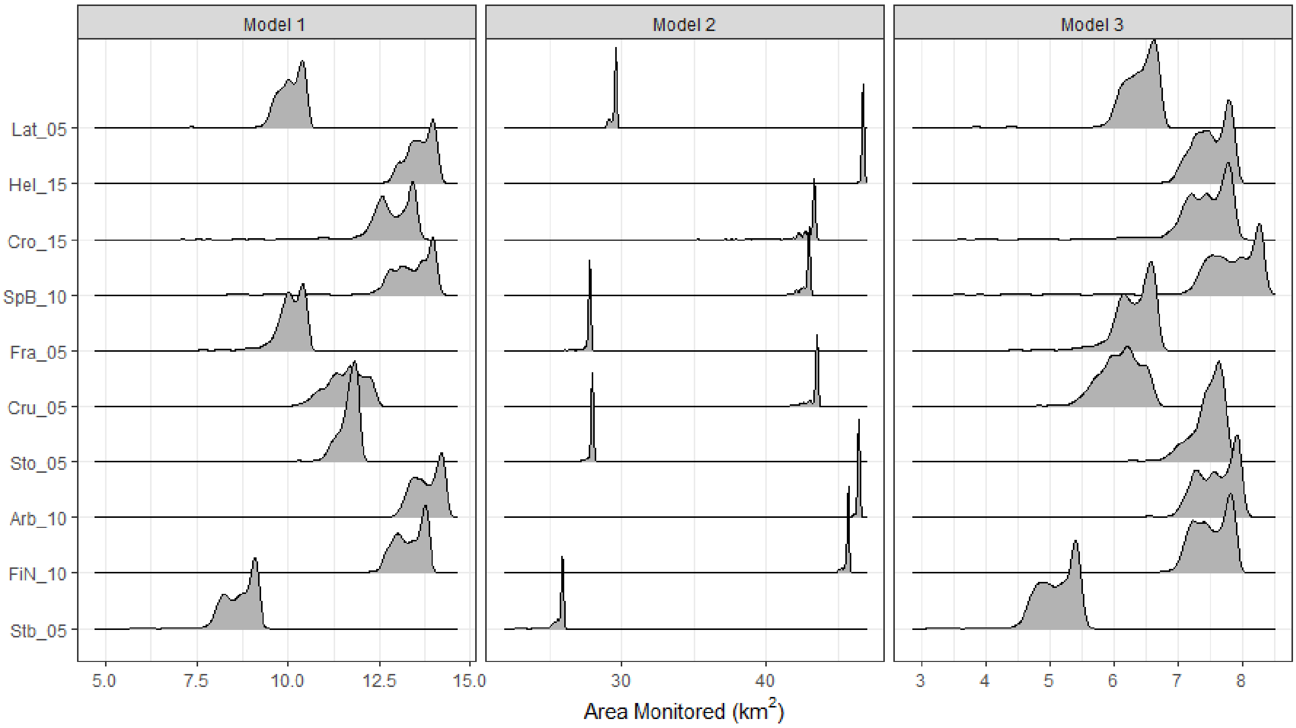


Figure 3-5 Density distribution of the monitored area estimates (km^2) for the 10 C-PODs with adjacent SM units throughout the 2013 and 2014 SM recording period. Model 1: SNR threshold = 1dB and integration window (τ_e) of 1500 µs, Model 2: SNR threshold=10dB and integration window (τ_e) of 5000 µs and Model 3: SNR threshold=15 dB and integration window (τ_e) of 8000 µs.

3.3.4. Modelled Acoustic Occupancy Rates

Acoustic occupancy rates differed significantly between deployment locations, where significance is defined by non-overlapping Bayesian highest probability density intervals (HPDI). In all models, the acoustic occupancy rates of the nearshore (05) units including Latheron, Fraserburgh, Cruden Bay and Stonehaven were significantly higher than the offshore (10 and 15) units. Similarly, relative acoustic occupancy rates showed considerable variation between the null model and those with disparate SNR and integration times (Figure 3-6, Table 3-4).

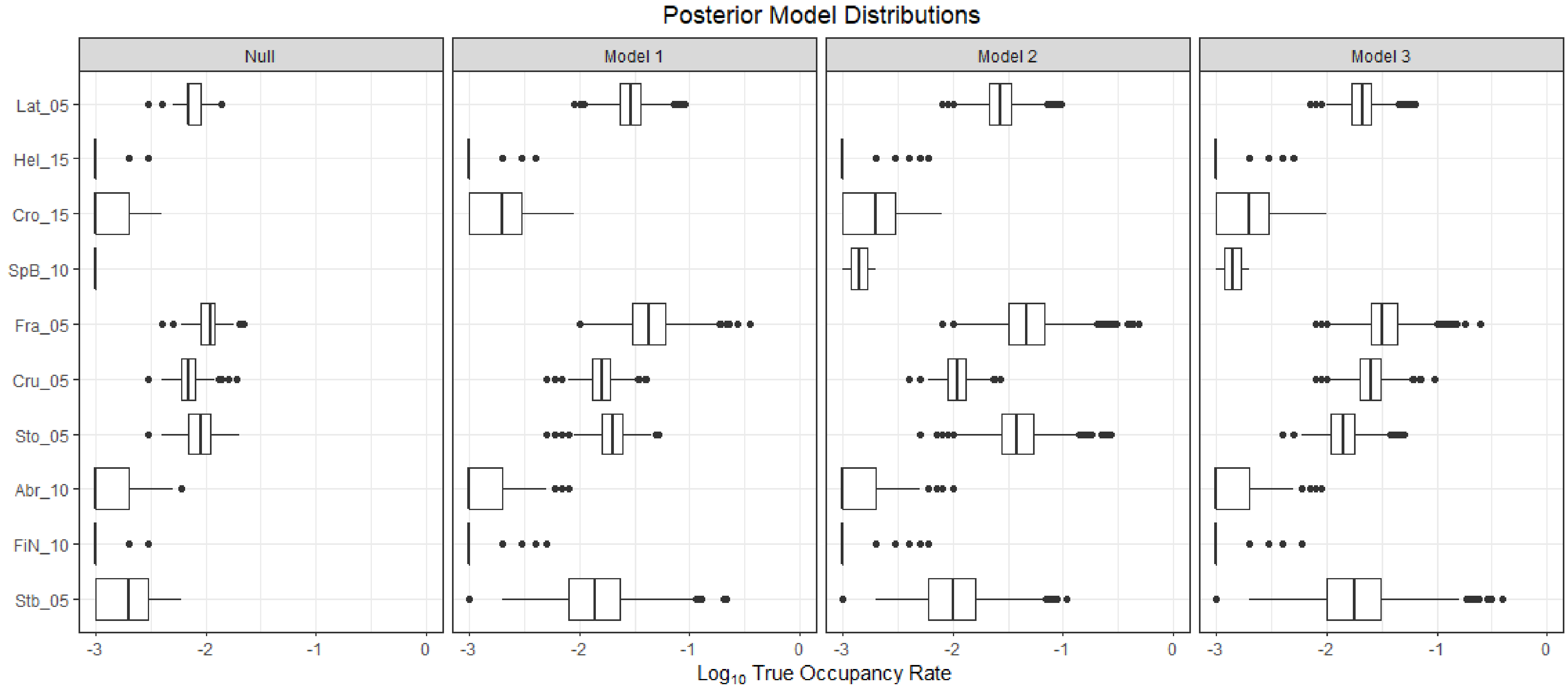


Figure 3-6 Natural log of the posterior distributions for the true occupancy rates for each deployment site and model. Integration periods (τe) and detector thresholds (TH) were 1 dB and 1500 µs for Model 1, 10 dB and 5000 µs for Model 2 and 15dB and 8000µs for Model 3.

Table 3-4 Median predicted percent (%) of acoustically occupied hours for the four different models (columns) at each of the 2013 and 2014 SM2M deployment sites (rows). In parenthesis are the 25th and 75th percentile values.

	Model			
	Null	**Model 1**	**Model 2**	**Model 3**
Latheron	0.2 (0.1-0.3)	1.4 (0.9-2.3)	1.0 (0.6-1.5)	1.9 (1.1-3.2)
Helmsdale	0.0 (0.0-0.1)	0.0 (0.0-0.1)	0.0 (0.0-0.1)	0.0 (0.0-0.1)
Cromarty	0.1 (0.1-0.1)	0.1 (0.1-0.2)	0.1 (0.1-0.2)	0.1 (0.1-0.2)
Spey Bay	0.9 (0.8-1.1)	2.0 (1.6-2.5)	3.7 (2.7-5.2)	1.4 (1.2-1.8)
Fraserburgh	0.7 (0.6-0.8)	1.6 (1.3-1.8)	1.1 (0.9-1.3)	2.5 (2.0-3.1)
Cruden Bay	1.1 (0.9-1.2)	4.2 (3.1-6.0)	4.5 (3.2-6.7)	3.3 (2.5-4.4)
Stonehaven	0.0 (0.0-0.0)	0.0 (0.0-0.0)	0.0 (0.0-0.0)	0.0 (0.0-0.0)
Arbroath	0.1 (0.1-0.2)	0.2 (0.1-0.3)	0.2 (0.1-0.3)	0.2 (0.1-0.3)
Fife Ness	0.0 (0.0-0.1)	0.0 (0.0-0.1)	0.0 (0.0-0.1)	0.0 (0.0-0.1)
St Abbs	0.2 (0.1-0.3)	1.4 (0.9-2.3)	1.0 (0.6-1.5)	1.9 (1.1-3.2)

3.4. Discussion

Analysis from this chapter suggests that the differential effects of ambient noise and site-specific transmission loss are sufficient to bias estimates of relative acoustic occupancy in the ECoMMAS survey area. . The nearshore deployment locations both detected more dolphin echolocation clicks and monitored a smaller area than the offshore deployment locations (Figure 3-5). Thus, the models including detection probability demonstrated a greater difference in acoustic occupancy between the near and offshore deployment location than the model that did not include detection probability. This, effectively, caused a greater difference in acoustic occupancy rates between the least and most occupied sites. In the case of the ECoMMAS array, the error introduced by varying detection probability likely results in overestimating habitat use of inshore areas. While no error is ideal, the bias in this case would not result in systematic changes in the management of the population given that the nearshore trend has been previously described in visual studies.

However, if the nearshore deployments either detected fewer echolocation clicks or monitored a smaller area than the offshore deployment locations, the interpretation of these results would change. Under this alternative scenario, the inclusion of detection probability would result in a smaller difference in acoustic occupancy between the least and most occupied sites. Thus, caution is warranted as teasing apart detection and acoustic occupancy probability would pose a considerable challenge to managers seeking to identify important areas.

Trends in median hourly noise levels in the 40.3 kHz 1/3rd octave band were highly correlated across sites (Figure 3-3). This suggests that storms, moving across large portions of the study area, dominate the hourly noise levels. The correlated noise levels and similar distributions suggest that relative impacts of noise at each sensor were small. However, correlation in Pearson's scores indicate a relationship between the level of correlation and the distance between sensors. Thus, the degree of correlation in noise levels reduces with distance. Future studies seeking to fully account for the effects of noise level on occupancy, density, or abundance metrics should consider this in their analysis. Accordingly, the results presented in Chapter 4 may incorporate limited bias introduced by varying ambient noise levels at distant survey locations. Previous studies have demonstrated that in areas of high tidal flow (<3m/s Macaulay pers. comm. 2/10/2017), high levels of ambient noise are present in the soundscape above 120kHz (Macaulay et al., 2017). The C-PODs in this study were subject to high tidal flow but were not deployed in extreme flow environments such as a tidal race. Therefore, while I expect that some degree of ambient noise is present above 48 kHz, I do not expect that the levels match those observed by Macaulay (2017). Similarly, the source level I used represented the maximum recorded peak-to-peak level reported by Wahlberg et al. (2011) and was therefore likely an overestimate of the average click source level produced in the wild. Finally, using frequencies below the peak frequency of echolocation clicks in the propagation model likely underestimates the transmission loss between the source and receiver. These were purposeful choices made to overcome the lack of explicit data concerning how the C-PODs may perform in this area. The combination of these decisions resulted in larger estimates of the area monitored and greater fluctuations in estimated detection probability due to ambient noise levels than previous studies have estimated and are likely the case (Nuuttila et al., 2013b, Roberts and Read, 2014, Sostres Alonso and Nuuttila, 2014). Because the relative acoustic occupancy rates were generally similar regardless of whether detection probability was incorporated in the model, I can be somewhat confident that the effects of ambient noise level and transmission loss will not severely skew the acoustic occupancy results in this study if they are not accounted for in analysis.

Results from this work are consistent with *in situ* studies that have shown that the likelihood of detecting an echolocating dolphin with a C-POD is influenced by the local conditions. Nuuttila et al. (2013b) and Roberts and Read (2014) investigated the maximum range at which bottlenose dolphins could be detected by C-PODs. Nuuttila et al. (2013b) report maximum detection ranges of ~2km for bottom-mounted C-PODs deployed in 17-22 m water. Roberts and Read (2014) report a maximum detection range of ~1km for units deployed at 4.5m depth. The difference in estimated detection ranges in these studies suggests that variation in propagation conditions with water depth may result in large changes in detection probability. Sostres Alonso and Nuuttila (2014) investigated this by comparing the click details resulting from C-PODs deployed at the same location but vertically spaced along the mooring. They found little difference in the number of detection positive minutes between units at the same mooring but noted that the average sound pressure level (as measured by the C-POD) was lower for C-PODs higher in the water column. However, since neither study reported noise levels it is impossible to judge whether differences in detection ranges were due to different noise levels, propagation conditions or a combination of the two.

Previous studies have shown that the probability and maximum detection range of bottlenose dolphins depends on the behavioural state of the animals (Nuuttila et al., 2013b). Because it was out of the logistical scope of this study, these considerations were not integrated into the model. Looking at behaviour across the array using the acoustic instruments is an interesting, albeit challenging prospect. One approach used by Pirotta (2014b) was to look at the proportions of click trains with low ICI clicks indicative of foraging.

This work incorporated several assumptions regarding the C-POD detection and classification system. Because so there were so few detections, use of the species-classification system developed in Chapter 2 was not possible. This may be a concern for future studies seeking to better understand how different species may be affected by changing noise and/or transmission loss characteristics. Thus, it is not possible to draw any firm conclusions regarding detection probability and how that may change between different species. Similarly, while I assumed all detections were bottlenose dolphin, the results may not hold under the source level constrains of other species. Future researchers seeking to investigate this may consider replacing click source levels and frequency distributions used here with those from different species (e.g. white-beaked or Risso’s dolphins). Moreover, studies looking to include multiple species in their density, occupancy, or abundance estimates may expand on the analysis code used here to incorporate source level distributions, species classification uncertainty (i.e. Caillat, 2013), and any number of environmental parameters.

The inability to discriminate between species in this portion of the analysis has the potential to bias occupancy rates under conditions where temporal trends in acoustic activity interact with changes in detection probability. For instance many species display variable diel acoustic activity (Carlström, 2005, Matthews et al., 2014, Baumann-Pickering et al., 2015) and differences between species would bias this research if conflated with diurnal fluctuations in ambient noise (Radford et al., 2008). Thus, one species producing sounds during a quieter part of the day would be more detectable than another producing calls when ambient noise levels were elevated, perhaps as boats return or leave the ports along the coast. Additionally, changes in detection probability were not modelled as a function of tidal state. However, tidal-drive changes in detection probability and species composition poses the same challenges to data interpretation. The continued use of C-PODs in such environments would benefit from more research in both these areas.

The choice of SNR thresholds and integration times was a based on a balance between available computing resources and the ability of the models to inform biological interpretations. The thresholds chosen represented three potential scenarios between the relative effects of ambient noise (within sensor variation) and transmission loss (between sensor variation). The first model represented a compromise between intra-sensor variation and intra-sensor variation. In the second model, the effects of transmission loss dominated and the variation between sensors greatly outweighed the variation within sensors. Finally, in the third model intra-sensor variation approached a similar scale as inter-sensor variation. This model would be chosen where site-specific noise regimes would be expected to dominate. A grid search of SNR thresholds and integration time would have provided a more comprehensive analysis of the potential area monitored by the systems. The approach used here was approximately the diagonal through the grid space and given the lack of variation in the results obtained it does not appear that a comprehensive search of all possible combinations of SNR and integration times would be worthwhile for ecological studies. More generally, the approach necessitated here represents linear approximation of what is undoubtedly a non-linear detection (C-Pod) and classification (Kerno) system. These simulations provide some insight into possible behaviour of the system. However, to appropriately integrating C-POD dolphin detections into ecological metrics including density, abundance will require controlled validation studies (e.g. Dahne *et al.,* 2013).

The assumptions necessitated by this chapter were necessitated the “black box” nature of the C-POD/KERNO system. This will continue to be a limitation of this and future studies using C-PODs as their primary data source(s). The major benefit of C-PODs is their ability to monitor very high frequencies (>200kHz) and to quickly process data for the presence of echolocation click trains in a cost-effective package. As costs associated with collecting and processing high frequency continuous recordings come down, researchers may consider more straightforward methods for effectively implementing large-scale acoustic studies. This may include replacing C-PODs with continuous recorders able to sample over longer durations.

This chapter investigated the potential effects of propagation conditions and ambient noise levels on the absolute and relative acoustic occupancy rates produced by C-PODs in the ECoMMAS array. The Bayesian approach used here is flexible and may easily incorporate both observation and ecological processes into the modelling (Pardo et al., 2015). The consistent noise levels recorded across the array in combination with acoustic occupancy rates robust to changes in detection probability suggest that, for this study, accounting for transmission loss and noise levels may not impact the survey outcome. Thus, in the addition to the Bayesian approach, the limited effects of transmission loss and noise level allow for multiple modelling approaches including GLMs and GEEs to be applied to the ecologically relevant aspects of the survey. While these results were not sensitive to the changes in detection probability modelled here, this will not be the case for many, if any, other large-scale acoustic studies. As advocated by previous authors, future studies must consider these effects on the probability of detecting an animal prior to making claims about acoustic occupancy (Marques et al., 2011, Helble et al., 2013).

Finally, this chapter presents a methodology that is suitable for investigating the effects of detection probability on acoustic occupancy surveys. This approach may be integrated into related methodologies including distance sampling and SECR to better understand whether non-detection in acoustic surveys results from animal absence or a reduction in the monitored by the instruments. Understanding this relationship is critical for monitoring large spatial scales as well as estimating population sizes for acoustically active animals.

3.5. Conclusions

In this chapter I found that the effects of ambient noise level and transmission loss were not sufficient to bias hourly acoustic occupancy rates at the subset of C-PODs that were co-deployed with the SM2/3Ms. Because median hourly noise levels were correlated across the array, noise caused by wind and wave action is unlikely to bias acoustic occupancy rates at C-PODs for which continuous noise monitoring was not available.

Chapter 4

Daily Acoustic Occupancy, Temporal Trends, and Spatial Modelling

4.1. Introduction

Conservation and management efforts require explicit knowledge of how plants and/or animals are distributed, how they utilise their available habitat, and how these distributions vary over time (Sutherland, 1998, Anthony and Blumstein, 2000, Embling et al., 2010, Onorato et al., 2011, Jaramillo-Legorreta et al., 2017). Knowledge of the temporal behaviour patterns of animals can shed light on the environmental, ecological, and /or anthropogenic factors that drive species distribution (Thompson et al., 2013a, Thompson et al., 2013c, Merchant et al., 2014b). These relationships can and should be integrated into ecological models such as those used to estimate the consequences of anthropogenic disturbance for populations (Liley and Sutherland, 2007, Harwood et al., 2014, King et al., 2015, Pirotta et al., 2015a).

Worldwide, bottlenose dolphins are often found in shallow coastal waters, although offshore populations also exist (Leatherwood and Reeves, 1983). Bottlenose dolphins are generalist predators, foraging on a variety of fish and molluscs (Connor et al., 2000, Hastie et al., 2004b, Nowacek, 2005, Sargeant et al., 2005, Bailey and Thompson, 2006, Weir et al., 2007). In the coastal waters of eastern Scotland, bottlenose dolphins are known to forage on migratory and diadromous fish including herring, mackerel and salmon (Janik, 2000a). They are also known to utilise geographic features such as deep channels and tidal fronts to optimise foraging efficiency (Mendes et al., 2002, Hastie et al., 2006, Sargeant et al., 2005).

Over the last three decades there has been considerable effort made to understand the population dynamics, distribution, and habitat use of this population of dolphins. Historically, however, the majority of the studies have taken place within the Moray Firth SAC and specifically within the Inner Moray Firth (Janik and Thompson, 1996, Wilson et al., 1997b, Hastie et al., 2003b, Bailey and Thompson, 2006, Hastie et al., 2006, Bailey et al., 2010, Pirotta et al., 2014b, Thompson et al., 2015). Visual and acoustic surveys of dolphins in the Moray Firth have elucidated much about the fine-scale habitat selection of the animals, functional mechanisms underlying some points of aggregation, and potential effects of man-made noise on this population (Thompson et al., 2013a, Wilson et al., 1999, Wilson et al., 2004, Cheney et al., 2018).

The SAC represents a small but important portion of the habitat used by the population (Arso Civil et al., 2019, Cheney et al., 2018). In addition to studies in the SAC, others have focused on points of aggregation elsewhere along the coast including Aberdeen harbour and the Firth of Tay (Anderwald et al., 2010, Arso Civil et al., 2019). In these locations, researchers have linked fine scale movement and foraging to tidal fronts and bathymetric features. There have also been a handful of regional scale surveys covering >100km of habitat. Anderwald et al. (2010) compile visual sightings from boat and land-based surveys covering much of the available habitat South and East of Inverness. Results from their report showed that much of the availability is occupied by bottlenose dolphins. Similarly, in addition to surveying the Firth of Tay and Firth of Forth, Arso Civil et al. (2019) covered much of the area between St Andrews and Aberdeen in a series of ten boat-based surveys between 2012 and 2013. Between 2001 and 2005 the southern coast of the outer Moray Firth extending from Lossiemouth to Fraserburgh was subject to visual survey effort consisting of 393 survey trips covering coastal habitat extending approximately 6 km from shore (Robinson et al., 2007, Culloch and Robinson, 2008). Finally, in 2007 and 2008, fourteen timing porpoise detectors (T-PODs, www.chelonia.co.uk) were deployed within the Moray Firth SAC and four units were deployed at key sites around the Scottish coastline (Thompson et al., 2011a). T-PODs record the timing of dolphin and porpoise clicks but do not document any species identification. Results from this survey indicated that high use areas identified in the T-POD data coincided with visual sightings of bottlenose dolphins and that temporal patterns of detection in summer and winter were similar between sites located within the Moray Firth SAC high-use areas and low-use areas outside of the Firth (Thompson et al., 2011a).

Boat-based survey efforts have historically focused their efforts in areas of high animal density in order undertake photo-ID research (Wilson et al., 1999). However, extensive offshore construction projects are planned for the coming years and animals will likely be exposed to noise and anthropogenic disturbance throughout their range. The differential use by animals within their range means that different individuals may be subject to different levels of exposure to different anthropogenic activities (Pirotta et al., 2015a). These activities included the construction and operation of offshore wind farms, as well as port developments in the Cromarty Firth, Aberdeen, Peterhead and Fraserburgh (Pirotta et al., 2015a, Graham et al., 2017).

Improving understanding of trends in occupancy throughout the species range will help to interpret how human activities may impact the population. Large scale ship or aerial line transect surveys of the eastern Scottish coastline are likely to suffer from low detection rates. Fixed passive acoustic monitoring (PAM) surveys represent an alternative to vessel-based surveys and can produce simultaneous high-resolution time-series data for multiple survey locations. This type of passive acoustic monitoring has proven successful in monitoring both harbour porpoise and dolphins within the Moray Firth (Pirotta et al., 2014a, Williamson et al., 2017). The ECoMMAS array seeks to build on previous studies by monitoring habitat use primarily outside of the previously studied areas of concentration.

Data collected by the ECoMMAS array are long term (~12 months over three years) and large scale (~400km of coastline) and these data may be sufficient to describe temporal patterns in occupancy as well as spatial analysis of habitat use. However, acoustic data pose various challenges that necessitate a flexible approach to their analysis. The ECoMMAS array provides extremely good temporal coverage (except, currently, in winter) but limited spatial coverage when compared to acoustic studies in the Moray Firth. Deployment groups in the ECoMMAS were spaced between 17 and 50 km apart whereas the CPODs used in Pirotta et al. (2014b) were generally less than 5 km apart. Moreover, that array consisted of 39 locations spread over a survey area of approximately 150km of coastline, though not all locations were surveyed every year. In comparison, the ECoMMAS covered approximately 400km of coastline with 2/3^{rds} of the units being greater than 5km from the nearest coastline. Additionally, ECoMMAS data, like all PAM data, are subject to misclassification errors (false positive detections, Chapter 2) and potentially fluctuating detection probabilities (Chapter 3). As in many ecological studies, autocorrelation in detections is present in passive acoustic surveys (Lichstein et al., 2002). Acoustic encounters lasting from minutes to days violate the assumption of independence in observations, as the probability of detecting an echolocating animal in any given period is often related to whether or not an animal was detected in the previous period. Thus, care is needed when working with time series data as failing to account for autocorrelation violates the assumption of independent sampling. Finally, the density of sensors in the array is low, which may preclude meaningful spatial analysis.

With these considerations in mind I took a three-step approach to analysing the ECoMMAS data. The first aim was to report acoustic occupancy rates from the ECoMMAS survey for the first three years of the study. This has not been done for acoustic data outside of the Moray

Firth and is useful baseline knowledge. Following on, the second aim was to model temporal trends in acoustic occupancy at the ten survey group sites. Identifying and characterising any consistent temporal patterns in annual occupancy may help to identify short and long-term changes in habitat use at the survey locations. These results should be informative in assessments of the effects of construction, operation, and decommissioning of offshore wind farms on dolphin habitat use throughout Scottish coastal waters. The final aim was to determine whether it was possible to produce a habitat scale spatial-temporal acoustic occupancy model for the eastern Scotland bottlenose dolphin population. In doing so I sought to identify and combine spatial and temporal predictors into a cohesive model for bottlenose dolphin habitat use along the Eastern Scottish coast.

Finally, the results in Chapter 4 indicate that varying detection probabilities across the spatial extent of the array could result in a biased interpretation of trends in habitat selection. To investigate this possibility, Appendix 5 includes a sensitivity analysis of the habitat models used in this analysis.

4.2. Methods

4.2.1. Data Collection

Thirty C-PODs were deployed in the spring of 2013, 2014 and 2015. In 2013 instruments were deployed between June 18th and July 30th, as weather allowed, and recovered in October (Figure 4-1). In 2014 the array was deployed between May 16th and May 19th and recovered in November of the same year. In 2015, the array was deployed and recovered twice. The first deployment took place between April 18th and 22nd. C-PODs were recovered and redeployed between July 5th and 13th and retrieved in November. With the exception of the first 2015 deployment which was recovered prior to internal resource exhaustion, all units ran continuously until either storage or battery capacity was exhausted (Figure 4-1). Recovery of the acoustic units occurred after the units had ceased recording.

4.2.2. Data Quality

C-POD data from the 2013-2015 ECoMMAS deployments were downloaded and processed with the KERNO classifier for the presence of high or moderate quality “other cetacean” click trains. All click trains were subsequently processed with the click train categorisation system described in Chapter 2. From the classified echolocation click train detections I created a daily acoustic occupancy table that documented whether or not (1/0) each of the three click train categories (broadband, frequency banded or unknown – see Chapter 2) was detected by the C-POD. Unfortunately, there is insufficient taxonomic resolution to discriminate between the click types of common (*Delphinus delphis*) and bottlenose dolphins encountered in eastern Scottish waters (Chapter 2). However, common dolphins are very rarely seen in the North Sea (Reid et al., 2003, Hammond et al., 2017). Thus, it is highly likely that all echolocation click trains classified as broadband represent bottlenose dolphins.

For each day of each C-POD deployment I calculated the probability that a broadband echolocation click train encounter was detected (P(*Broadband*); Appendix 2) by taking the average of the hourly probabilities obtained from the confusion matrix in Chapter 2 (broadband = 0.5, frequency banded = 0.06 and unknown = 0.5). The daily broadband detection probability was then used as the response variable in the temporal analysis.

4.2.3. Temporal Covariates

Temporal covariates comprised Julian day (1-365), season (spring, summer or autumn), and year. Spring was defined as the months of April and May (there were no data in March). Summer was defined as June, July, and August and autumn was defined as September, October, and November. Winter was not included as there were no data between the months of November and April.

4.2.4. Spatial Covariates

Spatial covariates were included as either continuous or factor variables based on the available degrees of freedom. Previous studies have identified the following spatial covariates as potential predictors for the presence of bottlenose dolphins: distance to nearest point of aggregation (e.g. Cromarty Firth and River Dee), distance to shore, depth, and slope (Thompson et al., 2015).

Points of aggregation included eight estuaries that were either of known or suspected ecological importance to the species. River estuaries were selected from the Atlantic Salmon Rivers Database (http://www.nasco.int/RiversDatabase.aspx). These included the Cromarty Firth, Firth of Tay, and the rivers Ness and Dee (Hastie *et al.*, 2004; Cheney *et al.*, 2013;

Quick *et al.*, 2014). To these known points of aggregation, the mouths of the rivers Spey, North Esk and Tweed were added (Table 4-1). Distance to nearest point of aggregation was reported as a continuous variable measured by the distance between each C-POD and the nearest point of aggregations.

Distance to shore was measured as either a three-level factor corresponding to whether each C-POD was deployed in nearshore (05), midshore (10), or offshore (15) habitat, or as a continuous predictor. For the spatial-temporal model of acoustic occupancy, distance to shore was reported as the continuous range between the deployment location and the distance to the nearest 0 m isobath (Pante and Simon-Bouhet, 2013).

Deployment depth (in metres) was recorded from the ship at the time of deployment. The gradient of the seabed (henceforth slope, measured in radians) was estimated from the NOAA ETOPO1 database (Amante, 2009), with 1 arc-second resolution (~30m). Spatial data were processed using the ‘marmap’ R package (Pante and Simon-Bouhet, 2013). Slope was calculated in radians using the Fleming and Hoffer algorithm through the ‘raster’ R package (Fleming and Hoffer, 1979, Hijmans and van Etten, 2014) . Both depth and slope were modelled as continuous predictors.

Table 4-1 Name and location of ecologically relevant and potentially relevant points of aggregation

Point of Aggregation	Latitude	Longitude
Cromarty Firth	57.6958	-3.9900
Spey	57.6658	-3.6386
Chaonory Point	57.5775	-4.0844
Dee	57.1447	-2.0603
North Esk	56.7044	-2.4447
Tay Firth	56.4506	-2.7731
Tweed	55.7639	-1.9836

4.2.5. Acoustic Occupancy Rates

The first goal of this work was to report daily acoustic occupancy rates at each of the 30 deployment sites for the entire survey duration. Data from the ECoMMAS array represents the first large-scale acoustic study of dolphins and porpoises outside of the Moray Firth. I report daily acoustic occupancy rates for C-PODs at all deployment locations represented in the ECoMMAS array (Figure 1-1).

Site-Specific Temporal Trends

The second goal of this work was to produce models capable of characterising as much of the temporal variation in the observed occupancy as possible. In this analysis I fit generalised estimating equations with cubic splines (GEEGAMs) to each of the ten deployment groups based on *a priori* knowledge that bottlenose dolphins forage at different locations throughout their range (Hastie et al., 2004b, Pirotta et al., 2014b). GEEGAMs are flexible modelling structures that are capable of handling binary data where the majority of the observations are 0. Even so, it is not possible nor valuable to fit curved splines to a series of all zeros. For that reason, I only included data from C-PODs where there were at least two detection positive days. Autocorrelations in detections were accounted for by including autoregressive correlation structure with detections grouped by C-POD deployment location and year was included into the models (Box et al., 2015).

Model selection focused on determining the form of the relationship between the daily probability of detecting a broadband echolocation click encounter and Julian day of year. For each deployment group I investigated four models. Predictor variables for all models included a factor indicating whether the C-POD location represented a near (05), mid (10) or offshore (15) deployment location (ShoreDist), a three-level factor for survey year and a continuous integer for Julian day of year. The first model (Equation 4-1) assumed an interaction between the shore distance and Julian day of year and that the pattern in detections throughout the year could be modelled by a cubic B-spline. The second model assumed an interaction between the cubic B-spline and the survey year (Equation 4-2). The third model (Equation 4-3) had no interactions between the cubic B-spline and the shore distance or survey year and the fourth model (Equation 4-4) assumed a parametric relationship between the daily probability of detecting a broadband echolocation click train and the Julian day of year. In accordance with previous studies, or cubic spline models, a single knot was set at the mid survey date (Pirotta et al., 2011). It was not possible to include more than one knot in the spatial models as the additional degrees of freedom prevented model convergence. All models were created in R v.3.3.2 using the ‘geepack’ package (Halekoh et al., 2006). B-splines were introduced into the models using the ‘splines’ package (R Core Team, 2016).

$$P(Broadband) \sim Year + ShoreDist * bs\big(JulienDay, knots = median(JulianDay)\big)$$

Equation 4-1

$$P(Broadband) \sim ShoreDist + Year * bs(JulienDay, knots = median(JulianDay))$$

Equation 4-2

$$P(Broadband) \sim ShoreDist + Year + bs(JulienDay, knots = median(JulianDay))$$

Equation 4-3

$$P(Broadband) \sim ShoreDist + Year + JulianDay$$

Equation 4-4

Alkaike’s information criterion (AIC) scores are commonly used to select between candidate GAM or GLM models. However, because GEEs are not likelihood-based models AIC scores cannot be calculated. Thus, I used the quasi-likelihood criterion (Pan, 2001) to select between the four temporal acoustic occupancy models. Quasi-likelihood criterion selection mirrors AIC selection. However, since QIC scores are calculated under the independence model criterion, they are appropriate for selecting between GEE models.

In assessing model fits, I followed the methods reported by Pirotta et al. (2011). For each deployment group, I used the model with the lowest QIC to predict the probability of detecting a broadband echolocation click. I then created receiver operating curves (ROCs) to determine the relationship between the detection threshold, and the false positive and false negative rates for each model. Using the ROC, I selected an optimal detection threshold above which I considered the model to have detected a broadband echolocation click encounter and below which I assumed that no broadband echolocation click encounter was detected. Using this detection threshold, I then created confusion matrices to measure the proportion of detection positive and detection negative days correctly identified by the model. Finally, I calculated the area under the curve (AUC) for the ROC curve to describe the model goodness-of-fit. With a binomial model, AUC scores of 0.5 indicate that the model correctly predicted 50% of the observations. Therefore, AUC scores at or below 0.5 represent a model that performed as well as would be expected by chance alone. I calculated AUC scores for each model for each deployment group (e.g. Latheron, Helmsdale etc.). I also calculated AUC scores for all 30 deployment locations to investigate site-specific model performance. These analyses were done in R using the ROCR v1.0-7 and PresenceAbsence v1.19 packages (Sing et al., 2005, Freeman, 2007).

4.2.6. Spatial-Temporal Habitat Modelling

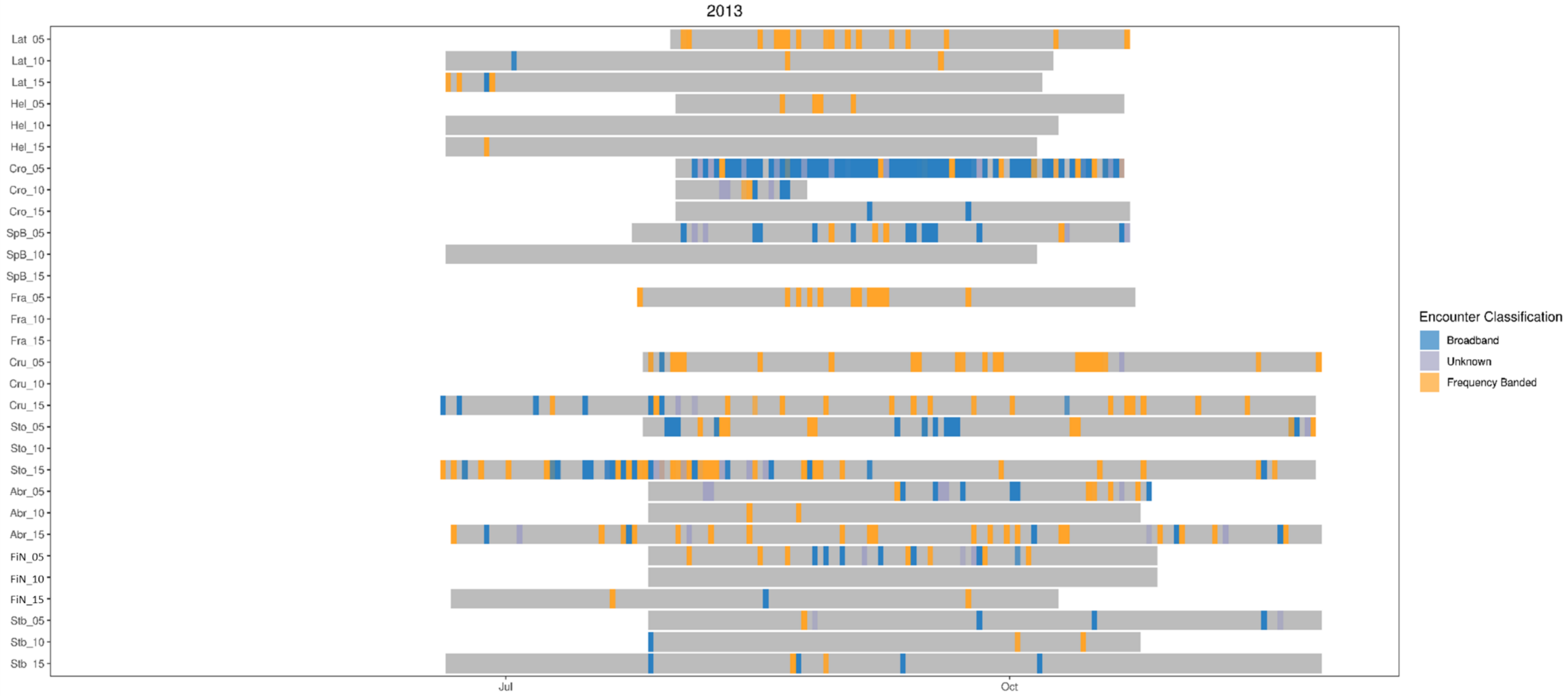
The third goal of this work was to produce a comprehensive spatial temporal model of bottlenose dolphin habitat use. I used generalised additive mixed models (GAMMs) (Wood, 2006) to incorporate both spatial and temporal variables, with unit location as a random effect. Bottlenose dolphins are known to move along the coast encountering different locations where foraging occurs (Wilson et al., 1997b, Quick et al., 2014). Thus, an ideal model would investigate interactions between the Julian day of the year, locations where animals are known to aggregate for foraging or other reasons, and the remaining spatial covariates (seabed slope, deployment depth, and distance to shore). Unfortunately, the small detection sample size meant that I was limited in the interactions that could be included. Instead, the full model included individual smooth terms of slope, distance to point of aggregation, depth, and distance to shore. As interactions in smooths are centred using the MGCV package, interaction factors were also added as a main effect as per package recommendations. As with site-specific temporal trends, an autoregressive correlation structure with detections grouped by deployment location was included in the model (Box et al., 2015).

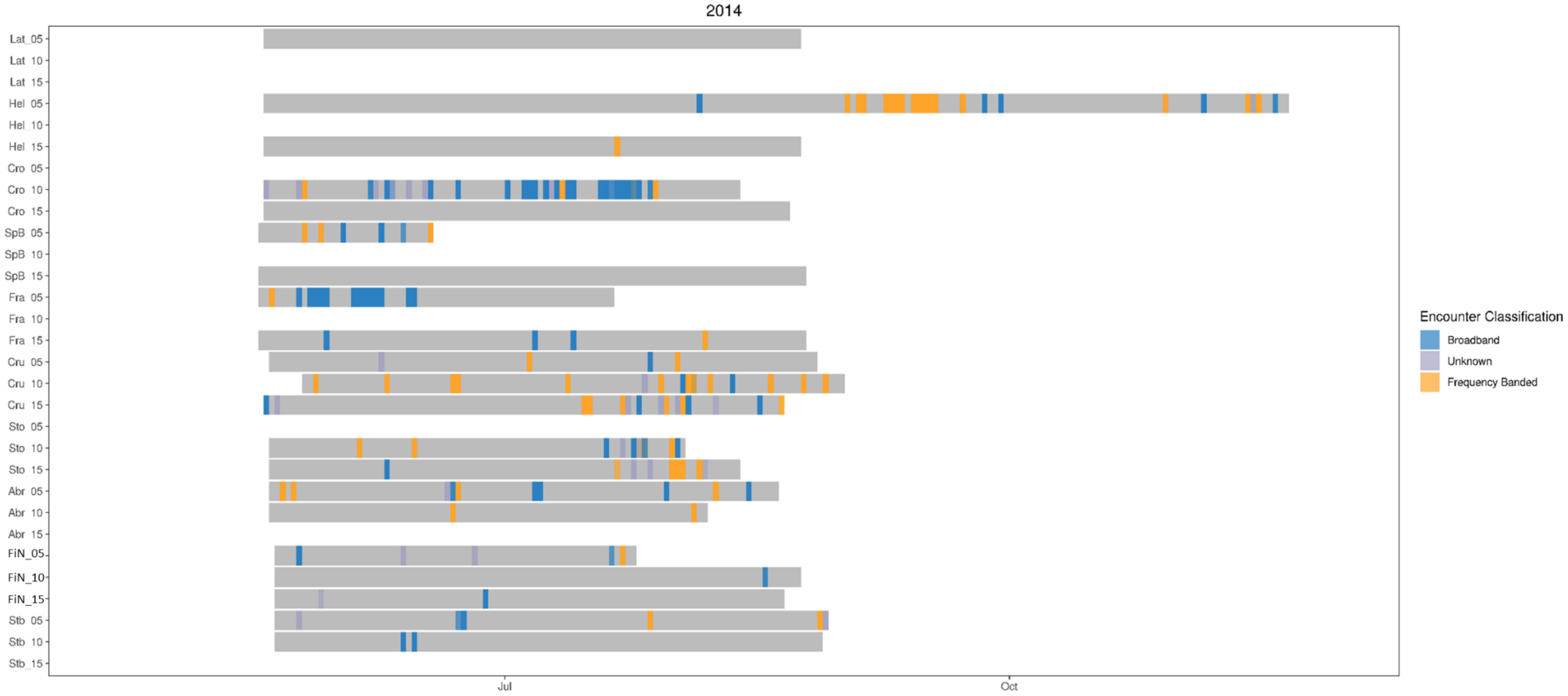
Model covariates were investigated for collinearity using variance inflation factors (VIF) and any covariates with VIF scores greater than three were considered collinear (Craney and Surles, 2002). Finally, adjusted R-squared and AUC scores were used to describe model fit.

4.3. Results

4.3.1. Acoustic Occupancy Rates

Together, the data retrieved from the C-PODs represented 11,663 days of monitoring. However, at only 16 of the 30 C-PODs deployment sites were devices retrieved in all three years. Periods of recording effort also differed between years (Figure 4-1). As expected, the C-POD deployed nearest to the Cromarty Firth (Cromarty 05) showed the greatest acoustic occupancy rate, with 78% of the days containing at least one broadband detection in 2013 and 83% in 2015. In 2014 the Cromarty 05 unit was displaced and not recovered (Table 4-2). There was a wide variation in both the rate of acoustic occupancy for all click trains as well as those identified as broadband by the click train classifier (Chapter 2). C-PODs deployed at the northerly and southerly ends of the survey area (Latheron and St Abbs) had very low (<5%) acoustic occupancy rates of broadband clicks for all survey years. In general, broadband acoustic occupancy rates at the nearshore (05) deployment locations were greater than the more offshore (10 or 15) locations (Table 4-2).


2013
Lat_05
Lat_10
Lat_15
Hel_05
Hel_10
Hel_15
Cro_05
Cro_10
Cro_15
SpB_05
SpB_10
SpB_15
Fra_05
Fra_10
Fra_15
Cru_05
Cru_10
Cru_15
Sto_05
Sto_10
Sto_15
Abr_05
Abr_10
Abr_15
FiN_05
FiN_10
FiN_15
Stb_05
Stb_10
Stb_15
Jul
Oct
Encounter Classification
Broadband
Unknown
Frequency Banded


2014
Lat_05
Lat_10
Lat_15
Hel_05
Hel_10
Hel_15
Cro_05
Cro_10
Cro_15
SpB_05
SpB_10
SpB_15
Fra_05
Fra_10
Fra_15
Cru_05
Cru_10
Cru_15
Sto_05
Sto_10
Sto_15
Abr_05
Abr_10
Abr_15
FiN_05
FiN_10
FiN_15
Stb_05
Stb_10
Stb_15
Jul
Oct
Encounter Classification
Broadband
Unknown
Frequency Banded

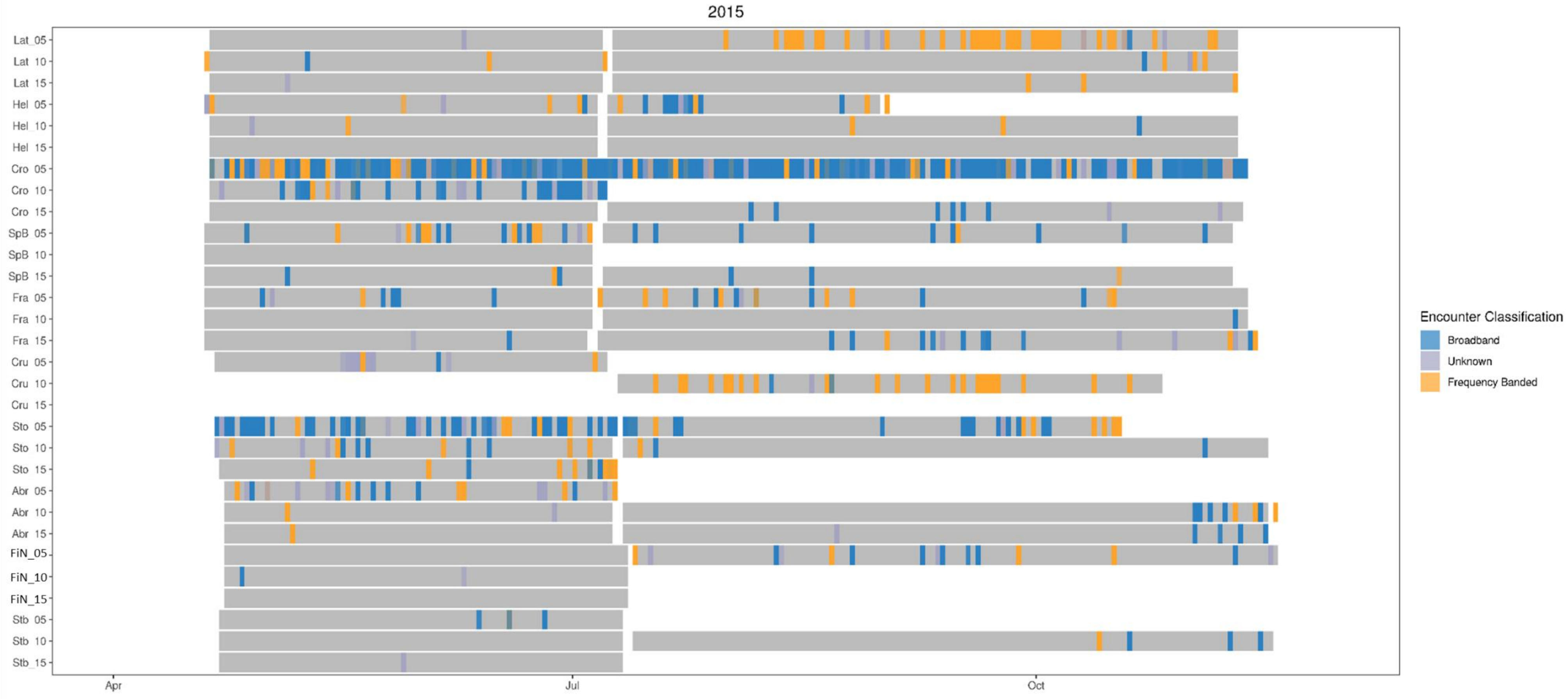


Figure 4-1 Spatial and temporal coverage (grey box) of ECoMMAS C-PODS for 2013 (top panel), 2014 (middle panel), and 2015 (lower panel). Coloured bars represent acoustic encounters. Encounters classified as broadband are coloured blue, frequency banded yellow, and encounters failing to meet either classification threshold are mauve.

C-PODs in the Stonehaven deployment group were notable for having the second highest overall acoustic occupancy rates. Moreover, a nearly even mix of both broadband and frequency banded echolocation click trains were recorded throughout the deployments (Figure 4-1). The C-PODs detected echolocation click trains on more than 15% of the survey days and broadband echolocation clicks indicative of either bottlenose or common dolphin echolocation click trains were identified on at least 10% of the survey days.

Table 4-2 Daily occupancy rates for unprocessed C-POD data (All) and detections classified as “broadband” by the classification system. 95% binomial confidence intervals in parenthesis

	2013		2014		2015	
	Occ. Rate (All)	Occ. Rate (Broadband)	Occ. Rate (All)	Occ. Rate (Broadband)	Occ. Rate (All)	Occ. Rate (Broadband)
Lat_05	0.19 (0.12 - 0.28)	0.00 (0.00- 0.04)	0.00 (0.00 - 0.04)	0.00 (0.00- 0.04)	0.20 (0.15 - 0.26)	0.00 (0.00- 0.03)
Lat_10	0.03 (0.01 - 0.08)	0.01 (0.00- 0.05)			0.04 (0.02 - 0.08)	0.01 (0.00- 0.04)
Lat_15	0.04 (0.01 - 0.09)	0.01 (0.00- 0.05)			0.02 (0.01 - 0.05)	0.00 (0.00- 0.02)
Hel_05	0.05 (0.02 - 0.12)	0.00 (0.00- 0.04)	0.12 (0.08 - 0.17)	0.03 (0.01 - 0.06)	0.14 (0.09 - 0.20)	0.07 (0.04 - 0.12)
Hel_10	0.00 (0.00 - 0.03)	0.00 (0.00- 0.03)			0.02 (0.01 - 0.06)	0.00 (0.00- 0.03)
Hel_15	0.01 (0.00 - 0.05)	0.00 (0.00- 0.03)	0.01 (0.00 - 0.06)	0.00 (0.00- 0.04)	0.00 (0.00 - 0.02)	0.00 (0.00- 0.02)
Cro_05	0.89 (0.8 - 0.94)	0.78 (0.68 - 0.86)			0.95 (0.91 - 0.97)	0.83 (0.77 - 0.87)
Cro_10	0.32 (0.17 - 0.52)	0.12 (0.04 - 0.3)	0.35 (0.26 - 0.46)	0.25 (0.17 - 0.35)	0.37 (0.27 - 0.48)	0.28 (0.19 - 0.39)
Cro_15	0.02 (0.01 - 0.08)	0.02 (0.01 - 0.08)	0.00 (0.00 - 0.04)	0.00 (0.00- 0.04)	0.04 (0.02 - 0.08)	0.03 (0.01 - 0.06)
SpB_05	0.22 (0.15 - 0.32)	0.13 (0.08 - 0.22)	0.21 (0.11 - 0.38)	0.09 (0.03 - 0.24)	0.14 (0.10 - 0.19)	0.08 (0.05 - 0.13)
SpB_10	0.00 (0.00 - 0.03)	0.00 (0.00- 0.03)			0.00 (0.00 - 0.05)	0.00 (0.00- 0.05)
SpB_15			0.01 (0.00 - 0.05)	0.01 (0.00- 0.05)	0.03 (0.01 - 0.06)	0.02 (0.01 - 0.05)
Fra_05	0.13 (0.08 - 0.21)	0.00 (0.00- 0.04)	0.21 (0.13 - 0.33)	0.2 (0.12 - 0.31)	0.11 (0.07 - 0.16)	0.06 (0.03 - 0.1)
Fra_10					0.00 (0.00 - 0.03)	0 (0.00- 0.03)
Fra_15			0.04 (0.02 - 0.10)	0.03 (0.01 - 0.08)	0.08 (0.05 - 0.13)	0.05 (0.03 - 0.09)
Cru_05	0.19 (0.13 - 0.26)	0.02 (0.00- 0.06)	0.04 (0.02 - 0.10)	0.01 (0.00- 0.05)	0.13 (0.07 - 0.22)	0.01 (0.00- 0.07)
Cru_10			0.15 (0.09 - 0.23)	0.04 (0.02 - 0.1)	0.00 (0.00 - 0.43)	0 (0.00- 0.43)
Cru_15	0.16 (0.11 - 0.23)	0.06 (0.03 - 0.10)	0.15 (0.09 - 0.23)	0.03 (0.01 - 0.09)		
Sto_05	0.17 (0.11 - 0.25)	0.10 (0.06 - 0.16)			0.36 (0.30 - 0.44)	0.27 (0.21 - 0.34)
Sto_10			0.12 (0.06 - 0.21)	0.05 (0.02 - 0.13)	0.07 (0.04 - 0.12)	0.04 (0.02 - 0.07)
Sto_15	0.30 (0.23 - 0.37)	0.11 (0.07 - 0.16)	0.10 (0.06 - 0.19)	0.01 (0.00- 0.06)	0.12 (0.06 - 0.20)	0.06 (0.03 - 0.14)

Abr_05	0.17 (0.11 - 0.26)	0.07 (0.03 - 0.14)	0.11 (0.06 - 0.18)	0.05 (0.02 - 0.12)	0.27 (0.18 - 0.38)	0.09 (0.04 - 0.17)
Abr_10	0.02 (0.01 - 0.08)	0.00 (0.00- 0.04)	0.02 (0.01 - 0.09)	0.00 (0.00- 0.05)	0.04 (0.02 - 0.08)	0.02 (0.01 - 0.06)
Abr_15	0.18 (0.13 - 0.25)	0.05 (0.03 - 0.1)			0.03 (0.01 - 0.06)	0.02 (0.01 - 0.05)
FiN_05	0.18 (0.12 - 0.27)	0.09 (0.04 - 0.16)	0.07 (0.03 - 0.16)	0.03 (0.01 - 0.1)	0.07 (0.04 - 0.11)	0.03 (0.02 - 0.07)
FiN_10	0.00 (0.00 - 0.04)	0.00 (0.00- 0.04)	0.01 (0.00 - 0.06)	0.01 (0.00- 0.06)	0.02 (0.01 - 0.09)	0.01 (0.00- 0.07)
FiN_15	0.03 (0.01 - 0.08)	0.01 (0.00- 0.05)	0.02 (0.01 - 0.07)	0.01 (0.00- 0.06)	0.00 (0.00 - 0.05)	0.00 (0.00- 0.05)
Stb_05	0.05 (0.02 - 0.10)	0.02 (0.01 - 0.07)	0.06 (0.03 - 0.12)	0.02 (0.01 - 0.07)	0.04 (0.01 - 0.10)	0.04 (0.01 - 0.1)
Stb_10	0.03 (0.01 - 0.09)	0.01 (0.00- 0.06)	0.02 (0.01 - 0.07)	0.02 (0.01 - 0.07)	0.02 (0.01 - 0.05)	0.01 (0.00- 0.04)
Stb_15	0.04 (0.02 - 0.08)	0.02 (0.01 - 0.06)			0.01 (0.00 - 0.07)	0.00 (0.00- 0.05)

4.3.2. Site-Specific Temporal Trends

Delta-QIC scores between the top and next best models were used for model selection. Low delta-QIC scores (<3) indicate considerable model selection uncertainty. Temporal model performance at some sites was poor with AUC scores at individual deployment sites less than 0.5 (Table 4-3). The low acoustic occupancy rates across most sites meant that all the temporal models generally did well at predicting periods without detections but poorly at predicting detection positive days. At least 50% of detection negative days were properly predicted by the models for each of the deployment groups. However, with the exception of the Cromarty group, no model was able to predict more than 6% of the broadband detection positive days. The minimum AUC score for the 10 models was 0.46 for the Latheron group indicating the model preformed no better than would be expected by chance. The maximum AUC was 0.9, observed at the Cromarty group. At individual C-POD deployment locations, AUC values ranged from 0.02 at the Latheron 15 location to .96 at the Cromarty 05 location (Table 4-3).

Large (>3) ΔQIC and high (>0.75) AUC scores indicated a more confident model selection and better model fit at the Latheron 05, Stonehaven 15 and Arbroath 10 deployment locations. Of these, only the Stonehaven 15 location contained broadband echolocation click trains on greater than 1% of the days. Thus, high AUC scores at the other locations are highly biased by the correct prediction of days without dolphin detections; the models essentially predicted 0 for all days and received high AUC scores because there were so few detections. In other words, they had very high precision but unacceptably low recall.

For sites with the highest acoustic occupancy of broadband click trains, Cromarty 05 and Stonehaven 15, GEEGLM models suggested peaks in the acoustic occupancy likelihood on August 15th and July 31st, respectively. At other locations, including deployment sites in the Fraserburgh, Arbroath and Fife Ness groups, temporal trends in acoustic occupancy were highly stochastic. Poor model fits (AUC <0.50) for deployment sites within these groups make it difficult to identify the presence and/or persistence of patterns in daily acoustic occupancy (Figure 4-2).

Table 4-3 Daily acoustic occupancy model results for the 10 deployment groups (Group). Model formula indicates the final model form selected via QIC selection where *P(Broadband)* is the probability of detecting a broadband echolocation click train (shortened from Equations 4-1 – 4-4). Model formula selected for each deployment group as well as the area under the ROC curve (AUC), proportion of presences correctly identified (Pres) and proportion of absences correctly identified (Abs) AUC is the area under the curve identified by through the ROC analysis and represents a measure of the goodness of fit. Presence and Absence represent the proportion of true presences and absences (within sample) correctly identified by the model. Dashes indicated location where modelling was not possible due to low numbers of detections or failure to recover the C-PODs deployed at that location. ShoreDist represents the three-level factor for the near (05), mid (10), and offshore (15) deployment locations.

Group	Formula	Delta QIC	Group AUC	Group Pres.	Group Abs.	Unit	Unit AUC	Unit Pres.	Unit Abs.
Lat	P(Broadband) ~ ShoreDist + Year + JulianDay	4.56	0.46	0	0.90	Lat_05	0.92	0.01	0.74
						Lat_10	0.38	0.01	0.92
						Lat_15	0.02	0.02	0.02
Hel	P(Broadband) ~ Year + ShoreDist * bs(JulianDay, knots = mean(JulianDay))	0.03	0.88	0.05	0.60	Hel_05	0.83	0.05	0.74
						Hel_10	0.95	0.00	0.93
						Hel_15	-	-	-
Cro	P(Broadband) ~ ShoreDist + Year + bs(JulianDay, knots = mean(JulianDay))	0.98	0.90	0.41	0.47	Cro_05	0.62	0.76	0.03
						Cro_10	0.66	0.19	0.41
						Cro_15	0.77	0.02	0.61
SpB	P(Broadband) ~ ShoreDist + Year + JulianDay	2.22	0.69	0.09	0.47	SpB_05	0.57	0.05	0.69
						SpB_10	-	-	-
						SpB_15	0.62	0.02	0.41
Fra	P(Broadband) ~ Year + ShoreDist *	0.49	0.77	0.02	0.87	Fra_05	0.81	0.04	0.82

	bs(JulianDay, knots = mean(JulianDay))								
						Fra_10	-	-	-
						Fra_15	0.69	0.06	0.53
Cru	P(Broadband) ~ ShoreDist + Year + JulianDay	3.89	0.63	0.1	0.3	Cru_05	0.64	0.04	0.64
						Cru_10	0.23	0.12	0.12
						Cru_15	0.61	0.03	0.71
Sto	P(Broadband) ~ Year + ShoreDist * bs(JulianDay, knots = mean(JulianDay))	5.69	0.79	0.1	0.71	Sto_05	0.71	0.16	0.58
						Sto_10	0.63	0.04	0.65
						Sto_15	0.81	0.10	0.75
Abr	P(Broadband) ~ Year + ShoreDist * bs(JulianDay, knots = mean(JulianDay))	13.93	0.79	0.09	0.43	Abr_05	0.60	0.10	0.55
						Abr_10	0.96	0.03	0.91
						Abr_15	0.78	0.07	0.50
FiN	P(Broadband) ~ ShoreDist + Year + bs(JulianDay, knots = mean(JulianDay))	1.64	0.82	0.05	0.76	FiN_05	0.81	0.06	0.69
						FiN_10	-	-	-
						FiN_15	0.69	0.00	0.67
Stb	P(Broadband) ~ ShoreDist + Year + JulianDay	3.93	0.64	0.02	0.59	Stb_05	0.57	0.04	0.39
						Stb_10	0.73	0.01	0.89
						Stb_15	0.46	0.03	0.23

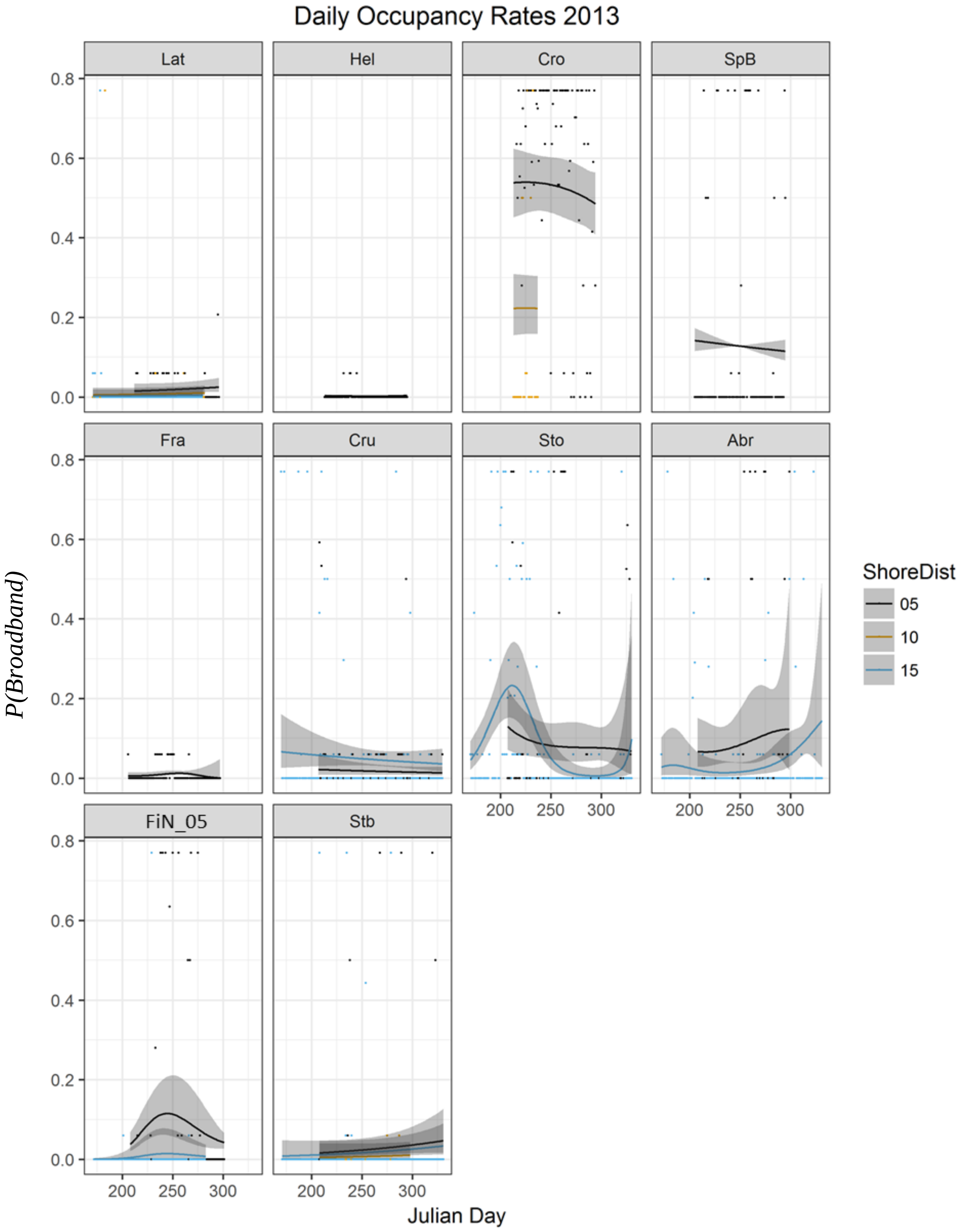


Figure 4-2 Observed (points) and 95% confidence interval of the modelled acoustic occupancy (shaded) for the near (05) mid (10) and offshore (15) deployment sites (panels) in 2013. Colour indicates shore distance.

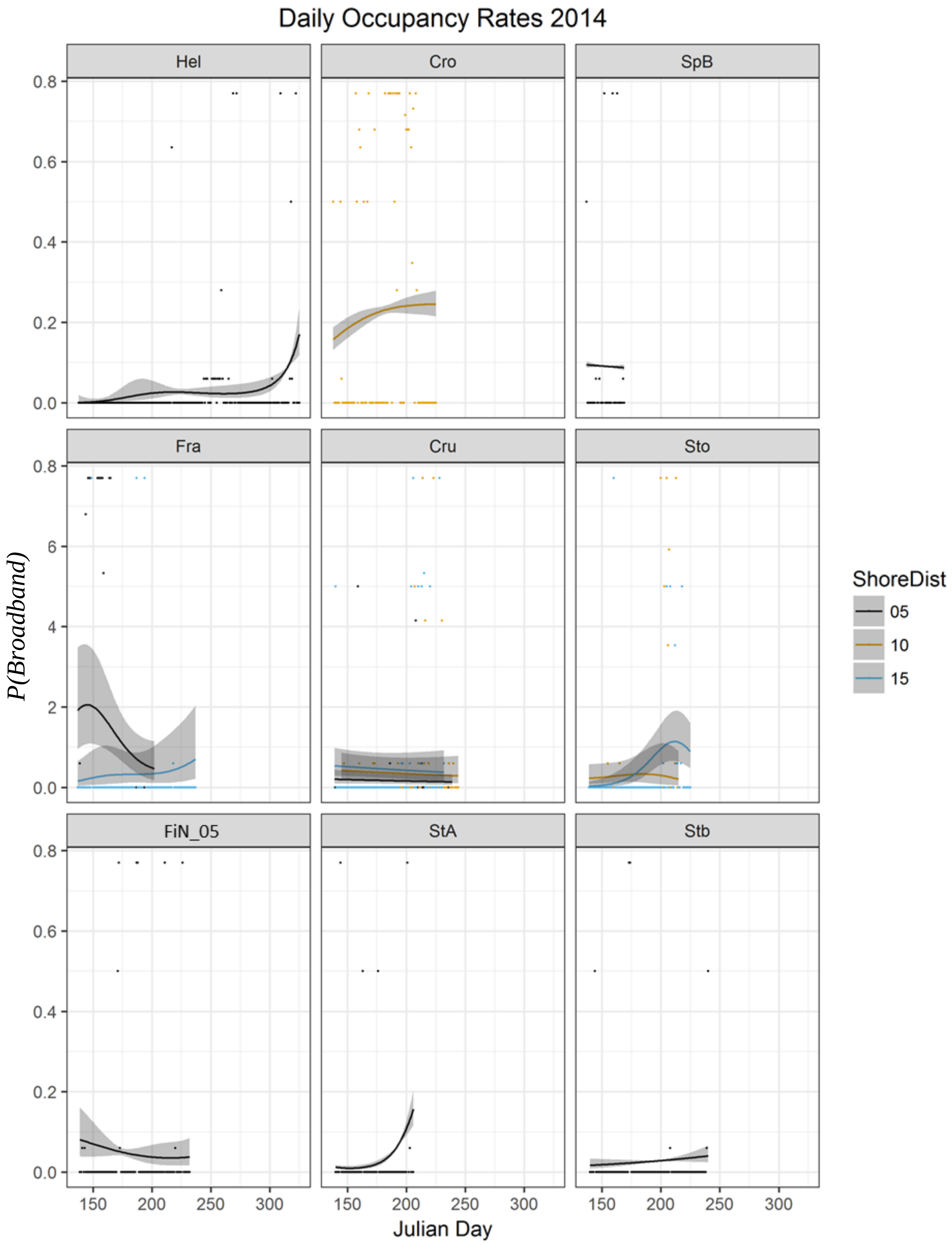


Figure 4-3 Observed (points) and 95% confidence interval of the modelled acoustic occupancy (shaded) for the near (05) mid (10) and offshore (15) deployment sites (panels) in 2014. Colour indicates shore distance.

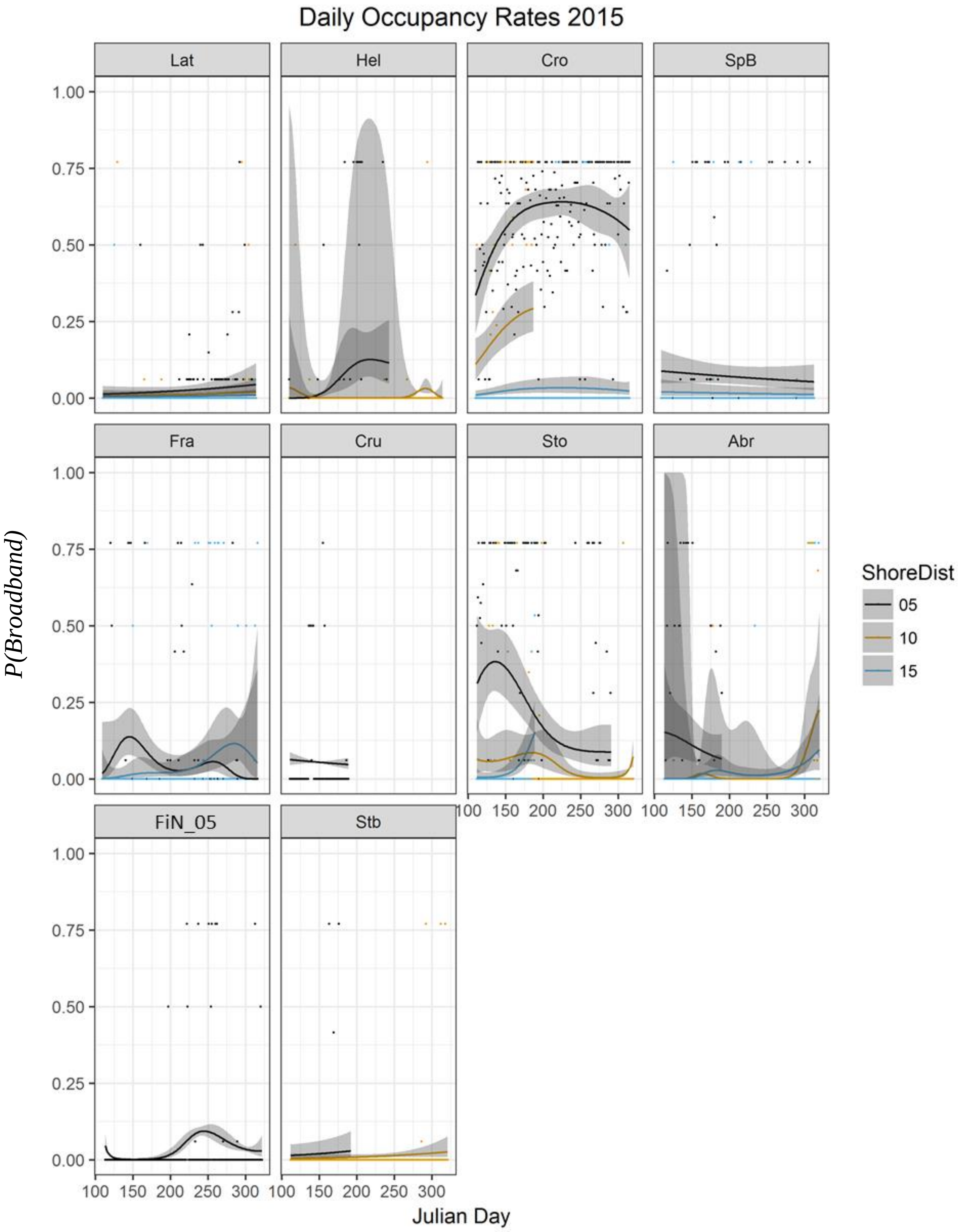


Figure 4-4 Observed (points) and 95% confidence interval of the modelled acoustic occupancy (shaded) for the near (05) mid (10) and offshore (15) deployment sites (panels) in 2015. Colour indicates shore distance.

4.3.3. Spatial-Habitat Modelling

Spatial covariates showed some degree of similarity but since VIF scores were less than three all model covariates were initially retained (Appendix 4). In the full model, the estimated degrees of freedom (EDF) for slope were less than one and thus this predictor was removed. In the final model all terms were significant with the exception of season (Table 4-4). The AUC score of the final model was 0.86.

Table 4-4 GAMM summary for the parametric and smooth coefficient estimates, standard errors, estimated degrees of freedom (EDF), reference degrees of freedom (Ref.df), F, t and p-values for the final habitat model. DistToPOA is the distance (in metres) to the nearest point of aggregation and POAName is the name of the nearest point of aggregation.

Model Formula

P(Broadband) ~ s(DistToPOa, bs = "ts", k = 3) + s(Depth, bs = "ts") + s(DistToShore, bs = "ts") + POAName + Season

Parametric coefficients

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-2.71	0.18	-15.28	<.001
POAName:Dee	-0.63	0.35	-1.81	0.07
POAName: North Esk	-1.02	0.31	-3.22	0.00
POAName:Spey	-1.24	0.28	-4.50	<.001
POAName:Tay Firth	-0.64	0.35	-1.83	0.07
POAName:Tweed	-2.41	0.44	-5.46	<.001
Season:Spring	-0.07	0.16	-0.40	0.68
Season:Summer	0.03	0.12	0.27	0.78

Approximate significance of smooth terms

	EDF	Ref.df	F	p-value
s(DistToPOA)	1.92	2	55.26	<.001
s(Depth)	4.69	9	6.23	<.001
s(DistToShore)	4.96	9	9.10	<.001

R-sq.(adj) = 0.322, Scale est. = 1, n = 9181

Modelling results suggested that the probability of detecting broadband echolocation click train encounters decreased with increasing distance to shore and distance to the nearest point of aggregation. However, across the extent of the array, the probability of detecting broadband echolocation encounters increased with increasing depth Figure 4-5.

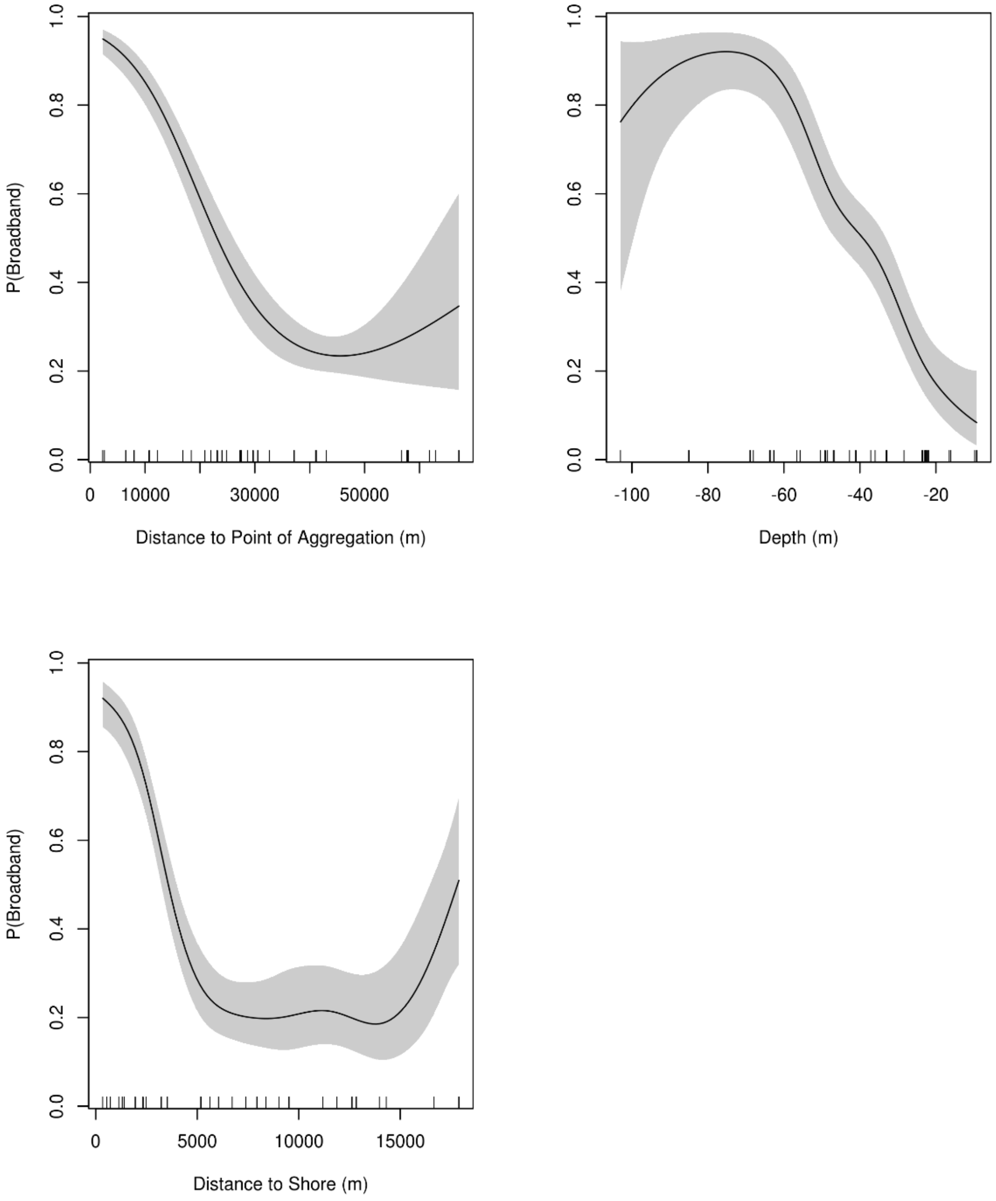


Figure 4-5 Two dimensional representations of the binomial smooths for the habitat GAM. Black line represents the probability of detecting a broadband echolocation click train on a given C-POD as a function of the C-POD’s distance to the nearest Point of Aggregation in metres (top left), deployment depth in metres (top right) and distance to shore in metres (bottom). Shaded areas represent 95% confidence intervals and dashes on X-axis are rug plot of deployment variables.

Figures 4-6 through 4-8 show the predicted daily broadband acoustic occupancy across the eastern Scottish coast. Prediction data were limited to those within the confines of the C-POD sampling locations, maximum distance from shore 17.9 km, depth 103 m, slope 0.3 radians and distance to nearest point of aggregation 67km. The model predicted increased detection probability at each of the points of aggregation included in the model (Table 4-1). The model predicted that detections were more likely close to shore throughout the east coast habitat between the Fife Ness and Cruden Bay units; in coastal areas in the Firth of Forth; in offshore areas between the Dee River, Stonehaven, and Spey Bay deployment groups; and in the extreme northern end of the survey area.

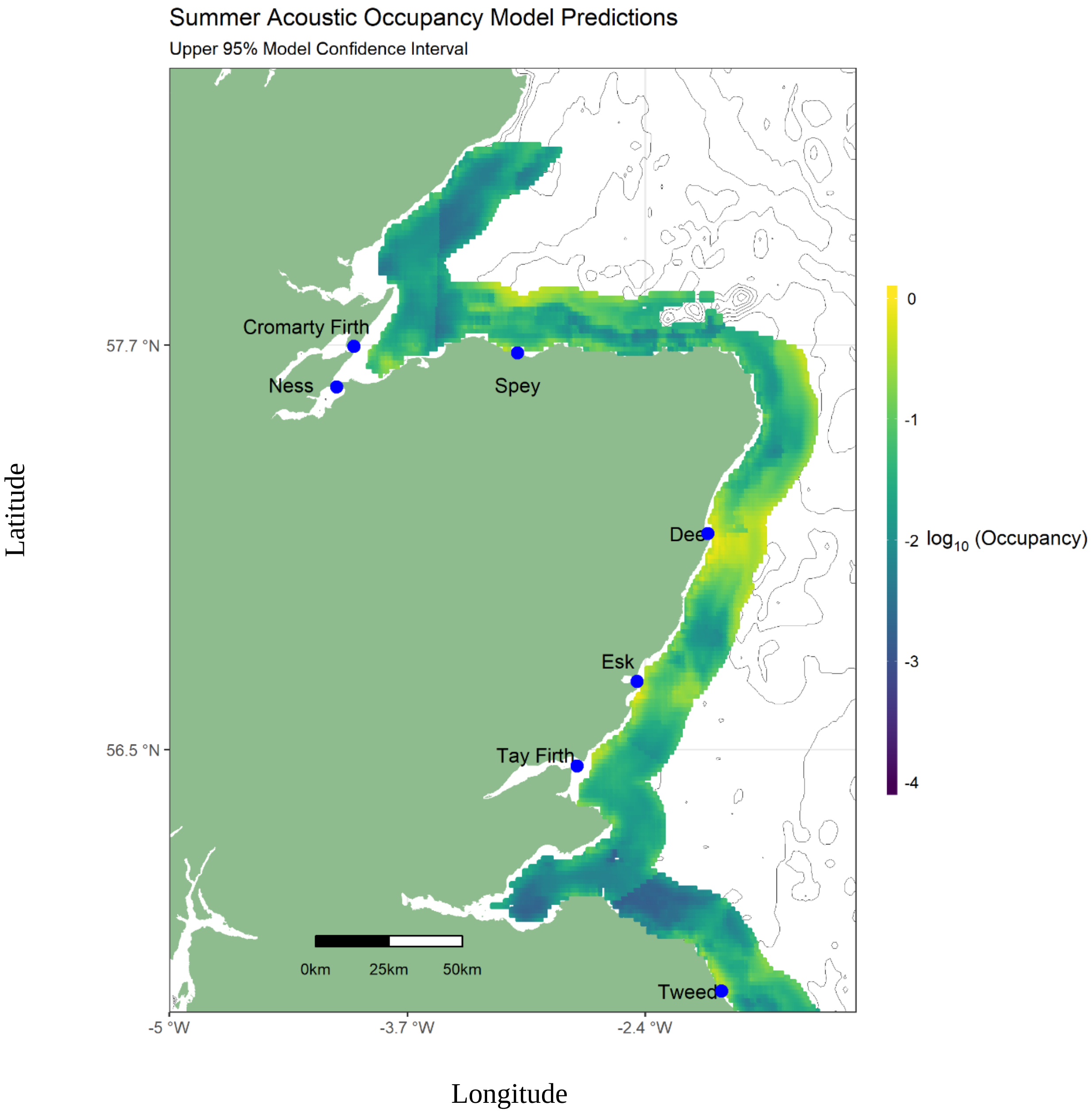


Figure 4-6 Median predicted daily likelihood of detecting a broadband echolocation click train throughout the study area. Blue dots represent the location of the points of aggregation.

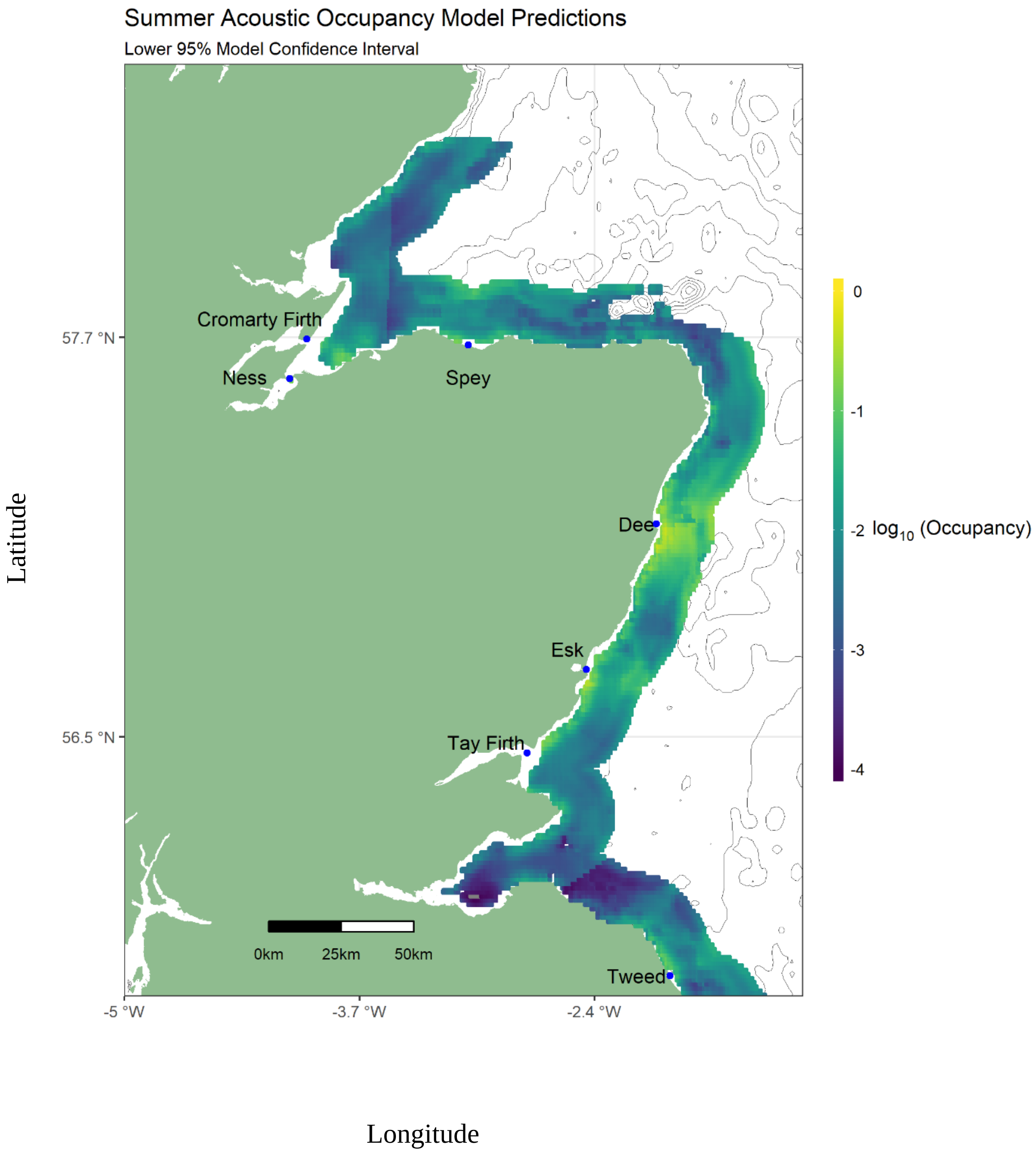


Figure 4-7 Lower 95% Confidence Interval of Predicted daily likelihood of detecting a broadband echolocation click train throughout the study area. Blue dots represent the location of the points of aggregation.

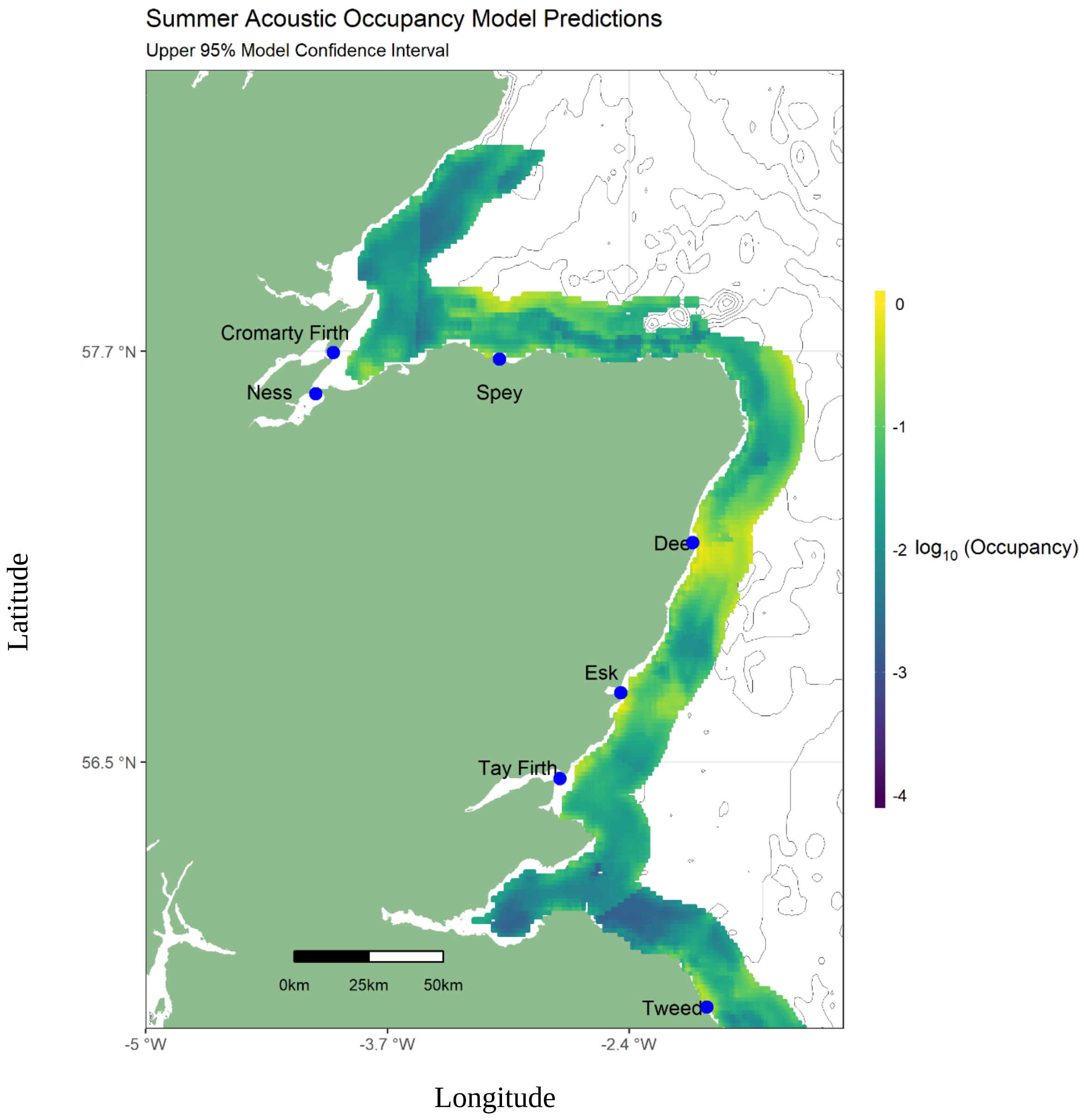


Figure 4-8 Upper 95% Confidence Interval of Predicted daily likelihood of detecting a broadband echolocation click train throughout the study area. Blue dots represent the location of points of aggregation.

4.4. Discussion

The goals of this chapter were to report acoustic occupancy rates at the 30 survey locations represented in the ECoMMAS array, identify temporal trends in acoustic occupancy at each of the survey groups, and to determine whether it was possible to produce a habitat-scale spatial-temporal acoustic occupancy model for the eastern Scotland bottlenose dolphin population. I reported acoustic occupancy rates for all C-PODs for all available years and found that temporal trends in acoustic occupancy data were highly stochastic. Temporal modelling results revealed a consistent peak in broadband detections at the Stonehaven 15 deployment location in late July, which may be indicative of important dolphin habitat warranting further investigation. The habitat modelling generally agreed with previous studies linking distance to shore with the probability of detecting bottlenose dolphins (Quick et al., 2014). However, unlike some previous studies (Pirotta et al., 2014a), this model suggests that animals are more likely to be detected in deeper water than shallow . Distance to the nearest point of aggregation was also retained in the model while bathymetry gradient was not. Unfortunately, the data did not contain sufficient degrees of freedom to model both spatial and temporal covariates together. Even when season, rather than Julian day, was included as the time covariate was not significant in the model (Table 4-4).

Acoustic occupancy results found that C-PODs deployed inshore (i.e. the 05 units) were more likely to detect broadband echolocation click trains than C-PODs deployed in offshore locations. The average broadband occupancy rate for the 05, 10 and 15 units was 0.12, 0.03 and 0.02 detections/day respectively. Even excluding the Cromarty 05 C-POD, the broadband occupancy rate for the nearshore deployments was 0.06 detections/day. This finding is consistent with visual studies that have suggested that this bottlenose dolphin population is primarily coastal and more likely to be observed in shallow waters less than 1-2km from the coast (Quick et al., 2014, Arso Civil et al., 2019).

Data presented in this chapter posed considerable challenges to the temporal modelling. For half of the deployment groups, temporal model selection (ΔQIC) did not strongly favour one model over another. Moreover, the models that were selected struggled to accurately predict rare occurrences (detections) and could not account for most of the variation present in the dataset. This indicates that there was insufficient information or too much variability in the

C-POD data to accurately characterise any temporal patterns present in the data. Either way, by themselves, these data cannot provide long-term temporal resolution of habitat use.

However, the lack of temporal resolution is unsurprising when considering the survey design and data availability. The data presented here represent only the first three years of a long term study and, furthermore, the ECoMMAS provided acoustic survey coverage for locations not thought to represent points of aggregation. Thus, low acoustic occupancy rates were expected. Even so, C-PODs have very low false positive rates but suffer considerably from false negatives (failing to detect dolphin presence). This becomes extremely problematic when dealing with habitats with low occupancy rates. Thus, as C-PODs are lost or retired from service, managers would do well to replace them with instruments where users can adjust the trade-off between false positives and false negatives based on their needs and the environmental conditions.

In addition to survey design, instrument loss and poor temporal replication were problematic. While some degree of trawling and displacement of instruments is an unavoidable consequence of passive acoustic monitoring, shifting boat time availability between years prevented consistent temporal coverage. For example, instruments were deployed during the month of August for all 30 deployment sites in all three years. However, in 2014 instruments were deployed in April and most exhausted their battery capacity prior to August which precluded almost any spatial/temporal replication for 2014. Thus, despite data being collected each year at each deployment site, only 3 of the 30 sites provided data for the month of August in all three survey years. For comparison, Pirotta et al. (2014b) used data from eight years of continuous surveys to produce estimates for dolphin foraging rates within the Moray Firth SAC. In addition to representing 2.5 times the duration of the present study, the data reported by Pirotta et al. (2014b) were not processed for the presence of different species, represented high acoustic and true animal occupancy rates and were collected from a much denser array of echolocation click detectors. The average spacing between deployment locations in Pirotta et al. (2014b) was 2-3km whereas spacing between deployment groups in the ECoMMAS array was 30-50km. Similarly, another acoustic study used data from 62 deployment locations within the inner Moray Firth to model diel trends in harbour porpoise activity (Williamson et al., 2017). Even though the array data in that study was more than twice as dense as the ECoMMAS array, the authors did not attempt to model daily acoustic occupancy. Finally, in both Pirotta et al. (2014b) and Williamson *et al.* (2017) there were sufficient degrees of freedom in the data to model spatial and temporal interactions whereas modelling efforts for the first three years of the ECoMMAS data could not support covariate interactions. Continuing deployments of the ECoMMAS array will ultimately provide better temporal coverage which should resolve trends in acoustic occupancy at each of the deployment sites and or groups. Well-fitting temporal models for the Eastern Scottish Coastline will require considerably more data and, ideally, more consistent data coverage.

The data in this chapter augment the existing surveys for this population (Wilson, 1995, Wilson et al., 1997b, Hastie et al., 2004b, Wilson et al., 2004, Thompson et al., 2011c, Cheney et al., 2013, Hammond et al., 2017, Cheney et al., 2018, Arso Civil et al., 2019) by collecting long-term acoustic data from across the majority of the eastern Scottish Coast. Moreover, this study demonstrated an approach for incorporating acoustic classifier output and uncertainty into ecological models. However, due to the limited nature of the validation data, it was not possible to characterise classifier bias which may skew the results. This classification does not account for known difference in species distributions. For example, bottlenose dolphins are sighted more frequently in nearshore waters than are other species. This *a priori* knowledge could be integrated into the habitat model to offset random error in the classification system. If that holds for the mid and offshore units as well, the models here would underrepresent habitat use. The converse is also true if the classifier skewed towards frequency banded click trains instead. The latter situation may explain the increased likelihood of acoustic occupancy near the outer edge of the survey areas. Should future studies need to better account for classifier uncertainty, a Bayesian approach may be justified (Caillat, 2013). The Bayesian approach is sufficiently flexible to account for other covariates not included in this survey including false negative and false positive rates.

Data from the ECoMMAS array revealed a mix of both broadband and frequency banded click trains at the Stonehaven 15 deployment location. These data suggest that the offshore habitat near Stonehaven may represent another area of relatively high occurrence. This finding also mirrors the continuous recordings collected from the SM unit at the Stonehaven 15 location, in which both broadband and frequency banded click trains were confirmed in 2013, 2014 and 2015 (Chapter 2). The consistency in the predictions between years at the Stonehaven 15 location suggests that the habitat may be ecologically meaningful to one or more dolphin species over the mid-summer period.

Unfortunately, the limited taxonomic resolution of the acoustic data (both continuous recordings and C-POD detections) means that it is not possible say with any degree of certainty which of the broadband or frequency banded species were present. Thus, the area may not be ecologically relevant to bottlenose dolphins, one of the primary targets of the ECoMMAS array. Similarly, several studies have noted that while bottlenose dolphins are primarily detected within 1-5 km of the coast, they are infrequently observed in offshore habitat (Thompson et al., 2011a, Hammond et al., 2017). With regard to the frequency banded click trains, both white-beaked and Risso's dolphins have been sighted from land and boat-based visual surveys but are more commonly seen offshore (Weir et al., 2007, Hammond et al., 2017). However, nearly all studies of delphinids in the area have found considerable variation in occupancy between survey years(Robinson et al., 2007, Culloch and Robinson, 2008, Cheney et al., 2014). Thus, visual studies will be needed for confirmation.

Results from the spatial model generally agreed with previous studies linking smaller distances to shore with increased probability of detecting bottlenose dolphins (Pirotta et al., 2014b, Arso Civil et al., 2019, Quick et al., 2014). However, unlike previous studies, the spatial modelling here suggested that broadband acoustic encounters were more likely to be detected in deeper water than shallow, and a slight increase in detections >15 km from shore. However, without concurrent visual surveys or more advanced click classification (Frasier et al., 2017) it is not possible to say whether these clicks represent bottlenose or common dolphins.

This study also found that distance to the nearest selected point of aggregation (often coinciding with river mouths) and depth were also important in predicting acoustic occupancy. The retention of distance to nearest point of aggregation in the model is supported by previous studies that have suggested that foraging opportunities outside the Moray Firth may have been a driving factor for the range expansion (Wilson et al., 2004, Cheney et al., 2014). Thus, locations where foraging may be focussed elsewhere along the coast, such as the Tay estuary (Arso Civil et al., 2019), may be as important as Chanonry Point and the Sutors within the SAC.

One of the limitations of this, and most passive acoustic studies is the inability to relate the number of detections to the number of animals present. Several studies have attempted to do this with more solitary species such as harbour porpoise and beaked whales (Kusel et al., 2011, Kyhn et al., 2012, Koblitz et al., 2014). Sound production by bottlenose dolphins is complex, population, and behaviour dependent (Connor and Smolker, 1996, Herzing, 1996, Janik, 2000a, Nowacek, 2005, Quick and Janik, 2008). Context specificity in both the quantity and quality (e.g. amplitude) of the clicks makes accurate estimation of density untenable without a-priori knowledge of the behaviour. This study, in particular, was also limited by the ‘black-box’ nature of the recording instruments (Nuuttila et al., 2013a, Nuuttila et al., 2013b, Robbins et al., 2016).

Marques et al. (2012) attempted to estimate animal density from acoustic detections for North Pacific right whales (*Eubalaena japonica*). However, the sounds produced by this species are omni-directional and relatively infrequent which allows analysts to readily discriminate between multiple calls. The same is not true for the dolphin echolocation click trains. Click trains may be produced by all animals in the group and the clicks themselves are highly directional. Thus, as an animal or group swims by a recorder a small proportion of the clicks produced will be detected by the recorder. One option for accounting for rapidly changing detection probabilities within a group of odontocetes is to localise individual animals and subsequently estimate group size. However, this methodology requires multiple hydrophones spaced within a few metres of each other and consequently not appropriate for the ECoMMAS array. Alternatively, where localisations are not available, some authors have used average group size as a multiplier (Kyhn et al., 2012). This assumes both explicit knowledge of group sizes and that the group sizes are stable within the analysis framework. Where stable group size estimate or localisations are available, single sensor recordings are a reasonable method to estimate animal density. Thus, in order to estimate animal density using the ECoMMAS array, future studies will need to incorporate a greater understanding of group size and spacing or reconfigure the array to allow for localisations and/or SECR analysis.

For the reasons above, I believe that there are limited circumstances in which estimating density or abundance from C-POD data alone is likely to provide robust results. However, presence and absence data from the instruments is valuable under a variety of other circumstances including studies of habitat use and site-specific acoustic behaviour. The manufacturer reports false positive rates of less than 4% using the C-POD data processed with the KERNO classifier alone. This value varies with deployment location and parameters chosen (Robbins et al., 2016). The data produced by C-PODs are also capable of differentiating between areas of known dense animal occupancy and those with lower occupancy, as confirmed by historic transect surveys (Pirotta et al., 2014b). Thus C-PODs may be an appropriate choice for preliminary studies or impact assessments that need only to determine whether an area is ecologically important for the species of interest, and in conjunction with visual surveys (Taylor et al., 2017).

Within the Moray Firth, Pirotta (2014b) found that seabed gradient was significant in predicting a higher proportion of foraging buzzes in acoustic encounters. While foraging buzzes were not modelled here, in this study seabed gradient was not a significant predictor of acoustic occupancy in the final habitat model. This suggests that seabed gradient is only important within the context of foraging activity.

Accurately defining which spatial covariates are meaningful predictors of bottlenose dolphin daily acoustic occupancy will require a considerable increase in the spatial extent of the ECoMASS array. This does not necessarily require deploying additional recording devices or modifying the survey design. Instead, visual survey data could be incorporated into the habitat models to provide the spatial data lacking in in the ECoMMAS array (Brookes et al., 2013, Thompson et al., 2015). Boat-based surveys in and around areas of known concentration of dolphins not covered by the array would be particularly well suited to complement the ECoMMAS data.

Foraging has been associated with deep channels which are similarly important for shipping. Thus far, it has not been possible to deploy acoustic recorders in active shipping lanes or near ports as the moorings are perceived as a potential navigational hazard. Moreover, loud and variable ambient noise associated with ports will severely bias the acoustic occupancy results (Chapter 3). Thus, small boat or land-based surveys may represent the best approach to monitoring daily acoustic occupancy rates in these areas. Finally, visual surveys of this population represent >25 years of continuous data collection. This vastly surpasses the available acoustic data for the population (>10yrs in the Moray Firth and five years of the ECoMMAS array of which only the first three years were included). Incorporating all visual and acoustic data available could be the best way to develop a cohesive spatial-temporal model of occupancy.

Previous studies have used dense arrays of passive acoustic instruments to look at density, abundance, and habitat use as well as spatial and temporal predictors of acoustically active species (Sherwin et al., 2000, Moretti et al., 2006, Pirotta et al., 2014b, Weirathmueller et al., 2014, Williamson et al., 2017). Thus, incorporating ancillary spatial data and/or rotating the acoustic monitoring stations could provide sufficient spatial replication to model acoustic occupancy outside of the SAC. Adding inshore sensors between each deployment group would provide replicates of shore distance, depth, and slope values while increasing the resolution for distance to the nearest point of aggregation.

Passive acoustic surveys off eastern Scotland will continue be faced with considerable misclassification error when identifying dolphin species, regardless of the recording device or sample frequency (Roch et al., 2011b, Caillat, 2013). Passive acoustics are also unable to distinguish between periods when animals are not present and periods when animals are present but not detectable, as may be the case at some of the ECoMMAS deployment locations. Together, these findings highlight the value of combining long term data from both visual and acoustic surveys. In doing so, researchers are able to provide robust data on long-term trends in dolphin occurrence throughout the habit and in particular for areas of ecological or commercial interest (Thompson et al., 2011a).

4.5. Conclusions

These data fill a gap in knowledge about the habitat use of Scottish bottlenose dolphins outside of the well-studied areas of concentration including surveying the northern and southern extent of the specie’s current main distribution. Results from this chapter support previous visual surveys indicating that dolphins are most likely to be detected in nearshore, deep and deep habitats. Acoustic results from this study also hinted at areas that may be used by more than one dolphin species and may be biologically important. Finally, these data represent the first three years of a multi-year longitudinal study. Data from the ECoMMAS array have the potential to provide meaningful insights into seasonal and annual variation in bottlenose dolphin habitat as well as how these trends may change over time in response to, among other things, the construction of offshore wind farms.

Chapter 5

Hourly Occupancy, Tidal State, and Diel Trends

5.1. Introduction

Diel trends in animal behaviour are ubiquitous. Birds, frogs, fish, insects, and mammals all display rhythms in behavioural activities that vary from diurnal, to nocturnal, and crepuscular (increased activity at dawn and dusk). Moreover, animals may shift their diel trends in response to environmental cues. For example, leatherback turtles (*Dermochelys coriacea*) show little or no diel rhythm in diving behaviour during their northern migrations. However, during the southern migration animals spend more time at the surface during the day but dive deeper at night. For this species the change in diel pattern between the phases of their annual migration has been linked to prey availability and thermoregulatory needs throughout their migratory cycle (James et al., 2006, Casey et al., 2014). Similarly, anadromous fish show considerable plasticity in behavioural rhythms across migration. Changes in water current strength and predation risk over even short time and small spatial scales can induce fish to switch between having no diel activity patterns to displaying either crepuscular or nocturnal peaks in activity (Keefer et al., 2013).

Knowing how animals use their environment(s) throughout their diel cycle can play a role in conservation and management efforts. Both endangered Florida panthers (*Puma concolor coryi*) and Scandinavian brown bears (*Ursus arctos*) require different habitats throughout their diel rhythm (Moe et al., 2007, Onorato et al., 2011). Early studies of both species focused on habitat selection during the daytime hours only. As Scandinavian brown bears and Florida panthers both display either crepuscular or nocturnal activity patterns, this meant that a large proportion of observations were associated with resting animals. Subsequently, managers were unaware that the species required different habitats and habitat features for the foraging and resting at different times of the 24 hr cycle. Similarly, in aquatic systems animals are known to shelter in reef-like habitats during daylight and forage over larger and/or open habitat at night (Lawton, 1987, Meyer et al., 2000, Keefer et al., 2013). These examples show how maintaining the integrity of all habitats selected by animals throughout their circadian cycle is important to long term conservation.

Worldwide, cetaceans are protected by a variety of regional and international legislation including the European Habitats Directive. For legislation to be effective in restoring or maintaining population levels, regulators must have a broad understanding of species' habitat use. This includes movement patterns and energy budgets. Presently, passive acoustic surveys are the most common methodology for monitoring cetaceans across the 24 hr scale. Fixed passive acoustic surveys are favoured for their ability to collect data over long timescales (Carlström, 2005, Wiggins et al., 2005, Baumann-Pickering et al., 2015). Results from fixed passive surveys, where instruments are moored in place, have shown that diel patterns in vocalisations are common among cetacean species (Munger et al., 2008, Todd et al., 2009, Mussoline et al., 2012, Matthews et al., 2014, Baumann-Pickering et al., 2015). In odontocetes, diel patterns in vocalisations have been linked to changes in behaviour predicated by differential prey availability and/or shifting foraging strategies throughout the 24 hr period (Friedlaender et al., 2009, Soldevilla et al., 2010b, Williamson et al., 2017). As with terrestrial systems, knowledge of diel patterns in habitat selection and or behaviour can inform conservation efforts by identifying how the use of habitats or habitat features may vary throughout their circadian cycles. Moreover, identifying diel variation in foraging and/or diving behaviour of protected marine mammals can inform mitigation efforts seeking to reduce the negative consequences of anthropogenic activities (Mussoline et al., 2012).

Understanding activity cycles allows monitoring of changes in behaviour that could indicate adverse environmental conditions or increased stress (Tyne et al., 2015). Bottlenose dolphins (*Tursiops truncatus*) display flexibility in their daily activity cycles at both spatial and temporal scales. For example, in the Indian ocean, bottlenose dolphins undergo an on/offshore diurnal migration that balances predation risk and preferred foraging habitat (Heithaus and Dill, 2002). Other populations are known to time foraging activity with tidal cycles in order to maximise foraging efficiency (Gregory and Rowden, 2001, Mendes et al., 2002, Pirotta et al., 2014b), including driving fish onto tidally exposed muddy banks while temporarily self-stranding (Hoese, 1971, Silber and Fertl, 1995). In such tidal habitats, animals time foraging attempts with tidal cycles in order to maximise their success rate. As with diel trends, knowledge of how animals change their behaviour over the tidal cycle can provide insights into the ecology of the animals as well as identifying important habitats (Hastie et al., 2003a, Hastie et al., 2016, Benjamins et al., 2017). In this chapter I investigate hourly trends in detections as a function of environmental variables across the spatial extent of the array. Data produced by the ECoMMAS study represents a potentially important large scale long-term acoustic survey of the eastern Scottish coast. As with Chapter 4, here I am limited by the taxonomic resolution of the C-POD data. Thus, I assume that broadband click detections are from bottlenose dolphins (see Chapter 2). This assumption, while imperfect, is reasonable for coastal deployments given the historically very low detection rate of common dolphins (*Delphinus delphis*) in the area (Hammond et al., 2002b, Reid et al., 2003, Weir et al., 2007, Anderwald et al., 2010, Hammond et al., 2013, Hammond et al., 2017, Arso Civil et al., 2019).

5.2. Methods

5.2.1. Data Collection and Quality

The hourly acoustic occupancy data collated in Chapter 4 was also used in Chapter 5. Since the goal of this analysis was to understand detection trends on a sub-daily scale, only days containing at least one echolocation click train were included in the analysis. This reduced the size of the dataset and reduced zero-inflation in the data and decreased the time needed to fit the models. Models presented in this chapter, therefore, represent the probability of detecting an echolocation click encounter conditional on at least one echolocation click encounter being detected during each day or tidal period (*P(Broadband)*). I again used probability values from the classifier to estimate the probability that a broadband click train was present. Where two or more encounter types (e.g. ‘Unknown’ and ‘Frequency banded’) were present during the same hour I assumed a broadband probability of 0.5.

Tidal Cycle and Tide State

Tidal heights were predicted for all C-POD deployments with one-hour resolution using POLPRED and POLTIPS software (NERC, 2016). POLPRED software uses a ‘Hydrodynamic DLL’ coupled with harmonic constants to predict tidal height for any time and for a given grid reference (Table 5-1). From the tidal height data, I used local extrema and zero crossings to calculate the approximate time of each high tide and subsequently the hours relative to high tide (±6hrs).

Table 5-1 C-POD Deployment latitudes and longitudes and grid centres from which tidal height predictions were calculated.

Hourly Occupancy, Tidal State, and Diel Trends

	Deployment		Prediction Grid	
UnitLoc	Lat	Lon	Lat	Lon
Lat_05	58.26933	-3.31819	58.2749	-3.3125
Lat_10	58.22935	-3.20642	58.2249	-3.2125
Lat_15	58.18674	-3.13592	58.1916	-3.1375
Hel_05	58.05338	-3.71525	58.0583	-3.7125
Hel_10	58.00506	-3.61084	58.0083	-3.6125
Hel_15	57.97570	-3.53584	57.9749	-3.5375
Cro_05	57.67490	-3.98821	57.6749	-3.9875
Cro_10	57.68919	-3.88175	57.6916	-3.8875
Cro_15	57.70668	-3.81072	57.7083	-3.8125
SpB_05	57.69019	-3.06247	57.6916	-3.0625
SpB_10	57.74148	-3.03882	57.7416	-3.0375
SpB_15	57.78698	-3.06426	57.7916	-3.0625
Fra_05	57.71135	-2.13012	57.7083	-2.1375
Fra_10	57.77115	-2.14043	57.7749	-2.1375
Fra_15	57.84919	-2.08981	57.8416	-2.0875
Cru_05	57.38019	-1.82836	57.3749	-1.8375
Cru_10	57.38021	-1.73809	57.3749	-1.7375
Cru_15	57.37728	-1.61809	57.3749	-1.6125
Sto_05	56.94694	-2.17671	56.9416	-2.1875
Sto_10	56.95942	-2.11339	56.9583	-2.1125
Sto_15	56.98064	-2.02174	56.9749	-2.0125
Abr_05	56.55405	-2.48332	56.5583	-2.4875
Abr_10	56.49980	-2.37990	56.4916	-2.3875
Abr_15	56.45966	-2.29863	56.4583	-2.2875
FiN_05	56.26498	-2.57206	55.9249	-2.1875
FiN_10	56.25789	-2.49931	55.9583	-2.1625
FiN_15	56.29006	-2.43306	56.0416	-2.0875
Stb_05	55.92920	-2.17711	56.2583	-2.5625
Stb_10	55.96349	-2.16185	56.2583	-2.4875
Stb_15	56.03335	-2.07541	56.2916	-2.4375

Hour Relative to Solar Noon

I report time of the day as hour relative to solar noon where solar noon is defined as the time at which the sun reaches its zenith, or daily maximum solar elevation angle (Michalsky, 1988). For each hour of each deployment I calculated the hour of the day relative to solar noon (-12 to 11).

5.2.2. Modelling Effects of Hour and Tidal State in and Outside of a Point of Aggregation

I used binomial GAMMs to model the effects of hour of the day and tidal state on the probability of detecting broadband echolocation click detections. As with the Chapter 4, the response variable was the hourly probability that a broadband echolocation click train was detected, *P(Broadband*). Hourly trends in acoustic occupancy were modelled as binomial distributions with the hourly *P(Broadband*) scores as the response variable. To account for temporal autocorrelation, I included an autoregressive correlation structure where hourly observations were grouped by date and deployment location (Wood 2011, p322). The deployment location (UnitLoc) was included as random effect. All models were created using the MGCV package (Wood, 2017) in R v.3.3.2 (R Core Team, 2016). Both hour and tidal state were modelled using cyclic cubic regression splines. The start and end points of cyclic splines are the same and thus they are appropriate for modelling oscillations such as tidal state and hour of the day (Williamson et al., 2017).

In this analysis candidate models were fit to two subsets of the data. The first subset included all deployment locations with the exception of Cromarty 05 ('non-Cromarty 05 data'). The second subset included only data from the Cromarty 05 deployments ('Cromarty 05 data'). This decision was based on two observations. First, C-POD detections from the Cromarty 05 location were associated with a known foraging location (Hastie et al., 2004b) whereas detections from other sites represented either locations not known to be areas where foraging occurs or relatively data deficient areas (Wilson et al., 2004). Second, observations from the Cromarty 05 location contained nearly as many occupied hours as the 29 other deployment location combined. Thus, data from the Cromarty 05 deployment site contained considerably more degrees of freedom with which to investigate multiple covariates. In comparison, many other deployment sites contained fewer than 10 hours with detections. Thus, patterns in detections from the Cromarty 05 site which contained greater statistical power than the remaining sites had the potential to bias observations at other locations in the array.

For the non-Cromarty 05 data, I compared five ecologically feasible models for the relationship between the probability of detecting a broadband echolocation click train and the hour of the day relative to solar noon, and hour relative to high tide. The first model modelled the probability of detecting a broadband echolocation click as two independent smooths of hour of the day and tidal state, without any interactions. The second model considered that Scottish bottlenose dolphins are known to utilise tidal races during specific periods of the tidal cycle (Mendes et al., 2002, Arso Civil et al., 2019) and therefore the relationship with tidal state may only be relevant to C-PODs deployed near the coast. This model built on the first model by adding a factor interaction between tidal state and whether the deployment represented a near (05), mid (10), or offshore (15) location. The third model was based on previous studies showing that odontocetes may vary their diel patterns in response to habitat type (Carlström, 2005, Soldevilla et al., 2010a, Williamson et al., 2017). This model investigated the possibility that diel trends in echolocation click trains change between different deployment groups and included an interaction between Group id (e.g. Latheron, Helmsdale, etc) and hour relative to solar noon. Unfortunately, there were insufficient degrees of freedom in the data to model deployment location specific interactions (n=30). The remaining two models represented logical extensions of the first three. The fourth model considered that the probability of detecting a broadband echolocation click may be a two-dimensional relationship between tidal state and hour and was subsequently modelled using a tensor smooth interaction. The fifth and most complex model considered that tidal state and hour of the day may interact with near, mid or offshore deployment locations (n=3). It was not possible to include interactions with the 2-D smooth for different groups (n=10) or different deployment locations (n=30) because of insufficient degrees of freedom.

With no deployment location interactions to consider, with distance from shore or deployment group for example, only two of the five models derived above were applicable to the Cromarty 05 subset. The first consisted of a smooth term for hour of the day relative to solar noon, and tidal state. The second model consisted of an interaction between time of the day relative to solar noon and tidal state. For both subsets of the data I used AIC to select the most likely of the candidate models tested and area under the curve scores (AUC) to assess model fit.

5.3. Results

5.3.1. Data Collection

The 2013-2015 ECoMMAS C-POD data represented 223,296 hours of acoustic monitoring (Table 5-2). Of those data, 1089 hours (0.49%) contained click detections classified as ‘broadband’. As expected, the C-PODs deployed nearest to the Cromarty Firth (Cromarty 05) contained both the greatest number of detections (158 and 450 in 2013 and 2015) and the highest proportion of detection positive hours (8.0 and 9.1% in 2013 and 2015) for broadband click trains. These values were nearly tenfold greater than those obtained from the next most frequently occupied site, Stonehaven 05, which had hourly acoustic occupancy rates of 0.6% and 1.9% for 2013 and 2015 respectively. When excluding Cromarty 05, the median acoustic occupancy rates for all units were 0.10%, 0.08% and 0.08% for 2013, 2014, and 2015 respectively, and the mean acoustic occupancy was 0.19 (n = 25, sd = 0.23), 0.29 (n = 21, sd = 0.23), 0.26 (n = 29, sd = 0.23) for the same periods.

Table 5-2 ECoMMAS Recording effort across the 30 deployment locations and 3 deployment years and the number (n) and percent (%) of the recording hours containing broadband click trains as identified by the classifier described in Chapter 2.

Deployment Location	Recording Effort (Hrs)			Number of Hours with Broadband Click Trains			Percent of Hours with Broadband Click Trains		
					— n —			— % —	
	2013	2014	2015	2013	2014	2015	2013	2014	2015
Lat_05	2040	2376	4896	0	0	2	0.00	0.00	0.04
Lat_10	2688	0	4896	1	–	2	0.04	–	0.04
Lat_15	2640	0	4896	1	–	0	0.04	–	0.00
Hel_05	1992	4512	3192	0	5	10	0.00	0.11	0.31
Hel_10	2712	0	4896	0	–	1	0.00	–	0.02
Hel_15	2616	2376	4896	0	0	0	0.00	0.00	0.00
Cro_05	1968	0	4920	158	–	450	8.03	–	9.15
Cro_10	600	2112	1872	4	46	32	0.67	2.18	1.71
Cro_15	2016	2328	4920	4	0	7	0.20	0.00	0.14
SpB_05	2184	792	4896	15	3	18	0.69	0.38	0.37
SpB_10	2616	0	1872	0	–	0	0.00	–	0.00
SpB_15	0	2424	4896	–	1	4	–	0.04	0.08
Fra_05	2208	1584	4968	0	27	18	0.00	1.70	0.36
Fra_10	0	0	4968	–	–	1	–	–	0.02
Fra_15	0	2424	4968	–	3	16	–	0.12	0.32
Cru_05	2976	2424	1896	5	2	1	0.17	0.08	0.05
Cru_10	0	2400	3072	–	4	1	–	0.17	0.03
Cru_15	3864	2256	0	9	4	–	0.23	0.18	–
Sto_05	2976	0	4296	18	–	82	0.60	–	1.91
Sto_10	0	1848	4992	–	8	9	–	0.43	0.18
Sto_15	3864	2088	1872	23	1	9	0.60	0.05	0.48
Abr_05	2208	2256	1872	6	5	10	0.27	0.22	0.53
Abr_10	2184	1944	4968	0	0	8	0.00	0.00	0.16
Abr_15	3840	0	4968	8	–	4	0.21	–	0.08
FiN_05	2256	1608	5016	10	2	8	0.44	0.12	0.16
FiN_10	2256	2328	1944	0	1	1	0.00	0.04	0.05
FiN_15	2688	2256	1944	1	1	0	0.04	0.04	0.00
Stb_05	2976	2424	1944	3	2	2	0.10	0.08	0.10

Stb_10	2184	2424	5016	2	2	4	0.09	0.08	0.08
Stb_15	3864	0	1944	4	–	0	0.10	–	0.00
Total	64416	47184	111696	272	117	700	0.42	0.25	0.63

5.3.2. Modelling Effects of Location, Time, and Tidal State

Of the five ecological models tested on the data excluding Cromarty 05, the third model was strongly preferred, with a delta-AIC of 39 units relative to the next model (Table 5-3). This model contained independent smooths for tidal state and hour of the day relative to solar noon, with an interaction between hour of the day and deployment group. In this model deployment group was significant ($\text{ANOVA}_{29,18571}$: F=3.7e-5, p<.001) as were interactions between the hour of the day and the Helmsdale, Cromarty, Fraserburgh, Stonehaven, Arbroath, Fife Ness and St Abbs deployment groups. The effect of tidal state was not significant (F = 0, p = 0.71; Table 5-4). The AUC score for this model was 0.75 and the adjusted r-squared was 0.02. R-squared, however, does not consider the large proportion of 0 detection hours and is therefore a biased representation of the model fit. All deployments in the non-Cromarty 05 subset where broadband echolocation click trains were common showed a minimum in detection probability around solar noon and higher detection rates throughout the hours of darkness (Figure 5-1). There was some variation in this relationship at sites with low acoustic occupancy rates such as Latheron, Cruden Bay, Fife Ness and St Abbs. At these locations the model suggested either no relationship with hour relative to solar noon (Latheron) or a slight shift in phase where the minimum detection rate occurred before or after solar noon (Cruden Bay, Fife Ness and St Abbs).

Table 5-3 Model specifications for the five models fitted to the data excluding Cromarty 05 (Non-Cromarty 05) and the two models fitted to the Cromarty 05 data. 'Hour' is the hour relative to solar noon and tidal state. 'S' represents smooth terms, 'te' represents tensor smooth terms and 'cc' represents cyclic cubic regression splines. Delta AIC scores (change in AIC from the best model) show a strong preference (Δ AIC) for third model for the Non-Cromarty data. For the Cromarty data, the second model was preferred over the first model (Δ AIC = 14).

Non-Cromarty 05 Data		
Model Formula	AIC	Δ AIC
P(Broadband) ~ s(Hour, bs='cc') + s(Tide, bs='cc')	117429	382
P(Broadband) ~ ShoreDist + s(Hour, bs='cc') + s(Tide, bs='cc', by = ShoreDist)	149487	32440
P(Broadband) ~ GroupId + s(Hour, bs = 'cc', by = GroupId) + s(Tide, bs = 'cc')	117047	0
P(Broadband) ~ te(Hour, Tide, by=ShoreDist, bs='cc')	117086	39
P(Broadband) ~ ShoreDist + te(Hour, Tide, by=ShoreDist, bs='cc')	117222	175
Cromarty 05 Data		
P(Broadband) ~ s(Hour, bs='cc') + s(Tide, bs='cc')	32429	14
P(Broadband) ~ te(Hour, Tide, bs='cc')	32415	0

Table 5-4 Model summary for the GAMM selected for the data excluding Cromarty 05 data.

Model Formula				
P(Broadband) ~ GroupId + s(Hour, bs = "cc", by = GroupId) + s(Tide, bs = "cc")				
Parametric coefficients:				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-4.69	0.32	-14.49	<0.001
GroupIdHel	0.38	0.47	0.82	0.410
GroupIdCro	1.56	0.36	4.30	<0.001
GroupIdSpB	1.08	0.39	2.79	0.005
GroupIdFra	1.14	0.38	2.97	0.003
GroupIdCru	0.51	0.40	1.28	0.200
GroupIdSto	1.20	0.35	3.44	<0.001
GroupIdAbr	0.53	0.41	1.28	0.200
GroupIdFiN	0.77	0.45	1.70	0.900
GroupIdStb	0.92	0.47	1.97	0.049
Approximate significance of smooth terms:				
	edf	Ref.df	F	p-value
s(Bahoura and Simard):GroupIdLat	<0.001	8	0.00	1.00
s(Bahoura and Simard):GroupIdHel	1.81	8	0.74	0.020
s(Bahoura and Simard):GroupIdCro	2.76	8	2.07	<0.001
s(Bahoura and Simard):GroupIdSpB	1.27	8	0.34	0.10
s(Bahoura and Simard):GroupIdFra	2.24	8	1.46	<0.001
s(Bahoura and Simard):GroupIdCru	1.41	8	0.40	0.08
s(Bahoura and Simard):GroupIdSto	2.81	8	2.77	<0.001
s(Bahoura and Simard):GroupIdAbr	2.59	8	2.09	<0.001
s(Bahoura and Simard):GroupIdFiN	2.20	8	1.15	<0.001
s(Bahoura and Simard):GroupIdStb	1.69	8	0.56	0.05
s(Tide)	<0.001	8	0.00	0.71
R-sq.(adj) = 0.0232		Scale est. = 1	n = 18600	

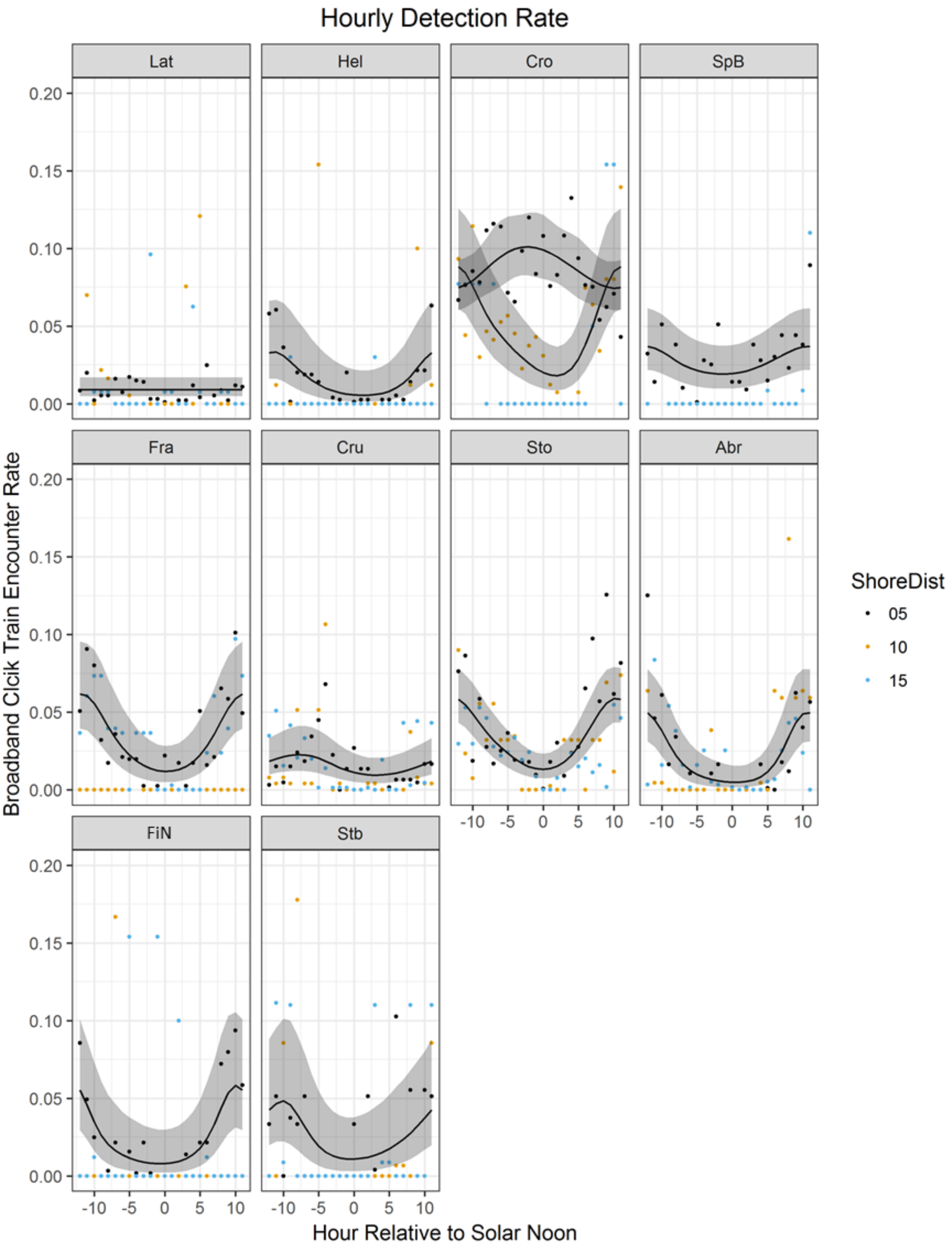


Figure 5-1 Observed (points) and modelled probability (black line) of detecting a broadband echolocation click train as a function of hour of the day relative to solar noon for each deployment group (panel). Shaded areas represent the 95% confidence intervals of the predictions for both models (Cromarty 05 and non-Cromarty 05). For plotting purposes, tidal state was set to 0 hours relative to high water. Excluded from the figure are 6 outlying observations at Cromarty 15 (0.2), Spey Bay 15 (0.22, 0.22), Fraserburgh 15 (0.77), Fife Ness 15 (0.51) and St Abbs 15 (0.34).

Of the two models tested for the Cromarty 05 dataset, the model with a tensor smooth between hour of the day and tidal state was strongly preferred over the model in which hour and tidal state were treated as independent smooths, with a delta-AIC of 14. In contrast to the models for the larger array, there was a slight increase in the likelihood of detecting a broadband echolocation click train at or around solar noon (Figure 5-1). Detections were also more likely in the hours preceding high tide and least likely four hours after high tide. However, the effect of tidal state was less pronounced than time of day (Figure 5-2). The AUC score for Cromarty 05 model the model was 0.57 and the adjusted R-squared was 0.003.

Table 5-5 Model parameters and significance for the Cromarty 05 model with the lowest AIC score. Parameter estimates (Estimates) for the parametric term (intercept) on the logit scale, standard error of the estimates (Std. Error), t value and P value (Pr(<|t|)).

Model Formula				
P(Broadband) ~ (Hour, Tide, bs = "cc")				
Parametric coefficients:				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-2.37	0.06	-42.16	<2e-16
Approximate significance of smooth terms:				
	edf	Ref.df	F	p-value
te(Hour, Tide)	3.39	15	0.588	0.0154
R-sq.(adj) = 0.0032		Scale est. = 1	n = 6408	

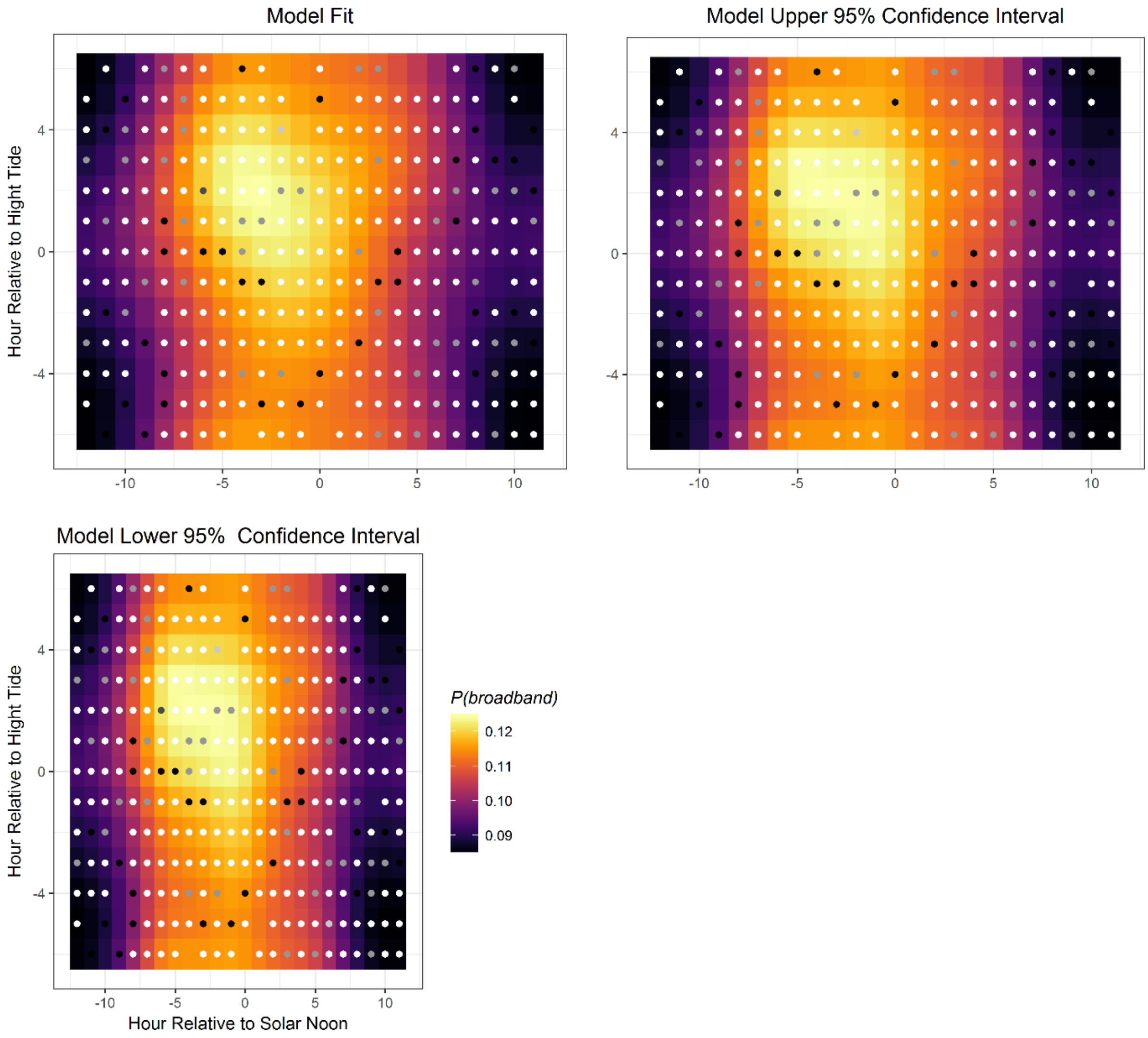


Figure 5-2 Model predictions (colour) and observations (points) for the Cromarty 05 model for the probability of detecting a broadband echolocation click train as a function of hour of the day relative to solar noon and tidal state. Point colours represent the proportion of click trains observed at each hour of the day tidal state where black equals zero and white equals one.

5.4. Discussion

In this study I looked for sub-daily trends in detections across the extent of the ECoMMAS array. I found two distinct diel patterns in the likelihood of detecting echolocation clicks conditional on whether or not the detector was deployed in or near a known foraging location. Near this location there was a slight diurnal trend in the detection of broadband echolocation click trains. Away from this location there was a nocturnal pattern in echolocation click detections. I also found that tidal state significantly impacted the likelihood of detecting broadband echolocation click trains at the Cromarty 05 location, but no effect was seen at the remaining deployment groups.

Tidal state was determined to be an important factor in predicting dolphin presence at the Cromarty 05 site. The relationship between tide and dolphin presence is well established both along the Scottish coast and worldwide. Arso Civil et al. (2019) noted changes in habitat selection concurrent with tidal speed and direction; animals were more often observed during periods and in areas of very low or high tidal flow as compared to times and locations with intermediate flow rates. Pirotta et al. (2014b) also noted a relationship between acoustic detections and tidal variables at numerous points within the Moray Firth. It is, therefore, not surprising that a relationship between tidal state (a proxy for other tidal variables) was retained during the model selection process. These results, in conjunction with visual studies lead credence to the notion that throughout the coastline tidal effects are an important predictor of bottlenose dolphin occupancy.

Using widely spaced moored acoustic instruments to describe the vocal behaviour of a wide-ranging predator is challenging as it is difficult to discriminate between animal movements and changes in vocal behaviour. For example, dolphins are known to migrate diurnally in order to either maximise foraging efficiency or minimise predation risk. In the Indian ocean bottlenose dolphins migrate daily between offshore resting habitat and inshore foraging habitat (Heithaus and Dill, 2002). It is conceivable that the diel pattern observed outside of the Cromarty location could be caused by migration. However, the most plausible explanation for the changes in diel patterns between the larger survey and the known foraging location is that the animals are changing their echolocation behaviour. In eastern Scotland bottlenose dolphins face little predation pressure so it is unlikely that temporal variation in predation risk affects sound production. While mammal eating killer whales are occasionally present, they are thought to primarily target pinnipeds (Bolt et al., 2009). Moreover, data from the first three years of the non-Cromary 05 sites in the ECoMMAS represented 213,456 hours of acoustic monitoring at 29 different locations spread across the majority of the coastline. Of the data collected, only 14 hours contained broadband detections within one hour of solar noon. In comparison, 121 hours contained detections between +11 and -12 hrs of solar noon. The paucity of detections near noon, regardless of survey location, strongly suggests that away from the Cromarty 05 site, dolphins have diurnal rhythms in their production of echolocation clicks.

Whether this pattern relates to the production or quality of the clicks remains to be determined. There is evidence to suggest that, in the absence of biological needs, bottlenose dolphins use echolocation sparingly (Jones and Sayigh, 2002, Gannon et al., 2005). For example, in the western North Atlantic, Jones and Sayigh (2002) found that bottlenose dolphins are more likely to produce echolocation clicks while foraging and the rate of echolocation per dolphin decreased with increasing group size. This finding was supported by playback studies of the same population that indicated dolphins passively listen for somniferous fish and produce echolocation clicks after detecting a potential prey item (Gannon et al., 2005). These studies suggest that the production of echolocation click trains is likely associated with a biological need or where the benefits of producing echolocation clicks is greater than those for remaining acoustically cryptic. The shallow waters habitat covered by this survey mean that during daylight periods light levels are likely sufficient to allow animals to travel or socialise without the need for echolocation. However, when actively foraging for highly mobile and/or visually cryptic prey, animals gain considerable advantage by employing both echolocation and vision. Alternatively, rather than producing fewer clicks during the daytime period, dolphins may be increasing the amplitude and therefore detectability of their clicks during periods of darkness (Au and Benoit-Bird, 2003).

AIC-based model selection suggested that the magnitude and phase of the diel trend in detections varied between each of the ten deployment groups. The low r2 value indicates that considerable amount of variance is not captured by the models. However, given the nature of the data this does not necessarily mean that the trends represented by the models are inaccurate. Much of the uncaptured variation can be attributed to sites with few detections. In these locations all predictions above 0 resulted in large error between the data and the models. However, designing models such that they minimized the r2 error produce models that predicted 0 for all times, thereby lacking the ability to predict times when detections are likely to occur. This is to say that r^2 values, like all metrics, should be interpreted within the context of the observations. For the Latheron deployment group there appeared to be no diel trend in detections whatsoever. For the remaining nine groups, the nadir in detections occurred within an hour or two of solar noon. Variation in the magnitude and phase-shift of the diel pattern could largely be attributed to variation in broadband echolocation click occupancy at the deployment groups. In the case of the Latheron group, there were only 5 hours containing broadband echolocation clicks detected despite 1824 hrs of monitoring over the 2013-2015 survey periods. Thus, the data contained insufficient power to determine whether or not diel trends were present at that deployment group. Similarly, Helmsdale and St Abbs contained less than twenty hours with broadband echolocation click detections despite a combined 49968 hours of monitoring over three years and three 6 C-PODs thereby reducing the power of the analysis at these locations. Excluding the Latheron deployment group from the data resulted in the first model, which did not include interaction terms nor the distance to shore factor, having the lowest AIC in the model set.

Outside of the Cromarty 05 deployment location, diel rhythms appeared to be the driving factor in predicting whether or not broadband echolocation click trains were detected. With so few detections, the data lacked sufficient power to identify both diel and tidal trends at the same time. Continued deployment of the ECoMMAS array will result in a greater number of days with dolphin detections thereby increasing the statistical power in the data. In future it should be possible to determine whether relationships between tidal covariates and broadband click detections are present at locations disparate from the Cromarty 05 site. However, considering potential confounding interactions between tidal state, detection probability, and detections, visual studies such as Arso Civil et al. (2019) represent a better approach to this specific question with fewer uncertainties requiring behavioural assumptions or mathematical gymnastics.

There was a significant relationship between the probability of detecting a broadband echolocation click train and tidal state at the Cromarty 05 deployment site. However, properly interpreting the behavioural implications of a relationship between acoustic detections and tidal aspects (i.e. phase, height, direction, or speed) is difficult. Within the Moray Firth, dolphins are known to use tidal races to corral fish, thereby increasing foraging efficiency (Mendes et al., 2002). It is therefore plausible that, like Chanonry point, dolphins near the Cromarty 05 site utilise tidal currents to maximise foraging efficiency. However, in shallow water the effect of tide on transmission loss is complex and changes in water depth will have major impacts on the area monitored by the acoustic sensors (Badiey et al., 2002). Thus, changes in the observed number of echolocation click detections may be attributable to changes in the area monitored by the system not accounted for in Chapter 3. If, for example, the local conditions were such that the area monitored by the sensors was largest at high tide but the animals had the lowest likelihood of producing clicks or were furthest from the sensors, peaks in detection rates would be observed just before and after high tide.

Findings from this study suggest that either the 29 non-Cromarty 05 deployment locations are not covering foraging hotspots, or that if the animals are foraging near these locations, their echolocation behaviour is different from their behaviour near the Cromarty 05 location. Visual surveys of this population have clearly shown that hotspots of foraging activity are present outside of the Moray Firth and especially in the Firth of Tay (Arso Civil et al., 2019). Unfortunately, it was not possible to deploy sensors near the entrance to the Firth of Tay. This means that it was not possible to determine whether the diel trend in detections observed at the Cromarty 05 site was indicative of patterns that would be seen at other points of aggregation, or whether the pattern is unique to the inshore Cromarty Firth area. Results from Chapter 4 suggested that the Stonehaven 15 deployment site may be, or may be close to, a previously undescribed area of high use. However, hourly patterns in detections at this site did not differ from the other non-Cromarty 05 locations (Figure 5-1). Thus, either the area is not a point of aggregation or the acoustic behaviour of the animals around the Stonehaven groups does not differ from the other non-foraging deployment locations.

How the presence of dolphins, behavioural drivers, and the physics of ocean acoustics interact to produce spatially and temporally distinct patterns in echolocation click detections is complex. As such, care is warranted when ascribing behavioural traits to trends in detections. For example, Au and Benoit-Bird (Au and Benoit-Bird) found that as dolphins approached a target, both the amplitude and peak frequency of their clicks decrease. Decreasing amplitude and peak frequency have opposite effects on the propagation range and subsequently detectability of echolocation click trains. Lower amplitude clearly results in a lower detection range. Conversely, within limits, lower frequencies propagate further and are subsequently more easily detected by passive acoustic systems. This relationship is further complicated by the black-box nature of C-PODs. Nuuttila *et al.* (2013b) empirically measured the detectability of bottlenose dolphin echolocation click trains by C-PODs under different behavioural states and group sizes. The authors found that for travelling dolphins, the area monitored by the C-PODs decreased with increasing group size, a counter-intuitive result. This corresponds with the decrease in echolocation click rate per dolphin while travelling described by Jones & Sayigh. However, Nuuttila *et al.* (2013b) also found that the effective area monitored by C-PODs was lower for foraging dolphins than for travelling dolphins. These findings highlight how complex interactions between the physics of detection system and the behaviour of the animals can produce intricate detection functions that are not easily generalizable to other locations survey locations.

One of the primary goals of the ECoMMAS array is to fill in knowledge gaps with regard to habitat use outside well-studied areas where animals concentrate. However, as with the majority of static acoustic arrays, the survey duration is limited by the battery capacity and memory in the recording systems. As a result, there is a paucity of data available over the winter period. Other populations of dolphins are known to produce acoustic signals only under certain behavioural states and or environmental conditions (Jones and Sayigh, 2002, Gannon et al., 2005). Thus, if future studies seek to understand acoustic occupancy over a greater portion of the annual cycle, it would be prudent to target the duty cycle of the ECoMMAS instruments to periods when the animals are most likely to vocalise.

Finally, knowing how diel trends in detection vary across the extent of the array will be useful in future studies looking at habitat use. Results from this chapter suggest that the probability of detecting an echolocation click train between greater than 10 hours before or after solar noon were approximately the same regardless of whether or not the sensor was in a foraging location. Thus, setting duty cycles of acoustic instruments to cover the night-time periods may extend data coverage without biasing daily acoustic occupancy rates. Targeting the duty-cycle of long-term deployments to cover this period would be the most effective way to increase survey coverage with minimal bias caused by diel clicking behaviour.

5.5. Conclusions

Data and modelling efforts from this chapter provided strong evidence that diel trends in bottlenose dolphin echolocation behaviour are site-dependent. Diel patterns in detections were nocturnal outside of a known foraging area and moderately diurnal near the foraging area. These data suggest that foraging is either less likely to occur at locations not associated with points of aggregation or that factors producing diel rhythms in foraging behaviour vary across the habitat of these dolphins.

Chapter 6

General Discussion

6.1. Aims

The primary aim of this thesis was to increase knowledge of bottlenose dolphin habitat use and behaviour outside of the well surveyed areas and times (daylight) in order to better serve the conservation goals for the population. This thesis has allowed for advancements in both these areas by including data coverage from the full 24hr cycle collected from areas outside well surveyed areas. Previous work has focussed on studying animals concentrated in certain areas (primarily Moray Firth, waters around Aberdeen, Montrose, St Andrews Bay and the Tay Estuary) with areas between these considered likely to be used as movement corridors (Cheney et al., 2013, Quick et al., 2014, Arso Civil et al., 2019). However, prior to this study, there was insufficient temporal or spatial resolution in the data to support this fully. Chapter 4 showed that daily acoustic occupancy in areas between previously studied concentrations is, as expected, low in comparison to in these previously studied areas. In Chapter 5, the data suggested that dolphins were present and acoustically active throughout the 24-hour cycle at a point of aggregation (Cromarty) but were either not present or present but not acoustically active during the daylight periods at other locations. However, other known points of aggregation including the Tay Estuary and Montrose Basin were not acoustically monitored. It is not possible to differentiate between the latter two hypothesises with passive acoustic data alone. While these findings alone are insufficient to confirm that previously unstudied areas are used primarily for transiting, they do suggest that areas outside those where studies have previously concentrated are not as frequently or continuously used as the studied areas, which include some specific foraging locations.

Like all methodologies, acoustic surveys are faced with limitations including species misclassification and uncertain detection probabilities. C-PODs are especially problematic in both of these aspects due to their black-box nature. Thus, better addressing species classification and detection probability were important contributions of this thesis. In Chapter 2, I addressed species misclassification by increasing the taxonomic resolution provided by the C-POD data and in Chapter 3 investigated whether site and noise dependent changes in detection probabilities were likely to bias occupancy rates. I found that it is possible to group C-POD echolocation click encounters into groups representing broadband or frequency-banded species of dolphin. I also found that changes in detection probability were unlikely to change the interpretation of the acoustic occupancy results presented here. Finally, in this chapter I suggest future research areas that have been highlighted by this thesis.

6.2. Key Findings and Interpretations

C-PODs are popular tools for monitoring odontocetes worldwide. They are predominantly used in habitats containing a single species of dolphin or porpoise where there is little risk of misclassification (Koschinski et al., 2008, Jaramillo-Legorreta et al., 2017, Williamson et al., 2016). However, occasionally C-PODs are deployed in multi-species habitats (Robbins et al., 2016). In such contexts there is a need for increasing the taxonomic resolution of data output from the instruments. Chapter 2 addressed classification by combining data from the SM units and the C-PODs deployed in ECoMMAS to increase the taxonomic resolution of the detector-classifier system of the C-PODs. This work represents the first successful attempt at discriminating between any dolphin species in C-POD data. While I was not able to build a classification system specifically for bottlenose dolphins, the grouping methodology initially advocated by Caillat (2013) and implemented here was efficient in identifying detections that were unlikely to be bottlenose dolphins (i.e. ‘frequency banded’ echolocation click encounters). These methodologies allowed me to calculate the probability that a ‘broadband’ echolocation click train was present in each hour of a C-POD detection history. The broadband probabilities were then used as the response variable in the binomial GEEGAMs in Chapter 4 and GAMMs in Chapter 5. By assigning a broadband click probability to each hourly observation, as opposed to a binary indicator for presence/absence, I was able to preserve some of the uncertainty in the classification system, which is an important aspect of passive acoustic surveys (Miller et al., 2011, Caillat, 2013). Furthermore, results from Chapter 2 suggest that it may be possible to discriminate between morphometrically similar groups of dolphins in other locations as well. To that end the classification model as well as the encounter likelihood code have been made freely available online (https://github.com/JPalmerK/C-POD-encounter-classification).

All ecological surveys are subject to environmental variations that impact the probability of detecting the target species (Bailey et al., 2007). In boat-based visual surveys this includes periods of darkness or elevated sea-state. In passive acoustic surveys, varying ambient noise levels and location-dependent transmission loss characteristics change the probability of detecting a vocalising animal at a given time and place. Previous studies have used the sonar equations in conjunction with simulations of diving animals and explicit knowledge of the detector performance to measure the bias caused by transmission loss and noise level (Kusel et al., 2011, Caillat, 2013, Helble et al., 2013, Frasier et al., 2016, Kusel et al., 2016). In Chapter 3, I applied the same principles to the C-POD instrument and detection system to estimate survey bias.

Where previous studies have explicitly calculated the probability of detecting vocalising animals, the ‘black-box’ nature of the C-POD and KERNO classification system precluded such analysis. I therefore adopted a simulation approach that focused on determining how transmission loss and ambient noise levels could bias the relative acoustic occupancy results rather than determine the exact detection probability. I relied on third party calibrations of the instrument sensitivity (Dahne et al., 2013) and made assumptions about the threshold and integration time of the KERNO classifier. These were then combined in a Bayesian framework with the noise levels measured by adjacent SM recordings and the detection positive hours reported by the KERNO classifier. I produced three models that related ambient noise levels and site-specific transmission loss to the probability of detecting a bottlenose dolphin echolocation click.

I found high levels of correlation in the median hourly noise levels from all SMs in the array. Unsurprisingly, noise levels from neighbouring instruments had the highest correlation values and correlation scores decreased with increasing distance between the sensors. However, even noise levels from SMs deployed at the extreme limits of the array (i.e. Latheron and St Abbs) were correlated up to ~20%. This suggested that the effects of noise level could bias absolute acoustic occupancy rates but would have limited effect on the *relative* acoustic occupancy rates. This was because all survey locations were likely affected by the same broad-scale noise variation such as storms. Transmission loss also varied considerably within the habitats monitored by the C-PODs, with nearshore and shallow water deployments monitoring smaller areas than offshore and/or deeper deployment locations.

Together, site-specific transmission loss and noise levels resulted in large changes in absolute detection probability. The estimated detection probabilities did, in fact, have the potential to bias relative acoustic occupancy rates at the survey locations. However, when I combined the hourly acoustic occupancy results from the C-PODs with the detection probabilities I found little evidence of *relative* bias in the acoustic occupancy results. This suggested that there was little value in including hourly detection probabilities in acoustic occupancy analyses in future ECoMMAS analysis.

The method developed in Chapter 3 was implemented in response to the need to address detection probability in C-PODs without undertaking concurrent visual surveys across the extent of the array (Kyhn et al., 2012, Roberts and Read, 2014). The simulation approach was necessitated due to the black-box nature of the C-POD detectors and KERNO classifier. However, the simulation approach I developed is flexible and may be applied to survey conditions where the detection system is well characterised, but the target animal's behaviour is less understood. For example, little is known about Bryde's whales in the Gulf of Mexico, including the depth at which they produce vocalisations (Sirovic et al., 2014). Without such information, simulation studies using Monte-Carlo models of sound production (e.g. Küsel *et al.*, 2011) are not reasonable as received levels are highly dependent on the depth at which the animal is calling. The approach presented in Chapter 3 represents a worst-case scenario that other researchers may use when the requisite animal behaviour data are lacking.

Chapter 4 represented a first attempt at modelling the Scottish east coast bottlenose dolphin population on a scale approaching its known range (Cheney *et al.*, 2013). I reported acoustic occupancy rates for areas between Latheron and St Abbs. I also looked at temporal trends at the survey locations and produced a habitat-scale model for acoustic occupancy. The GEEGAM and GAMM approach I used in Chapter 4 built on the habitat modelling presented by (Arso Civil et al., 2019). Where Arso Civil *et al.* (2019) dealt with autocorrelation in spatial observations arising from focal follows of groups of animals, I contended with temporal autocorrelation produced by the continuous nature of the ECoMMAS data. The findings from this chapter are largely in agreement with previous visual surveys that suggest animals are more likely to be found in certain areas in which foraging may be focussed, near the shoreline and in shallow water. However, I hypothesized that the bathymetry gradient, which has previously been identified as a predictor of dolphin foraging, was only meaningful in predicting acoustic occupancy when considered in the context of areas where foraging is focussed (Pirotta et al., 2014b). Supporting this finding, seabed gradient was not retained in the best habitat model in the set I tested. I was not, however, able to assess the effects of tidal current speed and direction as the POLPRED system is unable to produce predictions for these variables close to the shoreline.

In Chapter 5 I found compelling evidence that bottlenose dolphins display nocturnal patterns in echolocation outside previously studied high-use areas and diurnal trends near an area where foraging is focussed (Cromarty). In this study I found two distinct patterns in the likelihood of detecting echolocation click trains. Near a known foraging location there was a diurnal trend in the likelihood of detecting a broadband echolocation click, while elsewhere there was a strong nocturnal pattern in echolocation click detections. I also found that tidal state was significant in predicting echolocation presence near the foraging location, but not elsewhere. These findings provide important insights into the echolocation behaviour of bottlenose dolphins on a large spatial and temporal scale. Previous studies have shown that bottlenose dolphins display both spatial and temporal plasticity in their sound production and that many populations use echolocation sparingly in the absence of biological needs (Jacobs et al., 1993, Jones and Sayigh, 2002, Nowacek, 2005). For example, in the Northwest Atlantic, some groups of bottlenose dolphins are more likely to produce echolocation clicks while foraging and remain silent under other behavioural states (Jones and Sayigh, 2002; Gannon *et al.*, 2005). This pattern of decreasing click production while not actively foraging could result in the diel patterns observed here. Additionally, playback studies have indicated that animals may listen passively for prey items prior to producing echolocation clicks (Gannon et al., 2005). Thus, my findings support the hypothesis of behavioural plasticity in echolocation click production by showing an increase in the likelihood of acoustic detections during periods of increased darkness and in areas associated with prey availability.

As with most acoustic studies, this result is confounded by the ambiguity between when animals are present and not calling vs when animals are not present. Thus, it is possible that the paucity of detections during the daytime hours away from the foraging location was the result of animals not being present rather than changing their diel echolocation clicking behaviour. However, were animals moving away from the sensors during the day it begs the question - where are they going? Other populations of bottlenose dolphins are known to migrate offshore during the night to reduce predation risk (Heithaus and Dill, 2002). However, the Eastern Scottish bottlenose dolphins face little predation risk. Moreover, if the dolphins were making daily onshore/offshore migrations I would expect to see nocturnal patterns in detections at the offshore locations (e.g. 10 and 15 units) and diurnal patterns at the nearshore locations (05 units). That was not the case as nearly all deployments displayed nocturnal trends. Alternatively, the nocturnal trends in detections could have been caused by a daily onshore migration to habitat so close to the coastline that animals could not have been detected by the C-PODs. While this hypothesis is technically possible it would require that animals avoid the sensors across the entire array, with the exception of Cromarty 05, during the daylight hours. This movement pattern is improbable given that the ECoMMAS array is deployed over 400 km of habitat and encompasses a variety of distance to shore measures ranging from 350m at Spey Bay 05 to 17.5 km at the Arbroath 15 location. A third possibility could be that the animals move toward foraging locations during the daytime periods and away from them during the evenings. Thus, the Cromarty 05 deployment location could have been the only sensor near enough to a foraging location to identify a diurnal increase in detections. This scenario seems feasible, particularly since locations of bottlenose dolphin foraging activity are associated with areas of high flow rates (Arso Civil et al., 2019). Remaining in such areas while not foraging would therefore be energetically costly. Even so, under this scenario I would still expect to see a variety in diel rhythms between sites nearer to foraging locations (e.g. Cromarty 10) and sites further away (e.g. Cruden Bay and Fraserburgh deployment groups) and this pattern was not observed. Thus, while the movement hypothesis is worth exploring, it is not presently the most parsimonious explanation for the observed rhythms in diel detections.

Finally, Arso Civil et al. (2019) noted that the area between Stonehaven and Aberdeen is an important transiting and foraging area. Results from Chapter 5 confirm that the area off Stonehaven is frequented by more than one dolphin species. However, the diel patterns in echolocation click detections reported for this site did not differ from the remaining locations excluding Cromarty 05. This may suggest that the area outside of Stonehaven is primarily used for transiting or socialising as the pattern in diel detections differed from the known foraging location (Cromarty 05).

6.3. Limitations

The research presented here was limited in technical scope by the ‘black-box’ nature of the C-POD classification system and the ecological interpretations were limited by the low detection rates. In this thesis I chose to focus almost exclusively on the C-POD data to maximise the available spatial and temporal data available; the C-PODs in the array represented a several fold increase in data availability over the available SM units which were both fewer and duty-cycled. However, two chapters of this thesis were needed to begin to approach detection probability and species classification issues that have been effectively addressed in the continuous monitoring literature (Soldevilla et al., 2008, Frasier et al., 2016). Moreover, the taxonomic resolution achieved in Chapter 2 is less than could be managed with a simple classifier run without encounter analysis in freely available PAMGuard software (Gillespie et al., 2009, Caillat, 2013). The ecological limitations were partially a result of the choice of deployment locations and partially by the very high false negative rate of the C-PODs.

Similarly, Chapter 3 was primarily limited by a lack of published information about the KERNO classifier software. While the chapter would also benefit from knowledge of the sound transmission characteristics of the sediment at each location (e.g. shear speed), lack of knowledge of the KERNO classifier dominated the uncertainty. Independent research groups have compared visual detections to C-POD data classified with the KERNO system to establish false positive rates, which are generally very low (Kyhn et al., 2012, Nuuttila et al., 2013b, Roberts and Read, 2014). However, none of the studies considered the relationship between the detector performance and the SNR of the received click trains. Thus, while I am relatively confident that the effects of ambient noise on an hourly scale and site-specific transmission loss are unlikely to bias acoustic occupancy within the ECoMMAS survey area, these results are not applicable to other survey locations – each must be assessed taking into account the noise levels and transmission loss of the specific locations.

On the daily acoustic occupancy scale, it was not possible to create a single model for broadband likelihood as a function of survey location and time of the year. Models containing linear terms for each deployment location would not converge in either the GAMM or the GEEGAM framework. This was largely attributable to the low overall acoustic occupancy rates. With so many zeros and so few detections in the data, it was impossible to determine which of the covariates were the driving factor predicting the few observed occupied days. It is not, however, surprising that the models lacked statistical power. The data presented here represent only the first three years of the ECoMMAS project. Other spatial ecology studies of this population have either included data collected over a period ranging from eight to almost thirty years (Anderwald et al., 2010, Pirotta et al., 2014b), or relied on focal follows that increased the number of detection positive periods . Thus, as the ECoMMAS array continues to be deployed, the statistical power of models fitted to its data will undoubtedly increase.

In comparison to other survey methodologies, particularly visual, the data presented represented considerable limitations. Like many acoustic studies with small cetaceans we were not able to discriminate between some species, individuals, or many behaviours. It is possible to use static acoustic arrays and even C-POD arrays to assess population dynamics (Jaramillo-Legorreta et al., 2017). However, the use of static acoustic arrays for population dynamics is limited to study areas where the instruments can acoustically cover the entire habitat of the animal and, ideally, under circumstances where detection probabilities can be calculated with limited error (Kusel et al., 2011, Marques et al., 2011, Marques et al., 2012, Harris et al., 2013, Hildebrand et al., 2015).

6.4. The Value of Large-Scale Passive Acoustic Surveys

Passive acoustic monitoring is an important part of cetacean research. Acoustic devices can ‘listen’ for marine mammals during periods of darkness regardless of weather conditions. Furthermore, passive acoustic monitoring allows for surveys in areas inaccessible to visual studies (Van Parijs et al., 2009). The method is often described as cost effective and in many instances, it is. However, using acoustic studies to monitor habitat use is still relatively new when compared to visual surveys. Moreover, both delphinid species discrimination and survey effort quantification (i.e. determining the total area monitored at any given time) remain a challenge for all acoustic surveys (Binder and Hines, 2014, Frasier et al., 2016, Rankin et al., 2017). Unlike photo-id studies, it is not yet possible to easily discriminate between individual bottlenose dolphins, as the requisite catalogue of whistles has yet to be established for most populations (Sayigh et al., 2013, McCordic et al., 2016). It is therefore pertinent to consider whether large-scale passive acoustic surveys such as the ECoMMAS are, in fact, cost effective for monitoring this population. The following section presents a cost comparison of the ECoMMAS and a boat-based photo-id survey in the same area (Quick et al., 2014).

In this analysis I estimate the cost per effort hour of visual and acoustic studies in the same area. I also report the estimated cost per encounter (visual and acoustic) as this metric may be more relevant to some studies. Throughout this analysis a variety of cost assumptions are made. In each case I either provide a range of expected costs or estimate using the lowest reasonable estimate. This analysis will not consider post-processing equipment (e.g. computers) or time for either survey technique as the processing time is entirely dependent on the survey aims. For example, presence/absence studies may require very little processing time regardless of the survey technique. However, photo-id studies of individual animals require considerably more processing time. Additionally, some large funding bodies including the United States Office of Naval Research now preclude researchers from including computers in grant expenses.

The cost associated with visual and acoustic surveys can be divided into categories including equipment; vessel and crew; and analysis (not considered here). Initial equipment purchases for any long-term study are considerable but may be averaged over the life of the project. Thus, the average cost of a long-term project may decrease as the duration increases. In the following comparison, Quick (2014) embarked on a two-year study and the ECoMMAS covered three years. Subsequently, for average cost calculations I assume a third year of visual surveys. For this year I assume equipment costs are equal to the second survey year and the number of encounters and survey effort are the average of the previous two years. By this process, the initial equipment investment is averaged over three years for both visual and acoustic studies.

Equipment costs for the ECoMMAS included recording devices, moorings, and an underwater sound system to trigger the acoustic mooring. Because it is reasonable to deploy instruments with surface moorings, and some were, this analysis will not include underwater speakers or the acoustic release mooring. Instrumentation costs in the ECoMMAS included, C-PODs, SM2Ms, and chain weight moorings. Since all ecological inference derived from this study were provided by the C-PODs, the equipment costs will consider these instruments only. Moorings can be derived from a variety of materials including bar weights, chains (used here), and burlap bags of rocks. For the purposes of this analysis I assume the frugal choice of mooring material which can be acquired in most locations without incurring additional expense. At the time of writing, C-PODs retail for £2970 each.

Both visual and acoustic surveys require vessels and qualified crew. For the ECoMMAS, vessel and crew costs are limited to the time needed to deploy and retrieve the instruments. Visual studies such as Quick (2014) use vessels for the duration of the survey period. Vessel costs vary widely depending on the size of the ship and institutional fees. The ECoMMAS array was deployed and recovered using large (>20m) research vessels with several crew and scientists. However, C-PODs are relatively small, and deployment and recoveries could have been performed by chartering small vessels either from SMRU or coastal ports. Currently, the SMRU research vessels used for visual surveys quotes £500 per day for the use of the 7m research boat and the same for one member of crew for a total of £1000/day. Chartered boats are typically less expensive, costing approximately £600 per day plus £150 for a photographer. The ECoMMAS array required ~7 days each for deployment and recovery. Assuming one crew member and one paid researcher I estimate daily vessel costs between £750 for a chartered vessel with extra personnel and £1000 for the SMRU vessel. Equipment costs for the visual survey include £2000 the first year for a quality camera and £50 subsequent years for storage media.

Survey effort varied considerably between the two studies. Furthermore, there was imperfect overlap between the spatial coverage of the ECoMMAS and Quick (2014). Between 2012 and 2013 there were a total of 50 dedicated visual surveys between the Firth of Forth and Aberdeen representing 323 hours of effort. Visual surveys were divided into three sections: the Firth of Forth that included habitat primarily within the coastal waters of the forth, St Andrews Bay including the Firth of Tay, and the Montrose/Aberdeen section that covered habitat between Tayport and Aberdeen (henceforth ‘Aberdeen’). The Firth of Tay is a known high use area and was not covered by the ECoMMAS. Similarly, the University of Aberdeen typically surveys the Moray Firth including the Cromarty Firth, another high use area. Including high-use areas covered by one survey methodology but not the other would likely introduce bias into the analysis. Thus, the fairest way to compare the studies was to include only areas where there was survey effort for both methodologies. For this reason I included only the ‘Aberdeen’ section of the visual and the following ECoMMAS deployment groups: Cruden Bay, Stonehaven, and Arbroath C-POD groups. These sections of the two surveys (henceforth the Grampian region) covered approximately the same area and excluded high use areas.

The first three years of the ECoMMAS deployments in the Grampian region produced 65,064 of survey effort and documented 217 unique broadband acoustic encounters. Five C-PODs from the region were either lost or failed to collect data (Table 4-2). Assuming the total time needed to deploy and recover the C-PODs was eight days per season, the vessel costs for the ECoMMAS were between £6000 for a chartered vessel and £8000 for the SMRU vessel and extra crew member per year. Two C-PODs were also lost or failed to produce data in 2013 and 2014 and one in 2015. I assumed these C-PODs were replaced each year resulting in the purchase of 11, 2, and 1 C-PODs in 2013, 2014, and 2015 respectively. Thus, for the first year of the ECoMMAS in the Grampian region the total cost per collected hour of data was £1.76 -£1.86/hr in 2013 when eleven C-PODs were purchased (nine initial and two replacements) and £0.32-£0.39/hr in 2015 when only one unit was replaced (Table 6-1). The estimated cost per hour of visual data was £166.06-£197.31/hr in 2012 when the camera equipment was purchased and £94.53-£125.78 in 2013. The average cost per survey hour of the ECoMMAS was £0.92-£1.01/hr. The three-year average cost per survey hour was £109.06-£140.31/hr for the visual survey.

For the C-PODs in the Grampian the cost per broadband acoustic encounter ranged from £560.43– £589.42 in 2013 to £72.34– £88.48 in 2015. The visual surveys in the Aberdeen section represented 91.44 hours of effort and documented 49 visual encounters. (Arso Civil et al., 2019, Quick et al., 2014). This resulted in a cost per visual encounter of £328.08– £389.82 in 2012 and £158.67– £211.12 in 2013. However, after the initial instrumentation investment the cost per acoustic encounter dropped to £479.50– £580.83 and £72.34 – £88.49 in 2014 and 2015 respectively (Table 6-1). In total the cost per acoustic encounter was £166.06– £197.31/hr in 2012 when the camera equipment was purchased and £94.53– £125.78 in 2013. The average cost per visual encounter was £274.53– £302.21 and £164.38– £211.48 (Table 6-1).

Table 6-1 Cost comparison of Quick 2014 ‘Aberdeen’ visual surveys and the ECoMMAS survey within the Grampian region (Cruden Bay, Stonehaven, and Arbroath). To calculate average cost over three years in for the visual survey, a third survey year was assumed with equipment cost of £50. Survey effort and number of encounters was estimated as the average of the preceding years. Equipment cost for the acoustic survey includes initial C-PODs and replacement of lost C-PODs. For visual surveys equipment cost includes a high quality DSLR camera and lens (2012) and SD cards in 2013.

	Acoustic			**Visual**	
	2013	**2014**	**2015**	**2012**	**2013**
Equipment Purchase (C-PODs/ Camera)	32670	5940	2970	2000	50
Vessel Cost Lower Estimate	6000	6000	6000	2593.13	5979.38
Vessel Cost Upper Estimate	8000	8000	8000	3457.50	7972.50
Survey Effort (Hours)	21912	15216	27936	27.66	63.78
Number of Encounters	69	24	124	14	38
Cost Per Survey Hour (£)	1.76	0.78	0.32	166.06	94.53
	1.86	0.92	0.39	197.31	125.78
Cost Per Encounter (£)	560.43	497.50	72.34	328.08	158.67
	589.42	580.83	88.47	389.82	211.12
Three Year Average Cost Per Survey Hour (£)		0.92		109.06	
		1.01		140.31	
Three Year Average Cost Per Encounter (£)		274.56		164.38	
		302.21		211.48	

The cost analysis presented here does not account for the time needed to move from the data source (i.e. photographs, acoustic recordings, or C-POD detections) to response variables needed for statistical models (e.g. occupancy, behaviour, etc). For visual surveys of presence/absence it is a trivial task to determine when and animals were detected, but full photo-ID analysis is more involved and thus expensive. These data may come from either observer logs or inspection of the photographs and timestamps. Depending on the assumptions that the researchers are willing to accept the same could be said of C-POD detector. The manufacturer has designed the systems to produce daily and hourly occupancy tables with the click of a few buttons. In fact, several months of data from a single instrument can be processed in under ten minutes producing binary CSV files indicating, for each hour or day, whether or not an odontocete click was detected. Thus, in a single species context, analysis of C-POD data may be as efficient, if not more, than visual observations.

The most cost-effective survey technique is directly related to the research question, target species, and habitat. For example, with a few notable exceptions (Moretti et al., 2006, Jaramillo-Legorreta et al., 2017), visual transects and photo-id studies are the only way to discriminate between individual animals; assess animal health; and estimate population levels, survival rates, and birth rates (e.g. Arso-Civil *et al.*, 2019). In contrast, fixed acoustic arrays produce far superior temporal coverage for a given financial budget. Therefore, where researchers need continuous data for a given site, fixed passive acoustic arrays are generally a better choice. This is the case for environmental site assessment in areas of industrial interest. Real-time presence absence information such as ‘whale alarms’ that trigger ship speed regulations also rely on acoustic detections (Fladung et al., 2011). Finally, acoustic surveys are also the obvious choice when habitats are difficult to survey or where detections are thought to be sparse, such as the offshore deployment locations in the ECoMMAS. Here, fixed passive acoustic arrays produce exploratory data at very low cost. Thus, when more detections are recorded than expected, e.g. the Stonehaven group, these data can direct the distribution of survey effort to areas of interest.

For the Eastern Scottish bottlenose dolphin population, the most effective way to conduct future studies could be to combine acoustic data from ECoMMAS with focused photo-ID surveys in high-use areas (e.g. Cheney *et al.,* 2013). This approach would low-cost survey effort for low use areas and focus comparatively high-cost (per hour) visual surveys in areas where detailed detections are likely including the Firth of Tay and the Inner Moray Firth. Since both studies are ongoing, future research should seek to integrate these data.

When considering the costs benefits of the ECoMMAS array it is also important to consider that the range of commercially available passive acoustic monitoring instruments has expanded greatly in recent years. Therefore, the instruments presently used in the ECoMMAS array may not continue to be the most cost-efficient options. For example, although C-PODs produce very low false positive rates, their false-negative detection rates are notably worse than continuous recording systems. A comparison study of C-PODs and continuous recorders showed that C-PODs detected approximately half of the detection positive minutes than were reported for an adjacently deployed continuous recorder (Roberts and Read, 2014). Thus, the cost per acoustic encounter could drop significantly further if continuous recorders were used. There are presently continuous monitoring devices priced similarly to C-PODs that are capable of both detecting high frequency echolocation clicks as well as collecting continuous recordings at lower sample frequencies. Such instruments may be deployed for timescales similar to C-PODs but have fewer of the drawbacks associated with the proprietary software.

This review does not consider the non-trivial analysis costs. The magnitude of the cost of analysis varies considerably depending on the study objectives and, for acoustic surveys, instrumentation. For presence/absence studies the analysis cost of photo-id approaches negligibility as surveyors presumably are not taking photographs while animals are absent. Similarly, C-PODs and their associated software are designed to produce presence/absence data by default; providing user-friendly spreadsheets with no human auditing required. The presence/absence approach of C-PODs is useful for large-scale single-species surveys where a pressing conservation need requires a fast turn-around time (Koblitz et al., 2014, Jaramillo-Legorreta et al., 2017). However, multi-species acoustic studies require considerably more processing time to differentiate acoustically similar species and/or incorporate classifier uncertainty (e.g. Chapters 2 and 4). Even in high-quality recordings considerable species uncertainty may remain (Frasier et al., 2017). In contrast, species uncertainty typically presents a lesser challenge in photo-id surveys where high-quality photos are less likely to result in species uncertainty. As such, species-level photo-ID studies for presence/absence is likely more cost effective. Individual identification using passive acoustics has not yet been shown to be an effective approach in long-term or large-scale basis as has been for visual surveys. This makes studies of individual migration, fecundity, and population dynamics considerably more challenging for acoustic studies and not typically the method of choice except. Finally, measuring marine mammal density is an ongoing challenge for both visual and acoustic surveys. Neither is without challenges posed by changing detection probabilities,

6.5. Future Directions

This thesis represents the first analysis of the data output from the ECoMMAS array. The long-term dataset represented by the ECoMMAS has the potential to provide invaluable insights into the spatial ecology of coastal dolphins. As data from the 2016 and 2017 deployments are integrated into the analysis, numerous additional ecological questions may be asked. The following questions represent suggested future directions for analysis of the ECoMMAS array.

Where do bottlenose dolphins go over the winter months? One of the outstanding questions not addressed in this thesis is where bottlenose dolphins go over the winter months. The low light levels and adverse sea conditions generally preclude dedicated visual surveys for this population over the winter months. As such, the ECoMMAS array is particularly well suited to begin to answer these questions. Future studies should consider adding to or adjusting the survey design to monitor habitat use over the winter periods.

What is the relative importance of each of the points of aggregation? The distance to the nearest known point of aggregation has been shown to be an important indicator of bottlenose dolphin presence on both small and large spatial scales (Arso Civil et al., 2019) . However, in this study there were only 30 observation locations. Therefore, there were insufficient degrees of freedom in the spatial covariates to model distance to points of aggregation that could be important for foraging (river mouths) as a function of the location (e.g. Cromarty Firth, Aberdeen Harbour, etc). The ability to include the location of the point of aggregation in the spatial-temporal models is important for future studies seeking to investigate the relative use of the area around each point of aggregation. Including more spatial covariates into acoustic occupancy models could involve either adding more survey locations or-ideally- integrating data from boat-based surveys.

How important is foraging outside the well-studied areas? One study has shown that it is possible to infer foraging behaviour from C-POD detections based on the proportion of low inter-click-interval clicks within a click train (Nuuttila et al., 2013a). By modelling the likelihood of a foraging click train as a function of environmental covariates it is possible to infer spatial and temporal drivers of habitat use (Pirotta et al., 2014b). Understanding how animals use the available habitat for foraging, resting throughout their range is potentially important for managers seeking to maintain the integrity of key habitat features.

Unfortunately, there were an insufficient number of echolocation click trains detected during the first three years of the ECoMMAS to infer meaningful results from this type of analysis. Additional deployment of the ECoMMAS array will, however, produce sufficient acoustic encounters to allow behaviour analysis.

How does the construction of windfarms affect the distribution of bottlenose dolphins? Simulations of dolphin behaviour in and around the Moray Firth have suggested that the construction of offshore wind farms is unlikely to result in population-level effects (Pirotta et al., 2015a). The ECoMMAS project should contribute to an integrated monitoring system to determine whether this is the case more generally. As windfarms continue to be approved and construction commences, ECoMMAS array data should be combined with photo-id studies in high-use areas to understand what, if any, the effect of the construction operation and decommissioning of offshore wind farms has on the foraging behaviour, movements, and distribution of bottlenose dolphins.

Can whistles be used to increase certainty and track individuals? It is well established that including clicks and whistles can increase acoustic classifier performance in continuous recording PAM (Oswald et al., 2003, Rankin et al., 2017). The ECoMMAS array includes both continuous acoustic recorders and echolocation click detectors. Future studies may consider leveraging the whistle data to increase the taxonomic resolution provided by the C-POD classification system (Chapter 2), decreasing the uncertainty associated with the system. Similarly, it may be possible to track individual bottlenose dolphins based on signature whistles. The SM data collected in this study represents an ideal test case for this hypothesis.

What is the habitat use and distribution of the other species recorded by in the ECoMMAS study? This study did not consider the distribution or temporal trends in dolphins producing ‘frequency banded’ click trains nor harbour porpoise. Both groups are understudied in comparison to bottlenose dolphins. C-PODs are designed specifically for detecting high-frequency narrow-bandwidth echolocation click trains such as those from harbour porpoise. The ECoMMAS array represents the first opportunity to investigate porpoise distribution along the Scottish coast. Similarly, very little is known about the white-beaked and Risso’s dolphins that are occasionally spotted off the Grampian coast. Results from these data suggested a high likelihood of detecting one or both of these species off Stonehaven and Latheron. Thus, future photo-id surveys for these species may consider targeting these areas.

6.6. Conclusions

Bottlenose dolphins are, arguably, the best studied of all cetaceans and the Scottish East Coast population has been continuously monitored for last three decades (Hammond and Thompson, 1991). Yet much is unknown about this northernmost population of bottlenose dolphins. Bottlenose dolphins are flexible in their habitat use and behaviour which makes establishing effective long-term conservation measures a challenge (Wilson et al., 2004, Cheney et al., 2014). Passive acoustic monitoring has proved to be a cost effective method of monitoring animals in multiple habitats and can provide insights into animal behaviour and habitat use (Van Parijs et al., 2009). However, as with any survey methodology, care must be taken when interpreting the results. Of particular concern to passive acoustic studies is species misclassification and detection probability. This thesis contributed to both research areas by producing a categorisation system capable of increasing the taxonomic resolution of C-PODs as well as investigating how global (e.g. storms) and site-specific transmission loss could influence habitat models.

Previous visual surveys of this population have focused on high-use areas along the east coast of Scotland, primarily the inner Moray Firth and the St Andrews Bay/Tay area, but also waters off Aberdeen and Montrose. Conversely, the ECoMMAS almost exclusively monitored habitat outwith these high-use areas. Results from the ECoMMAS array largely supported the findings of visual surveys that suggested the east coast of Scotland bottlenose dolphins rely primarily on shallow water, coastal habitats, and target particular locations for foraging. Because habitat use may change over time, ongoing monitoring efforts are needed to ensure that the management measures in place to conserve the population continue to be effective.

The findings of this research were ultimately limited by the black-box nature of the C-POD instrument and KERNO classification system. While these instruments have served the field well, their continued use in fundamental research will become increasingly difficult to justify unless the manufacturer is more forthcoming with his algorithms. Competing continuous recorders are approaching similar price points for the same duration of acoustic coverage and the field of automatic detection and classification continues to improve. Providing open-source data processing and analysis software is increasingly normal practice and increasingly required by journals for publication. For this reason, as C-PODs are lost or retired, I strongly recommend that they are replaced with continuous recorders of similar prices.

The value of using acoustic instruments for monitoring habitat use by a coastal species comes from placing the instruments in areas that difficult to access, or seldomly occupied. In that regard, the ECoMMAS array represents an important component of ongoing monitoring efforts for this population of animals. However, because the ECoMMAS instruments have low detection probabilities, difficulty in discriminating between dolphin species, and are sparsely located, data from the array alone are not enough to allow researchers to gain a comprehensive understanding of the habitat use by this population of bottlenose dolphins.

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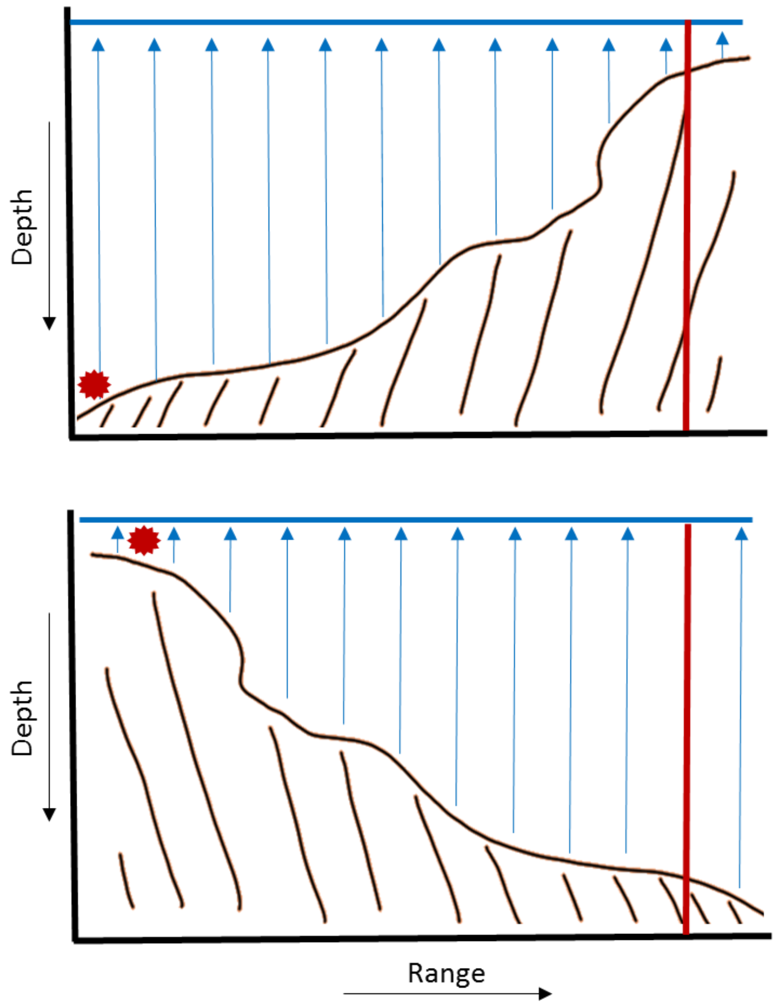
Appendices

Appendix 1- Bellhop Error

The transmission loss calculations relies on the assumption of acoustic reciprocity-where source and receiver locations may be switched. This principle holds even when the systems are subject to damping and friction "as long as they vary as with the first power of velocity" (Rayleigh, 1876). Thus, acoustic reciprocity is commonly incorporated into bioacoustic studies in order to increase model efficiency and reduce computational load (Kusel *et al.*, 2011; Helble *et al.*, 2013). However, the ray-tracing approximation implemented in the Bellhop model is imperfect and rounding errors are introduced as the distance between the source and receiver increases. This produces variance into the detection probability function which should be accounted for. In the following section I measure the changes in the total area monitored by the C-PODs when transmission loss is calculated with and without assuming reciprocity between source (dolphin) and receiver (C-POD) locations.

Here, I ran the transmission loss models described in Chapter 3 twice. In the first round I recorded the maximum detection range as a function of (θ, Equation 3-5) for all deployment locations and all frequencies of interest. The maximum range value was determined by the smaller of 5km or where the water depth was shallower than 2m. In the second run, reverse transmission loss grids were created by placing the source at the maximum detection range estimated using the above procedure and at a depth of 1.5m. Using the same procedures, I calculated the maximum detection range for each deployment site and each angle (θ). The new maximum rages were used to estimate the total area monitored by each sensor assuming noise level of 91 dB, 10dB SNR threshold, and 5000 μs integration. This process was repeated for the four frequencies included in the transmission loss modelling (30, 35, 40, and 45khz). On the second run I again calculated the maximum detection area run only this time transposing bathymetry and source locations.

Appendix 1- Bellhop Error



Appendix 1 Figure 1 Visualisation of the validation procedure. Top panel, simulated acoustic source placed at deployment location and the maximum detectable range (red line) is estimated. To validate the reciprocity assumption the simulated source is then placed at the maximum detectable range and the maximum range towards the original source location is measured (lower panel, red line). Changes in maximum ranges between the two simulations indicate that simplifications in the Bellhop ray-tracing algorithm are not justified.

For each deployment location I calculated the proportional difference between the maximum area monitored using either the standard or reversed bathymetry model. This was also done for four different frequencies within the 41kHz 1/3 octave band: 30, 35,40 and 45kHz. The mean variation between the models was converted to the standard deviation of the area monitored for each site and included in the Bayesian model (See Appendix 3 Simulation 2)

Appendix 1- Bellhop Error

Appendix 1 Table 1 Proportional difference between areas monitored assuming acoustic reciprocity principle (source at receiver/C-POD location) and testing the validity (Sources placed at maximum received distance)

	Proportional Differences in Total Area Monitored				
Deployment Location	30 kHz	35 kHz	40kHz	45khz	Mean
Arb_10*	0.04	0.03	0.02	0.01	0.03
Arb_15	0.00	0.00	0.00	0.01	0.00
Arb_05	0.04	0.04	0.05	0.06	0.04
Cro_10	0.01	0.02	0.02	0.03	0.02
Cro_15*	0.01	0.03	0.02	0.01	0.03
Cro_05	0.01	0.03	0.07	0.06	0.03
Cru_10	0.04	0.03	0.02	0.02	0.03
Cru_15	0.01	0.01	0.00	0.01	0.01
Cru_05*	0.00	0.01	0.01	0.02	0.01
Fra_10	0.07	0.03	0.02	0.01	0.03
Fra_15	0.06	0.06	0.06	0.05	0.06
Fra_05*	0.12	0.15	0.15	0.17	0.15
Hel_10	0.04	0.03	0.04	0.04	0.03
Hel_15*	0.01	0.00	0.01	0.00	0.00
Hel_05	0.00	0.00	0.01	0.01	0.00
Lat_10	0.03	0.05	0.03	0.04	0.05
Lat_15	0.00	0.00	0.00	0.00	0.00
Lat_05*	0.01	0.02	0.03	0.02	0.02
SpB_10*	0.04	0.04	0.02	0.01	0.04
SpB_15	0.04	0.02	0.01	0.01	0.02
SpB_05	0.01	0.01	0.00	0.02	0.01
Stb_10	0.15	0.17	0.17	0.18	0.17
Stb_15	0.00	0.01	0.00	0.00	0.01
Stb_05*	0.10	0.14	0.16	0.18	0.14
FiN_10*	0.01	0.00	0.00	0.01	0.00
FiN_15	0.01	0.00	0.02	0.01	0.00
FiN_05	0.22	0.15	0.11	0.07	0.15
Sto_10	0.00	0.00	0.00	0.00	0.00
Sto_15	0.01	0.01	0.00	0.00	0.01
Sto_05*	0.03	0.05	0.07	0.07	0.05

Appendix 2- Confusion Matrix

This document explores additional analysis undertaken since the publication of the C-POD classifier by Palmer 2017. One of the important critiques of the work was that there were insufficient encounters in 2013 to test out-of-sample performance of the classification system. However, the ECOMMAS array has been each year since and data are now available from 2014 through 2016. Following the verification procedures described in Palmer et al 2017, the 2014 and 2015 C-POD deployments were processed using the classifier and verified manually using the adjacent SM2M recordings.

The results of this work are represented in the confusion matrix (Appendix 2 Table 1) where rows represent the number of validated observations and columns represent number of classifications of each type. For example, in 2014 and 2015 there were a total of 71 validated broadband encounters detected by the C-PODs. Of those 56 were correctly classified as broadband and 15 were incorrectly classified as frequency banded. Unfortunately, in contrast to the 2013 data which contained a large number of verified frequency banded encounters but few verified broadband encounters, 2014/2015 contained only 6 verified frequency banded encounters. It is therefore difficult to determine exactly categorisation preforms on out-of-sample/validation encounters. In lieu of larger sample sizes, I combined classifier performance across all three years representing both in sample (2013) and out of sample (2014 and 2015) performance (Appendix 2 Table 2).

Appendix 2 Table 1 Confusion matrix for out-of-sample categorisation performance (2014 and 2015)

	GAM/Likelihood Categorization (Out of Sample)	
Verified Category	Broadband	Frequency Banded
Broadband	56	15
Frequency Banded	2	4

Appendix 2- Confusion Matrix

From the combined confusion matrix it was possible to determine the likelihood of a correct classification given a classifier output. Similarly, it was possible to calculate the probability that any given classification was broadband.

Appendix 2 Table 2 Confusion matrix for all available acoustic encounters (2013, 2014, 2015) Rows indicate number of verified acoustic encounters of each type and columns represent the classification assigned by the categorisation system described in Chapter 2. The last two rows indicate the probability that a given encounter was broadband or frequency banded given the classification provided by the categorisation |

	GAM/Likelihood Categorization (All)	
Verified Category	Broadband	Frequency Banded
Broadband	66	17
Frequency Banded	2	23
P(Broadband|Classification)	0.79	0.08
P(Frequency Banded|Classification)	0.21	0.82

Appendix 3- JAGS Models

Simulation 1

Simulation 1 assumes perfect detection probability

```
model{
  for(ii in 1:N){
    y[ii] ~ dbern(eff.p[ii])
    # Effective detection probability
    eff.p[ii]<-det.prob*occ.p[ii]
    # True Occupancy
    logit(occ.p[ii]) <- intercept+alpha.occ[Site[ii]]
  }
  ####  priors
  det.prob<-1 # Ignoring detection probability
  alpha.occ[1]<-0
  # Estimate the fixed effect of site location
  for(ii in 2:NSites){
        alpha.occ[ii] ~ dnorm(0, 10^-6)
            }

  intercept ~ dnorm(0, 10^-6)
  #data# N, y, NSites, Site
  # What we want to monitor:
  #monitor# alpha.occ, intercept, dic
  #inits# alpha.occ,intercept
```

Simulation 2

Simulation 2 incorporates fluctuating detection probabilities into the effective detection probability

```
model{
 for(ii in 1:N){
   y[ii] ~ dbern(eff.p[ii])

   # effective detection probability
   eff.p[ii]<-det.prob[ii]*occ.p[ii]

   # Deteciotn Probability
   det.prob_temp[ii] ~ dnorm(MedianArea[ii], 1/sqrt(sd[ii]))
   logit(det.prob[ii]) <- det.prob_temp[ii]

   # True Occupancy
   logit(occ.p[ii]) <- intercept + alpha.occ[Site[ii]]

 }

 ####  priors
 # Set Alpha1 to 0
  alpha.occ[1]<-0
   # Estimate the fixed effect of site location
   for(ii in 2:NSites){
         alpha.occ[ii] ~ dnorm(0, 10^-6)
           }
 intercept ~ dnorm(0, 10^-6)
```

```
  #data# N, y, NSites, Site, MedianArea, sd
  # What we want to monitor:
  #monitor# alpha.occ, intercept, dic
  #inits# alpha.occ, intercept


}
```

Appendix 4- Modelling Covariates and Results

Appendix 4 Table 1 Spatial covariates used in modelling habitat use. Distance to POA and name of POA name are the distance to and the name of the nearest known or hypothesised point of aggregation.

Unit Location	Latitude (decimal deg)	Longitude (decimal deg)	Distance to POA (m)	POA Name	Distance to Shore (m)	Slope (radians)	Depth (m)
Lat_05	58.27	-3.32	67174.11	Spey	343.71	0.03	-22.72
Lat_10	58.23	-3.21	61784.30	Spey	6716.45	0.00	-55.70
Lat_15	58.19	-3.14	56750.28	Spey	12820.23	0.00	-62.65
Hel_05	58.05	-3.72	42996.66	Cromarty Firth	1126.94	0.02	-23.06
Hel_10	58.00	-3.61	41081.71	Cromarty Firth	9003.51	0.00	-41.08
Hel_15	57.98	-3.54	41153.82	Cromarty Firth	14292.35	0.00	-49.15
Cro_05	57.68	-3.99	2303.34	Cromarty Firth	352.28	0.02	-9.28
Cro_10	57.69	-3.88	6495.62	Cromarty Firth	3218.44	0.00	-23.56
Cro_15	57.71	-3.81	10758.56	Cromarty Firth	6031.93	0.00	-16.13
SpB_05	57.69	-3.06	2597.30	Spey	2327.72	0.00	-9.79
SpB_10	57.74	-3.04	7990.26	Spey	7939.74	0.00	-22.46
SpB_15	57.79	-3.06	12258.46	Spey	12609.51	0.00	-36.00
Fra_05	57.71	-2.13	57758.17	Spey	1951.28	0.01	-37.15
Fra_10	57.77	-2.14	57950.65	Spey	8378.79	0.02	-102.98
Fra_15	57.85	-2.09	62913.85	Spey	16663.97	0.00	-85.00
Cru_05	57.38	-1.83	29669.71	Dee	1397.01	0.01	-22.00
Cru_10	57.38	-1.74	32621.90	Dee	5606.67	0.00	-68.88
Cru_15	57.38	-1.62	37142.66	Dee	11863.60	0.00	-68.04
Sto_05	56.95	-2.18	23127.84	Dee	529.00	0.03	-28.42
Sto_10	56.96	-2.11	20895.44	Dee	3503.34	0.00	-46.95
Sto_15	56.98	-2.02	18406.83	Dee	7371.00	0.00	-56.57
Abr_05	56.55	-2.48	16900.30	Esk	2475.08	0.01	-33.10
Abr_10	56.50	-2.38	23140.20	Esk	11158.14	0.00	-48.50
Abr_15	56.46	-2.30	28704.00	Esk	17855.55	0.00	-50.41
FiN_05	56.27	-2.57	24037.39	Tay Firth	704.20	0.01	-16.47
FiN_10	56.26	-2.50	27325.62	Tay Firth	5162.44	0.00	-42.70
FiN_15	56.29	-2.43	27528.97	Tay Firth	9485.96	0.00	-46.84
Stb_05	55.93	-2.18	22024.89	Tweed	1307.58	0.03	-32.88
Stb_10	55.96	-2.16	24862.57	Tweed	5187.84	0.00	-63.74
Stb_15	56.03	-2.08	30538.02	Tweed	13959.77	0.00	-63.58

Appendix 4 Table 2 Correlation scores of spatial covariates and variance inflation factor (VIF) scores for the GLM of the four spatial variables

	Slope	Distance to Shore	Distance to POA	Depth	VIF score
Slope	1.00				1.81
Distance to Shore	-0.58	1.00			2.36
Distance to POA	0.19	0.23	1.00		1.65
Depth	0.23	-0.62	-0.55	1.00	2.17

Appendix 4 Table 3 Model covariates for each deployment group GEE model

	Deployment Group									
Model Terms	Lat	Hel	Cro	SpB	Fra	Cru	Sto	Abr	StA	Stb
Intercept	-13.93	-5.95	-5.55	-5.49	-2.97	-2.80	-1.55	-1.25	-1.10	-0.94
ShoreDist10	6.71	-1.24	-	-0.80	0.78	-	-19.80	-	-1.40	-1.88
ShoreDist15	-	-0.34	-2.89	-1.48	1.01	-2.18	-14.19	-1.54	-3.94	-4.28
Year2014	2.20	0.65	2.03	-	-0.35	1.69	-0.66	-0.64	0.12	-0.86
Year2015	3.86	0.73	1.55	0.47	0.71	-0.23	-0.16	-0.80	0.42	0.15
JulianDay	-	0.01	-	0.01	0.00	-	-	0.00	-	-
Julian Day Knot 1	6.94	-	4.56	-	-	-7.29	-0.11	-	1.06	0.95
Julian Day Knot 2	9.28	-	-3.75	-	-	4.34	-2.24	-	1.37	-2.14
Julian Day Knot 3	7.05	-	4.60	-	-	-0.66	0.22	-	1.21	-1.38
Julian Day Knot 4	10.15	-	-6.05	-	-	-0.47	-0.82	-	0.88	-1.68
ShoreDist10: JulianDay Knot 1	-7.29	-	-	-	-	-	28.44	-	-	-1.52
ShoreDist10: JulianDay Knot 2	-31.68	-	-	-	-	-	1.34	-	-	5.08
ShoreDist10: JulianDay Knot 3	1.14	-	-	-	-	-	21.52	-	-	-5.24
ShoreDist10: JulianDay Knot 4	-16.11	-	-	-	-	-	20.99	-	-	3.78
ShoreDist15: JulianDay Knot 1	-	-	-0.58	-	-	-	15.58	-	-	-2.06
ShoreDist15: JulianDay Knot 2	-	-	5.04	-	-	-	11.16	-	-	12.56
ShoreDist15: JulianDay Knot 3	-	-	1.55	-	-	-	12.79	-	-	-2.54
ShoreDist15: JulianDay Knot 4	-	-	10.02	-	-	-	14.78	-	-	4.68

Appendix 5- Model Sensitivity Analysis

In Chapter 4 I created two model families. The first set of models looked at temporal trends in detections. That analysis would be sensitive to asynchronous variation in ambient noise levels but would be less sensitive to the local bathymetry. As such, and given the lackluster model fit with the existing covariates, incorporating the observation process was unlikely to change the interpretation.

The second model aimed to capture both spatial and temporal variation in acoustic occupancy. The spatial components of this model could be affected by the results of Chapter 3. Initially, a Bernoulli GAMM was chosen as to account for autocorrelation in the data (detections yesterday increase the likelihood of detections today) as well as non-linear interactions between covariates such as depth and distance to the nearest point of aggregation. Incorporating detection probability into this model was not possible because the GLM portion accepts only offsets (additive) not weights (multiplicative) which are more appropriate in this case. This meant that I could not compare the models presented in the thesis chapter to the same models with covariates accounting for relative detection probability.

Thus, to estimate whether variation in site-specific detection probability was likely to have influenced the interpretation of acoustic occupancy, I again added binomial models to the analysis. Detections and survey effort (monitored days) were binned across the entire survey and the scaled median area monitored was used to calculate model weights (Table 1). For the twenty sites that did not have noise level measurements, I used median noise levels from the nearest SM2M to estimate the median area monitored for all 30 deployment locations. I then compared the original Bernoulli model to the binomial models with and without weights to determine whether there were any consequential differences in predictions for the spatial covariates. For this analysis, the scaled area monitored was calculated by first calculating the median area monitored at each of the 30 deployment sites (*medianArea*). For each deployment location (j), the scaled area monitored was calculated as the negative median area monitored at the site (j) minus the mean of median area monitored for all sites divided by the standard deviation (*sd)* of the median area monitored for all sites (Equation 1).

$$ScaledArea(j) = -\frac{medianArea(j) - mean(medianArea)}{sd(medianArea)} \qquad \text{Equation 1}$$

Table 2- Modelling variables for the binomial occupancy model. Scaled Area Monitored is the transformed median area monitored by each C-POD relative to the mean area monitored at all C-POD deployment locations. Number of detections is the total number of days with at least one broadband acoustic encounter, and recording effort is the total number of days monitored by C-PODs at each location. The remaining columns are the spatial covariates included in the original GAMM.

Deployment Location	Number of Detections	Scaled Area Monitored	Recording Effort (d)	Distance to Point of Aggregation (m)	Distance to Shore (m)	Depth (m)	Point of Aggregation Name
Lat_05	1	-1.42194	388	67174.11	348.3342	22.72	Spey
Lat_10	3	0.747323	316	61784.3	6726.511	55.7	Spey
Lat_15	1	0.815956	314	56750.28	12832.87	62.65	Spey
Hel_05	14	-0.73243	404	42996.66	1128.979	23.06	Cromarty Firth
Hel_10	1	0.806094	317	41081.71	9019.115	41.08	Cromarty Firth
Hel_15	0	0.856988	412	41153.82	14312.38	49.15	Cromarty Firth
Cro_05	234	-2.16619	287	2303.339	348.1128	9.28	Cromarty Firth
Cro_10	47	0.528196	191	6495.624	3228.515	23.56	Cromarty Firth
Cro_15	8	0.40755	386	10758.56	6049.193	16.13	Cromarty Firth
SpB_05	32	-1.50757	328	2597.296	2326.304	9.79	Spey
SpB_10	0	0.360979	187	7990.257	7943.911	22.46	Spey
SpB_15	5	0.37342	305	12258.46	12624.89	36	Spey
Fra_05	25	-1.66052	365	57758.17	1943.69	37.15	Spey
Fra_10	1	-0.33662	207	57950.65	8381.02	102.98	Spey
Fra_15	13	0.247357	308	62913.85	16671.61	85	Spey
Cru_05	4	0.431141	304	29669.71	1407.862	22	Dee
Cru_10	4	0.41528	105	32621.9	5617.515	68.88	Dee
Cru_15	12	0.49049	255	37142.66	11872.56	68.04	Dee
Sto_05	61	-1.63868	303	23127.84	539.7511	28.42	Dee
Sto_10	12	0.828057	285	20895.44	3520.705	46.95	Dee
Sto_15	23	0.782991	326	18406.83	7390.412	56.57	Dee
Abr_05	18	0.462499	264	16900.3	2482.573	33.1	Esk

Abr_10	5	0.820151	379	23140.2	11184.97	48.5	Esk
Abr_15	12	0.81311	367	28704	17891.69	50.41	Esk
FiN_05	17	-1.28857	370	24037.39	713.8489	16.47	Tay Firth
FiN_10	2	0.719804	272	27325.62	5172.812	42.7	Tay Firth
FiN_15	2	0.877347	287	27528.97	9517.364	46.84	Tay Firth
Stb_05	8	-1.91303	306	22024.89	1313.59	32.88	Tweed
Stb_10	6	0.222643	401	24862.57	5195.129	63.74	Tweed
Stb_15	4	0.658167	242	30538.02	13969.05	63.58	Tweed

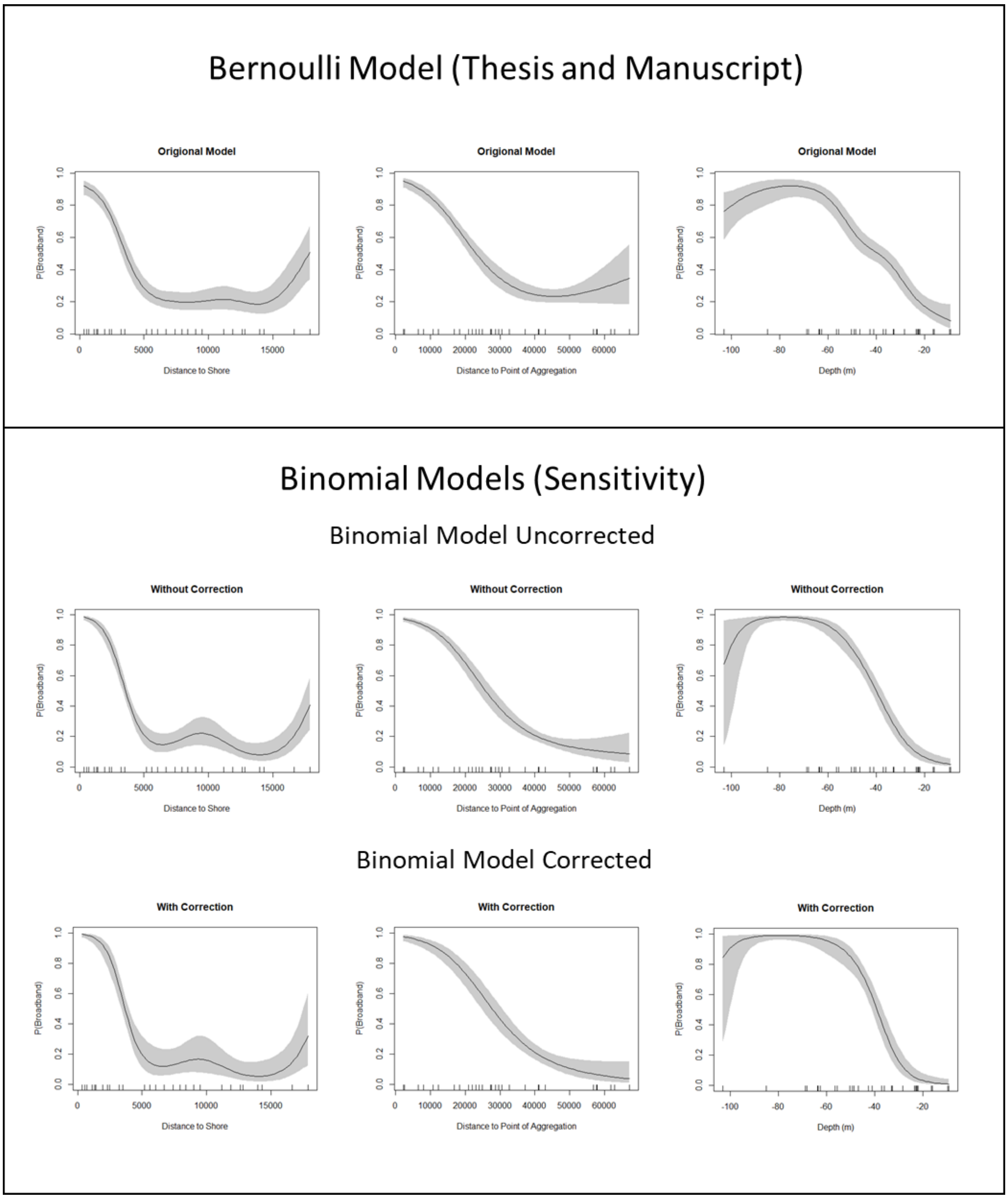


Figure 1 Comparison of model predictions for the Bernouli model (blue) and binomial models (orange). Uncorrected binomial model includes spatial covariates only, corrected binomial model includes spatial covariates and weight variable model weight (Table 2).

Figure 1 shows the results of the original GAMM compared to the GAMs with and without model weights accounting for the relative area monitored. In all three models, there was very little difference between predictions of acoustic occupancy as a function of distance to shore and distance to the nearest point of aggregation. With depth, there was some difference between the binomial and the Bernoulli model response, but little difference between the binomial models with and without weights. All models showed increasing likelihood of detecting animals with increasing depth. However, the binomial models suggest greater variation in deeper water than did the Bernoulli model.

Overall, differences between all three model predictions were small. For all instances, the probability of detecting a broadband echolocation click increased with decreasing distance to shore, point of aggregation and increasing depth. Thus, the interpretation and subsequent recommendations of the thesis and manuscript remains constant, regardless of which model is used.

Investigating the impacts of site-specific detection probability is a crucial aspect of acoustic modelling. While the results presented here were robust to the habitats covered by the C-PODs, I do not expect this to be the case in other locations. Specifically, areas in the SAC where large number of dolphins are present may show greater variability in model response depending on whether or not detection probability is included.

Appendix 5- Model Sensitivity Analysis

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