INFLUENCE OF NATURAL AND ANTHROPOGENIC PROCESSES ON THE SPATIO-TEMPORAL OCCURRENCE OF BOTTLENOSE DOLPHINS

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THESIS CONTENTS

AUTHOR'S DECLARATION

I declare that the work presented in this thesis is a record of work undertaken by me, or principally by myself in collaboration with others, and that it is of my own composition. No part of the recorded work has been accepted in any previous application for a degree. All quotations have been distinguished by quotation marks and the sources of information specifically acknowledged. Chapter 2 was published in a peer-reviewed journal and therefore includes contributions from co-authors.

Oihane Fernández

ABSTRACT

Animal spatio-temporal occurrence is the result of the cumulative effect of natural and anthropogenic processes. For protected species, understanding the drivers of their occurrence is key because it enables decision-makers to implement appropriate conservation and mitigation measures. This thesis aimed to investigate the effects of environmental cycles, prey fields, predator-prey interactions and offshore developments on the occurrence of bottlenose dolphins in the Moray Firth (Scotland). Passive acoustic monitoring collected from 2010 to 2016 highlighted that seasonal, tidal and diel cycles had site-specific effects on bottlenose dolphin occurrence. Analyses detected a previously unreported interaction between seasonal and diel cycles at two sites, where the occurrence was diurnal in summer and nocturnal in autumn. To determine the drivers of these patterns in occurrence I described, for the first time, the prey fields at two dolphin foraging hotspots throughout a year using newly developed small-scale acoustic surveys with a portable scientific echosounder. Data from 23 surveys during 2018 revealed seasonal, tidal and diel patterns of fish abundance, schooling behaviour and species composition that could explain these cyclic patterns of dolphin occurrence. I further investigated dolphin-prey interactions by extracting two foraging vocalizations, echolocation buzzes and bray calls, from acoustic recorders deployed in 2018. The presence of buzzes or brays led to longer dolphin encounters, confirming that area-restricted search behaviour is driven by an increase in encounters with prey. Lastly, a long-term dataset from 2010 to 2019 provided the first evidence of the far-field effects of impulsive noise on bottlenose dolphins. Analyses showed that impulsive noise from a seismic survey and pile-driving activities at two offshore windfarms did not displace dolphins from their coastal distribution but did cause short-term changes in vocalizations. This work provided key information on the spatio-temporal occurrence of dolphins that has implications for mitigating the impact of future developments.

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CHAPTER 1

GENERAL INTRODUCTION

CHAPTER 1: GENERAL INTRODUCTION

Knowing a species' relationship with its environment is essential to understanding its ecology (Austin 2007). Identifying the main processes that affect animal occurrence provides key information for implementing effective management strategies (Ferrier 2002). For instance, this knowledge can be used to model species distribution over large spatial scales (Rogan et al. 2017) and identify areas that require higher levels of protection (Crowder and Norse 2008). It is also useful for predicting animal distribution in new scenarios and to accurately forecast the effect that human activities may have on them (Davies et al. 2006; Rushton et al. 2004). This information is important for marine protected species since they are facing unprecedented human-induced habitat alteration (Avila et al. 2018).

Marine mammals are protected under national and international legislation (CITES 1973; CMS 1979; EU Habitats Directive 1992; MMPA 2016; OSPAR 1992; UNCLOS 1982); therefore, accurate knowledge of their spatio-temporal distribution is required to manage the areas they inhabit. Traditionally, static marine protected areas (MPA) have been designated to protect them (Hoyt 2018), but a sound knowledge of the drivers of their occurrence would enable the implementation of more dynamic approaches (Dunn et al. 2016; Hazen et al. 2018). Dynamic ocean management (DOM) is a flexible management approach that changes in space and time in response to the dynamic nature of the ocean and its users (Hobday et al. 2014). It is particularly useful for mobile species, such as marine mammals, because conservation measures can be implemented when and where they are needed (Howell et al. 2008). However, this approach requires, as a first step, a deep understanding of the drivers of animal occurrence (Scales et al. 2014).

Marine mammal occurrence is the result of the cumulative effect of natural and anthropogenic processes (Tardin et al. 2019). Natural fluctuations of the environment such as changes in temperature, salinity, hour of the day, prey density or predator risk affect their occurrence and behaviour (Benjamins et al. 2016; Hastie et al. 2016; Hodge et al. 2012; Holdman et al. 2019; Romagosa et al. 2019; Saijo et al. 2016; Wang et al. 2015). Human activities are also important drivers of environmental change that have the potential to impact marine mammal populations; such as pollution, habitat removal, food limitation or by-catch (Avila et al. 2018). Therefore, marine mammals will respond to both natural and anthropogenic drivers of environmental change (Castellote et al. 2015; Tardin et al. 2019).

NATURAL PROCESSES: ENVIRONMENTAL CYCLES

Environmental cycles such as seasonal, tidal and diel cycles are important drivers of habitat alteration in marine ecosystems. They cause cyclic changes in salinity, temperature, physical processes (currents, fronts, eddies) and light conditions, that shape the occurrence and behaviour of marine mammals at different spatio-temporal scales. Furthermore, these environmental cycles can have an indirect effect on marine mammals because they can also affect the distribution and abundance of their prey (Friedlaender et al. 2009; Hazen et al. 2011; Saijo et al. 2016).

In temperate marine ecosystems, the seasonal cycle is believed to be the main natural driver of cyclical change. It causes seasonal migrations and changes in animal behaviour that lead to major fluctuations in food availability and predation risk (Antonella et al. 2017; Dudgeon et al. 2013; Hagan and Able 2003; Lambert et al. 2016). Tides also cause dramatic physicochemical changes in coastal environments that lead to small spatial-scale animal movements and changes in behaviour (Benjamins et al. 2015). Furthermore, high energetic tidal areas enhance primary and secondary production which in turn attracts predators due to increased foraging opportunities (Brough et al. 2020; Cox et al. 2013; Zamon 2001). Finally, most marine animals have evolved rhythms in response to the diel cycle, which can also cause daily changes in prey species composition (Baumgartner et al. 2008; Benoit-Bird and Au 2006; Castillo-Rivera et al. 2010; Clark et al. 2003).

The effect of these cycles on marine mammals is highly variable and site-specific. For instance, studying dolphins in several marine protected areas (MPA) in the Mediterranean sea, Castellote et al. (2015) found different seasonal and diel patterns in each of the areas studied. The effect of tides is also highly variable. Benjamins et al. (2016) found that porpoises spent most of the time in low-energy environments but moved to high-energetic channels during the flood and ebb tide. Marubini et al. (2009) showed that porpoises preferred areas with high current speeds during high tide.

Research has shown that the dynamic nature of the environment needs to be considered when investigating the spatio-temporal occurrence of marine mammals (Cox et al. 2018a; Gilles et al. 2016; Williamson et al. 2017). Therefore, site-specific studies are needed to identify important spatial and temporal features in the distribution of these animals that may require higher levels of protection.

NATURAL PROCESSES: PREDATOR-PREY RELATIONSHIPS

Distribution and abundance of prey is one of the main natural processes that drives the distribution of a species (Begon et al. 2009). Theory predicts that predators should seek areas where prey abundance is higher in order to increase their fitness (Pyke 1984). However, in the marine environment this theory has proven challenging to test because most predator-prey interactions occur out of sight.

Acoustic fish surveys have become a well-established and useful technique to obtain information on the distribution and abundance of pelagic fish (Simmonds and Maclennan 2006). An increasing number of studies have used this technique to describe prey fields and understand marine mammal occurrence (Benoit-Bird et al. 2009; Eierman and Connor 2014; Hazen et al. 2011; Lawrence et al. 2016; Sveegaard et al. 2012b). However, relationships between marine mammals and prey distribution are not always detected (Lambert et al. 2019). For instance, Embling and Fernandez (2005) found that dolphin and prey distribution matched in some areas but not in others. Similarly Certain et al. (2011) found links between the occurrence of marine mammals and their prey only during some years. In the marine environment, prey is mobile, unpredictable and patchily distributed. Therefore, choosing the right spatio-temporal scale is key to assessing the links between marine predators and their prey (Hunsicker et al. 2011). However, due to the high costs and logistics of hiring research vessels, obtaining prey information at the spatio-temporal scale required to understand predator occurrence is often unfeasible. Furthermore, large research vessels are not suitable for navigating shallow coastal areas. New portable scientific echosounders give the opportunity to design cost-effective acoustic surveys because they can be mounted on smaller, more affordable boats while providing accurate and precise acoustic data (Demer et al. 2017; Lavery et al. 2017). As such, they can be used to perform small-scale surveys, in shallow coastal areas and collect the information on prey required to better understand predator occurrence.

Highly vocal animals such as cetaceans provide a unique opportunity to study predator-prey relationships because they produce specific vocalizations when feeding (Tyack and Clark 2000). Passive acoustic monitoring devices that record cetacean calls can be used to infer encounters with prey. For example, cetacean foraging behaviour has been inferred from echolocation buzzes (Brough et al. 2020; Nuuttila et al. 2017a; Pirotta et al. 2014b) and from other types of vocalizations such as brays (Janik 2000; King and Janik 2015). Thus, passive acoustic techniques enable researchers to assess the foraging behaviour of cetaceans and better understand the drivers of their occurrence.

ANTHROPOGENIC PROCESSES

Human activities can modify animal distribution directly through habitat destruction or degradation, or indirectly, by causing behavioural avoidance similar to the response to predation risk (Frid and Dill 2002). They introduce a variety of anthropogenic stressors to the marine environment, including underwater noise, climate change, habitat modification, pollution and resource overexploitation (Halpern et al. 2015).

Historically, overkilling was the major anthropogenic threat to marine mammal populations, but nowadays, habitat degradation and loss have become more evident threats (Harwood 2001). Overfishing is one source of habitat degradation that can adversely affect marine mammals (Demaster et al. 2001). It can cause prey depletion and the consequent decline of predators via bottom-up interactions (Bearzi et al. 2006). Climate change can also affect marine mammals both directly, through habitat loss, and indirectly, by modifying prey distribution and abundance (Laidre et al. 2008; Simmonds and Isaac 2007). Finally, human activities such as coastal construction, dredging and dumping are further potential drivers of marine habitat loss that can displace marine mammals (Todd et al. 2015; Van Lavieren et al. 2011).

Noise generated by anthropogenic activities is considered an important environmental stressor in the marine environment because hearing is the main distance sense for many aquatic animals (Francis and Barber 2013; Hawkins et al. 2017). In line with this, many studies have been developed in recent years to investigate the responses of aquatic life to anthropogenic noise (Booth 2016; Erbe et al. 2018). The effects of impulsive noise produced by pile driving, oil and gas exploration and sonar activities have received much attention due to the high levels of energy they introduce to the marine environment (Shannon et al. 2016). For mammals, impulsive noise is more hazardous than non-impulsive noise, due to its higher potential to physically damage their auditory systems (Henderson et al. 1991; Southall et al. 2019c). Therefore, there has been a proliferation of studies on the potential impacts of impulsive noise on them in recent decades (Gordon et al. 2003). However, this field is currently developing and still has many knowledge gaps, due to the challenges of collecting data on animal responses in the wild (Van Beest et al. 2018; Wisniewska et al. 2018). For instance, although responses to noise are species-specific, data on some species such as bottlenose dolphins are sparse and often limited to laboratory experiments (Branstetter et al. 2018; Finneran et al. 2015; Graham et al. 2017). Furthermore, most studies to date have focused on the near-field effects of acute noise, but the potential far-field effects remain poorly understood (Blackwell et al. 2015; Risch et al. 2012). Noise propagates very efficiently through the ocean, travelling long distances from the noise source, so it has the potential to affect a great number of animals (Tyack and Thomas 2019). Obtaining information on the far-field effect of impulsive noise in the wild is thus required to assess the consequences of human activities at sea.

COMMON BOTTLENOSE DOLPHINS

The common bottlenose dolphin (*Tursiops truncatus*; Montagu, 1821), hereafter bottlenose dolphin, is probably the most studied and well-known cetacean species (Würsig et al. 2017). They are found worldwide, from the tropical to temperate zones (Figure 1.1). Distinct populations inhabit a broad range of habitats in both deep oceanic (Klatsky et al. 2007) and shallow coastal areas, including bays and estuaries (Read et al. 2003). There are two ecotypes, offshore and coastal bottlenose dolphins (Wells and Scott 2009), with genetic, morphological and physiological differences as well as distinct habitat and dietary preferences (Costa et al. 2016; Díaz-Gamboa et al. 2018; Fruet et al. 2017; Oudejans et al. 2015).

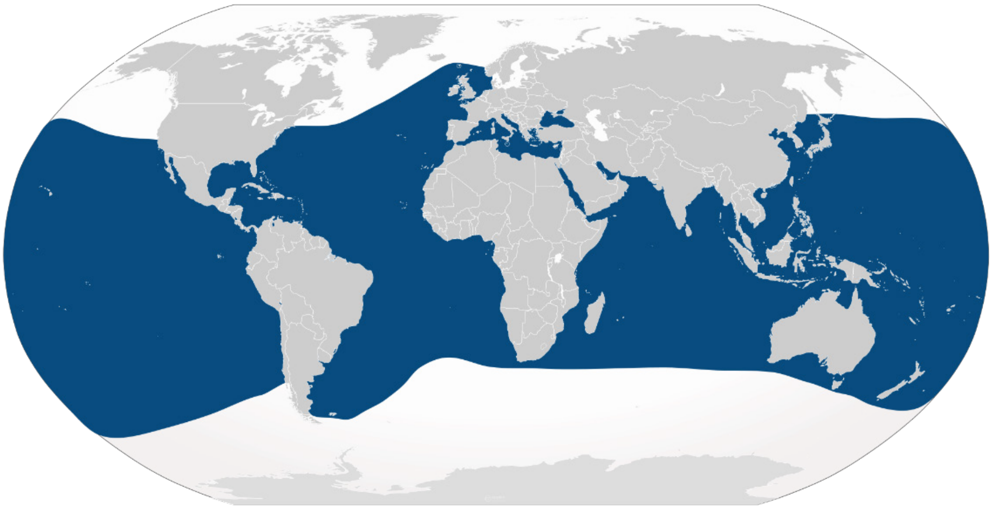

Figure 1.1: Worldwide distribution of the common bottlenose dolphin (Tursiops truncatus; navy shaded area). Source IUCN CC BY-SA 3.0.

They exhibit a wide variety of movements and site-fidelity, including year-round home ranges with little movement, seasonal migrations, occasional long-distance movements, periodic residency and nomadic behaviour with little residency (Currey et al. 2007; Gnone et al. 2011; Robinson et al. 2012; Wilson et al. 1997). Long-distance movements and range shifts of coastal bottlenose dolphins have been observed in response to environmental changes (Sprogis et al. 2018; Würsig et al. 2002). Bottlenose dolphins modify their behaviour and occurrence following both diel and tidal cycles and these patterns are site-specific (Allen et al. 2001; Benjamins et al. 2015; Berrow et al. 1996; Mendes et al. 2002; Nuuttila et al. 2017b).

They are selective opportunistic feeders that forage on a variety of prey, such as fish, squid and crustaceans, depending on the local habitat (Wells and Scott 2009). Individual, temporal and spatial variability in their diet has been observed due to differences in prey abundance (Eierman and Connor 2014; Pate and McFee 2012), ontogenetic requirements (Blanco et al. 2001), demographic groups (Secchi et al. 2016) and social factors (Kovacs et al. 2017). They have developed a wide range of foraging tactics both within and between distinct populations. Specialized foraging techniques can be performed by solitary animals, in cooperation with other conspecifics or even with other species of animals, including humans (see Wells 2019 for a review).

Bottlenose dolphins produce three main categories of sounds: echolocation clicks, whistles and burst-pulse sounds (Popper 1980). They use these vocalisations to communicate, forage and navigate (Herzing 2015; Nowacek 2005). Dolphin echolocation involves the production of broad-band pulses called clicks with peak frequencies between 40 and 130 kHz (Au 1993) that are emitted in trains. Dolphins can modify the amplitude, frequency and rate of the clicks and, like bats, they produce buzzes prior to prey interception by increasing their click rate dramatically (Wisniewska et al. 2014). Whistles are frequency and amplitude modulated tonal calls, with frequency ranges from 1 to 40 kHz (Hiley et al. 2016), used in communication and foraging (Janik and

Sayigh 2013; King and Janik 2015). Burst pulses are groups of click trains with specific patterns and a clear beginning and end point that are processed together as one unit (Herzing 2000; Tyack and Clark 2000). There are many burst pulse subtypes described in the literature and they have been linked to different social and feeding behaviours (Jones et al. 2019).

STUDY POPULATION

The bottlenose dolphin population of the east coast of Scotland is the only resident population in the North Sea (Wilson et al. 1997). Their main distribution includes the Moray Firth and St Andrews Bay, with notable movements of individuals between them (Figure 1.2; Arso Civil et al. 2019; Cheney et al. 2013). In response to the European Union Habitats Directive (92/43/EEC), the Moray Firth SAC was designated in 2005 to protect the core area of their distribution. The latest estimate of the population size is 209 individuals (95 % highest posterior density interval 189-230; Arso Civil et al. 2019) and the population is considered to be increasing (Cheney et al. 2018). The proportion of dolphins that uses the SAC has declined in recent years, thought to be due to the overall increase in the population size (Cheney et al. 2012) and a range expansion (Wilson et al. 2004). However the inner Moray Firth is still intensively used, with > 50 % of the population visiting the SAC in any one year (Cheney et al. 2014).

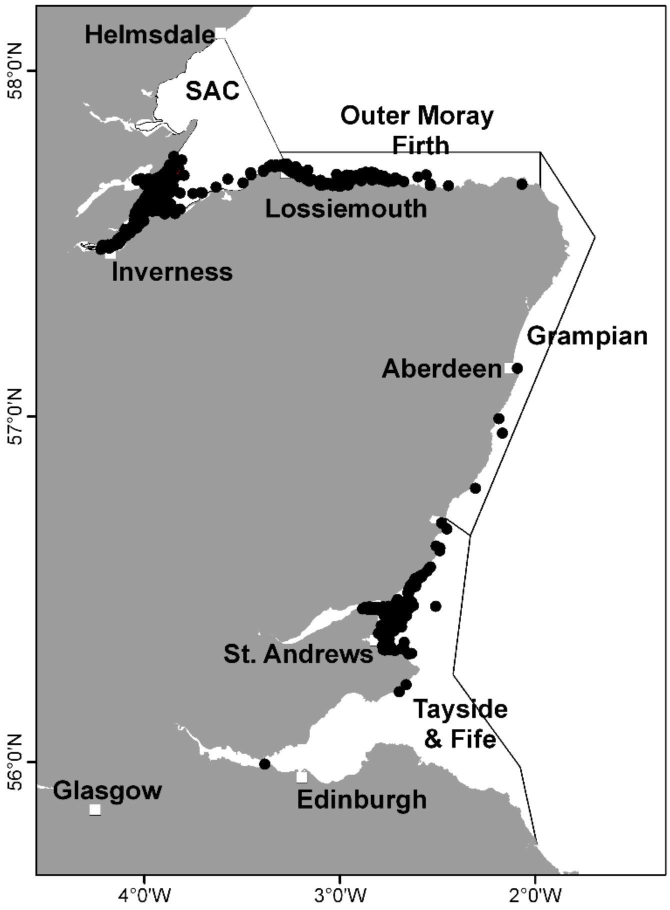

Figure 1.2: Locations of bottlenose dolphin encounters (black dots) observed during photo-ID surveys conducted from 1990 to 2010 (Cheney et al. 2014).

Dolphins occur in the inner Moray Firth year-round, but their abundance is lower during winter months (Wilson et al. 1997). Stratified movement of individuals has been detected, with the most frequently observed animals found further inshore in summer than the animals detected only occasionally in the area (Wilson et al. 1997).

Previous studies have found site-specific patterns of occurrence and foraging behaviour linked to tides in areas with rapid tidal flows. In the Kessock channel, dolphin occurrence increased during the flood tide (Mendes et al.

2002). In Chanonry, another channel < 10 km apart, Bailey et al. (2013) found inter-annual variability in the preferred tidal stage, with animals targeting low or flood tide in different years. The effect of the diel cycle on the occurrence of these dolphins over the complete 24 hours has not been yet described.

Information about the diet of this population of dolphins is very limited. Analysing the stomach contents of 10 animals, Santos et al. (2001) identified several species of fish (including Gadidae, Salmonidae and Cottidae), cephalopods and, to a lesser extent, crustaceans and polychaetes. Seasonal differences in prey taxa were found; however, conclusions about their diet were constrained by the study's small sample size, the bias towards sick animals inherent to the sampling method and the unknown origin of the stranded animals. Other studies based on behavioural observations from land detected frequent predation events of migrating salmonids (*Salmo salar* and *Salmo trutta*) by these dolphins (Hastie et al. 2004; Janik 2000).

Although orcas (*Orcinus orca*) occur occasionally within the distribution range of this bottlenose dolphin population (Robinson et al. 2017), there is no evidence of predation (Wilson et al. 2004).

STUDY AREA

The Moray Firth is a triangular embayment on the North East of Scotland with an area of 5,230 km^2 (Adams and Martin 1986). It is generally less than 80 m deep except in the southeast, where a fault system reaches 200 m (Chester and Lawson 1983). Tides are semidiurnal and relatively weak except in the tidal narrows in the inner Moray Firth where flow rates can exceed 0.75 m s^{-1} (Adams and Martin 1986; Mendes et al. 2002).

The main fish species in the area include gadoids, such as cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and whiting (*Merlangus merlangius*), sandeels (*Ammodytes marinus*), and the clupeids, herring (*Clupea harengus*) and sprat (*Sprattus sprattus*). Their relative abundance varies seasonally: gadoids are more abundant in winter; sandeels in summer; and, clupeids in autumn (Greenstreet et al. 1998). Eighteen major rivers, which have historically supported populations of adult Atlantic salmon (*Salmo salar*), flow into the Firth (Williamson 1988), although their abundance has been in long-term decline (Macandrew 2019).

The Moray Firth is a very active area with a high number of anthropogenic activities, such as shipping (Merchant et al. 2014), the oil and gas industry (Thompson et al. 2013a), marine renewables (Bailey et al. 2014), sediment dumping (Marine Scotland 2014), coastal developments (Graham et al. 2017) and ecotourism (Pirotta et al. 2015b) amongst others (Senior et al. 2008). Studies based on visual surveys highlighted the importance of the inner Moray Firth during summer for bottlenose dolphins (Hastie et al. 2003a; Wilson et al. 1997). Therefore, mitigation measures have been focused on summer and some activities, such as spoil dumping, have been encouraged in autumn to minimise their negative effects on dolphins (Marine Marine Scotland 2014).

RESEARCH AIMS AND OBJECTIVES

The overall aim of this study was to gain insights into the effect of natural and anthropogenic factors on bottlenose dolphins in the Moray Firth to better understand their drivers of occurrence in the core area of their distribution.

The effect of environmental cycles on marine mammals is highly variable and site-specific, and their combined effect on the population of dolphins in the inner Moray Firth remained unknown. In Chapter 2, I aim to describe the combined effect of the seasonal, tidal and diel cycles on the occurrence of bottlenose dolphins. Using a long-term passive acoustic monitoring dataset, I investigated the effect of these cycles on their occurrence at three different sampling sites in the core area of their distribution. The objectives were to determine the relative importance that environmental cycles had on the occurrence of dolphins, explore potential interactions between them, investigate whether patterns were consistent in time and space and assess the implications for the conservation and management of this population.

Although foraging is one of the main drivers of predator occurrence, there was no up-to-date information on prey resources in the inner Moray Firth. In Chapter 3, I aim to describe the variation in prey abundance and behaviour at two foraging hotspots to better understand the cyclical patterns of dolphin occurrence observed in Chapter 2. We developed a cost-effective method for performing small-scale (< 10 km) fish acoustic surveys from a RIB and collected data on potential prey throughout one year. The objectives were to describe the seasonal, tidal and diel variation in fish abundance, schooling behaviour and prey species composition, and to explore links with the occurrence of dolphins.

In Chapter 4, I aim to investigate in more detail how foraging behaviour modulates dolphin occurrence. Using passive acoustic devices, I assessed whether the variation in prey encounters influenced area-restricted search behaviour in dolphins. I used foraging vocalisations as proxies for predator-prey encounters and tested whether dolphin encounter duration was linked to the detection of those proxies.

Since marine mammals use sound to communicate, navigate and forage, there is concern about the potential adverse effects of anthropogenic noise. In Chapter 5, I aim to investigate whether the far-field impulsive noise generated by offshore developments resulted in displacement of dolphins from coastal waters. I used a long-term passive acoustic monitoring dataset and investigated the effect of three offshore developments: a 2D seismic survey and the installation of foundations for two windfarms. The objectives were to assess the variation in dolphin detections in areas exposed to different levels of noise from these developments.

Finally, in Chapter 6, I summarise the main findings from Chapters 2 to 5, consider the wider implications of the results and provide suggestions for future research.

CHAPTER 2

FINE SCALE SPATIAL VARIABILITY IN THE INFLUENCE OF ENVIRONMENTAL CYCLES ON THE OCCURRENCE OF DOLPHINS AT COASTAL SITES

CHAPTER 2: FINE SCALE SPATIAL VARIABILITY IN THE INFLUENCE OF ENVIRONMENTAL CYCLES ON THE OCCURRENCE OF DOLPHINS AT COASTAL SITES[1]

ABSTRACT

Environmental cycles often influence the presence of animals, creating patterns at different temporal scales, which may mean that their effects overlap and/or interact. Interactions between diel and seasonal cycles have been reported to influence fish behaviour but little is known about such interactions in marine top predators. Here, I studied the combined effect of seasonal, tidal and diel cycles on the occurrence of bottlenose dolphins (*Tursiops truncatus*) at three coastal sites within a Marine Protected Area in Scotland. The analyses were based on echolocation detections from passive acoustic devices (CPODs) deployed between 2010 and 2016. I described patterns of dolphins' occurrence using circular statistics and then used generalised additive mixed models to explore the relative importance of each cycle and any interactions between them. I found site-specific cyclical patterns of presence that remained constant across years. There was a highly significant interaction

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between seasonal and diel cycles at two sites around deep channels, where occurrence was diurnal in summer but became nocturnal in autumn. This study demonstrates the highly plastic behaviour of bottlenose dolphins and shows a previously unreported behaviour that has management implications for this and other marine protected areas.

INTRODUCTION

Environmental cycles create rhythmic patterns that modify the abiotic conditions of ecosystems, and biological rhythms that match these cycles are widespread (Hut et al. 2013). In mid and high latitudes, seasonal changes in temperature and day length lead to major changes in the abundance and distribution of many species across trophic levels (Coma et al. 2000; Lambert et al. 2016; Maes et al. 1998). The daily light-dark cycle results in diel activity patterns which may be diurnal, nocturnal or crepuscular. The trade-off between foraging success and predation risk is considered the most critical influence on diel behaviour (Becker and Suthers 2014; Owen-Smith et al. 2010). In coastal environments, the tidal cycle also causes dramatic physiochemical changes that result in periodic movements of many species. The main driver of tidal migrations in coastal areas is the avoidance of unsuitable conditions, but tidal currents are also used for transport, feeding, predator avoidance and reproduction (Gibson 2003).

Since these environmental cycles can create patterns at different temporal scales, their effects may interact. The interaction most often studied in marine organisms is the one between seasonal and diel cycles. In winter, animals must choose between adapting to local, often harsh, conditions and migrating to more favourable habitats. For animals with a flexible diel behaviour, one strategy they can follow to adapt to local conditions is to modify their diel activity patterns. Examples of such seasonal changes in diel activity patterns can be found across many taxa (see Hut et al. 2012 for a review). The diel behaviour of fish is known to be very plastic (Reebs 2002). For example, salmonids and sea bass may be diurnal in summer but nocturnal in winter (Fraser et al. 1995), while other species such as cod exhibit more complicated seasonal diel shifts (Righton et al. 2000).

The influence of environmental cycles on top predators is not only direct, they are also affected by the rhythmicity of their prey. Therefore, their cyclic patterns of behaviour often match those of their prey (Cozzi et al. 2012; Monterroso et al. 2013; Penteriani et al. 2013). In the marine environment, predators have developed highly flexible behaviour in response to the dynamic environment in which they live (Montevecchi et al. 2009). As an example of that flexibility, marine mammals exhibit a full spectrum of responses to environmental cycles. Studies of the effect of seasonal, tidal and diel cycles on their behaviour have produced highly variable results (de Boer et al. 2014; Nuuttila et al. 2017b). However, whilst interactions between different environmental cycles have been described for some of their prey, there is a lack of information about more complex responses in marine mammals.

Understanding behavioural variation due to natural cycles is not only key to our knowledge of animal behaviour in the wild but, for protected species, it is also key to their conservation management. In recent years, many Marine

Protected Areas (MPA) have been designated to protect marine mammals (Hoyt 2012). More dynamic approaches with flexible spatial and temporal boundaries that protect the core areas have been recommended for mobile species (Hyrenbach et al. 2000). Habitat modelling has been used as a method to identify key areas for target species (Cañadas et al. 2005) and many authors have highlighted the importance of including dynamic environmental variables because static physical features on their own do not capture the complexity of the habitat selection process (de Boer et al. 2014; Jones et al. 2014). For instance, without including temporal variables in the models, it was found that a sandy bank was an important site for harbour porpoises in the Moray Firth (Brookes et al. 2013). However, once the diel cycle was included, it was found that adjacent muddy areas were also important habitats for them during the night (Williamson et al. 2017). The management of potential stressors relies on accurate information about the distribution of focal species; consequently, the inclusion of both spatial and temporal variables becomes necessary to implement efficient protection measures for highly mobile species.

The present study aims to explore the combined effects of seasonal, tidal and diel cycles on the presence of bottlenose dolphins in an MPA in the Moray Firth, NE Scotland. Previous studies in this area have identified relationships with some of these cyclic variables, and there is evidence that there may be fine-scale spatial variation in these patterns (Bailey et al. 2013; Hastie et al. 2003b) that could have implications for managing this protected population. Early boat-based visual surveys demonstrated that individuals from this population remained in the area all year round, with a higher number of encounters during summer (Wilson et al. 1997). However, whilst subsequent studies in one tidal channel detected relationships with both time of day and tidal cycles (Bailey et al. 2010a; Bailey et al. 2013), no tidal or diurnal effects were identified at a second nearby channel with similar physical characteristics (Hastie et al. 2003b). Determining whether this represents real spatial variation in the importance of these different environmental variables was not possible because these studies were undertaken at different times, using slightly different methodologies. Furthermore, these earlier assessments of diel patterns were constrained to analyses of daylight observations, preventing an analysis of the full diel cycle and the interactions between these different cycles.

Long-term passive acoustic studies provide unique opportunities for exploring variation in the occurrence and behaviour of cetaceans across whole seasonal and diel cycles that would be impossible to sample representatively using visual methods (Dede et al. 2013; Verfuß et al. 2007). Here we use a 6 year time series of passive acoustic recordings to compare temporal patterns of dolphin occurrence at three sites within the Moray Firth, that include the two potentially contrasting sites studied by Hastie et al. (2003b) and Bailey et al. (2013). Our specific objectives were to (1) determine the relative importance that environmental cycles had on the presence of dolphins, (2) explore possible interactions between them, (3) assess whether patterns were consistent in time and space, and (4) explore the potential implications of the results for the conservation and management of this population of dolphins. Our main hypothesis was that environmental cycles would have site specific effects on the presence of bottlenose dolphins. Drawing upon the findings of the previous studies at individual sites, we predicted that our results would exhibit spatial variation in temporal patterns of occurrence, and that the relative importance of different environmental cycles would differ between sites. To do so, we used echolocation detections (CPOD; Chelonia Ltd.) coupled with circular statistics (Rayleigh test; Fisher 1993) and generalized additive mixed models (GAMM; Wood 2006) to assess fine-scale temporal patterns of dolphin presence. I studied three discrete sites (Sutors, Chanonry and Spey Bay) which have been identified as important sites for this population in several studies (Culloch and Robinson 2008; Hastie et al. 2003a; Pirotta et al. 2014b) and which differ in their physiographic characteristics such as tidal regime and bathymetry.

METHODS

Study Area

The Moray Firth is a large coastal embayment on the East Coast of Scotland, which contains a Special Area of Conservation (SAC) that was designated for its resident population of bottlenose dolphins under the EU Habitats Directive (92/43/EEC; Cheney et al. 2014).

Three discrete sites were studied: Sutors (57° 41.41' N, 03° 59.18' W), Chanonry (57° 35.14' N, 04° 5.85' W) and Spey Bay (57° 41.32' N, 03° 5.14' W) (Figure 2.1 and details in Figure 2.2). All three sites are in the core area of this bottlenose dolphin population's distribution, where the presence of other species of dolphins is rare (Thompson et al. 2015). Sutors and Chanonry are constricted channels in the inner part of the firth that are subject to strong tidal currents and are used intensively by this population (Hastie et al. 2003a; Wilson et al. 1997). Spey Bay, located on the southern coast of the outer Moray Firth, has also been identified as an important area for this population (Culloch and Robinson 2008). It is a shallow coastal area with a low energy tidal regime (Reid and McManus 1987).

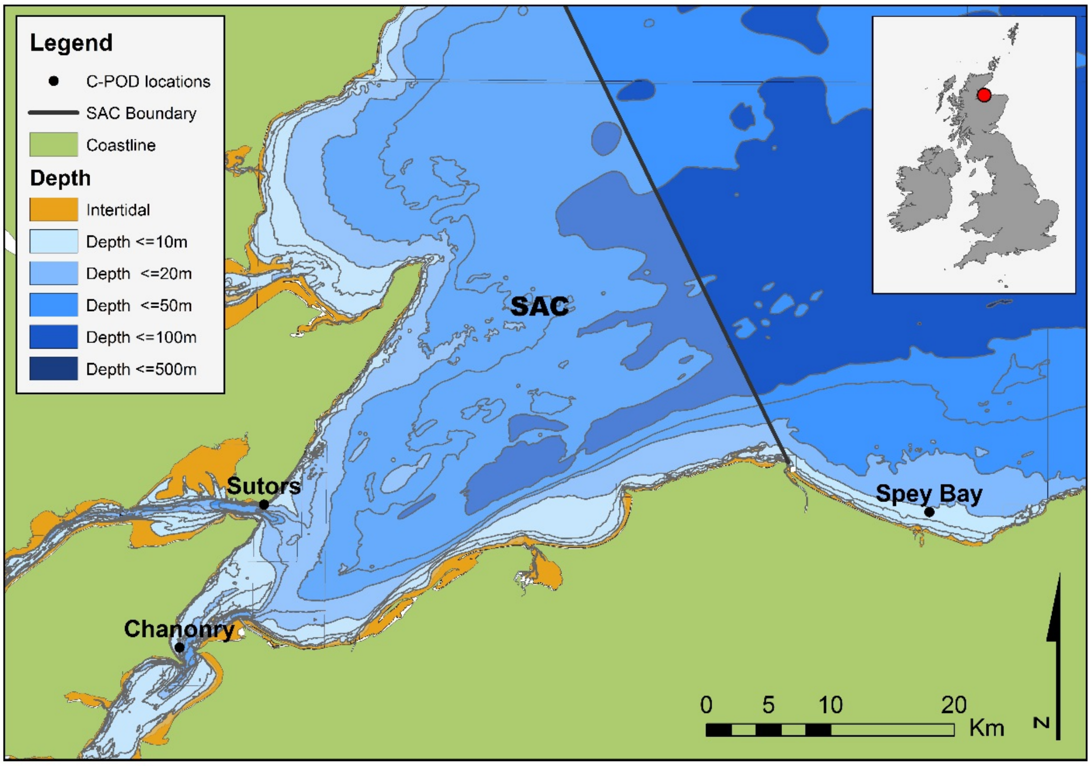


Figure 2.1: Map of the Moray Firth and the three sites studied: Sutors, Chanonry and Spey Bay. Detailed bathymetry and aerial photographs of the three sites are provided in Figure 2.2.

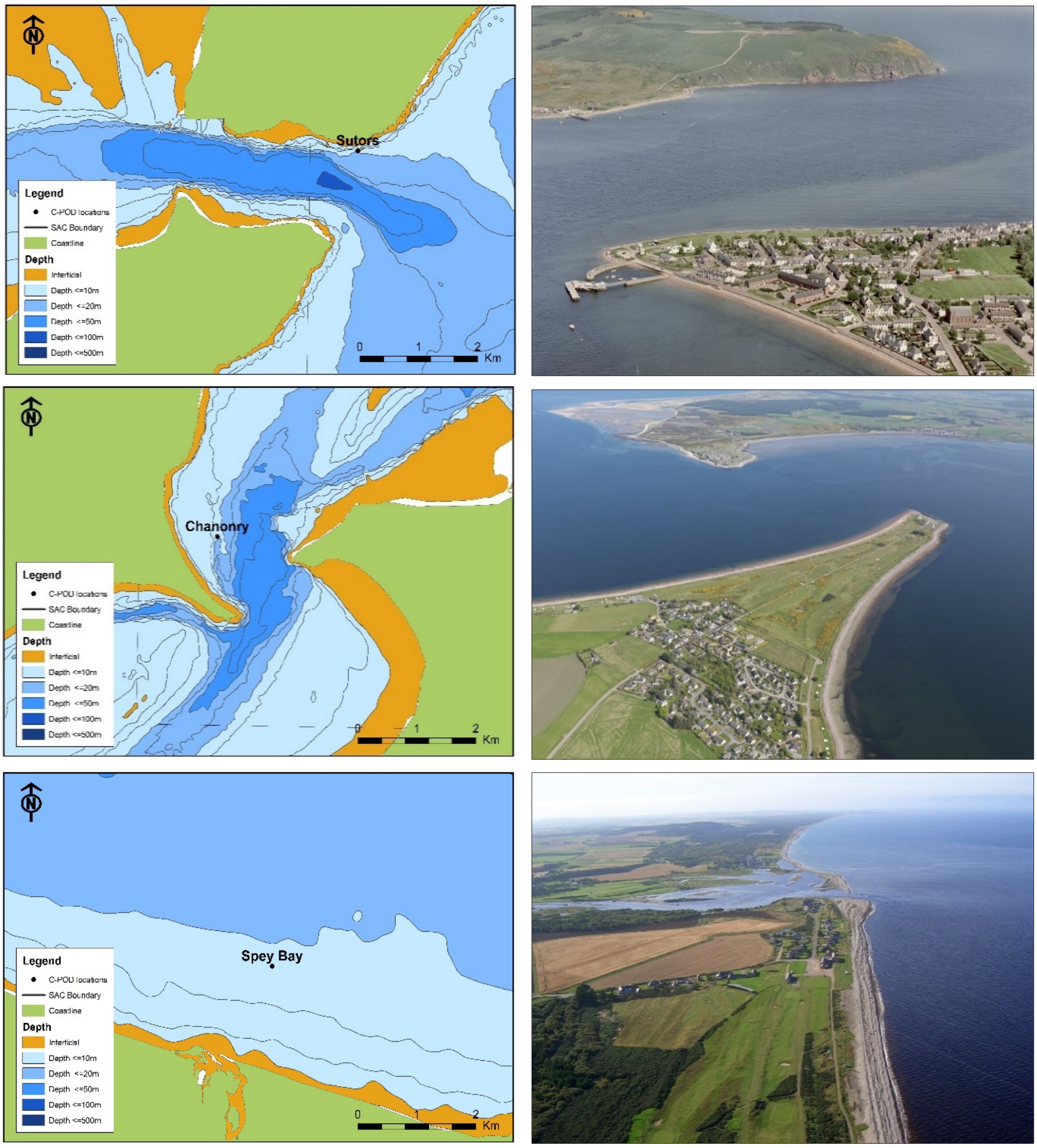


Figure 2.2: Detailed bathymetry and aerial pictures of the study sites. Top right and middle right images retrieved from CANMORE National Record of the Historic Environment - © Crown Copyright: Historic Environment Scotland. Bottom right image belongs to the University of Aberdeen.

Acoustic data collection

CPODs (Chelonia Ltd, UK) were used to provide data on temporal variation in the occurrence of dolphins at the three study sites. CPODs are acoustic data loggers, specifically designed to detect marine mammal echolocation clicks that have been widely used in recent years (Benjamins et al. 2016; Nuuttila et al. 2013a; Pirotta et al. 2014b). CPODs record data continuously on the time of occurrence of tonal clicks, as well as many other variables, within the frequency range 20 kHz to 160 kHz for up to 4 months. In this study, data were used from deployments made between January 2010 and March 2016. CPODs were moored in shallow waters (< 13m) using moorings with either a subsurface acoustic release or a surface buoy as described by Bailey et al. (2010a). A target frequency of 50 kHz and a reference frequency of 70 kHz were used. The *scan limit* (maximum number of clicks recorded in each scan) was set to a maximum of 4096 clicks per minute to conserve memory.

CPOD validation

CPOD performance within our study system was evaluated by comparing their detection rate to the one obtained through analyses of broadband recordings from SM2M devices (Wildlife Acoustics, MA, USA) using PAMGuard software (Gillespie et al. 2009). This comparison used existing datasets generated in a previous study (Pirotta et al. 2015b), where the authors designed a conservative dolphin click classifier and a Gaussian mixture-model to identify buzzes (click trains associated with attempted prey captures). Here, those click and buzz detections were compared to data recorded by CPODs that had been deployed on the same mooring as the SM2M recorder between

May and July of 2013. PAMGuard detections were considered to be an indicator of dolphins' presence following the methodology described by Garrod et al. (2018).

Environmental data

High and low tide times were obtained from the United Kingdom Hydrographic Office (*www.gov.uk/ukho*) using reference ports within 12 km of each sampling site (Port of Cromarty: 57° 40' N, 04° 00' W, for Sutors and Chanonry; Port of Lossiemouth: 57° 43' N, 03° 17' W, for Spey Bay). Sunrise and sunset times were calculated for each of the sites using the 'maptools' library (Bivand and Lewin-Koh 2016) in R (R Core Team 2016).

Data analyses

Data from the CPODs were processed using the manufacturer's CPOD software (*www.chelonia.co.uk*). As recommended by the manufacturer, only click trains classified as *High* and *Moderate Quality* were used in this study. The statistical programme R v. 3.3.1 (R Core Team 2016) was used in all subsequent analyses.

Individual click trains were grouped into encounters. Encounters were defined as groups of click trains at least 10 minutes apart (Graham et al. 2017; Philpott et al. 2007). Since the main focus was on studying rhythms, circular statistics were used to describe the effect of each of the environmental cycles. For this, the time of the mid-point of each encounter was transformed into three different cyclical indices derived from its position in each of the cycles (diel, tidal and seasonal). The *diel* variable was obtained by measuring the time difference between the encounter and the previous sunset. Due to the high latitude of the research area and the variability of day length across the year, its values were normalized: 0 and 1 corresponded to sunset whereas sunrise was fixed to 0.5, meaning that the time span between 0 and 0.5 varied as a function of the season (Booth et al. 2013). The *tidal* variable was calculated following the same methodology: 0 and 1 corresponded to high tide and 0.5 to low tide. For the *seasonal* variable the 0 was set at Julian day 1 (Figure 2.3). Rayleigh tests were performed to determine whether encounters were significantly clustered around a mean (Fisher 1993). For diel and tidal cycles, tests were conducted on a monthly basis for each month with ≥ 25 encounters in order to increase the statistical power. For the seasonal cycle, analyses were conducted on a yearly basis. When the null hypotheses were rejected ($P < 0.05$), the mean vector (peak of dolphin presence) and mean resultant length (length of the mean vector, an indicator of the dispersion of the data) were calculated. Analyses were conducted using the R package ‘circular’ (Agostinelli and Lund 2013).

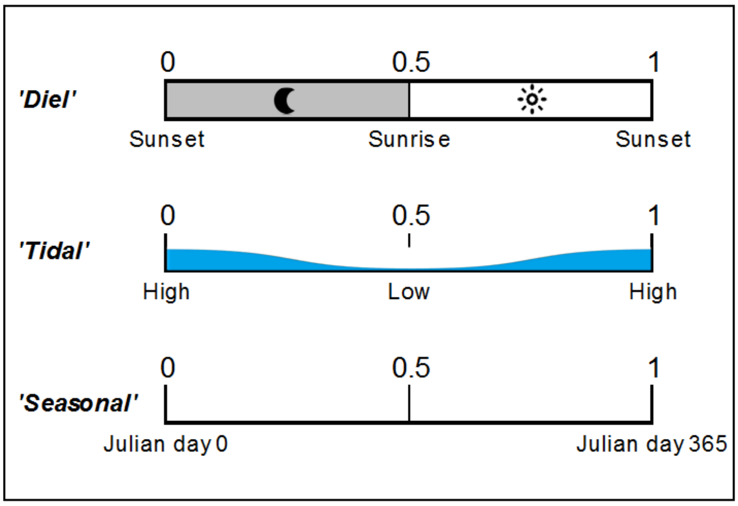


Figure 2.3: Schematic of the assignment of values for the diel, tidal and seasonal variables. All variables ranged from 0 to 1.

Generalized additive mixed models (GAMMs) were then used to explore non-linear effects of the diel, tidal and seasonal cycles on the presence of bottlenose dolphins. Presence/absence of dolphin encounters per hour was set as the response variable. *Diel*, *tidal* and *seasonal* were included as explanatory variables and defined by cyclic cubic regression splines. *Year* was introduced as a factor. All possible interactions were included in the models as tensor products (function '*ti*'), as recommended when the main effects and any lower interactions are also present (Wood 2017). The importance of each term was determined by removing them sequentially from the model (Nuuttila et al. 2017b) and exploring the variation in the Akaike Information Criterion (AIC;(Bolker et al. 2009b). Once the main interactions were determined for each of the sites, full tensor product smooths (function '*t2*' and '*te*') were used in the final models.

The binomial GAMMs above were fitted using the ’gamm4’ library (Wood and Scheipl 2016). Because ‘gamm4’ does not allow accounting for the inherent temporal autocorrelation in the model residuals, the presence of dolphin encounters in the previous hour was included as a fixed effect in the models (Brandt et al. 2016). Finally, the robustness of all models were checked by also using the function ‘gamm’ in the ’mgcv’ library (Wood 2017). This may in some cases be less stable for binomial data but does account for residual autocorrelation. In these models, temporal autocorrelation was assumed to be produced by an autoregressive process of order 1 (corAR1) within each day.

Data from the three sites were modelled separately to assess variability at each location and to avoid unnecessary complexity with site interactions. Multicollinearity between explanatory spline functions was checked using the concurvity function. Autocorrelation plots (ACF) and partial autocorrelation plots (pACF) were used to check the level of autocorrelation in residuals.

RESULTS

Deployments were made almost continuously at all three study sites during the 6-year study period, providing data with only a few gaps due to battery or equipment failure. The maximum number of clicks was reached in a very small proportion (< 0.11%) of minutes, meaning that the CPODs were sampling for dolphin presence > 99.8% of the time in all sites. In total, datasets included more than 23000 encounter-positive hours. The highest number of encounters was recorded in Sutors (n = 15188), followed by Chanonry (n =

8406), with smaller numbers in Spey Bay (n = 4316) (summary in Table 2.1 and details in Table 2.2).

Table 2.1: Summary of acoustic data obtained from 2010 to 2016.

	Sutors	**Chanonry**	**Spey Bay**
Location	57° 41' 25.02'' N	57° 35' 9.36'' N	57° 41' 23.53'' N
	3° 58' 51.30'' W	4° 5' 53.40 W	3° 5' 36.06'' W
Hours recorded	49 028	44 445	47 448
% time max. num. clicks reached	0.104%	0.001%	0.062%
Total number of encounters	15188	8406	4316
Total encounter positive hours	12516	7038	3749

Table 2.2: Total number of encounters per year and month at each site.

	Months												
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	***Tot. Num. Encounters***
Sutors													
2010	69	58	108	352	419	380	348	331	202	360	388	146	*3161*
2011	73	35	84	261	380	300	292	298	81	271	193	228	*2496*
2012	130	50		128	464	377	332	275	161	303	165		*2385*
2013				101	332	335	382	230	172	181	216	135	*2084*
2014	193	75	56	184	403	292	359	255	204	275	271	154	*2721*
2015	59	70	60	165	202	232	294	246	159	217	243	210	*2157*
2016	123	32	22										*177*
Chanonry													
2010	185	170	159	99	179	158	256	219	168	99	34	74	*1800*
2011	24	46	15	1	116	187	151	146			17	43	*746*
2012	11	8	45	103	110	113	213	240	109	32	57	18	*1059*
2013				127	184	224	317	334	226	213	187	125	*1937*
2014	186	94	20	99	218	259	265	184	172	105	20		*1622*
2015			9	86	99	133	141	196	167	136	131	97	*1195*
2016			47										*47*
Spey Bay													
2010	68	6	7	66	110	129	51	36	25	60	63	26	*647*
2011	7	11	42	99	102	146	136	141	98	50	25	22	*879*
2012	5	12	7	48	112	103	82						*369*
2013				46	129	154	105	102	68	26	26	26	*682*
2014	13	15	3	68	158	157	151	110	101	79	48	22	*925*
2015	7	2	14	66	126	198	105	63	47	38	40	108	*814*
2016	22	2	12										*36*

CPOD validation

Using PAMGuard click detections as a baseline, CPODs predicted dolphin presence with high accuracy at both filter settings: High-Moderate (98%) and High quality (100%) whereas their ability to predict dolphin absence was lower, 71% and 66% for High-Moderate and High quality trains respectively (Table 2.3). The false positive rate was very low (0-1%) and the true negative rate was very high (100-98%).

Table 2.3: Results of PAMGuard dolphin click and buzz detection and corresponding true positive (TP), false positive (FP), true negative (TN) and false negative (FN) hours and ratios and positive predictive (PPV) and negative predictive (NPV) values using High and High and Moderate quality trains from CPOD software.

PAMGUARD				**CPOD**						
Detection type	**Total Effort (h)**	**Dolphin Present (h)**	**Dolphin Absent (h)**	**Filter**	**TP (h, TPR)**	**FP (h, FPR)**	**TN (h, TNR)**	**FN (h, FNR)**	**PPV**	**NPV**
Clicks	1215	957	258	Hi	458, 48%	0, 0%	257, 100%	499, 52%	100%	66%
				Hi-Mo	568, 59%	3, 1%	253, 98%	395, 41%	98%	71%
Buzzes	1215	714	501	High	440, 62%	19, 4%	482, 96%	274, 38%	94%	72%
				Hi-Mo	529, 74%	38, 8%	463, 92%	185, 26%	90%	78%

Overall, CPODs produced fewer dolphin detection positive hours than PAMGuard when using either train quality filter setting. Despite this, both PAMGuard and CPODs detected the same diel pattern over the whole deployment (Figure 2.4).

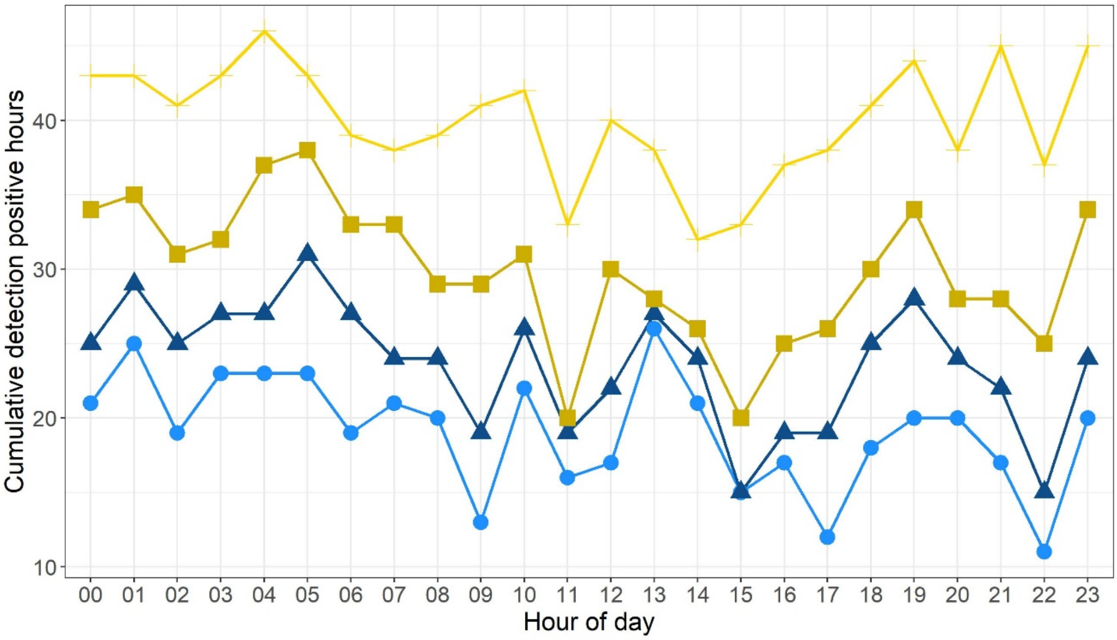


Figure 2.4: Cumulative detection positive hours for both SM2M and CPODs for each hour of the day during the whole deployment. Cross: SM2M click detections; Solid square: SM2M buzz detections; Solid triangle: CPOD detections High-Moderate quality trains; Solid circle: CPOD detections High quality trains.

Effect of each environmental cycle

In Sutors the number of encounters exceeded 25 in most months, allowing the Rayleigh test to be performed for almost the whole period. In Chanonry and Spey Bay, the number of encounters was sometimes fewer than 25 per month, especially in winter, so the Rayleigh test could not be performed in all cases.

The relationship between the diel cycle and the occurrence of dolphins differed between sites (Figure 2.5a). In Sutors and Chanonry, times of encounters were significantly different from a uniform distribution over the diel cycle for most months (Figure 2.6). At these two sites, encounters most often occurred during daytime in summer and during night-time in autumn and early winter (circular mean vector during day and night respectively, Table 2.4). In Spey Bay, fewer months were statistically significant and the Raleigh test provided no evidence for the seasonal variation in diel pattern seen at the other two sites.

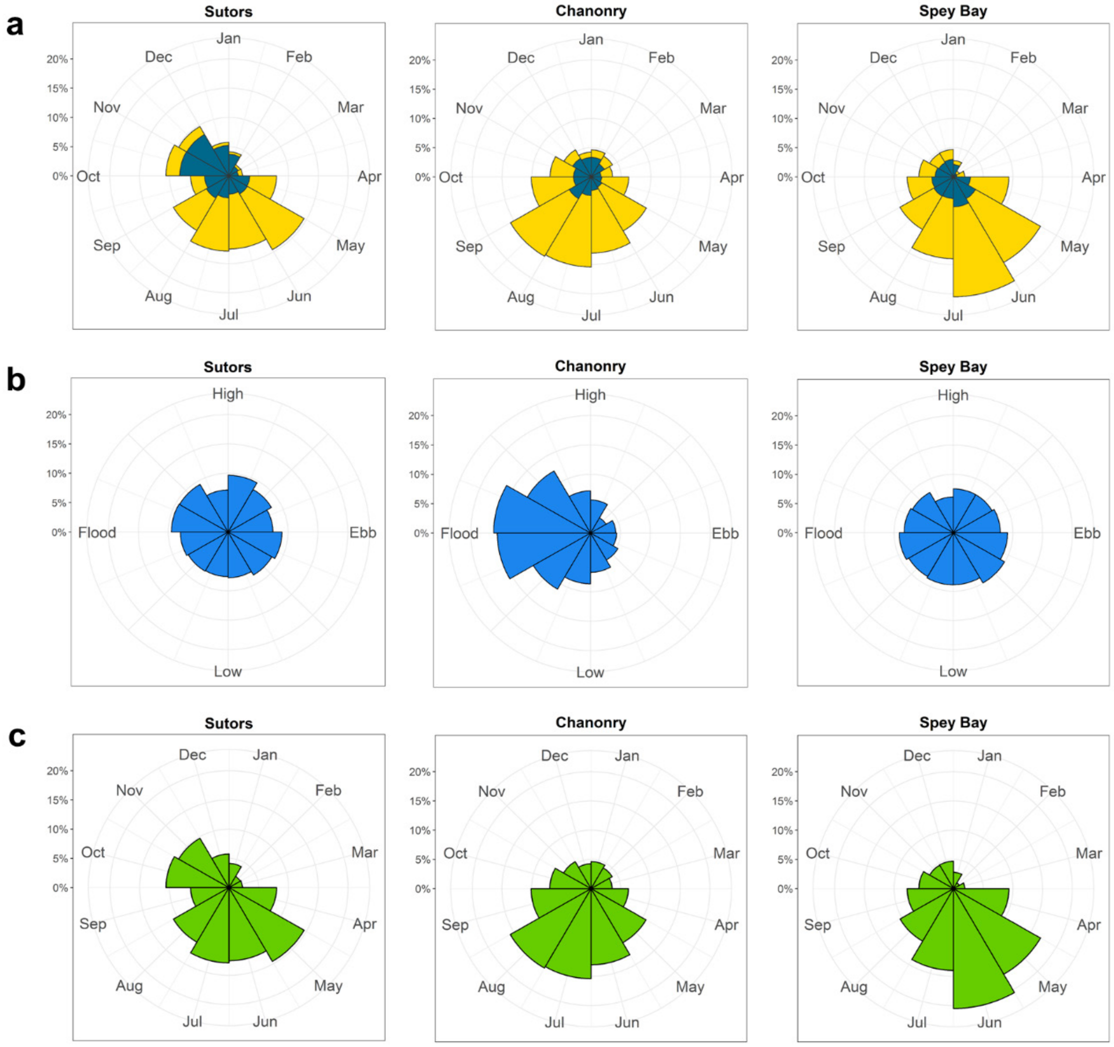
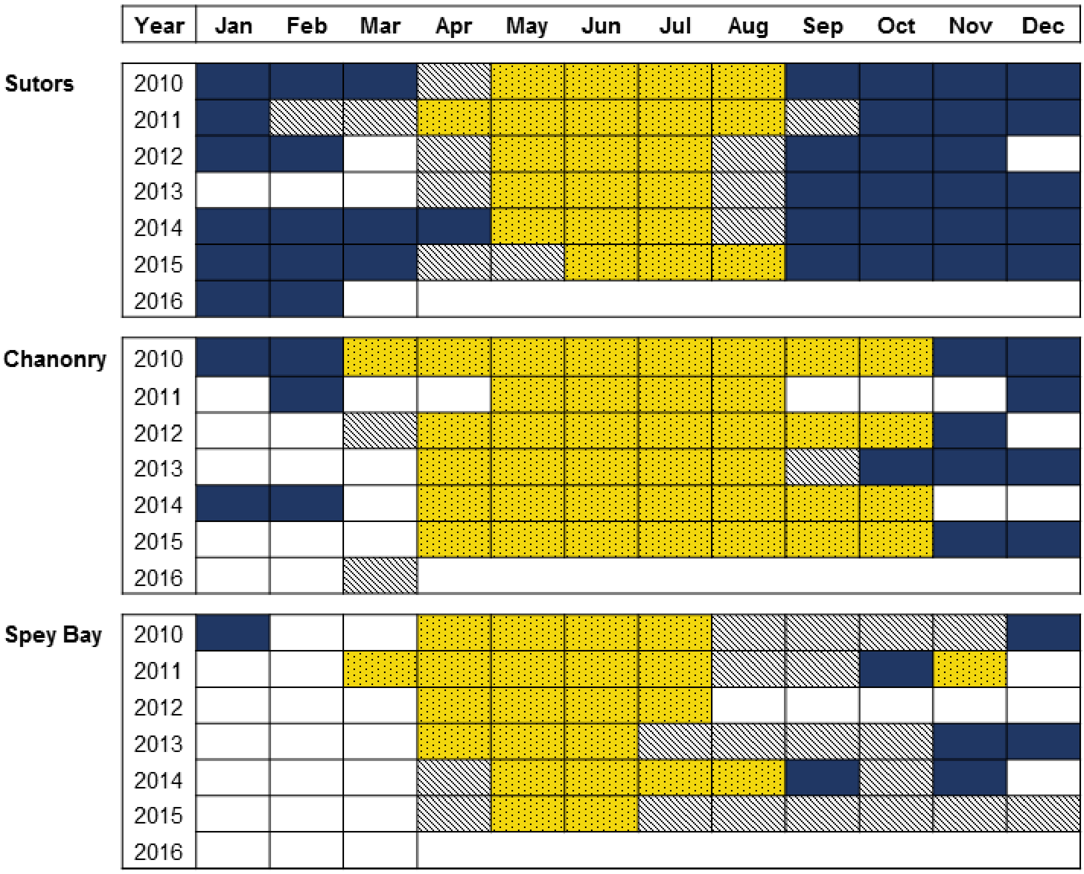


Figure 2.5: Proportion of encounters relative to the a) diel cycle (yellow: encounters during the day; dark blue: encounters during the night), b) tidal cycle and c) seasonal cycle at the three sampling sites for the whole period studied (2010-2016).



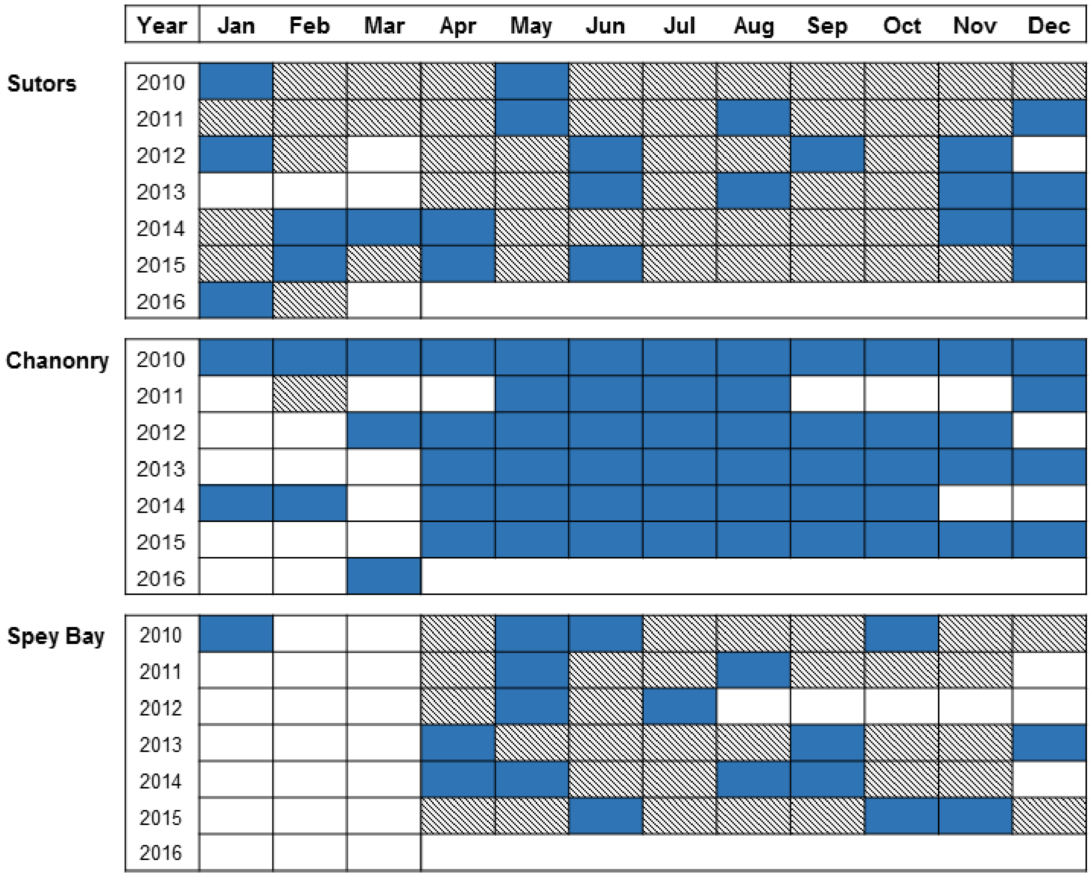
	Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Sutors	2010	🟦	🟦	🟦	▨	🟨	🟨	🟨	🟨	🟦	🟦	🟦	🟦
	2011	🟦	▨	▨	🟨	🟨	🟨	🟨	🟨	▨	🟦	🟦	🟦
	2012	🟦	🟦	⬜	▨	🟨	🟨	🟨	▨	🟦	🟦	🟦	⬜
	2013	⬜	⬜	⬜	▨	🟨	🟨	🟨	▨	🟦	🟦	🟦	🟦
	2014	🟦	🟦	🟦	🟦	🟨	🟨	🟨	▨	🟦	🟦	🟦	🟦
	2015	🟦	🟦	🟦	▨	▨	🟨	🟨	🟨	🟦	🟦	🟦	🟦
	2016	🟦	🟦	⬜									
Chanonry	2010	🟦	🟦	🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟦	🟦
	2011	⬜	🟦	⬜	⬜	🟨	🟨	🟨	🟨	⬜	⬜	⬜	🟦
	2012	⬜	⬜	▨	🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟦	⬜
	2013	⬜	⬜	⬜	🟨	🟨	🟨	🟨	🟨	▨	🟦	🟦	🟦
	2014	🟦	🟦	⬜	🟨	🟨	🟨	🟨	🟨	🟨	🟨	⬜	⬜
	2015	⬜	⬜	⬜	🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟦	🟦
	2016	⬜	⬜	▨									
Spey Bay	2010	🟦	⬜	⬜	🟨	🟨	🟨	🟨	▨	▨	▨	▨	🟦
	2011	⬜	⬜	🟨	🟨	🟨	🟨	🟨	▨	▨	🟦	🟨	⬜
	2012	⬜	⬜	⬜	🟨	🟨	🟨	🟨	⬜	⬜	⬜	⬜	⬜
	2013	⬜	⬜	⬜	🟨	🟨	🟨	▨	▨	▨	▨	🟦	🟦
	2014	⬜	⬜	⬜	▨	🟨	🟨	🟨	🟨	🟦	▨	🟦	⬜
	2015	⬜	⬜	⬜	▨	🟨	🟨	▨	▨	▨	▨	▨	▨
	2016	⬜	⬜	⬜									

Figure 2.6: Months in which significant Rayleigh tests indicated that dolphin encounters were more likely in daytime are shown in yellow, and those in which encounters were more likely at night are shown in dark blue. Those months in which Rayleigh tests were not significant (P > 0.05) are shown with diagonal shading and white cells represent months with fewer than 25 encounters.

Table 2.4: Summary data table for the diel cycle. Bold: direction of the circular mean vector (0: Sunset; 180: Sunrise). In brackets: length of the mean vector which provides an indicator of the strength of the relationship.

	Month											
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Sutors												
2010	**75.7** (0.5)	**57.2** (0.3)	**49.4** (0.3)		**280.3** (0.3)	**268.4** (0.3)	**273.1** (0.3)	**270.5** (0.3)	**78.0** (0.2)	**65.1** (0.4)	**78.0** (0.5)	**79.2** (0.6)
2011	**87.9** (0.4)			**242.9** (0.3)	**256.0** (0.3)	**289.9** (0.3)	**266.0** (0.2)	**302.0** (0.1)		**65.6** (0.4)	**64.7** (0.5)	**70.3** (0.6)
2012	**72.5** (0.6)	**72.3** (0.5)			**259.7** (0.4)	**252.1** (0.3)	**271.2** (0.2)		**64.9** (0.4)	**55.9** (0.5)	**71.4** (0.5)	
2013					**263.4** (0.4)	**263.2** (0.3)	**275.1** (0.2)		**62.4** (0.3)	**55.7** (0.5)	**80.0** (0.5)	**71.5** (0.6)
2014	**74.8** (0.6)	**85.2** (0.6)	**77.1** (0.5)	**91.6** (0.1)	**261.6** (0.3)	**255.6** (0.3)	**240.6** (0.3)		**51.6** (0.2)	**63.2** (0.4)	**62.7** (0.6)	**73.0** (0.6)
2015	**64.5** (0.6)	**93.9** (0.5)	**86.2** (0.3)			**271.5** (0.4)	**278.2** (0.2)	**264.6** (0.1)	**62.9** (0.4)	**76.4** (0.5)	**64.4** (0.4)	**77.3** (0.5)
2016	**68.8** (0.6)	**57.3** (0.7)										
Chanonry												
2010	**112.4** (0.4)	**120.9** (0.3)	**192.0** (0.2)	**287.0** (0.3)	**278.9** (0.6)	**270.0** (0.6)	**258.2** (0.4)	**264.1** (0.3)	**233.5** (0.4)	**231.7** (0.3)	**148.2** (0.4)	**78.5** (0.5)
2011		**113.2** (0.4)			**263.3** (0.4)	**265.6** (0.5)	**269.8** (0.5)	**247.5** (0.6)				**97.1** (0.4)
2012				**266.2** (0.5)	**311.9** (0.4)	**282.7** (0.3)	**254.1** (0.4)	**256.1** (0.4)	**238.9** (0.3)	**222.3** (0.5)	**106.7** (0.5)	
2013				**326.9** (0.2)	**262.5** (0.3)	**287.2** (0.3)	**272.6** (0.4)	**293.9** (0.1)		**154.8** (0.3)	**114.5** (0.3)	**84.5** (0.3)
2014	**89.9** (0.3)	**31.0** (0.2)		**290.6** (0.5)	**268.6** (0.3)	**262.1** (0.3)	**281.7** (0.3)	**228.7** (0.4)	**245.4** (0.4)	**215.4** (0.3)		
2015				**249.5** (0.3)	**266.2** (0.5)	**268.4** (0.6)	**261.6** (0.2)	**248.0** (0.3)	**254.2** (0.4)	**221.6** (0.3)	**146.6** (0.3)	**126.3** (0.4)
2016												
Spey Bay												
2010	**69.6** (0.5)			**305.2** (0.4)	**267.8** (0.2)	**283.0** (0.4)	**227.6** (0.4)					**51.7** (0.4)
2011			**279.8** (0.3)	**303.7** (0.3)	**291.4** (0.3)	**280.2** (0.2)	**263.1** (0.4)			**141.0** (0.3)	**195.2** (0.5)	
2012				**318.6** (0.3)	**327.1** (0.3)	**243.9** (0.4)	**246.0** (0.3)					
2013				**308.6** (0.4)	**273.4** (0.5)	**283.2** (0.2)					**65.6** (0.4)	**90.3** (0.3)
2014					**291.8** (0.3)	**285.4** (0.3)	**264.2** (0.2)	**271.1** (0.3)	**6.4** (0.3)		**79.3** (0.4)	
2015					**300.4** (0.4)	**264.8** (0.3)						
2016												

The effect of the tidal cycle on the occurrence of dolphins also varied between sites. There was a strong relationship between dolphin presence and the tidal cycle at Chanonry (Figure 2.7), where a high proportion of encounters occurred during the flood tide (Figure 2.5b). Although some months showed a relationship with tidal cycle at the other sites (Figure 2.7), occurrence did not peak consistently at any particular stage of the tide (Figure 2.5b and Table 2.5).



	Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Sutors	2010	🟦	▨	▨	▨	🟦	▨	▨	▨	▨	▨	▨	▨
	2011	▨	▨	▨	▨	🟦	▨	▨	🟦	▨	▨	▨	🟦
	2012	🟦	▨	□	▨	▨	🟦	▨	▨	🟦	▨	🟦	□
	2013	□	□	□	▨	▨	🟦	▨	🟦	▨	▨	🟦	🟦
	2014	▨	🟦	🟦	🟦	▨	▨	▨	▨	▨	▨	🟦	🟦
	2015	▨	🟦	▨	🟦	▨	🟦	▨	▨	▨	▨	▨	🟦
	2016	🟦	▨	□									
Chanonry	2010	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦
	2011	□	▨	□	□	🟦	🟦	🟦	🟦	□	□	□	🟦
	2012	□	□	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	□
	2013	□	□	□	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦
	2014	🟦	🟦	□	🟦	🟦	🟦	🟦	🟦	🟦	🟦	□	□
	2015	□	□	□	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦
	2016	□	□	🟦									
Spey Bay	2010	🟦	□	□	▨	🟦	🟦	▨	▨	▨	🟦	▨	▨
	2011	□	□	□	▨	🟦	▨	▨	🟦	▨	▨	▨	□
	2012	□	□	□	▨	🟦	▨	🟦	□	□	□	□	□
	2013	□	□	□	🟦	▨	▨	▨	▨	🟦	▨	▨	🟦
	2014	□	□	□	🟦	🟦	▨	▨	🟦	🟦	▨	▨	□
	2015	□	□	□	▨	▨	🟦	▨	▨	▨	🟦	🟦	▨
	2016	□	□	□									

Figure 2.7: Months in which significant Rayleigh tests indicated that dolphin encounters were related to the tidal cycle, shown in blue. Those months in which Rayleigh tests were not significant (P > 0.05) are shown with diagonal shading and white cells represent months with fewer than 25 encounters.

Table 2.5: Summary data table for the tidal cycle. Bold: direction of the circular mean vector (0: High tide; 180: Low tide). In brackets: R, length of the mean vector which provides an indication of the strength of the relationship.

	Month											
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Sutors												
2010	**81.7** (0.4)				**339.0** (0.1)							
2011					**350.1** (0.1)			**278.2** (0.1)				**12.8** (0.1)
2012	**340.9** (0.2)					**263.7** (0.1)			**13.1** (0.2)		**31.0** (0.2)	
2013						**268.8** (0.1)		**304.3** (0.1)			**36.4** (0.1)	**62.9** (0.2)
2014		**61.9** (0.2)	**7.7** (0.3)	**270.8** (0.2)							**30.2** (0.2)	**30.3** (0.2)
2015		**58.7** (0.2)		**293.5** (0.2)		**37.1** (0.1)						**59.6** (0.1)
2016	**94.4** (0.2)											
Chanonry												
2010	**249.9** (0.3)	**248.4** (0.4)	**263.9** (0.4)	**254.8** (0.5)	**301.1** (0.4)	**263.3** (0.3)	**259.5** (0.3)	**262.8** (0.3)	**262.3** (0.4)	**263.2** (0.5)	**271.0** (0.7)	**274.3** (0.6)
2011					**263.1** (0.4)	**237.8** (0.2)	**254.7** (0.4)	**239.9** (0.4)				**281.9** (0.5)
2012			**261.1** (0.5)	**267.0** (0.5)	**289.1** (0.5)	**246.3** (0.3)	**262.1** (0.4)	**254.4** (0.3)	**263.0** (0.5)	**262.1** (0.4)	**279.3** (0.4)	
2013				**263.5** (0.4)	**245.6** (0.4)	**255.2** (0.4)	**246.8** (0.2)	**248.3** (0.2)	**262.1** (0.3)	**278.2** (0.3)	**292.8** (0.3)	**278.1** (0.4)
2014	**245.5** (0.3)	**250.5** (0.2)		**249.1** (0.2)	**232.9** (0.4)	**254.7** (0.3)	**264.8** (0.4)	**263.6** (0.4)	**259.7** (0.3)	**271.4** (0.4)		
2015				**298.9** (0.5)	**322.2** (0.4)	**285.2** (0.4)	**265.1** (0.5)	**260.5** (0.4)	**280.7** (0.4)	**265.9** (0.3)	**283.1** (0.5)	**285.9** (0.5)
2016			**309.6** (0.3)									
Spey Bay												
2010	**270.1** (0.3)				**122.3** (0.3)	**33.5** (0.2)				**101.9** (0.2)		
2011					**172.9** (0.2)			**163.3** (0.2)				
2012					**164.5** (0.3)		**201.3** (0.2)					
2013				**99.9** (0.3)					**184.7** (0.3)			**252.2** (0.4)
2014				**239.8** (0.3)	**177.0** (0.2)			**3.2** (0.2)	**138.5** (0.2)			
2015						**233.3** (0.2)				**204.7** (0.4)	**207.4** (0.3)	
2016												

Encounters were distributed significantly differently from a uniform distribution over the seasonal cycle in all years at all sites (Rayleigh test: $P < 0.01$) with most encounters occurring during summer months (circular mean vector during summer; Table 2.6). Overall, mean length values (R) were slightly lower in Sutors than in the other two sites. Thus, while the highest proportion of encounters occurred in summer in all sites (Figure 2.5c), seasonality was stronger in Chanonry and Spey Bay. In Sutors, the proportion of encounters remained high in autumn.

Table 2.6: Rayleigh Test results for the seasonal cycle in the three sites between 2010 and 2015. The Mean value shows the month in which the peak of dolphin encounters occurred. R is the length of the mean vector which provides an indication of the strength of the relationship.

	Sutors			**Chanonry**			**Spey Bay**		
	p	**Mean**	**R**	**p**	**Mean**	**R**	**p**	**Mean**	**R**
2010	< 0.0001	July	0.238	< 0.0001	June	0.166	< 0.0001	June	0.227
2011	< 0.0001	July	0.239	< 0.0001	June	0.545	< 0.0001	July	0.486
2012	< 0.0001	July	0.403	< 0.0001	July	0.515	-	-	-
2013	< 0.0001	July	0.486	< 0.0001	Aug	0.458	< 0.0001	July	0.576
2014	< 0.0001	July	0.216	< 0.0001	July	0.351	< 0.0001	July	0.482
2015	< 0.0001	July	0.279	< 0.0001	Aug	0.431	< 0.0001	June	0.370

Interactions between cycles and their relative importance

The relative importance of each of the cycles varied among sites (Table 2.7). Diel and seasonal cycles were statistically significant at all sites. The tidal cycle was significant in Chanonry and Sutors but not in Spey Bay. The only interaction to have an effect on the presence of dolphin encounters was the interaction between diel and seasonal cycles. Based on the change in AIC, the most important covariates were the interaction *diel*seasonal* in Sutors, *tidal* in Chanonry and *seasonal* in Spey Bay.

Table 2.7: Summary results for the GAMM using tensor products (ti) smooths. ΔAIC: variation in the AIC value by removing the covariate. AIC Rank: relative importance of each covariate. Covariates ranked from 1 (highest AIC weight) to 5 (lowest).

Covariate	**Chi-sq**	**P**	**ΔAIC**	**AIC Rank**
Sutors				
Diel	617.17	< *0.0001*	-26.4	5
Tidal	98.88	< *0.0001*	-85.88	3
Seasonal	397.27	< *0.0001*	-361.39	2
*Diel*Seasonal*	461 726.1	< *0.0001*	-658.41	1
Year			-74.37	4
Chanonry				
Diel	327.2	< *0.0001*	-200.89	3
Tidal	1307.3	< *0.0001*	-1333.9	1
Seasonal	368.8	< *0.0001*	-36.15	5
*Diel*Seasonal*	863.1	< *0.0001*	-199.99	4
Year			-292.59	2
Spey Bay				
Diel	187.5	< *0.0001*	-162.95	2
Tidal	-	*NS*	-	-
Seasonal	198.9	< *0.0001*	-175.2	1
*Diel*Seasonal*	39 660.4	< *0.0001*	-37.89	4
Year			-55.1	3

Final GAMM models included *tidal*, the full tensor product *diel*seasonal* and *year* in Sutors and Chanonry. *Tidal* was not retained in Spey Bay. Both GAMM approaches, using temporal correlation corAr1 and gamm4, gave similar results.

Dolphin encounters showed site-specific relationships with each of the temporal cycles and results matched patterns previously observed with circular statistics (Figure 2.8). In Sutors, the diel behaviour was diurnal in summer and nocturnal in autumn (Figure 2.8.1a). At this site, the probability of encounters remained high all day long during summer, with the highest probability during daytime. By the end of the year, around October-November, the situation changed and the probability of encounters was high only during night-time. In Chanonry the diel behaviour was diurnal during summer months with a higher probability of encounters during day-time (Figure 2.8.2a). During the rest of the year the diel pattern was not clear but the probability was slightly higher at night. In Spey Bay a diel pattern was only evident during summer months (Figure 2.8.3a). There the diel behaviour was crepuscular, with a higher probability of encounters around sunrise and sunset.

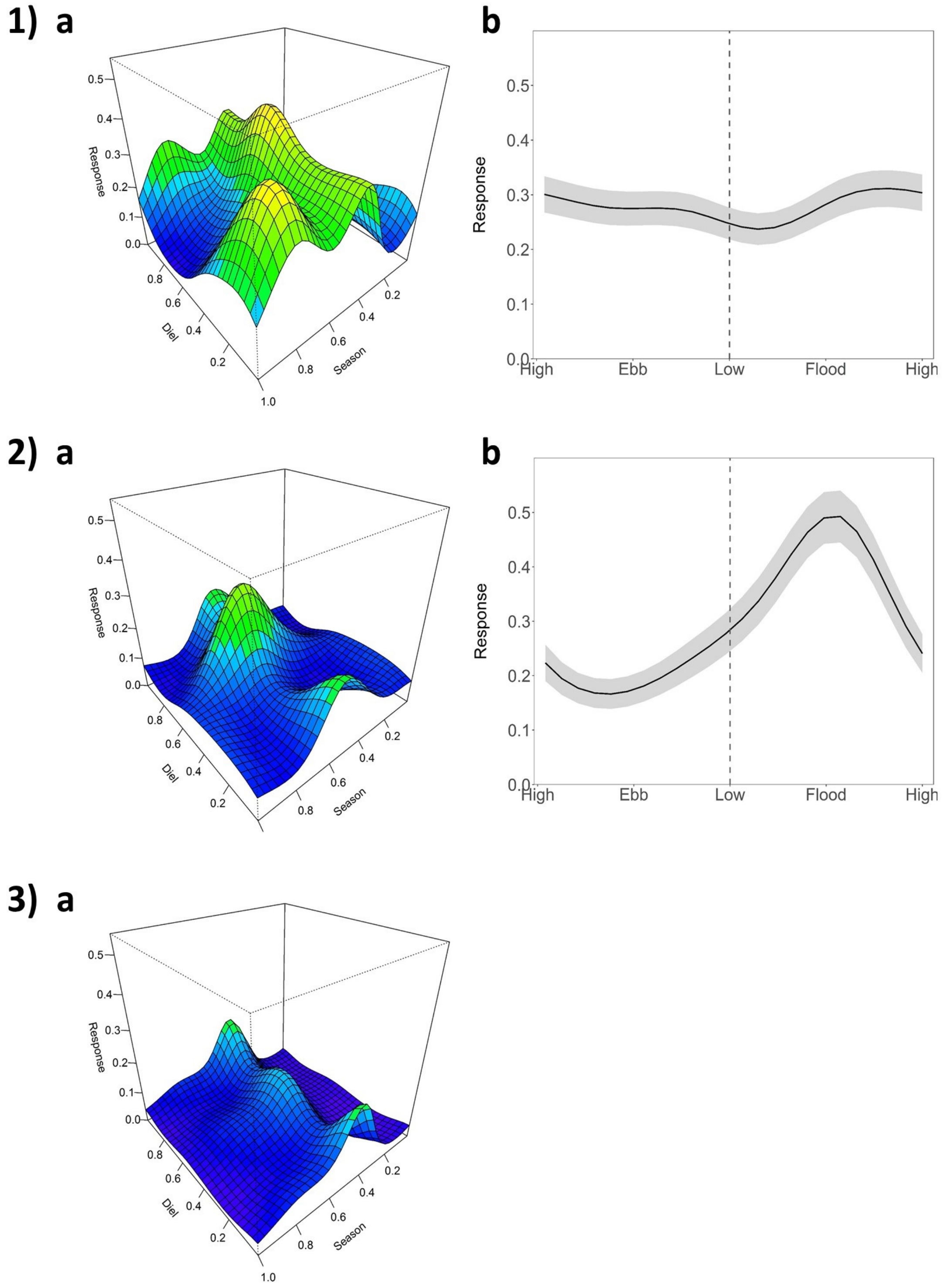


*Figure 2.8: GAMM modelling results for 1) Sutors, 2) Chanonry and 3) Spey Bay. Representation on the response scale of the effect of the a) interaction diel*seasonal b) tidal variable (95% confidence intervals represented by grey areas) on the probability of dolphin encounters*

The importance of the tidal cycle was clear in Chanonry with the highest probability of encounters concentrated around the flood stage of the tide (between the low and high tide; Figure 2.8.2b). In Sutors, although the variable was significant, the tidal influence was much weaker, with only a slight reduction in use after low tide and a small peak before high tide (Figure 2.8.1b). As stated before, this variable was not significant in Spey Bay.

The probability of encounters showed the highest values during summer months at all sites. Seasonality was more evident in Chanonry and Spey Bay, with the highest values concentrated around the middle of the year. In Sutors, values remained higher than in the other two sites during the whole year, but especially around October-November.

Temporal correlation issues were corrected using both GAMM approaches, GAMM4 and temporal correlation corAr1. No collinearity was found between the variables included in the final models.

DISCUSSION

Our analyses of changes in acoustic detections allowed us to compare the relative importance of tidal and diel cycles in the occurrence of dolphins at our three different sampling sites. Cetaceans are considered less likely to be influenced by tides in open coastal areas than in narrow channels (Mellink and Orozco-Meyer 2006; Pierpoint 2008). In line with this, there was no effect of the tidal cycle at the most open of our study sites in Spey Bay (Figure 2.7). In contrast, occurrence at Chanonry was strongly influenced by tide in all months of the year (Figure 2.7 & Figure 2.8.2b). This site was within a narrow channel and subject to strong tidal flows which are known to influence fine-scale spatial movements of dolphins in this area (Bailey and Thompson 2010). Our acoustic data extended the results of previous visual surveys (Bailey et al. 2013) by confirming that this pattern dominated during both day and night. The Sutors site was within a similar, albeit slightly wider, channel, where previous visual studies had not detected strong tidal effects (Hastie et al. 2003b). Our results show that the amplitude of the tide effect on dolphin activity is smaller than at Chanonry overall (Figure 2.8a), yet the differences are highly significant and the pattern of use is clearly qualitatively different at the latter site, despite apparent similarities in the physiography of these two sites. Similarly, Pirotta et al. (2014b) found that a tidal mixing parameter and tidal speed had a stronger influence on foraging behaviour in Chanonry than in Sutors. Together, these studies highlight more subtle differences in the oceanography and/or prey populations at these sites that warrant further investigation. The diel cycle showed marked differences between sites, with evidence of consistent diurnal, nocturnal and crepuscular patterns of behaviour through the study period (Figure 2.8). At a larger scale, Castellote et al. (2015) also found contrasting diel patterns in occurrence of bottlenose dolphins within Mediterranean MPAs located 90 km apart. Our results highlight that site-specific variability in both tidal and diel behaviour persists at much smaller spatial scales (13.5 km).

By considering interactions between temporal variables, we revealed a consistent seasonal shift in diel behaviour, with dolphin occurrence within these inshore sites becoming highly nocturnal in autumn. This is particularly seen in Sutors, as the overall use of the other two sites is considerably reduced outside summer. As far as we know, this is the first time that a seasonal shift in diel presence has been documented in a resident population of marine mammals. Many authors have suggested that the cyclical behaviour of marine mammals is related to the avoidance of their predators or to the cyclicity of their prey (Baird et al. 2008; Benoit-Bird and Au 2003; Samarra et al. 2017), but obtaining direct evidence to test these alternative hypotheses remains challenging. Although Orca (*Orcinus orca*) occur occasionally in this area (Robinson et al. 2017), there is no evidence of this dolphin population being regularly exposed to natural predators. Whilst predator avoidance behaviours may also occur in response to anthropogenic disturbance (Lima and Dill 1990), there is no evidence of a similar seasonal shift in diel patterns of any human activity that could elicit the patterns observed in our data. In contrast, the importance of these sites has been linked to foraging in the past (Hastie et al. 2004; Pirotta et al. 2014b), suggesting that observed changes in occurrence are most likely related to differences in prey distribution (Gilles et al. 2016), prey density (Wang et al. 2016), prey behaviour (Benoit-Bird and Au 2003) or prey catchability (Allen et al. 2001). There are limited data on temporal and spatial variation in potential prey in the Moray Firth (Greenstreet et al. 1998; Marine Scotland 2016), but no recent data that can be used to assess spatial variation at a scale relevant to our three study sites. Nevertheless, older data on fisheries and marine mammal predator-prey interactions might provide insights into the drivers of the cyclic patterns observed in this study. The Moray Firth had an important fishery for clupeids that overwintered in the area (Hopkins 1986) and in the late 1980s it was shown that these winter fish stocks were important for harbour seals. Pierce et al. (1991) discovered that harbour seals performed a seasonal shift in their diet and targeted clupeids in winter. Harbour seals are benthic foragers

(Tollit et al. 1998) and Thompson et al. (1991) linked the daily vertical migration of clupeids to the diel behaviour of seals which appeared to forage in daytime while fish were in tight schools in the deep channels of the inner Moray Firth. In later years, clupeid stocks declined in the area and inter-annual variation in seal diet and physiology was found (Thompson et al. 1997). The variation in dolphin use of these same areas might be due to a recent recovery of fish stocks. I hypothesise that an influx of clupeids could be the driver of the diel behaviour of dolphins observed in autumn. Bottlenose dolphins may be using the deep channels to forage at night when the fish are closer to the surface, a foraging strategy that may be energetically more efficient (Williams et al. 2000). However, studies of predator-prey behaviour would be needed in the area to prove this theory.

The seasonal cycle dominated patterns of occurrence at all sites, with a greater proportion of encounters in summer (Figure 2.5c & Figure 2.8). These results confirm those observed in earlier boat-based visual studies of this population (Bailey et al. 2013; Hastie et al. 2003b; Wilson et al. 1997). However, our results suggest that previous visual studies could have underestimated the importance of night-time use at the most intensively used of these sites (Sutors, Figure 2.8a). In our study, acoustic data collected throughout the 24 h cycle showed that there was a high probability of detection during night-time in autumn. This highlights how acoustic studies may help overcome the restriction of visual surveys to daylight hours. At the same time, it is important to recognise that CPOD detection rates may be influenced by dolphin behaviour (Nuuttila et al. 2013b). Marine mammal click beams are highly directional (Au et al. 2012) so that only clicks directed towards the acoustic device have the potential to be detected. Additionally, bottlenose dolphins echolocate mainly when traveling and foraging, and whistle when socialising (Au 1993; Cook et al. 2004). Our comparison of CPOD detections and analysis of simultaneous broadband recordings support previous studies that demonstrate that CPODs provide a robust and conservative measure of dolphin occurrence within a range of almost 1000m (Bailey et al. 2010a; Garrod et al. 2018; Roberts and Read 2015). However, this comparison also highlighted that click absences should always be interpreted cautiously because the use of this conservative metric means that these will include some false negatives and could also represent either an absence of animals or a change in acoustic behaviour. Broad band acoustic devices that detect other vocalisations (Van Parijs et al. 2009) could be used to explore this issue further. In the meantime, we assume that the most likely cause of observed changes in click detections is a change in dolphin occurrence, although we cannot rule out the possibility that this could reflect some other behavioural change.

This study highlights the importance of understanding temporal variation in behaviour to underpin more dynamic management of Marine Protected Areas. Although nocturnal activity has been detected in many studies of these animals (Castellote et al. 2015; Temple et al. 2016; Williamson et al. 2017), visual methods are still widely used to study their distribution (Marini et al. 2015; Pitchford et al. 2016). Visual surveys only provide data during daylight hours and may be underestimating the importance of certain locations during the night (Williamson et al. 2017). For example, our Sutors and Chanonry study sites are two of the most important areas for bottlenose dolphins within the Special Area of Conservation (SAC) that was established to protect their population (Hastie et al. 2004; Wilson et al. 1997). However, these areas are also subject to a wide range of human activities, including vessel traffic and spoil dumping (Merchant et al. 2014; Pirotta et al. 2015a). Previous studies have recognised the importance of these areas (Hastie et al. 2003a; Wilson et al. 1997), but the visual sightings used to underpin that mitigation work were focused on the summer months (Marine Marine Scotland 2014). As result, some activities such as spoil dumping have been encouraged in autumn, when our results indicate that animals continue to use some of these sites albeit nocturnally.

In summary, this study presents evidence that environmental influences on dolphin behaviour can be highly site-specific, even at relatively fine spatial scales. These findings demonstrate the need to include dynamic environmental variables and interactions between them when modelling the habitat use of small cetaceans. Environmental cycles can interact with one another, producing the consistent seasonal shift in diel behaviour observed in this population. Similar patterns are likely to occur elsewhere but may have gone unnoticed. The challenge now is to develop a better understanding of the key drivers underpinning these patterns, and to identify how best to integrate this information into more effective marine management measures.

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AUTHOR CONTRIBUTIONS

OFB, IMG & PMT designed the study based on data collection that had been led by IMG & PMT. OFB and TC designed the generalized additive modelling analysis. All analyses were conducted by OFB and supervised by IMG. OFB drafted the MS and prepared all the figures. All authors reviewed the manuscript.

ADDITIONAL INFORMATION

Data availability: Data used in these analyses are available at https://datadryad.org/stash/dataset/doi:10.5061/dryad.k378542.

CHAPTER 3

SEASONAL, TIDAL AND DIEL PATTERNS OF PREY DRIVE DOLPHIN OCCURRENCE IN A FORAGING HOTSPOT

CHAPTER 3: SEASONAL, TIDAL AND DIEL PATTERNS OF PREY DRIVE DOLPHIN OCCURRENCE IN A FORAGING HOTSPOT

ABSTRACT

Quantifying the distribution of prey is important for understanding habitat use of marine predators and can inform management and conservation. However, marine top predator studies frequently lack information on prey at the required spatio-temporal scales. In this study, a series of fisheries acoustic surveys were conducted to understand potential drivers of dolphin occurrence at two foraging hotspots in NE Scotland. Seasonal, tidal and diel variation in fish abundance, schooling behaviour and position in the water column were investigated together with seasonal changes in fish species composition. In 2018, data were collected during 36 surveys using a split beam 38 kHz scientific echosounder operated from a small Rigid Inflatable Boat. An increase in fish density during summer corresponded with increases in dolphin occurrence at both sites. A greater number of fish tracks per kilometre was detected during flood tide, supporting earlier hypotheses that increases in prey availability may drive observed increases in dolphin occurrence during this tidal stage. A combination of a higher fish density, lower fish aggregation and a change in fish species composition also reflected diel patterns of dolphin behaviour. These results highlight the link between prey and predator occurrence in these two foraging hotspots and demonstrate the potential for using portable

echosounders in fine-scale surveys that can be integrated into studies of coastal marine predators.

INTRODUCTION

Identifying the drivers of predator occurrence is key for their conservation and management (Boyd et al. 2006). Understanding predator habitat preferences can support predictions of the potential effects of environmental change (Baker and Harris 2020) and help identify measures to avoid or mitigate these impacts. Prey availability is recognised to be a key driver of predator occurrence (Begon et al. 2009), and efforts to model predator habitat use are likely to be most robust when they can include information on prey (Ainley et al. 2009; Schick and Lutcavage 2009; Waggitt et al. 2018). However, obtaining prey data in the marine environment remains challenging. Consequently, marine top predator studies are frequently constrained by limited information on the distribution, abundance and spatio-temporal variability of potential prey (Gilles et al. 2016; Hall et al. 2019; Sharples et al. 2012).

Information on marine prey fields is often collected from large scientific vessels, with scientific echo sounders, performing fisheries acoustic surveys (Simmonds and Maclennan 2006). These surveys are typically large-scale, expensive and require complicated logistics that compromise their repeatability (Hilborn and Walters 2013; Simmonds and Maclennan 2006). Furthermore, they provide just snapshots of the fish abundance and behaviour in the surveyed areas. Due to the heterogeneous and dynamic nature of prey distribution, these snapshots do not always provide accurate information on predator-prey associations. Although theory predicts that predator occurrence should match the spatio-temporal distribution of their prey, finding positive correlations between predator and prey distribution remains challenging in the marine environment (Astarloa et al. 2019; Torres et al. 2008). Therefore in highly dynamic ecosystems, finding the right temporal and spatial scales when collecting prey information is key to understanding predator-prey interactions (Benoit-Bird and McManus 2014; Cox et al. 2013; Embling et al. 2012; Grigg et al. 2009).

Portable scientific echo sounders have become more affordable in recent years, offering excellent potential for obtaining parallel data on prey in coastal areas being used by marine predators (Wang et al. 2019). These devices can be operated from a variety of different vessels, such as small rigid inflatable boats (RIBs). This makes studies at fine temporal and spatial scales more cost-effective and, also, facilitates work in shallow coastal waters that may be inaccessible for large vessels.

Prey field studies in temperate estuaries may benefit from these affordable techniques because these ecosystems exhibit complex diel, tidal and seasonal changes that are challenging to capture with larger vessels. On a seasonal scale, due to the ontogeny and life cycle of animal species, estuaries exhibit major seasonal changes in fish species composition (Hagan and Able 2003; Selleslagh and Amara 2008). Estuaries act as nursery areas for many species of fish which in turn attract other fish predators, causing seasonal changes in fish assemblages (Greenstreet et al. 1998). Furthermore, migratory species such as salmonids, perform seasonal movements that also modify estuarine fish composition through the seasons (McCormick et al. 1998; Methven et al. 2001). On a smaller temporal scale, horizontal and vertical movements of fish linked to the tidal and diel cycles also cause changes in the fish assemblage in the water column (Becker et al. 2011; Hagan and Able 2008). For instance, clupeids spend the day in deeper waters and spread out throughout the water column at night (Blaxter and Hunter 1982). On the other hand, sand eels perform a daily movement in the opposite direction, spending the day closer to the surface and burying in the seabed at night (Freeman et al. 2004). Other fish species perform daily horizontal movements linked to tides and day-night cycles in order to exploit varying resources of coastal habitats (Becker et al. 2015; Childs et al. 2008). Furthermore, diel and tidal cycles also cause changes in the behaviour of fish (Embling et al. 2013; Rieucau et al. 2015; Taylor et al. 2013b). For instance, the day-night cycle modifies the schooling behaviour of fish, generally, fish being aggregated during day-time and dispersed during night-time (Cardinale et al. 2003; Fréon et al. 1996). Strong tidal currents can also affect fish school cohesion and cause the breakup of schools by disorienting fish (Robinson et al. 2007a). Overall, estuaries support diverse animal populations that undergo a complex mixture of cyclical patterns. Comprehending the cyclicity of the species that inhabit these areas is key to understanding the ecosystem functioning and manage them better (Field et al. 2010).

Previous studies have identified site-specific seasonal, tidal and diel patterns in the occurrence of bottlenose dolphins (*Tursiops truncatus*) at two foraging hotspots in the Moray Firth (Fernandez-Betelu et al. 2019). The occurrence of dolphins increased during summer and, at one of the sites, during the flood tide. Furthermore, there was a seasonal shift in the diel behaviour of dolphins as they were present 24 h a day in summer but became highly nocturnal in autumn. Based upon the findings in Chapter 2, I hypothesised that these patterns of dolphin occurrence were being driven by temporal patterns of prey. However, there was no existing information on prey at relevant scales to test this hypothesis.

The aim of this study was to investigate seasonal, tidal and diel variation in fish abundance and behaviour in these two foraging hotspots to better understand factors affecting the occurrence of dolphins in these areas. To achieve this, we developed a method to perform fisheries acoustic surveys at small spatial scales (< 10s km) from a small RIB. I hypothesised that we would find differences in prey density, prey position in the water column, prey aggregation or prey species composition that could explain the site-specific patterns of occurrence previously observed in dolphins.

METHODS

Study Area

Sutors (57° 41.41'N, 03° 59.18'W) and Chanonry (57° 5.14'N, 04° 5.85'W) are two channels connecting the Moray Firth to large inshore fjord-like bays (Scotland, Figure 3.1). Both channels are relatively deep (maximum depth 55 m) and narrow (maximum width 1.7 km) and are both are considered foraging hotspots for the resident population of bottlenose dolphins (Hastie et al. 2004).

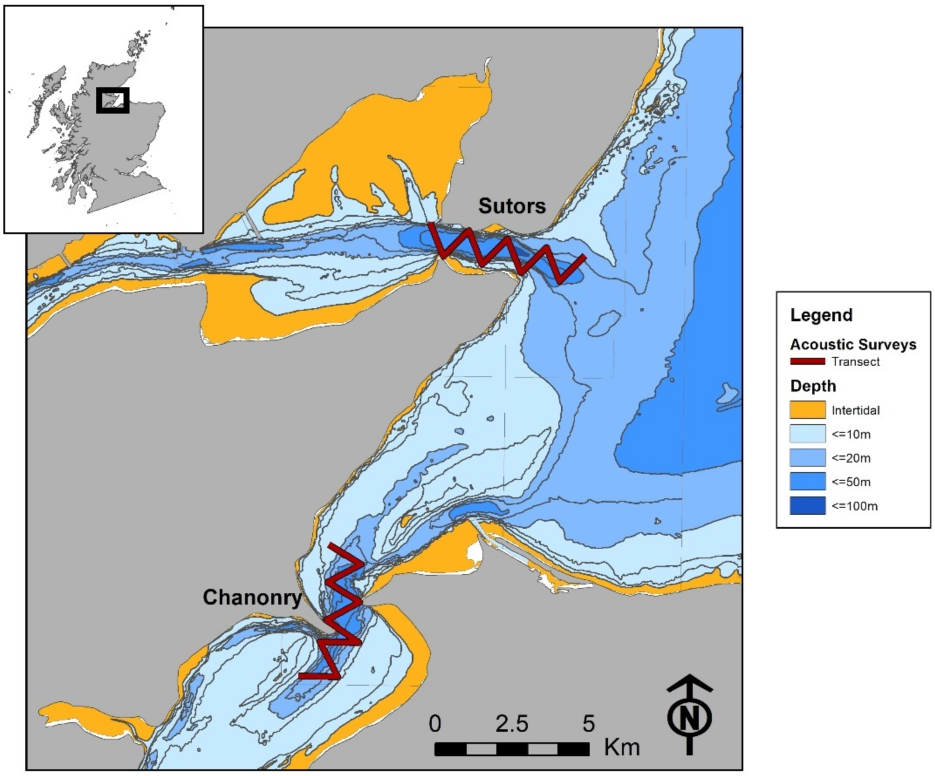


Figure 3.1: Map of the Inner Moray Firth, with an example of the zig-zag acoustic surveys performed in the two sites: Sutors and Chanonry. Inset shows the location of the firth relative to Scotland. Grey lines are bathymetric contours at 10 m intervals and deeper blue shading indicates greater depths. Orange shading shows the intertidal area.

The Moray Firth is also an important overwintering area for juvenile herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) (Hopkins 1986). During summer, sand eels (*Ammodytes marinus*) are the most abundant fish in the firth (Greenstreet et al. 1998). The main rivers that flow into the Moray Firth support populations of Atlantic salmon (*Salmo salar*), which spend much of their adult life at sea and return to their home rivers to spawn between spring and summer.

Acoustic surveys

Monthly surveys were conducted throughout 2018 in Sutors and Chanonry to explore the differences in fish density, schooling behaviour, position in the water column and fish species composition in these two areas. To study seasonal differences, monthly surveys were performed during daytime and flood tides in both channels to minimise potential extra variation in the data. To study differences between tidal stages, additional surveys during ebb tides were performed between May and August in both channels. Finally, to study the diel differences between summer and autumn, surveys were performed during the night in Sutors between July and December (Figure 3.2). Whenever possible, the surveys comparing flood/ebb and day/night were performed on the same day to minimise the effect of day-to-day variation.

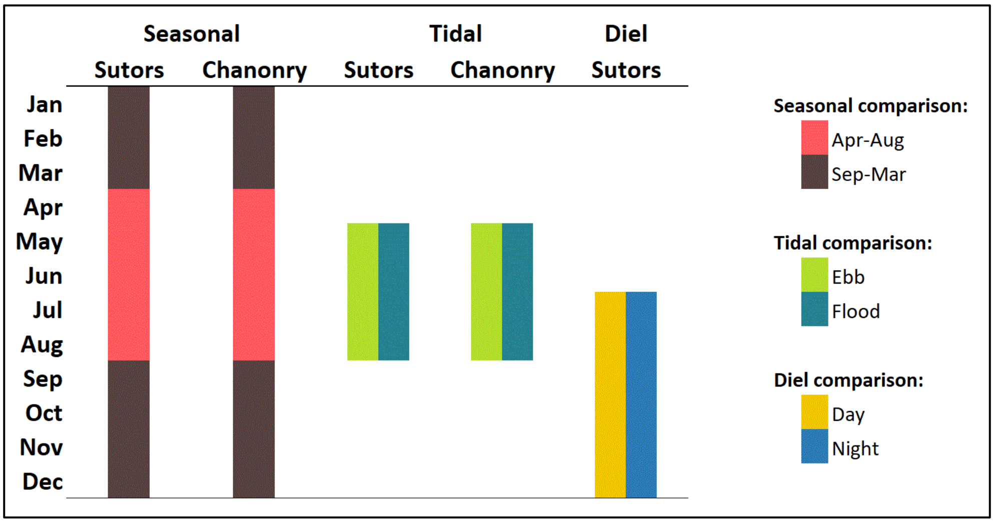


Figure 3.2: Acoustic surveys, comparison diagram for the statistical analysis at each of the temporal scales.

Zigzag survey designs were chosen due to the shape and size of the survey areas (Simmonds and Maclennan 2006). The survey area was consistent throughout the study, but the location of the starting point was randomized every month. Transects were followed as close to shore as safe navigation allowed, to a minimum depth of 4 m and to within a minimum distance of 100 m to the harbour. Whenever dolphins were encountered along the planned transect, boat direction was modified to avoid the area that animals were using and minimise any potential disturbance.

The acoustic transects were performed using a small RIB (5.85 m). A portable and battery-powered SIMRAD WBT Mini EK80 echo sounder and a 38 kHz split-beam transducer were operated from a laptop computer. A removable frame was specifically designed for the transducer. The frame was vertically adjustable and kept the transducer approximately 0.5 m below the surface off the starboard side of the RIB during surveys (Figure 3.3). A standard boat speed of ~ 2 $m.s^{-1}$ (4 knots) was maintained. The echo sounder operated continuously at a rate of 1 ping every 600 ms and a pulse length of 0.256 ms in all the surveys. An external GPS was connected to the laptop to obtain the location information for the acoustic data. The equipment was calibrated in July 2018 at slack tide in Sutors, using a tungsten carbide sphere of 38.1 mm following standard procedures (Demer et al. 2015). CTD casts were performed at the beginning and the end of each transect using a RBR Concerto CTD (RBR Ltd., Ottawa, Canada). The mean temperature and salinity for the whole water column were used in post-processing.

Figure 3.3: Pictures of the equipment used in the echo sounder surveys. Frame-mounted transducer on the RIB (left), transducer submerged during an acoustic transect (top right) and battery powered laptop and echo sounder during a survey (bottom right).

Acoustic data processing

All acoustic processing was conducted in EchoView 10 (Echoview Software Pty Ltd., Hobart, Australia).

Data were filtered using a processing threshold of -60 dB to remove unwanted weaker targets such as krill or plankton (Simmonds and Maclennan 2006). Data from the top 5 m and from 0.7 m above the seabed were removed from the analysis to avoid the nearfield transmit pulse and any errors in seabed detection.

Fish abundance and behaviour was studied using two methods: echo integration of fish schools and echo counting of fish tracks. Fish schools were detected using the SHAPES algorithm (Coetzee 2000) implemented in EchoView. The software was configured to detect aggregations with a minimum length and height of 2 m. The maximum vertical linking distance was set to 2 m and the horizontal to 10 m. Regions that corresponded to birds, tidal fronts and dolphins were classified manually, based on visual inspection of the echograms (Benoit-Bird and Lawson 2016; see Figures S3.1 in supplementary material for examples on classified regions). Diagonal or “V” shape regions that originated from the surface were classified as birds. Vertical regions that were visible in the first meters of the water column (< 5 m from the surface) were classified as tidal fronts. Regions with high target strengths (> -22 dB) detected during bottlenose dolphin encounters were classified as dolphins. To avoid any miscalculation in the echo-integration, regions classified as birds, tidal fronts, and dolphins were excluded from the analysis. A mask that included only the aggregations classified as fish schools was created and it was divided into 1000 m long elementary distance sampling units (EDSU). The following echo-integration variables from that mask were extracted (Table 3.1): the nautical area scattering coefficient (NASC), a proxy of fish density in the area; the centre of mass (CM), an estimator of the mean vertical location of fish in the water column; and the index of aggregation (IA), an indicator of the aggregation levels of the fish schools detected (Urmy et al. 2012).

Table 3.1: Variables used to describe the abundance and behaviour of fish schools in the GLMM analysis.

Variable	**Symbol**	**Units**	**Definition**
Nautical area scattering coefficient	NASC	m^2 nmi^{-2}	Proxy of fish density in the water column.
Centre of mass	CM	m	Average of the depths of all the detected fish schools weighted by their volume backscatter coefficient values.
Index of aggregation	IA	m^{-1}	Proxy of the level of patchiness of the fish schools. IA is high when fish distribution is patchier i.e. certain areas have higher fish density than others.
Number of fish tracks per km	No.FT/km	nFT km^{-1}	Number of single fish tracks per kilometre. A fish track was considered a combination of at least three single target detections.

For the echo counting of fish tracks, a mask was created removing all the aggregations detected through SHAPES. Echoview was configured to detect single targets using a TS threshold of -60 dB. Single targets were combined into fish tracks using the target-tracking algorithm implemented in EchoView (Blackman 1986). A track had to contain a minimum number of three single targets separated by less than three pings to be considered a fish track. Number of detected fish tracks per kilometre was used in further analyses.

Statistical data analysis

To test for seasonal, tidal and diel differences in fish density and schooling behaviour, a series of generalised linear mixed models (GLMM) was conducted. The variables extracted from Echoview (NASC, centre of mass, index of aggregation and number of fish tracks per kilometre) were used as response variables in separate models. The NASC variable was log-transformed (log[NASC+1]) to meet the assumption of normality and homoscedasticity.

For the seasonal comparison April-August data were compared with September-March data. This division was used because the presence of dolphins increases during day-time from April to August and during night-time from September to March (Fernandez-Betelu et al. 2019). To avoid the confounding effect from the tidal and diel cycles, the seasonal comparison was based on the transects performed during daytime and at the flood stage of the tide. To test the effect of tides, a flood/ebb comparison was performed on the data collected between May and August during daytime. In both seasonal and tidal comparisons, an interaction with site was included to test for differences between the channels. For the diel comparison, day/night data collected during flood were aggregated into two groups: summer (July-August, when dolphins are present all day long) and autumn (September-December, when dolphins become highly nocturnal). Day/night and summer/autumn differences, and their interaction, were tested. Month was used as a random effect in the GLMMs to account for autocorrelation of the data. The acf and pacf functions in R were used to check the autocorrelation in the residuals. A Gaussian distribution was used for the NASC, a gamma distribution for the centre of mass and for the index of aggregation and negative binomial for the number of fish tracks per kilometre.

For the seasonal cycle, Principal Component Analysis (PCA) and cluster analysis of school descriptors were performed to investigate the seasonal species composition in the area. Since validation samples were not available, an unsupervised clustering algorithm was conducted. Robust sparse k-means clustering (RSKC) was chosen due to its robustness to the presence of outliers (Gastauer et al. 2017; Kondo et al. 2016). The optimal number of clusters was estimated via the *clest* algorithm. To categorise schools into different clusters, ten school descriptors were extracted for each school: five energetic, three morphologic and two bathymetric variables (Table 3.2). The energetic descriptors were the mean backscattering volume (Sv mean, dB re $1m^{-1}$), maximum Sv (Sv max), Sv Kurtosis, Sv Skewness and beam geometry corrected Sv (MVBS, dB re $1m^2m^{-3}$). The morphologic school descriptors were the corrected area of the school (Area, m), corrected vertical dimension (Thickness, m) and corrected length (Length, m). The bathymetric variables were the mean depth of the school (Depth, m) and mean distance from the seabed (Altitude, m). Clustering of the detected fish schools was performed using all school descriptors. Night-time schools were removed from the clustering analysis since diel vertical migration of fish has been observed in the area (Thompson et al. 1991). Once the schools were divided into the different clusters, the total PRC_NASC (the weighted NASC for the intersection of a region within an integration cell) of each cluster was used to measure the acoustic relative density of each group in each of the seasons.

Table 3.2: Fish school descriptors used in the PCA and cluster analysis.

Descriptor	**Units**	**Definition**
Sv mean	dB re 1m^{-1}	Mean volume backscattering strength
Sv max	dB re 1 m^{-1}	Maximum Sv detected in the school
Kurtosis		Statistical measure of the combined weight of the tails relative to the rest of the distribution of the Sv
Skewness		Statistical measure of how skewed the distribution of the samples within the school are
Corrected MVBS	dB re 1m^{2}m^{-3}	Mean Sv of the school represented by a region on an echogram corrected for the known beam geometry according to the system of Diner (1998)
Area	m^{2}	Cross-sectional area of the school in the plane of the echogram for the known beam geometry according to the system of Diner (1998)
Thickness	m	Vertical dimension of the school corrected according to the system of Diner (1998)
Length	m	Horizontal dimension of the school corrected according to the system of Diner (1998)
Depth	m	Mean depth of all good data points in the school
Altitude	m	Average distance from the seabed to the centre data points in the school

All the analyses were performed in R 3.5 (R Core Team 2018) , using the *lme4* (Bates et al. 2015) and *RSKC* packages (Kondo et al. 2016).

RESULTS

Thirty-six acoustic surveys were carried out during 2018 (Table 3.3). We were unable to perform two surveys due to the weather conditions (Chanonry-January and Chanonry-September). Chanonry transects in April, July, May and August had to be altered due to the presence of dolphins (Table 3.3 and Figure 3.4).

Table 3.3: Details of acoustic surveys and sampling effort performed at each site.

Date	Site	Day-night	Tide	No. ESDU	Total survey length (km)	Dolphins observed	Transect modified due to dolphins
25/01/2018	Sutors	Day	Flood	11	10.661	No	No
-/01/2018	Chanonry	-	-	-	-	-	-
20/02/2018	Chanonry	Day	Flood	10	9.794	No	No
19/02/2018	Sutors	Day	High	10	9.122	No	No
08/03/2018	Chanonry	Day	Flood	9	8.612	No	No
19/03/2018	Sutors	Day	Flood	10	9.595	No	No
19/04/2018	Chanonry	Day	Flood	8	7.225	Yes	Yes
18/04/2018	Sutors	Day	Flood	10	9.320	No	No
16/05/2018	Chanonry	Day	Ebb	9	8.847	No	No
16/05/2018	Chanonry	Day	Flood	8	7.616	Yes	Yes
13/05/2018	Sutors	Day	Ebb	10	9.084	Yes	No
13/05/2018	Sutors	Day	Flood	10	9.226	No	No
26/06/2018	Chanonry	Day	Ebb	9	8.460	No	No
28/06/2018	Chanonry	Day	Flood	9	8.329	Yes	No
27/06/2018	Sutors	Day	Ebb	10	9.760	No	No
27/06/2018	Sutors	Day	Flood	10	9.589	Yes	No
13/07/2018	Chanonry	Day	Ebb	9	8.113	Yes	No
13/07/2018	Chanonry	Day	Flood	9	8.278	Yes	Yes
12/07/2018	Sutors	Day	Ebb	10	9.928	Yes	No
12/07/2018	Sutors	Day	Flood	10	9.441	Yes	No
19/07/2018	Sutors	Night	Flood	10	9.728	Yes	No
10/08/2018	Chanonry	Day	Ebb	9	8.985	Yes	No
10/08/2018	Chanonry	Day	Flood	9	8.507	Yes	Yes
02/08/2018	Sutors	Day	Ebb	10	9.448	No	No
02/08/2018	Sutors	Day	Flood	10	9.812	Yes	No
04/08/2018	Sutors	Night	Flood	10	9.333	No	No
18/09/2018	Sutors	Day	Flood	10	9.435	No	No
20/09/2018	Sutors	Night	Ebb	10	9.354	No	No
-/09/2018	Chanonry	-	-	-	-	-	-
10/10/2018	Chanonry	Day	Flood	9	8.882	No	No
08/10/2018	Sutors	Day	Flood	10	9.592	No	No
11/10/2018	Sutors	Night	Flood	11	10.545	No	No
11/11/2018	Chanonry	Day	Flood	8	7.499	No	No
01/11/2018	Sutors	Day	Flood	10	9.655	No	No
01/11/2018	Sutors	Night	Flood	11	10.782	Yes	No
11/12/2018	Chanonry	Day	Flood	8	7.214	No	No
10/12/2018	Sutors	Day	Flood	10	9.377	No	No
10/12/2018	Sutors	Night	Flood	10	9.568	No	No

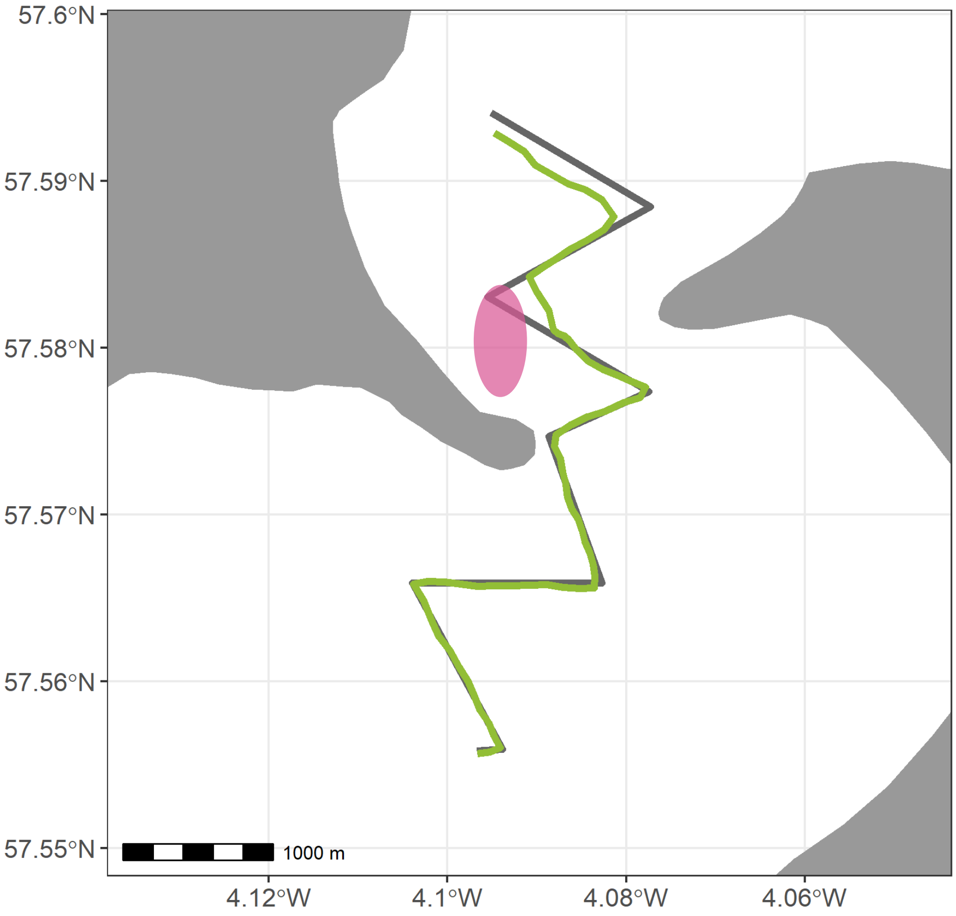


Figure 3.4: Example of transect modification due to the presence of dolphins (Chanonry: May during flood). Dark grey: planned transect. Green: performed transect. Pink: area with dolphins.

The SHAPES algorithm detected a total number of 783 regions in Sutors and 593 in Chanonry (Table 3.4). 172 regions were manually classified as either tidal fronts, birds or dolphins at each of the sites and were removed from the analyses (see echogram examples in Supplementary material Figures S3.1).

Table 3.4: Total number of regions in each of the channels after the manual classification of the regions detected by the SHAPES algorithm of EchoView.

	Fish schools	**Tidal fronts**	**Birds**	**Dolphins**
Sutors	611	50	94	28
Chanonry	421	118	47	7

Seasonal patterns in fish density, schooling behaviour and species composition

Fish density was significantly higher in April-August than in September-March in both sites (Table 3.5, Figure 3.5 and Table 3.6). The centre of mass was significantly deeper in September-March than in April-August in both channels (Figure 3.5a and Table 3.6). The interaction between site and season was significant for the index of aggregation (Table 3.5 and Figure 3.5). In Sutors, the index of aggregation was lower in April-August than in September-March, while the opposite occurred in Chanonry (Figure 3.5a and Table 3.6) but those differences were not statistically significant (Kruskal-Wallis Sutors: X^2 = 3.2020, p-value = 0.0735; Chanonry: X^2 = 1.5735, p-value = 0.2097). The number of fish tracks was higher in September-March than in April-August in both channels (Figure 3.5a; see echogram examples for the seasonal comparison in Supplementary material Figures S3.2).

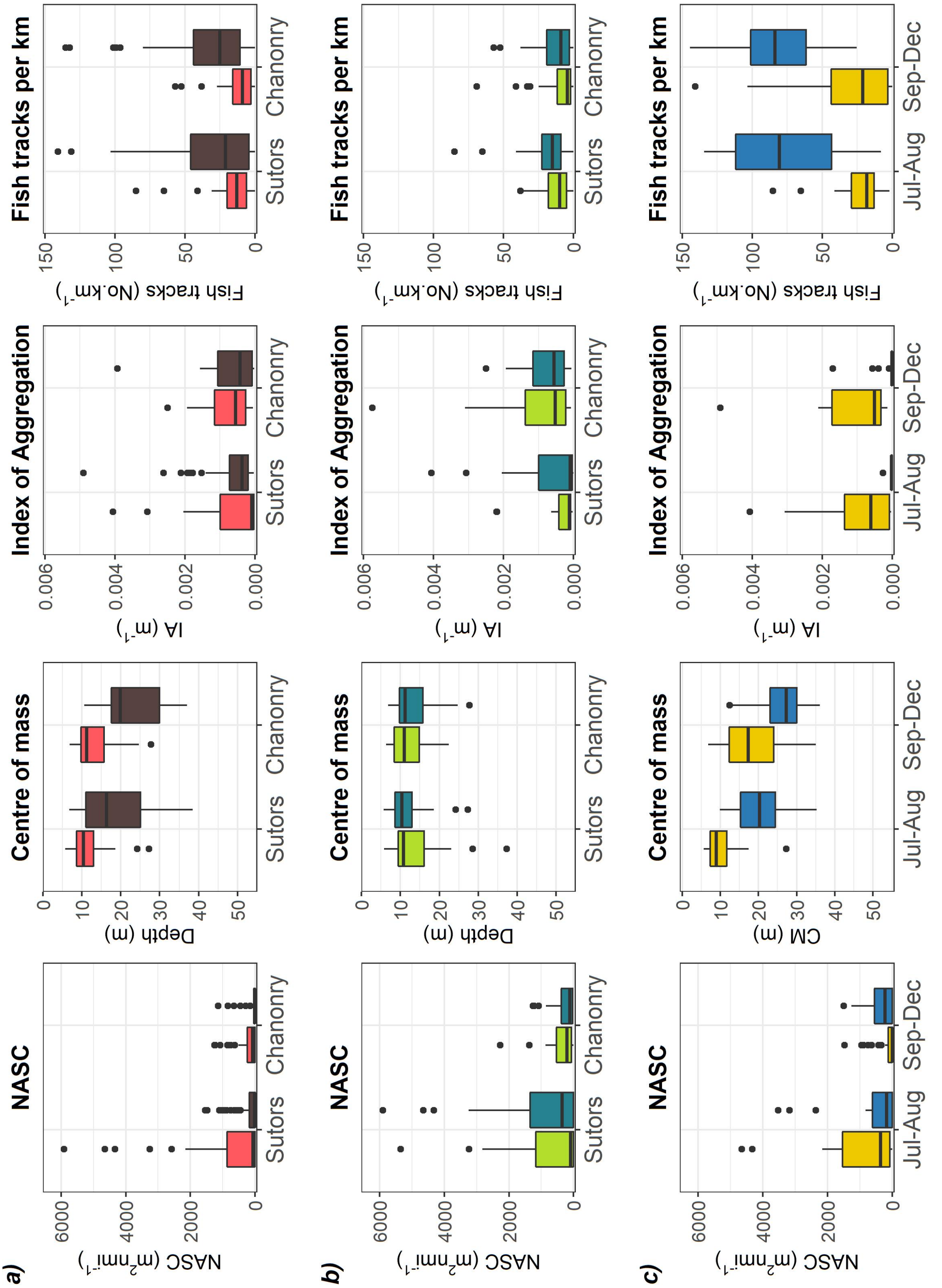


Figure 3.5: Boxplots of fish density (NASC, left), centre of mass (middle-left), index of aggregation (middle-right) and number of fish tracks per kilometre (right) for a) seasonal (April-August: bright pink; September-March: dark brown), b) tidal (ebb: bright green; flood: dark turquoise) and c) diel comparison (day-time: yellow; night-time: dark blue).

			NASC	Center of mass	Index of aggregation	no. Fish Tracks per km
Seasonal comparison:						
Sutors	Apr-Aug		**62.6** (0-867.8)	**10.4** (8.6-13)	**0.0001** (0-0.001)	**13.0** (6-20)
	Sep-Mar		**5.4** (0-170.4)	**16.4** (11.1-25.1)	**0.0004** (2e-04-7e-04)	**21.0** (4.3-46.1)
Chanonry	Apr-Aug		**74.0** (0-242)	**11.2** (9.8-15.7)	**0.0006** (3e-04-0.0012)	**9.0** (3-16)
	Sep-Mar		**0.0** (0-37)	**19.9** (17.6-30)	**0.0004** (1e-04-0.0011)	**25.1** (10.8-43.8)
Tidal comparison						
Sutors	Flood		**353.5** (0-1338.6)	**10.4** (8.6-13)	**0.0001** (0-0.001)	**15.0** (9-22.5)
	Ebb		**98.6** (0-1333.6)	**10.8** (9.5-16.1)	**0.0001** (1e-04-4e-04)	**10.0** (5-18)
Chanonry	Flood		**114.5** (33.2-377.4)	**11.2** (9.8-15.7)	**0.0006** (3e-04-0.0012)	**9.0** (3-19)
	Ebb		**199.0** (62.1-533)	**11.1** (8.4-14.8)	**0.0005** (2e-04-0.0014)	**4.5** (2-11.5)
Diel comparison:						
Sutors	Jul-Aug	Day	**353.5** (66.4-1534.5)	**8.9** (7.4-11.7)	**0.0006** (1e-04-0.0014)	**18.0** (13-29.1)
	Jul-Aug	Night	**270.0** (0-2560.1)	**20.3** (15.3-24.4)	**0.0000** (0-0)	**83.5** (46-131.3)
	Sep-Dec	Day	**0.0** (0-113.5)	**17.3** (12.4-24)	**0.0005** (3e-04-0.0017)	**21.0** (3.1-43.6)
	Sep-Dec	Night	**213.6** (0.4-550)	**27.3** (23.1-30)	**0.0000** (0-0)	**84.1** (61.9-105.1)

Table 3.5: Summary table of the variables used in the generalised linear mixed models. Median values in bold, lower and upper quartiles in brackets.

Table 3.6: Results of the GLMM models describing the effect of time and space on fish school backscatter. The table shows the response variable and predictor variables used in each model. P-values in bold indicate significance at p < 0.05 level. Interaction removed from the model when p > 0.05.

				F				p-value		
Model	**Response**	**Predictor1**	**Predictor2**	**Predictor1**	**Predictor2**	**Interaction**	**Df**	**Predictor1**	**Predictor2**	**Interaction**
Seasonal comparison:										
	log(NASC)	site	season	0.7729	13.9886	-	1	0.9390	**0.0001**	-
	CM	site	season	0.7113	26.1274	-	1	0.3990	**< 0.0001**	-
	IA	site	season	8.1505	0.2219	19.9713	1	< 0.0001	0.0089	**< 0.0001**
	No.FT/km	site	season	0.0437	22.6160	-	1	0.8344	**< 0.0001**	**-**
Tidal comparison:										
	log(NASC)	site	tide	0.4890	0.1852	-	1	0.3852	0.4670	-
	CM	site	tide	0.0030	0.0015	-	1	0.8996	0.9393	-
	IA	site	tide	6.8195	0.0303	-	1	**0.0142**	0.5284	-
	No.FT/km	site	tide	8.7990	7.7305	-	1	**0.0066**	**0.0063**	-
Diel comparison:										
	log(NASC)	day	season	5.8454	0.9763	6.8711	1	0.4458	0.1560	**0.0087**
	CM	day	season	44.8150	16.4630	-	1	**< 0.0001**	**< 0.0001**	-
	IA	day	season	22.4981	0.4524	-	1	**< 0.0001**	0.5012	-
	No.FT/km	day	season	99.3778	0.2359	-	1	**< 0.0001**	0.6148	-

In the cluster analyses of the school descriptors, the *clest* algorithm determined an optimal number of two clusters of fish schools (Table 3.7).

Table 3.7: Results of the clest algorithm. K: number of clusters; Test.stat: test statistics; obsCER: observational classification error rate; refCER: reference classification error rate; p-value: probability of the absolute CER being higher than the CER under the null hypothesis.

k	test.stat	obsCER	refCER	p-value
2	-0.0208	0.0809	0.2891	0.00
3	-0.0.04	0.2120	0.2425	0.35
4	-0.0642	0.7979	0.1440	0.05

During the clustering, the energetic (Sv_max, Sv_mean, MVBS) and bathymetric (Depth mean, Altitude) variables were the most important school descriptors (Figure 3.6, Table 3.8). The first two principal components explained 66% of the variance contained within the data: the first (PC1) and second (PC2) components accounted for 35.92% and 30.22% of the variance respectively. The fish schools grouped under cluster one had higher backscattering strength, were at higher altitude from the seabed and were shallower in the water column compared to the schools in cluster two (Table 3.9 and Figure 3.7). In Sutors, and to a lesser extent Chanonry, cluster one was more abundant in April-August than in September-March (Figure 3.8). In both channels, cluster two increased in September-March although only slightly in Chanonry.

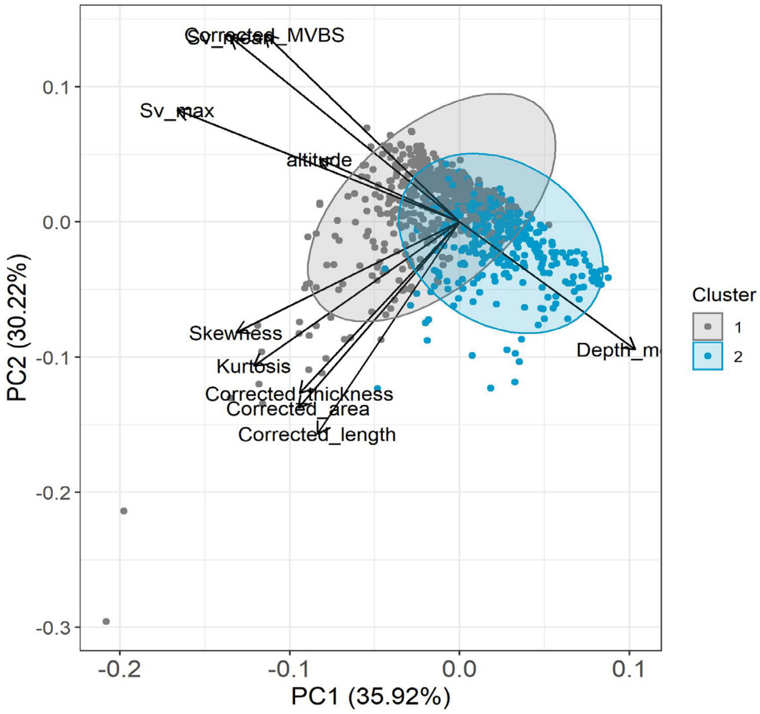


Figure 3.6: Biplot of the first (PC1) and second (PC2) principal components of the clustering including the pulling direction of the school descriptors used in the PCA analysis.

Table 3.8: Weights of the school descriptors in the robust sparse k-means clustering (RSKM weights) and their contributions to the first (PC1) and second (PC2) components of the Principal Component Analysis.

Variable	RSKM Weights	PC1	PC2
Sv max	0.11	-0.86	0.39
Sv mean	0.17	-0.70	0.65
Kurtosis	0.01	-0.63	-0.51
Skewness	0.01	-0.68	-0.39
MVBS	0.10	-0.60	0.66
Area	0.01	-0.49	-0.65
Thickness	0.00	-0.49	-0.60
Length	0.03	-0.43	-0.75
Depth mean	0.95	0.54	-0.45
Altitude	0.20	-0.43	0.22

Table 3.9: Median (in bold) and lower and upper quartiles (in brackets) of each of the school descriptors used in the clustering analysis.

	Cluster 1	**Cluster 2**
Sv max	**-30.99** (-34.13 to -27.37)	**-36.39** (-40.16 to -33.24)
Sv mean	**-43.78** (-46.17 to -40.85)	**-49.1** (-52.16 to -45.98)
Kurtosis	**20.58** (12.6 - 36.91)	**18** (10.58 - 30.57)
Skewness	**3.97** (3.21 - 5.07)	**3.7** (2.85 - 4.78)
MVBS	**-43.43** (-45.97 to -40.44)	**-48.45** (-51.76 to -44.7)
Area	**18.86** (9.54 - 58.16)	**19.29** (10.9 - 38.74)
Thickness	**3.2** (2.35 - 4.77)	**3.03** (2.27 - 4.2)
Length	**13.39** (6.32 - 32.04)	**20.21** (9.29 - 37.02)
Depth mean	**9.26** (7.35 - 12)	**30.09** (23.13 - 34.71)
Altitude	**19.06** (11.58 - 28.01)	**5.2** (2.43 - 9.92)

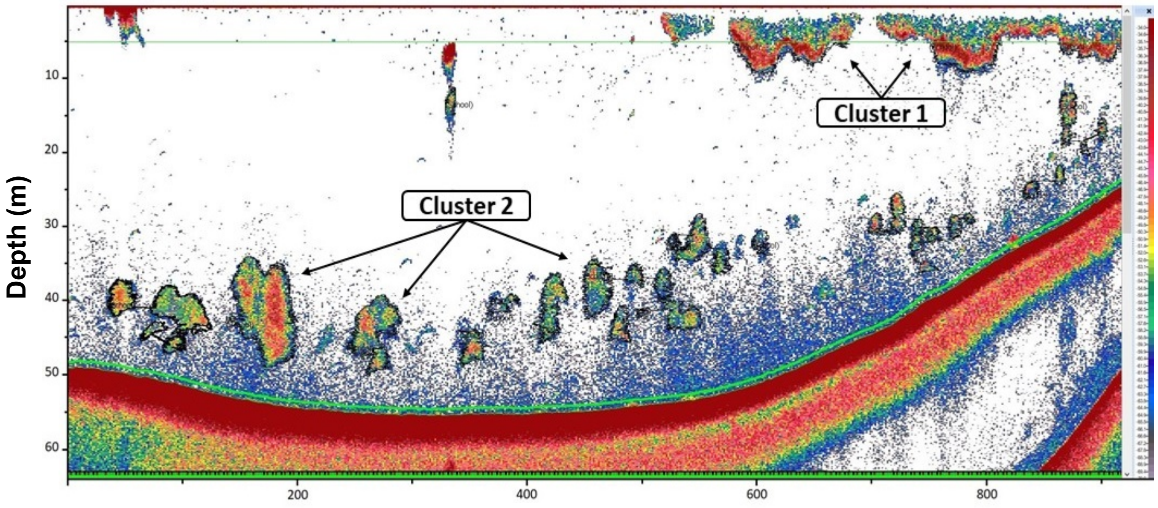


Figure 3.7: Echogram with examples of the 2 clusters obtained in the cluster analysis.

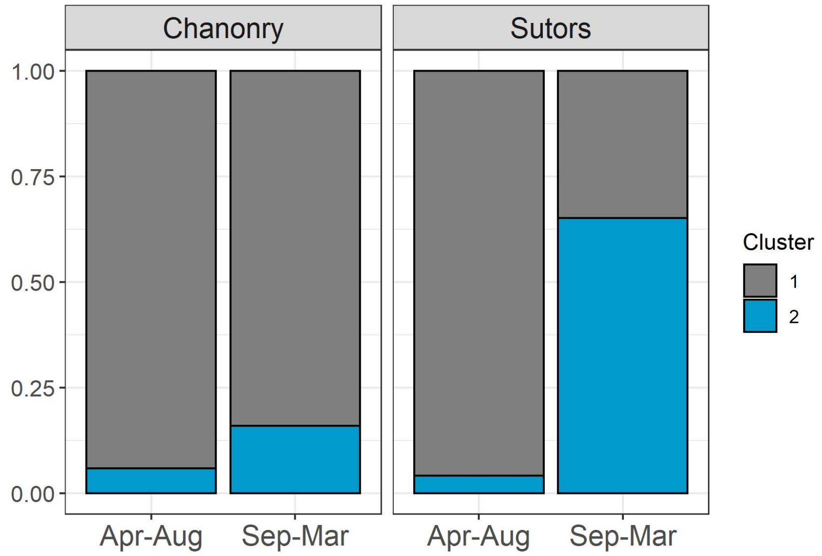


Figure 3.8: Proportion of acoustic biomass (PRC_NASC) during day-time divided into the two groups obtained via cluster analysis (cluster 1: grey; cluster 2: blue).

Tidal patterns in fish density and schooling behaviour

There were no differences in fish density or centre of mass between tidal stages, either in Sutors or Chanonry (Table 3.5,Table 3.6 and Figure 3.5b). The index of aggregation varied between sites but not between tidal stages (Table 3.5) and was higher in Chanonry than in Sutors during both flood and ebb (Figure 3.5b). The number of fish tracks was higher during flood than during ebb and it was higher in Sutors than in Chanonry (Figure 3.5b; see echogram examples for the tidal comparison in Supplementary material Figures S3.3).

Diel patterns in fish density and schooling behaviour

The interaction between day-night and season was significant for fish density in Sutors (Table 3.5). In summer no significant differences were found in the diel cycle for acoustic biomass (Kruskal-Wallis: X^2 = 0.0819, p-value= 0.7747), but in autumn it was higher during the night than during the day (Kruskal-Wallis: X^2 = 8.2848, p-value= 0.0039). The centre of mass was shallower during daytime than during night-time and shallower in summer than in autumn (Figure 3.5c and Table 3.6). The index of aggregation was higher during the day than during the night in both seasons (Table 3.5 and Figure 3.5c). The number of fish tracks per kilometre was higher during the night than during the day in both seasons (Table 3.5 and Figure 3.5c; see echogram examples for the diel comparison in Supplementary material Figures S3.4).

DISCUSSION

This study documented substantial temporal variability in prey density and behaviour (fish aggregation) in two marine mammal foraging hotspots that could explain patterns in dolphin occurrence. We also developed a methodology to perform small-scale fish acoustic surveys in coastal areas from a small RIB.

This study found that acoustic fish abundance increased during summer months in two narrow estuarine channels. This is in line with studies performed in other temperate estuaries that described an increase in fish abundance and biomass during the warmest seasons (Acuña Plavan et al. 2010; Hagan and Able 2003). Here, the increase in fish acoustic density matched the increase in dolphin occurrence (Fernandez-Betelu et al. 2019), suggesting that changes in fish biomass may be driving seasonal patterns in dolphin occurrence in the Moray Firth. These results are consistent with other studies that found marine mammal preferences for areas with higher fish density (Benoit-Bird et al. 2004; Hazen et al. 2011; Romagosa et al. 2019; Sigler et al. 2012).

In these narrow channels, fish were more aggregated during the day, while the number of individual fish tracks increased during the day (Figure 3.5). These findings are in line with the general daily activity pattern of fish, since, most fish species are aggregated during day-time and dispersed during night-time (Cardinale et al. 2003; Fréon et al. 1996). Fish are generally unable to maintain the school cohesion during the night (Pitcher 2001) because light levels play a critical role the schooling behaviour of fish (Pavlov and Kasumyan 2000). These cyclical aggregation patterns may be a strategy to reduce individual risks to predation (Clark and Levy 1988).

The combination of diel patterns of prey density throughout the seasons, diel differences in index of aggregation and seasonal differences in fish species detected in this study may explain the seasonal shift in the diel behaviour of dolphins. Dolphin occurrence in the area was higher when fish density was higher: in summer prey density was higher during the day than at night, whereas the opposite occurred in autumn. Furthermore, in autumn, the index of aggregation was higher during the day than at night, indicating a highly patchy prey distribution during daytime. Patchiness increases the relative importance of resource limitation (Benoit-Bird and McManus 2012). Therefore, from September to December, the combination of low biomass and high school aggregation may be making the area insufficiently productive for dolphins during daytime. However, observed day-night differences in fish density might be partly due to the bias caused by the vertical migration of fish. Fish in shallower waters produce stronger acoustic backscatter and, hence, higher biomass values (Ona 2003). Nocturnal vertical migration of clupeids has been observed in these channels (Thompson et al. 1991), therefore fish density during the night may have been overestimated.

The variation in fish species composition observed in this study could also contribute to the seasonal shift in the diel behaviour of dolphins. The unsupervised cluster analysis performed in this study revealed two differentiated clusters, one that was more abundant in summer and a second that was more abundant in autumn (Figure 3.7 and Figure 3.8). These results are consistent with historic fisheries data and earlier studies that demonstrated seasonal changes in the species composition of prey schools in the inner Moray Firth (Greenstreet et al. 1998; Hopkins 1986). Sand eels, which increased in abundance in summer and which have high frequency response at 38 kHz (Johnsen et al. 2009), could be represented by cluster one. Herring and sprat, which overwinter in the Moray Firth, match with the echotraces and seasonal pattern of abundance of cluster two (Figure 3.7 and Figure 3.8). Although our cluster analysis results are limited by the lack of ground-truth data (McClatchie et al. 2000), they do provide some contemporary support for the seasonal changes in fish species composition reported in earlier studies (Greenstreet et al. 1998; Thompson et al. 1991). Information about the diet of bottlenose dolphins in this area is very limited (Santos et al. 2001). Studies elsewhere suggest that dolphins are generalist predators that take advantage of seasonally or locally abundant prey (Klinowska 1991). Opportunistic pictures of bottlenose dolphins feeding events obtained in the area are in line with this theory (see Appendix I). Shifts in prey distribution are often suggested to be the main drivers of changes in dolphin habitat use (Bearzi et al. 2008; Gnone et al. 2011) Similarly, dolphins can modify their foraging strategies between seasons switching from nocturnal to diurnal behaviour when they target different fish species (Markowitz et al. 2004). Therefore, in the inner Moray firth, dolphins may be present during daytime in summer to take advantage of high levels of sand eel biomass, a species that buries in the sand at night (Freeman et al. 2004). Whereas in autumn, when biomass of sand eels decreases and herring increases (Greenstreet et al. 1998), dolphins may become nocturnal and forage on herring when they spread in the water column at night to feed (Cardinale et al. 2003). Herring’s escape capabilities decrease in low-density schools (Rieucau et al. 2014) and when they are feeding (Fernö et al. 1998). Predator foraging success increases when they target more vulnerable prey (Quinn and Cresswell 2004). Dolphins in this area may thus be targeting herring at night, when fish are more vulnerable.

Previous studies in deeper off-shore waters have often linked dolphin occurrence with vertically migrating prey (Benoit-Bird and Au 2003; Benoit-Bird et al. 2019; Scott and Chivers 2009). For air-breathing predators, targeting prey that are closer to the surface reduces the energetic costs of foraging (Doniol-Valcroze et al. 2011; Tyson et al. 2016). For this reason, I hypothesised in Chapter 2 that dolphins became nocturnal in autumn because feeding at night, when herring migrate towards the surface (Thompson et al. 1991), might be more cost-effective for them (Fernandez-Betelu et al. 2019). However, our study has been unable to show any diel change in the centre of mass that could explain the seasonal interaction with the diel occurrence of dolphins. The CM was not closer to the surface at night than during the day in autumn. This discrepancy may be explained by the fact that CM is the average of the depths of all the detected schools weighted by their volume backscatter coefficient values (Urmy et al. 2012). Therefore, it might not be a good indicator of the vertical migration of a particular species, especially, as in this case, when there are two species migrating in opposite directions. Additional studies specifically focused on dolphin diving behaviour are suggested to further investigate this theory.

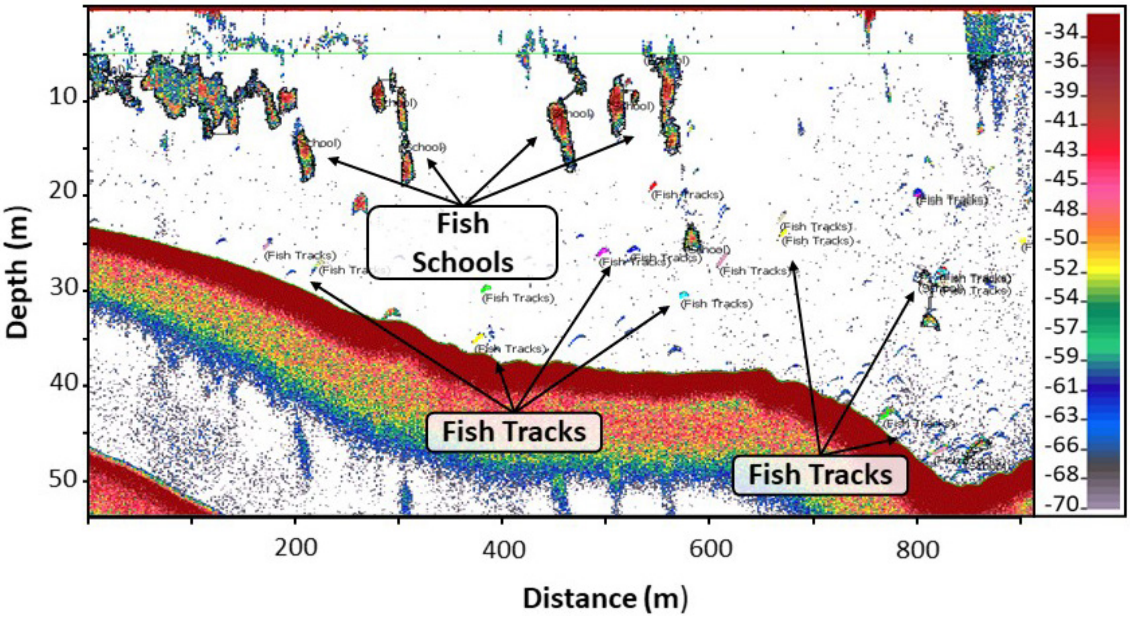
The increase in the number of fish tracks per kilometre during flood partially explains the increase in dolphin occurrence during this tidal stage. Previous studies in the area linked the presence of tidal fronts with foraging behaviour of dolphins and hypothesised that fronts increased dolphin foraging success (Bailey and Thompson 2010). Many studies described fronts and eddies as highly productive areas that exhibit higher prey concentrations (see Benjamins et al. 2015 for a review). It is believed that tidal streams have the potential to increase prey availability and encounter rate (MacKenzie and Leggett 1991; Zamon 2003). Additionally, strong currents enhance fish vulnerability to predation by disorienting them and breaking up fish school cohesion (see Benjamins et al. 2015 for a review). In this line, may studies described tidal fronts as key oceanographic drivers of predator occurrence (Cox et al. 2018a; Mendes et al. 2002; Scott et al. 2010; Waggitt et al. 2016). Our results are consistent with these studies, the increase in single fish detections during flood tide may be exploited by dolphins to enhance their foraging success. However, we detected a higher number of fish tracks in Sutors than in Chanonry whereas dolphin occurrence is linked to tides in Chanonry but not in Sutors (Fernandez-Betelu et al. 2019). A possible explanation for this might be that there was a mismatch in the spatial scale of our surveys in Chanonry. Bottlenose dolphins show preference for small, localised areas within the channel when they are foraging in Chanonry (Bailey and Thompson 2006). The transects performed in this study covered a much larger area so we might have diluted any potential tidal variation from the dolphins' perspective. Furthermore, when dolphins were present in the channel, we had to avoid the area they were using to prevent any potential disturbance, so we might have missed important information. Alternatively, previous studies in the area have suggested that, in summer, dolphin occurrence might be driven by salmon (Hastie et al. 2004; Wilson et al. 1997). Salmon are likely to have been poorly detected by our echo sounder as data from tagged adults shows that they typically remain in the top few meters of the water column during their return migration (Godfrey et al. 2015). Therefore, adult salmon are likely to have either avoided our boat or fallen inside the surface dead-zone of the transducer. Further focussed studies would be needed to investigate the link between salmon and dolphin occurrence in these channels.

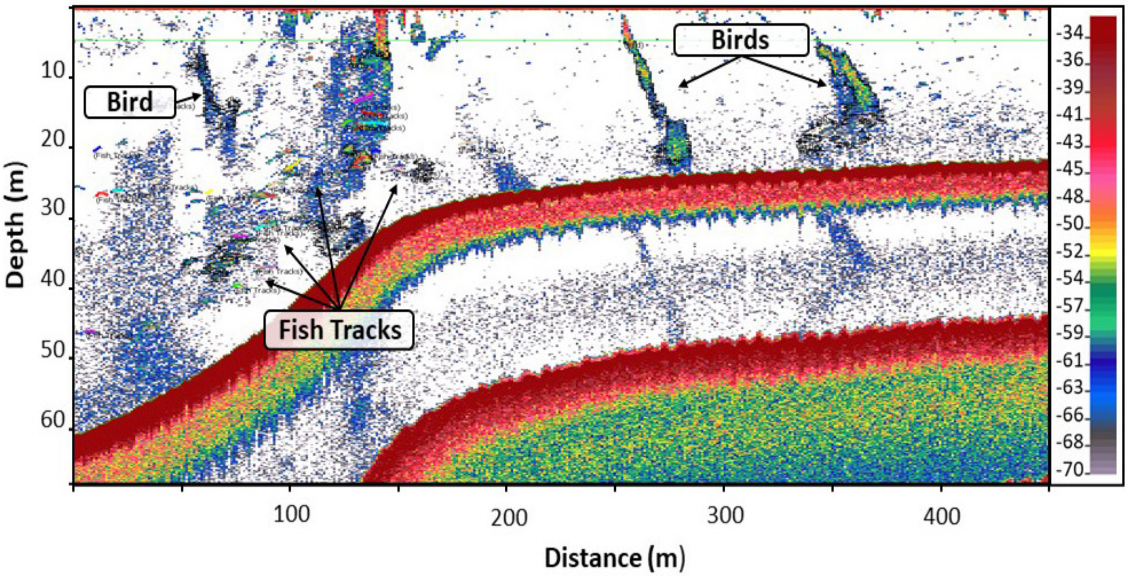
The methodology developed in this study highlights the potential for other researchers to perform fish acoustic surveys at small spatial scales. We demonstrated that robust data can be obtained from a small RIB using a scientific echo sounder and a frame-mounted transducer. Scientific vessels are expensive to operate and less suitable for studying shallow coastal areas. The method used here is more cost-effective but remains challenging, particularly under winter conditions. Furthermore, boat-based acoustic transects provide only snapshots of prey abundance and may not be a good reflection of prey availability from the predator's perspective. For example, our design was unable to account for other sources of temporal variability such as day-to-day variability or the spring-neap tidal cycle. The weather (Lehodey et al. 2006) and the lunar cycle (Numata and Helm 2014) are known to affect fish abundance and behaviour in coastal ecosystems, and both these factors may constrain small boat survey designs. Some studies have been able to use seabed-mounted echo sounders to obtain longer time-series data (Fraser et al. 2018; Kaartvedt et al. 2009) and overcome some of these logistic issues. In future, research using moored systems could be used to acquire a more thorough knowledge of prey field variability in these dolphin foraging hotspots.

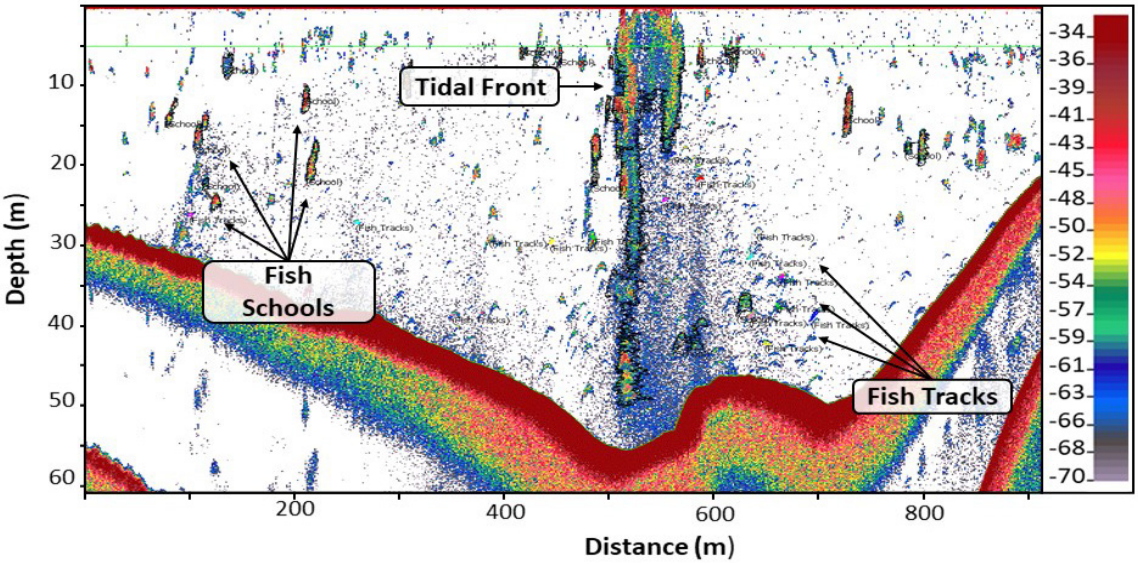
This study was performed at two foraging hotspots of a protected population of dolphins (Hastie et al. 2004) and provided insight into the prey resources that these protected animals might be exploiting. Furthermore, the design developed here is a robust method that could be applied in other projects where hiring large scientific vessels is not feasible. For protected marine predators, knowledge about the distribution and abundance of their prey is key since foraging opportunities influence predator behaviour and demographic trends (New et al. 2013b). Furthermore, understanding the drivers of animal occurrence is essential to inform marine spatial planning and correctly identify potential anthropogenic impacts (Benoit-Bird et al. 2020). The findings on temporal variability in prey abundance and behaviour from this chapter suggest several hypotheses and highlight the need for additional research to better understand the link between bottlenose dolphins and their prey.

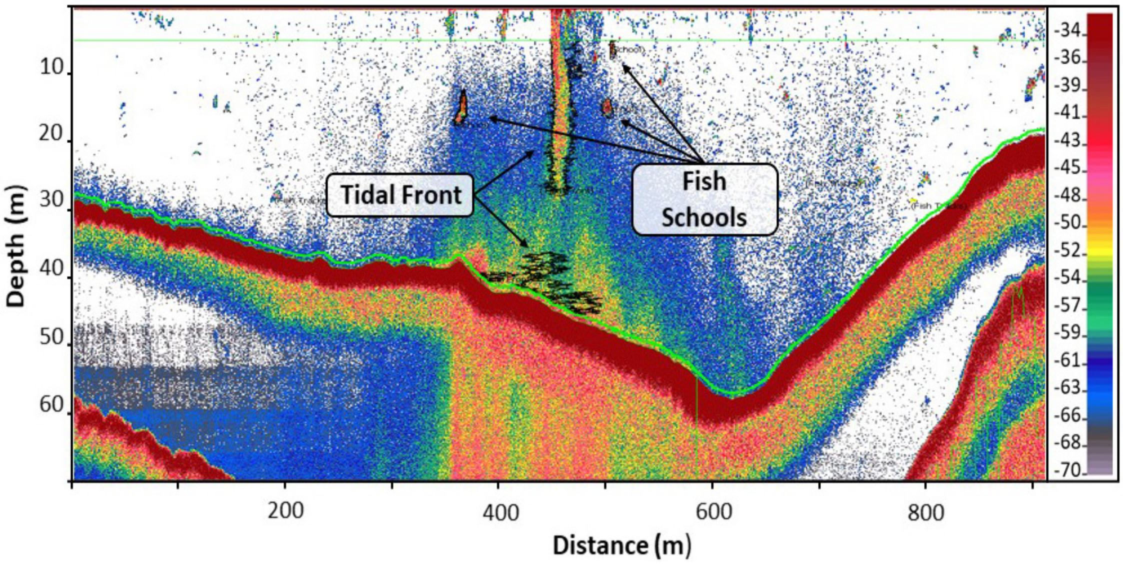
SUPPLEMENTARY MATERIAL

Supplementary Figures S3.1: EchoView screenshots with examples of classified regions:






Tidal Front
Fish Schools
Fish Tracks
Depth (m)
10
20
30
40
50
60
Distance (m)
200
400
600
800
-34
-36
-39
-41
-43
-45
-48
-50
-52
-54
-57
-59
-61
-63
-66
-68
-70


Tidal Front
Fish Schools
Depth (m)
10
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Distance (m)
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-39
-41
-43
-45
-48
-50
-52
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-68
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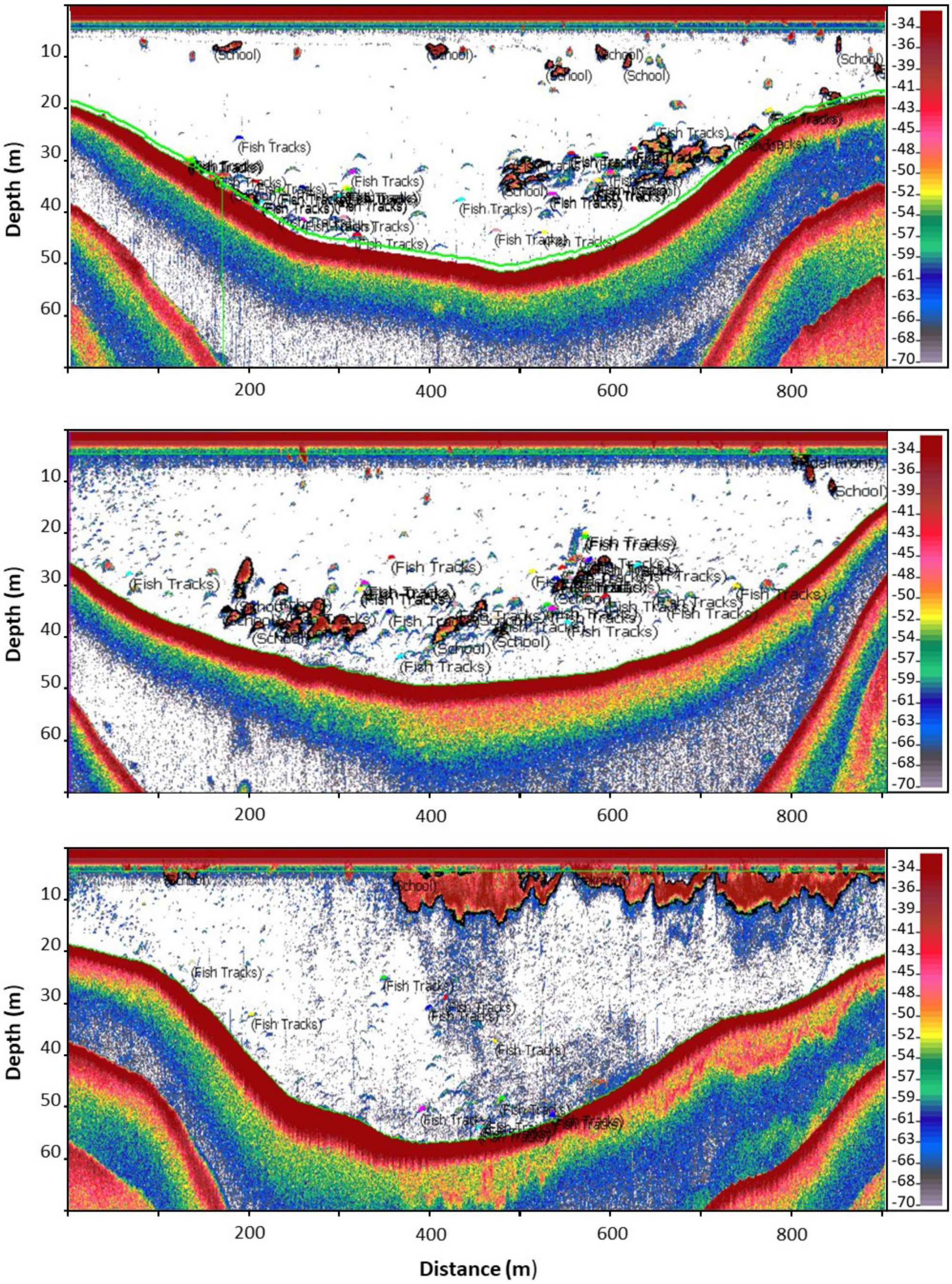
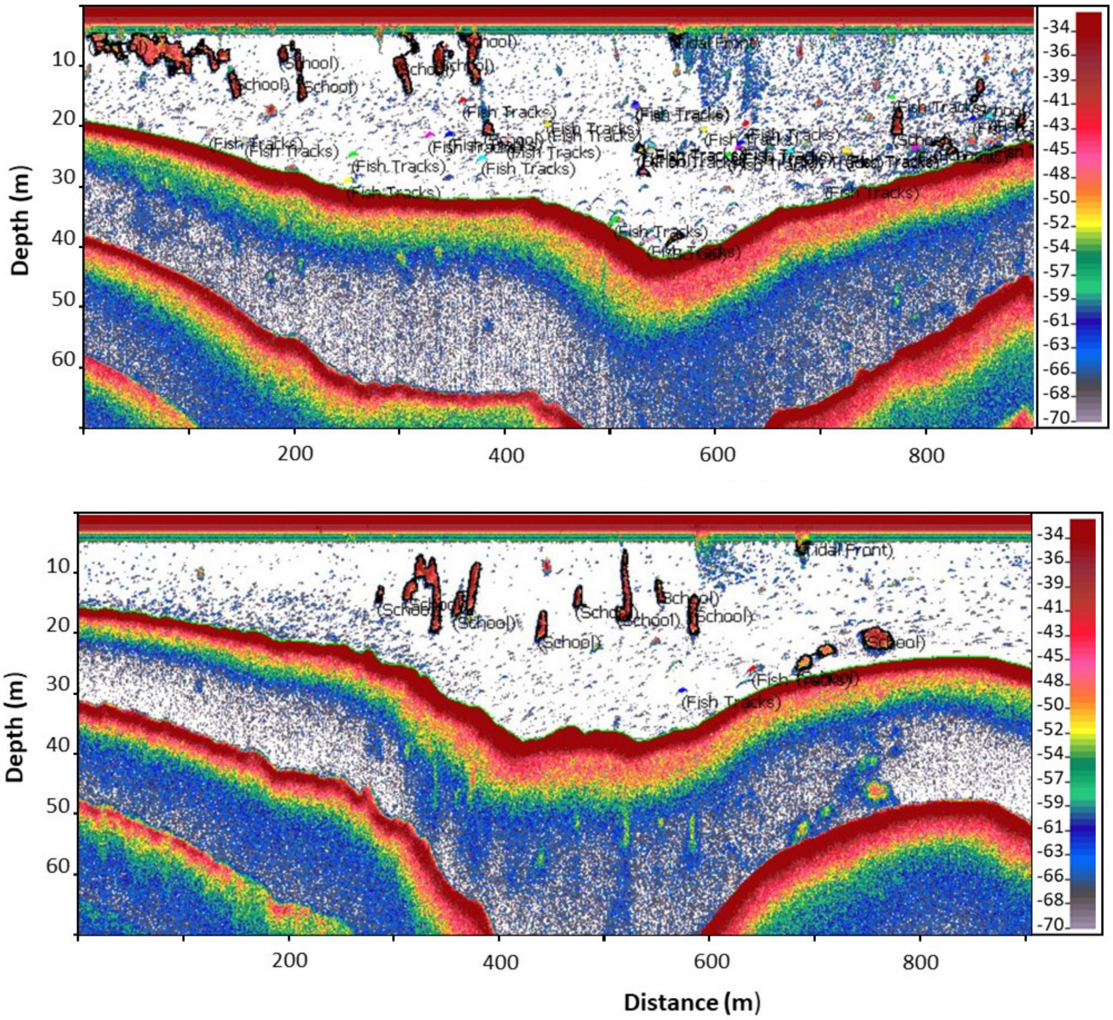
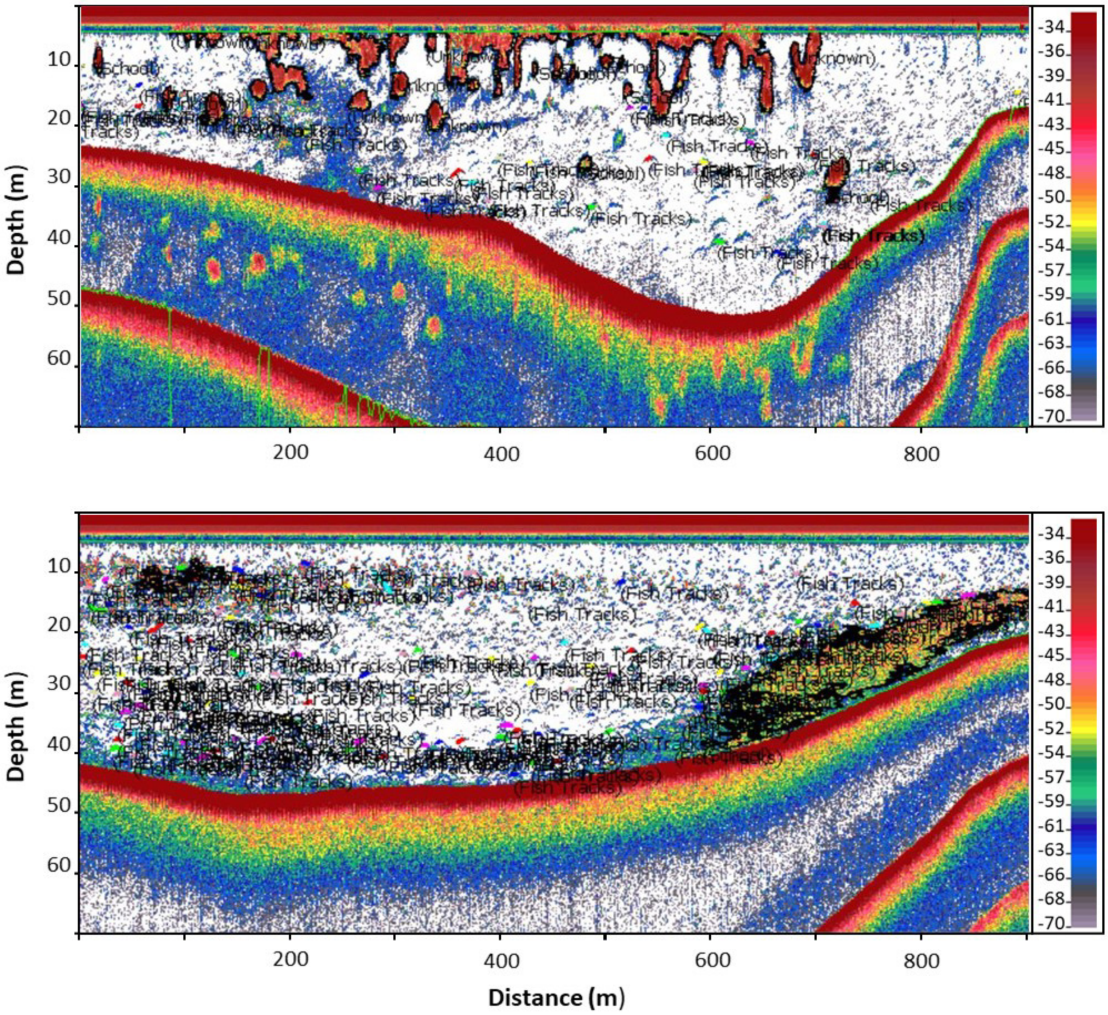
Supplementary Figures S3.2: EchoView screenshots showing seasonal differences in fish school and fish track detections. Images show the echograms obtained with the 38 kHz transducer in January (top), October (middle) and July (bottom) during daytime and flood tide in Sutors



Supplementary Figures S3.3: EchoView screenshots showing tidal differences in fish school and fish track detections. Images show the echograms obtained with the 38 kHz transducer during flood (top), and ebb (bottom) in June during daytime in Chanonry.



Supplementary Figures S3.4: EchoView screenshots showing diel differences in fish school and fish track detections. Images show the echograms obtained with the 38 kHz transducer during the day (top), and night (bottom) in July during flood, in Sutors.



CHAPTER 4

VARIATION IN FORAGING ACTIVITY INFLUENCES AREA-RESTRICTED SEARCH BEHAVIOUR BY BOTTLENOSE DOLPHINS

CHAPTER 4: VARIATION IN FORAGING ACTIVITY INFLUENCES AREA RESTRICTED SEARCH BEHAVIOUR BY BOTTLENOSE DOLPHINS

ABSTRACT

Area-restricted search (ARS) behaviour is often inferred from animal movements using telemetry and biologging devices. However, tagging small cetaceans is challenging, restricted to a limited number of individuals and not always feasible. Passive acoustic monitoring is an inexpensive alternative for animals that produce vocalizations when feeding. Here, I used passive acoustics to investigate ARS behaviour in a population of dolphins by testing whether the duration of encounters increased when foraging occurred. To do so, we deployed two arrays of passive acoustic devices (CPODs and SoundTraps) within two key bottlenose dolphin foraging areas between May and September 2018. Analyses were based on two independent foraging descriptors: echolocation buzzes, widely used as foraging proxies and bray calls, specifically linked to salmon predation attempts. Buzzes were identified with a mixture model of detected echolocation inter-click intervals and bray calls were manually extracted by visual inspection of the spectrograms. The results revealed that the presence of buzzes or brays led to longer encounters, supporting the theory that bottlenose dolphins initiate ARS behaviour in response to higher prey encounter rates. The presence of bray calls had a

greater effect on encounter duration than echolocation buzzes, which suggests that bray calls may provide a more robust foraging proxy in this study system during the salmon run. This study provided evidence of ARS behaviour in dolphins using bray calls for the first time, corroborating that passive acoustic monitoring is a valuable method for studying ARS behaviour in vocal animals.

INTRODUCTION

Many studies have demonstrated the importance of tidal narrows as foraging habitat for coastal marine mammals and seabirds (see Cox et al. 2018a for a review). In Chapter 2, I used long-term data from echolocation devices (CPODs) to explore how the occurrence of bottlenose dolphins varied over different temporal scales in two important foraging areas located in tidal narrows within the Moray Firth; the Sutors and Chanonry narrows. The distributional range of these animals extends along the east coast of Scotland (Arso Civil et al. 2019; Cheney et al. 2013) but they regularly move into these areas to forage (Hastie et al. 2004), with a peak in dolphin occurrence during summer and autumn (Fernandez-Betelu et al. 2019). They feed on a variety of prey (Santos et al. 2001; see Photo Appendix I) and previous studies highlighted that prey patches vary seasonally, with an increase in abundance of returning Atlantic salmon in summer (Janik 2000) and an influx of clupeids in autumn (Thompson et al. 1991).

Animals should adopt foraging strategies that maximise their energy intake, because obtaining adequate food supply affects their survival, growth, and reproductive success (Pirotta et al. 2019). Area-restricted search (ARS) theory suggests that, in patchy environments, animals should increase search effort after detecting a prey item due to the higher probability of detecting other prey nearby (Hoskins et al. 2015; Kareiva and Odell 1987). As a result, predators are expected to increase their residency times within productive areas where foraging success is high before continuing wide range exploration (Benhamou 1992). The detection of productive areas where ARS occurs provides valuable information for conservation management (Lascelles et al. 2016) and it is particularly critical for protected species such as marine mammals (Panigada et al. 2017).

In the marine environment ARS behaviour has been demonstrated across a wide array of taxa using satellite tags (Adachi et al. 2017; Freitas et al. 2018; Sommerfeld et al. 2013; Stalder et al. 2020). Area-restricted movements are generally inferred from an increase in the tortuosity of animal tracks and a decrease in travel speed (Carter et al. 2016; Cox et al. 2018b). However, finding empirical evidence of the drivers of ARS behaviour in marine predators remains challenging due to the difficulties of linking their movements or occurrence to feeding events at sea (Votier et al. 2013; Watanabe and Takahashi 2013). Furthermore, tagging some species such as small cetaceans remains challenging, often limited to a small number of individuals and not always feasible.

Marine mammals that use acoustic cues when foraging, such as echolocation or vocalizations, enable researches to investigate ARS behaviour using passive acoustic techniques. For instance, recent research by Bailey et al. (2019) found empirical evidence that ARS behaviour in bottlenose dolphins was linked to foraging activity by deploying single echolocation detectors at four open water sites at 15 km intervals off the East coast of the USA shelf waters. Using echolocation detections to detect both the occurrence of dolphins (Nuuttila et al. 2013b) and the presence of foraging buzzes (Pirotta et al. 2014b), they found that the probability of bottlenose dolphins leaving areas within the detection range of each CPOD (< 1000 m; Roberts and Read 2015) decreased when a higher proportion of foraging buzzes was detected during the first third of an encounter. Given that ARS behaviour assumes that animals remain in an area after detecting prey (Kareiva and Odell 1987), the probability of animals leaving the area would also be expected to decrease whenever foraging calls were detected. However, contrary to ARS theory, Bailey et al. (2019) also found that the probability of animals leaving the area increased when there was a higher proportion of foraging during the last third of the encounter. To explain these results, Bailey et al. (2019) hypothesised that the restricted range of the single echolocation detectors used in this study (< 1000 m) may not have captured the complete period of ARS behaviour in each foraging patches. Consequently, the initial start and/or cessation of foraging could have been missed due to a mismatch between the passive acoustic device's detection range and the restricted-search area used by the animals.

In this chapter, I built upon the approach used by Bailey et al. (2019) to investigate whether variation in prey encounters influenced ARS behaviour of dolphins using the Sutors and Chanonry channels. As in Bailey et al. (2019), previous acoustic studies in these channels had typically been based on single CPODs at long-term monitoring sites that covered just part of the channels

(Fernandez-Betelu et al. 2019; Pirotta et al. 2015b). However, visual surveys have shown that dolphins may occur across wider areas within these channels (Bailey and Thompson 2010; Cheney et al. 2014; Hastie et al. 2003b). Therefore, whilst single CPODs can be used to investigate larger scale patterns of presence in the area (Chapter 2) they may not capture the detailed characteristics of dolphin encounters within these channels. In this study, a broader array of CPODs was deployed across the two sites to improve the characterisation of dolphin encounters within each of these key foraging areas. CPODs and broadband sound recorders were deployed in summer, when dolphins are known to feed on returning salmon (Figure 4.1; Butler et al. 2006), because dolphins produce a specific call when feeding on these fish (bray calls; Janik 2000) which provides an opportunity for an independent proxy for prey encounters. I tested whether the ARS behaviour of dolphins could be linked to foraging in these channels by using two different foraging proxies to characterise prey encounters. Following Bailey et al. (2019) methodology I extracted echolocation buzzes, which have been widely used as foraging descriptors (Arranz et al. 2019; Pirotta et al. 2015b; Wisniewska et al. 2018). In addition, bray calls, which are specifically linked to salmon catching attempts, and which have also been used as foraging descriptors (Cascao et al. 2020; King and Janik 2015), were extracted from parallel deployments of broadband acoustic recorders (SoundTraps*; Ocean Instruments, NZ*). To further investigate findings by Bailey et al. (2019), I tested whether detecting these two foraging proxies at the beginning or end had different effects on the encounter duration. More specifically, I hypothesised that (1) dolphins would remain longer in these channels when foraging occurred and (2) the duration of those encounters in which foraging occurred would increase, regardless of whether proxies of foraging were detected at the beginning or end of the encounter.

Figure 4.1: Bottlenose dolphin feeding on Atlantic salmon at Sutors. Photo by Dr B. Cheney - © Lighthouse Field Station, University of Aberdeen.

MATERIAL AND METHODS

Acoustic deployments

Passive acoustic monitoring was conducted from May to September 2018 at Sutors (57° 41.41’N, 03° 59.18’W) and Chanonry (57° 5.14’N, 04° 5.85’W), two channels within the Moray Firth SAC (NE Scotland, Figure 4.2). They are both narrow channels considered to be foraging hotspots for the population of bottlenose dolphins in the area (Hastie et al. 2004).

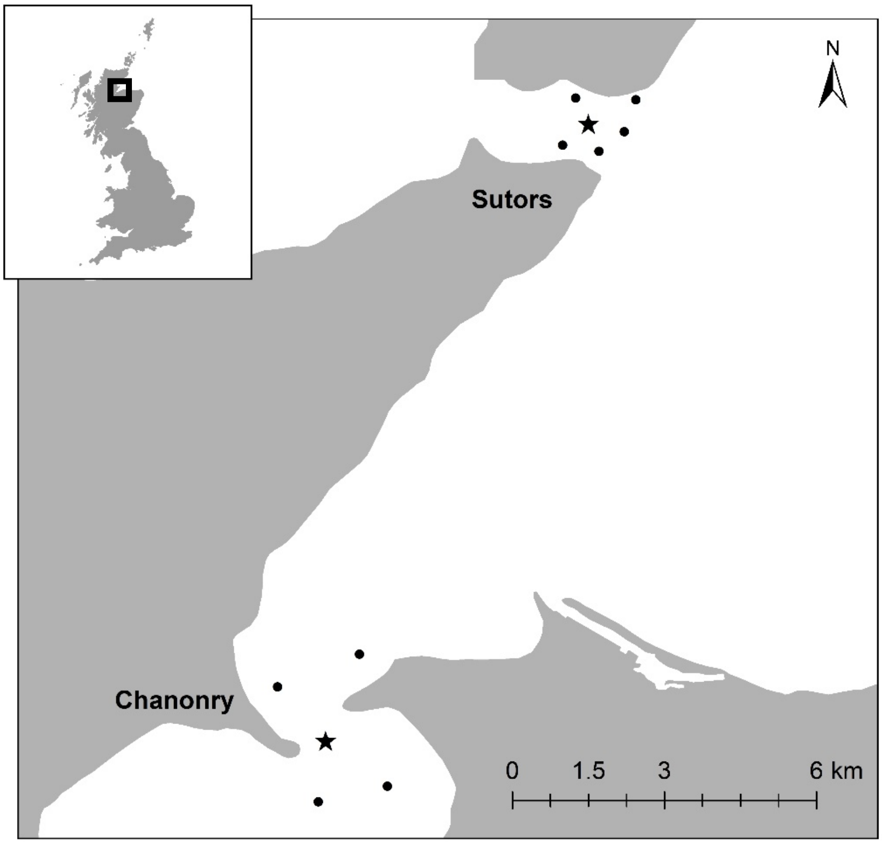


Figure 4.2: Map showing the passive acoustic monitoring arrays deployed at Sutors and Chanonry in NE Scotland: (●) C-POD and (★) C-POD+SoundTrap locations.

Echolocation detectors (CPODs*;* Chelonia Ltd, UK) were deployed 2 m above the seabed to record continuously at five sites within the Chanonry narrows and six sites within the Sutors. The arrays were thus designed to optimise coverage across both channels and maximize the detection of echolocating dolphins at each site. A single broadband sound recorder (SoundTrap ST300HF; Ocean Instruments, NZ) was deployed at the mooring in the middle of each array (Figure 4.2) and was duty cycled to record 10 min in every 20 min at a 48 kHz sampling rate.

Encounter definition

Unique encounters within each site were defined based on the echolocation clicks detected on each of the two arrays of CPODs. Dolphin encounter was defined as a group of clicks, detected by any CPOD in the array, containing no gaps longer than the 95th quartile of the time gap distribution between click-detection positive minutes. To do this, dolphin click details classified as *High* and *Moderate quality* were downloaded using the manufacturer's custom software (www.chelonia.co.uk). Click detections were grouped by CPOD array and all minutes containing dolphin click detections on at least one of the CPODs within each array were extracted. The distribution of time intervals between these detection-positive minutes was investigated and the 95th quartile of the distribution was calculated. Following the methodology used by Bailey et al. (2019), only encounters exceeding 5 minutes in duration were used in further analyses.

Data processing

Two different proxies of dolphin foraging behaviour were used: echolocation buzzes and bray calls, extracted from the CPODs and SoundTraps respectively. Echolocation buzzes are click trains with low inter-click intervals (ICI), that have been linked to prey capture attempts and are used as foraging activity descriptors (Arranz et al. 2019; Pirotta et al. 2015b; Wisniewska et al. 2018). Bray calls are low frequency vocalizations that have been linked to salmon predation attempts in the area (Janik 2000). Each single bray consists of two parts, a long multiband burst-call and a short tonal downsweep, with most of their energy below 2 kHz (Figure 4.3).

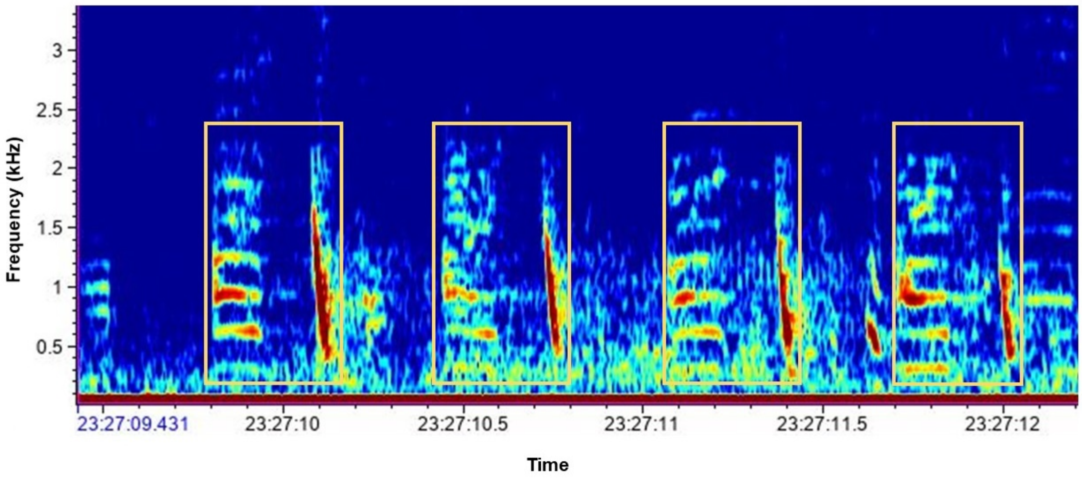


Figure 4.3: Example of spectrogram (Raven Pro 1.6) with four bray calls highlighted with yellow squares.

To extract echolocation buzzes, I grouped echolocation click detections by CPOD array and performed a Gaussian mixture model (Pirotta et al. 2014b). Encounters shorter than 20 min were divided into two halves, with the first half representing the beginning and the second half representing the end of the encounter. To ensure the buzz dataset was comparable with the duty cycled acoustic recordings, for encounters of longer than 20 minutes only the first and last 10 minutes were used, to represent the beginning and end of the encounter respectively.

Dolphin bray calls were identified manually using Raven Pro 1.6.1 software through visual inspection of the spectrograms (0 - 3.5 kHz, Hann window, window size 1,024, 85 % overlap; Figure 4.3), following the description by Janik (2000). Given the extensive dataset, the manual extraction of bray calls was limited to a subsample of dolphin encounters from July (the peak in salmon run in the area; Butler et al. 2006) in which at least 5 minutes of SoundTrap recordings were available. Given that bottlenose dolphin occurrence has been linked to tides in the area (Fernandez-Betelu et al. 2019), the tidal stage at the middle point of each encounter was calculated and encounters were divided into four groups (high-ebb-low-flood). Encounters were subsequently subsampled following stratified random sampling to obtain a representative sample with a variety of tidal stages for the manual extraction of bray calls. For encounters longer than 20 minutes, only two sound files were processed: the first (beginning of encounter) and last (end of encounter) sound files with at least 5 minutes inside the encounter.

Statistical analysis

I tested the two hypotheses using four generalized linear models (GLM) with encounter duration as the response variable. To test whether dolphins remained longer in the area when foraging occurred, I included the presence of buzzes (Model 1) and brays (Model 2) in an encounter as binary explanatory variables (0/1) in separate models. Presence of foraging was defined as positive (1) when at least one buzz or bray call was detected during that encounter. To test whether encounter duration was affected differently by the point at which foraging occurred within the encounter, I defined four encounter states by the presence or absence of foraging at the beginning and end of the encounter: “Not foraging-Not foraging” (0-0), “Not foraging-Foraging” (0-1), “Foraging-Not foraging” (1-0) and “Foraging-Foraging” (1-1). I included buzz encounter states (Model 3) and bray encounter states (Model 4) as explanatory variables in separate models. I used Tukey post-hoc tests for multiple comparisons to investigate potential differences between encounter states. I excluded encounters with only one SoundTrap file from this second analysis. To investigate potential differences between sites I included an interaction with site as an explanatory variable in all four models.

RESULTS

The distribution of time gaps between successive dolphin echolocation click detections ranged from 1 to 1581 min (26.35 h) in Sutors and from 1 to 2012 min (33.53 h) in Chanonry, the 95th quartile being 8 and 26 min respectively. Sutors 95th quartile was discarded because a 10 min time gap to define encounters caused temporal autocorrelation in a previous study suggesting that a longer threshold was needed (Fernandez-Betelu et al. 2019). Chanonry data was thus selected to differentiate encounters and the threshold was rounded up to 30 min to be consistent with previous studies in NE Scotland (Palmer et al. 2017). Therefore, I defined a dolphin encounter as a group of click trains, detected by any CPOD in the array, containing no gaps longer than 30 minutes. The buzz dataset comprised a total of 1283 dolphin encounters of which 96 were processed in Raven for the manual extraction of bray calls (Table 4.1 and Figure 4.4). No obvious seasonal trend in encounter duration was observed at either site (Figure 4.5).

Table 4.1: Number of bottlenose dolphin encounters and total hours processed for the two sites.

		Total processed encounters	**Total processed hours**	**Median Encounter Duration (min)**
Buzz dataset	*Sutors*	706	218.18	45.62
	Chanonry	577	168.42	37.99
Bray dataset	*Sutors*	49	13.27	56.47
	Chanonry	47	12.81	60.81

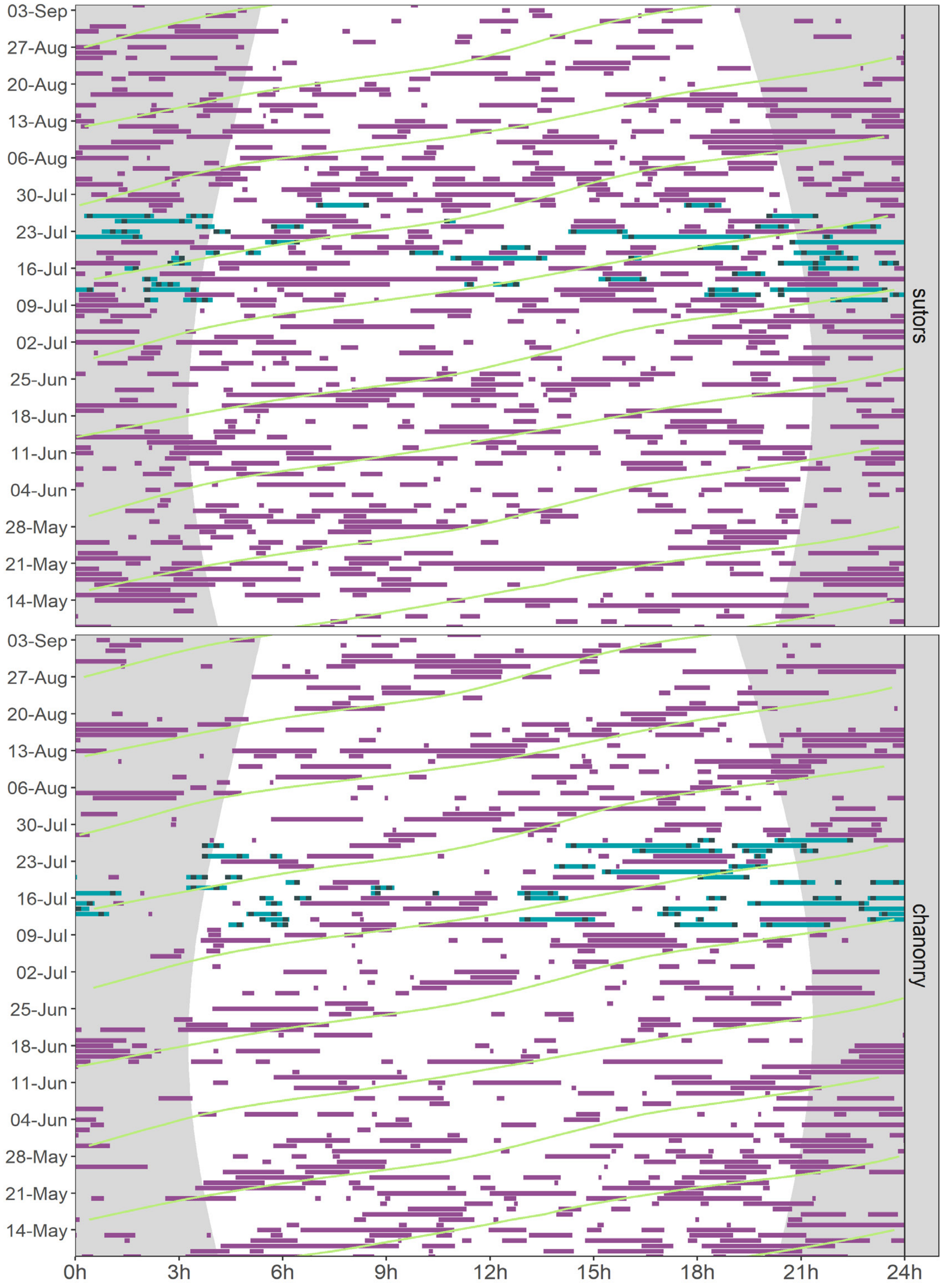


Figure 4.4: Dolphin encounters for the entire CPOD deployment defined by CPOD click detections (purple). Subsample of encounters included in the bray dataset (blue) and corresponding SoundTrap files processed in Raven Pro 1.6 for the extraction of bray calls (black) per day and site: Sutors above, Chanonry below. Daytime (white area), night-time (grey area) and high tide (light green line).

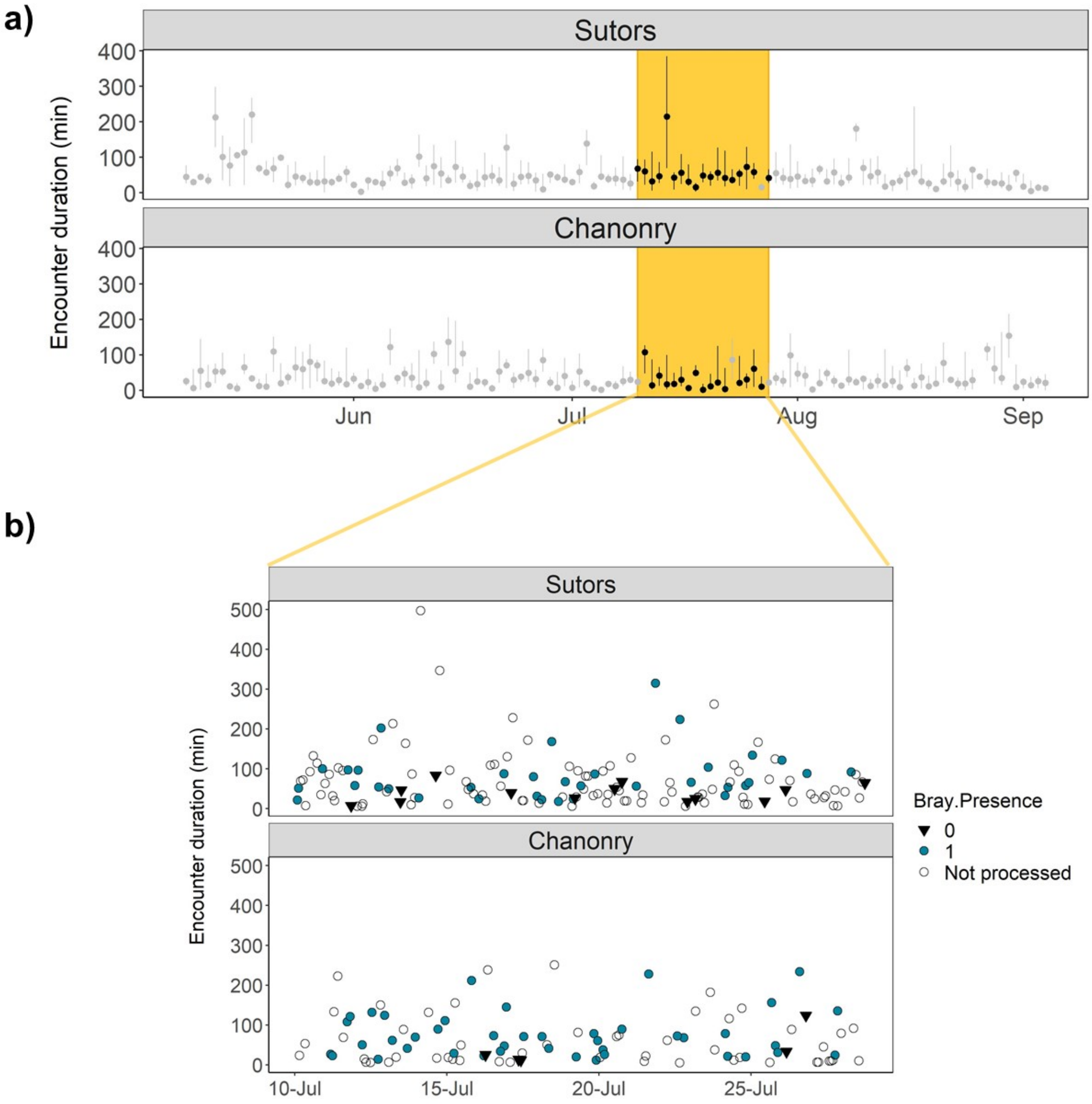


Figure 4.5: a) Median dolphin encounter duration and inter-quartile ranges for the entire CPOD deployment (May-Sept. 2018), days with encounters processed for the bray extraction in black; b) Duration of each of the encounters processed in Raven for the bray extraction (black triangles: encounters without brays; blue circles: encounters with brays; empty circles: encounters not processed in Raven).

As predicted from my first hypothesis, dolphin encounters were significantly longer when either echolocation buzzes (GLM: X^2 = 19.700, Df = 1, p-value < 0.001) or foraging bray calls (GLM: X^2 = 10.147, Df = 1, p-value =

0.001) were detected. The effect of bray calls on encounter duration was greater than the effect of buzzes: median encounter duration was 117% longer in the presence of brays (from a median of 30 mins to 65 mins) and 60% longer in the presence of buzzes (from a median of 30 mins to 48 mins; Figure 4.6a-b).

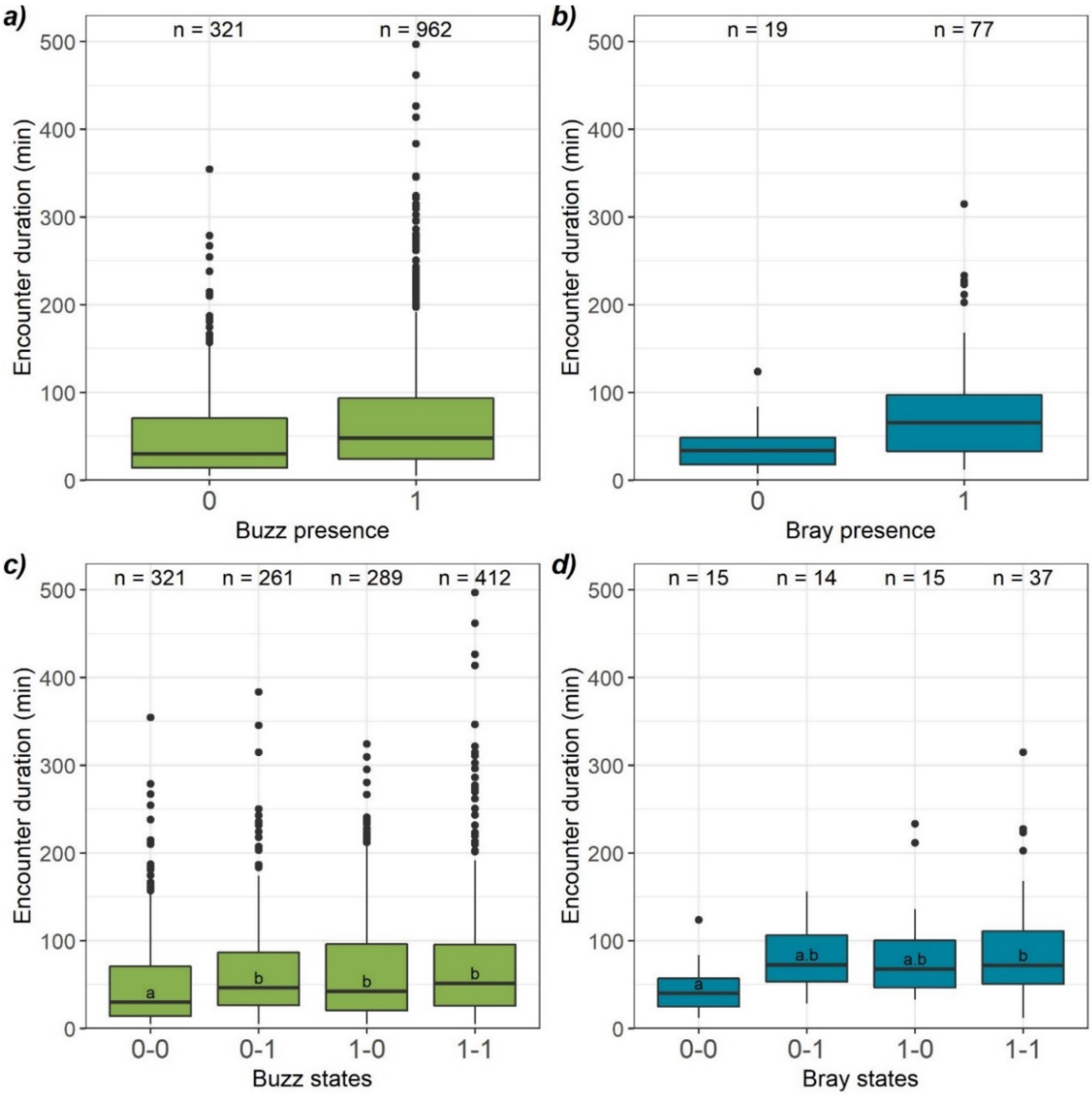


Figure 4.6: Encounter duration in minutes per a) Buzz presence (Model 1), b) Bray presence (Model 2), c) Buzz encounter states (Model 3) and d) Bray encounter states (Model 4). N indicates total number of encounters per group. Unlike letters denote state groups that differed statistically from each other in Tukey post-hoc test (e.g. a and b: p < 0.05; a and a.b: p > 0.05).

Supporting my second hypothesis, dolphin encounters were significantly longer when buzzes were detected at any time of the encounter (0-1, 1-0, 1-1; Model 3, Figure 4.6c) than encounters without any buzzes (0-0; Table 4.2). A similar pattern was seen with brays (Model 4; Figure 4.6d), but sample sizes were much smaller and only one contrast was statistically significant: encounters with brays in both the beginning and end (1-1) were significantly longer than encounters without any brays (0-0; Table 4.2).

Table 4.2: Pairwise comparisons between buzz states (Model 3) and bray states (Model 4) using Tukey's method to adjust for multiple comparisons. Significant contrasts in bold.

	Contrast	Estimate	SE	Z-ratio	p-value
Model 3: Buzz states					
	0-0 - 0-1	-13.31	4.95	-2.692	**0.0358**
	0-0 - 1-0	-14.86	4.86	-3.059	**0.0119**
	0-0 - 1-1	-22.49	4.65	-4.838	**< 0.0001**
	0-1 - 1-0	-1.54	5.60	-0.276	0.9927
	0-1 - 1-1	-9.17	5.42	-1.692	0.3279
	1-0 - 1-1	-7.63	5.34	-1.428	0.4816
Model 4: Bray states					
	0-0 - 0-1	-33.92	16.43	-2.065	0.1646
	0-0 - 1-0	-42.12	17.25	-2.442	0.0694
	0-0 - 1-1	-44.68	12.81	-3.487	**0.0027**
	0-1 - 1-0	-8.20	20.97	-0.391	0.9797
	0-1 - 1-1	-10.76	17.51	-0.614	0.9275
	1-0 - 1-1	-2.56	18.28	-0.140	0.9990

All the results were consistent between sites: neither site nor the interaction with site were significant in any of the models (Table 4.3).

Table 4.3: Generalised Linear Model (GLM) results for each of the 4 models performed.

	Explanatory Variables	Chisq	Df	p-value
Model 1				
	Buzz presence	19.7001	1	**< 0.0001**
	Site	0.1275	1	0.7210
	*Buzz presence * Site*	0.0103	1	0.9195
Model 2				
	Bray presence	10.1467	1	**0.0014**
	Site	0.2418	1	0.6228
	*Bray presence * Site*	0.0660	1	0.7972
Model 3				
	Buzz states	23.5113	3	**< 0.0001**
	Site	0.2785	1	0.5977
	*Buzz states * Site*	2.2750	3	0.5173
Model 4				
	Bray states	10.3125	3	**0.0161**
	Site	0.7902	1	0.3740
	*Bray states * Site*	2.9643	3	0.3972

DISCUSSION

Understanding of mechanisms underlying movement patterns of marine top predators is often constrained by limited information on encounters with prey (Hunsicker et al. 2011; Redfern et al. 2006). Here, arrays of different passive acoustic detectors allowed us both to characterise patterns of dolphin occurrence within two foraging areas and obtain acoustic proxies of encounters with prey. In line with the ARS theory, the presence of buzzes or brays led to longer encounters at both sites, supporting my first hypothesis that dolphins would remain longer in an area when feeding occurred. Support for the second hypothesis was found when using echolocation buzzes as foraging proxy, encounters with buzzes were longer regardless of whether they were detected at the beginning or end of the encounter.

Both the detection of echolocation buzzes and bray calls were linked to longer dolphin encounters at the studied sites suggesting that the detection of prey induced ARS behaviour. This is in line with ARS theory, which predicts that animals should spend more time in an area when they find prey because it increases the probability of finding additional prey nearby (Kareiva and Odell 1987). Although it is assumed that predators should adjust their movements in response to prey, the detection of prey does not always induce ARS behaviour in marine predators (Hamer et al. 2009; Weimerskirch et al. 2007). Usually, ARS behaviour is studied tracking animal movements (Hamer et al. 2009; Hoskins et al. 2015; Planque et al. 2020), but many factors hinder our ability to find empirical evidence of ARS behaviour in the marine environment with this methodology. For instance, the inherent difficulties in detecting predator-prey interactions at sea (Watanabe and Takahashi 2013), the need to correctly infer foraging behaviour from animal movements (Sommerfeld et al. 2013), and the importance of choosing the correct spatial scales (Pinaud and Weimerskirch 2005). By using passive acoustic techniques and foraging vocalizations, I was able to link predator-prey encounters without inferring them from predator movements. Furthermore, the acoustic devices were deployed in dolphin foraging hotspots (Hastie et al. 2004) where ARS behaviour should be confined. The use of passive acoustic techniques thus allowed me to overcome some of the limitations faced by animal tagging systems and enabled me to find empirical evidence of ARS behaviour in bottlenose dolphins at two foraging areas.

Results from this study highlighted that the presence of bray calls had a greater effect on encounter duration than echolocating buzzes. There are several possible explanations for these findings. One explanation is that bray calls may provide a more robust foraging proxy for our study system than echolocation buzzes during the salmon run. While bray calls have only previously been recorded in association with salmon feeding events (Janik 2000), echolocation buzzes have been linked both to foraging and to social communication (Herzing 1996; Martin et al. 2019). The buzzes extracted in this study may, therefore, be a mixture of foraging and social buzzes, potentially making these calls a less accurate foraging proxy than bray calls. Further research is required to investigate the different contexts in which bottlenose dolphins use buzzes in the area and the extent to which they can be used as foraging proxies. Another possible explanation is that salmon may be triggering stronger ARS behaviour in this population of dolphins, leading to longer encounters when dolphins detect them. Large and high-quality prey items enhance ARS behaviour in some species (Walsh 1996; Weimerskirch et al. 2007). Salmon are among the largest prey species of these dolphins (Santos et al. 2001; see Photo Appendix I) and they are a high-quality food source (Fritz and Hinckley 2005), with a high lipid and protein content (Machovsky-Capuska and Raubenheimer 2019). They have been suggested as key drivers of the occurrence of this population of dolphins (Hastie et al. 2004; Robinson et al. 2007b; Stockin et al. 2006; Wilson et al. 1997), highlighting their importance as a prey species which may thus cause a stronger ARS behaviour. Lastly, another explanation is that the mechanics of salmon capture themselves may increase dolphin encounter duration. Due to their large size, when dolphins capture a salmon, they may manipulate it for 10 to 15 minutes before swallowing it (B. Cheney, personal communication, June 2020). This increased handling time on its own however, would not suffice to explain the 117% increase (> 30 minutes) in encounter duration observed here.

Supporting my second hypothesis, dolphin encounters were longer when buzzes were detected at any time of the encounter. Consistent with ARS theory (Benhamou 1992), encounter durations were not influenced by how far through the encounter buzzes were detected. Conversely, Bailey et al. (2019) found that the probability of animals leaving the area increased when foraging occurred during either the first minute or the last third of the encounter, but recognised that this could have resulted from the limited detection range (< 1 km; Roberts and Read 2015) around their single CPODs. While Bailey et al. (2019) studied 4 offshore sites, we focused our deployments in two constrained areas where dolphins are known to forage (< 6 km^2; Bailey and Thompson 2010; Hastie et al. 2004). Furthermore, I defined encounters within each of those foraging areas using the combined detections of arrays of five to six CPODs. By doing this, the effective sampling area was increased and there was a greater probability of detecting the complete period of ARS behaviour.

Although the model to test my second hypothesis was not significant using brays as a foraging proxy (Table 4.2), patterns of variation in encounter durations were similar for both buzzes and brays (Figure 4.6c-d). However, sample sizes for brays were smaller and less precisely linked to different stages of the encounter. This was partly because limited battery and data capacity meant that the acoustic recorders could not be deployed for as long as the CPODs. Duty-cycling allowed us to sample for an extended period but meant that we were often unable to analyse the exact first and last 10 minutes of each encounter. Additionally, the duty-cycle and the need to match SoundTrap files with dolphin encounters caused the bias towards longer encounters observed in the bray dataset (Table 4.1). This bias may have caused shorter encounters without brays to be missed, which in turn may have hindered the ability to detect significant differences between bray state groups. Future work using continuous acoustic recordings would be needed to investigate the effect of brays on dolphin encounters in more detail. Another source of mismatch between the bray dataset and dolphin encounters is the different detectability range between brays and echolocation clicks. Here, echolocation clicks detected by CPODs were used to define the beginning and end of dolphin encounters and these devices are known to have a high false negative rate (Fernandez-Betelu et al. 2019). The beams of echolocation clicks are highly directional and, although CPODs can detect dolphin clicks up to 1000m away (Roberts and Read 2015), only the clicks that are directed towards the acoustic device will be detected. On the other hand, since brays are omnidirectional low-frequency calls (< 3 kHz), their detectability should be higher and over bigger ranges than echolocation clicks. This difference in detectability might have caused a mismatch between the beginning and end of encounters based on either short-range echolocation clicks or other omnidirectional long-range calls such as brays.

A caveat of this study is that other factors, such as tides, time of day or boat presence, may have a combined effect on the duration of dolphin encounters in the area. Diel and tidal cycles are known to affect the occurrence of these dolphins at these sites (Fernandez-Betelu et al. 2019). The presence of boats also has an effect on marine mammals (Erbe et al. 2019) and previous studies in the area found that boats modified the behaviour of these dolphins

(Pirotta et al. 2015b). Therefore, these unexplored factors may also have an effect on the duration of dolphin encounters, but the limited number of encounters in the dataset hindered my ability to investigate this in detail. Future research, based on a bigger sample size, should include these sources or variability in the analyses. However, the detection of brays through visual inspection of the spectrograms is a time-consuming activity. It limited the amount of SoundTrap files we could process and extracting vocalizations from a greater number of acoustic recordings would be even more challenging. Lately, artificial intelligence (AI) and machine-learning technologies have been successfully used to automatically detect marine mammal vocalisations from acoustic recordings (Bergler et al. 2019; Harvey 2018). A challenge faced when using AI is that these methods require training with large labelled datasets (Zhou et al. 2017). However, once trained they can process amounts of data that are far beyond the capabilities of manual processing. This study was constrained by the limited amount of SoundTrap files that could be manually processed for the bray extraction. Future research using AI methodology could overcome the limitations of this study and investigate my second hypothesis with a bigger sample size.

The results of this study corroborate the ideas of Bailey et al. (2019) who suggested that passive acoustic techniques are a valuable method for studying ARS behaviour in echolocating animals. These analyses provided evidence of ARS behaviour in bottlenose dolphins by using, for the first time, two foraging proxies: echolocation buzzes and bray calls. Although similar patterns in foraging behaviour were observed with both proxies, results suggest that bray calls may be a better foraging proxy in this area during the salmon run.

Studying in more detail when in the encounter foraging calls occur and linking foraging behaviour with dolphin movements will be an interesting area of further research.

Passive acoustic monitoring is an inexpensive method for investigating marine mammal occurrence. Bailey et al. (2019) proved that echolocation clicks could be used to investigate the ARS behaviour of dolphins. This study broadened those findings, by detecting ARS behaviour using other vocalizations linked to feeding, which will be useful for studying vocal animals that do not echolocate. The development of new technologies to automatically detect animal vocalizations, such as deep learning, will open new opportunities to investigate this behaviour in vocal animals.

CHAPTER 5

FAR-FIELD EFFECTS OF IMPULSIVE NOISE ON BOTTLENOSE DOLPHINS

CHAPTER 5: FAR-FIELD EFFECTS OF IMPULSIVE NOISE ON BOTTLENOSE DOLPHINS[2]

ABSTRACT

Increasing levels of anthropogenic underwater noise have caused concern over their potential impacts on marine life. Offshore renewable energy developments and seismic exploration can produce impulsive noise which is especially hazardous for marine mammals because it can induce auditory damage at shorter distances and behavioural disturbance at longer distances. However, far-field effects of impulsive noise remain poorly understood, causing a high level of uncertainty when predicting the impacts of offshore energy developments on marine mammal populations. Here I used a 10-year dataset on the occurrence of coastal bottlenose dolphins over the period 2009-2019 to investigate far-field effects of impulsive noise from offshore activities undertaken in three different years. Activities included a 2D seismic survey and the pile installation at two offshore wind farms, 20-75 km from coastal waters known to be frequented by dolphins. Passive acoustic data in key coastal areas were collected and I used a Before-After Control-Impact design to investigate variation in dolphin detections in areas exposed to different levels of impulsive

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noise from these offshore activities. I compared dolphin detections at two temporal scales, comparing years and days with and without impulsive noise. Passive acoustic data confirmed that dolphins continued to use the impact area throughout each offshore activity period, but also provided evidence of short-term behavioural responses in this area. Unexpectedly, and only at the smallest temporal scale, a consistent increase in dolphin detections was observed at the impact sites during activities generating impulsive noise. I suggest that this increase in dolphin detections could be explained by changes in vocalization behaviour. Marine mammal protection policies focus on the near-field effects of impulsive noise; however, these results emphasize the importance of investigating the far-field effects of anthropogenic disturbances to better understand the impacts of human activities on marine mammal populations.

INTRODUCTION

Ambient noise in the marine environment has increased since the 1950s due to the rise of human activities at sea (Frisk 2012). In response to the heightened concerns about the potential impacts of noise on marine life, many countries have reached international agreements to monitor underwater noise levels (OSPAR 2017; Reeve 2019; Van der Graaf et al. 2012). In Europe, the Marine Strategy Framework Directive (MSFD) requires Member States to avoid sound sources that are likely to cause significant impact in the marine environment (Tasker et al. 2010). The MSFD sets out a series of indicators to assess the environmental status of an area, which for underwater noise is the proportion and spatial distribution of days on which sound sources exceed levels likely to entail significant impact.

Human activities such as pile-driving, seismic surveys and sonars produce some of the most powerful sounds underwater (Gordon et al. 2003). These impulsive sounds are defined as acute, broadband, transient signals with a rapid onset and a rapid decay (< 1 s) and are considered particularly hazardous to marine mammals (Southall et al. 2007). However, during the propagation, the acoustic characteristics of sound change at rates that vary according to the specific environmental conditions. The greatest change in the acoustic characteristics of impulsive sounds occurs within ~ 10 km from the source (Hastie et al. 2019) and, therefore, the hazardous characteristics of these sounds will vary with distance (Southall et al. 2007). Impulsive sounds have the potential to impact cetaceans through direct injury at shorter distances (here near-field) and through behavioural disturbance at longer distances (here far-field; Erbe et al. 2018). Measures to mitigate near-field effects from injury are widely adopted (Bröker et al. 2015; Verfuss et al. 2016). However, potential far-field behavioural effects and the longer-term consequences of any short-term disturbance remain challenging to assess (Pirotta et al. 2018). To date, most of the studies on the effect of impulsive noise on wild marine mammals have focused on harbour porpoises (*Phocoena phocoena*) and seals (*Phoca vitulina*) (e.g. Brandt et al. 2018; Graham et al. 2019; Russell et al. 2016). Other species, such as bottlenose dolphins (*Tursiops truncatus*), may react differently to this disturbance but information on this is sparse (David 2006; Finneran et al. 2015; Graham et al. 2017). Due to the lack of empirical data, estimates of potential behavioural effects required for the regulation of marine energy developments have a high level of uncertainty for these animals (Merchant 2019).

This uncertainty can be especially challenging where offshore energy developments are being considered within or near to areas used by protected cetacean populations. Over the last decade, three major energy developments have been undertaken in NE Scotland, near a Special Area of Conservation (SAC) that was established in the Moray Firth to protect bottlenose dolphins. These included a 2D seismic survey for oil and gas exploration in 2011, and the installation of foundation piles for two offshore wind farms in 2017 (Beatrice Offshore Wind Farm) and 2019 (Moray East Offshore Wind Farm), all of which are known to result in high levels of impulsive underwater noise (Madsen et al. 2006; Thomsen et al. 2011). The Habitats Directive (92/43/EEC) requires regulators to ensure that the Favourable Conservation Status of the SAC is maintained. Therefore, higher levels of assessment and protection were required prior to all three of these projects. The Appropriate Assessments undertaken by the regulator, concluded that there were no likely long-term impacts on the protected bottlenose dolphin population and permissions were granted (Berr 2007; MS-LOT 2014; MS-LOT and Marine Scotland Science 2014). However, significant objections were raised during some of these processes, arguing that dolphins could be displaced from the southern coast of the Moray Firth, an important area for this population (Cheney et al. 2013).

Given the sensitivities surrounding this issue and the level of uncertainty in the predictions, I used passive acoustic monitoring (PAM) to investigate whether far-field effects of impulsive noise from these offshore activities resulted in displacement of dolphins from coastal waters in the southern Moray Firth. To do so, echolocation data loggers (CPODs) were deployed to study variation in dolphin detections in areas exposed to different levels of impulsive noise. First, year-to-year variability in dolphin occurrence was investigated in each of those areas. Second, Before-After Control-Impact analyses (BACI; Smith 2002; Underwood 1992) were performed at two temporal scales to assess potential differences in detections within these areas. At the medium temporal scale, the BACI analysis compared years in which impulsive noise from offshore activities was present or absent. At the small temporal scale, finer-scale patterns within years with offshore activity were explored by comparing days in which impulsive noise was present or absent. Lastly, during the construction of Moray East wind farm, a more extensive PAM array was deployed in the coastal area nearest this development to investigate whether dolphins were displaced away from it and towards the coast during piling days.

METHODS

Study area and Moray Firth Developments

The study was carried out in the Moray Firth, a large triangular embayment of the North Sea that covers approximately 5230 km^2. The seabed gradually slopes from the coast to depths of up to 200 m and, in the centre, there is a shallow sand bank of 40 to 50 m depth called the Smith Bank (Eleftheriou et al. 2004). The Firth is frequented by a range of cetacean species (Risch et al. 2019; Robinson et al. 2017; Thompson et al. 2015) that includes animals from a protected population of bottlenose dolphins that uses the Moray

Firth SAC (Figure 5.1). The distribution of this population is primarily coastal (Thompson et al. 2015) and, although individuals show interannual variability in their range (Pirotta et al. 2015c), the population shows high site fidelity at a broader scale (Cheney et al. 2014). The area most intensively used by these dolphins is the inner Moray Firth, in the south-western part of the Firth, which is considered to be their core area of distribution (Cheney et al. 2013). However, a large proportion of the population uses other areas further south along the east coast of Scotland, such as St Andrews Bay and the Tay Estuary (Arso Civil et al. 2019). The southern coast of the Moray Firth is also intensively used by these dolphins and acts as a corridor between the SAC in the Moray Firth and the other key areas around the east coast (Arso Civil et al. 2019; Cheney et al. 2013; Culloch and Robinson 2008).

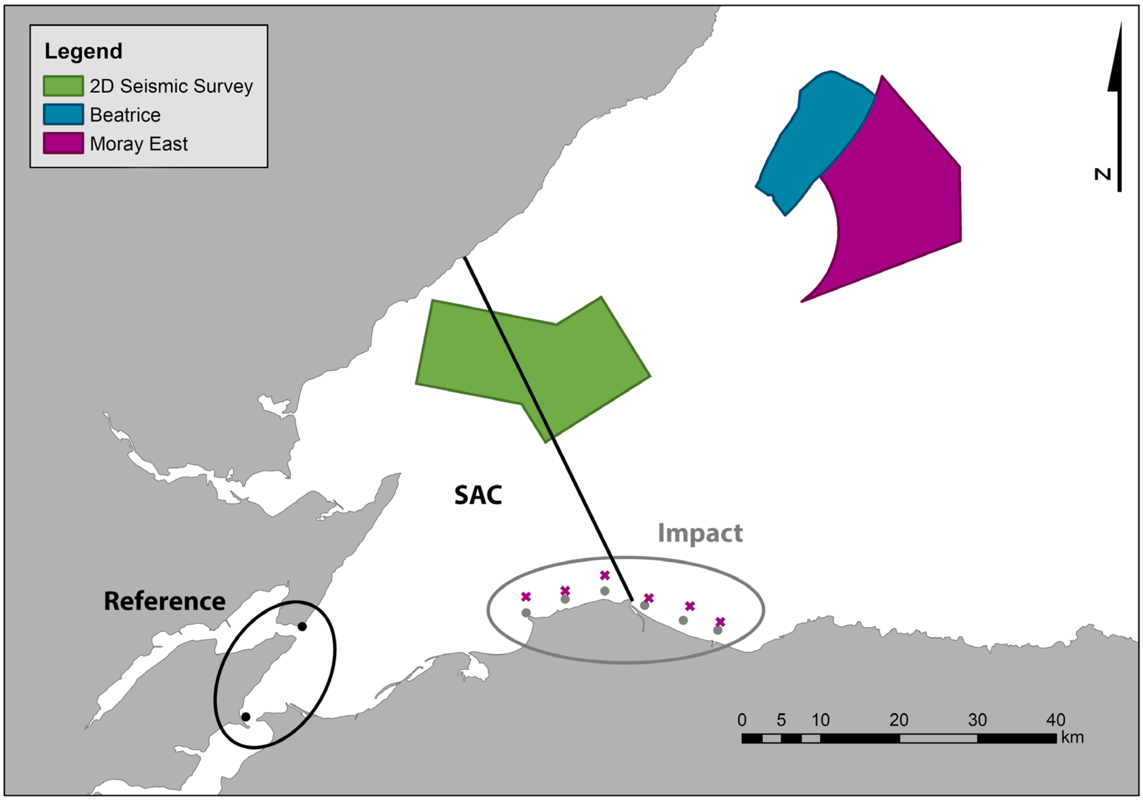


Figure 5.1: Map of the Moray Firth showing the boundary of the Moray Firth SAC (solid line) and the areas in which different offshore projects were undertaken (2D seismic survey and Beatrice and Moray East wind farms). Circles (●): CPODs deployed from 2009 to 2019 (circled in black: Reference Area array; circled in grey: Impact Area array); X-shaped crosses (x): CPODs deployed in 2019 only (Impact Outer array).

In 2011, between the 2nd and the 11th of September, 2D seismic surveys were undertaken within the central Moray Firth, at minimum distances of 18 and 42 km from the southern coast and inner Moray Firth respectively (Figure 5.1 and Table 5.1). They were conducted with a 470 cubic inch airgun array and a 5-6 s shot interval (see Thompson et al. 2013b for survey details and modelled predictions of received noise levels). Between the 2nd April and the 2nd December 2017, the 344 pile foundations for the Beatrice wind farm were installed on the Smith Bank at least 53 km from the southern coast and 80 km from the inner Moray Firth. Each pile was hammered into the seabed using impulsive pile driving techniques with a maximum hammer energy of 2299 kJ (see Graham et al. 2019 for modelled predictions of received noise levels). On the 30th May 2019, construction started at the Moray East wind farm next to Beatrice; 264 pile foundations were installed between May and December 2019 (see MORL, 2016 for modelled predictions of received noise levels). Piles were installed using similar impulsive pile driving techniques and a maximum hammer energy of 2071 kJ (see Table S5.1 and Table S5.2 in supplementary material for detailed piling timelines from Beatrice and Moray East).

Table 5.1: Summary table with distance to the development and maximum received noise levels expressed as unweighted single-pulse sound exposure levels (SEL: dB re 1 μPa^{2}s; Thompson et al., 2013; MORL, 2016; Graham et al., 2019).

		Reference	**Impact**
2D Seismic	Minimum distance (km)	42	18
	Max Received noise levels (SEL)	132	140
Beatrice	Minimum distance (km)	80	53
	Max Received noise levels (SEL)	100	128
Moray East	Minimum distance (km)	78	45
	Max Received noise levels (SEL)	93	141

Passive acoustic monitoring

Echolocation detectors (CPODs, Chelonia Ltd.) were used to collect information on temporal patterns of occurrence in areas known to be frequented by bottlenose dolphins (Cheney et al. 2014). CPODs were deployed between 2009 and 2019 following previously described techniques (Bailey et al. 2010a; Graham et al. 2019; Thompson et al. 2013b). Two CPODs were deployed at sites within the inner Moray Firth where the impact was expected to be lowest; hereafter the *Reference Area* (Figure 5.1; Fernandez-Betelu et al. 2019). These reference sites were located at minimum distances of 42, 80 and 78 km from the seismic survey, Beatrice and Moray East wind farm developments respectively. Six CPODs were deployed along the southern Moray Firth coast, the part of the dolphin population's coastal range that was closest to all three offshore activities, where the impact was expected to be highest, hereafter the *Impact Area* (Thompson et al. 2010). These impact sites were located at minimum distances of 18, 53 and 45 km from the seismic survey, Beatrice and Moray East wind farm developments respectively. In 2019, during the construction of Moray East wind farm, six extra CPODs were deployed in the *Impact Area* at greater distances from the coast (from 3 to 4 km), hereafter *Impact Outer* area. With this array we aimed to investigate whether dolphins from further out at sea were displaced towards the coast in the southern Moray Firth by impulsive noise. Although data were collected year round at some locations, data from November to April were excluded from all the analyses due to the low occurrence of dolphins during those months along the southern Moray Firth coast (Fernandez-Betelu et al. 2019).

CPOD data were downloaded and trainfiltered using the manufacturer's software (*www.chelonia.co.uk*) to identify which echolocation clicks were produced by dolphins. As recommended by the manufacturer, only click trains classified as high and moderate quality were used in this study. Since previous photo-ID, line transects and aerial surveys confirmed that the presence of other species of dolphins is rare in the studied sites (Thompson et al. 2015), all detected echolocation clicks were assumed to be produced by bottlenose dolphins. Detection Positive Hours per day (DPH) was the metric derived from the click train detections that we chose as the proxy for dolphin occurrence. DPH describes the number of hours in each day in which a dolphin click train was detected on each CPOD and is a robust proxy for studying odontocete occurrence (Brookes et al. 2013; Williamson et al. 2016). I used the statistical program R v. 3.5.1 (R Core Team 2018) in all subsequent analyses.

Inter-annual variability in dolphin occurrence

Inter-annual variability in the occurrence of dolphins in the *Reference* and *Impact Areas* was characterized from a sub-set of comparable data from 4 long-term CPODs, two in each of the areas, that provided complete datasets for August and September from 2009 to 2019 (see timeline with CPOD deployments in supplementary material Figure S5.1). I calculated the DPH per day for these months and assessed the year-to-year variability in dolphin occurrence within these areas. Comparisons between years were made using non-parametric Kruskal-Wallis tests because data were not normally distributed.

Far-field effects on bottlenose dolphin occurrence in relation to seismic and wind farm projects: medium and small temporal scales

I performed BACI analyses (Smith 2002; Underwood 1992) to investigate whether there was a change in dolphin detections in the *Impact Area* relative to the more distant *Reference Area* during each offshore activity. In the BACI analyses we performed generalized linear mixed models (GLMM) with a

Poisson family distribution and square root link function (Bolker et al. 2009a). I used dolphin DPH as the response variable and included area (*Reference Area/Impact Area*) and period (*Baseline period/Activity period*) as fixed effects in interaction. At the medium temporal scale, the *Activity period* comprised years when offshore activities were undertaken and the *Baseline period* years without these offshore activities. At the small temporal scale, the *Activity period* included days in which impulsive noise was generated and the *Baseline period*, days in which impulsive noise was not generated (Table 5.2). I included CPOD location and day within a year as random intercepts to remove patterns in the residuals and improve the fit of GLMM models at both temporal scales.

Table 5.2: Data used in the BACI analyses for the medium and small temporal scales. Table includes the total number of days in each of the periods (Baseline period/Activity period) and the percentage of days with impulsive noise in August and September in brackets.

			Baseline period	**Activity period**
Medium temporal scale	**2D Seismic**	Dates	01-14 Sep	02-11 Sep
		Years	2009, 2010, 2013, 2014	2011
		Tot. ndays	60	10
	Beatrice	Dates	May-Sep	May-Sep
		Years	2014, 2015, 2016, 2018	2017
		Tot. ndays	611	153
	Moray East	Dates	May-Sep	May-Sep
		Years	2014, 2015, 2016, 2018	2019
		Tot. ndays	611	153
Small temporal scale	**2D Seismic**	Dates	23 Aug-01 Sep, 12-21 Sep	02-11 Sep
		Years	2011	2011
		Tot. ndays	20	10 (16.4%)
	Beatrice	Dates	Non piling days May-Sep	Piling days May-Sep
		Years	2017	2017
		Tot. ndays	68	85 (52.4%)
	Moray East	Dates	Non piling days May-Sep	Piling days May-Sep
		Years	2019	2019
		Tot. ndays	101	52 (24.6%)

Far-field effect on bottlenose dolphin occurrence in relation to Moray East wind farm: displacement from the southern Moray Firth at a fine spatial scale.

During foundation installation at Moray East wind farm I investigated the occurrence of dolphins in the *Impact Area* at a fine spatial scale and assessed whether dolphins were displaced towards the coast during piling days. To do so, I assessed differences in dolphin DPH between the CPODs closer to the shore (*Impact Inner* array) and the CPODs further from the coast (*Impact Outer* array) in the impact area (Figure 5.1). I used GLMM and introduced array (*Impact Inner/Impact Outer*) and period (Piling/Non piling days) as explanatory variables in interaction. CPOD location and day within a year were included as random intercepts.

RESULTS

CPODs were successfully deployed from 2009 to 2019 and provided more than 10,000 days of CPOD data. Gaps in the dataset occurred due to a combination of device failure and logistical constraints. Data from 2012 were removed from these analyses because only one CPOD was recovered that year from the *Impact Area* (supplementary material, Figure S5.1).

Inter-annual variability in dolphin occurrence

The seismic survey, Beatrice and Moray East wind farm construction resulted in impulsive noise being produced within the Moray Firth on 16.4 %, 52.4 % and 24.6 % of days in August and September 2011, 2017 and 2019 respectively (Table 5.2).

For the comparable subset of data from August-September, there were significant inter-annual differences in the daily occurrence of dolphins (DPH) in both areas (Figure 5.2A). The median DPH ranged between 3 and 7 h in the *Reference Area* (X^2 = 102.26, df = 10, p-value < 0.0001) and between 0 and 3 h in the *Impact Area* (X^2 = 139.4, df = 10, p-value < 0.0001; Figure 5.3 and Table 5.3). Dolphin detections were higher in the *Reference Area* than in the *Impact Area* during all years: dolphins were detected on 77-98 % of the days in the *Reference Area*, compared to 45-89 % of the days in the *Impact Area* (Figure 5.2B).

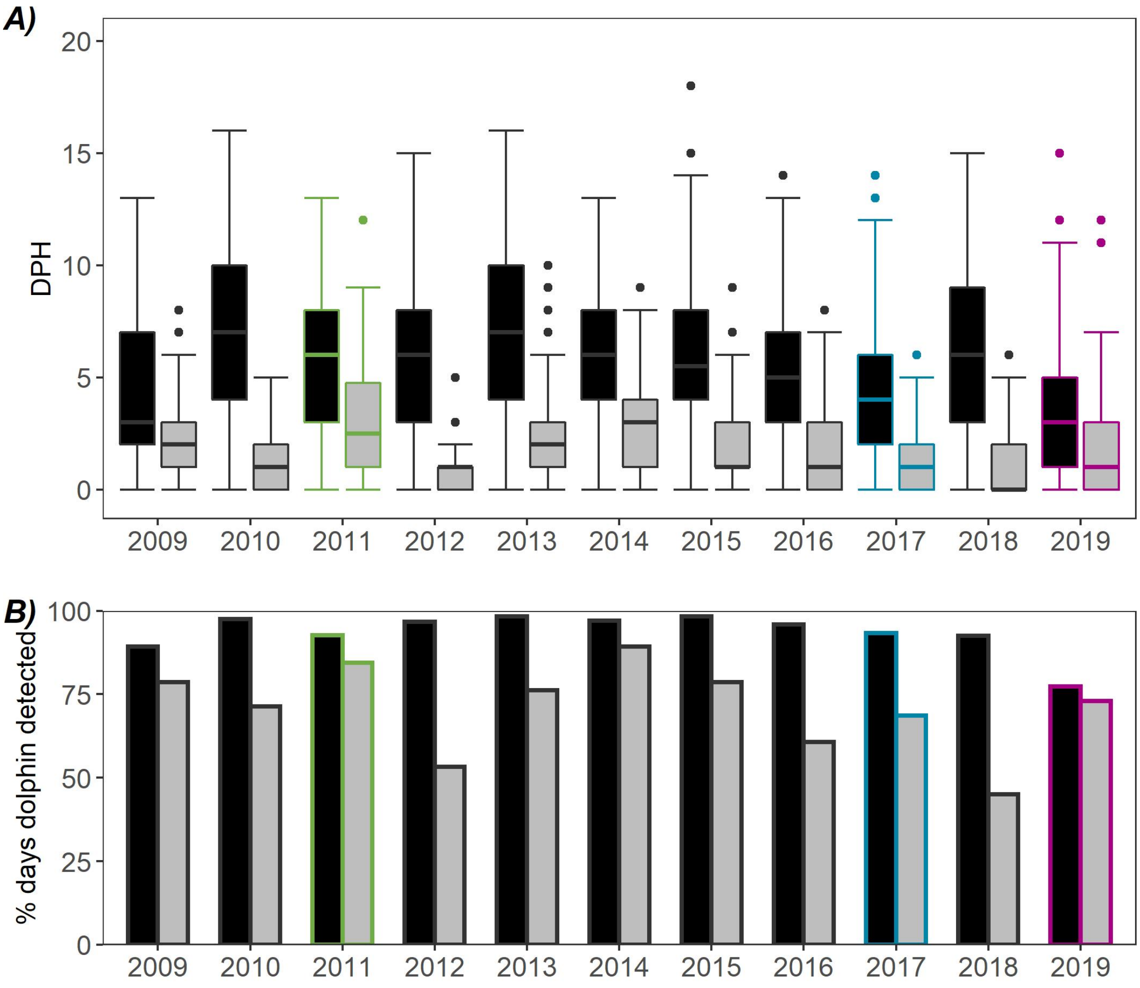


Figure 5.2: Inter-annual variation in (A) dolphin Detection Positive Hours per day and (B) percentage of days that dolphins were detected in Reference Area (black) and Impact Area (grey). Data from August-September 2009 to 2019 from the 4 long-term CPODs. Coloured borders indicate years when offshore activities took place (2011: 2D seismic survey; 2017: Beatrice wind farm construction; and 2019: Moray East wind farm construction).

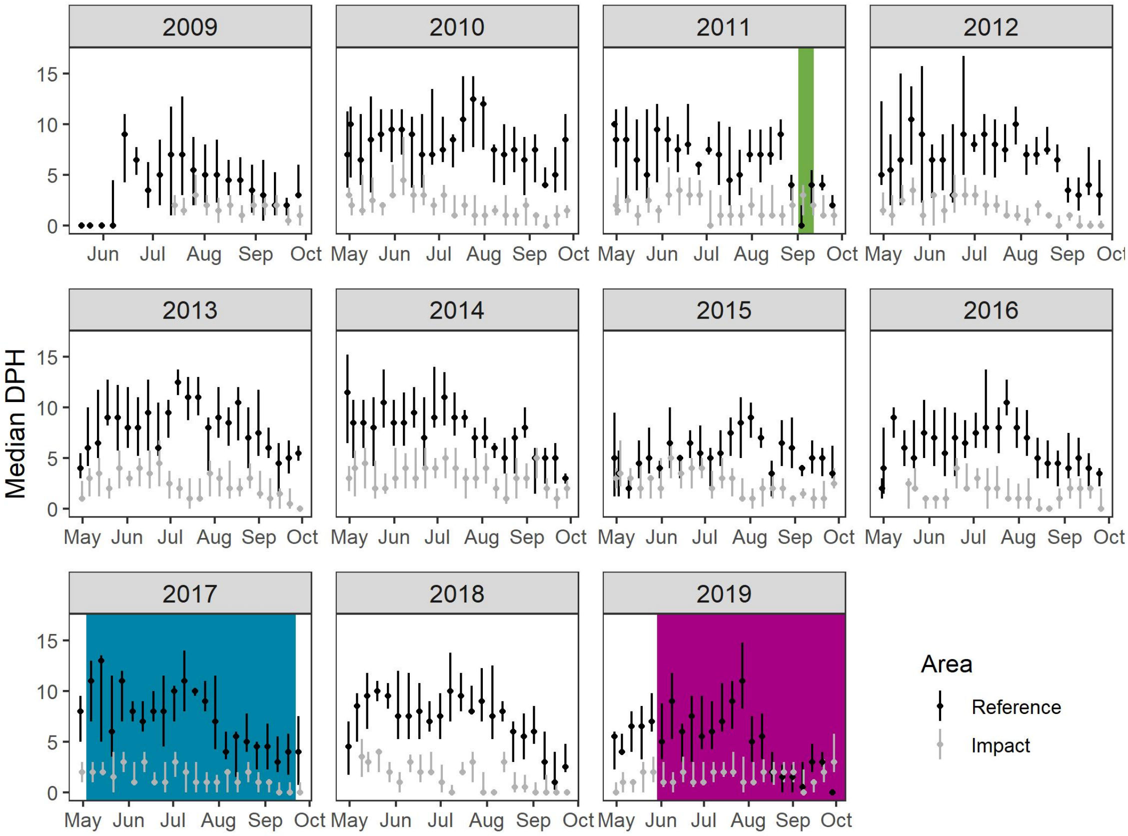


Figure 5.3: Weekly median Detection Positive Hours (DPH) and inter-quartile ranges in the Reference Area (black) and Impact Area (grey) in each of the years studied. Coloured areas indicate when offshore activities took place (green: 2D seismic survey; blue: Beatrice wind farm construction; magenta: Moray East wind farm construction).

Table 5.3: Summary data from the four long-term CPODs from August and September 2009-2019. N: number of days on which CPOD data were available). Values are median detection positive hours (DPH) and percentage of days that dolphins were detected in each of the areas.

	Reference			**Impact**		
Year	**N**	**Median DPH**	**% days dolphins detected**	**N**	**Median DPH**	**% days dolphins detected**
2009	61	3	89.26	61	2	78.69
2010	61	7	97.54	61	1	71.31
2011	61	6	92.68	61	2.5	84.43
2012	61	6	96.69	60	1	53.33
2013	61	7	98.35	61	2	76.23
2014	61	6	96.72	61	3	89.34
2015	61	5.5	98.36	61	1	78.69
2016	61	5	95.90	61	1	60.66
2017	60	4	93.28	61	1	69.57
2018	61	6	92.50	61	0	45.08
2019	61	3	76.58	61	1	72.95

Far-field effects on bottlenose dolphin occurrence in relation to seismic and wind farm projects: medium and small temporal scales

At the medium temporal scale, the BACI analysis did not identify any consistent relationship between observed inter-annual variability and the occurrence of impulsive noise from these offshore activities (Figure 5.4 and Table 5.5). There were significant impacts of both the seismic survey and Beatrice wind farm construction, but the effects were in opposite directions. For the seismic survey in 2011, dolphin detections in the *Impact Area* increased by 50 % (to a median of 3 h per day) compared to baseline years but reduced by 100 % (to a median of 0.5 h per day) in the *Reference Area* (GLMM: X^2 = 32.975, d.f = 1, p-value < 0.001; Figure 5.4A). In contrast, during the Beatrice wind farm piling campaign in 2017, compared to baseline years, dolphin detections decreased by 50 % in the *Impact Area* (to a median of 1 h per day) and decreased by 14 % (to a median of 6 h per day) in the *Reference Area* (GLMM: $X^2 = 39.342$, d.f = 1, p-value < 0.001; Figure 5.4B). Finally, when impact piling was conducted at Moray East wind farm in 2019, no significant difference in dolphin detections between areas was found compared to baseline years (GLMM: $X^2 = 0.9451$, d.f = 1, p-value > 0.05; Figure 5.4C and Table 5.5).

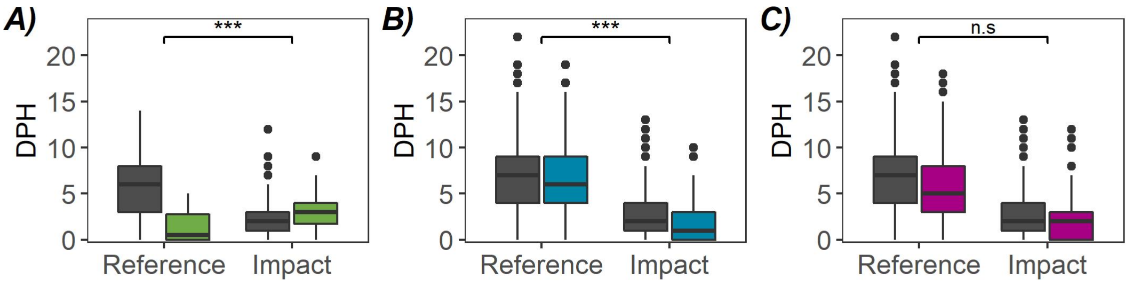


*Figure 5.4: Dolphin Detection Positive Hours (DPH) in the inner Moray Firth (Reference Area) and the southern Moray Firth (Impact Area) during the Baseline period (dark grey) and the Activity period (coloured) at the medium temporal scale: (A) 2D seismic survey, (B) Beatrice wind farm construction and (C) Moray East wind farm construction. Significance of the interaction between period and area is indicated above the bar at the top: *** P < 0.001; n.s. P > 0.05.*

Table 5.4: Results of the Poisson generalized linear mixed models used to investigate the effect of impulsive noise from offshore activities on the acoustic detection of dolphins at sites in the inner Moray Firth (Reference Area) and the southern Moray Firth (Impact Area) in the medium and small temporal scales.

			Estimate	Std. Error	Df	P Value
Medium temporal scale	**2D Seismic Survey**	*Intercept*	0.777	0.089	1	< 0.001
		Period	0.240	0.154	1	0.119
		Area	0.910	0.137	1	< 0.001
		Period:Area	-1.617	0.286	1	< 0.001
	Beatrice	*Intercept*	0.786	0.066	1	< 0.001
		Period	-0.338	0.046	1	< 0.001
		Area	1.078	0.127	1	< 0.001
		Period:Area	0.270	0.041	1	< 0.001
	Moray East	*Intercept*	0.786	0.069	1	< 0.001
		Period	-0.205	0.046	1	< 0.001
		Area	1.085	0.132	1	< 0.001
		Period:Area	0.039	0.040	1	0.331
Small temporal scale	**2D Seismic Survey**	*Intercept*	0.502	0.163	1	0.002
		Period	0.478	0.170	1	0.005
		Area	1.147	0.350	1	0.001
		Period:Area	-0.186	0.298	1	< 0.001
	Beatrice	*Intercept*	0.274	0.093	1	0.003
		Period	0.286	0.089	1	0.001
		Area	1.428	0.141	1	< 0.001
		Period:Area	-0.174	0.077	1	0.023
	Moray East	*Intercept*	0.385	0.121	1	< 0.001
		Period	0.327	0.086	1	< 0.001
		Area	1.209	0.208	1	< 0.001
		Period:Area	-0.162	0.074	1	0.028
Fine spatial scale	**Moray East**	*Intercept*	0.471	0.397	1	0.235
		Period	0.245	0.082	1	0.003
		Area	-2.211	0.603	1	< 0.001
		Period:Area	0.153	0.980	1	0.121

At the small temporal scale, the BACI analysis identified a significant impact of all three offshore activities, with an increase in dolphin detections in the impact area during those days on which impulsive noise was generated

(Figure 5.5 and Table 5.5). For the seismic survey, an increase in dolphin detections of 200 % (to a median of 3 h per day) was obtained in the *Impact Area* whereas a reduction of 90 % (to a median of 0.5 h per day) was detected in the *Reference Area* (GLMM: $X^2 = 38.861$, d.f = 1, p-value < 0.001; Figure 5.5A). During pile-driving at Beatrice wind farm, an increase in dolphin detections of 100 % was found in the *Impact Area* (to a median of 2 h per day) whereas there was no change in the *Reference Area* (GLMM: $X^2 = 5.198$, d.f = 1, p-value < 0.05; Figure 5.5B). For the Moray East wind farm development, dolphin detections increased by 100% (to a median of 2 h per day) in the *Impact Area* and increased by 20 % (to a median of 6h per day) in the *Reference Area* (GLMM: $X^2 = 4.807$, d.f = 1, p-value < 0.05; Figure 5.5C and Table 5.5).

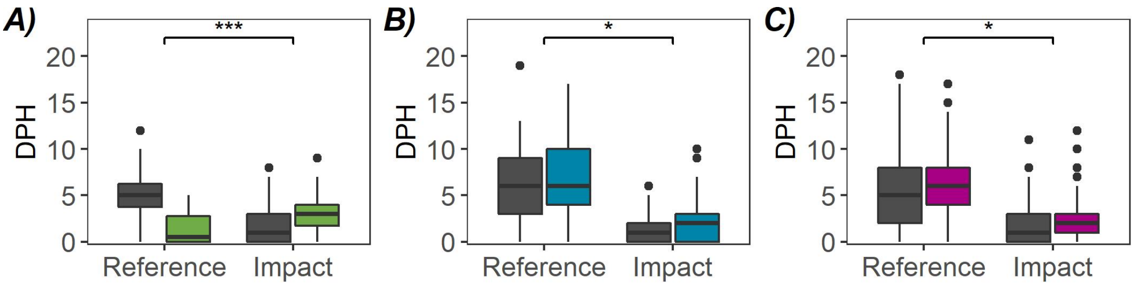


*Figure 5.5: Dolphin Detection Positive Hours (DPH) in the inner Moray Firth (Reference Area) and the southern Moray Firth (Impact Area) during the Baseline period (dark grey) and the Activity period (coloured) on the small temporal scale: (A) 2D seismic survey, (B) Beatrice wind farm construction and (C) Moray East wind farm construction. Significance of the interaction between period and area is indicated above the bar at the top: *** P < 0.001; * P < 0.05.*

Far-field effects on bottlenose dolphin occurrence in relation to the construction of Moray East wind farm: fine spatial scale

There was a significant increase in dolphin detections during piling days in both *Impact Inner* and *Impact Outer* arrays compared to non-piling days (GLMM: X^2 = 8.932, d.f = 1, p-value = 0.003; Figure 5.6). Dolphin detections were significantly higher at the *Impact Inner* array than at the *Impact Outer* array (GLMM: X^2 = 14.659, d.f = 1, p-value < 0.001). The interaction between array and period was not significant (GLMM: X^2 = 2.406, d.f = 1, p-value > 0.05; Table 5.5).

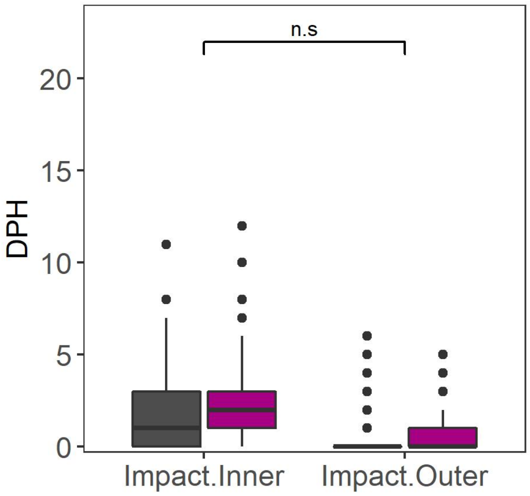


Figure 5.6: Dolphin DPH for the Impact Inner and Impact Outer CPOD arrays in the Impact Area during the construction of Moray East wind farm (2019): non-piling days (dark grey) and piling-days (magenta). Significance of the interaction between period and array is indicated above the bar at the top: n.s. P > 0.05.

DISCUSSION

The analysis of ten years of PAM data highlighted that dolphins used Moray Firth inshore areas regularly, albeit the extent of use varied from year to year without any consistent relationship to the impulsive noise generated by offshore activities. Nevertheless, at a fine temporal scale within offshore activity years, there was a significant change in dolphin occurrence depending upon the presence or absence of impulsive noise on different days.

The results of this study suggest that the impulsive noise generated by offshore activities did not cause any dolphin displacement from the southern coast of the Moray Firth. The southern coast is the closest area to the offshore activities within this bottlenose dolphin population's range (Arso Civil et al. 2019): the seismic survey took place 20-30 km away, and piling at Beatrice 50-70 km and Moray East 40-70 km, from the southern coast. Predicted maximum received noise levels were 139 dB and 128 dB re 1 μPa^{2}s during the seismic survey and during piling at Beatrice wind farm respectively (unweighted single pulse SEL; Graham et al. 2019; Thompson et al. 2013b) and 141 dB re μPa^{2}s in the worst-case scenario for Moray East wind farm (MORL 2016). My analyses showed that dolphins continued using the southern coast of the Moray Firth during the seismic survey and impact pile-driving. These results are in line with recent studies that found that displacement of marine mammals from impulsive noise sources only occurs at shorter distances. For instance, displacement of harbour porpoises and baleen whales, which are more sensitive to noise (Southall et al. 2019c), has been reported up to 20 km away from impulsive noise sources (Dähne et al. 2013; Dunlop et al. 2018; Graham et al. 2019;

Sarnocińska et al. 2020; Southall et al. 2019b). There are no similar studies for bottlenose dolphins but, since they are less sensitive than baleen whales and harbour porpoises to noise, shorter ranges of displacement would be expected.

Contrary to expectations, the BACI analysis at the smaller temporal scale, showed an increase in dolphin detections on the southern Moray Firth coast on days with impulsive noise. Furthermore, this increase was consistent between all three offshore projects. The short-term increase in dolphin detections observed only at the smallest temporal scale is in line with previous studies that found that behavioural alterations due to noise exposure last less than a day (Thompson et al. 2013b; Van Beest et al. 2018). These findings are consistent with those of Bailey et al. (2010b) who, based on criteria in Southall et al. (2007) suggested that dolphins in this study area might exhibit modifications in behaviour at around 50 km away from a piling vessel. Acute noises can modify marine mammal group size and group behaviour (Curé et al. 2021; Visser et al. 2016), which in turn can cause changes in vocalizations (Henderson et al. 2012). Therefore, one possible explanation for the observed increase in dolphin detections is that noise modified bottlenose dolphin group sizes or group behaviour. Although whistle vocalization rates have been linked to group sizes (Quick and Janik 2008), echolocation click rates cannot be directly linked to the size of bottlenose dolphin groups (Nuuttila et al. 2013b). Since this study was based on echolocation data loggers, we cannot test whether the increase in noise levels modified dolphin group sizes. Moreover, since CPOD detections and the number of individuals are not directly linked (Nuuttila et al. 2013b), it does not follow that the increase in detections observed here is indicative of changes in group size. Changes in marine mammal vocalizations due to distant (> 20 km) anthropogenic noise sources have been observed previously (Blackwell et al. 2013; Risch et al. 2012; Shannon et al. 2016). Therefore, another explanation of the increase in detections is that dolphins might have changed their vocalization rate (Blackwell et al. 2015) or the amplitude of their calls (Holt et al. 2009; Parks et al. 2011) in response to the impulsive noise generated by the offshore activities. In an experiment with captive bottlenose dolphins, the playback of pile driving noise resulted in an increase in the number of clicks produced by these animals (Branstetter et al. 2018). Caution is required when extrapolating information from trained to wild animals, but an increase in the click rate could explain the observed increase in detections by our CPODs during the impulsive noise events. Results obtained from the fine scale spatial analysis during the construction of Moray East wind farm also support this hypothesis. No displacement from the outer towards the inner array was observed during piling days, while a subtle but consistent increase in dolphin detections was observed on both arrays. Research is needed to further investigate potential changes in the acoustic characteristics of bottlenose dolphin clicks during far-field impulsive noise events. Passive acoustic devices that collect information on marine mammal click characteristics could be deployed during future offshore developments to explore in more detail whether these activities can be linked to differences in dolphin click rates or click amplitude.

At the medium temporal scale, comparing dolphin occurrence to baseline years, the results were not consistent between offshore activities. During the seismic survey, an increase in dolphin detections was observed on the southern coast. During the construction of Beatrice wind farm, a decrease was detected in the same area and during the construction of Moray East wind farm, no significant difference was detected. In line with previous studies, dolphin detections overall were higher in the *Reference Area* of the inner Moray Firth, compared with the *Impact Inner* area on the southern coast, but the extent of use varied between years and through the season (Fernandez-Betelu et al. 2019; Thompson et al. 2015). The difference in detections at the medium temporal scale therefore seems likely to be related to the natural inter-annual variation in occurrence that was also reflected in my analyses here (Figure 5.2). Although potentially modified by anthropogenic factors, bottlenose dolphin occurrence is largely influenced by a range of natural drivers, such as prey abundance and oceanographic processes (Benjamins et al. 2015; Heithaus and Dill 2002). These results suggest that the effect of far-field noise is less important than these other natural drivers in affecting the occurrence of dolphins in this study area.

I used a BACI design to investigate the effect of impulsive noise on the coastal occurrence of dolphins. This methodology is based on the comparison of data from two similar areas (Impact and Control) in situations where only one of them is affected by a disturbance. However, finding control sites with similar ecological characteristics to impact sites, while being distant enough to be unaffected by the disturbance, is not always feasible (Underwood 1992, 1994). The sites defined here as reference sites were chosen because they were located at greater distances from the developments but were still within the bottlenose dolphin population’s range. However, a complete lack of disturbance cannot be assured there, hence the term *Reference* instead of *Control Area*. For instance, during the construction of Moray East wind farm an increase in detections was observed at both *Reference* and *Impact Areas* during piling days, potentially indicating that noise levels might also have affected dolphins at reference sites. Nevertheless, these ten years of passive acoustic monitoring data provided a robust dataset to investigate the effects of three offshore projects, while overcoming some of the limitations of the BACI design. The consistent results at the smallest temporal scale strengthened my hypothesis that a change in vocal behaviour may have caused the observed increase in dolphin detections. While the contrasting results at the medium temporal scale from multiple offshore activities prevented me from suggesting misleading effects that might have been inferred from work conducted only during a single project. Overall, these analyses showed that long-term datasets such as this provide opportunities to detect relatively subtle differences in bottlenose dolphin behaviour linked to the far-field impulsive noise generated by offshore activities.

Management implications

Limited data on localised cetacean populations can constrain environmental assessments for new developments, particularly where these occur in or near protected areas. In the Moray Firth, concerns over the potential impacts of offshore developments on the protected population of bottlenose dolphins required additional research and survey effort in the area to inform licensing decisions.

The findings of this study support the Appropriate Assessments' conclusions that these offshore activities would not have a major impact on the bottlenose dolphin population using the SAC (Berr 2007; MS-LOT 2014; MS-LOT and Marine Scotland Science 2014). My results also concur with recent photo-ID studies of this dolphin population that showed increasing trends in both population size (Cheney et al. 2014) and vital rates (Cheney et al. 2019), supporting the lack of any large-scale impacts on the population. My analysis showed that dolphins continued using the area of their range where the impact was expected to be highest when these projects took place. The monitoring of the far-field responses of dolphins provided evidence of potential short-term changes in vocalisations as reported for other marine mammal species (Gomez et al. 2016). Developers are required to perform marine mammal monitoring for several years to create a sufficient baseline and assess potential impacts (Diederichs et al. 2008). However, in places with high inter-annual variability in the presence of marine mammals, analyses using data from other years as a baseline may produce misleading results.

Marine mammal protection policies are focused on minimising the near-field acute effects of impulsive noise (Bröker et al. 2015; Verfuss et al. 2016). While the risk of death or injury is limited to the first hundreds of metres from the sound source (Southall et al. 2019c), behavioural responses, such as changes in vocalisations, can occur at greater distances (hundreds of km) potentially affecting a greater number of animals (Risch et al. 2012). Here, I suggested that distant impulsive noise sources may have caused modifications of bottlenose dolphin vocalisations. Further research is now required to test this hypothesis and describe the extent of any change in more detail, given that moderate modifications of vocal behaviour have the potential to affect foraging and individual vital rates (Southall et al. 2007). The challenge in future research will be linking modifications of vocal behaviour to changes in energetic costs (Booth

2020; Pirotta et al. 2021) and, ultimately, population level consequences (Pirotta et al. 2015a; Reed et al. 2020).

SUPPLEMENTARY MATERIAL

Table S5.1: Beatrice Offshore Windfarm Ltd. piling timeline with turbine location, maximum hammer energy (kJ) and maximum unweighted single pulse SELs (dB re 1 µPa^{2}s) per area (see Graham et al. (2019) for information on noise modelling and BOWL (2015) for detailed information on piling strategy).

					Max SEL	
Date	**Turbine**	**Lat**	**Long**	**Energy (kJ)**	**Reference**	**Impact**
04/05/2017	J5	58.23653	-2.85008	737	97.407	125.523
05/05/2017	G6	58.23973	-2.88406	1007		
06/05/2017	G6	58.23973	-2.88406	773		
10/05/2017	G5	58.22937	-2.88757	958	98.753	125.842
11/05/2017	F6	58.23614	-2.90281	887		
17/05/2017	F5	58.22580	-2.90629	884	98.548	126.249
18/05/2017	E6	58.23256	-2.92155	1059		
19/05/2017	E5	58.22222	-2.92503	954		
21/05/2017	D3	58.19991	-2.95003	1018		
22/05/2017	C4	58.20512	-2.96581	942		
23/05/2017	D5	58.21862	-2.94376	1130		
25/05/2017	D5	58.21862	-2.94376	1307		
26/05/2017	D5	58.21862	-2.94376	1888		
27/05/2017	G3	58.20907	-2.89544	2299		
28/05/2017	G3	58.20907	-2.89544	2295		
29/05/2017	E8	58.25326	-2.91459	1061		
30/05/2017	E8	58.25326	-2.91459	1091		
31/05/2017	D7	58.23932	-2.93681	1035		
01/06/2017	E7	58.24291	-2.91807	1099		
02/06/2017	D8	58.24968	-2.93332	999		
03/06/2017	J8	58.26758	-2.83955	1101	97.694	124.862
11/06/2017	J8	58.26758	-2.83955	1209	97.694	124.862
13/06/2017	D6	58.22898	-2.94029	947		
14/06/2017	C7	58.23574	-2.95553	838		
16/06/2017	B6	58.22180	-2.97773	1560		
17/06/2017	G4	58.21903	-2.89106	790		
18/06/2017	H4	58.22260	-2.87232	2042		
19/06/2017	H5	58.23295	-2.86883	824		
20/06/2017	H5	58.23295	-2.86883	1186		
21/06/2017	J6	58.24687	-2.84658	818		
22/06/2017	D4	58.20828	-2.94723	999		

					Max SEL	
Date	Turbine	Lat	Long	Energy (kJ)	Reference	Impact
01/07/2017	E4	58.21186	-2.92851	1408	100.312	128.172
02/07/2017	E4	58.21186	-2.92851	1356	100.312	128.172
03/07/2017	F2	58.19474	-2.91675	993		
04/07/2017	F4	58.21544	-2.90979	1626		
05/07/2017	F12	58.29824	-2.88184	819		
06/07/2017	H8	58.26400	-2.85832	740		
07/07/2017	G8	58.26042	-2.87708	1267		
08/07/2017	H7	58.25365	-2.86182	1243		
10/07/2017	C6	58.22539	-2.95902	1082		
11/07/2017	C5	58.21504	-2.96249	1671		
12/07/2017	B5	58.21145	-2.98121	1709		
14/07/2017	A5	58.20785	-2.99993	940		
15/07/2017	E9	58.26361	-2.91109	799		
16/07/2017	D9	58.26003	-2.92984	1272		
17/07/2017	C8	58.24609	-2.95206	1054		
18/07/2017	B7	58.23215	-2.97427	1750		
24/07/2017	L8	58.27471	-2.80203	1765	99.392	124.953
27/07/2017	M9	58.28862	-2.77973	1805		
28/07/2017	M10	58.29897	-2.77619	1399		
29/07/2017	L10	58.29540	-2.79497	1350		
30/07/2017	L9	58.28506	-2.79849	1577		
31/07/2017	K8	58.27114	-2.82079	1704		
03/08/2017	J9	58.27792	-2.83605	1492		
04/08/2017	K9	58.28149	-2.81727	266		
05/08/2017	K9	58.28149	-2.81727	1647		
06/08/2017	J7	58.25722	-2.84308	1966		
07/08/2017	K6	58.25045	-2.82782	1512		
08/08/2017	K7	58.26079	-2.82431	1608		
12/08/2017	D11	58.28073	-2.92288	1409	98.475	124.880
13/08/2017	D11	58.28073	-2.92288	1348	98.475	124.880
14/08/2017	E12	58.29466	-2.90062	795		
18/08/2017	G12	58.30181	-2.86306	1029	96.019	122.635
19/08/2017	G11	58.29147	-2.86657	965		
20/08/2017	K10	58.29184	-2.81376	994		
21/08/2017	K10	58.29184	-2.81376	1125		
24/08/2017	K11	58.30219	-2.81024	1453		
25/08/2017	K11	58.30219	-2.81024	1780		
26/08/2017	J11	58.29861	-2.82902	1462		
27/08/2017	J12	58.30896	-2.82549	1684		
28/08/2017	C9	58.25644	-2.94859	1106		
30/08/2017	D10	58.27038	-2.92636	266		

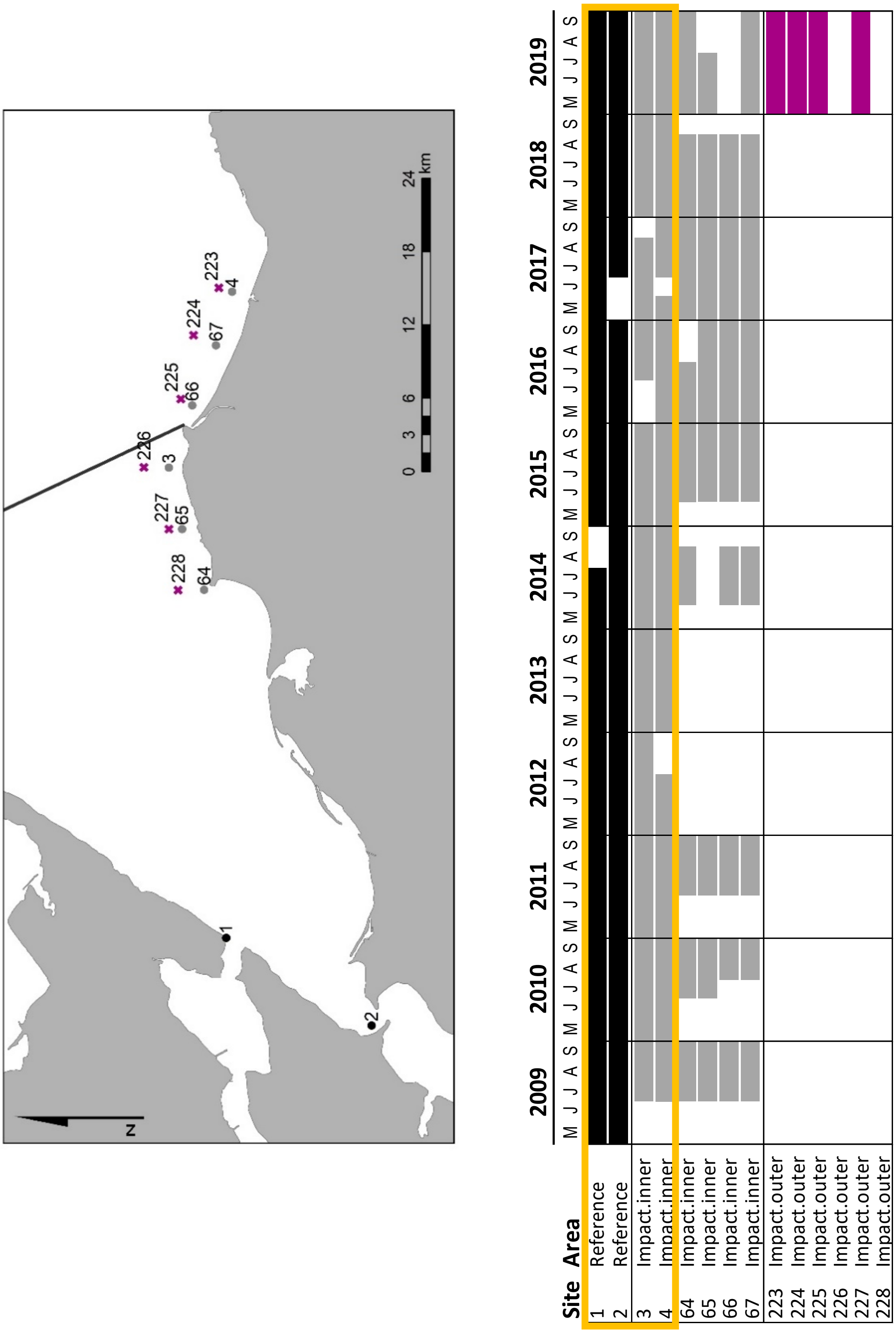
Date	Turbine	Lat	Long	Energy (kJ)	Max SEL	
					Reference	Impact
31/08/2017	D10	58.27038	-2.92636	740		
01/09/2017	E10	58.27397	-2.90760	934		
07/09/2017	F11	58.28790	-2.88534	1356	97.757	124.344
08/09/2017	H12	58.30539	-2.84428	965		
09/09/2017	H12	58.30539	-2.84428	993		
10/09/2017	F13	58.30859	-2.87834	1045		
12/09/2017	G13	58.31217	-2.85956	1609		
13/09/2017	G13	58.31217	-2.85956	1890		
14/09/2017	G14	58.32252	-2.85604	1936		
18/09/2017	E11	58.28431	-2.90411	883	96.161	122.559
19/09/2017	E11	58.28431	-2.90411	1096	96.161	122.559
20/09/2017	F10	58.27754	-2.88883	1117		
21/09/2017	F9	58.26719	-2.89233	1527		

Table S5.2: Moray East Offshore Windfarm piling timeline with turbine location and maximum hammer energy (kJ) (see MORL (2016) for detailed information on piling strategy).

Date	Turbine	Latitude	Longitude	Energy (kJ)
30/05/2019	ME-K17	58.23648	-2.60222	1234
31/05/2019	ME-K16	58.22583	-2.60510	1310
02/06/2019	ME-J17	58.23620	-2.63133	1909
05/06/2019	ME-I19	58.25668	-2.65750	1241
07/06/2019	ME-I20	58.26683	-2.65740	1463
08/06/2019	ME-H19	58.25692	-2.68387	1784
09/06/2019	ME-G19	58.25713	-2.71023	1201
16/06/2019	ME-G18	58.24698	-2.71032	1199
17/06/2019	ME-G17	58.23685	-2.71040	1619
19/06/2019	ME-H17	58.23663	-2.68403	1524
20/06/2019	ME-J18	58.24633	-2.63123	1638
21/06/2019	ME-J16	58.22605	-2.63143	913
23/06/2019	ME-H16	58.22650	-2.68413	1311
24/06/2019	ME-G16	58.22672	-2.71048	909
27/06/2019	ME-G15	58.21658	-2.71055	1309
28/06/2019	ME-H14	58.20623	-2.68432	1011
30/06/2019	ME-J14	58.20578	-2.63165	1027
02/07/2019	ME-J13	58.19565	-2.63175	836
04/07/2019	ME-H13	58.19608	-2.68440	993
05/07/2019	ME-G13	58.19630	-2.71072	1065
07/07/2019	ME-E14	58.20685	-2.76330	1402
08/07/2019	ME-C14	58.20725	-2.81597	1419
09/07/2019	ME-B14	58.20743	-2.84230	1409
10/07/2019	ME-C15	58.21738	-2.81592	1123
11/07/2019	ME-D16	58.22732	-2.78952	1033
12/07/2019	ME-C16	58.22752	-2.81585	1201
13/07/2019	ME-D17	58.23747	-2.78945	1217
14/07/2019	ME-E19	58.25753	-2.76297	1434
14/07/2019	ME-E18	58.24740	-2.76303	1434
16/07/2019	ME-F21	58.27760	-2.73645	1523
17/07/2019	ME-G22	58.28753	-2.70998	1215
18/07/2019	ME-H22	58.28732	-2.68358	1748
21/07/2019	ME-H21	58.27718	-2.68368	1411
22/07/2019	ME-G21	58.27740	-2.71007	1429
24/07/2019	ME-H20	58.26705	-2.68377	1012
25/07/2019	ME-L12	58.18505	-2.57923	1102
27/07/2019	ME-L09	58.15463	-2.57958	925
27/07/2019	ME-L11	58.17490	-2.57935	925
29/07/2019	ME-K10	58.16500	-2.60577	1426
29/07/2019	ME-K11	58.17515	-2.60565	728
04/08/2019	ME-J10	58.16523	-2.63207	1426
05/08/2019	ME-H09	58.15555	-2.68477	728

Date	Turbine	Latitude	Longitude	Energy (kJ)
07/08/2019	ME-G09	58.15575	-2.71105	2071
08/08/2019	ME-H18	58.24677	-2.68395	1124
17/08/2019	ME-I18	58.24655	-2.65758	2071
18/08/2019	ME-G10	58.16590	-2.71097	1371
19/08/2019	ME-OSP2	58.21678	-2.73690	1194
20/08/2019	ME-OSP3	58.16547	-2.65837	1901
21/08/2019	ME-OSP1	58.12577	-2.76383	1420
22/08/2019	ME-J08	58.14497	-2.63228	1014
23/08/2019	ME-J07	58.13483	-2.63238	1066
24/08/2019	ME-G07	58.13548	-2.71122	2045
29/08/2019	ME-F08	58.14583	-2.73742	1955
30/08/2019	ME-C05	58.11602	-2.81643	939
01/09/2019	ME-B04	58.10607	-2.84273	1660

Figure S5.1: Detailed map with all CPOD locations and availability of data for each, from May to September 2009-2019. Coloured cells represent months with more than 10 days of available data, white cells represent no data. Four long-term CPOD deployments highlighted in yellow. Gaps in the acoustic time series of the long-term sites resulted from equipment failure and logistic constraints.



CHAPTER 6

GENERAL DISCUSSION

CHAPTER 6: GENERAL DISCUSSION

Sound knowledge of spatio-temporal patterns in animal occurrence enables decision-makers to forecast how animals may respond to ecosystem changes and implement appropriate conservation and mitigation measures (Hays et al. 2019). This is particularly critical for protected species, such as marine mammals, because gaps in our understanding of the drivers of animal occurrence challenge our ability to protect them while managing the areas where they occur (Williams et al. 2014).

The Moray Firth Special Area of Conservation (SAC) was designated under the European Union Habitats Directive (92/43/EEC) to protect the only known resident population of bottlenose dolphins in the North Sea (Wilson et al. 1997). The SAC includes the main core area of their distribution (Cheney et al. 2013). However, it is an area with a high level of human activity including the offshore renewable industry (Bailey et al. 2014), oil and gas exploration (Pirotta et al. 2014a; Thompson et al. 2013b), ecotourism (Pirotta et al. 2015b), marine traffic (New et al. 2013a), sediment dumping (Marine Scotland 2014) and coastal developments (Graham et al. 2017). These dolphins have been studied for more than 25 years (Cheney et al. 2013), however, there are still gaps in our knowledge about their patterns of occurrence and foraging behaviour that need to be addressed to ensure their protection in such an anthropogenically active area.

The overall aim of this study was to better understand the natural and anthropogenic factors affecting the occurrence of bottlenose dolphins in the Moray Firth. More specifically, I investigated the combined effect of environmental cycles (seasonal, tidal and diel cycles) on the occurrence of dolphins in the core area of their distribution (Chapter 2). I updated information on the prey field at two known foraging hotspots for these dolphins to better understand the drivers of their occurrence (Chapter 3) and investigated in more detail how foraging behaviour modulates dolphin presence at those two sites (Chapter 4). Lastly, I studied the effect of three offshore developments, a seismic survey and the construction of two windfarms, on the coastal distribution of dolphins (Chapter 5).

MAIN FINDINGS OF THIS THESIS

Seasonal, tidal and diel cycles affect marine mammal occurrence but their effect is highly variable and site-specific (Antonella et al. 2017; Benjamins et al. 2015; Nuuttila et al. 2017b; Zein et al. 2019), and their combined effect on the population of dolphins in the inner Moray Firth was unknown. This study described the fine-scale variability in dolphin occurrence linked to environmental cycles at three sites in the core area of their distribution (Chapter 2). The results highlighted that cyclic patterns of occurrence were consistent throughout the study period (6 years) and varied at fine spatial scales (< 15 km). For instance, dolphin occurrence was strongly influenced by the tidal cycle in one of the channels studied (Chanonry), whereas no tidal pattern was found in another similar channel located 13.5 km away (Sutors; Figure 2.5b, Figure 2.7 and

Figure 2.8). This study also showed site-specific effects of the diel cycle, with diurnal, nocturnal and crepuscular patterns of dolphin occurrence detected throughout the area. Site-specific variability in both tidal and diel occurrence had already been observed for this species at a larger scale (> 90 km; Castellote et al. 2015). However, these new results highlighted that such variability can occur at a much smaller spatial scale. Furthermore, these data revealed, for the first time, a consistent seasonal shift in diel behaviour, with dolphins becoming highly nocturnal in autumn. To the best of my knowledge, a seasonal shift in diel presence has never previously been described in a resident population of marine mammals. In line with earlier boat-based visual studies (Bailey et al. 2013; Wilson et al. 1997), the results of my study showed a high probability of dolphin encounters in summer. However, these results also showed a high probability of dolphin encounters in autumn, but these were during night-time when they would be underestimated by visual studies.

Based on the results in Chapter 2, I hypothesised that the cyclical patterns of occurrence observed in dolphins were driven by the temporal patterns of their prey. However, there was no up-to-date information on prey at the required spatial and temporal scales to test that hypothesis. Chapter 3 filled knowledge gaps on information about the prey fields at two key foraging areas for the dolphin population in the Moray Firth, Sutors and Chanonry. The results of this study showed changes in prey abundance, behaviour and composition that could explain the patterns in dolphin occurrence previously observed in Chapter 2. For instance, seasonal variability in fish biomass matched the seasonal occurrence of dolphins. Prey biomass is often linked to the occurrence of marine mammals (Romagosa et al. 2019; Sveegaard et al. 2012a). Here, the increase in dolphin occurrence observed in the Chapter 2 during summer months may be driven by the increase in prey biomass also observed during those months. The detected increase in fish tracks during the flood tide could also partially explain the higher probability of dolphin occurrence at that stage of the tide. Single fish are more vulnerable to predation than schooling fish (Magurran 1990). Therefore, I suggested that dolphins might be targeting tidal stages with higher numbers of single targets to enhance their foraging success. A combination of prey proxies such as acoustic biomass, number of fish tracks and changes in species composition could also explain the seasonal shift in diel behaviour observed in dolphins. I hypothesised that the nocturnal behaviour of dolphins was linked to the influx of overwintering clupeids in the area. I suggested that dolphins were targeting herring at night because these fish might be more vulnerable when they spread out in the water column to feed (Domenici and Batty 1997; Fernö et al. 1998; Rieucau et al. 2014). Elsewhere, marine mammals have been shown to feed on herring at night (Richard et al. 2017; Thomas et al. 2011). In contrast, previous studies on harbour seals in this area suggested that they were feeding on clupeids during the day (Thompson et al. 1991). One possible explanation for this is that harbour seals are specialised in benthic feeding (Grigg et al. 2009; Wilson et al. 2014). Therefore, targeting these fish during the day, when they are close to the seabed (Blaxter and Parrish 1965), might be more beneficial for seals than for dolphins. Another explanation is that seals and dolphins may rely on different sensory systems when foraging and these differences may lead to their divergent foraging strategies. Dolphins rely on echolocation (Au 1993), a sophisticated system that allows them to pursue prey under any light conditions. Seals, on the other hand, use other sensory systems, including vision and hearing, to forage (Kilian et al. 2015; Schusterman et al. 2000). Herring produce noise during the day, when they are in dense schools (Langård et al. 2008) and these noises fall within seals' hearing capabilities (Reichmuth et al. 2013). Seals may, thus, be using a mixture of visual and acoustic cues to feed on clupeids during the day.

This thesis described in more detail how two foraging proxies, echolocation buzzes and bray calls, could be used to explore how dolphin presence at these sites was affected by prey encounter rates (Chapter 4). Here, I provided empirical evidence that area-restricted search (ARS) behaviour occurred in response to changes in these proxies for prey encounters. Buzzes are echolocation clicks with low inter-click intervals (ICI) widely used as foraging proxies (Arranz et al. 2019; Pirotta et al. 2014b) and brays are low frequency calls specifically linked to salmon predation attempts (Janik 2000). This study described how foraging modulates dolphin presence at the two foraging hotspots studied in Chapter 2 and showed that animals remained longer in each of these areas when foraging calls were detected (Fig. 4.6). These results are in line with ARS theory, which states that animals expend more time in areas where they detect prey, since it increases the probability of detecting more prey in the surrounding area (Kareiva and Odell 1987). The results of this study also suggested that bray calls may be a better proxy of foraging behaviour in the area than buzzes, at least in summer, during the salmon run.

In addition to natural drivers, anthropogenic disturbances such as marine developments, also have the potential to modify marine mammal occurrence. Marine mammals rely on acoustic cues to travel, forage, hunt and communicate so any human activity that increases underwater noise levels has the potential to impact them (Erbe et al. 2018). Over the last decade, three offshore developments were undertaken in the Moray Firth: a 2D seismic survey and the construction of two windfarms (Beatrice Offshore Wind Ltd, BOWL; and Moray East Offshore Wind Farm, MEOW). Their appropriate assessments concluded that they would not cause any long-term effects on the protected population of dolphins (Berr 2007; MS-LOT 2014; MS-LOT and Marine Scotland Science 2014). However, the potential displacement of dolphins from the southern coast of the Moray Firth could not be dismissed, and some stakeholders were concerned that this would cause a barrier effect, preventing dolphins from moving between foraging areas. This thesis described the far-field effect of the impulsive noise generated by these offshore developments on the coastal distribution of dolphins (Chapter 5). In line with their appropriate assessments, this study did not detect any long-term effect on the distribution of dolphins linked to the three developments (Fig. 5.2). The analyses also showed that animals were not displaced from the southern Moray Firth during the seismic survey or pile driving. These findings were consistent with previous studies that found that porpoise and baleen whale displacement from impulsive noise sources only occurs at shorter distances (< 20 km; Graham et al. 2019; Sarnocińska et al. 2020). Contrary to expectations, there was a consistent increase instead of a decrease in dolphin detections on the southern coast of the Moray Firth when the impact was expected to be highest. However, this was a short-term increase that was detected only at the smallest temporal scale, comparing days in which construction activity was present or absent (Fig. 5.4). Unlike displacement, changes in vocalisation behaviour linked to distant impulsive noise (> 20 km) have been detected previously in several marine mammal species (Blackwell et al. 2013; Risch et al. 2012). Therefore, I hypothesised that, in response to the impulsive noise, bottlenose dolphins may have modified their vocalisation behaviour by increasing either the amplitude of their calls (Holt et al. 2009) or their echolocation rate (Branstetter et al. 2018).

WIDER IMPLICATIONS

Understanding how animals use their habitat and how/where they spend their time is key for management and conservation plans (Krausman 1999). This thesis provides valuable information on the temporal and spatial occurrence of this protected population of bottlenose dolphins that may enable marine spatial planners to use a more dynamic approach (Dunn et al. 2016). Prior studies based on visual surveys highlighted the importance of the inner Moray Firth during summer months for these dolphins (Wilson et al. 1997). Therefore, mitigation measures linked to human activities in the area were focused on summer, while activities such as spoil dumping were encouraged in autumn (Marine Scotland 2014). However, findings in Chapter 2 highlighted the importance of the area in autumn for this dolphin population, particularly during the night, information that should be considered in future development plans.

Several key findings within this thesis have implications which extend beyond the regional management of this protected population, providing insights for research and management of marine mammal populations in other parts of the world. This study showed that environmental cycles can have highly site-specific effects on the occurrence of dolphins, with contrasting tidal patterns of occurrence at fine-spatial scales and diel patterns that changed through the year. Researchers should thus consider these sources of variability in their survey and statistical analysis designs when studying marine mammal occurrence. For instance, the seasonal shift in diel occurrence described in this study was detected because interactions between variables were included in the analysis. This shift might be happening elsewhere but might have gone unnoticed because interactions between environmental cycles are often not included when modelling marine mammal occurrence (Brough et al. 2020; Leroy et al. 2016; Munger et al. 2016). Furthermore, this study highlighted the utility of passive acoustic devices in studying marine mammal patterns of occurrence. Many studies use only visual observations to inform marine spatial planning (Passadore et al. 2018; Weir et al. 2019), missing potentially important information during night-time or poor weather conditions. By using passive acoustic monitoring, this thesis detected the highly nocturnal behaviour of dolphins in autumn, which would have been undetectable with visual observations. These results support previous research highlighting that, since passive acoustic devices collect data through the 24-h cycle, they provide more comprehensive information for conservation and management plans (Mussoline et al. 2012; Thompson et al. 2015; Williamson et al. 2017).

Investigating predator-prey links is key to understanding marine ecosystem functioning and implementing holistic management methods (Cox et al. 2018a; Hooker et al. 2011; Hunsicker et al. 2011). However, due to the difficulties inherent in studying the marine environment, marine top predator research often lacks information about potential prey. For instance, in the Moray Firth, the bottlenose dolphin population has been studied for more than 25 years (Cheney et al. 2013), but information about fish has not been updated for more than 20 years (Greenstreet et al. 1998; Hopkins 1986; Thompson et al. 1991). Results in Chapter 3 provided up-to-date information on prey density and behaviour that will be useful for future studies, not only for bottlenose dolphins but also for all other marine predators in the inner Moray Firth. Furthermore, the technique developed here to perform fisheries acoustic surveys is also relevant for small-scale studies on prey fields. We successfully developed a method to collect fish data using a scientific echosounder from a small rigid-inflatable boat. This technique enables future research on prey fields, without relying on expensive research vessels, to better understand the drivers of marine mammal occurrence.

In the designation of marine protected areas, policy makers often target areas where area-restricted search behaviour (ARS) occurs because theory suggests they might be important foraging areas (Hays et al. 2019; Lascelles et al. 2016). However, finding empirical evidence of ARS behaviour in the marine environment remains challenging due to the difficulties in detecting predator-prey interactions (Watanabe and Takahashi 2013). Based on the methodology developed by Bailey et al. (2019), this study inferred predator-prey interactions by deploying passive acoustic monitoring devices and using dolphin foraging vocalisations as a proxy for prey encounters. For the first time, ARS behaviour in dolphins was evidenced using two foraging vocalisations: echolocation buzzes and bray calls. ARS behaviour is often studied by tracking animal movements (Adachi et al. 2017; Freitas et al. 2018; Sommerfeld et al. 2013), but tagging marine mammals, especially small cetaceans, is not always feasible. The results of this thesis supported Bailey et al. (2019), showing that passive acoustic techniques are a valuable method for studying ARS behaviour in echolocating animals.

Far-field effects of anthropogenic disturbances on marine mammal occurrence are poorly understood because empirical evidence about these effects is very limited. In the environmental impact assessment process, knowledge gaps cause a high level of uncertainty when predicting potential impacts and therefore, precautionary approaches need to be implemented (Dolman et al. 2016). The information in Chapter 5 will be useful for future developments planned along the East coast of Scotland, because analyses did not find any evidence that the impulsive noise generated by offshore developments caused any far-field displacement of the protected population of bottlenose dolphins. Therefore, for similar received sound exposure levels, bottlenose dolphin displacement should not be expected. These findings are also useful for developments near protected populations of dolphins elsewhere, because they showed that changes in behaviour can occur at long distances (> 20 km) from the impulsive noise source. Information about the effects of impulsive noise on bottlenose dolphins is sparse (Finneran et al. 2015; Graham et al. 2017), and this thesis provided evidence of changes in echolocation detections linked to far-field impulsive noise sources that require further research. Overall, these results emphasise the importance of obtaining empirical evidence on the effect of anthropogenic disturbances on marine mammal populations and fill a knowledge gap on the far-field effects of impulsive noise on bottlenose dolphins.

The long-term acoustic data set analysed in Chapter 5 highlighted that there was high year-to-year variability in animal occurrence. Marine developers are often required to monitor marine mammal populations for several years in order to investigate the potential impacts of their developments. However, the results did not show any clear change in dolphin occurrence that could be linked to the generated impulsive noise from the three offshore developments when using other years as a baseline. In contrast, short-term changes in occurrence were detected when comparing days with and without impulsive noise. High variability in the baseline during non-development years suggests that natural drivers, such as prey abundance, have a greater effect on the occurrence of dolphins than the far-field anthropogenic noise. Therefore, in areas with high inter-annual variability, using occurrence during days prior to developments might be a better approach to investigate the impacts of marine developments (Graham et al. 2019).

FUTURE RESEARCH

This thesis addressed some knowledge gaps on the factors that modulate bottlenose dolphin occurrence in the Moray Firth. However, it raised new questions related to dolphin habitat use, foraging strategies, predator-prey relationships and responses to disturbance that should be addressed in future research.

Patterns in dolphin occurrence in this thesis was investigated mainly using CPODs. Although CPODs are reliable devices when studying dolphin occurrence (Bailey et al. 2010a; Roberts and Read 2015) they also present some limitations: first, they cannot be used to identify dolphins to the species level; second, number of individuals cannot be inferred; third: individual animals cannot be identified. The first limitation might not be an issue in my study site because I focused my analyses on sites where the presence of other species of dolphins than bottlenose dolphins is rare (Thompson et al. 2015). Therefore, I could safely assume that all detected echolocation clicks were produced by bottlenose dolphins. On the other hand, the second and third limitation might have caused some constraints to my research. For instance, the analysis of CPOD data in Chapter 2 showed a switch in diel occurrence in autumn, but due to the limitations of the data it was not possible to investigate the seasonal and diel acoustic behaviour of particular individuals. Intra-specific competition can lead to diversification in resource use among members of a single population (Svanback 2007). Habitat partitioning has been detected previously in populations of dolphins (Fury and Harrison 2008; Kiszka et al. 2012), caused by socially learned behaviours (Kovacs et al. 2017), ontogenetic (Giménez et al. 2017) or sex-specific dietary differences (Browning et al. 2014). Stratified movement patterns have been observed previously in this population of dolphins, which suggests that competition may be shaping their spatial distribution (Wilson et al. 1997). Therefore, the diel pattern in the occurrence of dolphins observed in Chapter 2 (Fig 2.8) could be explained by the co-occurrence of two distinct groups in the Moray Firth: one with diurnal behaviour that uses key sites in the inner Moray Firth predominately in summer to feed on returning adult salmon and a second with nocturnal behaviour that is present in summer but remains in autumn to feed on the overwintering clupeids. Using broadband sound recorders, which record not only echolocation clicks but also other dolphin vocalisations, would enable us to test this theory. Dolphins produce signature whistles, stereotyped whistles that can be used to identify individuals (Janik and Sayigh 2013; Longden et al. 2020). The deployment of broadband sound recorders in combination with signature whistle identification techniques would enable researchers to investigate whether resource partitioning occurs within this population of dolphins.

Nowadays, arrays of hydrophones can be used to accurately detect and track cetaceans by using their echolocation clicks (Gillespie et al. 2020; Macaulay et al. 2017; Malinka et al. 2018). This technology would enable studies to fill new knowledge gaps that arose from this thesis. For instance, highly site-specific patterns of dolphin occurrence were detected in Chapter 2, but patterns of movements between those sites remain unknown. Arrays of hydrophones could thus be used in the core area of the distribution of these dolphins to get more detailed information about their movement patterns. These devices could also expand our knowledge about the 3D habitat use of these animals and provide information on the water depths they use. For example, in Chapter 2 it was suggested that dolphins became nocturnal in autumn because feeding at night, when their prey are closer to the surface, might be energetically beneficial for them. This hypothesis could be tested by deploying 3D hydrophone arrays in summer and autumn and comparing information on dolphin diving depths through the 24-h cycle.

Information on prey in this thesis was collected by conducting boat-based acoustic surveys. This is a good approach to obtain data on fish abundance and distribution over wide spatial scales (Simmonds and Maclennan

2006). However, it provides a snapshot of the prey field that may not be a good reflection of prey availability from the predator perspective. For instance, they are unable to capture vertical movements of fish that may affect prey availability and, therefore, predator occurrence and behaviour (Baird et al. 2001; Baird et al. 2008; Benoit-Bird and Au 2003; Scott and Chivers 2009). Furthermore, boat surveys, due to logistic constraints, are often unable to account for the day-to-day variability that fish communities may present (Bruno et al. 2013; Hernández-Miranda et al. 2003). Bottom-mounted echosounders overcome these limitations providing data over longer periods of time (Fraser et al. 2018; Kaartvedt et al. 2009; Viehman and Zydlewski 2017). The deployment of one of these devices in a key foraging area would provide more comprehensive data on prey and would enable researchers to study predator-prey relationships in more detail. For instance, it could be deployed for several days to investigate prey abundance and behaviour over complete tidal and diel cycles overcoming the limitation of the day-to-day variability (Ariza et al. 2016; Solberg and Kaartvedt 2017; Viehman and Zydlewski 2017). Furthermore, since marine mammals can sometimes be detected and identified with an echo sounder (Benoit-Bird 2004; Benoit-Bird and Au 2003; Geoffroy et al. 2016), there may be opportunities for studies that investigate predator-prey links by investigating marine mammal echotraces directly from the echosounder data (Benoit-Bird et al. 2009; Doksæter et al. 2009; Pyć et al. 2016). Bottlenose dolphins in the Moray Firth use very constrained areas to forage (Hastie et al. 2004). Therefore, a bottom-mounted echo sounder may provide opportunistic detections of marine mammals during feeding events (Benoit-Bird and Lawson 2016).

Echosounders are increasingly used in marine research to describe predator habitat and study predator-prey relationships (Benoit-Bird and McManus 2012; Embling and Fernandez 2005; Lambert et al. 2019; Lawrence et al. 2016; Southall et al. 2019a). Frequencies usually used in scientific fish acoustic surveys produce sound within the hearing range of marine mammals (Southall et al. 2019c) and therefore have the potential to affect their behaviour (Schlundt et al. 2007). While the effect of naval sonars on marine mammals has been widely documented (see Harris et al. 2018 for a review), information about how marine mammals react to echosounders is sparse (Cholewiak et al. 2017; Quick et al. 2017) and there is no specific information about bottlenose dolphins. The ability to detect a sound does not necessarily imply that it will cause any behavioural disturbance (Southall et al. 2008). Therefore, empirical data on bottlenose dolphin responses to these devices are needed to investigate the effect they may have on these animals. This knowledge gap could be filled by deploying a duty-cycled bottom-mounted echosounder combined with devices to track dolphins, such as the 3D hydrophone arrays already described. This methodology would provide the required empirical information on the behavioural responses of dolphins to echosounder activity.

One of the limitations of the work in Chapter 3 was the lack of ground-truth data for the fish acoustic surveys we carried out (McClatchie et al. 2000). In fisheries acoustics, ground-truthing consists of obtaining information on fish sizes and species composition of the acoustic echotraces detected by the echo sounder. There are several methods to ground-truth fish acoustic detections but the inner Moray Firth has proven to be a challenging area. Fisheries acoustic surveys usually rely on trawl sampling to identify the fish species or species groups detected (Simmonds and Maclennan 2006). However, big research vessels equipped with echosounders and trawling gear are not suitable for shallow coastal areas like this. Another method to ground-truth acoustic information is the comparison of the echosounder data with commercial captures (McClatchie et al. 2000). However, this information is not available because fishing with mobile or active gear is not allowed within the SAC (Scotland 2004). Furthermore, due to this prohibition, there was no small fishing boat equipped with suitable fishing gear that could be hired to perform small-scale acoustic trawl surveys. Underwater camera techniques have been used successfully to characterise fish communities in coastal areas where fishing is a challenge (see Mallet and Pelletier 2014 for a review). Baited remote underwater video (BRUV) is a cost-effective sampling method (Langlois et al. 2010) that could be used to describe the fish assemblage of the inner Moray Firth. BRUV surveys have several sources of bias, such as the selection of bait type (Ghazilou et al. 2016), time in the diel (Myers et al. 2016) and tidal cycles of the deployments (Taylor et al. 2013a), the short-term variability in fish assemblages (Munks et al. 2015) or the species-specific responses of fish to the lights of the system (Birt et al. 2019). Due to the dynamic nature of the inner Moray Firth, a pilot study would be required to optimise the sampling methodology, but overall, this approach should prove to be a robust methodology to study fish assemblages in the area (Becker et al. 2010; Gladstone et al. 2012).

A further limitation of the acoustic surveys performed in this thesis was that they did not provide any specific information on Atlantic salmon (*Salmo salar*). Salmon has long been considered an important prey species for this population of dolphins (Hastie et al. 2004; Robinson et al. 2007b; Stockin et al. 2006; Wilson et al. 1997). However, information about salmon movements and habitat use in the inner Moray Firth is still lacking. For instance, it is still unknown how much time they spend in the area before going up their home rivers, whether they use tidal currents to go through the channels or what their diel behaviour is. In 2018 and 2019 an adult salmon tracking project was undertaken in the Moray Firth to study salmon movements and survival rates (Ness District Salmon Fishery Board 2018, 2019). Arrays of acoustic receivers were deployed in the Sutors and Chanonry narrows and around 200 adult salmon were successfully tagged. Salmon were captured by deploying a net during the flood tide near Chanonry, tagged and immediately released once recovered from the anaesthesia (< 10 minutes). Since most of the salmon remained in the narrows for less than 24 h (Marine Scotland Science Unpublished data), and all the salmon were released at the same location in Chanonry, during daytime and around the flood tide, the dataset could not be used to investigate their diel or tidal preferences. Some salmon tracking studies involve relocating and releasing tagged fish several hours after their capture (Reischel and Bjornn 2003; Russell et al. 1998). The feasibility of relocating salmon and releasing them at different stages in the diel and tidal cycles should be explored in future studies in order to obtain a more randomised sample to study adult salmon migration behaviour in this area.

When studying the ARS behaviour in dolphins in Chapter 4, the analysis was based on duty-cycled sound recorders that were recording 50% of the time. Therefore, studying the presence of foraging calls throughout complete dolphin encounters and investigating their link with dolphin occurrence was unfeasible. In the future, continuous broadband recordings would be needed to disentangle this link in more detail. This thesis was also constrained by the time needed to manually extract dolphin calls. If devices were set to record continuously, this process would be even more challenging making it necessary to first develop an automatic detector for dolphin vocalisations. Historically, the extraction of marine mammal calls has been performed manually, via visual inspection of the spectrograms (Mellinger et al. 2007). Even though this method is very accurate, it is extremely time-consuming and limits the amount of data that researchers can process. Lately, artificial intelligence (AI) and machine-learning technologies have been used to automatically detect animal vocalisations with great success (Bergler et al. 2019; Mac Aodha et al. 2018; Shiu et al. 2020). Initially, these techniques are very data demanding, with algorithms that need to be trained using large annotated datasets (Zhou et al. 2017). However, once trained, AI can process large amounts of data that far exceed those that can be processed manually. The Lighthouse Field Station in collaboration with researchers from the Friedrich-Alexander University (Germany), has started to develop an automatic detector for bottlenose dolphin vocalisations. The project is in its first phase of development, training the algorithm, and once working it will enable researchers to deal with the increasing amount of acoustic data new projects are collecting.

It was hypothesised in Chapter 4 that the echolocation buzzes extracted in the analysis may be a mixture of foraging and social buzzes. Social buzzes have been detected in bottlenose dolphins (Herzing 1996), but there is no information about the behavioural contexts in which bottlenose dolphins use buzzes in the Moray Firth. This could be investigated following a methodology similar to that described by Martin et al. (2019): during dolphin photo-ID surveys a CPOD and a SoundTrap could be deployed while the surface behaviour of dolphins is recorded. These data would enable researchers to explore how often social buzzes are produced and assess their suitability as a foraging proxy. Previous studies in harbour porpoises found acoustic differences in repetition rates between foraging buzzes and buzzes produced in social contexts (Sørensen et al. 2018). Similarly, potential differences between social and foraging buzzes in bottlenose dolphins could be explored to investigate whether they could also be differentiated.

CONCLUSION

This study substantially contributes to the knowledge base on the drivers of occurrence of the Scottish east-coast bottlenose dolphin population in the core area of their distribution. This thesis described how environmental cycles, foraging and offshore developments affect the coastal distribution of bottlenose dolphins. The results emphasized the need for empirical data to effectively predict the occurrence of these animals and enable decision-makers to implement adequate measures to protect them. The studies presented in this thesis also highlighted the importance of both passive and active acoustic methods when investigating drivers of cetacean occurrence and exploited new techniques to perform fisheries acoustic surveys that could be useful in future research. Hopefully, the combined findings of this thesis will encourage further studies aiming to investigate predator-prey relationships in more detail and ultimately to understand the fine-scale habitat use of bottlenose dolphins in this area.

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PHOTO APPENDIX I

Opportunistic pictures of bottlenose dolphins feeding in the inner Moray firth.

Picture	**Date**	**Location**	**Prey species**
Figure AI.1	14-Jun-10	57.688 N -3.962 W	Salmon (*Salmo salar*)
Figure AI.2	20-Jul-10	57.735 N -3.912 W	Salmon (*Salmo salar*)
Figure AI.3	05-Aug-13	57.601 N -3.969 W	Mackerel (*Scomber scombrus*)
Figure AI.4	24-Aug-16	57.087 N -4.107 W	Likely: Mullet (*Chelon spp.)*
Figure AI.5	01-Sep-10	57.709 N -3.946 W	Unknown
Figure AI.6	01-Sep-10	57.593 N -4.081 W	Likely: Sand eel (*Ammodites spp.*)
Figure AI.7	02-Sep-09	57.688 N -3.952 W	Likely: Squid (*Loligo spp.*)
Figure AI.8	Unknown	57.087 N -4.107 W	Flat fish

Figure AI.1: Bottlenose dolphin feeding on salmon (Salmo salar). Photo Dr Barbara Cheney ©Lighthouse Field Station, University of Aberdeen

Figure AI.2: Bottlenose dolphin feeding on salmon (Salmo salar). Photo Dr Barbara Cheney © Lighthouse Field Station, University of Aberdeen.

Figure AI.3: Bottlenose dolphin feeding on mackerel (Scomber scombrus). Photo Dr Barbara Cheney © Lighthouse Field Station, University of Aberdeen.

Figure AI.4: Bottlenose dolphin feeding on, likely, mullet (Chelon spp.). Photo © Charlie Phillips/WDC.

Figure AI.5: Bottlenose dolphin with an unidentified fish prey. Photo Dr Barbara Cheney © Lighthouse Field Station, University of Aberdeen.

Figure AI.6: Bottlenose dolphins feeding on, likely, sand eels (Ammodites spp.). Photo Dr Barbara Cheney © Lighthouse Field Station, University of Aberdeen.

Figure AI.7: Most likely squid (Loligo sp.) captured in pictures during a bottlenose dolphin feeding event. Photo Dr Barbara Cheney © Lighthouse Field Station, University of Aberdeen.

Figure AI.8: Bottlenose dolphin feeding on a flat fish (unidentified species). Photo © Charlie Phillips/WDC.