MSc Thesis

Fine-scale use by harbour porpoise of a high energy coastal environment

Ellen E. Blanchard

PRIFYSGOL BANGOR UNIVERSITY

Supervised by Dr Peter Evans and Dr James Waggitt
School of Ocean Sciences, Bangor University
Collaborating institution: Sea Watch Foundation (SWF)

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Abstract:

With the UK setting renewable energy targets of delivering 15% of its energy consumption from renewable sources by 2020, new marine renewable technologies are emerging, including tidal energy. Although this form of energy extraction is environmentally sustainable, the high energy areas in which the tidal technologies would be deployed are also favoured by the small cetacean species, the harbour porpoise. To assist the assessment of tidal energy developments, and the potential impacts they may cause, knowledge of how harbour porpoise utilise these high energy coastal environments is needed. To do so, data were collected from land-based watch points, from 5th June to 21st July 2018, at two sites Point Lynas and Bull Bay headland, using direct visual observations, supplemented by a tripod mounted camcorder, filming the movement of the individual animals. The recordings taken were then analysed and response variables were related to surface features, and hydrodynamic models of turbulence, current speed, depth and tidal range developed for the areas. Results showed that harbour porpoise in the area show movements suggestive of foraging during all tidal states, but primarily during the ebb and high slack tides at Point Lynas and during flood and low slack tides at Bull Bay. Results highlighted turbulence as a significant factor influencing behaviour and movement at Point Lynas, with porpoise showing concentrated movements of fast foraging in areas of high turbulence.

Contents:

Figures and tables:

Figures:

Tables:

1.0 Introduction

1.1 Human impacts on cetaceans:

Globally, there are numerous human activities that threaten the whale, dolphin and porpoise species that collectively make up the mammalian order Cetacea (Simmonds and Brown, 2011), with many occurring in waters around the UK (Reid et al, 2003; Parsons et al, 2010). Although whale hunting in UK waters stopped several decades ago, hunting continues to occur in a minority of countries, including Japan, Norway and Iceland (IFAW, 2018) and can cause a significant threat to local cetacean populations. In UK waters the biggest human activity threat extends from the incidental death of cetaceans as a product of 'by-catch' in fishing gear (Simmonds and Brown, 2011). Boat traffic is also a threat to cetaceans by causing collisions that injure or kill animals, as well as contributing to marine noise pollution by emitting noise into surrounding waters (Simmonds and Brown, 2011). Other threats to cetaceans as a result of human activities in UK and global waters include pollution, climate change and prey reductions due to fishing pressures.

A relatively new emerging human activity that has the potential to cause a negative impact to cetaceans is the installation of marine renewable energy (MRE) sources (Wilson et al, 2013; Waggitt et al, 2017), including wind power, and wave and tidal stream technologies (DECC, 2011; The Crown Estate, 2012). Wind power is currently recognised as the predominant MRE source in the UK, with the UK offshore wind market the largest in the world (DECC, 2011; The Crown Estate, 2017). However, with the UK setting renewable energy targets of delivering 15% of its energy consumption from renewable sources by 2020, through the Renewables Obligation, the target is unlikely to be met by using wind power alone (RED, 2009; DECC, 2011). Therefore, new marine renewable technologies of wave and tidal stream are emerging (DECC, 2011; The Crown Estate, 2012). Along with wind power, these new marine renewable technologies have potential effects/risks on marine life that, although still relatively poorly unknown, are primarily negative. For cetacean species which inhabit areas where MRE sources are installed, the potential risks they face are shown in Table 1, including collision with devices, disturbance from the construction and device operation, noise emission and increased contamination (Teilmann et al, 2006; Evans, 2008; Thomsen, 2010; Simmonds and Brown, 2011; Mann and Teilmann, 2013; Wilson et al, 2013; Waggitt et al, 2017).

Table 1: Potential impacts of marine renewable-energy industry on cetaceans. Source: Simmonds and Brown (2011).

1. Increased noise	2. Physical interactions	3. Habitat changes	4. Increased contamination	5. Effects on prey
Construction phase: pile driving, drilling, dredging, increased shipping/aircraft movements. **Operation phase:** operating turbines and other renewable devices and other, maintenance vessels/aircraft. **Decommissioning phase**: explosives, cutting equipment, increased movements of vessels/aircrafts.	**Entrapment/ entanglement** with e.g. mooring or other cables. **Collisions** with e.g. floating or submerged structures potential including rotating blades of current driven turbines.	**Predominantly transient**: increased turbidity, resuspension of potentially polluted sediments during construction and cable laying. **More persistent**: physical and biological consequences of presence of structures in water column, e.g. artificial reef effect.	**Leaks or spills** of e.g. hydraulic fluid from operating devices or from increased shipping. **Use of biocides** to control marine fouling organisms on operating devices.	**Changes in food webs and prey** caused by increased noise, physical interactions, habitat changes and increased contamination alone or in combination.

1.2 Tidal stream renewable energy:

Tidal stream technologies are still at a relatively early stage of development. However, the potential for tidal resources in the UK is large, in the context of supplying power to meet the UK electricity demand, and both tidal stream and wave technologies are being considered as a new extraction source (Figure 1; DECC, 2011; The Crown Estate, 2012). Tidal stream technologies require movements of water in order to capture and convert kinetic energy into electricity. Therefore, favourable environmental characteristics for the installation of tidal stream sources are periodically fast-flowing, turbulent conditions (Benjamins et al, 2015). These high energy tidal stream environments are frequently found around headlands/islands and through narrow channels where currents and energy increase (Johnston et al, 2005b; Benjamins et al, 2015; Waggitt et al, 2017). Along with having favourable conditions for the extraction of renewable energy, high energy tidal stream environments are also frequent sites for cetaceans, who use the environments for a range of reasons which are likely to vary between populations, age, or gender of the same species, but include foraging or saving energy (Benjamins et al, 2015; Waggitt et al, 2017). However, as already stated, the installation of MRE sources in areas of cetacean occupancy could have potential negative impacts on species, affecting their habitat and prey along with causing other problems like increased noise (Teilmann et al, 2006; Evans, 2008; Thomsen, 2010; Simmonds and Brown, 2011; Mann and Teilmann, 2013; Wilson et al, 2013; Waggitt et al, 2017). In order to focus on, and perhaps mitigate, these potential impacts, it needs to be known how and why cetaceans are using areas of interest for energy extraction, specifically in terms of their habitat use and small-scale distribution (Wilson et al, 2013). Currently, however, these potential impacts remain poorly known due to the complexity of tidal stream environments, the technological difficulties of conducting research on mobile species in fast-flowing, turbulent waters, and the gap in knowledge of how tidal stream environments are used by cetaceans and their prey (Wilson et al, 2013; Benjamins et al, 2015).

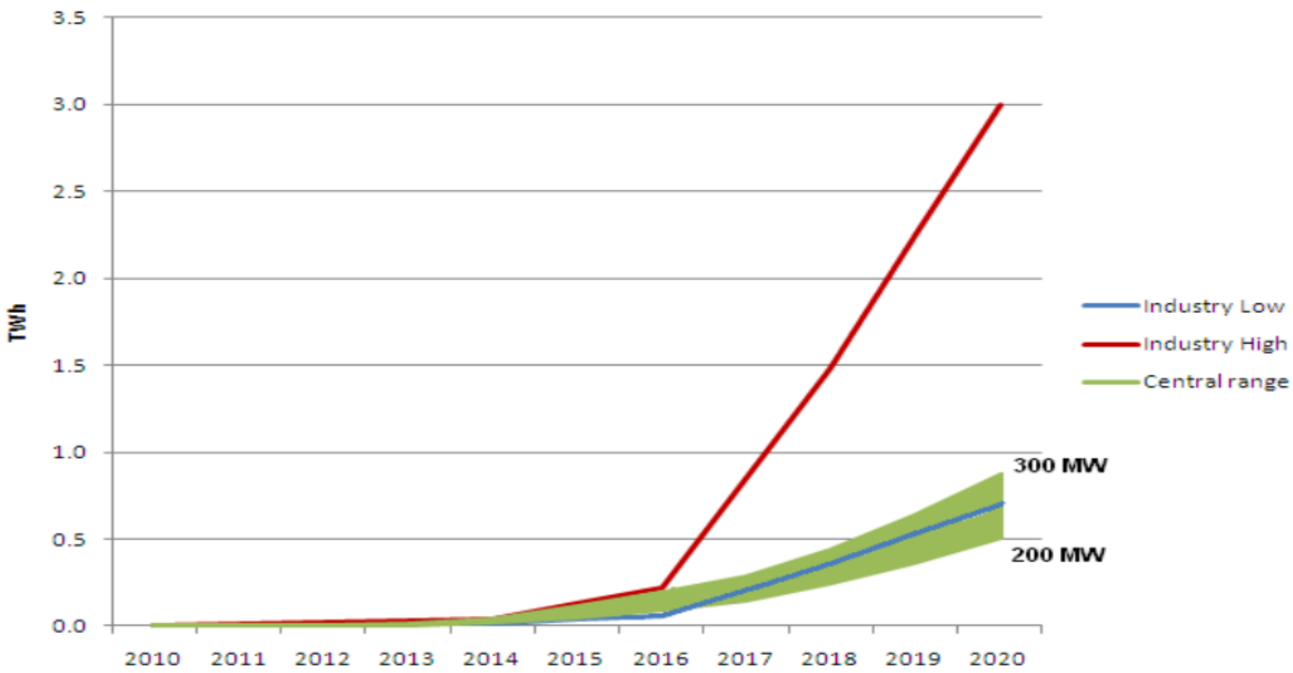

Figure 1: Deployment potential, in TeraWatt hours (TWh), for marine energy (wave and tidal) in the UK by 2020. Source: DECC, (2011).

1.2.1 Tidal stream environments:

Tidal stream environments are referred to when a site has a structure of topography and coastlines that cause tidal flows to pass through narrow channels or around headlands/islands (Benjamins et al, 2016). The strong currents of these environments provide a range of logistical and technological difficulties in studying tidal stream sites and the ecology within them, making it difficult to deploy and recover moorings or carry out boat-based surveys (Benjamins et al, 2015). The characteristics of tidal steam environments that make them suitable for both cetaceans and tidal stream renewable energy extraction are the fast-flowing, turbulent water conditions (Benjamins et al, 2015), which for renewable energy extraction provide a reliable source of energy and for cetaceans are assumed to provide areas of opportunistic foraging

(Benjamins et al, 2015; Waggitt et al, 2017). Cetaceans also benefit from the headlands and islands around which tidal streams are frequently found, as the features generate complex three-dimensional secondary flows, which produce physical and biological fronts (Wolanski and Hamner, 1988). Fronts are boundaries between two different water masses and they affect the distribution of sediments and aggregations of weak nekton and plankton within the water column (Wolanski and Hamner, 1989). Aggregations of weak nekton and plankton change the distribution and density of small consumers, which results in patches of concentrated prey for marine predators like cetaceans (Wolanski and Hamner, 1988; Evans, 1990; Johnston et al, 2005b; Ingram et al, 2007; Shucksmith et al, 2009; Jones et al, 2014).). Along with making prey more abundant, tidal stream environments can also enhance the vulnerability of prey to capture. The strong turbulence of the areas provides a mechanism which confuses and disorientates the prey and increases the cost to maintain orientation, making prey easier to catch (Benjamins et al, 2015). Therefore, cetaceans may choose to forage in tidal stream environments because their prey are more abundant, more diverse or more vulnerable to predation at particular phases of the tide (Benjamins et al, 2015). Steep velocity gradients connected with tidal stream environments allow cetaceans to enter the faster flowing currents to capture prey, before returning into calmer waters or other oceanographic features formed as a result of headlands and islands, such as eddies and upwellings (Wolanski and Hamner, 1988; Johnston et al, 2005a; Ingram et al, 2007; Benjamins et al, 2015). The conditions of these strong tidal currents found in the development areas of eddies and upwellings are favoured by certain cetacean species (Pierpoint et al, 1998; Weare, 2003; Isojunno et al, 2012, notably the harbour porpoise (*Phocoena phocoena*).

1.3 Harbour porpoise:

The harbour porpoise is one of the smallest cetacean species, inhabiting the northern hemisphere and considered a mainly coastal dwelling species (Koopman, 1998; Lockyer, 2003; Reid et al, 2003; Santos et al, 2004 Around the British Isles the harbour porpoise is the most commonly sighted cetacean, with a wide coastal distribution around the UK (Reid et al., 2003; Evans et al., 2008; Marubini et al, 2009). As the species lives mainly in temperate waters, their layer of blubber has a deeper and higher lipid content in comparison to similar-sized cetaceans (Koopman, 1998). The small body size of the harbour porpoise makes them unable to store substantial amounts of energy (Santos et al, 2004), and therefore they depend on being able to locate abundant prey resources regularly to maintain their level of energy (Heide-Jørgensen et al, 2011). Small pelagic schooling species, such as sprat, sandeel, and whiting are their main prey source, along with demersal fish such as flatfishes and cod (Reijnders, 1992; Santos and Pierce, 2003). However, even though a wide range of prey species have been recorded for the harbour porpoise, studies have found that populations in one area tend to primarily feed on two to four main species (Santos and Pierce, 2003).

Harbour porpoise are the only cetacean species on the UK Biodiversity Action Plan that are prioritised due to earlier declines in UK waters (Bennett et al, 2010) They are also listed under Annex II and IV of the EU Habitats Directive (European Commission 1992) due to their vulnerability to anthropogenic threats including disturbance and by-catch (European Commission, 2009). Under the Habitats Directive, the UK has an obligation to identify and evaluate risks that may pose a threat to the conservation status of harbour porpoise within UK waters (Evans and Anderwald, 2016; Evans, 2018 Therefore, with the recent developments of human activities in offshore shelf waters, and the increase of anthropogenic threats, the harbour porpoise has become a focal species in terms of management of human impacts and marine habitat conservation plans (Skov and Thomsen, 2008).

1.3.1 Harbour porpoise and tidal stream environments:

Tidal stream environments are common habitats for the harbour porpoise (Evans, et al, 2015; Waggitt et al, 2017). Fine-scale studies have found that the conditions of said environments are favoured by harbour porpoise, especially the strong tidal currents produced by areas of upwelling and eddies (Peirpoint et al, 1998; Weare, 2003), representing important foraging habitats for numerous populations of the species worldwide (Evans, 1990; Johnston et al, 2005b; Pierpoint, 2008; Marubini et al, 2009; Isojunno et al, 2012; Jones et al, 2014; Waggitt et al, 2017). As already mentioned, the small body size of the harbour porpoise makes them unable to store substantial amounts of energy (Santos et al, 2004; Wisniewska et al, 2016), and so high energy coastal environments may be of particular importance for harbour porpoise in finding regular sources of food (Marubini et al, 2009; Heide-Jørgensen et al, 2011; Isojunno et al, 2012; Ijsseldijk et al, 2015). Whilst these environments are likely to be challenging for harbour porpoise to exploit, due to the fast flow and turbulence, it is thought that, along with providing enhanced foraging opportunities, tidal stream environments may facilitate movement or increase interaction with other porpoise travelling through the area (Benjamins et al, 2015), making the cost of exploiting energy in these sites profitable.

Due to the high abundance of the species within tidal stream environments, and the importance it has for the species around the world (Johnston et al, 2005b; Pierpoint, 2008; Marubini et al, 2009; Isojunno et al, 2012; Jones et al, 2014; Waggitt et al, 2017), an increase of renewable tidal stream energy extraction in these environments could be a problem. Therefore, reducing the impacts from renewable tidal stream energy extraction is currently a conservation priority (Waggitt et al, 2017). In order to accurately select locations which will maximise the energy output of tidal stream extraction, but also mitigate the interactions with porpoise populations, an understanding of harbour porpoise distribution, at a regional scale, and their fine-scale uses of each tidal stream environment is needed (Wilson et al, 2013; Benjamins et al, 2015; Macaulay et al, 2017; Waggitt et al, 2017). However, basic knowledge of species ecology, inter-annual variability and habitat preferences, for not only the harbour porpoise but for many other cetacean species which inhabit tidal stream environments, is currently inadequate in many areas (Marubini et al, 2009). And the relationship between porpoise presence and use of tidal environments appears variable across many areas where porpoise are found (Benjamins et al, 2015). However, studies have been and are still trying to increase knowledge and understanding.

1.4 Studies on harbour porpoise:

1.4.1 Harbour porpoise ecology:

Studies on harbour porpoise began with focusing on their ecology, firstly looking into abundance and distribution of the species in many areas around the world (e.g. Evans, 1980; Kraus et al, 1983; Watts and Gaskin, 1985; Barlow, 1988; Barlow et al, 1988; Raum-Suryan and Harvey, 1998; Hammond et al, 2002). The general distribution of harbour porpoise is mainly affected by depth and temperature, with the species inhabiting inshore shallower areas in temperate waters around the world (Evans, 1980; Barlow, 1988; Hammond et al, 2002). The general abundance of the species makes it the most common and widespread cetacean in British waters (Evans, 1980; Hammond et al, 1995; Reid et al, 2003, Evans et al, 2015). The abundance of the species on a finer scale is largely influenced by tidal cycles, with certain tidal states and speeds leading to an increased number of porpoise. However, it is apparent that the influence of tidal cycles is complex and varies between areas, as the abundance of harbour porpoise is reported to increase during high tide (Leeney, 2003; Weare, 2003; Marubini et al, 2009; Boonstra et al, 2013), low tide (Leeney, 2003; Weare, 2003; Embling et al, 2010), the ebb tide (Leeney, 2003; Hall, 2011; Jones et al, 2014) and the flood tide (Johnston et al, 2005b) in different areas which harbour porpoise inhabit. Porpoise abundance can also be influenced by depth (Watson and Gaskin, 1985; Raum-Suryan and Harvey, 19898; Marubini et al, 2009), seabed slope (Raum-Suryan and Harvey, 1998; Booth et al, 2013), and distance from the land (Booth et al, 2013). Harbour porpoise also appear to use various habitats throughout their distribution for different reasons, such as using areas as feeding sites, and other areas as resting or socialising sites (Leeney, 2003; Pierpoint, 2008; Benjamins et al, 2015; Gilles et al, 2016).

A main habitat of the harbour porpoise that has become a key focus are the high energy tidal stream environments. Studies looking into the distribution and abundance of the porpoise have highlighted these areas as habitats where porpoise are regularly seen, with many reporting that their behaviour in these environments seems representative of foraging or feeding (Evans et al, 1993; Evans and Borges, 1995; Borges and Evan, 1997; Leeney, 2003; Goodwin, 2008; Pierpoint, 2008; Shucksmith et al, 2009). As previously mentioned, these environments are regions of enhanced relative vorticity and result in patches of concentrated prey, which are assumed to facilitate foraging for harbour porpoise (Wolanski and Hamner, 1988; Johnston et al, 2005b; Goodwin, 2008; Shucksmith et al, 2009; Jones et al, 2014). The distribution of porpoise in tidal streams can be influenced by many factors including the local bathymetry, current speeds, oceanographic conditions and the abundance, distribution and behaviour of prey species, and are likely to change over short spatio-temporal scales (Benjamins et al, 2015). The focus of studies on harbour porpoise has shifted from large-scale synoptic surveys, providing context on general distribution and abundance, to small-scale focused efforts quantifying the fine-scale habitat use of porpoise in tidal stream environments (Benajmins et al, 2015). In high energy environments, porpoise abundance is strongly related to certain areas, areas which contain fine-scale oceanographic features driven by tidal circulation (Johnston et al, 2005b, Johnston and Reed, 2007). On a meso-scale, hydrodynamics of high energy environments, such as eddies forming by an island wake, have been associated with high concentrations of prey species and/or increased porpoise abundance (Borges and Evans, 1997; Johnston et al, 2005a; Johnston et al, 2005b; Johnston and Reed, 2007; Jones et al, 2014). Again, like with the relationship between tidal current and porpoise abundance, although many studies on harbour porpoise habitat use have found that tidal flow and the hydrography of the environment affects the abundance and use of harbour porpoise, the relationship between presence and use against tidal flow speed and phase is irregular between different studied areas (Benjamins et al, 2015).

Habitat use of tidal stream environments by harbour porpoise change with the tidal phase and speed. In some areas, presence and feeding behaviours have been observed to increase during the ebb tidal phase, when current speeds are thought to be at a faster rate (Pierpoint, 2008; Hall, 2011). On the other hand, in other areas porpoise tend to feed during the flood tidal phase (Calderan, 2003). In several studies, porpoise were more abundant in areas of low currents, as opposed to the presence increasing when flow is fast (Marubini et al, 2009, Embling et al, 2010; de Boer et al, 2014). Results from porpoise habitat use highlight that no single tidal variable can fully explain the effect of tide on harbour porpoise occurrence in tidal stream environments, and as a result, habitat use changes also, with the preferred tidal phase or speed varying across the studies (Evans and Borges, 1995; Calderan, 2003; Embling et al, 2010; Pierpoint, 2008; Marubini et al, 2009; Hall, 2011; Isojunno et al, 2012; Booth et al, 2013; Benjamins et al, 2015). Instead of a particular tidal condition influencing their fine-scale use, it is more likely that porpoise select a range of currents and topography that increase relative vorticity and concentrate prey in patches (Johnston et al, 2005b; Isojunno et al, 2012). However, it has now been proven that tides, along with providing different phases and speeds, do produce hydrodynamic features, such as baroclinic flows and lee waves, which may be important for providing foraging opportunities for porpoise (Jones et al, 2014).

1.4.2 Methodology:

In terms of the methodology for studying the ecology of harbour porpoise, abundance and distribution studies began with visual boat-based or land-based surveys (e.g. Watts and Gaskin, 1985; Barlow et al, 1988; Hammond et al, 1995; Pierpoint, 2008; Shucksmith et al, 2009; Baines and Evans, 2012; de Boer et al, 2014; Evans et al, 2015). These involved reporting of porpoise sightings, usually over a time-scale of a few months, to give an insight into the distribution and *abundance* of harbour porpoise in different areas of the world. The land-based watches usually involve surveying over a given area (Leeney, 2003; Goodwin, 2008; Evans et al, 2015), whereas the boat-based watches tend to survey on given line transects (Pierpoint, 2001; Shucksmith et al, 2009; Baines and Evans, 2012). The results from these types of studies gives a good idea of porpoise distribution generally, and the areas where they are most abundant, sometimes in relation to the tidal cycle. However, as only visual watches are used, any other information reported during the surveys, such as habitat use by porpoise, or changes in physical features and porpoise behaviour, are just speculation as results obtained at coarse scales may not reliably identify small-scale habitat use (Watts and Gaskin, 1985; Leeney, 2003; Pierpoint, 2008; Shucksmith et al, 2009; Embling et al, 2010; Benjamins et al, 2015). Advanced methods to support the visual surveys are needed if fine-scale habitat use by porpoise are to be determined with certainty.

Acoustic methods of detecting porpoise are used to give a more accurate recording of porpoise distribution and abundance in areas. The devices can detect and track porpoise movements, giving an insight into the number of porpoise in an area as well as their behaviours (Skov and Thomsen, 2008; Gordon et al, 2014). The results from acoustic methods usually support visual surveys of the same area, along with being compared against physical parameters, such as current velocity and temperature which can be recorded using an ADCP and temperature sensor (Ijsseldijk et al, 2015). The addition of a more precise method of tracking porpoise, along with physical conditions for an area, means that the behaviours and abundance of porpoise against parameters such as depth, temperature, tidal phase and flow speed can be determined. However, the physical variables used to explain the ecology of harbour porpoise within tidal stream environments in these fine-scale studies tend to use methods with easily obtained variables, such as depth and temperature (Booth et al, 2013; Ijsseldijk et al, 2015). For a full understanding of what is driving the behaviours of porpoise, more complicated variables need to be tested, for example turbulence within the area.

More recent studies on harbour porpoise in tidal stream environments are moving from standard acoustic techniques to using moored passive acoustic detectors (e.g. C-PODs) to survey harbour porpoise abundance and distribution (Boonstra et al, 2013; Nuuttila et al, 2013; Wilson et al, 2013; Benjamins et al, 2016; Cox et al, 2017; Macaulay et al, 2017; Nuuttila et al, 2017). These moored passive acoustic detectors provide continuous recordings of porpoise in the area of interest, offering a new and rapid way to investigate porpoise occurrence (Wilson et al, 2013). This form of study has been widely used on harbour porpoise but is still a relatively new form of technique within tidal steam habitats, due to the complicated nature of the environment (Wilson et al, 2013; Benjamins et al, 2016). This means many studies carried out so far in tidal stream habitats have acted as pilot studies for the technique, highlighting the appropriate spatio-temporal scales in which to carry out more advanced studies, which will then provide information on the fine-scale site use of harbour porpoise (Boonstra et al, 2013). Information regarding harbour porpoise fine-scale use of tidal stream habitats is critical for the future developments in both the renewable energy sector and for the conservation of the species. Knowledge currently is inadequate in many areas.

1.5 Gaps in knowledge:

The difficulties in using standard techniques to study highly mobile species, like the harbour porpoise, in energetic tidal stream environments, means that though studies have been ongoing for several years, there are still gaps in the knowledge of how porpoise use these high energy environments (Wilson et al, 2013; Benjamins et al, 2015). Although visual and acoustic studies have shown that tidal stream environments provide foraging opportunities to the species, little is known as to why these underlining mechanisms generate such events. In particular, few studies have looked at the prey element of how porpoise use the areas. Whilst many have linked the increased presence of porpoise to the movements of their prey (e.g. Johnston et al, 2005b; Goodwin, 2008; Shucksmith et al, 2009; Booth et al, 2013; de Boer et al, 2014), not many have explained why the prey are behaving in the tidal stream environments in a way that increases their abundance or availability, or how harbour porpoise capture their prey in the environments (Evans and Borges, 1995; Borges and Evans, 1997; Johnston and Read, 2007; Benjamins et al, 2015). Other studies have also neglected to link the physical forces within the area with the foraging behaviours of the species, missing out on recognising the bio-physical mechanisms that drive foraging (Johnston et al, 2005a; Waggitt et al, 2017). The precise variables that affect harbour porpoise within tidal environments are also unknown. Studies use methods with variables that, although favourable for research purposes (such as current and depth), are probably not the variables directly influencing the observed behaviours. Instead, it is more likely that they are proxies for other variables that are affecting the species, with many studies conceding that it is plausible their studies miss out, or do not account for, all factors that influence behaviour (Booth, 2010; Embling et al, 2010; Booth et al, 2013; Ijsseldijk et al, 2015; Waggitt et al, 2017).

Studies have currently managed to record the distribution of harbour porpoise in many cold temperate and subarctic regions around the world, highlighting the importance or tidal stream environments for the species, but understanding the fine-scale movements of porpoise within the environment is still lacking (Pierpoint, 2008). Where they are found, and certain properties of high energy environments that are attractive to porpoise are known. However, knowledge on how they move and use the environments is lacking. To allow for the appropriate management of both conservation areas and MRE developments, we need to understand which habitats are important for harbour porpoise, in particular how and why they are using the areas (Shucksmith et al, 2009; Wilson et al, 2013). This project attempts to address this knowledge gap, recording the fine-scale behaviours of harbour porpoise by tracking their movements and usage within high energy environments.

1.6 Aims and Hypotheses:

The project will involve using a relatively novel method, along with rarely used measurements of turbulence, to examine the fine-scale use by harbour porpoise at two high energy sites in north Anglesey: Point Lynas and Bull Bay headland, identifying where the animals forage in relation to surface physical features. The changes to porpoise foraging patterns during varying current strengths, at different stages of the tidal cycle, and between spring and neap tides, will also be tested. The project will seek to answer the following primary hypotheses:

H_1 Harbour porpoise will show concentrated movements in areas of high turbulence.

H_2 Harbour porpoise will show movements suggestive of foraging during certain tidal states.

2.0 Methods:

2.1 Study site:

The survey data collected during the research project were taken from two high energy sites in north Anglesey, Point Lynas (53˚ 25' 0.59" N 004˚ 17' 19.21" W) and Bull Bay headland (53˚ 25' 25.39" N 004˚ 22' 5.77" W) from land-based watch points (Figure 2). Point Lynas is situated on the northeast tip of Anglesey, with Bull Bay slightly to the northwest, around 6km along the coastline from Point Lynas. Observations during the land-based surveys focussed around a 1km radius of the watch point at each site (Figure 3), which allowed for fine-scale (1 to 10km) behaviours of harbour porpoise in the area to be seen and identified (Johnston et al, 2005b), but if sightings were easily seen past the 1km radius, they were included. Both sites have been classified as high energy, with current speeds surpassing 1.5ms^{-1} at certain tidal states (Shucksmith et al, 2009; Robins et al, 2014). Point Lynas and Bull Bay are also known sites of regular high encounters with harbour porpoise, particularly during the summer months (Evans et al, 2015), with conditions representative of important foraging habitats for the species (Pierpoint et al, 1998; Johnston et al, 2005b; Shucksmith et al, 2009; Waggitt et al, 2017). These characteristics made the two sites appropriate for observing the foraging behaviour of harbour porpoise in high energy environments.

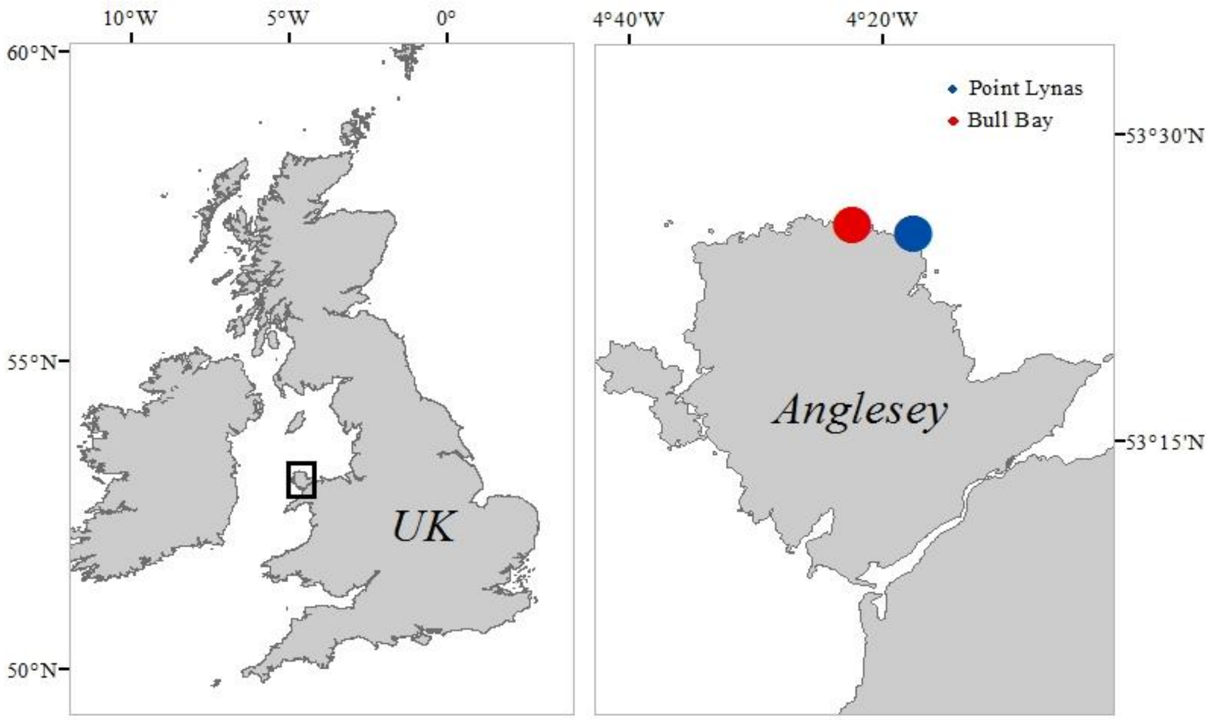

Figure 2: The locations of the two sites, Point Lynas and Bull Bay, used for the watch-based surveys during the project. The location of Anglesey in the UK is shown by a box.

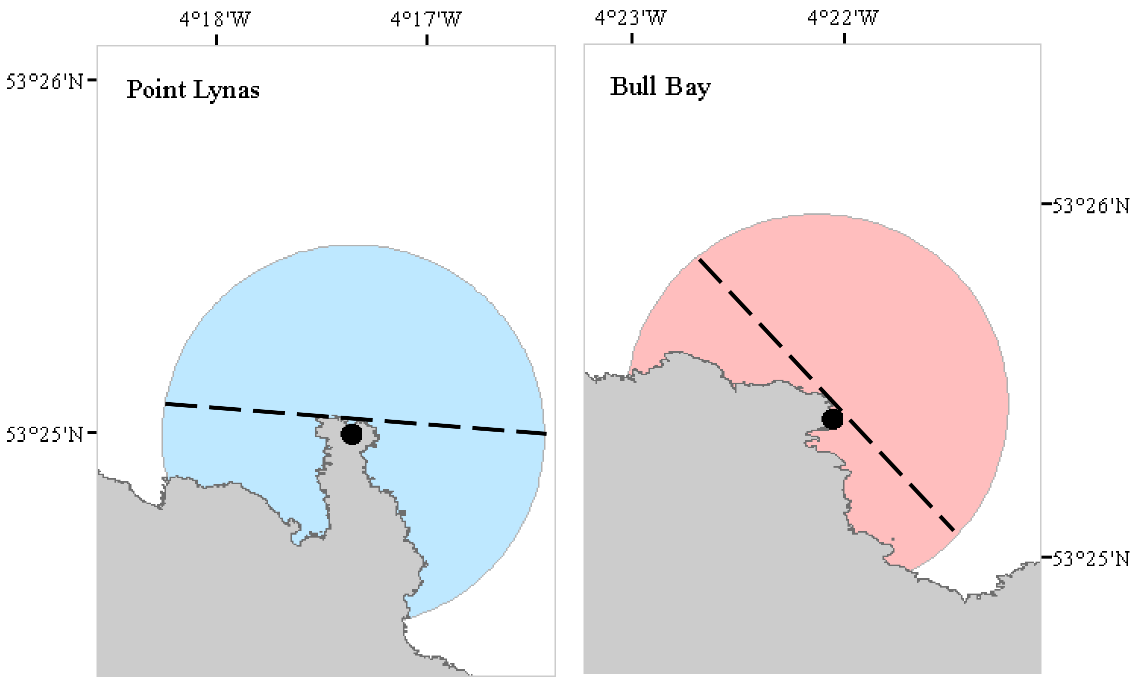

Figure 3: The 1km radius at each surveying site used for focussed observations. The points represent the locations of the watch points. Dashed line shows the area (above line) more likely to be surveyed.

2.2 Land-based surveys:

Land-based watch surveys took place at the two sites from 5th June to 21st July 2018, with a total of 27 surveys carried out at Point Lynas and 23 surveys at Bull Bay. Surveys were conducted using direct visual observations, supplemented by a tripod-mounted camcorder (Canon Legria HF21 with 15x optical zoom) filming the movement of the individual animals. A tripod-mounted theodolite was also utilised to supplement the visual observations and camcorder recordings, providing the precise location of the harbour porpoise in relation to the chosen watch points. At each site, a specific position for both the camcorder and theodolite was chosen at the first survey, with these positions used throughout the remainder of the fieldwork. To accompany the theodolite recordings, the elevation of each survey site was taken from a handheld GPS, and the theodolite height, measured from the base of the theodolite tripod leg to the theodolite eyepiece, was recorded. Each survey lasted either 1 hour and 30 minutes or 2 hours, with a few surveys cut shorter than the stated time due to bad weather conditions.

At the beginning of each survey, an effort and environmental data form was filled out, noting the environmental conditions for that site and the date including the sea state, swell height, time of day, tidal height and time of high water/low water (see Appendix 1), and subsequently, every 15 minutes during the survey. Additional notes were also made every 15 minutes, commenting on boat activity in the area, seabird activity and other marine mammal species seen. A panoramic video of the survey area was taken at the beginning, half way through and at the end of each survey, along with four pictures of the site, to record a visual representation of the environmental conditions of the area. When a sighting was made, video recording focused on capturing the conditions of the area, along with porpoise behaviours. Harbour porpoise seen in small groups were recorded as a group if behaviours were the same. However, if individuals behaved differently or moved from one another, the recording aimed at the individual nearest to the coastline, where possible.

All sightings data and information to accompany the camcorder were recorded on a land-based effort and sightings recording form under the 'Sightings' section (see Appendix 1). Species identification of harbour porpoise in the field were determined by size, appearance, dorsal fin shape and behaviour. Harbour porpoise are relatively small cetaceans, with dark body coloration and small triangular shaped dorsal fins. They also tend to be slow swimmers, travelling either individually or in small numbers. These key features were used to identify the porpoise with certainty before recording the sighting as that species. When porpoise were first seen, the time was recorded, along with group size, behaviour, the heading, and location. If possible, a theodolite reading (both vertical and horizontal), was taken of where the porpoise was first seen. Harbour porpoise seen either in pairs or groups had position data recorded for the nearest individual to the coastline, to correspond with the video recordings. If porpoise then stayed in the area for half an hour, their new position was recorded using the theodolite, and subsequently every half hour after that. Once porpoise left the area, their last time seen was recorded along with their last seen position. Additional information regarding porpoise sightings were also recorded, such as whether the group contained a mother and calf, and any associations observed with their feeding patterns. For example, seabirds can be associated with cetacean feeding, and seabird species regularly indicate the prey of the porpoise at the time (Evans, 1982; Evans and Borges, 1995; Pierpoint et al, 1998; Weare, 2003). If porpoise were seen for 5 minutes or more, a timed interval sightings form was filled out to help accompany the video recordings and as a backup in case the video recordings were unable to be utilised (see Appendix 2). A new record of porpoise position and heading was made every subsequent 5 minutes if the porpoise were still seen within the survey area. The location definitions for the timed interval form were more descriptive than with the land-based sighting form, as rather than using slack, normal or rippled water to describe the location in which porpoise were seen, mixtures of the three different water types were used, for example slack-rippled or normal-slack, along with the standard normal, slack and ripple descriptive (Figure 4). Using more detailed locations allows the corresponding visual sightings and camcorder recordings to be related with certainty, and should the video recordings have failed, the detailed locations could then be used for analysis.

The survey involved a minimum of two surveyors, with one using the camcorder to record the individual porpoise movements and the other using the theodolite to record harbour porpoise position and filling out the land-based effort and sighting form, along with the timed-interval form. The target for the survey was to cover as many stages of the tidal cycle as possible, meeting the aim of identifying if harbour porpoise foraging patterns change at the different tidal cycle stages. Local topography and diurnal tidal cycle alter both spatially and temporally within the two sites (Waggitt et al, 2017), and so it was important that the survey included all stages of the tidal cycles at each site. To maximise this chance, in the first month of the fieldwork process, surveying occurred as and when, with 4 to 6 days of surveying taking place each week, each day consisting of between 1 and 3 surveys. Once a sufficient amount of data had been collected, the number of surveys and videos taken at each tidal state were worked out, with the objective of using the last 2 weeks of surveying to focus on the tidal states with the least amount of data. This allowed for a minimum of 3 surveys at each site, during the spring and neap tides of both the high slack, low slack, ebb and flood tides.

As the survey was visual, watches could only be started in conditions of Beaufort Sea State (SS) 4 or less. In general, as the sea state increases, and visibility decreases, the probability of spotting cetaceans decreases. This problem is particularly acute for small, undemonstrative species such as the harbour porpoise (Hammond et al, 2002; Teilmann, 2003; Shucksmith et al, 2009). And even though in sea states higher than 2, it can often be harder to spot this diminutive species, an increase in sea state can change their behaviour, and so it was important to survey during sea states 3 and 4 as well, in case behaviour changed. Therefore, the suitability of the weather was assessed each day and, if concluded as appropriate, a day of surveying followed. If surveying already began and then bad weather, e.g. heavy rain or wind, occurred, procedures were put in place to try and complete the survey, for example, covering the video camera with an umbrella and the theodolite with plastic casing. However, on occasion, the weather affected the visibility of spotting harbour porpoise, and prevented the video camera from seeing the porpoise, and so surveying stopped for that day.

A)

B)

C)

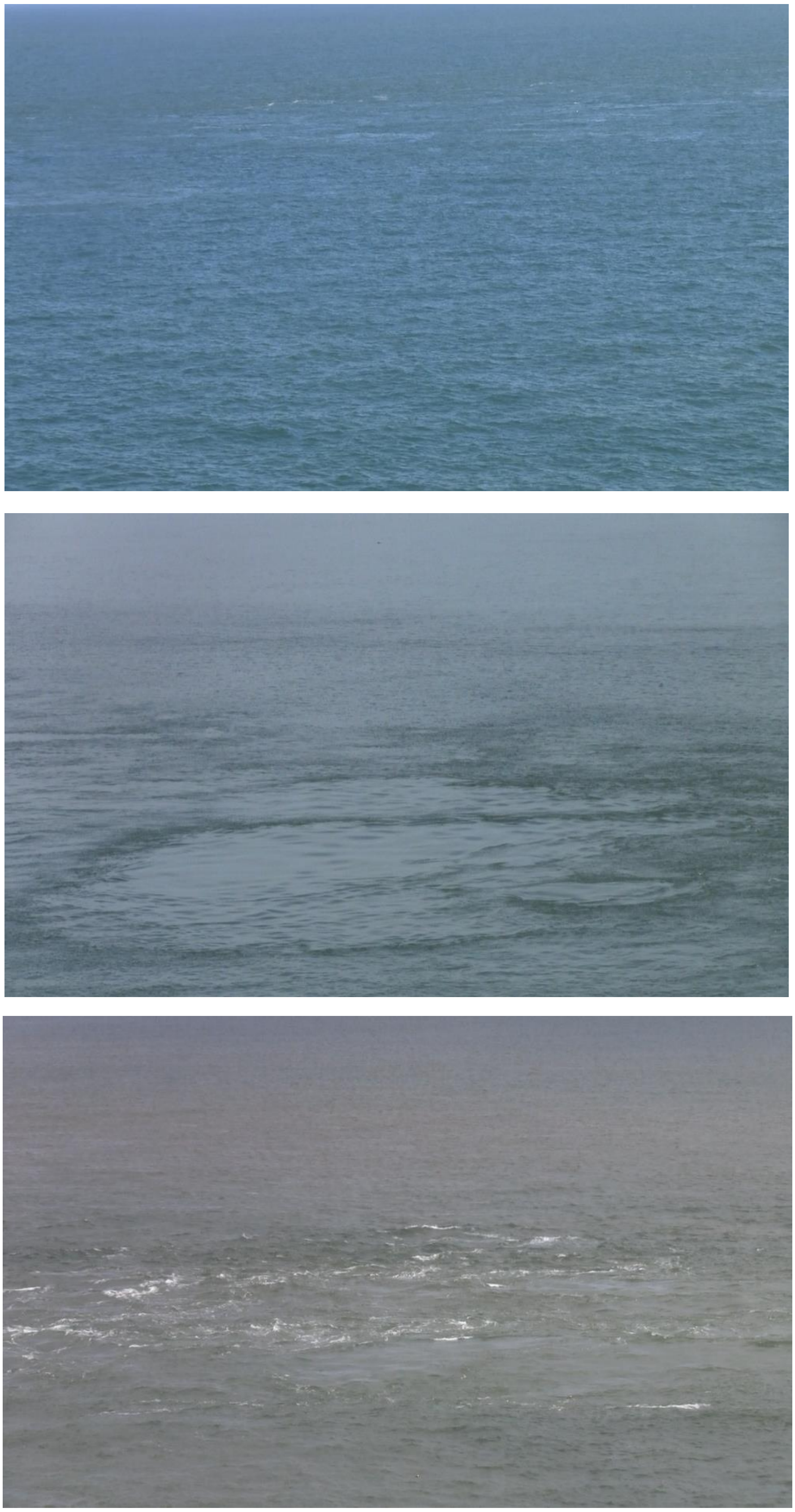

Figure 4: A) Normal water at Point Lynas, Anglesey, B) Slack water with rippled water on the right, creating a ripple-slack/slack-ripple boundary, and normal water above, below and left, creating a normal-slack/slack-normal boundary at Point Lynas, C) Rippled water with normal water above and below, creating a normal-ripple/ripple-normal boundary at Point Lynas.

2.3 Data analysis:

The video recordings taken of the individual movements of porpoise, along with effort and sighting data and theodolite recordings, were transferred onto a computer and sorted daily during the fieldwork part of the project. Each individual video was edited to only include the tracks of the porpoise, ready for further analysis. Theodolite recordings taken in the field had to be converted to give the position of the sighted porpoise. This involved converting the vertical and horizontal recordings into decimal days and using the decimal day recordings along with the distance from the theodolite to produce numbers which could be converted into latitude and longitude positions of porpoise. Distance from theodolite was calculated by adding together the elevation of the sites and measured theodolite height, to give the actual theodolite height (m) from sea level. This output was placed into a tangent equation and multiplied by 180 minus the vertical decimal day, giving the distance from the theodolite. Along with the decimal day recordings and the distance from the theodolite, the latitude and longitude position for each porpoise were calculated, giving the exact position they were seen during the survey.

The video tracks were given a video ID, along with the date and time they occurred, the site, tidal state and the latitude/longitude position of the porpoise in the video. Only video tracks containing porpoise that had a latitude/longitude position were used in the data analysis. Each video was then watched through twice, the first time counting the number of dives the targeted porpoise made and the second watch timing the length of each dive. The number of dives made in each video was then converted into the number of dives per minute. Along with timing the dives in the second watch, each time the targeted porpoise surfaced, its primary behaviour was noted down, either travelling or foraging. As previously mentioned, due to their small size, porpoise need to feed regularly (Santos et al, 2004; Wisniewska et al, 2016), and so it is assumed that much of their time is spent foraging or looking for food. For this reason, only travelling and foraging were chosen as potential behaviours, as it is relatively easy to distinguish between the two and the majority of porpoise time is spent doing one or the other. When travelling, the porpoise travel through the site or to a specific spot with no stopping or milling, but when foraging, the porpoise stay in a relatively similar area with seemingly no directional movement. Along with the primary behaviour of each dive, if foraging was the primary behaviour seen, a secondary behaviour was recorded in terms of whether the foraging was a slow or fast forage. The speed of the forage was determined by eye, with the faster forages assumed to be more representative of the porpoise chasing prey or in direct food capture. The size of the group at every dive was also recorded, usually noted as an individual porpoise, but if direction, behaviour and time of dive were the same with more than one porpoise, they were classed as the same sighting and the number of porpoise displaying the same characteristics as noted as the group size. In addition, the location of each dive was recorded, following the same definitions as the timed-interval sightings sheet, and the distance from the feature for each dive assessed. Distance from the feature was classified in a numerical sequence from 1 to 3. If the porpoise dived in a rippled or slack feature, its distance was classified as a 1, if in a rippled-normal, normal-slack, etc, then distance was classified as 2, and if in the normal water the distance from the feature was 3. The variables noted from the video tracks were then compared with the visual timed-interval recordings taken during the surveys, to ensure the locations and timings were correct. Model outputs from a TELEMAC-2D hydrodynamic model from Marco Piano provided measurements of current speed (m/s), depth (m) and turbulent energy (J/kg) at 50m and 1-hour resolutions (Piano et al, 2015). The TELEMAC-2D model is a robust hydrodynamic model that simulates high-resolution spatial distribution of currents in coastal environments (Piano et al, 2015). Sightings were matched to the nearest value in space and time, using the date and hourly time of each video, along with the latitude and longitude positions of the porpoise recorded, allowing the corresponding videos to be related to the environmental conditions for the area. The model also included the tidal range for each day, giving an accurate tidal state, in terms of spring and neap tides, for each video track.

Data from the two sites were treat separate, firstly looking into how the number of porpoise per hour at the two sites differed in relation to environmental variables such as the tidal state and turbulence for the area. Next, the environmental data were checked for collinearity, by plotting variables against one another. Collinear variables should not be plotted together, as the influencing factor which is important will be unclear. Current speed and turbulence were found to be collinear, and so each model was run with turbulence as an explanatory factor, and then with current speed Video tracks were then analysed as a product of four response variables against explanatory variables of interest and importance. The explanatory variables were chosen by carrying out simple linear models against the response variables to see which showed an influence. Table 2 shows the explanatory variables against which the four response variables were originally tested for each site, each model was run twice, once including turbulence and once including current speed. Linear models with numerous explanatory variables were used, which consider multiple synergistic variables and can be used to determine the relative influence of each variable. By running each model against all variables, the importance of each influencing factor is given, through the P value. The models were run multiple times, each time removing the variable with the highest P value, until all variables left had a significant influence on the response (*P<0.05*).

Table 2: Original statistical tests (linear models with numerous explanatory variables) carried out in R version 3.2.4.

Model Number	Site	Response Variable	Explanatory Variable	Explanatory data
			Travelling/foraging behaviour	Categorical
1	Point Lynas		Distance from feature	Numerical
		Number of dives	High/low slack, flood, ebb	Categorical
2	Bull Bay		Spring/Neap	Numerical
			Turbulence or Current speed	Numerical
			Depth	Numerical
			Distance from feature	Numerical
3	Point Lynas		High/low slack, flood, ebb	Categorical
		Probability of foraging	Spring/Neap	Numerical
4	Bull Bay		Turbulence or Current speed	Numerical
			Depth	Numerical
			Distance from feature	Numerical
5	Point Lynas		High/low slack, flood, ebb	Categorical
		Probability of fast foraging	Spring/Neap	Numerical
6	Bull Bay		Turbulence or Current speed	Numerical
			Depth	Numerical
			Travelling/foraging behaviour	Categorical
7	Point Lynas		Distance from feature	Numerical
		Dive duration	High/low slack, flood, ebb	Categorical
8	Bull Bay		Spring/Neap	Numerical
			Turbulence or Current speed	Numerical
			Depth	Numerical

When inspecting the analysis of number of dives and dive length, the models showed overdispersion in the data, which can result in an unrepresentative P value, and so a quasi-poisson dispersion along with the use of a general linear model (GLM) were used to adjust the P values based on the overdispersion. The categorical variable of behaviour was analysed as a product of other characteristics using a binomial distribution. As foraging behaviour is of key interest to the analysis, a binomial GLM was used to give the probability of foraging and fast foraging occurring compared with potential influencing factors. For the models including turbulence or depth as explanatory variables, a generalised additive model (GAM) was then run. This model is used on factors with expected non-linear relationships, with all other variables modelled as either linear or categorical. Table 3 shows a summary of the final analysis taken for the sites separately, showing the four response variables in each model for each site, the explanatory variables used for each model due to their significant influence, and the distribution fix.. All data analysis was carried out in R version 3.2.4 and ArcGIS.

Table 3: Summary of final statistical tests carried out in R version 3.2.4.

Model Number	Site	Response Variable	Explanatory Variable	Explanatory data	Distribution fix
1	Point Lynas	Number of dives	Travelling/foraging behaviour	Categorical	Quasipoisson
			Distance from feature	Numerical	
			High/low slack, flood, ebb	Categorical	
			Spring/Neap	Numerical	
			Turbulence or Current speed	Numerical	
			Depth	Numerical	
2	Bull Bay	Number of dives	Travelling/foraging behaviour	Categorical	Quasipoisson
			Distance from feature	Numerical	
			High/low slack, flood and ebb	Categorical	
			Turbulence or Current speed	Numerical	
3	Point Lynas	Probability of foraging	Distance from feature	Numerical	Binomial
			High/low slack, flood, ebb	Categorical	
			Spring/Neap	Numerical	
			Turbulence or Current speed	Numerical	
4	Bull Bay	Probability of foraging	Distance from feature	Numerical	Binomial
			Spring/Neap	Numerical	
			Depth	Numerical	
5	Point Lynas	Probability of fast foraging	Distance from feature	Numerical	Binomial
			High/low slack, flood, ebb	Categorical	
			Turbulence or Current speed	Numerical	
			Depth	Numerical	
6	Bull Bay	Probability of fast foraging	Distance from feature	Numerical	Binomial
			High/low slack, flood, ebb	Categorical	
			Spring/Neap	Numerical	
7	Point Lynas	Dive duration	High/low slack, flood, ebb	Categorical	Quasipoisson
			Turbulence or Current speed	Numerical	
8	Bull Bay	Dive duration	Travelling/foraging behaviour	Categorical	Quasipoisson

3.0 Results:

3.1 Harbour porpoise sightings:

The 27 surveys carried out at Point Lynas and 23 surveys at Bull Bay resulted in 199 sightings of harbour porpoise over the two sites between 5th June and 21st July 2018. At Point Lynas, 126 sightings were recorded, with 71 captured on video and theodolite. At Bull Bay, 73 sightings were recorded, with 40 captured on video and theodolite (Figure 5). Overall, 111 sightings were used in the data analysis, with some sightings recorded on the camcorder multiple times, resulting in 233 video tracks analysed.

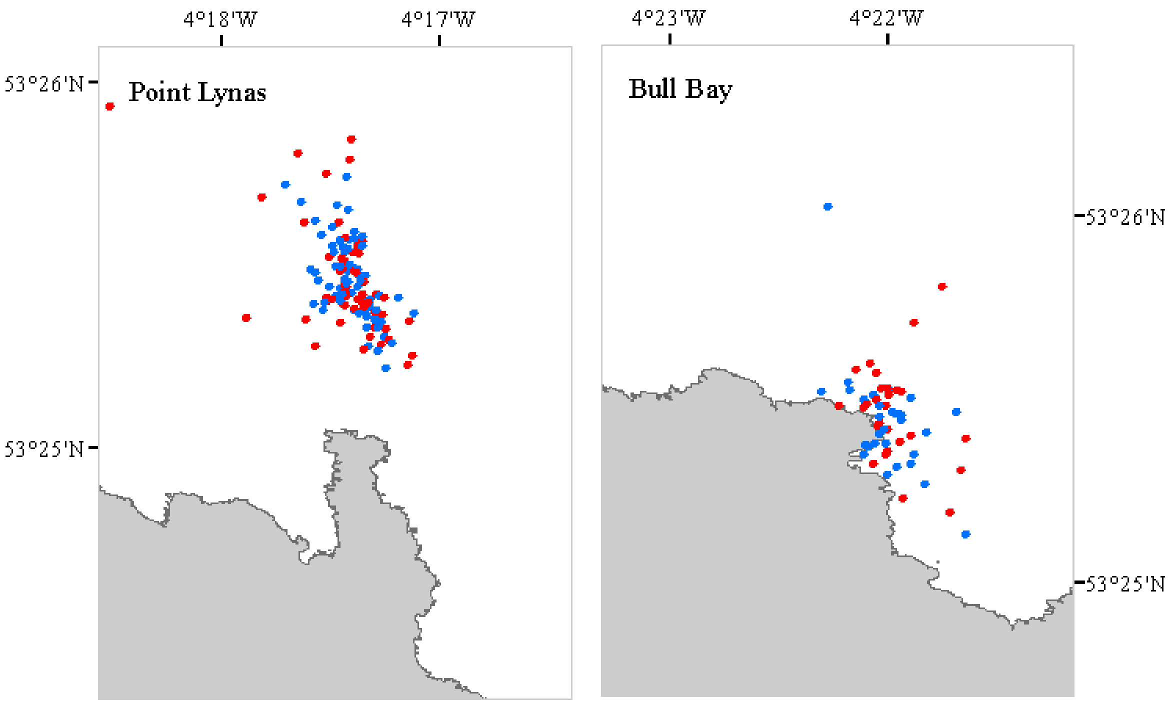

Figure 5: Positions of harbour porpoise sightings captured on video at Point Lynas (n=71) and Bull Bay (n=40), and positions of harbour porpoise sightings not captured on video at Point Lynas (n=55) and Bull Bay (n=33). Blue circle shows sightings captured on video, red circle shows the sightings not captured on video.

When looking at the data from Point Lynas and Bull Bay separately, regarding the sightings of porpoise, an increase in the tidal range at Point Lynas, on average, tends to increase the number of porpoise sighted per hour ($Chi^2(1)$ = 3.48, *P=0*.069, Figure 6a). On the other hand, tidal range has very little influence on the number of porpoise seen at Bull Bay, with the average sightings remaining around 5 porpoise per hour regardless of tidal range ($Chi^2(1)$ = 0.23, *P=0.639*, Figure 6b). The influence of the tide on porpoise abundance changes the number of sightings per hour at Point Lynas ($Chi^2(3)$ = 1.87, *P=0.15*, Figure 7a). During the ebb tides, porpoise numbers per hour are higher than numbers recorded during the other three tidal states. On the other hand, at Bull Bay the tides seem to have little influence on the number of porpoise seen ($Chi^2(3) = 0.47$, *P=0.71*, Figure 7b).

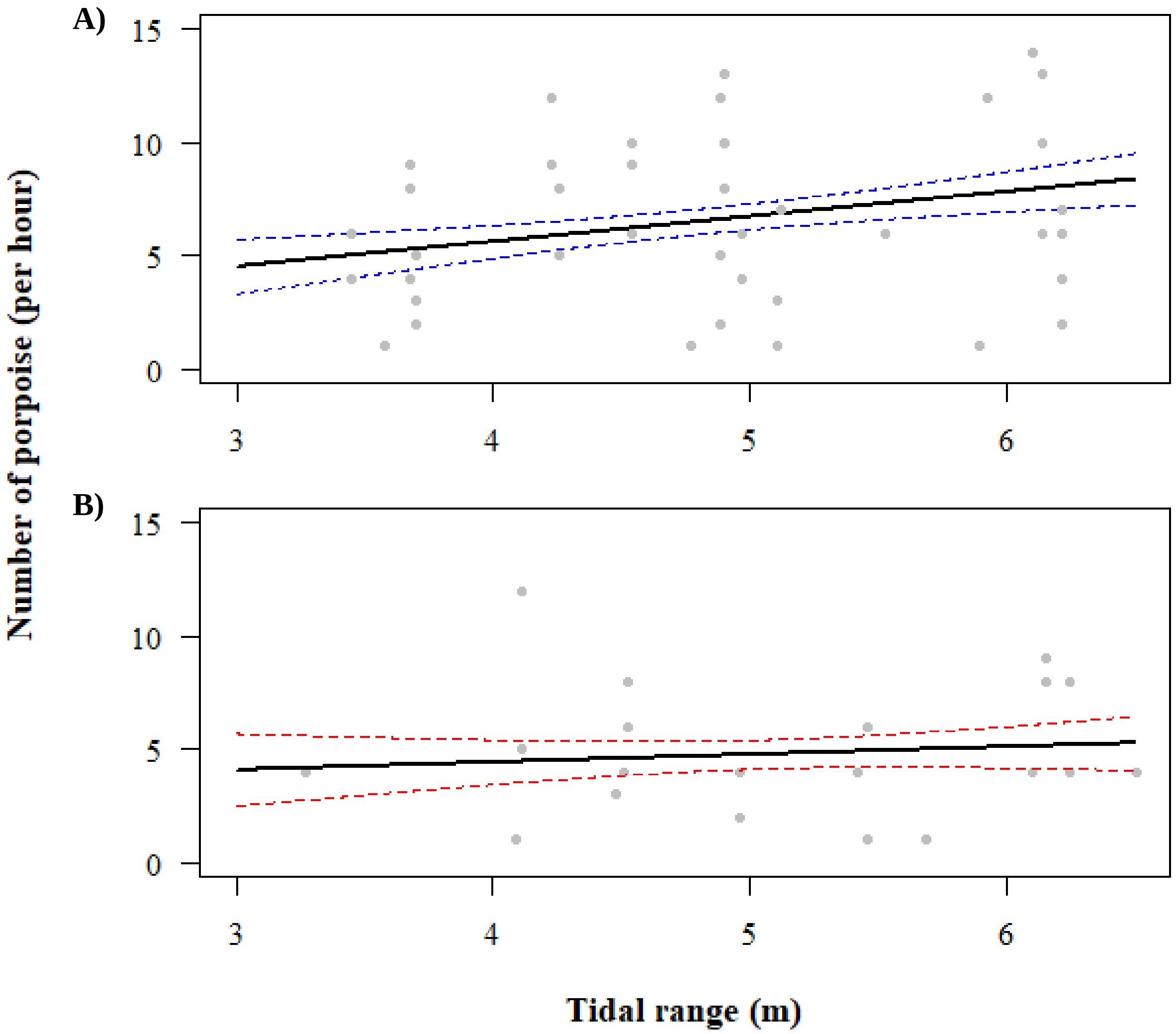

Figure 6: Mean (± 1SE) number of porpoise (per hour) sighted at A) Point Lynas B) Bull Bay as a factor of the tidal range (m), raw data shown as grey circles.

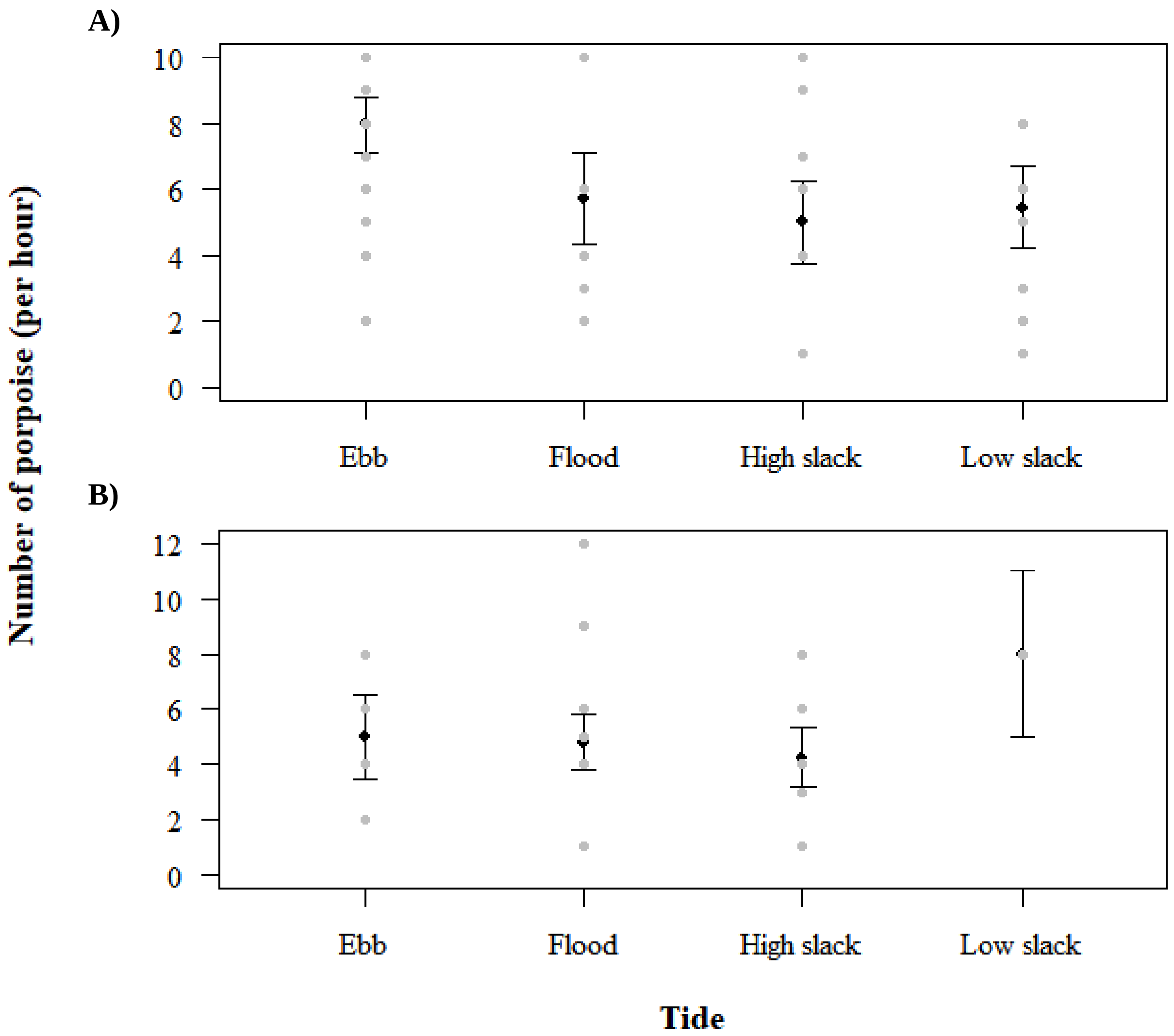

Figure 7: Mean (± 1SE) number of porpoise (per hour) sighted at A) Point Lynas B) Bull Bay as a factor of tide, raw data shown as grey circles.

As with the tidal range, the influence of turbulence on the number of porpoise sighted at Point Lynas leads to a significant increase in porpoise numbers as the turbulence increases ($Chi^2(1) = 11.87$, *P=0.001*, Figure 8a). For the sightings at Bull Bay, average porpoise numbers remain around five porpoise for all turbulence values ($Chi^2(1) = 0.0004$, *P=0.985*, Figure 8b). However, the range of turbulence recorded at Bull Bay is much smaller compared with that found at Point Lynas, which may account for the lack of change in average porpoise numbers with increasing turbulence.

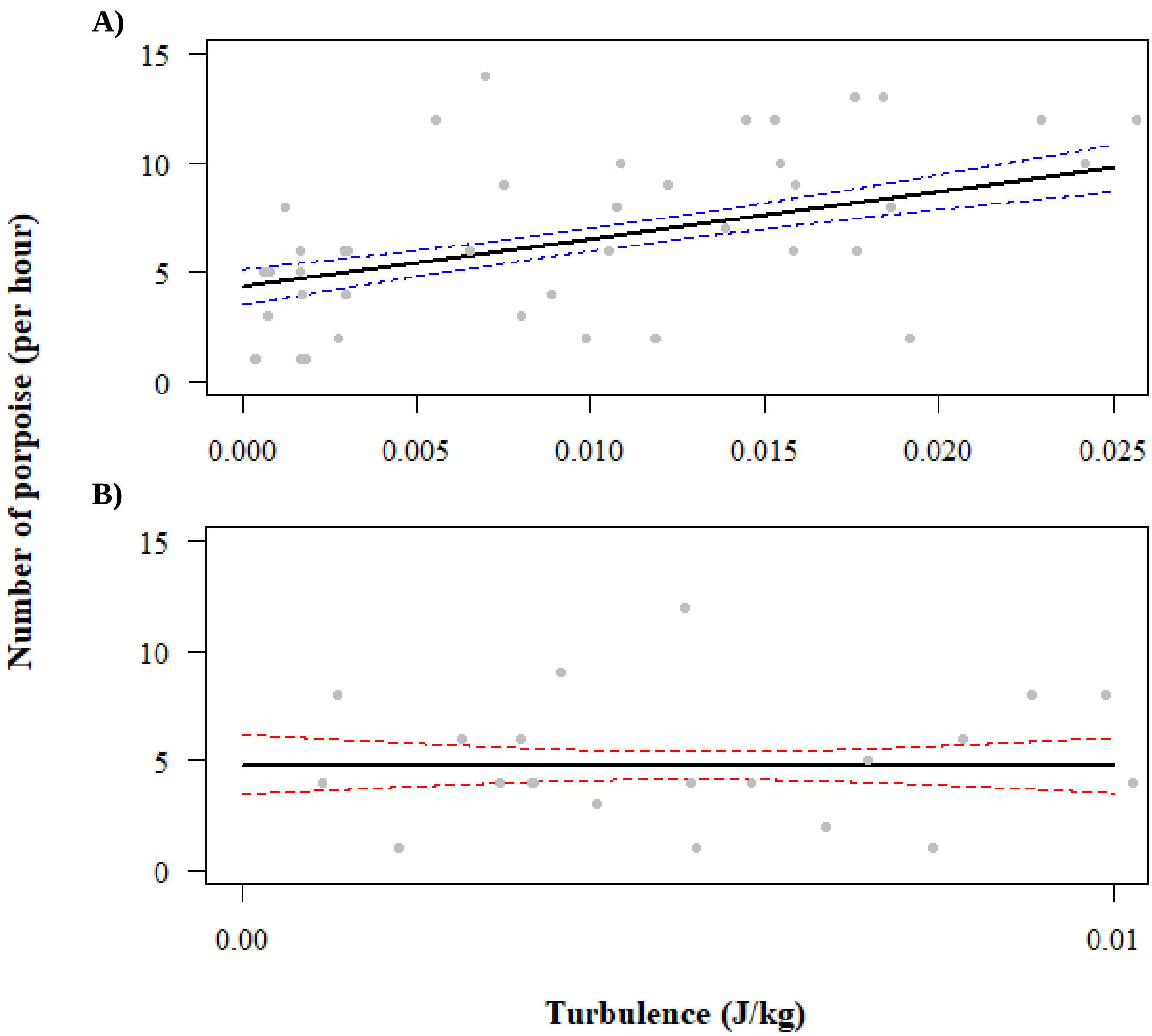

Figure 8: Mean (± 1SE) number of porpoise (per hour) sighted at A) Point Lynas B) Bull Bay as a factor of turbulence (J/kg), raw data shown as grey circles.

The influence of current speed on number of porpoise is similar to that of turbulence, with the number of porpoise sighting at Point Lynas increasing as current speed increases ($Chi^2(1) = 14.65$, $P<0.001$, Figure 9a). For the number of porpoise at Bull Bay, current speed does not have a significant impact on porpoise sightings ($Chi^2(1) = 0.01$, $P=0.9124$), with the number of sightings remaining relatively similar for all recorded current speeds (Figure 9b).

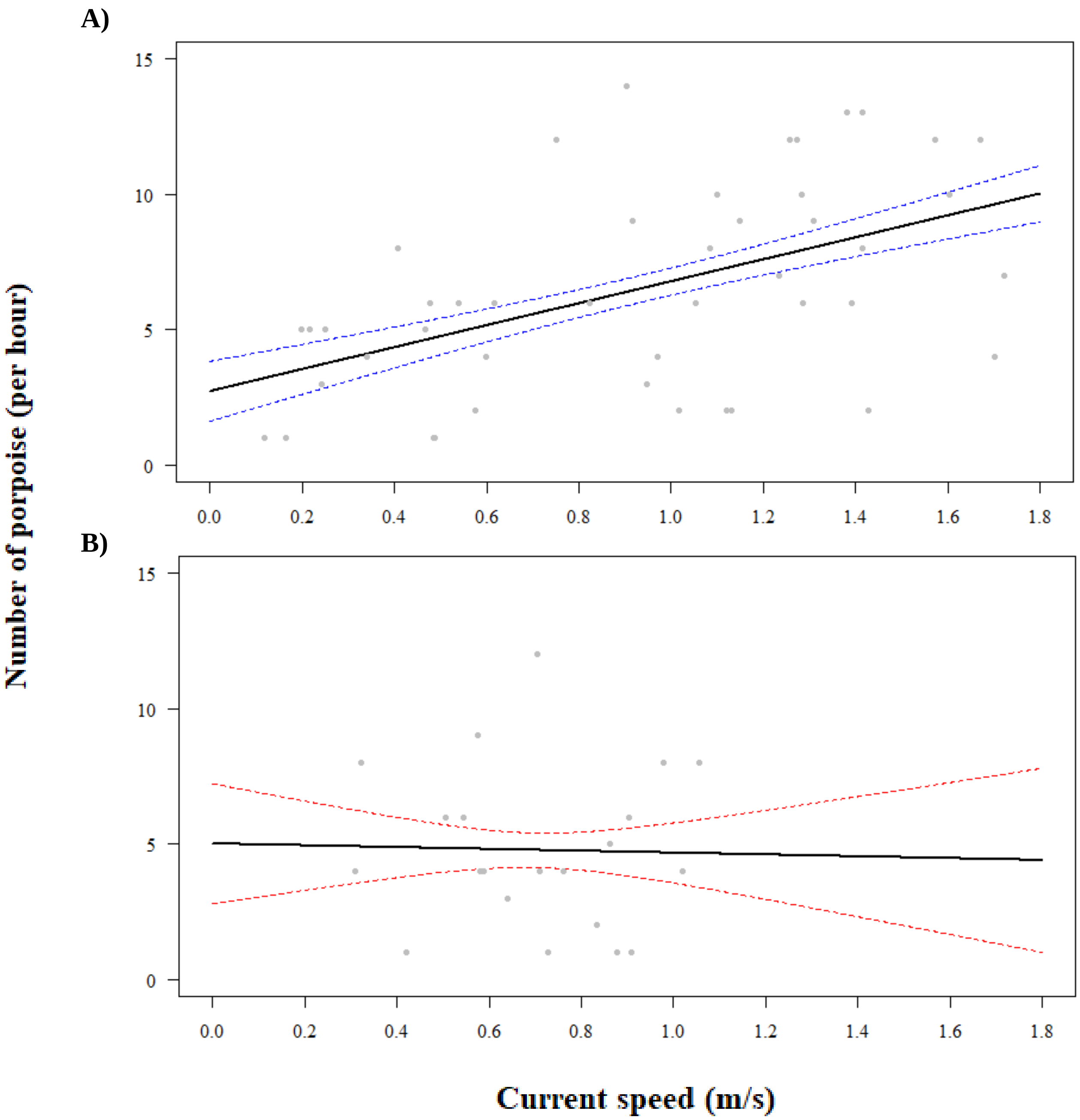

Figure 9: Mean (± 1SE) number of porpoise (per hour) sighted at A) Point Lynas B) Bull Bay as a factor of current speed (m/s), raw data shown as grey circles.

3.2 Model outputs:

3.2.1 Number of dives per minute:

The analysis of number of dives per minute at Point Lynas recorded from the video tracks found six explanatory variables with a significant influence, when using turbulence as an explanatory variable. The tidal cycle showed the greatest significant difference ($Chi^2(3) = 31.43$, $P<0.001$). The tidal cycle of the survey areas was split into high slack (±1 hour from high tide), low slack (±1 hour from low tide), flood tide and ebb tide, with the number of dives per minute significantly greater during the ebb and high slack tides (Figure 10a). Turbulence showed the second greatest significant difference ($Chi^2(1) = 56.99$, $P<0.001$), with the number of dives per minute significantly increasing with increased turbulence (Figure 10b). The recorded behaviours of the porpoise, either foraging or travelling, also showed a significant difference ($Chi^2(1) = 29.73$, $P<0.001$). The number of dives was significantly higher when the porpoise displayed foraging behaviours, by comparison to the number of dives when porpoise showed travelling behaviours (Figure 10c). Distance from the feature reported significantly more dives the further from the feature ($Chi^2(1) = 11.27$, $P<0.001$, Figure 11a) and tidal range showed less dives the greater the range ($Chi^2(1) = 11.74$, $P<0.001$, Figure 11b). The spring/neap tide is represented by the tidal ranges of the survey areas, with neap tidal cycles occurring when tidal range is low (~ < 4m), and the spring tidal cycles occurring at greater tidal ranges (~ > 4m). Depth also had a significant influence on the number of dives per minute ($Chi^2(1) = 5.61$, $P=0.018$), with the number of dives decreasing with increasing depth (Figure 11c) and seeming to level off around 30m. Depth as an explanatory variable of the number of dives had less impact compared with the five other explanatory variables, but still showed a significant difference in the number of dives as depth changed.

The same explanatory variables showed similar significant impacts when analysed with current speed (tidal cycle; $Chi^2(3) = 29.02$, $P<0.001$, behaviour; $Chi^2(1) = 26.94$, $P<0.001$, distance from feature; $Chi^2(1) = 6.96$, $P=0.008$, tidal range; $Chi^2(1) = 30.38$, $P<0.001$, depth; $Chi^2(1) = 5.55$, $P=0.019$), with the influences seen when using turbulence the same as with current speed for all explanatory variables. Current speed also showed a significant impact ($Chi^2(1) = 32.41$, $P<0.001$), with the number of dives decreasing as current speed increases, to begin with, and then increasing between 0.8 and 1.0m/s (Figure 12).

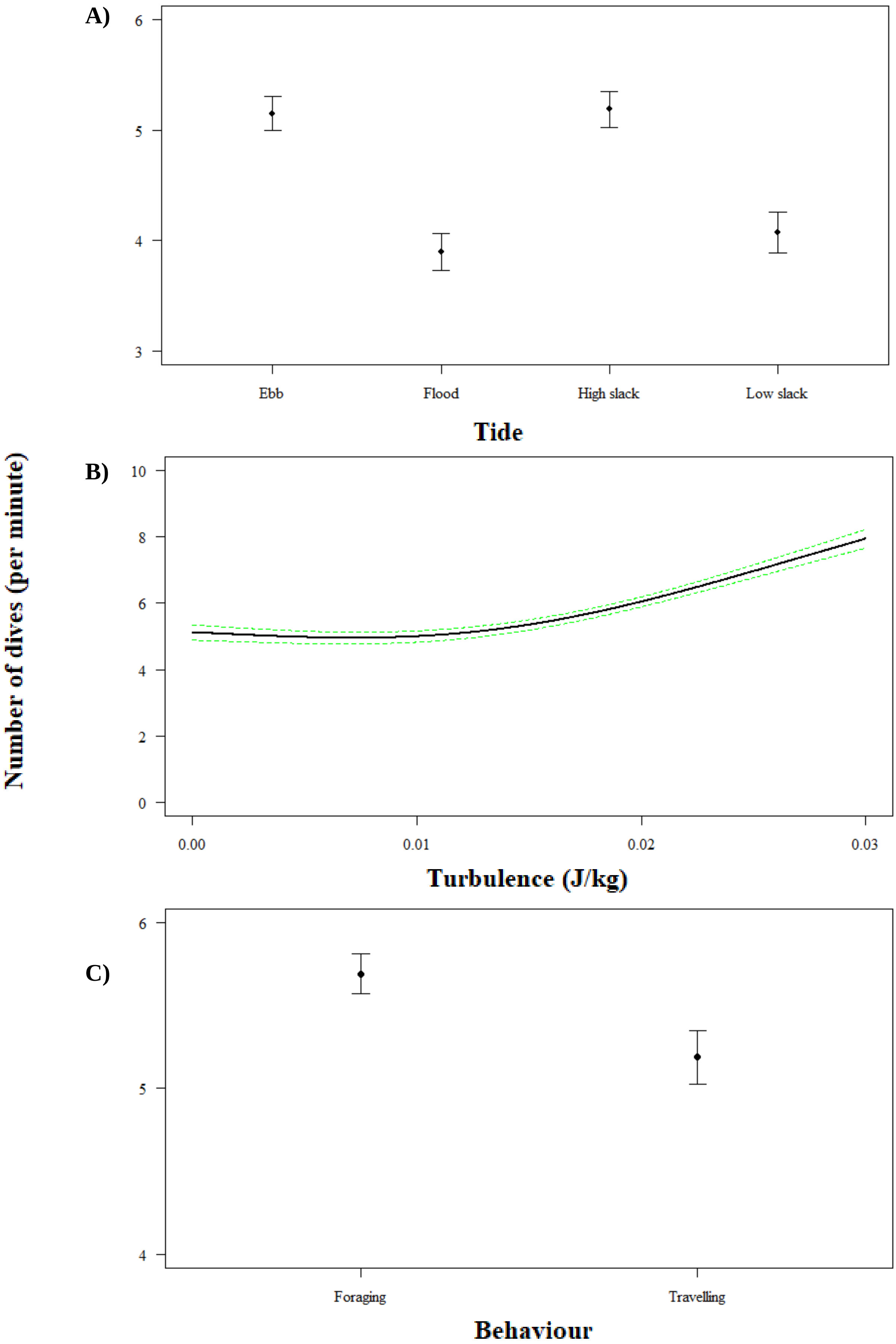

Figure 10: Output from model 1 showing mean (± 1SE) number of dives (per minute) as a factor of A) tide, B) turbulence (J/kg) and C) behaviour. Data from Point Lynas, Anglesey.

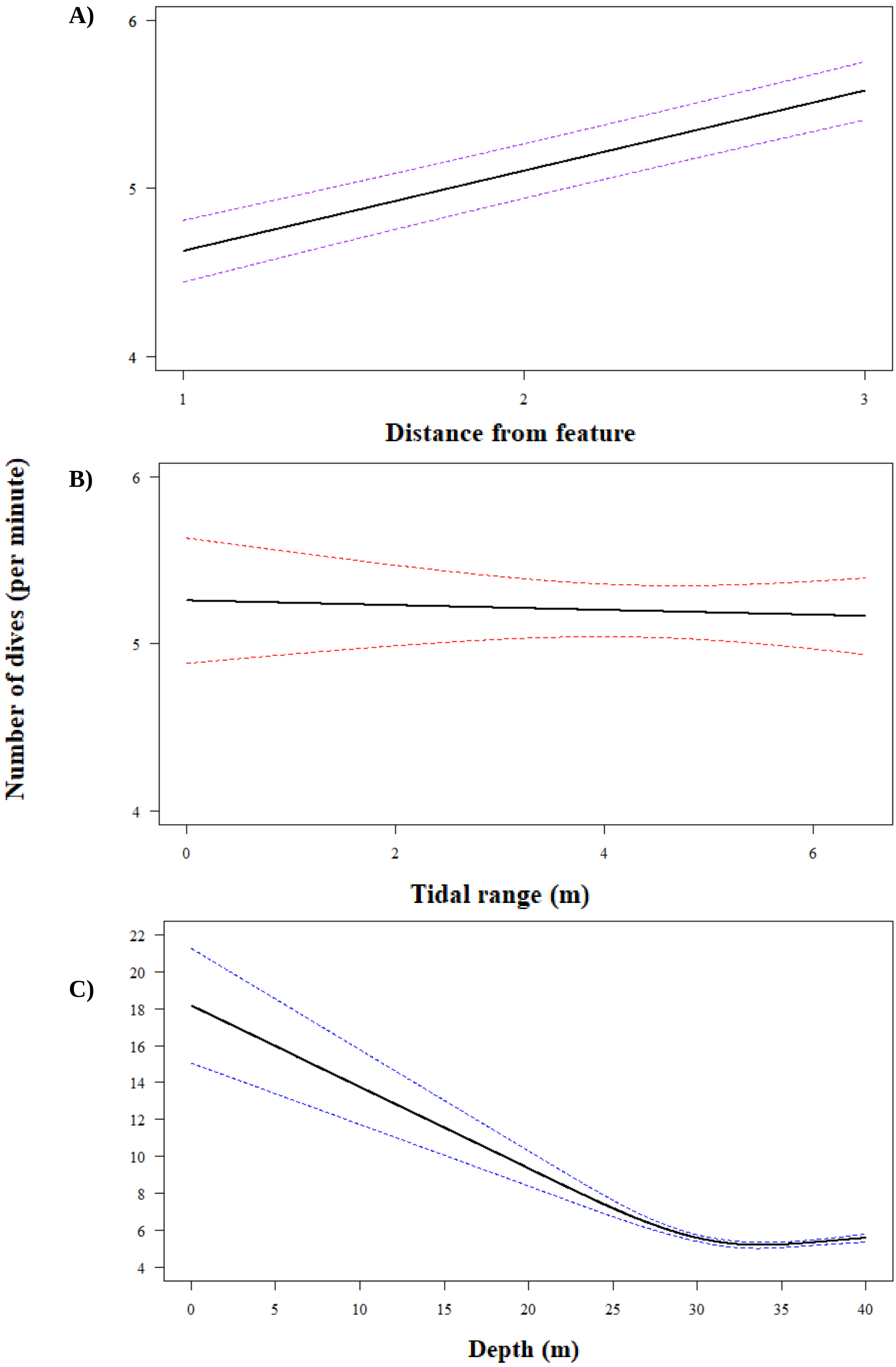

Figure 11: Output from model 1 showing mean (± 1SE) number of dives (per minute) as a factor of A) distance from feature, B) tidal range (m) and C) depth (m). Data from Point Lynas, Anglesey.

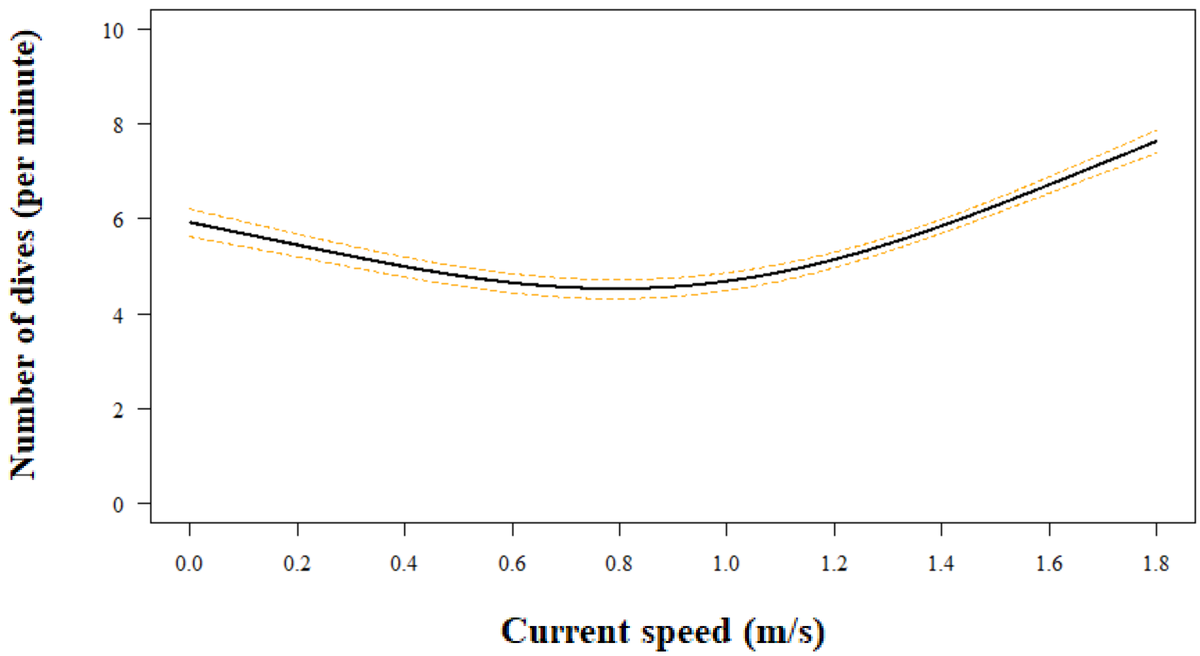

Figure 12: Output from model 1 showing mean (± 1SE) number of dives (per minute) as a factor of current speed (m/s). Data from Point Lynas, Anglesey.

The number of dives recorded at Bull Bay by porpoise were influenced by four explanatory variables. Turbulence and the tide had the greatest significance on the number of dives, with dives increasing as turbulence increased ($Chi^2(1) = 127.23$, $P<0.001$, Figure 13a). When influenced by tide, number of dives significantly increased during low slack and flood tides ($Chi^2(3) = 48.14$, $P<0.001$, Figure13b), showing the opposite influence to that found at Point Lynas. The distance from the feature also had a significant impact on the number of dives reported ($Chi^2(1) = 52.95$, $P<0.001$), with the number of dives decreasing with increased distance from a feature (Figure 13c) The last explanatory variable with a significant impact on the number of dives at Bull Bay is the behaviour of the porpoise ($Chi^2(1) = 9.49$, $P=0.002$). The number of dives was significantly higher when the porpoise displayed foraging behaviours, by comparison to the dive number when porpoise was travelling (Figure 13d). When the model was run a second time, substituting current speed in for turbulence, as with at Point Lynas, the explanatory variables showed the same influence on number of dives (tidal cycle; $Chi^2(3) = 50.20$, $P<0.001$, distance from feature; $Chi^2(1) = 33.04$, $P<0.001$, behaviour; $Chi^2(1) = 7.43$, $P=0.007$). Current speed had a significant impact on the number of dives recorded at Bull Bay ($Chi^2(1) = 112.58$, $P<0.001$). The relationship between current speed and number of dives shows an increase in dives as current speed increased (Figure 14).

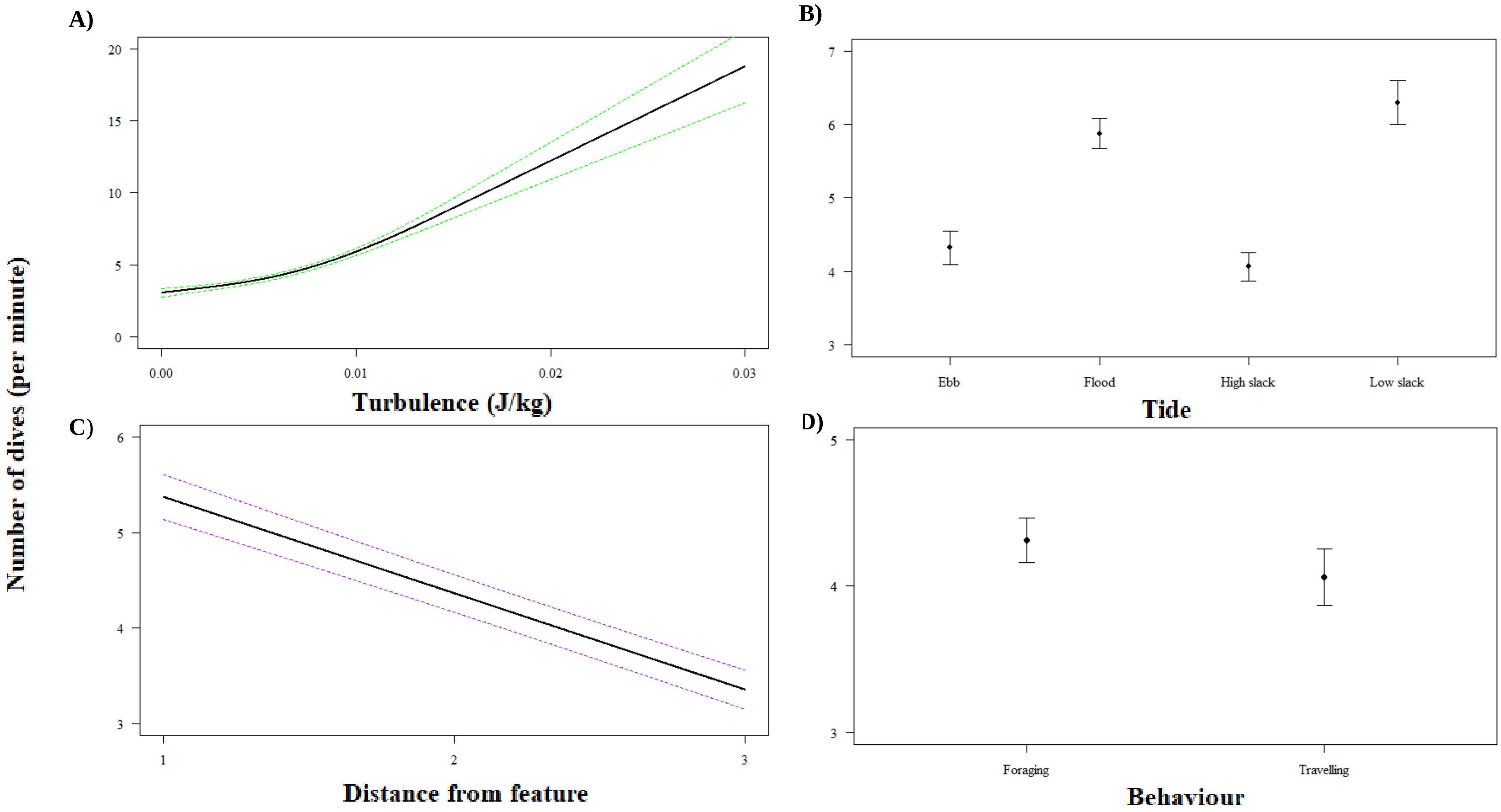

Figure 13: Output from model 2 showing mean (± 1SE) number of dives (per minute) as a factor of A) turbulence (J/kg), B) tide, C) distance from feature and D) behaviour. Data from Bull Bay, Anglesey.

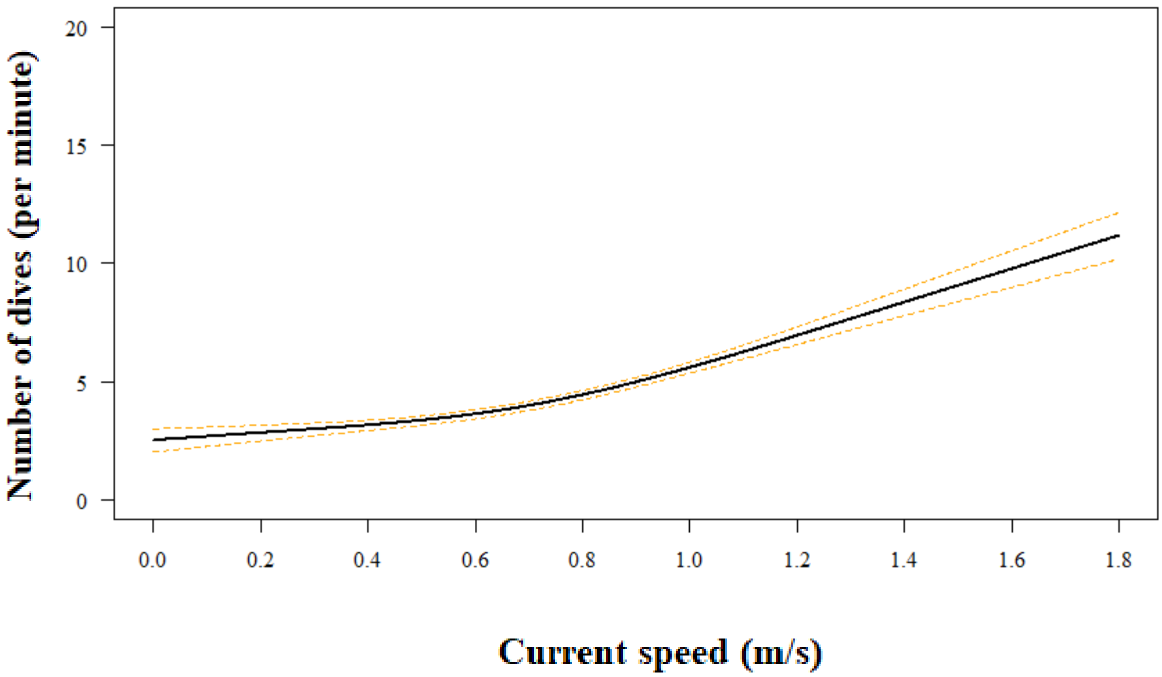

Figure 14: Output from model 2 showing mean (± 1SE) number of dives (per minute) as a factor of current speed (m/s). Data from Bull Bay Anglesey.

3.2.2 Probability of foraging:

The focus of the next analysis was the foraging behaviour of harbour porpoise, with four explanatory variables showing significant differences in the probability of foraging at Point Lynas when the model was run using turbulence. Tidal cycle and distance from features showed the greatest influence on foraging behaviour. With the tidal cycle giving a significant difference in the probability of foraging between the four tidal states ($Chi^2(3) = 234.52$, $P<0.001$). The results showed that the probability of foraging was highest during the ebb tide (Figure 15a), with foraging next likely to occur during high slack. Although foraging during the flood tide was the least probable, the probability of it occurring was still over 0.5, meaning that the probability of harbour porpoise showing a foraging behaviour during high slack, low slack, flood and ebb was always greater than them showing a travelling behaviour. Although it was not the explanatory variable with the greatest significant difference, spring/neap was another tidal variable found to influence the probability of foraging (Chi^2(1) = 8.10, *P=0.004*). The probability of foraging decreased as tidal range increased (Figure 15b), indicating that during the neap tidal cycles, foraging behaviour is more likely to occur than during the spring tidal cycles.

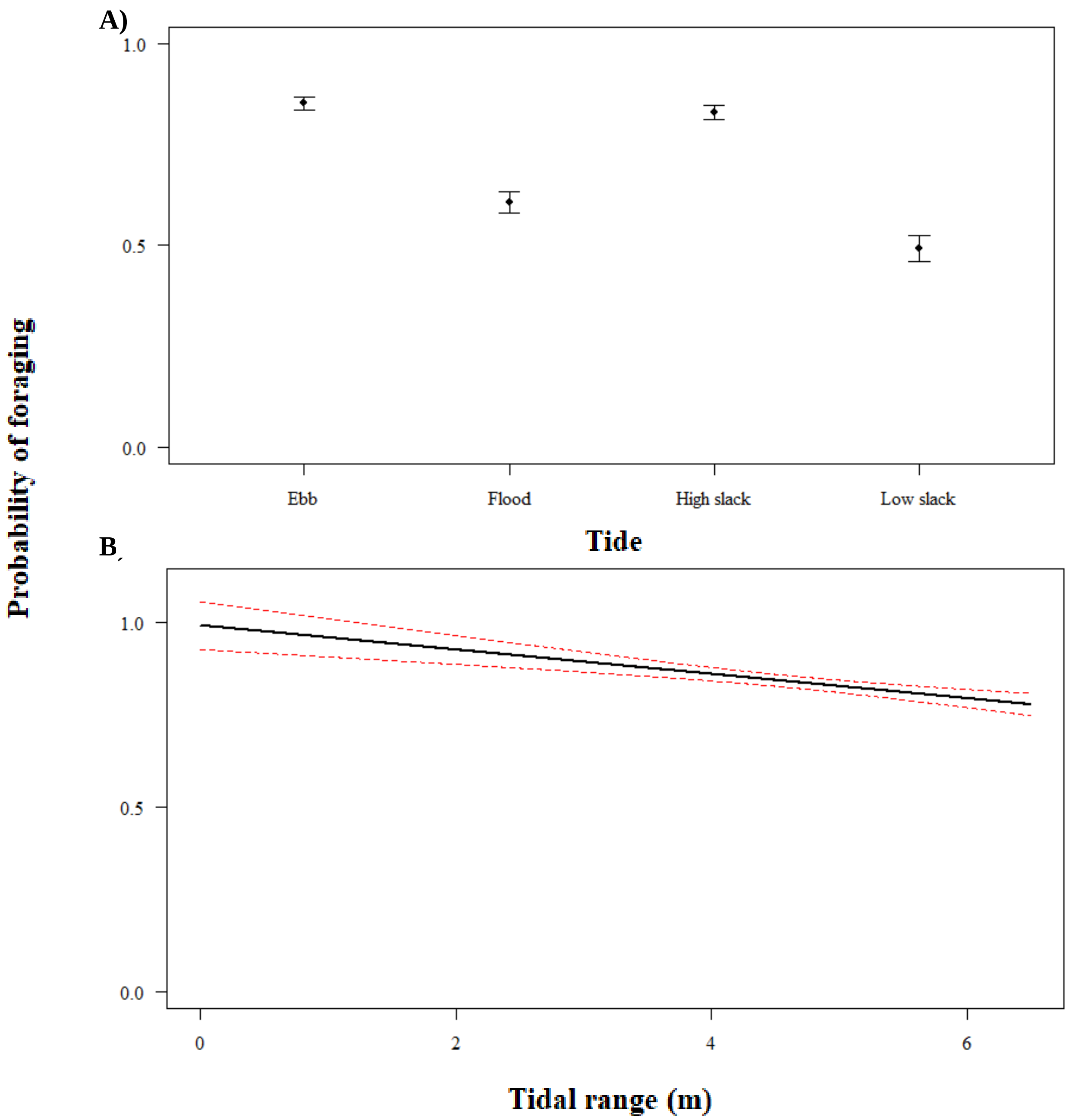

Figure 15: Output from model 3 showing mean (± 1SE) probability of foraging as a factor of A) tide and B) tidal range (m). Data from Point Lynas, Anglesey.

The distance from features, the features being either rippled water or slack water, gave a significant difference in terms of the probability of foraging behaviour by the harbour porpoise ($Chi^2(1) = 84.04$, *P<0.001*). It showed that with increased distance from a feature, the probability of foraging decreases (Figure 16a). When porpoise were within the features, their probability of foraging was very high, decreasing as they move to the edges of the features and then into normal water, where foraging behaviours were least likely. However, as mentioned with the probabilities shown as a factor of tide, and with the tidal ranges, foraging behaviour was still more probable than travelling behaviour at all distances. Finally, turbulence also showed a significant difference in terms of foraging probability ($Chi^2(1) = 18.42$, *P<0.0011*). As turbulence increased, the probability of foraging decreased (Figure 16b). This seems to contradict the findings on the number of dives, which increased both with foraging behaviour and increased turbulence. However, again the probability of foraging was still higher than that of travelling, even at the increased rates of turbulence, and unlike with the number of dives, where turbulence and behaviour had the greatest influence, for foraging behaviour the tides and distance from feature appeared to have a greater impact. As can be seen, all explanatory variables for foraging behaviour had a highly significant influence on their probability, but with tides and distance to feature having the greater impact. When using current speed, the tidal cycle ($Chi^2(3) = 234.52$, *P<0.001*), distance ($Chi^2(1) = 80.64$, *P<0.001*). and tidal range ($Chi^2(1) = 12.77$, *P<0.001*). showed the same influence on foraging behaviours. The probability of porpoise foraging decreased significantly as current speed increased at Point Lynas ($Chi^2(1) = 18.09$, *P<0.001*, Figure 17).

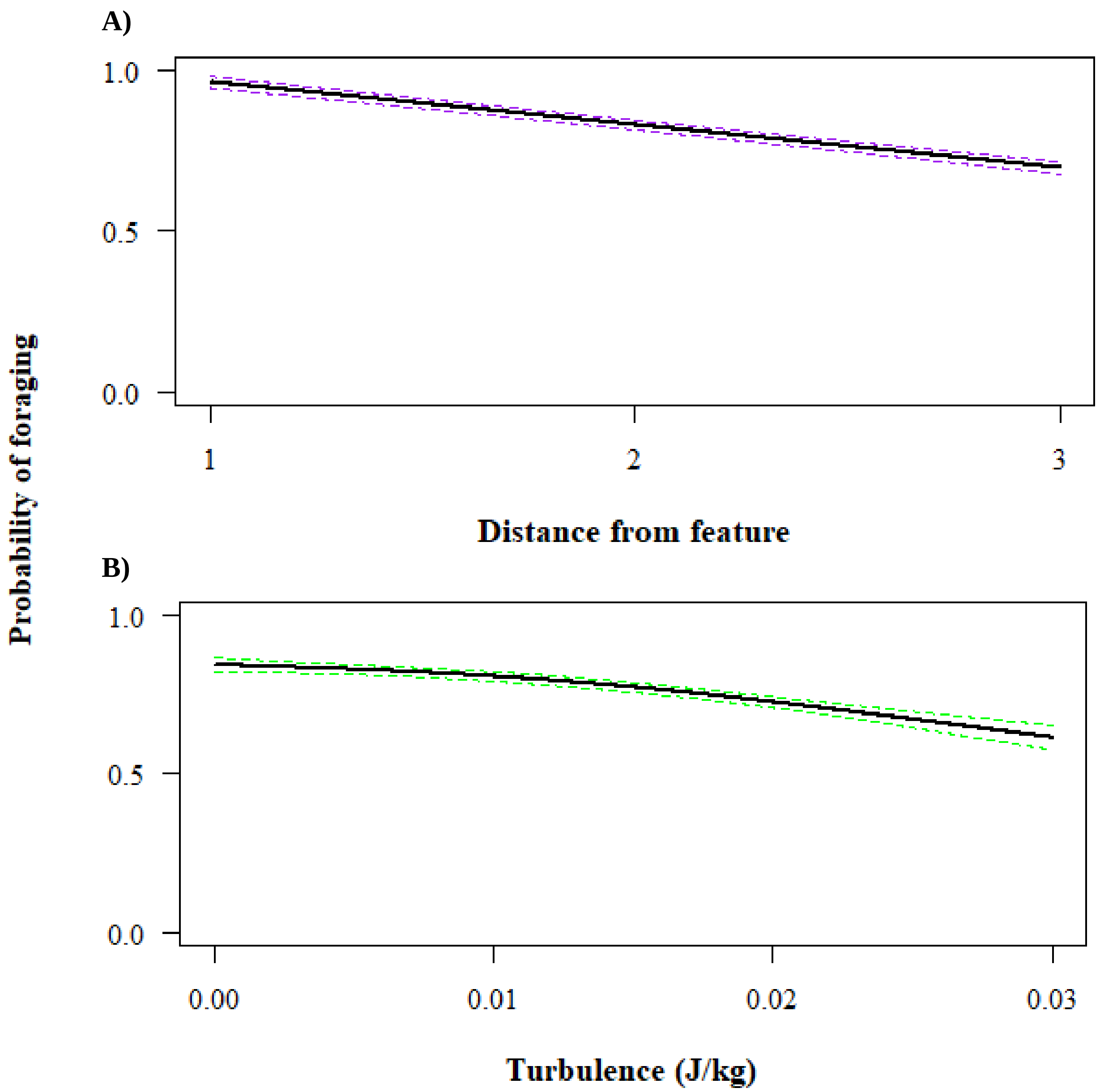

Figure 16: Output from model 3 showing mean (± 1SE) probability of foraging as a factor of A) distance from feature and B) turbulence (J/kg). Data from Point Lynas Anglesey.

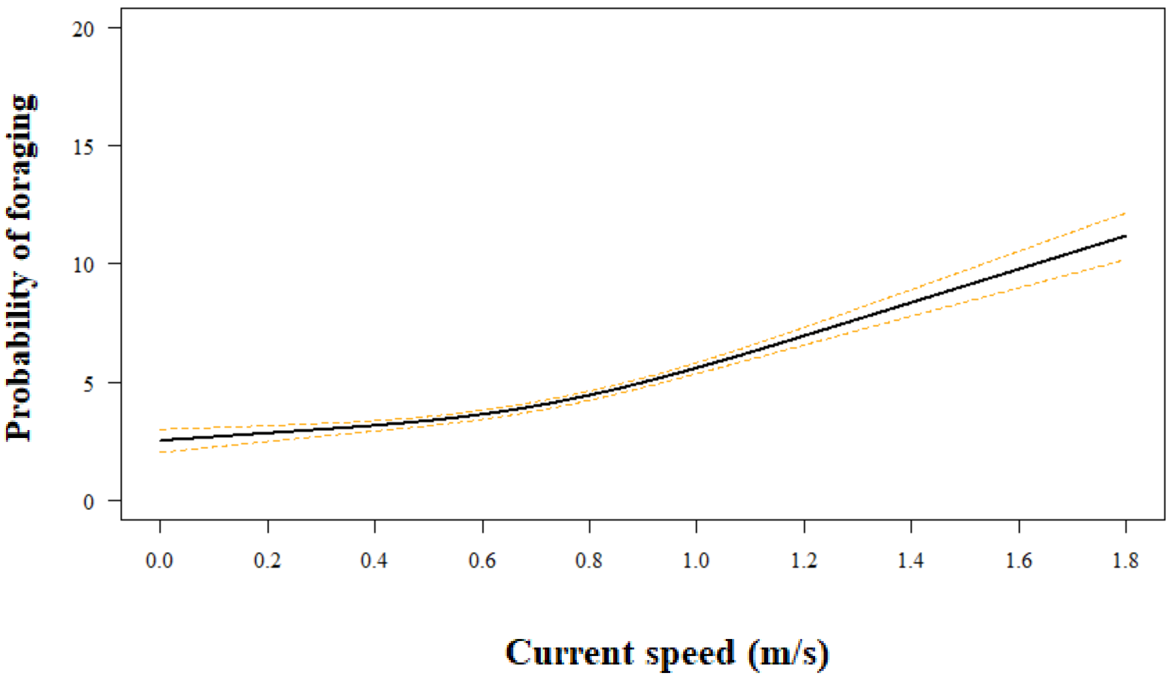

Figure 17: Output from model 3 showing mean (± 1SE) probability of foraging as a factor of current speed (m/s). Data from Bull Bay Anglesey.

Foraging behaviour at Bull Bay are predominantly influenced by three explanatory variables of distance from a feature, depth and tidal range. Distance from features had the greatest significant difference ($Chi^2(1) = 54.26$, *P<0.001*), with the probability of porpoise displaying foraging behaviours decreasing with increased distance from a feature (Figure 18a). Tidal range also shows a significant difference in terms of the probability of foraging ($Chi^2(1) = 7.65$, *P=0.006*). The probability of foraging is higher when tidal range is smaller, meaning that during the neap tidal cycle, when tidal range is less, foraging is more likely in comparison with the spring tidal cycle (Figure 18b). The last explanatory variable to influence foraging behaviour at Bull Bay is the depth of the area ($Chi^2(1) = 5.00$, *P=0.025*). In the shallower areas, the probability of foraging remains fairly level, around 25m the probability increases and continues growing with increasing depth (Figure 18c).

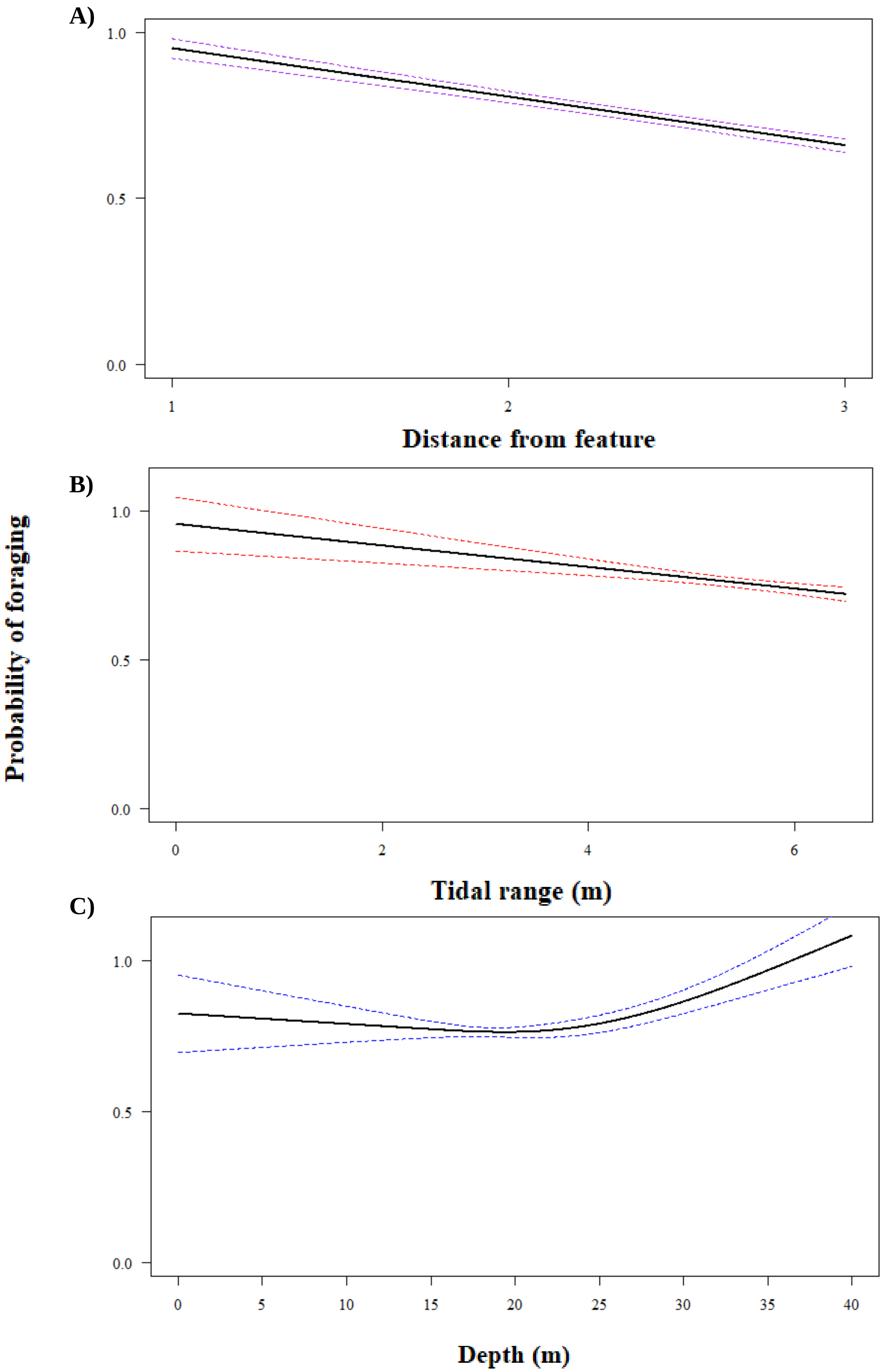

Figure 18: Output from model 4 showing mean (± 1SE) probability of foraging as a factor of A) distance from feature B) tidal range and C) depth (m). Data from Bull Bay, Anglesey.

3.2.3 Probability of fast foraging:

For this analysis only, the video tracks showing the primary behaviour of foraging, were used, to compare the probability of fast foraging against slow foraging. Four explanatory variables were found to cause a significant difference to the probability of fast foraging at Point Lynas, with the variables being tide, turbulence, distance from a feature, and depth. As with the probability of foraging, tide and distance from a feature showed the greatest significant differences. Examining tide first, there is a significant difference in the probability of fast foraging across the four tides ($Chi^2(3) = 124.64$, $P<0.001$). Fast foraging was more likely to occur during the ebb and high slack tides (Figure 19a), with the probability less for the flood and low slack tides. Distance from a feature also gave a strong significant difference in terms of the probability of fast foraging ($Chi^2(1) = 168.96$, $P<0.001$). The relationship between distance and fast foraging shows that the further from a feature, the less probable the behaviour of fast foraging (Figure 19b). Within a feature, harbour porpoise were most likely to show fast foraging behaviour, with this probability dropping rapidly as they move from the feature into normal water, where behaviours were more probable to be representative of slow foraging.

Turbulence also showed a significant difference in the probability of fast foraging ($Chi^2(1) = 28.36$, $P<0.001$). The relationship between these two variables appears to be more complex than with the other explanatory variables, in that probability of fast foraging starts decreasing with increasing turbulence, but then around 0.01J/kg it increases again, to a higher probability of fast foraging with increased turbulence (Figure 19c). This means that with higher turbulence, slow foraging is less probable. This may help explain the results seen, with foraging behaviour decreasing with high turbulence but yielding an increased number of dives. Slow foraging, which decreases during fast turbulence, contributes to the decreased foraging behaviour seen in the previous analysis, with an increase of turbulence. This may also help to explain why foraging behaviour decreases but the number of dives increases. Depth is the final explanatory variable found to influence the probability of fast foraging ($Chi^2(1) = 4.79$, $P=0.029$). As depth increases, the probability of fast foraging decreases (Figure 19d). The current speed model showed the same explanatory variables with the same effect on the fast foraging (tidal range; $Chi^2(3) = 124.04$, $P<0.001$, distance from feature; $Chi^2(1) = 180.68$, $P<0.001$, depth; $Chi^2(1) = 4.52$, $P=0.033$). Probability of fast foraging decreases as current speed increases, until 1.0m/s where it significantly increases as current speed increases ($Chi^2(1) = 15.06$, $P<0.001$, Figure 20).

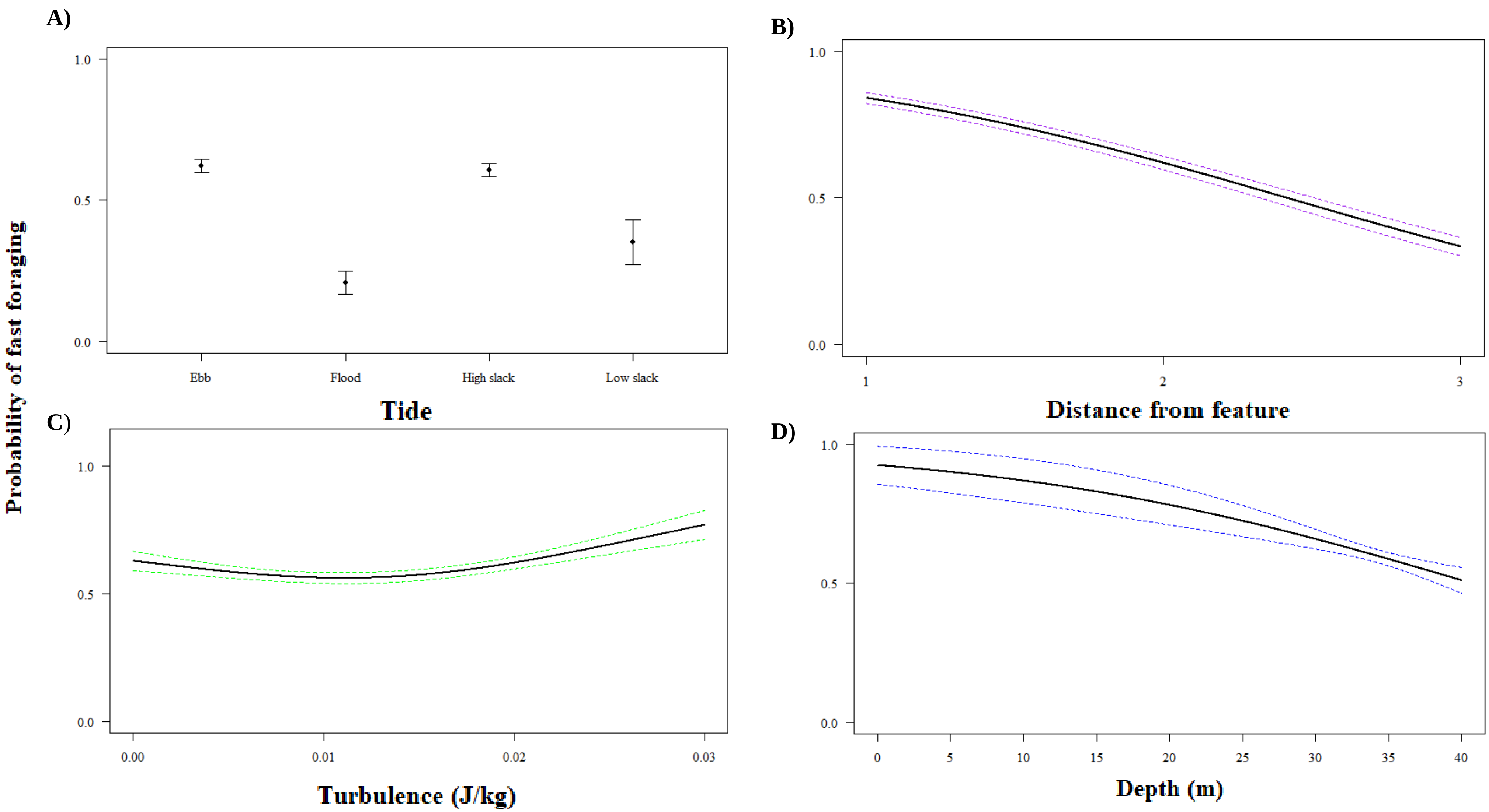

Figure 19: Output from model 5 showing mean (± 1SE) probability of fast foraging as a factor of A) tide, B) distance from feature, C) turbulence (J/kg) and D) depth (m). Data from Point Lynas, Anglesey.

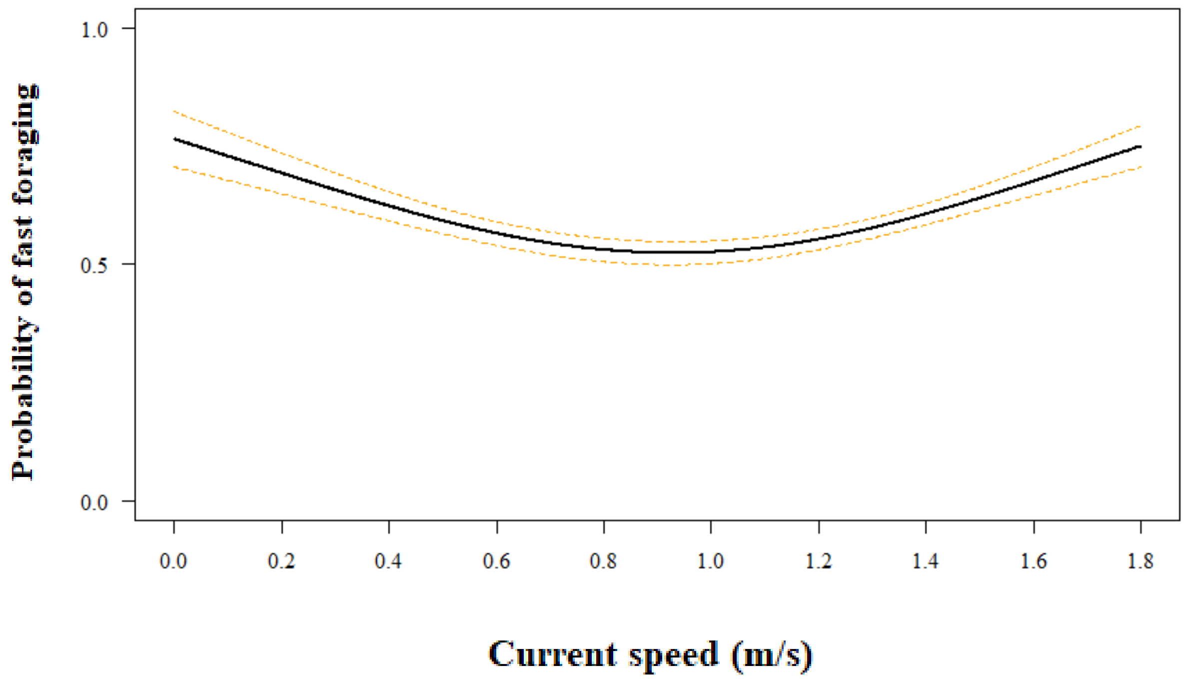

Figure 20: Output from model 5 showing mean (± 1SE) probability of fast foraging as a factor of current speed (m/s). Data from Bull Bay Anglesey.

Fast foraging behaviour at Bull Bay was influenced by the tidal cycle, distance from features and the tidal range. The tidal cycle gives a significant difference in the probability of fast foraging behaviours between the four tidal states ($Chi^2(3) = 84.29$, $P<0.001$), with fast foraging most probable during flood tides (Figure 21a). The distance from a feature also gives a significant impact ($Chi^2(1) = 276.20$, $P<0.001$). The further from the feature the less probable it is that porpoise at Bull Bay will display fast foraging behaviours (Figure 21b). The last explanatory variable for fast foraging probability is the tidal range ($Chi^2(1) = 4.03$, $P=0.045$), with fast foraging behaviour increasing the greater the tidal range (Figure 21c).

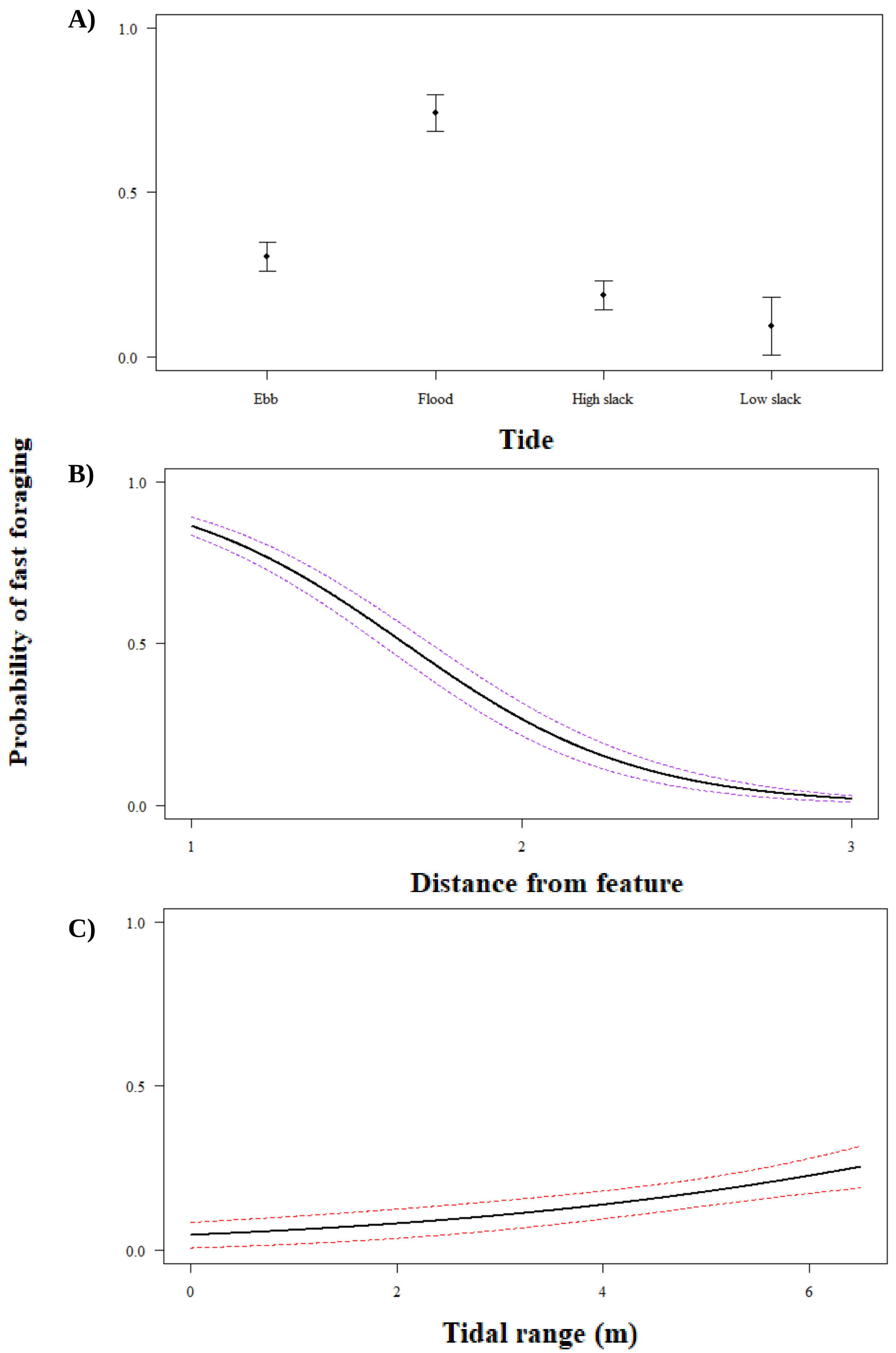

Figure 21: Output from model 6 showing mean (± 1SE) probability of fast foraging as a factor of A) tide, B) distance from feature and C) tidal range (m). Data from Bull Bay, Anglesey.

3.2.4 Dive durations:

The final analysis examined the length of the dives recorded from the video tracks. For this response variable, only two explanatory variables, tide and turbulence, showed a significant difference at Point Lynas. Tide gave the strongest difference ($Chi^2(3) = 3.53$, $P<0.014$), with dive lengths significantly shorter during ebb and high slack tides, and longer during flood and low slack tides (Figure 22a). Turbulence also had a strong influence on the length of dives recorded ($Chi^2(1) = 4.29$, $P=0.038$), showing a significant decrease in dive lengths with faster turbulence (Figure 22b), indicating that longer dives occurred when turbulence was less, and shorter dives occurred when turbulence was greater.

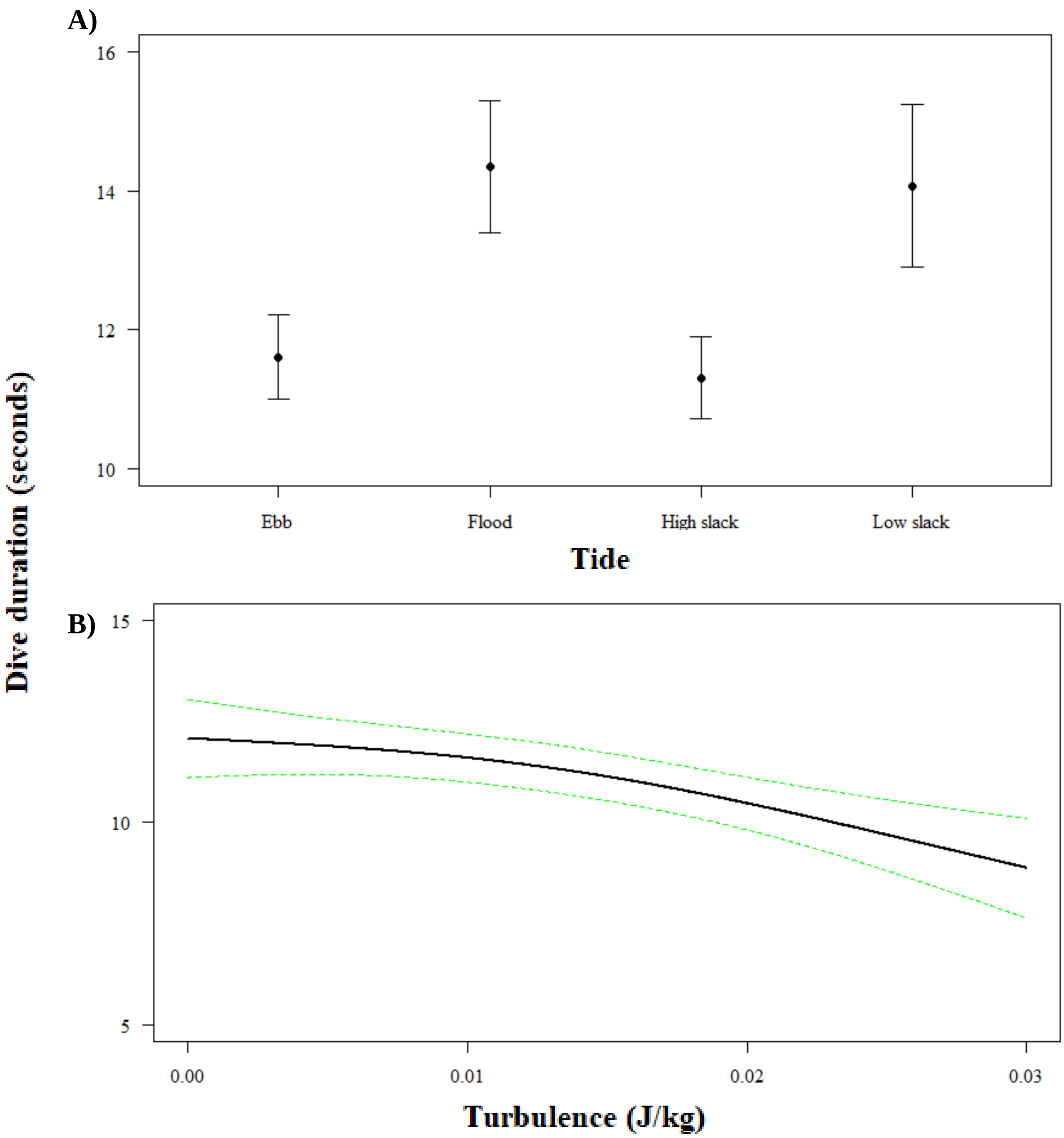

Figure 22: Output from model 7 showing mean (± 1SE) dive lengths (seconds) as a factor of A) tide and B) turbulence (J/kg). Data from Point Lynas, Anglesey.

For dive duration at Bull Bay one explanatory variable was found to have a significant difference, the behaviour of the porpoise ($Chi^2(1) = 8.32$, *P=0.004*). Dive duration was significantly shorter when harbour porpoise displayed foraging behaviours, in comparison to longer dives when travelling (Figure 23).

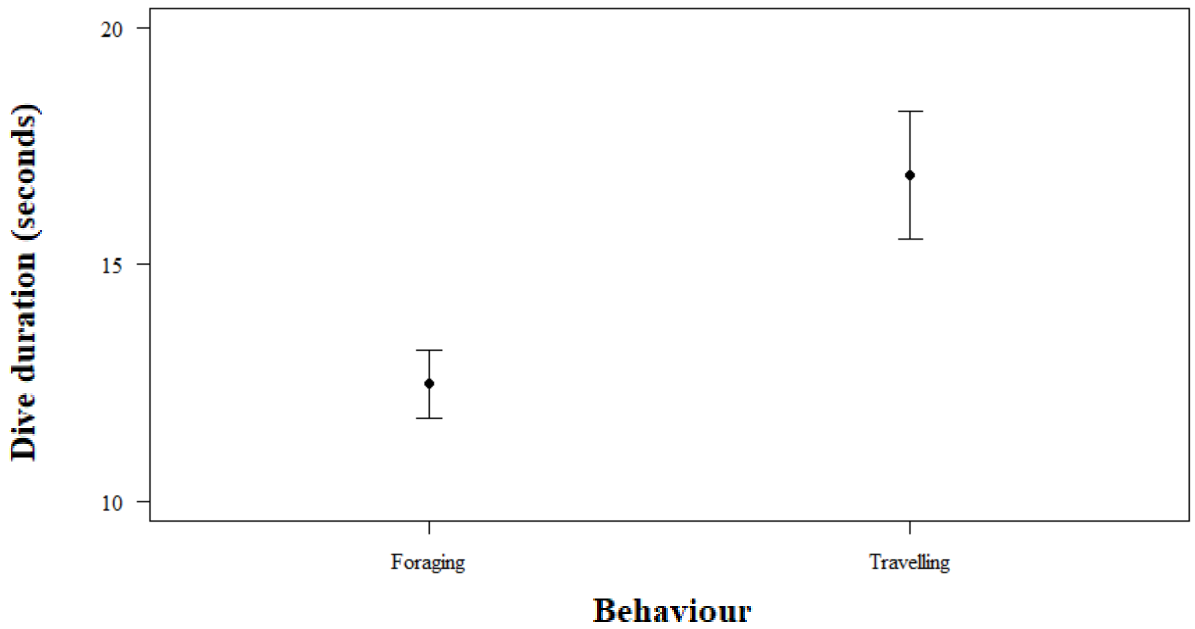

Figure 23: Output from model 8 showing mean (± 1SE) dive lengths (seconds) as a factor of behaviour. Data from Bull Bay, Anglesey.

4.0 Discussion:

The results show that harbour porpoise fine-scale use of the high energy environments at Point Lynas and Bull Bay, Anglesey, are influenced by a range of explanatory variables, with the influence of these variables also depending on other factors occurring in the area. The first important variable found to have a strong impact was turbulence within the area. Turbulence was the only explanatory factor to produce significant differences in all four of the key response variables at Point Lynas, having less of an impact on porpoise behaviours at Bull Bay, only influencing their number of dives. At Point Lynas the results show that porpoise dive more often in areas with higher turbulence, the higher number of dives likely representing foraging behaviour. When turbulence was used as an explanatory variable for foraging, less foraging was found to occur in the more turbulent areas. On the other hand, foraging in turbulent waters was more likely than travel. In fact, in all types of water, porpoise are likely to forage, as they are assumed to need to feed for much of their time to maintain energy levels (Santos et al, 2004; Heide-Jørgensen et al, 2011; Wisniewska et al, 2016). Fast foraging was the behaviour most likely to be recorded in the higher turbulent areas at Point Lynas and is thought to represent a higher probability of the porpoise feeding or chasing prey, rather than just searching for prey. The non-linear relationship between turbulence and fast foraging may show that turbulence provides the most favourable conditions for fast foraging if at Point Lynas. Current speed also showed a non-linear relationship with fast foraging behaviour for porpoise at Point Lynas, again showing that for harbour porpoise to forage, there is an optimal current speed. Porpoise also tend to take shorter dives in higher turbulence, suggesting that in those areas they are diving more frequently, for less time, and are therefore likely to be foraging. Current speed as an explanatory variable also had a greater impact on the behaviours of porpoise at Point Lynas in comparison to porpoise behaviour at Bull Bay, showing similar results to that caused by turbulence, in that porpoise diving and fast foraging behaviour increases in areas of high speed. The reported values for turbulence and current speed were also greater at Point Lynas in comparison to the values reported at Bull Bay, which may contribute to the effect found. This gives the first key fine-scale use by the porpoise at Point Lynas, utilising the turbulent, higher speed areas of the higher energy environments for foraging, and most likely feeding.

Linked with turbulence is the effect of distance from a feature, which had a strong impact on behaviour at both sites. The closer to the feature, the more probable it was that porpoise were foraging or fast foraging. As the ripple and slack features of the area are produced by the nature of the high-energy environments at Point Lynas and Bull Bay, including headlands and high current speeds, it is likely that these features, particularly the rippled parts, are areas of high turbulence, more so at Point Lynas. Although the relationship between turbulence and distance from a feature is not completely linear, it is likely that differing turbulence of the features and normal water play a part in attracting porpoise to forage and feed in the featured areas, as opposed to foraging in the calmer normal waters. In both analyses using distance from a feature, the probability of a travelling or slow foraging behaviour is greatest in normal waters. Another explanatory variable that showed a significant impact on harbour porpoise fine-scale use is that of the tidal state, more specifically the tide and tidal range. The tidal cycle had significant opposite effects on behaviour and the number of dives of the porpoise at the two sites. Although porpoise were likely to forage during all tidal state, at Point Lynas they were significantly more likely to do so during the ebb and high slack tide, when tidal range was shorter, i.e. the neap tidal cycles. Number of dives also increased during these tidal states. On the other hand, at Bull Bay porpoise were most likely to show a foraging behaviour and dive more during the flood and low slack tides, and when tidal range was shorter. Fast foraging behaviour was also more likely during the ebb and high slack tides at Point Lynas, and during the flood and low slack at Bull Bay. This highlights a possible movement of the porpoise between the two sites at different tidal states. The porpoise may utilise Point Lynas mainly during the ebb and high slack, and then travel to Bull Bay to utilise the area during the flood and low slack tides.

Behaviour, as an explanatory variable itself, influences the number of dives at both sites and dive duration of the porpoise at Bull Bay, with frequently more shorter dives when foraging, and longer but fewer dives when travelling. As behaviour is influenced by numerous other variables, these are indirectly influencing the number of dives and dive duration. This functions by the environmental variables, such as turbulence and tidal state, changing behaviour, which in turn affects the characteristics of the behaviour such as the number of dives or the length of the dives. This supports the finding that, in general, although porpoise are found foraging in all waters, they are more likely to be showing foraging behaviours, such as shorter dive lengths but more diving, in turbulent waters. As the determination of behaviour was purely made by eye, it may be that the characteristics of the dive gives a better representation as to whether porpoise are foraging/feeding in certain areas.

By grouping the influences of the explanatory variables together, we can learn how and when harbour porpoise are using high-energy environments at Point Lynas and Bull Bay. The results show that porpoise tend to use the featured areas of the environment for their fast foraging activities which coincide with their use of the more turbulent areas. The characteristics of these foraging behaviours seem to include shorter, more frequent, dives with travelling behaviours displaying opposite characteristics. The porpoise are also influenced by the tidal state, showing more foraging behaviours during the neap cycles and ebb and high slack tides at Point Lynas and during flood and low slack tides at Bull Bay. These variables give a good indication as to the processes influencing porpoise use of these areas, but whether similar processes affect harbour porpoise and other cetaceans in other high energy tidal environments, is still largely unknown.

4.1 Fine-scale use by harbour porpoise:

4.1.1 Effect of tidal states on harbour porpoise:

Many studies on the fine-scale use of tidal stream environments by harbour porpoise have found varying factors that increase their abundance. One in particular is the tidal cycle, including the high slack, low slack, flood and ebb tides along with whether the tides occur during the spring or neap tidal cycle (Leeney, 2003; Weare, 2003; Johnston et al, 2005b; Marubini et al, 2009; Embling et al, 2010; Hall, 2011; Boonstra et al, 2013; Jones et al, 2014). Among the many studies which have reported on porpoise abundance, and the influence of tides, the main outcome is that the influence varies between sites. This is supported by the results from the surveys conducted at Point Lynas and Bull Bay. Although these two sites are relatively close, and both represent important foraging habitats for harbour porpoise (Shucksmith et al, 2009; Waggitt et al, 2017), the effect of the tidal cycle on porpoise abundance differs. Point Lynas is heavily affected by the tides, with abundance increasing during the ebb tides and neap tidal cycle. Whereas, at Bull Bay, there is little effect on abundance. A simple explanation for this may be the varying amount of surveys carried out at each site, with more occurring at Point Lynas, possibly providing a sufficient amount of data for the patterns to be highlighted. However, all tidal states were surveyed at least three times at both sites, and so it is more likely that the site-specific nature of tidal trends is causing the difference (Goodwin, 2008; Benjamins et al, 2015).

Comparing other studies on habitat use with the findings from this project, it can be concluded that porpoise use in high energy environments also changes based on the tidal cycle (Johnston et al, 2005b; Goodwin, 2008; Pierpoint, 2008; Isojunno et al, 2012). Regardless of other environmental factors that play a part in attracting porpoise, and influencing their behaviour, the tidal cycle changes not only porpoise abundance but also how they behave and use the environments. Pierpoint (2008) carried out observations at three sites in Ramsey Sound, Pembs (North Sound, Treginnis and South Sound), relating the observations to tidal currents and topography. South Ramsey Sound waters are a high-energy environment, where tide race, overfalls, and upwellings form during the ebb phase; this was found to be the site which harbour porpoise preferred to visit to feed, almost entirely during only the ebb tidal phase (Pierpoint, 2008). It was theorised that seabed topography and the tidal currents combine in this area to form a foraging resource which porpoise can then exploit regularly and predictably (Pierpoint, 2008). A similar process may occur at Point Lynas, and possibly Bull Bay. Using Point Lynas as an example, during the ebb tide the specific topography of the area along with the tidal currents produced during an ebb tide, create an area that porpoise can then recognise as a place where prey will be found at regular intervals, increasing the abundance and foraging/feeding behaviours seen during this tidal state (Pierpoint, 2008).

As with the site-specific nature of tidal trends changing porpoise presence, studies have also highlighted site-specific habitat use because of the tides (Leeney, 2003; Goodwin, 2008; Isojunno et al, 2012). A study by Goodwin (2008) on harbour porpoise in North Devon, UK, found that habitat use at two sites differed, along with the effect that the tidal cycle had on their uses. At Morte Point, porpoise aggregated in areas of high tidal flow, and were assumed to be using the site as a feeding area. However, no differences in porpoise occurrence at the site were observed during diurnal and tidal cycles (Goodwin 2008). On the other hand, the second site surveyed, that of Lee Bay, showed tidal variation in porpoise behaviour, with porpoise spending part of their time feeding but much of their time travelling (Goodwin, 2008). It was concluded that Morte Point was used as a feeding site, whereas Lee Bay provided a corridor between more productive feeding sites (Goodwin, 2008). For Point Lynas and Bull Bay, the main behaviour of the porpoise recorded strongly represented foraging or feeding, regardless of the number of porpoise in the area, and so the sites were classified as mainly feeding sites for the porpoise (Shucksmith et al, 2009; Waggitt et al, 2017), however, as previously mentioned the utilisation of the sites differs with tidal state. Although both sites are classed as feeding sites for the porpoise, there is a site-specific nature of the tidal trends which is affecting the tidal state the porpoise forage and feed at.

4.1.2 Effect of turbulence on harbour porpoise:

The effect of turbulence on harbour porpoise has been relatively unstudied, with most studies focusing on tidal states, topography and water depth as explanatory variables. However, in this study it has been highlighted as having an important influence, in particular for porpoise at Point Lynas, effecting every aspect of harbour porpoise behaviour, including their foraging tendencies and associated behaviours, including the number of dives and dive duration. Other studies have mentioned it as a variable that could potentially influence the distribution of prey, and therefore foraging (Johnston et al, 2005b; Jones et al, 2014), but few have investigated why exactly turbulence can alter the distribution of prey. Studies have found that porpoise regularly aggregate in shear-lines, or slack water, that form between fast laminar and slow eddying flows produced by the obstruction of headlands/islands (Johnston et al, 2005b; Jones et al, 2014; Waggitt et al, 2017). In these areas, increased turbulence can disorientate and break up shoals of prey, with circular currents aggregating the shoals, making it easier for the porpoise to search for and capture the prey (Johnston and Read, 2007; Waggitt et al, 2017). However, if turbulence/current speed is relatively fast, the movement can help transport the prey away from the waters rather than aggregating them into a smaller area (Waggitt et al, 2017). This may explain why in higher turbulence and high current speed, the probability of foraging behaviour decreased at Point Lynas in comparison to reduced turbulence and speed. Potentially, if the horizontal movement of turbulence is too high, prey are transported further away, making it more difficult for the porpoise to find a high density in a relatively small area. However, theories on increased speed transporting prey have only examined current speed (Waggitt et al, 2017). Although when compared against one another, turbulence and speed showed a linear relationship, and both had similar effects on the four response variables tested, the effect of turbulent energy and current speed on prey distribution cannot be concluded as the same. However, it can be assumed that the current speed at Point Lynas is having an effect on the prey distribution, as has been found in other studies (Waggitt et al, 2017), and it is likely that turbulence is a contributing factor. Along with making prey more abundant, turbulence can also change the behaviour of the prey (Benjamins et al, 2015).

Features of tidal stream environments can make prey more abundant to harbour porpoise. However, porpoise may also be attracted to tidal stream environments because of the vulnerable nature of the prey in such environments (Benjamins et al, 2015). In areas of strong turbulence, it has been found that prey seem to be disorientated and confused, and this disorientation adds a metabolic cost for the prey as they try to remain orientated. Turbulence can also impact the cohesion of schooling prey, potentially breaking up the schools and providing easier predation of individuals (Benjamins et al, 2015). Prey are may also be less able of an escape reaction to foraging porpoise as water movement pulls them in directions beyond their control. The influence of turbulence on the prey creates not only an area where prey are more concentrated but also an area where prey are easier to catch, providing favourable foraging conditions for porpoise (Jones et al, 2014).

4.2 Cetaceans and tidal stream environments:

Many studies on tidal stream environments have focused effort on other coastal cetacean species, reporting findings and conclusions like those found in harbour porpoise studies, and which could improve knowledge regarding harbour porpoise habitat use in high energy environments. The main species studied has been the bottlenose dolphin (*Tursiops truncatus*; e.g. Wilson et al, 1997; Mendes et al, 2002; Bailey et al, 2013), with a few studies also on the Indo-pacific humpback dolphin (*Sousa chinensis*; Karczmarski et al, 2000; Lin et al, 2013), finless porpoise (*Neophocaena phocaenoides*; Akamatsu et al, 2010), fin (*Balaenoptera physalus*) and minke whales (*Balaenoptera acutorostrata*; Johnston et al, 2005a; Ingram et al, 2007; Anderwald et al, 2012). As with the harbour porpoise, studies on those cetacean species have found that their presence and habitat use can alter with the effect of tides and other environmental variables, including topography of the area (Acevedo, 1991; Berrow et al, 1996; Wilson et al, 1997; Harzen, 1998; Mendes et al, 2002; Akamatsu et al, 2010; Bailey et al, 2013; Lin et al, 2013; Zanardo et al, 2017).

Johnston and Read (2007) conducted oceanographic observations and remote sensing surveys to identify mesoscale biophysical links between the hydrodynamics in the Bay of Fundy, and how these changed the foraging behaviour of cetaceans in the area. The findings showed that during the flood tide (the tidal state with the highest abundance of minke and fin whales in the area), an island wake aggregates and structures the distribution of zooplankton and weak nekton (Johnston and Read, 2007). During the flood tide, the northerly flow along the eastern coastline of the island increases, producing shear lines that deflect and shed eddies. The results give an ecological context to the aggregation of cetaceans during certain tidal states. However, the study was conducted over a large spatial scale, and so, physical processes, for example secondary flows, may have affected their findings (Johnston and Read, 2007; Jones et al, 2014). Nevertheless, the study highlights that in tidal stream environments, topography along with tidal movement have the ability not only to increase the abundance of prey, but to aggregate them into a concentrated area (Johnston and Read, 2007). This occurs through the increased productivity of plankton and weak nekton within the area due to environmental factors, which the prey of the porpoise feed on. Porpoise prey track the plankton and weak nekton in the area and in doing so, a larger abundance of prey becomes accessible to the cetaceans (Evans and Borges, 1995; Johnston and Read, 2007). Similar processes could be occurring off Point Lynas and Bull Bay, where porpoise foraging and feeding is highest during the ebb and high slack tides at Point Lynas and during the flood and low slack tides at Bull Bay.

It may be the case that during these tidal states at the two sites, productivity of plankton increases, leading to prey aggregated and distributed in a way that increases foraging behaviour in the porpoise (Johnston et al, 2005b; Johnston and Read, 2007). These aggregations of prey may be important to the harbour porpoise, due to its small body reserves and cold living environments (Johnston et al, 2005b; Evans et al, 2008; Isojunno et al, 2012). Instead of particular tidal conditions, or environmental variables, porpoise are likely to select a variety of topographic and current regimes that enhance relative vorticity and concentrate prey species into accessible patches (Borges and Evans, 1997; Johnston et al, 2005b; Isojunno et al, 2012).

All the above cetacean studies, including those on harbour porpoise use in tidal stream environments, show that the distribution of species is directly influenced by the distribution of their prey (Acevedo, 1991; Evans & Borges, 1995; Berrow et al, 1996; Sveegaard, 2011), which is indirectly affected by environmental variables that are expected to predictably influence the distribution of prey and the foraging behaviour, including water depth, topography, tidal flow, turbulence and stratification (Watts and Gaskin 1985; Johnston et al, 2005b; Embling et al, 2010; Jones et al, 2014).

4.3 Harbour porpoise fine-scale use in North Anglesey:

Previous studies on harbour porpoise in North Anglesey have focused on Point Lynas along with a number of other sites around Anglesey (Calderan, 2003; Leeney, 2003; Weare, 2003; Shucksmith et al, 2009; Waggitt et al, 2017), but none have used Bull Bay as a study site. Some findings coincide with the results from this study, with Point Lynas used as a feeding area, and higher frequencies of porpoise occurring mainly during the ebb and high slack tides (Leeney, 2003; Weare, 2003), whereas other studies have found increased encounters during the flood tide, with feeding behaviour significantly higher during the flood tidal phase compared with the ebb phase (Calderan, 2003; Waggitt et al, 2017). The varied results show that even within the same site, the use and presence of porpoise can alter depending on tidal state, which suggests that no single tidal variable can fully explain the effect that tide has on harbour porpoise. The preferred tidal phase or speed does vary across studies, even with studies in the same areas (Isojunno et al, 2012).

Headlands such as the one at Point Lynas, which produces eddies and upwellings as a fast-moving tide passes through, have been identified by other fine-scale studies as favourable areas for harbour porpoise to forage within (Pierpoint et al, 1998; Weare, 2003; Johnston et al, 2005b), and are likely to be what causes the rippled and slack features seen during the project. These areas were found to promote foraging and fast foraging behaviours in the porpoise at both sites, most likely due to the aggregation of prey in the area. It is likely that similar processes occur at Bull Bay, with the headland causing a construction for the fast-flowing tide to pass through, although the speed and turbulence of the tides at Bull Bay have less of an effect (Pierpoint et al, 1998; Weare, 2003; Johnston et al, 2005b). Waggitt et al (2017) studied the spatial and temporal occupancy of harbour porpoise within tidal environments around north Anglesey using similar explanatory hydrodynamic variables as those used in this project. They found, much as this study did, that a combination of characteristics can to an extent explain variations in the presence of harbour porpoise in tidal stream environments. However, some patterns were unable to be explained, for example the increased encounter rates reported during flood tides at Point Lynas (Waggitt et al, 2017). Although this does not coincide with the findings of increased porpoise abundance and foraging behaviour during the ebb and high slack tide, it was theorised that a lack of explanation could be down to the little knowledge of the detailed bathymetry of the area, which can create strong hydrodynamic features, and could lead to either increased or decreased occupancy (Waggitt et al, 2017). Although knowledge of the fine-scale bathymetry is still poor, depth was found to be an explanatory variable for both the number of dives and probability of fast foraging at Point Lynas and the probability of foraging at Bull Bay. Of interest is the changing impact depth has on foraging and fast foraging at the two sites. For Point Lynas, increasing depth decreases fast foraging probability, whereas for Bull Bay deeper depths increase foraging probability. Although not completely relatable, as foraging at Bull Bay includes both fast and slow foraging, it may be that at the differing depths of the two sites particular topographic features which lead to a hydrodynamic effect, such as turbulence, aggregates prey and encourage porpoise to the area (Johnston et al, 2005b; Johnston and Read, 2007). As depth changes slightly during the tidal cycle, these multiple variables working together are likely to cause an environment preferred by the porpoise for foraging at the two sites. However, without a complete understanding of the bathymetry of the areas, and how it produces and changes the hydrodynamic features, the reason for an increase of porpoise behaviour and presence at different tidal states can only be presumed.

4.4 Sampling issues:

The sampling issues associated with the project mainly relate to the surveys, in particular the weather needed to accurately undertake them, as in order to visibly see porpoise, the weather needed to be relatively calm. For the most part, the weather over the two survey months was very suitable, however, a few surveys were cancelled or stopped due to bad weather. The use of the equipment also was an issue at times, as the camera could not be used in the presence of rain or mist. In light rain and no wind, the camera was set up with an umbrella and the theodolite covered with a plastic causing, but in heavy rain and wind, the camera steamed up and was unable to film the porpoise. Another issue with the camera was the battery life of just 90 minutes. Since each survey was of either 1.5 or 2 hours, the battery life was generally too short. Although a second battery was purchased it took a few weeks to arrive, and so it did mean that in the first few weeks, one had to work with a short battery life. One tried to be selective with recording sessions, but it was decided that if a survey was particularly busy then it was better to record the porpoise and collect the data than only record a small amount in order to save the battery life for the next survey. This did mean that on some days, when two or three surveys were planned, only one or two could be carried out as the battery needed re-charging. Other issues arose when trying to survey every tidal state at both sites a sufficient amount of times. As surveying times were for the most part selected at random, it did result in some tidal states, for example the ebb tide during the spring tidal cycle at Point Lynas, being surveyed more than others. However, all were surveyed at least three times, and effort was considered when recording the number of dives. The length of the survey could also be considered a sampling issue, as although in the time frame it was not possible to lengthen the time put aside for surveying, to fully understand the fine-scale use of the porpoise it would be useful to know how the explanatory variables affect porpoise throughout the whole year, and whether the time of year has any effect on this. As this project only focused on the summer months, when the porpoise are most abundant, it can only be assumed how they would have reacted in other months. However, despite all of the above issues, a good number of surveys were undertaken, and all tidal states were sampled a acceptable amount for patterns and influences to been seen.

Regarding the data analysis, although the process of collecting the data from the video recordings was relatively simple, deciphering the porpoise behaviour from the videos may have led to a few errors. Deciding between foraging and travelling was relatively straightforward, as they swim in a set direction when travelling, but tend to stay in a similar area, or travel in random directions when foraging. The issue came when deciding between a fast or slow forage, as the diving speed could appear between the two set speeds. When this was the case, the speeds of the dives taken before and after were examined, along with the location and the behaviours of other porpoise, if in the shot, in order to try to choose which speed category was more likely.

5.0 Conclusion:

The fine-scale use by harbour porpoise in high energy environments appears complex and varied. It can be concluded that they do use these high energy tidal stream environments for foraging, and often for feeding, with underlying variables aggregating their prey into concentrated areas. However, as with many other studies, no single environmental variable was found to fully explain the fine-scale use of the porpoise in the area. The hypotheses for the project that one, harbour porpoise will show concentrated movements in areas of high turbulence and two, harbour porpoise will show movements suggestive of foraging during certain tidal states, can both be accepted. Harbour porpoise showed concentrated movements, in the form of fast foraging, in areas with high turbulence, however only at Point Lynas, and at both sites they showed movements suggestive of foraging in all tidal states but were more likely during the neap cycle, and during ebb and high slack tides at Point Lynas and during flood and low slack tides at Bull Bay. These findings show that the environments at Point Lynas and Bull Bay are important foraging/feeding habitats for the species, and if tidal marine renewable energy sources were to be installed in these areas, or areas with similar importance, it may have an impact on the ability of porpoise to reliably and predictably find food. The gap in knowledge regarding how harbour porpoise move around and use their environment has been filled to an extent by these results. The results have also reinforced early findings that these two sites are important feeding grounds for the species, but with Point Lynas seemingly the more active of the two sites, and the more influenced by hydrodynamic variables. The porpoise use the rippled and slack features created by the fast-flowing tide passing through headlands as their main feeding grounds, as prey are aggregated and confused in the areas of high turbulence. To accurately guide MRE installations towards locations with high energy but low porpoise interactions, similar studies are needed in other coastal areas where porpoise are commonly found, to highlight their feeding grounds and the grounds they use mainly to travel through. As highlighted in this project, even between relatively close sites, use by porpoise can vary significantly. This method is a non-intrusive way to analyse how porpoise use their environment and considers a range of environmental factors.

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Appendices:

Appendix 1: Effort and sightings form for used in the field.

LAND-BASED EFFORT & SIGHTINGS RECORDING FORM

Date: __________**Site Name**: ___________________ **Latitude**:______˚__________' N **Longitude**: ______˚__________' W

Start time (BST):________**End time (BST)**:________**High water time/height**:_______ _____m **Low water time/height**:_______ _____m

Effort and Environmental Data: record every 15 minutes

Effort time (BST)	**Sea state**	**Swell height (m)**	**Tidal height (m)**	**Rain /fog**	**No. of porpoise**	**Additional notes (e.g. boat activity- vessel and number)**

Sightings: make a new record for each sighting

Sighing time		**Group size**	**Behaviour**	**Animal heading**	**Location**	**Associated seabirds**	**Theodolite**		**Additional notes**
First seen	**Last seen**						**Vertical**	**Horizontal**	

DATA DEFINITIONS: *Use categories provided below where possible*
Sea state: 0 = Sea calm, wind speed under 1 knot, wave height 0 cm, 1 = Ripples, wind speed 1 – 3 knots, wave height 10cm, 2 = Small wavelets, wind speed 4 – 6 knots, wave height 20cm, 3 = Large wavelets, wind speed 7 – 10 knots, wave height 60cm, 4 = Small waves, wind speed 11 – 16 knots, wave height 1m. **Rain/fog:** 0 = none, 1 = Fog < 500m, 2 = Rain < 500m, 3 = Rain and fog < 500m, 4 = Rain or fog > 500m. **Behaviour:** SW = Normal swimming, MI = Milling, BR = Breaching, FE = Feeding, LO = Logging/resting at surface, O = Other. **Location:** 1 = slack water, 2 = normal water, 3 = ripples. **Boat vessels:** RB = rowboat, kayak, JS = jet ski, MB = motor boat, SB = speed boat, YA = yacht, FI = fishing boat, LS = large ship.

Appendix 2: Timed interval form used within field.

Date: __________**Site Name**: ___________________ **Start time (BST)**:___________**End time (BST)**:___________

LAND-BASED SIGHTINGS RECORDING FORM – TIMED INTERVALS

Timed intervals: make a new record of animals position every 5 minutes

Time (BST)	Location	Animal heading

Time (BST)	Location	Animal heading

Time (BST)	Location	Animal heading

DATA DEFINITIONS: *Use categories provided below where possible*

Location: S = Slack water, R = Rippled water, N = Normal water, SR = Slack-Rippled (animal occurs in calm water on the edge of the mixed), RS = Rippled-Slack (animal occurs in the mixed water on the edge of the calm), SN = Slack-Normal (animal occurs in calm water on the edge of the normal), NS = Normal-Slack (animal occurs in the normal water on the edge of the calm), RN = Rippled-Normal (animal occurs in the rippled water on the edge of the normal), NR = Normal-Rippled (animal occurs in the normal water on the edge of the rippled).