Harbour Seals (*Phoca vitulina*) in a Tidal Stream Environment: Movement Ecology and the Effects of a Renewable Energy Installation

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“Deep in the human unconscious is a pervasive need for a logical universe that makes sense. But the real universe is always one step beyond logic.”

Frank Herbert, *Dune*

Thesis Abstract

Despite ever increasing information on the importance of oceanographic processes for marine predators, movement ecology of higher trophic level species in tidal stream environments remains relatively under-studied. This represents a significant knowledge gap for certain species which spend large portions of their lives in these energetic habitats. In this thesis I show that a top predator, the harbour seal (*Phoca vitulina*), inhabiting one of the most tidally energetic regions in Europe, the Pentland Firth, shows a complex range of behaviours as a consequence of the strong current flows they are subjected to. Both horizontal movement and diving behaviour elucidate a degree of foraging plasticity, hitherto undocumented in a single population of harbour seals. I also demonstrate that, by using multiple perspectives of movement, researchers can better tease apart ecologically important areas for animals inhabiting these habitats. Given the importance of tidally energetic systems for harbour seals, I then go on to study the impact of tidal energy installations on their movements and physical fitness. Using telemetry data, I determine an overt avoidance response of the local population to an operational turbine array and demonstrate the effect this can have on our understanding of collision risk. To further augment our predictions of the population level effect of these devices, I then go on to demonstrate that not all collisions between seals and tidal turbine blades are likely to result in fatality. In combination, these results suggest that currently held views on the lethal effects of tidal turbines are overly-conservative, and the likely behavioural and physical responses to these devices may result in a more ecologically favourable outcome than previously assumed.

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Chapter 1

The importance of tidally dominated regions to the ecology of marine vertebrates

"May the [tidal] force be with you"

1.1 Abstract

The role of marine predators in balancing delicate marine ecosystem dynamics is a vital trophic cascade that has a significant effect on ecological resilience. Increasing evidence suggests that tidally influenced features ranging from mixing fronts to tidal streams are vitally important habitat for many marine vertebrates both for migration and foraging. Previous studies demonstrate that taxon-specific behaviour and distribution in these regions is nuanced and often enigmatic given the challenges in data collection. Marked behavioural plasticity is often apparent and is likely to function as a means of effectively exploiting these variably productive and available features. The energetic costs of movement appear to be successfully offset by increases in foraging opportunities as a result of increased productivity, lower trophic level aggregations and disorientation of prey species. Owing to the increasing industrialisation of the world's oceans, some marine populations have been heavily negatively impacted at various scales ranging from the oceanic effects of climate change and plastic pollution to more localised effects of fisheries by-catch and collisions with shipping. Given the evident ecological importance of these regions, and the potential for tidal energy extraction, it is vital that the renewable energy industry and academic institutions collaborate to expand our understanding of the fine-scale behaviour of animals in areas proposed for anthropogenic exploitation. This will require flexible frameworks to allow for temporally varied ecological issues. Future research should focus on a combination of mechanistic and empirical approaches to provide a holistic view of species-specific behaviour. Here I (1) review interactions between physical oceanographic features and marine vertebrates in these habitats (2) discuss the fine-scale behaviour of these animals in a temporally and spatially heterogeneous environment and (3) explore how the advent of the tidal energy industry may impact these animals.

1.2 Introduction

An animal's movement can be driven by a range of life-history goals (Alerstam, Hedenström & Åkesson 2003). The ability of individuals to successfully forage and breed often hinges on the ability to move efficiently between sites. In general, terrestrial animal movement is achieved solely through propulsion and their own energetic expenditure (Cavagna *et al.* 1977). However, air-borne and aquatic animals must deal with a further challenge; that they are often subjected to the considerable additional force of flow (Chapman *et al.* 2011). The movement over ground of an animal moving from one location to another, in water and air, is the vector sum of both its locomotion and that of the surrounding flow. As a consequence, birds, flying insects and aquatic fauna have evolved a suite of techniques to exploit or temper this forcing by either (a) moving at favourable times and altitudes/depths when prevailing flow compliments the ultimate goal destination or (b) orienting themselves into the prevailing flow so as propulsion balances or outweighs the advective forces (Dickinson *et al.* 2000; Chapman *et al.* 2011). If the goal destination is upstream of the prevailing flow, the ability to employ the second strategy is entirely dependent on the animal being able to swim/fly above the speed of the opposing flow. This limits the applicability of this strategy for many less physically capable species.

The behavioural strategies employed by animals in flow are influenced by the goal of movement, and by predator avoidance or opportunistic foraging, and are ultimately constrained by their physiological limitations. Some animals have been observed to move almost exclusively in a manner consistent with assisted transport, regardless of their likely ability resist and move against water and air movement (Metcalfe, Hunter & Buckley 2006; Gill *et al.* 2009; Campbell *et al.* 2010). Alternatively, some species which are not characteristically fast swimmers or flyers, have developed strategies to counter flow by varying their orientations, altitudes/depths and propulsion speeds at various points along a track (Krupczynski & Schuster 2008; Alerstam *et al.* 2011; Klaassen *et al.* 2011). Prevailing flow has often been shown to be the most prominent and enduring extrinsic force acting on large-scale, goal-oriented migrating animals. It is therefore likely that, over relatively long distances and varying flow conditions, a combined approach of compensation for flow-induced drift and goal directed down-stream transport is the most favourable strategy (Alerstam 1979). For shorter distance movements, such as foraging trips, the short-term driver of movement may result in different strategies. If a target goal, such as a discrete foraging patch or individual food item, exists upstream of a significant wind or current it may be an optimal strategy for an animal to continually move in the opposing or perpendicular direction of the flow to achieve its goal (Riley *et al.* 1999; Krupczynski & Schuster 2008). This may also provide future benefits for central place foragers returning to the starting location in a downstream orientation after loading mass (Alerstam, Bäckman & Evans 2019). Although understanding the mechanisms underlying animal movement in flow can be challenging, it is clear that a range of intrinsic and extrinsic factors influence how an animal orientates itself to, and expends energy in, flow conditions. The ability of animals to withstand or counteract flow forces appears central to their endurance and fitness both at a population and individual level. Disentangling the active movement of an animal from movement due to environmental flows has been highlighted as a key question in understanding how animals use dynamic environments (Hays *et al.* 2016).

Tidal processes can have significant impacts on the structure and dynamics of shelf-seas and coastal environments. Tides generate currents, which shape the bathymetry, advect sediment and greatly affect the distribution of less mobile, lower trophic level plankton and nekton (Brown 1999). Being cyclical, they create dynamic habitats which are variable but predictably available to different species. In shallow, coastal waters this often results in markedly different species assemblages at different tidal states (Sogard, Powell & Holmquist 1989; Gibson 2003) presumably due to dramatic changes in food availability, shelter and migratory corridors. Given the seasonally variable nature of these processes and their cascading influence on the distribution of primary productivity and immotile lower trophic level species, tides can be seen to largely govern the food-web in these regions, both spatially and temporally (Otto *et al.* 1990; Zhao, Daewel & Schrum 2019).

Predator distribution is primarily driven by prey distribution and availability, and individuals will often be observed in localised patches (Boyd 1996; Hastie *et al.* 2004). Prey patches in the marine environments can often be associated with hydrographical and oceanographic features and, in lieu of direct observations of foraging events, reasonable assumptions can be made as to prey distributions as a function of these features (e.g. Hazen & Johnston 2010). Oceanographic features ranging from mesoscale tidal mixing fronts to fine-scale tidally energetic current features such as eddies and rips have been associated with increases in biodiversity suggesting them to be vitally important for efficient migration and foraging for multiple taxa (Begg & Reid 1997; Johnston, Westgate & Read 2005; Ingram *et al.* 2007; Scott *et al.* 2010).

To understand predator distributions in dynamic environments, many empirical studies of space use and how they associate with fixed and mobile features have been carried out (e.g. Cox *et al.* 2017; Lieber *et al.* 2018). The advent of integrated biologging technology such as GPS-CTD tags (Boehme *et al.* 2009) and D-Tags (Johnson & Tyack

2003) and the rapid development of sophisticated mechanistic models have advanced this field of research considerably over the past decade and allow inferences on behaviour, as well as distribution, to be made (McClintock & Michelot 2017; Jonsen *et al.* 2018). However, little is still known about the subtleties of marine animal movement in some of the most energetic and dynamic regions in the ocean. While the importance of tidally dominated regions is clear, the behavioural adaptations which allow animals to efficiently use these areas remains enigmatic and presents the next step in understanding the biological complexities of these systems. In this chapter, I review the ecology and dynamic physical properties of coastal environments, with a particular emphasis on the behaviour and foraging strategies of predators in tidally energetic areas.

1.3 Multi-scale, tidally influenced marine dynamics

Since Newton (1687) first described the equilibrium (astronomical) tides as a function of gravitational forces acting on the earth by the Sun and Moon, oceanographers have had the foundation from which to study the movement of water governed by the tide. In fact, Newton's description, while groundbreaking and fundamental, only provided scientists with the basis by which ocean dynamics occur in the absence of variability, and there are a suite of hydrodynamic reactions to this water movement that need to be considered when predicting tidal processes.

Tidal forcing results from the gravitational pull of the Moon and the Sun *and* the centrifugal force of the Earth's rotation (Simpson & Sharples 2012). Consequently, the strength of the tide is both temporally cyclical and heterogeneous across space at any given time. Tides and tidal currents have a cyclical pattern on three general scales: diurnal (or semi-diurnal), lunar/solar and equinoctial. The position of the lunar/solar cycle governs the height of the tide and therefore the strength of tidal currents, as driven by gravitational forces of the moon and the sun and their relative positions with respect to the Earth. This is commonly referred to as the spring/neap cycle. Diurnal or semi-diurnal cycles refer to the timing of flood and ebb tides (high and low waters) and cycle on just above a 12-hour basis, resulting in a slight forward shift in the timings of high and low waters each day. Equinoctial cycles refer to the bi-annual effect of the axial tilt of the earth and its orbit around the Sun where the position of the Sun in relation to the equator changes. This results in highest astronomical tides (HAT) during the Vernal and Autumnal equinoxes when the plane of the equator passes the centre point of the Sun. This fundamental physical force governs oceanographic processes ranging from micro-scale turbulent features to large scale marine currents.

1.3.1 Tidal features in shelf-seas: physical properties and biological importance

Shallow shelf-seas are mediated by seasonal and tidal processes (Simpson & Hunter 1974; Pingree & Griffiths 1978; Simpson & Sharples 2012). Tidal currents are often the main flow constituent in these areas (Otto *et al.* 1990) and they drive turbulence, upwelling and mixing processes which underpin the regional ecology. Tidal stirring caused by near constant movement results in perpetually mixed water in coastal regions however, further offshore, seasonal thermal stratification occurs periodically (Hill *et al.* 2008). The boundary between these stratified and mixed waters, referred to as tidal mixing fronts, are among the largest, tidally mediated features in shelf-seas, often being greater than 100 km in length (Suberg 2015). Due to the seasonal effect on stratification, tidal mixing fronts are seasonally persistent. In general, they form in shallow seas with strong tidal currents and sloping bathymetry when the boundary layer of turbulence caused by friction at the seabed propagates sufficiently through the water column to mix the overlying layers (Fig. 1). In deeper waters, the boundary layer does not penetrate high enough into the water column to affect the pycnocline and counteract the buoyant effects of surface heat flux, resulting in stratification.

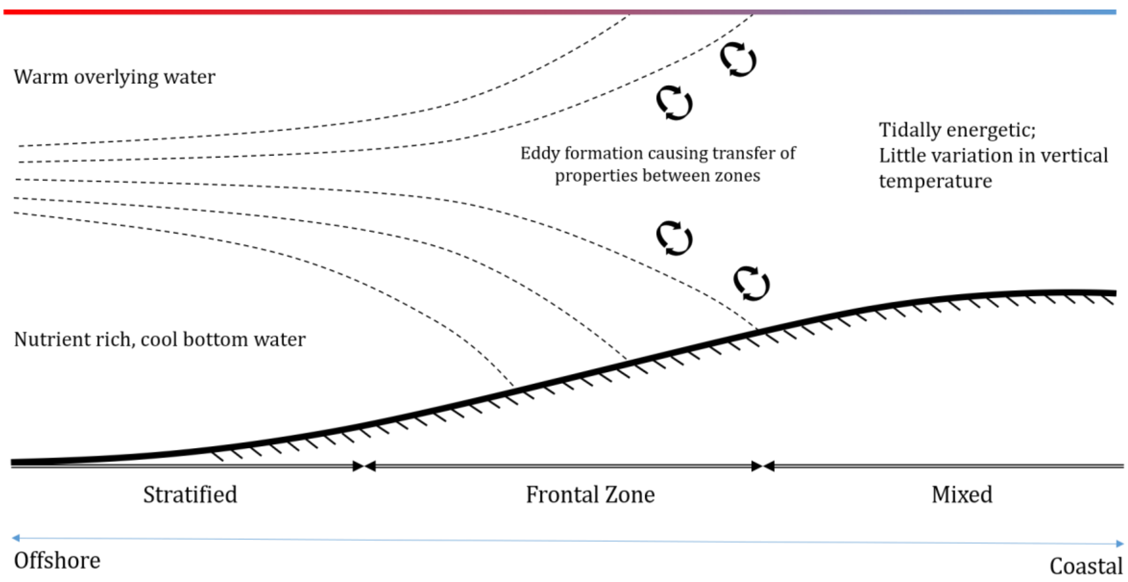


Figure 1 **Large-scale, tidally mediated features in shelf-seas and coastal habitats.** Dashed lines indicate isotherms and circular arrows represent eddies. Adapted from Van Heist (1986).

Consequently, the location of tidal fronts is predictable due to the dependence of mixing on the ratio between bathymetric depth (H) and tidal velocity (u), the so-called Simpson Hunter parameter, H/u^3 (Simpson and Hunter 1974). Local environmental conditions such as heat-flux and surface wind stress can affect this value by altering the buoyant properties of the turbulent layer and kinetic energy, shifting the position of tidal mixing fronts, however, they are predominantly influenced by the strength of tidal forcing. Recent studies have also highlighted the importance of other variables such as salinity gradients and non-tidal flows in the formation of these fronts (Sheehan *et al.* 2018). Primary productivity is often high at tidal mixing fronts due to the combined physical properties of comparatively deep photic zones in stratified offshore waters and nutrient retention from coastal mixing (Franks 1992). Convergent flows also serve to redistribute small or immotile phytoplankton, zooplankton and fish species (Epstein & Beardsley 2001) which aggregate pelagic foragers and create high levels of seasonally varying biodiversity (Cox *et al.* 2018).

1.3.2 Tidally energetic coastal waters

Tidally influenced currents can be found throughout the world's oceans but are most prominent in coastal regions. The effects of tidal forcing are particularly pronounced in mid-shelf and coastal regions, where interactions between mobile water masses and static features (e.g. land masses) can result in fast-flowing water being funnelled through channels and peeling off headlands. Further, the strength of currents is regionally specific and can also be affected by a range of stochastic features such as wind stress and heat flux. As water masses interact with landmasses, significant potential and kinetic energy can be generated through compression (Vogel 1994). In comparison to the mid-shelf regions of seasonally stratified waters, boundary layer propagation through the relatively shallow waters creates a perpetual and vertically consistent mixed layer, restricting the prevalence of primary productivity due to increased turbidity, and results in a near-surface pycnocline.

The majority (~75%) of tidal energy supplied by gravitational forces is dissipated in shelf seas and coastal systems, supporting tidal flows (Wunsch & Ferrari 2004). As a consequence of the large amount of energy dissipation to coherent structures in these systems, they are characteristically turbulent and variable environments. Various coherent structures such as eddies, boils, wakes and jets can be generated at different scales at these sites, depending on the topography and amount of energy supplied to the system. Consequently, the ability of animals to exploit these environments is likely to be spatially and temporally constrained.

1.3.3 Biodiversity in tidal mixing fronts

The mobility of water can affect marine predators at a range of scales. Like all animals in mobile features, they must account for the direction and strength of water movement when attempting to get from one location to another. This may be advantageous or detrimental depending on the speed and direction of the current. Such interactions can occur on large spatial scales, along migration routes, or at small scales in coastal tidal streams or at confluences where dynamic water masses meet relatively static, stratified waters causing frontal systems.

Given the entrainment of primary production at tidal mixing fronts, multiple trophic levels have been reported to forage at sites of convergent flow (Bost *et al.* 2009; Embling *et al.* 2012; Scales *et al.* 2014b). In particular, surface and pelagic predators, and suspension feeders are relatively abundant. For example, several cetacean species have been observed to associate with tidally influenced frontal systems and they have even been suggested to affect migratory phenology (Bailleul *et al.* 2013). Doniol-Valcroze *et al.* (2007) described spatial partitioning between mysticete species within frontal systems suggesting interspecific differences in foraging tactics. Pelagic delphinids such as bottlenose dolphins (*Tursiops* sp.) and common dolphins (*Delphinus delphis*) have also been reported to be strongly associated with tidal mixing fronts, and have been predominantly observed favouring the offshore, stratified side of the boundary (Franks 1992; Cox 2016; Cox *et al.* 2017). Smaller-scale fronts in UK waters have been noted to attract basking sharks (*Cetorhinus maximus*) which display almost completely passive movement during foraging bouts, tracking the trajectory of the prevailing current and 'following' dense aggregations of zooplankton over several days (Sims & Quayle 1998). This may be an efficient foraging tactic for grazing species as their relatively immotile prey is aggregated by the currents. Further, dense, diverse aggregations of plankton can allow enhanced prey selection, resulting in further energetic benefits when targeting these regions (Vlietstra *et al.* 2005).

Several central-place foragers have been observed utilising prey aggregations and productivity at tidal-mixing fronts; however, these usage patterns are more seasonally dependent than their pelagic counterparts (Cox *et al.* 2018). Seasonal use of these features has been suggested to be driven by proximity, given that trip distance from haulouts or nesting areas is a key limiting factor in at-sea distribution, and tidal-mixing fronts may only be within home-ranges when increased heat-flux in spring and summer shifts the fronts closer to the coast (Holt & Umlauf 2008). For example, short-tailed shearwaters *(Puffinus tenuirostris*) in the Bering Sea have been observed to be dependent on euphausids associated with near-shore thermal fronts during summer when stratified waters encroach further towards land (Jahncke *et al.* 2005). Piscivorous seabirds have also been noted to heavily use tidal mixing fronts, foraging on species presumably attracted to similar resources as planktivorous species. Durazo, Harrison and Hill (1998) noted four species, razorbills (*Alca torda)*, black-legged kittiwakes (*Rissa tridactyla*), common guillemots (*Uria aalge*) and Manx shearwaters (*Puffinus puffinus*) foraging around tidal mixing fronts when performing concurrent line-transect surveys of foraging assemblages and CTD casts in the Irish Sea. Similarly, northern gannets (*Morus bassanus*) have been shown to be more likely to perform foraging like movements when in close proximity to frontal systems (Scales *et al.* 2014a; Grecian *et al.* 2018). While these studies are useful indicators of the importance of fronts to higher trophic levels, it is important to note that birds have a markedly different relationship with mobile environments such as tidal mixing fronts and currents when compared to exclusively marine or semi-aquatic animals. Specifically, animals which commute and forage in water are continually subjected to the forces of currents and often must adjust their locomotion in order to maximise their energy intake. Conversely, birds can effectively avoid these advective forces by flying between discrete patches or prey aggregations more directly.

There is a relative lack of information as to the distribution of pinniped species around tidal mixing fronts. This is curious given the fact that many pinnipeds occupy the same ecological niches as seabird and cetacean species which rely heavily on the prey assemblages in these zones. This may be due to the comparatively high dependence on benthic and demersal prey sources by pinniped species which solely occupy shelf seas (Bowen, Beck & Austin 2009); in these cases, tidal mixing fronts may not provide elevated foraging opportunities due to productivity being concentrated in the upper photic zones. Consequently, stratified areas further offshore may be preferred given the high levels of nutrients in the colder, denser underlying waters. Ongoing research is beginning to point towards the contrary; however, there are still limited data sets in which to answer this question. For example, pinnipeds on the east coast of the UK have been shown to associate with the Flamborough frontal system (Carter *et al.* in prep), a tidal mixing front in the North Sea (Hill *et al.* 1994). There is, however, evidence which points towards phocid use of coastal, well-mixed, tidally energetic waters (Zamon 2001; Hastie *et al.* 2016; Jones *et al.* 2017; Lieber *et al.* 2018) where nutrients are entrained and transported throughout the water column and foraging opportunities can present themselves at varying temporal and spatial scales and depths.

1.3.4 Air breathing predators in tidally energetic waters

Several predatory species appear to target tidal stream environments; however, there is often a pronounced interspecific and cyclical pattern in abundance which correlates with tidal phase (e.g. Bailey & Thompson 2010; de Boer *et al.* 2014; Hastie *et al.* 2016). Tidal currents can reach speeds as high as 10 $m.s^{-1}$ (Eliassen, Heggelund & Haakstad 2001), so predators attempting to forage during peak flow periods must possess the ability to identify important features and navigate through energetically demanding water in order to effectively find and catch prey. Consequently, the strategies required for piscivorous predators to efficiently forage in these environments are likely to be markedly different than in calmer waters.

Productivity in tidally energetic regions depends heavily on the seasonal flux of nutrients from the deeper, stratified waters further offshore (Brink 2013). Regardless of the comparatively low levels of primary productivity, these regions demonstrate cyclical periods of increased biomass; migratory animals seek reduced costs of transport through enhanced travel speeds in prevailing flow directions, and piscivorous and planktivorous predators exploit boosted foraging opportunities due to the inability of smaller zooplankton and nekton to resist the strong forces of upwelling and turbulence (Gibson 2003; Benjamins *et al.* 2015). The predictable nature of tidal forcing presents a potentially important energy source for larger animals if they are able to withstand or exploit the energetic forces themselves.

1.3.4.1 Pinnipeds

While many pinniped species have been observed in association with mesoscale and sub-mesoscale oceanographic frontal structures (e.g. Lea *et al.* 2006; Bailleul *et al.* 2007;

Baylis, Page & Goldsworthy 2008; Charrassin *et al.* 2008; Della Penna *et al.* 2015), few have been observed in consistent association with tidal streams.

As such, quantitative studies of seal distributions in relation to tidally energetic areas are sparse; however, a number of animal-borne telemetry studies suggest that these areas may be important to some. For example, Brown and Mate (1983) observed harbour seals holding position, swimming directly into the prevailing flow at river mouths during flooding tides in Oregon, USA foraging on chum salmon. The seals were likely targeting large salmon which were using tidally assisted movement to return to their spawning grounds and so represented a predictable, highly calorific food source. Similarly, Zamon (2001) observed a strong association between harbour seal foraging behaviour and tidal currents. Seals spent more time foraging for salmon at the mouth of a river during slow, flooding tides suggesting a threshold above which seals may not be capable of efficiently targeting these high flow spots. This study also provided a basis for the still commonly held ‘tidal coupling hypothesis’ where tidal currents mediate fish species aggregations when flows exceed their physiological capabilities and provide profitable foraging sites for piscivorous predators (Zamon 2001; Zamon 2003).

Conversely, Thompson (2012) observed what appeared to be a different, relatively passive foraging tactic with juvenile grey seals moving forwards and backwards with the tide repeatedly diving to the bottom suggesting foraging activity in the fast-moving tidal currents off Anglesey and Ramsey Sound, Wales. In similar tracking studies on the west coast of Scotland, Thompson (2013) and Hastie *et al.* (2016) observed adult harbour seals demonstrating foraging techniques in tidal rapids that suggested utilisation of smaller scale coherent structures. Seals repeatedly swam (or were advected) downstream with the flow while diving to mid-water. It was postulated that they were continually targeting mid-water fish species such as mackerel. In order to continue this process throughout the flooding tide, seals potentially “escaped” the flow by swimming into associated eddies which allowed them to move into slower moving water at the periphery of the channel and swim upstream before repeating the process (Hastie *et al.* 2016).

While foraging activity may partly explain the pinniped distributions during different phases of the tidal cycle, it is important to consider that haul-out behaviour and breeding strategies may also play a role in the observed patterns. For example, the availability of intertidal haul-out sites decreases during flooding tides resulting in an increasing proportion of seals being at-sea during this time (Thompson *et al.* 1997). Studies have noted higher seal abundance in narrow channels during flooding tides compared to ebbing tides (Zamon 2001; Zamon 2003), some with markedly different cyclical haul-out patterns between flood and ebb tides that are not directly centred around high tide (Hastie *et al.* 2016). This suggests that the observed patterns are not directly related to haulout availability. Nevertheless, studies of the relationships between tidal state and foraging activity of pinnipeds must consider haulout availability when interpreting observed patterns. Similarly, Van Parijs, Hastie and Thompson (1999) noted reproductive strategies of harbour seals were spatially and temporally affected by tide cycles with male reproductive vocalisations being significantly greater in narrow channels, during flooding tides suggesting the complexity of tidal usage by phocids may have a phenological component at certain times of year.

1.3.4.2 Odontocetes

Harbour porpoises (*Phocoena phocoena*) are widely distributed in most shelf-sea waters and sightings are common in many coastal regions (Hammond *et al.* 2002). The highest concentrations of porpoises in UK waters have been seen in areas with strong tidal features such as the Inner Hebrides (Northridge *et al.* 1995; Embling *et al.* 2010). However, there are contrasting observations suggesting that the use of high tidal energy sites may vary between different geographical locations. Several studies of harbour porpoise spatial usage in tidal areas of Europe have reported higher abundance (observation rates) during periods of strong tidal flow (Pierpoint 2008; Marubini *et al.* 2009; Jones *et al.* 2014; Ijsseldijk *et al.* 2015). Behavioural observations have also indicated foraging primarily during fast, ebb tides where individuals would adopt the strategy of using the flow to hold position and ambush prey swimming with the prevailing flow (Pierpoint 2008). However, it is important to highlight that geostationary porpoises would likely be more easily seen and recorded than a porpoise increasing its speed over ground by swimming with a current, so alternate strategies may be as prevalent but less likely to be observed. In a study using drifting porpoise recording systems, Benjamins *et al.* (2016) noted that porpoise presence was not correlated with flow speed and that a more complex interaction occurred where porpoises consistently travelled downstream with prevailing currents. In addition, porpoise distributions can vary markedly within, as well as between, discrete tidal phases (Benjamins *et al.* 2017). In contrast, Embling *et al.* (2010) used habitat models to predict relative densities in the southern Inner Hebrides and found that maximum tidal current was the best predictor of distribution with greater numbers predicted in areas of low current. The apparent differences may be a result of the tidal differences in the study areas or due to subtle differences in the analytical methods. For example, Embling *et al.* (2010) considered separate spatial and temporal measures of tide rather than a single temporal measure which is more commonly used. Arguably this method has more explanatory power as the state of tide can vary dramatically over a relatively small area and modelling flow rates over the entire study area concurrently can give a broader perspective on the movements and spatial usage of a dynamic marine predator. Recent investigations in the Sound of Islay and Kyle Rhea, Scotland have concluded that it is not the tidal narrows themselves but turbulent eddies, formed as a result of tidal outflow from the channels, that harbour porpoises utilise more frequently (Wilson, Benjamins & Elliott 2013). Regardless of the reasons behind the differences, it seems clear that tidal currents play a significant role in their distribution.

Several delphinid species have been observed using tidally active regions and tidally generated structures. Bottlenose dolphins (*Tursiops truncatus*) are commonly observed in tidally influenced regions; however, as generalist predators, their activity is not always predictable or consistent and the importance of energetic regions on their foraging opportunities remains uncertain. Blair, Scott and Kauffman (1981) observed that bottlenose dolphins in Palma Sola Bay, Florida swam more frequently against the current and at the periphery of channels where tidal flow diminished, possibly indicating opportunistic foraging. Similarly, Shane (1980) observed a higher abundance of bottlenose dolphins during peak ebb tides in southern Texas and were repeatedly observed swimming against the current. This behaviour coincided with anecdotal evidence of increased fish abundance (local fisheries catch records) during these periods and indicated a possible foraging tactic similar to that identified in porpoises in the UK (Pierpoint 2008). However, as with all studies of this nature, they must be caveated by the fact that animals swimming against a flow will be more available to observers than animals moving with a current, assuming no change in surface behaviour.

1.3.4.3 Birds

Although several bird species utilise tidal streams for foraging, there do not appear to be any species that specialise exclusively on high energy tidal streams with generalist tendencies often noted (Benjamins *et al.* 2015). There is also a high degree of interspecies variability in foraging tactics such as shallow surface diving, plunge-diving, deep diving and less often, surface foraging.

The Auk family varies in both body size and prey selection, but are a common feature is their ability to dive relatively deep. For example, common guillemots (*Uria aalge*), have been recorded diving up to 180 metres (Piatt & Nettleship 1985). When using tidal environments, foraging behaviour is limited by tide cycles due to the energy required to either swim against currents or travel back to important foraging areas after swimming with currents. Consequently, multiple studies have noted differences in dive behaviour and abundance during changes in tidal current direction and speed (Holm & Burger 2002; Zamon 2003; Furness *et al.* 2012; Waggitt & Scott 2014).

Holm and Burger (2002) observed significant differences in densities, between slack and flood/ebb tides, of ancient murrelets (*Synthliboramphus antiques*) and pigeon guillemots (*Cepphus columba*) in the strong tidal currents of Vancouver Island, Canada. The use of fast-flowing tidal currents for foraging by pigeon guillemots was also noted in this area. Similarly, foraging behaviour by black guillemots (*Cepphus grylle*), razorbills and common guillemots has been reported in tidally energetic sites in the UK (Furness *et al.* 2012; Waggitt & Scott 2014). Zamon (2003) observed that not only do rhinoceros auklets (*Cerorhinca monocerata*) utilise tidal flows of the San Juan archipelago, USA to forage but they are significantly more abundant during flooding tides than ebbing tides.

Several studies have noted foraging in tidal currents by phalacrocoracids in Northe America (Zamon 2003; Ladd *et al.* 2005; Elliott *et al.* 2008). Further, Wade *et al.* (2013) observed foraging activity within the tidal system of inner Pentland Firth, UK by the European shag (*Phalacrocorax aristotelis*). They noted that diving shags often surfaced upstream from the point of submergence indicating swimming against the current. This was interpreted as foraging activity; the increased costs of swimming against a fast-flowing current would presumably require the individual to offset this by consuming more prey. Similar to the behaviour of alcids, Zamon (2003) also noted *Phalacrocorax* species exploiting flooding tides of the San Juan archipelago with reduced activity during ebbing tides.

Gulls and gannets (family: Laridae and Sulidae respectively) have been observed using high energy sites to varying degrees and it is likely they profit from increased prey concentrations caused by both tidal currents and prey aggregation by deep divers. For example, Elliot (2004) found a high abundance of black-legged kittiwakes and northern gannets (*Morus bassanus*) in the Gulf of Corryvreckan (a tidally dominated, high energy site on the west coast of Scotland).

1.4 Animal movements in tidally energetic regions

As described above, there are numerous reports of use of tidal features by marine predators; however, the range of foraging and travelling behaviours observed indicates stark differences in the drivers of abundance in these areas. Although the use of these regions must impart an energetic benefit for animals found in them, the mechanisms underlying the benefit remain unclear. However, it is likely to be based on reduced expenditure through current use to aid transit or through increased prey acquisition.

1.4.1 Discrete behaviours

Many fish species have been shown to passively use tidal currents through selective tidal stream transport (STST, Forward & Tankersley 2001; Gibson 2003). Metcalfe, Arnold and Webb (1990) noted adult plaice (*Pleuronectes platessa*) migrating into the water column during one phase of the tide and then returning to the seabed on the reciprocal tide. It was suggested that this represented a strategy for energetically efficient migration between feeding and spawning grounds. More commonly, STST is observed in larval and juvenile fish and crustacea (Forward & Tankersley 2001; Gibson 2003) which are less capable of active movement in tidally driven waters. Migratory pelagic fish species have also been recorded using tidal currents and channels to aid transit. For example, Lacoste (2001) tracked pre-spawning movements of herring (*Clupea harengus*) in the tidally active region of the St. Lawrence estuary, Canada. Herring translocated to a tidal channel, repeatedly swam towards spawning grounds regardless of the state of tide, gaining more ground during concurrent movement than they lost when actively resisting flow. Further, no STST was observed which indicated energetically effective use of the channel; no significant energetic deficit was being incurred as a result of swimming against the current given the ground being made up by swimming with the current.

While larger marine vertebrates may be more capable of combatting fast-flowing currents, several species have also been seen to use tidally driven movement to aid transit between foraging patches. de Boer *et al.* (2014) observed that harbour porpoise use of a high energy tidal site in Wales dropped significantly either side of slack water; however, the authors consistently observed individuals “hitch-hiking the current” through the channel rather than actively swimming at the periphery of the flow. Raya

Rey *et al.* (2010) also noted that transit between nest sites and foraging grounds of Magellanic penguins (*Spheniscus magellanicus*) in the Beagle channel always occurred with the prevailing current flow during chick-rearing, when net energy gain is most important for successful breeding. Although foraging behaviour in channels subject to strong currents would seemingly require animals to actively swim against the direction of flow in order to target resident prey, it is possible that individuals may use tidally induced hydrodynamic features (e.g. eddies or coastal friction) or static structures to counteract the effects of displacement (Liao 2007).

The leading hypotheses as to why predators may be attracted to these regions are 1) increased abundance of prey, and 2) increased vulnerability of prey to capture due to turbulent waters (Benjamins *et al.* 2015). Theoretically, prey concentrations will periodically increase in these sites due to the bottom-up effects of the advection of zooplankton from productive, stratified waters of the mid-shelf region (Zamon 2002). Coupled with the frequency of STST movement by benthic and demersal fish and active reproductive migrations of pelagic fish we could expect prey species to be in high abundance throughout the water column. However, it has been argued that the behaviour of forage fish and their increased vulnerability due to disorientation and advection during high flow periods may be the major driver of tidally mediated predator abundance (Liao 2007; Fauchald 2009; Ferguson, Kingsley & Higdon 2012). Multiple tactics to exploit the disorientation of prey in tidal streams have been theorised for marine predators. Some hypotheses are based on laboratory and field-based observations of predatory fish species such as using flow refuges to ambush prey (McLaughlin & Noakes 1998) and using turbulent structures to increase closing speeds to disoriented prey (Lewis & Pedley 2001). However, for larger predators such as marine mammals and birds, fine-scale behaviours have generally been inferred from horizontal and vertical movement strategies and there are few direct observation of predator-prey interactions (Zamon 2001). Nevertheless, it seems clear that tidal streams are a periodically important foraging habitat for several marine predators.

1.4.2 Challenges of assessing movement in high flow conditions

Measuring movement and foraging behaviour in tidal flows is challenging due to the relative difficulties of tracking individual animals in fast-flowing environments. As such, most studies have been limited to short-term observational studies of animals at the surface (e.g. Wade *et al.* 2013; Lieber *et al.* 2018). However, as foraging behaviour generally occurs underwater and over larger time-scales, the inferences that can be made are limited. The spatial and temporal complexity of these systems in three dimensions further compounds the difficulties in measuring fine-scale, sub-surface behaviour using only surface observations, whether they be GPS records of horizontal movement or direct observations.

The exploration of these underwater behaviours is hindered by the difficulty in measuring 3-dimensional hydrodynamic conditions at these sites while simultaneously collecting high-resolution movement data (Lieber *et al.* 2018). Consequently, most studies have relied on modelled predictions or interpolated in-situ measurements in concurrence with animal movement observations (both from biologging, observational and acoustic surveys). While quantitative analysis can be carried out with these kinds of data, mechanistic and empirical frameworks will inevitably overlook fine-scale features which, when analogously scaled up, are of evident importance to predators foraging in the realms of meso- and macroscale oceanographic structures.

A critical component when looking to understand animal movement in tidally energetic areas is that movement patterns are necessarily a function of both the locomotion of the individual and the flow vector of the immediately surrounding medium (Richardson 1990; Gaspar *et al.* 2006). In other words, an observed animal trajectory in a tidally influenced habitat is governed by the movements of both animal and the current (Fig. 2). This becomes problematic when trying to use mechanistic approaches to defining animal movements in energetic environments as the movement behaviour is not being directly measured by observation alone. Even if we consider discrete behaviours, without accounting for oceanographic conditions we omit the information required to robustly interpret the animal's behavioural state (Gaspar *et al.* 2006). To date, researchers have generally not considered this potential issue when investigating animal movements in tidally energetic sites. However, in the past 30 years, studies of large scale migrations of pelagic species and avian movements have begun to resolve this issue.

Richardson (1990) compiled evidence of 'drift compensation' in migratory birds and demonstrated that, given that following winds are sporadic or sometimes absent on many important migratory corridors, certain species must adjust their orientation and speed in order to efficiently travel. This technique was then applied to large scale movements of marine animals subjected to ocean currents (e.g. Loughlin 1999; McConnell *et al.* 2002). Gaspar *et al.* (2006) then suggested, using the example of leatherback turtle GPS tracks in the western Atlantic, that neglecting the influence of ocean currents could result in misclassifications of discrete behavioural modes. This idea has been developed somewhat over the past decade with large scale movements of pelagic foragers being adjusted for physical ocean movement in an attempt to tease apart subtleties in behaviours as a response to oceanographic variables (Horton *et al.* 2011; Bon *et al.* 2015; Dodge, Galuardi & Lutcavage 2015; Briscoe *et al.* 2016; Trudelle *et al.* 2016). However, they are largely hampered in their ability to robustly detect small-scale, oceanographically influenced movements given the typically coarse scale of hydrodynamic information.

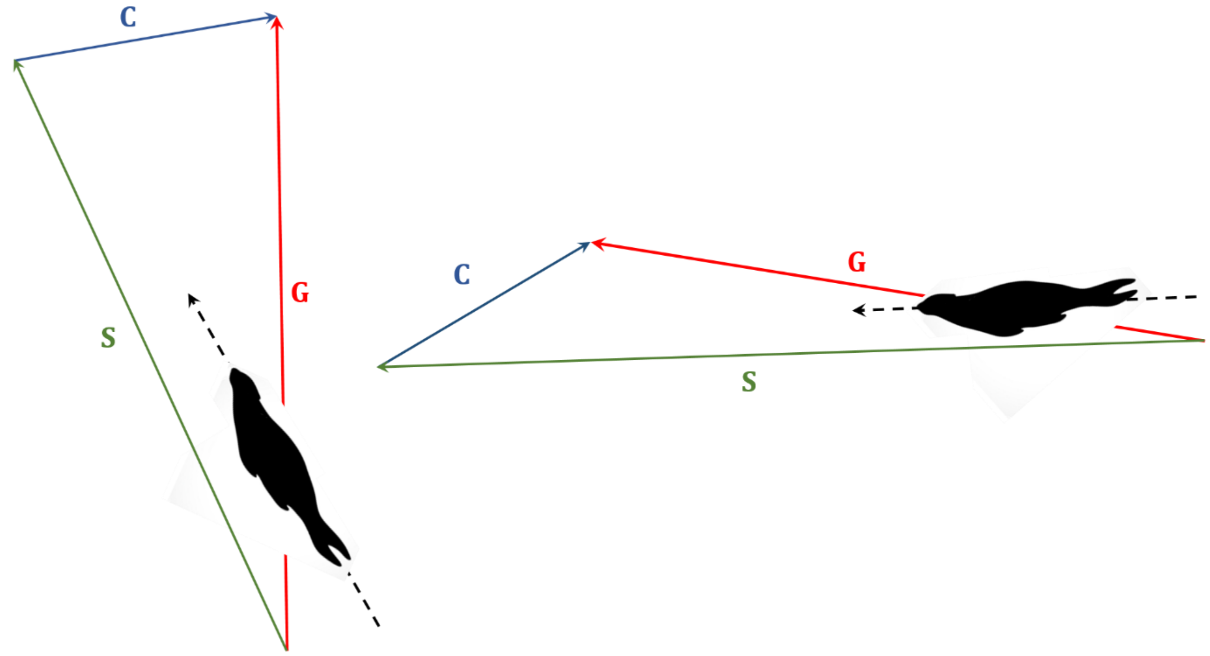


Figure 2: **Animal movement vs current.** In the marine environment, an observed movement vector over ground (G) is the vector sum of the animal's swimming vector (S, also known as heading) and the current vector (C). Animals must compensate movement in increasing currents by swimming in opposing angles to current direction such that in currents moving in the opposite direction to the target destination, animals must swim at a 180° orientation to the prevailing flow.

Recently, environmental data has begun to be collected onboard tags (Boehme *et al.* 2009) as well as researchers using oceanographic measurement tools such as ADCPs to validate tidal forecasting models (e.g. Murray & Gallego 2017). These developments particularly aid the interpretation of diving animal behaviour given that flow conditions of a given area are heterogeneous in both the horizontal and vertical planes. However, as described above, these analyses still rely on broad-scale assumptions of fluid dynamics and are heavily scale dependant. Consequently, the application to tidal streams has remained relatively untouched, given the inherent fine-scale heterogeneity of physical features in mid-shelf to coastal waters, the more pronounced effects of meteorological conditions on tidal currents in shallow waters and the difficulties of measurement therein.

1.5 Tidal stream energy industry

The role of marine predators in marine ecosystem dynamics is a vital trophic cascade that has a significant effect on ecological resilience (Soule *et al.* 2003; Hughes *et al.* 2005; Heithaus *et al.* 2008). As a result of the increasing industrialisation of the oceans, several populations have been heavily negatively impacted at various scales ranging from the oceanic effects of climate change (Moore & Huntington 2008; Gremillet & Boulinier 2009) and plastic pollution (Vegter *et al.* 2014; Nelms *et al.* 2016) to more localised effects of fisheries by-catch (Lewison *et al.* 2004) and collisions with shipping (Laist *et al.* 2001) and renewable energy installations (Desholm & Kahlert 2005). Effective conservation presents many challenges owing largely to the highly mobile and enigmatic behaviour of many species; some of which occupy several ocean basins or exist in areas which are difficult to survey (Wilson 2016). Furthermore, the establishment of static protected areas may over-simplify the effective conservation of several species whose distribution is driven primarily by temporally and spatially heterogeneous conditions. While mitigation of anthropogenic degradation is imperative, effective strategies to improve population trajectories and re-establish distributions can only be achieved with an improved understanding of fundamental vertebrate ecology.

Geographical areas of interest to the marine renewable energy industry appear to overlap with the geographic ranges of several marine species and it is therefore important to assess the potential environmental consequences of the installation and operation of the industry. Over the past decade, growing concerns about anthropogenically induced climate change has resulted in significant developments of the renewable energy industry. Global renewable energy capacity is dominated by biomass digestion plants and hydroelectric power, with a rapidly increasing contribution from on-shore wind sources (Panwar, Kaushik & Kothari 2011). However, offshore wind, wave and tidal power (marine renewables) are an increasingly attractive alternative due to the public perception of cosmetic landscape effects of terrestrial structures (Green *et al.* 2016) and the magnitude of wind offshore, and predictability of tidal power (DECC 2011). Tidal stream energy devices typically function in a similar way to wind turbines, by converting the kinetic energy of the tidal flow into electricity. In general, they have tapered blades attached to a central hub which rotates and activates a generator to produce electricity at a rate proportional to the tidal current velocity.

At present, there is a high degree of uncertainty regarding the potential environmental impacts of the marine renewable energy industry, particularly when considering the abundance of animals which inhabit areas of interest. Predicted impacts vary markedly both between and within the renewable industries due to the variation in the physical properties and the installation and operational strategies of the devices. The primary concern for marine mammals with regards to offshore wind farms derives primarily from the high sound levels as a result of pile driving during the installation phases (Bailey *et al.* 2010; Brandt *et al.* 2011; Hastie *et al.* 2015; Russell *et al.* 2016).

Operational phases have been suggested to be relatively benign (Russell *et al.* 2016) with some evidence suggesting that the turbine foundations provide increased foraging opportunities through artificial reef effects (Russell *et al.* 2014). Conversely, although some tidal power generation devices do require potentially acoustically damaging installation phases, key concerns about the potential impacts of the tidal industry are potential collisions between animals and the rotating blades of tidal turbines during the operational phase, with the potential for injury or death (Wilson *et al.* 2006). Other potential impacts include avoidance behaviour leading to displacement from key habitats or barrier effects (Hastie *et al.* 2017). The concerns may be compounded as high flow periods, where the blades are rotating at their fastest, are often associated with high densities of marine animals (Williamson *et al.* 2019).

Due to the relative infancy of the tidal industry, there is a general lack of information to determine whether the perceived impacts are valid. Further, there is a paucity of data on marine predator distributions and behaviour in tidally energetic areas, particularly those with operational tidal turbines. To date, only three studies have measured the effects of an operational turbine on animal movement and distributions, and these have suggested a degree of avoidance. Sparling, Lonergan and McConnell (2017) and Joy *et al.* (2018) used GPS quality tracking data on harbour seals to observe movements around the SeaGen Tidal Turbine device in Strangford Lough, Northern Ireland. These studies report an overall decrease in density of seals close to the turbine during operation, with animals transiting past the turbine at the periphery of the narrow channel as compared to their general mid-channel transits in the absence of the turbine. Joy *et al.* (2018) suggested that the observed degree of spatial avoidance could reduce collision risk by >90%. In contrast, although Long (2017) observed that the numbers of most bird species in the region of the European Marine Energy Centre (EMEC) Falls of Warness tidal turbine test site in Orkney, Scotland reduced during installation phases, they recovered to baseline levels during operations. This result suggests that, for bird species, the installation phase may cause a larger avoidance effect than the device itself. While informative, these studies were limited in spatial and temporal resolution and focussed on the effects of single, test turbines with sporadic operations so cannot be generalised to large commercial scale devices. Furthermore, data on the direct physical consequences of collisions to animals are lacking, resulting in potentially overly conservative approaches of population effects being adopted (Band *et al.* 2016). As a result, a number of attempts to estimate population-level impacts have used theoretical models based on animal movement data in the absence of tidal turbines; collision risk models (CRMs) or encounter rate models seek to estimate the frequency of interactions, and the consequences to individuals and populations as a result of the interactions (Wilson *et al.* 2006; Band *et al.* 2016).

Currently, CRMs require information on animal movement to estimate the number of times an animal would be predicted to encounter a turbine blade in the absence of close-range evasion responses. To date, there are two CRMs widely used to quantify collisions between marine mammals and tidal turbines: 1) the Scottish Association for Marine Science (SAMS) Research Services Limited (SRSL) Encounter Rate Model (Wilson *et al.* 2006) which estimates the overall rate of collisions between animals and turbines using an adaptation to a predator-prey model by Gerritsen and Strickler (1977), and 2) the modified Band collision risk model (Band *et al.* 2016) which estimates the risk posed to individual seals during a nominal number of transits through a simulated turbine. There is, however, very few data to inform the potential for fine-scale avoidance behaviour (Wilson *et al.* 2014a; Bald *et al.* 2015), so estimates from these models are often un-realistic. General scalars are included in these models to account for an assumed near-field evasion and large-scale avoidance of animals however, they are self-admittedly non-informative given the lack of data to support them. Given the hydrodynamic performance of many diving animals in these regions it is likely that they are capable of evading turbine blades at ranges closer than previously used tracking techniques have been capable of resolving. Future studies will attempt to rectify this issue using high resolution, near field acoustic tracking (Hastie *et al.* 2019a; Hastie *et al.* 2019b) but presently, large scale avoidance measurement remains the only tool to assess behavioural responses to tidal turbines.

Recent attempts to measure avoidance behaviour of marine mammals to operational tidal turbines are limited. Sparling, Lonergan and McConnell (2017) provided the first investigation of the effects of operating tidal turbines on the behaviour of marine mammals. While no overt barrier effects were reported, the authors noted that harbour seals adjusted their transit frequency and behaviour in response to turbine operations and provided the first evidence of potential avoidance behaviour. Similarly, Joy *et al.* (2018) used the same data to suggest there was an overall reduction in collision risk as a response to the presence of an operating tidal turbine and an avoidance response apparent up to 200 metres from the turbine location. Hastie *et al.* (2017) showed similar avoidance patterns by tagged harbour seals to playbacks of sounds of a tidal turbine indicating that avoidance behaviour may partly be a result of auditory cues. Carlson *et al.* (2014) and Copping *et al.* (2017) were the first to assess the potential physical ramifications of tidal turbine collision on killer whales (*Orcinus orca*) and harbour seals respectively. Through computational modelling of soft tissue trauma as a result of ‘worst-case scenario’ interactions, neither study found concrete evidence of likely fatality however, the effect on harbour seals remained reasonably unclear.

In order for the industry to develop in an environmentally sound manner, filling the key data gaps addressed in this section is essential. More robust information on movements, dive behaviour, responses to operational devices and arrays, and the consequences of physical collisions with these devices are needed. Moreover, these data need to be applied in frameworks which inform mitigation and allow the industry to make key planning decisions which do not significantly impact populations.

1.6 PhD Objectives

The objective of this thesis is to understand the movement and spatial ecology of harbour seals in tidally energetic areas with a specific focus on potential interactions with tidal turbines. I investigate the importance of these ecosystems for harbour seals and measure the potential of an operational tidal energy turbine array.

1.6.1 Harbour seals of the UK: status and threats

Harbour seals are the most widely distributed pinniped species, common in the temperate and sub-polar waters of the North Atlantic and North Pacific (Perrin, Würsig & Thewissen 2009). Natal site-fidelity has resulted in five genetically and geographically distinct subspecies; the European population being constituted solely of *Phoca vitulina vitulina* (Stanley *et al.* 1996). The UK harbour seal population constitutes ~30% of the entire European stock (~80,000 individuals), of which 80% breed and moult in Scotland (Duck *et al.* 2011; Thompson *et al.* 2019).

Inter-regional differences in population trends within Europe has resulted in harbour seals being listed in Annex II of the EU Habitats Directive stating the necessity to designate special areas of conservation (SAC) to establish and maintain favourable conservation statuses. As a member state, the UK has followed this directive by the establishment of nine designated harbour seal SACs. Additional protection is provided in the UK under the Conservation of Seals Act 1970 (England and Wales), the Marine Act 2010 (Scotland) and the Wildlife Order 1985 (N. Ireland). To ease management and trend reporting, the entire UK population is divided into 15 seal management units based on the spatial distribution of breeding haulout sites (Thompson *et al.* 2019; Fig. 3). In recent decades several of these management units have shown rapid increases in population size; for example, counts of harbour seals in South-east England have increased exponentially (2.8% per annum) since the culmination of the PDV epidemic of 2002 (Thompson *et al.* 2019). Conversely, some populations, such the North Coast and Orkney seal management unit, are undergoing steady declines the causes of which are still uncertain (Thompson *et al.* 2019).

Several proximate causes have been postulated for local harbour seal declines in the UK such as competition between and predation pressure from the rapidly growing grey seal (*Halicheorus grypus*) population (Brownlow *et al.* 2016; Thomas *et al.* 2019), predation pressure from killer whales (Bolt *et al.* 2009), persistent effects from population crashes due to phocine distemper virus epidemics (Thompson *et al.* 2019) and exposure to harmful algal toxins such as domoic acid and saxitoxins (Jensen *et al.* 2015). While no single event has yet been linked to the declines, it is likely that a combination of pressures has led to deleterious effects being felt at the population level. Given the protection required for Annex II species, these declines require any local anthropogenic activity to be exhaustively monitored and assessed to determine whether environmental impacts may exacerbate the declines, at which point mitigation measures must be pursued or new ventures abandoned. This has created a paradoxical situation as the UK government has pledged to offset carbon emissions by shifting energy generation towards renewable sources such as wind and tidal, but in the process have identified that these ventures can potentially serve to negatively affect local ecosystems (including harbour seals) through long and short term, direct and indirect impacts if not mitigated (Boehlert & Gill 2010; Wright 2014).

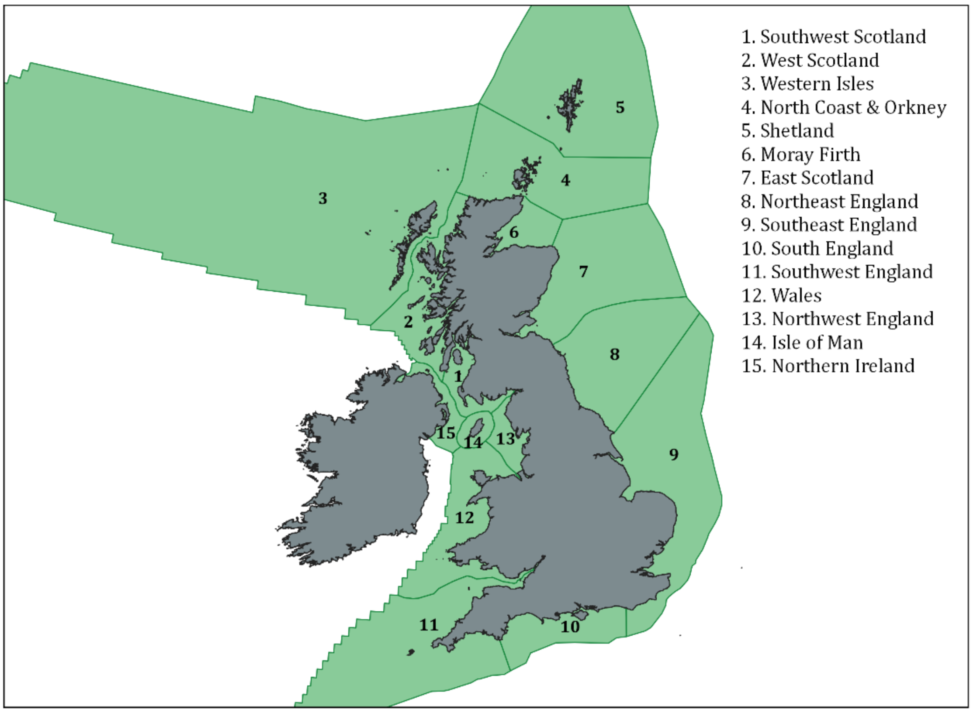


Figure 3 **Seal management units of the United Kingdom (Thompson *et al.* 2019)**

One such issue exists in the Pentland Firth, Scotland; the fast tidal flows in the region have been identified as a potential source for commercial scale tidal energy extraction however, the leased development site overlaps with the local population of harbour seals which has been undergoing significant declines in recent years (Jones *et al.* 2017;

Thompson *et al.* 2019). The concerns of direct and indirect negative effects from collisions (Wilson *et al.* 2006) and barrier effects reducing accessibility to key foraging sites (Sparling, Lonergan & McConnell 2017) render further investigation into this site crucial as the development progresses. Under the guidance of the OSPAR Convention EcoQO management actions are required if local populations decline by more than 10% over a decade (OSPAR 2009). Using potential biological removal as a tool to estimate the maximum number of individuals available for removal through anthropogenic action (direct and indirect), research programmes have identified that the North Coast and Orkney SMU can afford no additional mortality sources if the 10% per decade threshold is to be achieved (SCOS 2017; Arso-Civil *et al.* 2018). Therefore, any identified threat posed by the turbine array development could curb further licensing and cause significant environmental and economic difficulties.

1.6.2 The Pentland Firth: study site and project plan

The Pentland Firth is a body of water separating mainland Scotland from the Orkney Islands. It is characterised by strong tidal currents created by geographical bottlenecks through the channel and around small islands, producing currents in excess of 5 $m.s^{-1}$ during peak, spring flood and ebb tides; speeds which exceed the maximum burst speeds of the harbour seals which inhabit the area (Williams & Kooyman 1986; Thompson, Hiby & Fedak 1992). Between May and August, approximately 85 harbour seals haul out to breed and moult at sites along the north coast of the mainland, and exhibit at-sea distributions primarily within the Pentland Firth (Jones *et al.* 2017). Due to the significant energy resource produced by the tidal currents, a lease site has been consented by the Scottish Government and developed by SIMEC Atlantis Energy Ltd. which represents the world’s first commercial sized tidal energy array (MeyGen 2017).

However, uncertainty around it's environmental impact is a cause for concern given the overlap with the geographic range of the declining local harbour seal population.

Given the lack of information on the potential environmental risks posed by large arrays such as this, consenting has progressed under the scientific knowledge generated from modelling approaches and investigation of the effects of single, test devices (Wright 2014; Sparling, Lonergan & McConnell 2017; Joy *et al.* 2018). This is a necessity in lieu of large scale arrays however, with installation of scaled up deployments, comes the opportunity and the requirement to assess the effects to the local ecosystem. The Pentland Firth therefore provides a unique opportunity to study both the effects of operational renewable energy devices on harbour seals and how these animals navigate a fast-flowing, dynamic system to achieve energetically efficient movement; complimentary investigations which could yield information key for conservation and elucidate nuances of movement ecology in dynamic systems, hitherto undocumented.

In Chapter 2, I therefore explore the movement ecology of seals in relation to their geo-spatial movements and swimming behaviour and quantify the relative use of these to understand how seals forage in dynamic environments. The aim of this work is to further the biological knowledge of the animals' movement patterns in relation to environmental conditions, and in so doing aid in our interpretation of potential threats to the animal by, or indeed their resilience to, proposed anthropogenic activity.

Specifically, I tagged Fourty-eight harbour seals with GPS devices over 4 deployments. I apply hidden-Markov models to geo-referenced movement parameters as well as tidal current vector corrected values to compare the differences between geo-centric movement and swimming behaviour. I then use environmental covariates to describe behavioural state-switching and to understand fine-scale, horizontal movement in the context of tidal currents.

In Chapter 3, I quantify seal dive behaviour and present variations in water column use as a function of tidal currents, seasons and a range of other environmental covariates. I also compare the dive data to the behavioural data from Chapter 2 and make a series of inferences about dive function. Similarly to chapter 2, this work aims to both clarify how animals use diving to navigate an exploit fast flowing systems and how their depth use could inform their susceptibility to tidal turbine arrays.

In Chapter 4, I use cutting-edge modelling techniques to measure the impacts of the world's first commercial-scale tidal turbine array on the at-sea distributions of harbour seals. I use both the presence of the turbines and their operational state to evaluate potential long-term and short-term effects of tidal turbine arrays. This work directly aims to inform the tidal energy industry on best practices by demonstrating how animals may react to their devices.

In Chapter 5, I develop a novel experimental protocol and investigate the effects of collisions between seals and tidal turbine blades. This is designed to provide an empirical measure of threshold collision speeds, above which are likely to be fatal; implications for collision risk models and the tidal energy industry are discussed.

I will finally discuss the major implications of this work in the context of future directions in marine research and industry. Together, this thesis provides detailed insights into harbour seal behaviour, and aims to advance the field of movement ecology . It will also inform how researchers seeking to study these dynamic habitats collect and interpret data in the future. Finally, it will serve as a benchmark for future projects in these increasingly commercially important environments and provide baseline information on the ecology of a threatened population to ensure future development and industrialisation of coastal ecosystems is carried out sustainably.

Chapter 2

Intraspecific foraging plasticity of a predator in a highly dynamic environment

"You mean the tidal force controls your actions?"

"Partially, but it also obeys your commands"

2.1 Abstract

Quantifying and describing animal behaviour allows us to understand the ways in which environmental drivers affect energy acquisition. With the aid of new technologies and analytical techniques, the interpretation of discrete behavioural traits has become easier at the individual and population levels. However, characterising behaviour in dynamic ecosystems requires more complex analyses than simply quantifying observed geocentric movement. In this study, GPS quality tracking data was combined with model-derived hourly estimates of tidal current vectors to quantify the differences between geocentric movement and swimming behaviour of harbour seals in a tidally energetic habitat. I used discrete-time Hidden Markov Models (HMMs) to identify behavioural states for both perspectives of movement (geo-spatial and hydro-spatial) and included hydrodynamic covariate effects to estimate the probabilities that an animal would transition from one state to another. Three functional behavioural states were identified; localised, dispersed, and travelling which were described by different distributions of relative step-length and turning angles. A significant difference in the activity budgets of the seals between the two perspectives was identified, including a higher percentage of time spent foraging from 52.1% (s.d. 11.2%) to 57.5% (s.d. 14.9%) when using a hydro-spatial as opposed to geo-spatial perspective. Covariate effects of tidal currents revealed a high degree of foraging plasticity which showed to what extent seals could remain resident, were forced to travel, or drifted with prevailing currents. This study presents, for the first time, how activity budgets for animals in dynamic marine environments, can potentially be misclassified when taking a single perspective of movement into account. The plasticity in behaviour also supports the assertion that harbour seal populations in the UK are predominantly made up of generalist predators, capable of responding to significant changes in oceanographic conditions.

2.2 Introduction

The importance of oceanographic drivers of marine animal behaviour is well established for multiple taxa (McConnell *et al.* 2002; Gaspar *et al.* 2006; Bost *et al.* 2009; Grecian *et al.* 2016; Hastie *et al.* 2016; Abrahms *et al.* 2018). Features ranging from ocean currents at the scales of kilometres to eddies and tidal boils at scales of tens of metres have been linked to foraging activity (Zamon 2001; Mann & Lazier 2005; Benjamins *et al.* 2015; Grecian *et al.* 2016). Highly dynamic, tidally influenced marine ecosystems provide a series of relatively unique challenges, such as potentially high transport costs due to water currents, and benefits, such as spatially predictable prey patches (Genin 2004; Gómez-Gutiérrez, Martínez-Gómez & Robinson 2007). Foraging predators must therefore seek to balance these contrasting features to forage successfully and maintain suitable fitness for growth and reproduction.

The development of animal-borne tags has provided researchers with the means of collecting high-resolution movement data for many marine species (Cooke *et al.* 2004; Carter *et al.* 2016). These data can be compared to environmental conditions to answer questions about drivers of distribution and population dynamics (Zucchini, MacDonald & Langrock 2009; Morales *et al.* 2010). In recent years, growth in the field of movement ecology has also given rise to statistically robust methods of inferring foraging behaviour from telemetry and observational data (Morales *et al.* 2004; Jonsen, Flemming & Myers 2005; Langrock *et al.* 2012b; Auger-Méthé *et al.* 2017; Patterson *et al.* 2017). Typically, movement tracks are partitioned into discrete states which are related to underlying behaviours. The most common sets of inferred states for marine species are foraging/resting (characterised by high residence times and low directional persistence) and travelling (characterised by low residence times and high directional persistence (Zucchini, MacDonald & Langrock 2009; Carter *et al.* 2016). Studies have also investigated drivers that lead to animals switching behavioural states by measuring the effects of intrinsic and extrinsic covariates on the probability of transitioning between states, such that contemporaneous environmental conditions are now often explicitly modelled as independent variables (Patterson *et al.* 2009; Dragon *et al.* 2012; Pinto, Spezia & Freckleton 2016). Although studies have demonstrated environmental effects on behavioural transitioning (Towner *et al.* 2016; Leos-Barajas *et al.* 2017b; Grecian *et al.* 2018), few have investigated the effects of environmental covariates on the state determination itself which has potentially led to a restricted view of how behaviours can develop and adapt over different time-scales (McClintock & Michelot 2017).

More recently, state-space models and analogous frameworks have been refined to allow the incorporation of environmental covariate effects on the probability distributions which relate to the movement characteristics of the individual (Auger-Méthé *et al.* 2017; McClintock & Michelot 2017). However, in dynamic environments, the interpretation of the behavioural mechanisms underlying movements is complicated due to the animal's observed movement pattern being necessarily a function of both the individual's movement and the movement of the environment immediately surrounding it (Richardson 1990; Gaspar *et al.* 2006). Consequently, key signals which are traditionally used to inform behavioural classification in marine animal movements may be misinterpreted, which may give rise to inaccuracies in behavioural classification and the identification of foraging habitats.

The measured trajectory of an animal is a vector sum of the speed and orientation of propulsive movement and the speed and orientation of its immediately surrounding medium (Richardson 1990). This often results in animals adjusting their movement through air or water to maximise energetic efficiency (Able 1977; Weimerskirch *et al.* 2000; Wakefield *et al.* 2009; Gaspar *et al.* 2012; Gutierrez Illan *et al.* 2017) or exploit resources within physically energetic regions (Gaspar *et al.* 2006; Della Penna *et al.* 2015). Gaspar *et al.* (2006) first described the mismatch between inferences of behavioural data for a marine species with the comparison of geo-referenced tracks and the swimming trajectories of a leatherback turtle in the North Atlantic. It was noted that simply using geo-referenced tracks to detect periods of high residence time produced an underestimate of foraging effort in faster moving currents. To date, current correction has not been explicitly resolved for species in dynamic, micro-scale features such as tidally forced currents, but several authors have caveated their inferences with this issue (Jonsen, Myers & James 2007; Bailey *et al.* 2008; McClintock *et al.* 2012). Consequently, our understanding of the foraging strategies employed by species in dynamic marine ecosystems is limited.

Harbour seals have been shown to exhibit highly localised at-sea distributions in tidally energetic channels, potentially exploiting fine-scale hydrodynamic features to forage on predictable prey sources (Hastie *et al.* 2016; Jones *et al.* 2017). In many cases, consistency in the use of such tidal channels has been shown to be linked to tidal state (Zamon 2001; Jones *et al.* 2017); however, some populations have been noted foraging in a range of energetic conditions. Tidal features in these regions have a clear influence on harbour seal foraging but how individuals adjust to varying degrees of tidal currents to efficiently forage remains unclear.

In the present study, the foraging strategies of harbour seals in a highly dynamic tidal environment were investigated. Using both geo-referenced locations and current corrected (hydro-referenced) locations, the disparity between activity budgets of the two processing methods was quantified to gain insights into the foraging strategies of seals and the potential links between tidal currents and behaviour. Specifically, harbour seal telemetry data collected within the Pentland Firth, on the north coast of Scotland was analysed within a movement modelling framework (a discrete-time hidden Markov model; HMM).

2.3 Methods

2.3.1 Study Site: The Pentland Firth

The Pentland Firth is a body of water separating mainland Scotland from the Orkney Islands. It is characterised by strong tidal currents created by geographical bottlenecks through the channel and around small islands, producing currents in excess of 5 $m.s^{-1}$ during peak, spring flood and ebb tides (Fig. 1). Water depths are less than 85 metres and the benthos is composed mainly of shells, sand and gravel (Fig. 2). Between May and August, approximately 85 harbour seals haul out to breed and moult at sites along the north coast of the mainland, and exhibit at-sea distributions primarily within the Pentland Firth (Jones *et al.* 2017). The HMM framework was selected as it has been demonstrated to be a robust means of extracting behavioural state-switching for GPS derived movement data when compared to other methods such as first-passage time or kernel density estimation (Dragon *et al.* 2012; Bennison *et al.* 2018).

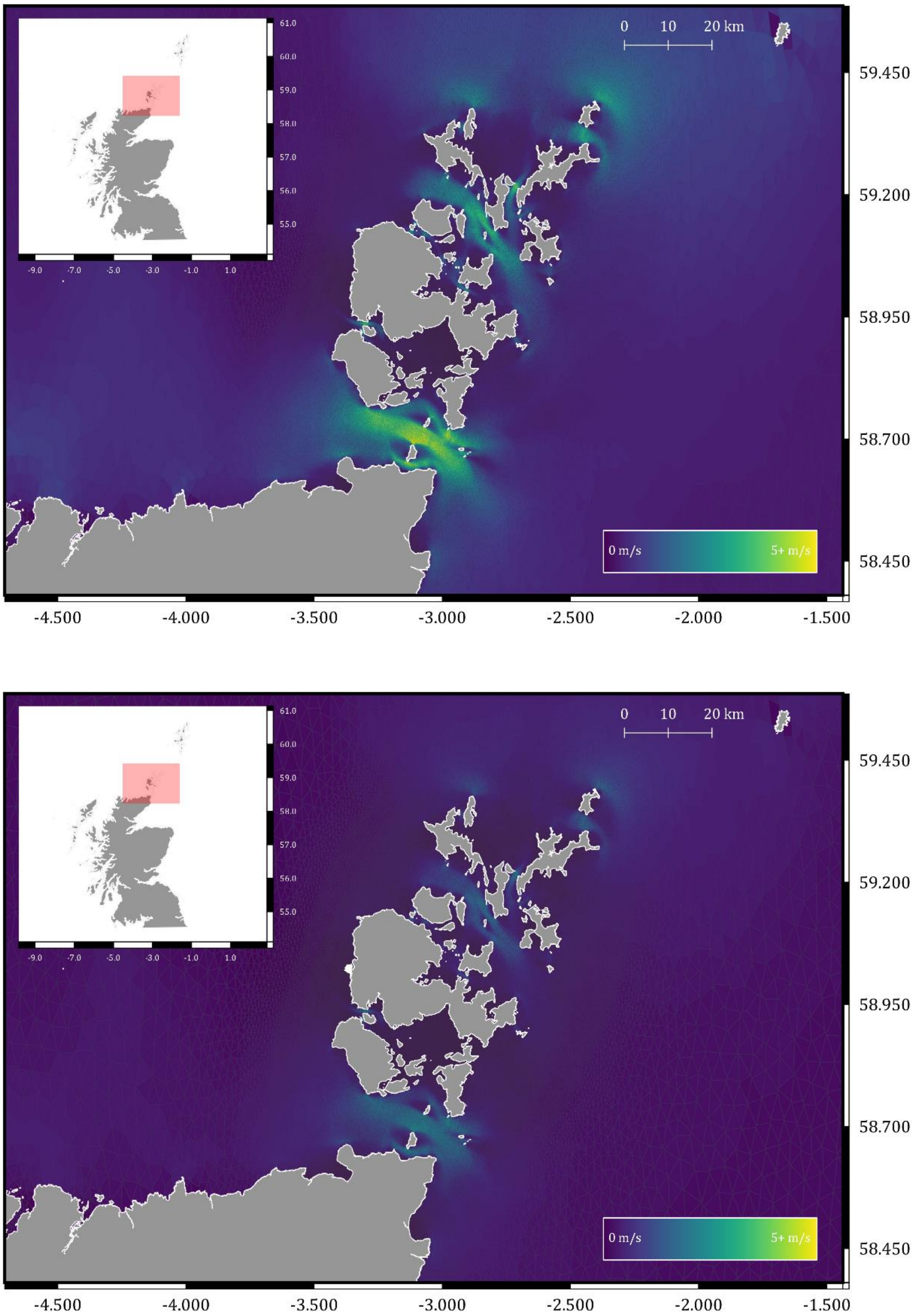


Figure 1 **Mean annual tidal flow speed for the Pentland Firth and Orkney Waters.** Mean speeds are provided for both spring tides (top panel) and neap tides (bottom panel). Flow speed estimates were generated from the Pentland Firth and Orkney Waters sub-domain of the Scottish Shelf Model (Wolf *et al.* 2016).

2.3.2 Telemetry Data

Fastloc® GPS/GSM tags (SMRU Instrumentation) were deployed on 14 harbour seals in 2011 and Fastloc® GPS/UHF tags (Pathtrack Ltd.) were deployed on 40 harbour seals over 4 deployments in 2016, 2017 and 2018 in the Pentland Firth, Scotland (Table 1, Fig. 2). All seals were caught on or close to haulout sites using tangle nets in the water or hoop-nets on land. All Seals were weighed and then anesthetised with intravenously administered Zoletil$_{100}$® at a dose rate of 0.005 mg.kg^{-1} prior to further handling (Sharples *et al.* 2012). GPS tags were glued to the fur at the back of the neck using Loctite 422^{TM} cyanoacrylate adhesive. All capture and handling protocols were carried out under UK Home Office licences #60/4009 and #70/7806 in accordance with the Animals Scientific Procedures Act 1986.

Both GPS tag types collected data at irregular intervals; GPS/GSM tags attempt to record a position every 5 minutes while the GPS/UHF tags attempt to record a position at a maximum of once every 3 minutes. GPS/GSM tags transmitted data via the Global System for Mobile Communication (GSM) network when the seal came within signal coverage (McConnell *et al.* 2004). UHF tags collected and stored data on-board the tag and transmitted to UHF base stations placed overlooking haulout sites along the coast once the tag had been dry for 30 minutes (Hastie *et al.* 2016). In addition, individual at-sea locations could be broadcast if a seal surfaced within line-of-sight of a base-station.

GPS locations with large errors were identified and removed using a filter based on number of satellites and thresholds of residual error (Russell *et al.* 2015). Further location uncertainty was partially resolved by measuring the estimated swim speed, assuming straight line movement, between sequential geo-referenced locations and removing any location demonstrating swim speeds greater than 2 m.s^{-1} after maximum estimated assistance from currents was taken into account. The 2 $m.s^{-1}$ threshold was used as the assumed maximum, sustained speed of a harbour seal (Williams & Kooyman 1986; Thompson, Hiby & Fedak 1992; Hind & Gurney 1997; Gallon *et al.* 2007). The speed threshold removed 0.07% (n=156) of locations. Haulout behaviour for GPS/GSM tags were identified on-board the tag using a wet/dry sensor; seals were assumed hauled out when the tag was dry for 10 minutes and the haul out period ended when the sensor had been wet for 40 seconds. Haulout behaviour for GPS/UHF tags was identified using a pre-scheduled temporal threshold for location acquisition; once the tag was dry, five consecutive locations were collected at precisely 3 minute intervals after which subsequent location intervals were collected at precisely 30 minute intervals until the wet/dry sensor was wet for 15 seconds. Haul out data were removed from any further analyses as the primary focus of this study was to observe at-sea movements.

Table 1 **Capture details for the all seals telemetry tagged in this study**. All animals were qualitatively assessed as being of breeding age. Animals tagged in 2011 were fit with SMRU Instrumentation GPS-GSM tags which include embedded time-depth recorders so dual tagging was not necessary.

TAGGING DATE	CAPTURE LOCATION	SEX	GPS BODY NUMBER	TDR BODY NUMBER	LENGTH (CM)	AXIAL GIRTH (CM)	MASS (KG)
29-MAR-11	Gills Bay	F	pv24-598-11	NA	136	114	84.6
29-MAR-11	Gills Bay	F	pv24-580-11	NA	146	114	89
30-MAR-11	Brough Bay	M	pv24-165-11	NA	143	112	90.6
30-MAR-11	Brough Bay	M	pv24-541-11	NA	153	118	96.8
30-MAR-11	Brough Bay	M	pv24-394-11	NA	128	89.5	49.6
30-MAR-11	Brough Bay	M	pv24-590-11	NA	133	92	49.8
31-MAR-11	Brough Bay	M	pv24-x625-11	NA	151	114	98.6
31-MAR-11	Brough Bay	M	pv24-622-11	NA	151	111	91.4
24-SEP-11	Scotland's Haven	M	pv24-155-11	NA	154	109	95
24-SEP-11	Scotland's Haven	M	pv24-112-11	NA	156	122	92.8
24-SEP-11	Castle Mey	M	pv24-148-11	NA	143	126	76.2
25-SEP-11	Scotland's Haven	M	pv24-151-11	NA	140	117	84.8
26-SEP-11	Gills Bay	F	pv24-150-11	NA	136	119	86.6
26-SEP-11	Gills Bay	F	pv24-153-11	NA	144	100	72
28-SEP-16	Brough Bay	M	65254	51031	153	110	89.2
29-SEP-16	Brough Bay	F	65231	51019	110	80	33.6
30-SEP-16	Gills Bay	F	65199	51025	148	110	91.6
30-SEP-16	Scotland's Haven	M	65191	51011	144	110	92.6
01-OCT-16	Scotland's Haven	M	65201	51009	115	104	85
01-OCT-16	Scotland's Haven	M	65334	51020	165	116	106.2
01-OCT-16	Scotland's Haven	M	65246	51030	155	96	75.4
01-OCT-16	Scotland's Haven	M	65242	51026	147	116	100.2
02-OCT-16	Scotland's Haven	M	65446	51022	154	115	93
02-OCT-16	Scotland's Haven	M	65239	51029	153	114	102
02-APR-17	Ham	M	65257	51104	149	108	87

TAGGING DATE	CAPTURE LOCATION	SEX	GPS BODY NUMBER	TDR BODY NUMBER	LENGTH (CM)	AXIAL GIRTH (CM)	MASS (KG)
02-APR-17	Ham	M	65500	51120	147	101	81.4
02-APR-17	Ham	M	65243	51105	151	110	92.6
03-APR-17	Harrow Harbour	F	65507	51109	147	112	103.4
03-APR-17	Harrow Harbour	M	65513	51111	137	99	73.6
07-APR-17	Harrow Harbour	F	65195	51101	142	115	103.2
07-APR-17	Brough Bay	F	65502	51119	143	121	110.7
07-APR-17	Harrow Harbour	M	65504	51100	159	116	112
07-APR-17	Ham	M	65499	51112	156	112	108
08-APR-17	Harrow Harbour	F	65506	51114	146	109	86.4
08-APR-17	Ham	M	65505	51116	148	99	74.6
09-APR-17	Harrow Harbour	F	65496	51115	142	105	88.4
13-APR-17	Gills Bay	F	65503	51108	146	106	97.6
13-APR-17	Gills Bay	F	65512	51117	135	103	76
16-APR-18	Brough Bay	F	64315	51129	151	108	92.7
17-APR-18	Brough Bay	F	64313	51128	139	118	93.9
17-APR-18	Brough Bay	F	64312	51134	151	111	97.1
18-APR-18	Castle Mey	F	64318	51125	138	104	88.5
18-APR-18	Ham	M	64304	51124	143	99	76.9
18-APR-18	Ham	M	64305	51130	153	115	101.7
19-APR-18	Castle Mey	F	64321	51131	135	102	77.7
19-APR-18	Castle Mey	F	64308	51122	145	104	84.3
20-APR-18	Brough Bay	M	64309	51121	140	105	78.7
21-APR-18	Gills Bay	F	64316	51110	138	103	85.9
21-APR-18	Gills Bay	F	64301	51132	137	103	83.1
21-APR-18	Gills Bay	F	64300	51102	142	111	93.1
21-APR-18	Gills Bay	F	64303	51136	135	102	77.7
22-APR-18	Gills Bay	M	64320	51127	155	112	101.9
22-APR-18	Gills Bay	M	64314	51126	145	105	86.7
24-APR-18	Brough Bay	M	64302	51118	153	112	90.1

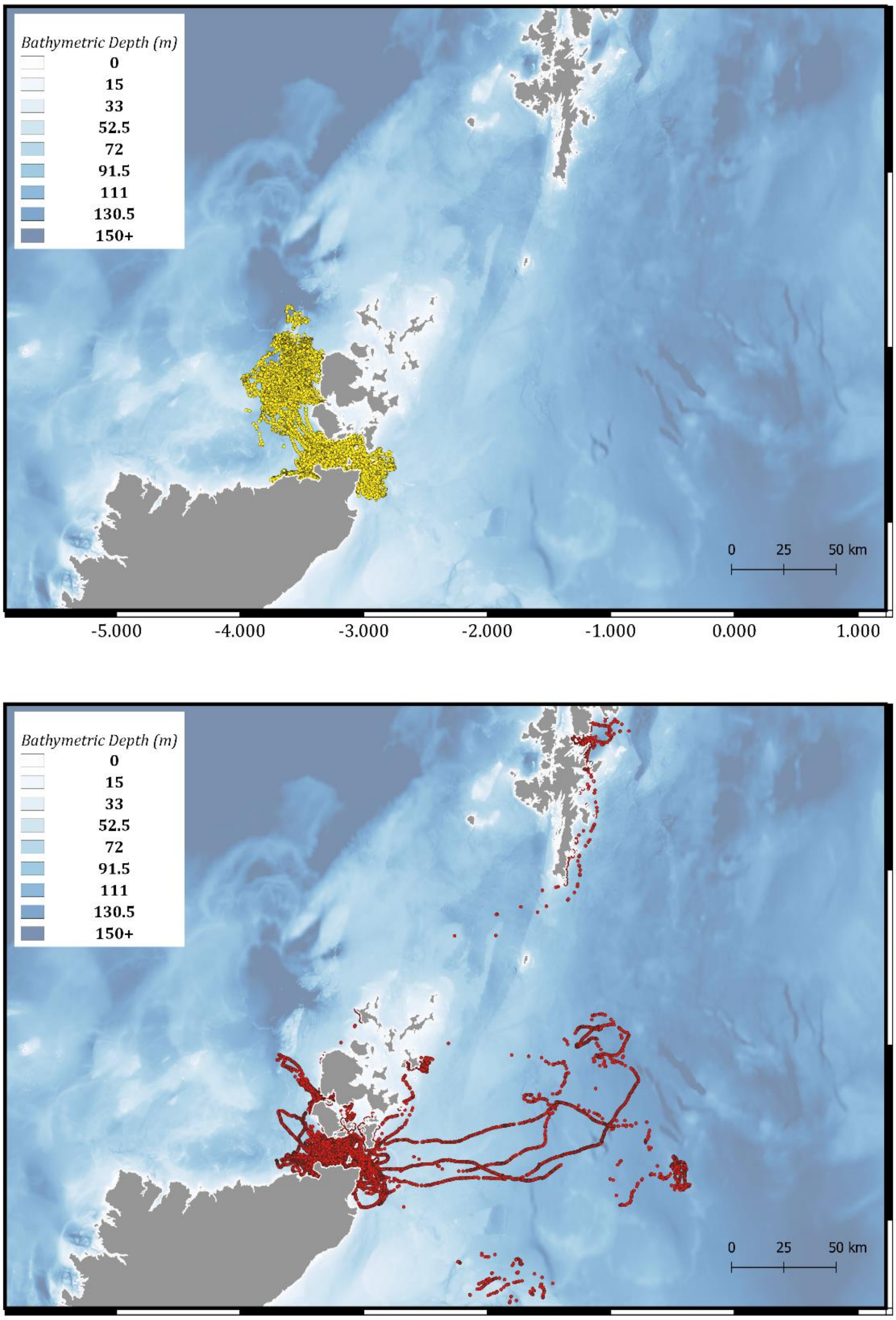


Figure 2 **All GPS data collected for harbour seals in the Pentland Firth**. (top panel) Cleaned tracks from 14 harbour seals instrumented with GSM-GPS tags between 2011-2012 and (bottom panel) 40 UHF-GPS tags between 2016-2018. Bathymetric data represents depth at lowest astronomical tide and were downloaded from EMODnet Digital bathymetry database (EMODnet 2016).

2.3.3 Hydrodynamic Data

Data on estimated, depth averaged current vectors (velocity and direction) were extracted from a Finite Volume Community Ocean Model (FVCOM) of the Pentland Firth and Orkney Waters; a sub-domain of the Marine Scotland Scottish Shelf Model which produces hydrodynamic projections for Scotland's coastal waters. The model simulates hydrodynamic conditions within its boundaries, on an unstructured grid for a given date range based on bathymetric data, forcing data and calibration data. As an unstructured grid, the resolution is non-uniform throughout its range. Maximum resolution (150 metres between vertices of triangular elements) occurs in the inner sound of the Pentland Firth and becomes coarser in a broadly analogous way to the densities estimated by the at-sea behaviour of tagged seals in this study rendering it ideal for use with this telemetry data set (Fig. 1, Appendix I). Horizontal resolution is largely based on the extent and resolution of the bathymetric and geographical data. Grid-meshes were generated so as to ensure the grid sizes varied smoothly; resolution in areas towards the northern periphery were 2.5 – 3 km whereas within the Pentland Firth and Orkney waters the grid-cells rarely exceed 250 m. Depth averaging is carried out over 10, equally spaced, binned depths throughout the water column, resulting in coarser vertical resolution in deeper areas. However, flow rate is more vertically uniform in deeper areas given boundary conditions representing smaller proportions of the water column so coarser resolution is more defensible.

The numerical model has been validated using existing Acoustic Doppler Current Profiler (ADCP) data collected by the British Oceanographic Data Centre (BODC; Baston and Harris, 2011) and the Environmental Research Institute (ERI) in 2001 and 2009 respectively (Wolf *et al.* 2016). Further, Price *et al.* (2016) and Murray & Gallego (2017) calibrated the model using available contemporary tidal forcing, temperature and salinity data from the National Oceanography Centre Atlantic Margin Model and meteorological forcing data (i.e. wind) and wave data from the Met Office.

The baseline model was acquired, with given hydrodynamic covariate estimates at hourly averages for a calendar year. The number of unique grid cells used by the seals was calculated as the number of unique grid-cells that raw GPS location fixes from the seal tags were recorded in. The hydrodynamic conditions for each of these grid cells were estimated for the date-range of the seal tag data via a harmonic analysis whereby the tidal peaks from the base-line model were matched to tide height data during the seal telemetry deployment. Hydrodynamic estimates were computed for each hourly time-step and then the model element and the hourly time-step in which the data point appeared were matched to produce the estimated velocity vector at each seal GPS location. Hydrodynamic data analysis and extraction was carried out in MATLAB (V 9.3.0.7).

2.3.4 Current Correction

To estimate seal swim direction and speed, current correction was carried out; the observed velocity of a seal's movement ($\overrightarrow{w_g}$) is necessarily a sum of the seal's swim vector through the water ($\overrightarrow{w_s}$) and the water movement vector ($\overrightarrow{w_c}$) (Gaspar *et al*. 2006) such that re-arranging allows assessment of the vector of the animal through hydro-space (Eq. 1) giving:

$$\begin{pmatrix} us \\ vs \end{pmatrix} = \begin{pmatrix} ug \\ vg \end{pmatrix} - \begin{pmatrix} uc \\ vc \end{pmatrix} \qquad \text{(Eq. 1)}$$

Northerly and easterly current velocities, which were estimated from the hydrodynamic model, were used to calculate depth averaged current speed and direction for each seal location at the point of departure. Current speed was then calculated using the standard vector formula (Eq. 2):

$$v_c = \sqrt{U^2 + V^2} \qquad \text{(Eq. 2)}$$

Where U is easterly current speed and V is northerly current speed. Current direction was computed through the circular trigonometric equation (Eq. 3):

$$\theta c = \left(\arctan\left(\frac{U}{v}, \frac{V}{v}\right)\right) * \frac{180}{\pi} \qquad \text{(Eq. 3)}$$

Which calculates flow orientation on the scale of -180° to +180°. Negative values are then adjusted to represent geostrophic orientation where -1° = 359°, -2°=358°…….-180° = 180°. Seal swim speeds (v_s) were calculated as distance over time for sequential raw, cleaned GPS location fixes. Distance was calculated using the Haversine formula (Eq. 4):

$$d = r \cdot \Phi \qquad \text{(Eq. 4)}$$

Where d is the great circle distance between two lat/lon locations, r is the radius of the Earth (usually given as the mean radius, 6,371 km) and Φ is the central angle which in turn is calculated using the trigonometric equation (Eq. 5):

$$\Phi = 2 \cdot \arctan\left(\sqrt{a}, \sqrt{1-a}\right) \qquad \text{(Eq. 5)}$$

Where a is given as:

$$a = \sin^2(\Delta\varphi/2) + \cos\varphi_1 \cdot \cos\varphi_2 \cdot \sin^2(\Delta\lambda/2) \qquad \textit{(Eq. 6)}$$

Swim direction was calculated using the forward azimuth formula (Eq. 7):

$$\theta_s = \arctan(\sin\Delta\lambda \cdot \cos\varphi_2 \cos\varphi_1 \cdot \sin\varphi_2 - \sin\varphi_1 \cdot \cos\varphi_2 \cdot \cos\Delta\lambda) \qquad \textit{(Eq. 7)}$$

A current corrected vector (Vs) was then produced by subtracting the current vector (Vc = v_c, θ_c) from the seal movement vector (Vg = vg, θ_g) for each time step, as per Gaspar *et al.* (2006). Vs ultimately describes the direction and speed a seal would have to swim in a given current to produce the measured movement track over ground and is demonstrated in figure 3.

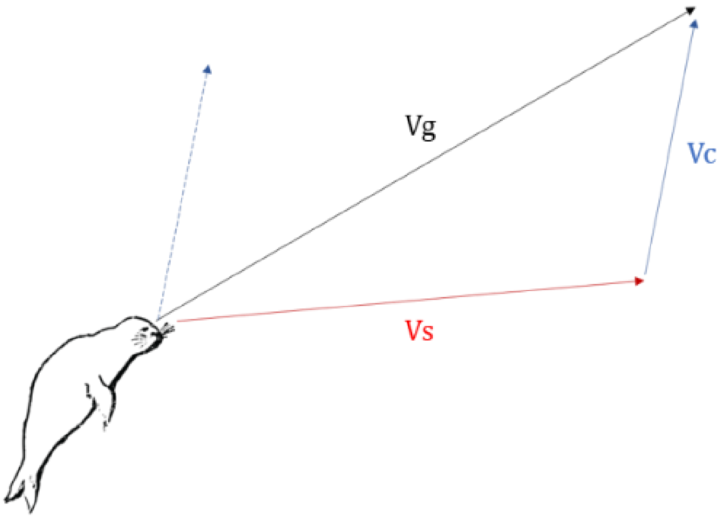


Figure 3 **Animal heading velocity and current flow velocity**. An animal's track vector (Vg), i.e. velocity over ground is the vector sum of its swim vector (Vs) and the current vector (Vc). The dashed blue line represents the current flow velocity at the point of departure to provide temporal context, however, is the same magnitude and direction as the solid blue line.

Location data were finally interpolated to a constant 15-minute time-step due to the requirement of regular intervals for HMM fitting. Several interpolation intervals were tested to establish the minimum reasonable value which did not violate model assumptions but was robust to the fact that several data gaps occurred within the data and data resolution differed between the two tag types. The final interpolation value was determined by the comparatively longer median inter-location interval of the GSM tags compared to the UHF tags (Fig. 4). Data were separated into bouts of locations whereby a new bout was specified if the observed location frequency was ≥ 45 minutes. Interpolated locations between these points were flagged as 'unreliable' and were excluded from further analysis, post-hoc. Tag durations ranged from 13 – 119 days (median: 72 days); tags with <28 days of data were removed from the study after the 7-day period immediately following deployment was removed. This ensured (a) a comparable sample size was used to ensure state frequency could be reliably linked between individuals (Zuur, Ieno & Elphick 2010) and (b) representative behavioural data was used, discounting any potentially abnormal post-capture effects (McKnight 2011).

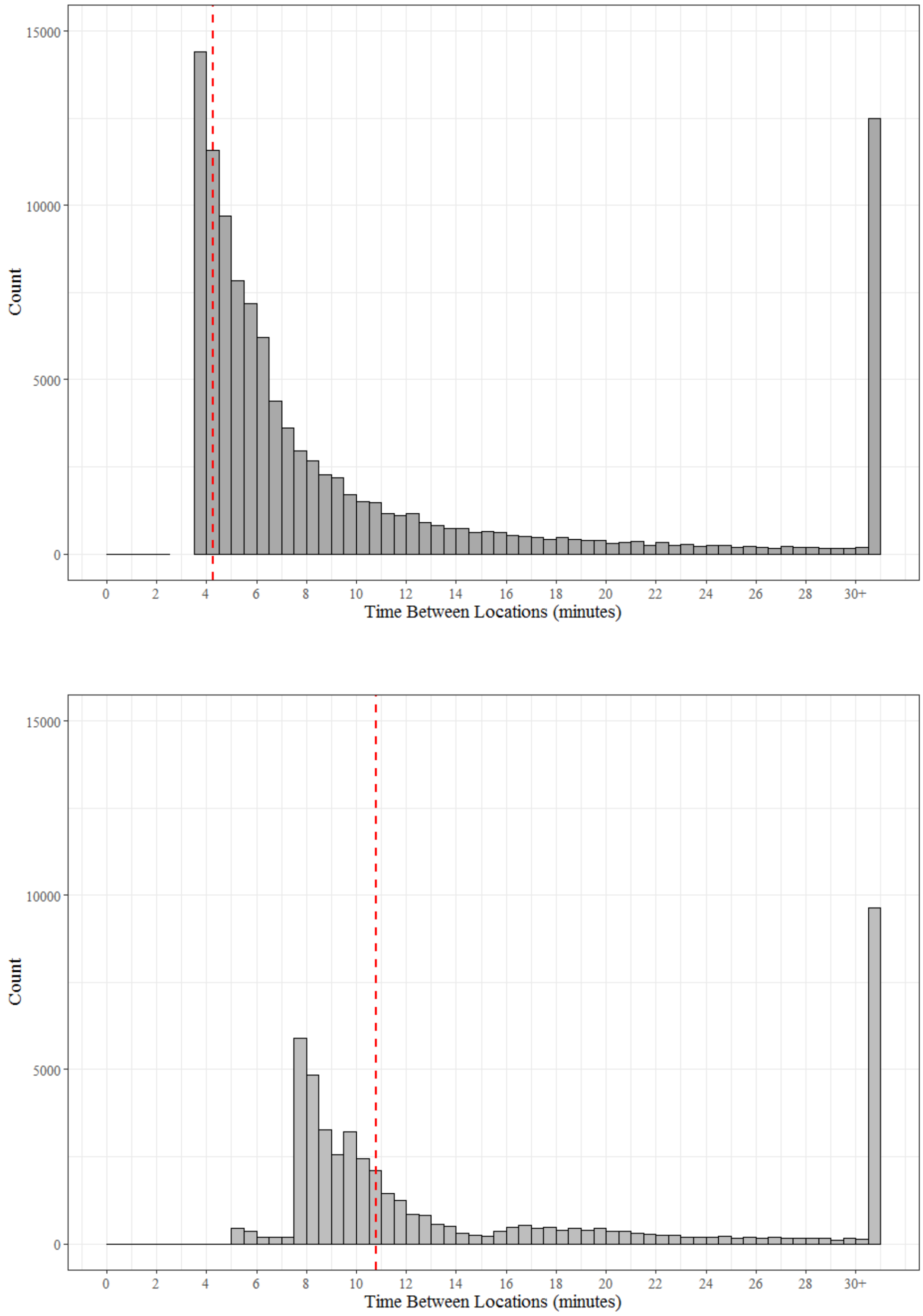


Figure 4 **Time intervals between filtered GPS locations.** Histograms are shown for GSM-GPS tags (below) and UHF-GPS tags (above). Dashed red lines indicate median values. Peaks at >30 minutes indicate extent of haulout behaviour and data gaps.

2.3.5 Hidden Markov Model (HMM)

Separate discrete time, 3-state, multivariate HMMs were developed for both the hydro-spatial corrected movement and geo-spatial movement from the regularised tracking data using the momentuHMM package (McClintock & Michelot 2017). Models were parametrised using the movement metrics step length (s_t, the Euclidian distance travelled in one time-step) and bearing (φ, turning angle in radians between consecutive locations). Discrete states were estimated in the model through identification of modes in the distributions of the movement metrics. Each location was assigned to one of three latent states: zt ∈ [*Tr, Fe, Fd*]. Three states were used rather than the widely used 2-state models (traditionally inferring travelling and foraging/resting) to ensure enough flexibility in the model to allow a variety of movement behaviours, that may not be apparent in more static environments, to be described. For example, animals may exhibit larger step lengths during area-restricted search behaviour in higher flow rates rendering separation of travelling and putative foraging more difficult. Following previous studies (Jonsen, Flemming & Myers 2005; McClintock *et al.* 2012; Russell *et al.* 2015) step length followed a gamma distribution ($s_{n,t}|z_{n,t = i} \sim \text{Gamma}(\mu_{n,i}/\sigma_{n,I}, \sigma_{n,i})$) where the state-specific mean step and shape parameter were greater than 0. A circular distribution, the VonMises distribution, was assumed for bearing (φ) (Langrock *et al.* 2012).

To maximise the likelihood function through exploration of the parameter space, initial distributions are required (mean and standard deviations for each parameter) for model estimation (Zucchini, MacDonald & Langrock 2009). Model convergence does not necessarily require the selection of meaningful initial parameter values. However, resulting state-dependent distributions can be heavily influenced by these values. The state process of the model is initiated by probabilistically sampling the unobserved state at the first time-step to be one of *n* possible states (3 possibilities in the present case) driven by the initial parameter values provided. Establishing starting values for the parameter estimates was therefore conducted using an iterative process due to the possibility of a local rather than global maximum likelihood being reached if poor starting values were provided. Starting parameter means and standard deviations were a random combination of between 0-6.3 km for step length and between 0-π radians for turn angle, for each iteration. The models were run 50 times with different, randomly selected combinations of values, and the likelihood functions were compared to establish the global maximum likelihood which was estimated using the forward algorithm.

Given the apparent inter-individual variation in spatial distributions, each model was run separately for each individual. Resulting probability distributions were graphically compared to assess whether pronounced individual variability was evident. Variation in the tidal dynamics of the study site was also likely to affect the parameter estimation and transition probabilities, and this approach allowed for the assessment of any inter-individual variations in behaviour. State sequences were then decoded using the Viterbi algorithm and assigned to the original time-intervals of the interpolated data to determine activity budgets.

Previous studies have described challenges associated with separating resting and foraging behaviour in two-dimensional models of movement. For example, harbour seals have been observed to spend over 5% of their time resting at sea (Russell *et al.* 2015). The limited availability of concurrent dive data to inform these assignments resulted in the inability to include multiple data streams to augment assumptions made purely from step length and turn angle measurements. Available dive data were, however, extracted for all intervals for which surface locations were known; i.e. when the beginning and the end of a dive had contemporaneous GPS locations. A comparison of the model with the dive data was conducted and the results are presented in Chapter 3.

To establish whether state-switches were driven by environmental variables, a novel, ‘known state’ sequence model was then fit using predicted flow rate as a covariate on state-transition probabilities. The ‘known state sequence’ involved the Viterbi derived state-sequences for both geo-spatial and hydro-spatial models being pooled for each time-step to create a new state sequence for each individual. This resulted in a 9-state system which represented all possible combinations of geo-spatial and hydro-spatial states (Table 2). The model was parameterised assuming the states were known and correct. In other words, the model was not permitted to estimate state dependant distributions of discrete states during fitting but only estimate transition probabilities between states. Due to the necessity of modelling state-dependant distributions being alleviated, all individuals were pooled for this analysis. The effect of tidal current flow rate was implemented on the transition probability matrix using a multinomial logit link function, using the starting parameter values estimated from the iterative process described above. This allowed assessments of behavioural switching as it relates to the local oceanographic dynamics.

Model selection was carried out by comparing delta AIC between the model with the covariate effect acting on the transition probability matrix and the intercept only model. The covariate model was considered superior if inclusion of the covariate resulted in a ΔAIC of <2 (Burnham & Anderson 2002). Final models were validated by visual inspection of qq-plots and pseuo-residual trends as well as an assessment of auto-correlation functions for the pseudo-residuals. Similarly, model fit was considered good if pseudo-residuals showed no discernible trends and qq-plots deviated minimally from a 1:1 ratio (Patterson *et al.* 2009; Appendix I).

Table 2 **Combined, known states.** Each state used as the input, known state sequence for the combined HMM. Accompanying descriptions of the combined states are provided to clarify the swimming trajectory of the seal given the observed geospatial and hydrospatial states.

State Number	*Geospatial State*	*Hydrospatial State*	*State Description*
1	Dispersed	Dispersed	Geo-Hydro Dispersed
2	Dispersed	Localised	Drifting-tortuous
3	Dispersed	Travel	Advection assisted travel
4	Localised	Dispersed	Cross-current localised
5	Localised	Localised	Geo-Hydro Localised
6	Localised	Travel	Swimming against current
7	Travel	Dispersed	Cross-current travel
8	Travel	Localised	Drifting - directed
9	Travel	Travel	Geo-Hydro travel

2.4 Results

2.4.1 Trip characteristics

A total of 3,677 foraging trips (periods of at-sea movement between individual haul out events) provided 71,7668 hours of tracking data across 24 individuals. Of the remaining seals, the tags either did not produce more than 2 weeks of data, produced tracks with large data gaps during offshore periods or failed entirely for unknown reasons, and were removed from further analysis. At-sea locations were concentrated within the Pentland Firth and relatively close to haulouts (Fig 2). This was reflected in the resulting trip distance and duration metrics; mean trip duration was 11.12 hours (4.52 – 71.42 hours) and mean trip distance (maximum distance from haulout of departure) was 5.22 km (3.12 - 19.27 km). Hourly resolved, depth-averaged hydrodynamic predictions were available for all locations for the 32 individuals included in the final modelling procedure (detailed below). Daily mean distance travelled for geo-spatial and hydro-spatial tracks across all individuals was 24 km (s.d. 18.9 km) and 34.3.3 km (s.d. 22.1 km) respectively (Fig. 5; Appendix I, Fig A1.1).

2.4.2 Hidden Markov Models

Hidden Markov Models converged for both geo-spatial and hydro-spatial data for all individuals included. Three discrete states were captured for both geo-spatial and hydro-spatial data; a dispersed state, a localised state and a directed state. Mean speeds of the localised state were 0.11 m.s^{-1} (s.d. 0.12 m.s^{-1}) and 0.16 m.s^{-1} (s.d. 0.14 m.s^{-1}) for geo-spatial and hydro-spatial movement respectively. In contrast, mean speeds for the dispersed state were 2.77 m.s^{-1} (s.d. 3.34m.s^{-1}) and 3.88 m.s^{-1} (s.d 5.55 m.s^{-1}) for geo-spatial and hydro-spatial movement respectively. This indicated little difference in speed between the two states in geo-referenced data (0.03 m.s^{-1}) compared with a more pronounced difference in the hydro-referenced data (0.72 m.s^{-1}). Following previous state-space approaches to characterise phocid at-sea behaviour the three states were defined by the following: 1. Dispersed foraging: longer step lengths with high tortuosity, 2. Localised foraging: shorter step lengths with high tortuosity and 3. Travelling: longer step lengths with low tortuosity (Figs. 6 and 7). A 2 state-model was also run to compare foraging designation. State-sequences indicated several time-intervals which were determined to be travelling in the 2-state model but dispersed foraging in the 3-state model, justifying the inclusion of the third state given the difference in turn-angle state dependant distributions between these 2 observed states.

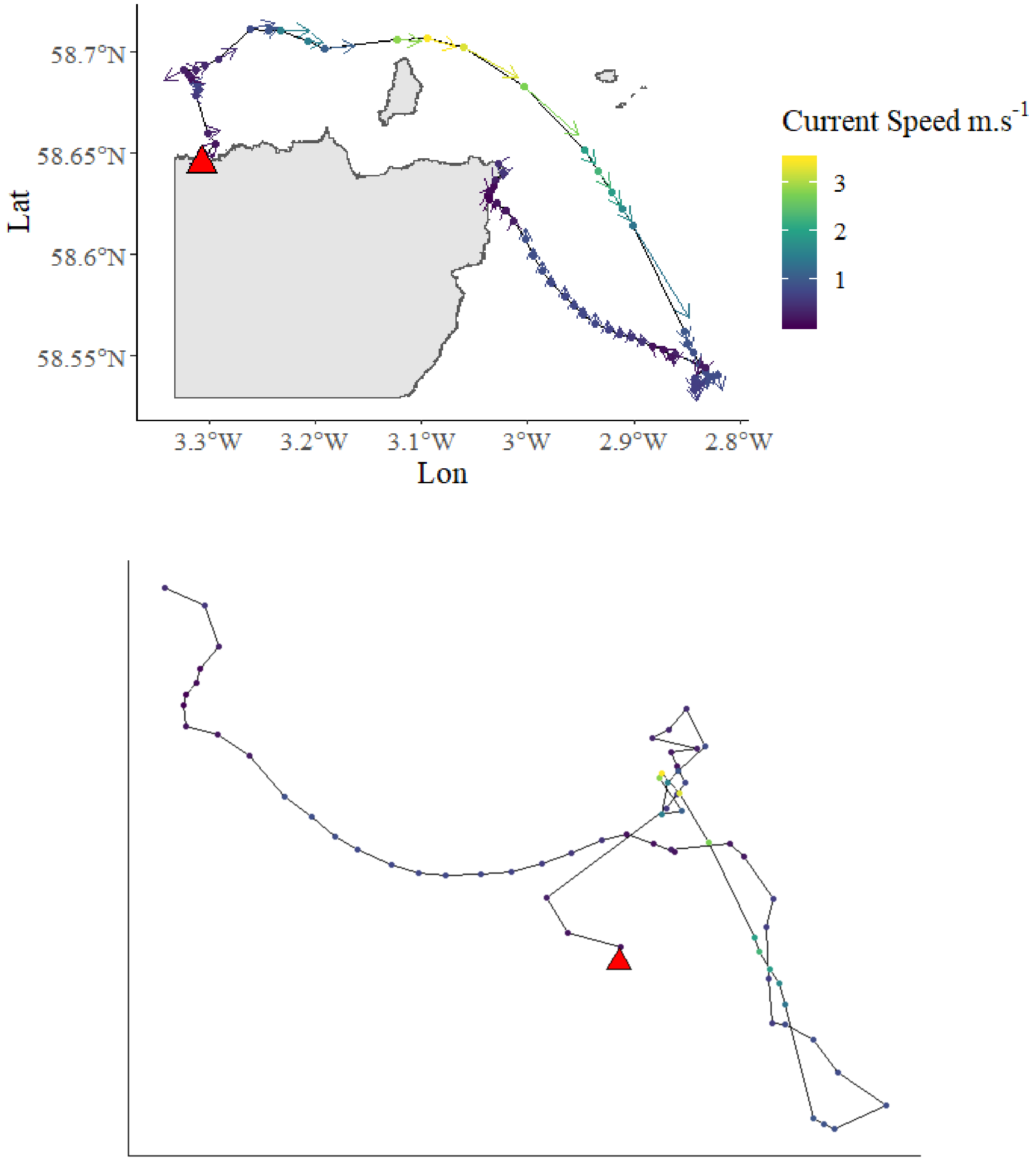


Figure 5 **Geo-spatial vs Hydro-spatial tracks**. (top panel) Cleaned geo-referenced tracks (before interpolation) of a male harbour seal during a 16-hour trip to sea with associated current vector estimates for each time interval. Current trajectory (shown by the arrows) and strength (colour coding) is given estimated at the first of each pair of locations. (bottom panel) Current-corrected track using the vectors displayed in the top panel to represent the swimming vector of the seal. Hydro-spatial movement is presented without landmass features as it represents the animals swimming track through hydro-space. Locations are coloured by estimated current strength at that location using the same scale as the top panel. Red triangles show the point of departure of the trip.

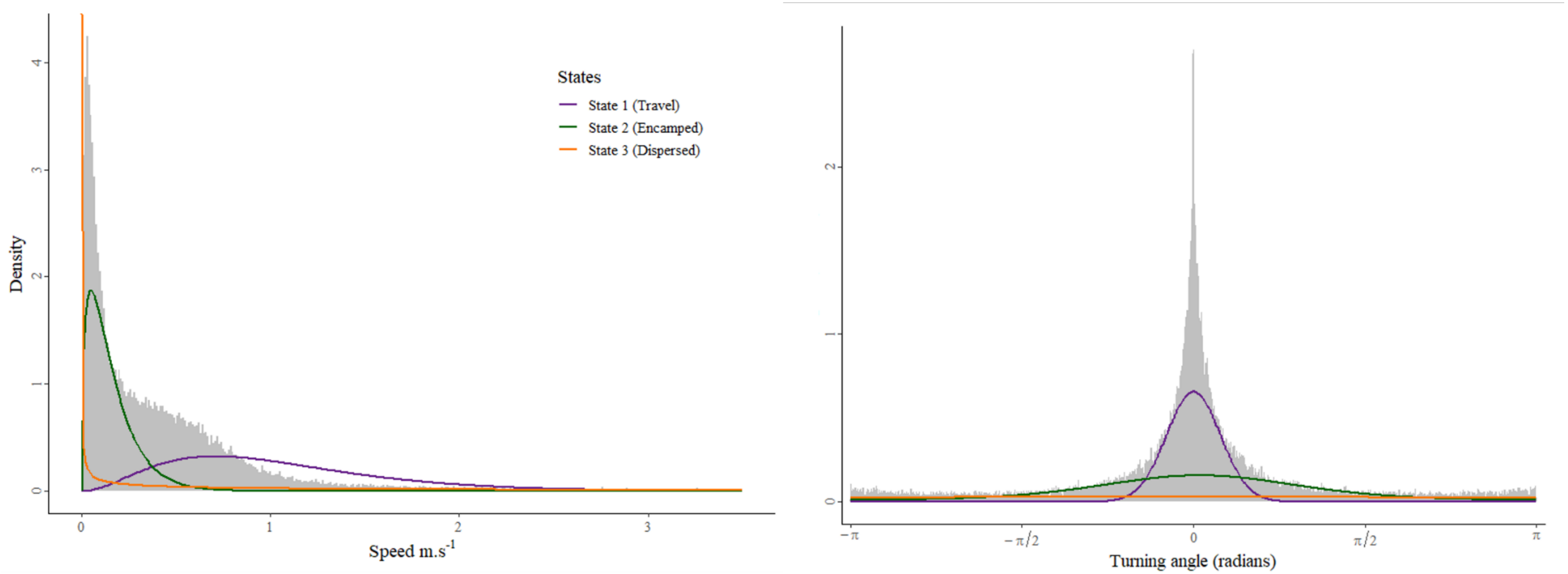


Figure 6 **State dependant distributions of step length and turning angle in hydro-space**. (left panel) step length (speed) and (right panel) turn-angle distributions. Histograms show the underlying movement parameters of the 15-minute regularised data (grey bars) and the discrete state distributions colour coded by state number and description of the hidden states.

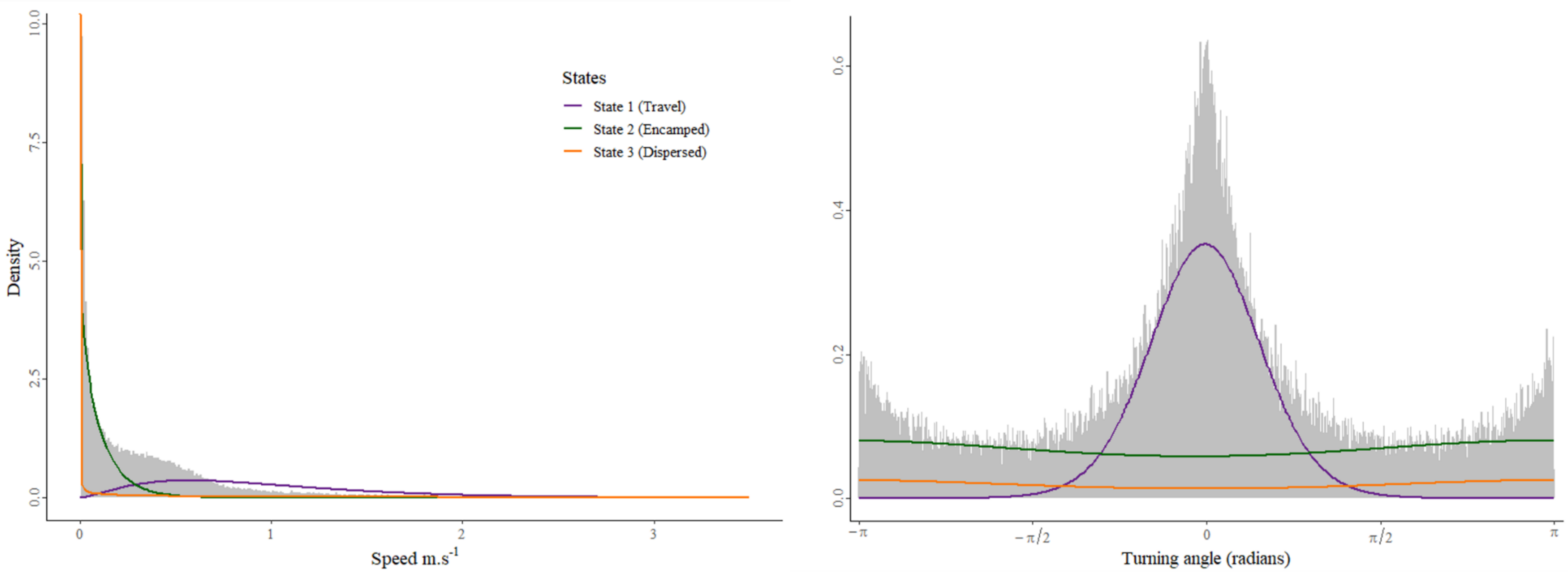


Figure 6 **State dependant distributions of step length and turning angle in geo-space**. (left panel) step length (right panel) turn angle distributions. Histograms show the underlying movement parameters of the 15-minute regularised data (grey bars) and the discrete state distributions colour coded by state number and description of the hidden states.

Track tortuosity was highest in localised and dispersed foraging states for both models; however, the difference between the states was more pronounced in hydro-spatial data compared with geo-spatial. Dispersed foraging behaviour in hydro-referenced tracks showed peaks in turn angle centred around 180° (±π) whereas localised foraging behaviour was normally distributed around 0°. Tortuosity was lowest for travelling states in both models (Figs. 6 and 7).

In terms of the environmental drivers of state-transition, the combined geo-space and hydro-space HMM (geo-hydro model) converged with the inclusion of the flow-rate covariate on the state-transition probability matrix. Final state-dependent distributions can be seen in Figure 8. Evident modality in the frequency of states was observed in the combined state-sequence where geo-spatial and hydro-spatial models concurred i.e. where geo-spatial and hydro-spatial models converged on the same Viterbi derived state assignation (Fig. 9).

Model selection retained the covariate of flow-rate on the state transition probabilities for the geo-hydro model. The most notable transition relationships were from a state where the animal was estimated to be localised foraging in both geospace and hydrospace (hereafter referred to as *Geo/Hydro localised foraging)*. The probability of switching to a hydrospatially localised-geospatially travelling state (drifting with the current) from *Geo/Hydro localised foraging* increased markedly above flowrates of 1 $m.s^{-1}$ (Fig. 10). The probability of switching to a hydrospatially travelling-geospatially localised state (swimming against a current) increased rapidly up to flowrates of ~2 $m.s^{-1}$ and then decreased rapidly towards 0 (Fig. 11). The probability of remaining in a *Geo/Hydro localised foraging* state decreased markedly with increasing flow rate to 0 at 2.76 $m.s^{-1}$ (Fig. 12). Additionally, the probability of transitioning from a known travelling state to a geo-spatially traveling, hydro-spatially dispersed state increased consistently from 0 m.s^{-1} to 4 m.s^{-1} flowrates (Fig. 13).

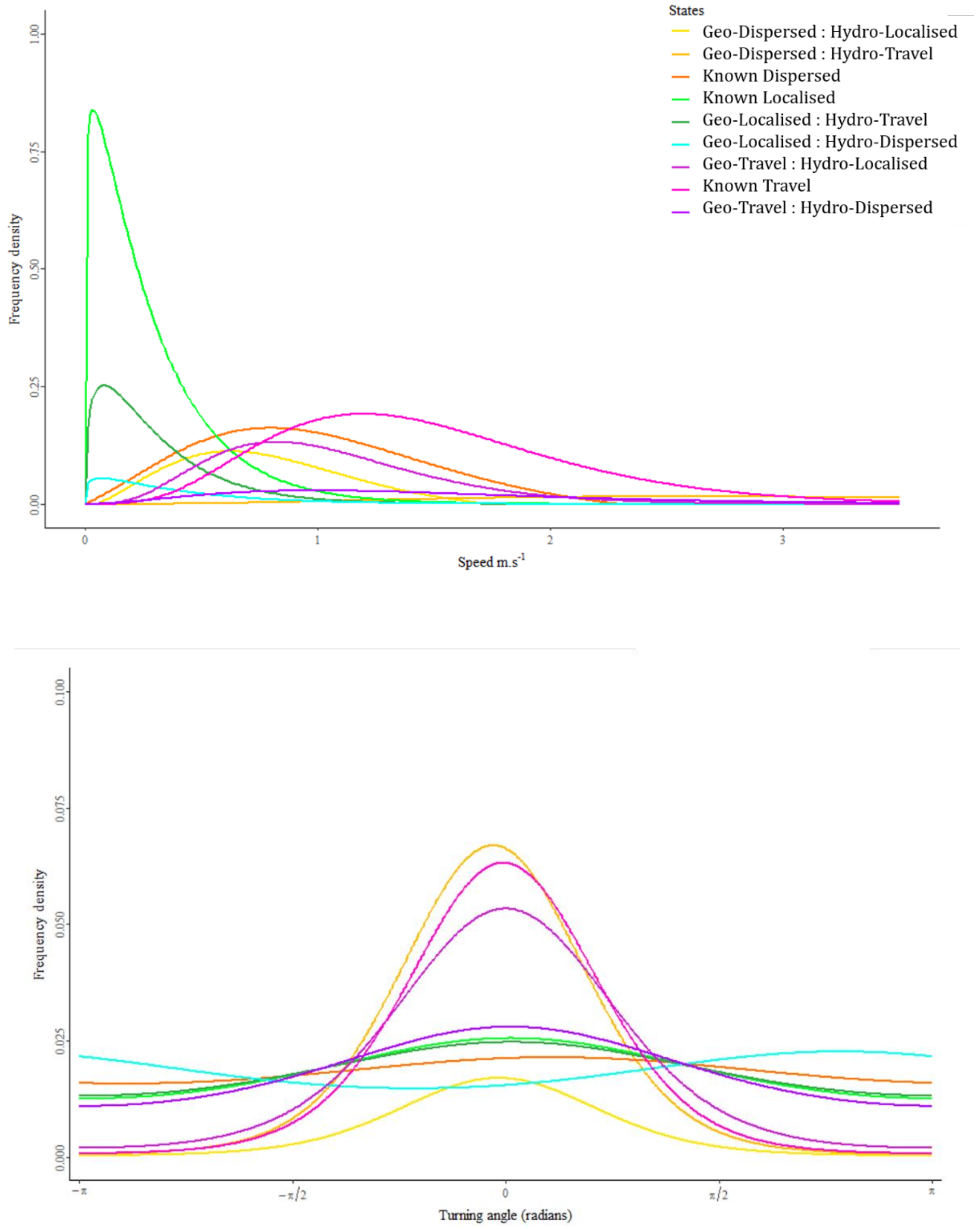


Figure 8 **State dependent distributions for the geo-hydro model.** Speed (top panel) and turning angle (bottom panel) distributions for all 9 combination states. Legend denotes the combination assignation with the three states in each model being localised, dispersed or travelling. Prefix of Geo or Hydro denotes geo-spatial or hydro-spatial state assignation, respectively. Underlying movement parameters are drawn from the geo-referenced data.

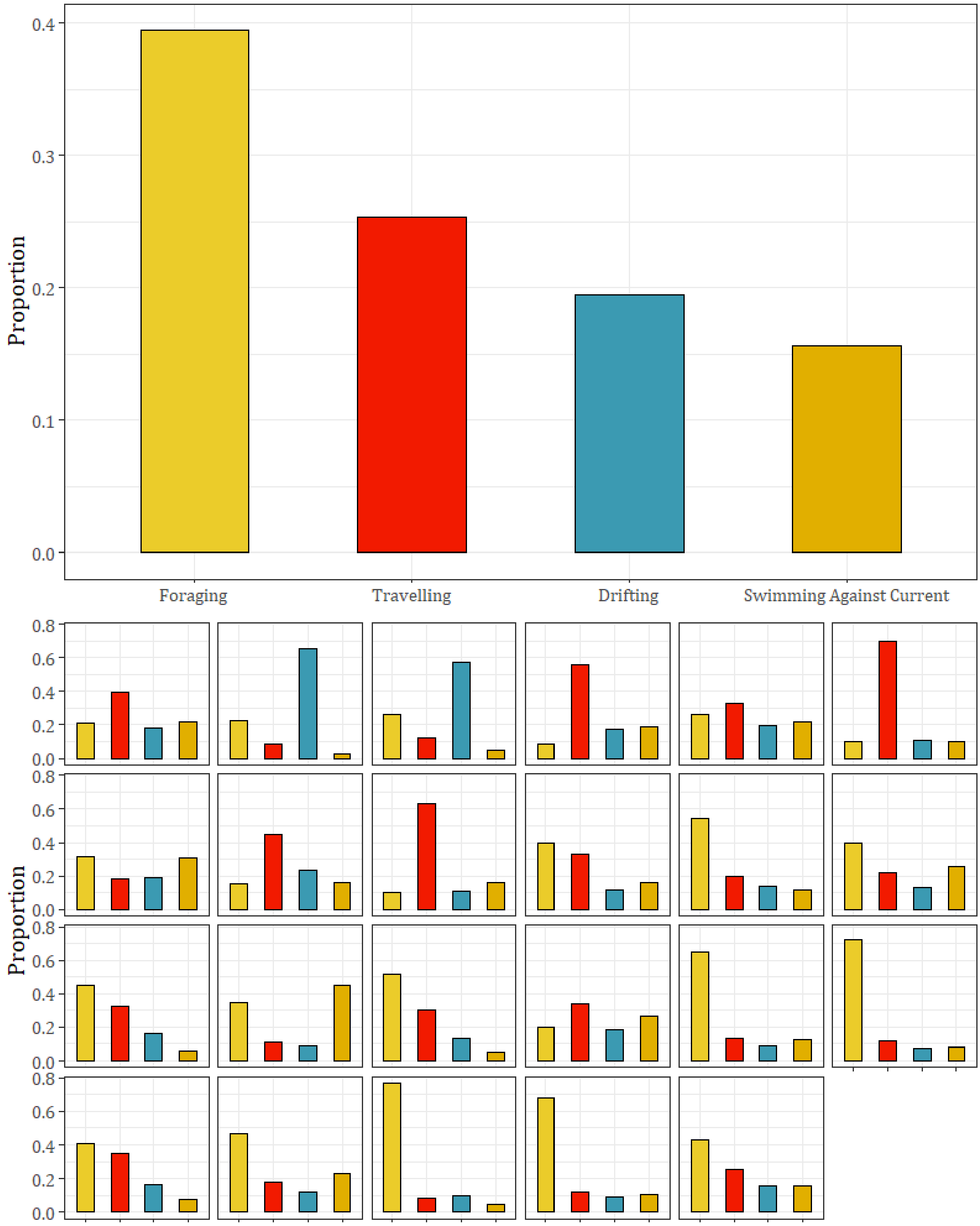


Figure 9 **Overall proportion of time spent in inferred activity across all individuals (top) and per individual (below).** Inferred foraging and travelling indicate when both geospatial and hydrospatial movements estimated localised or dispersed observed states. Drifting indicates when an animal was moving rapidly with a current with no apparent swimming assistance.

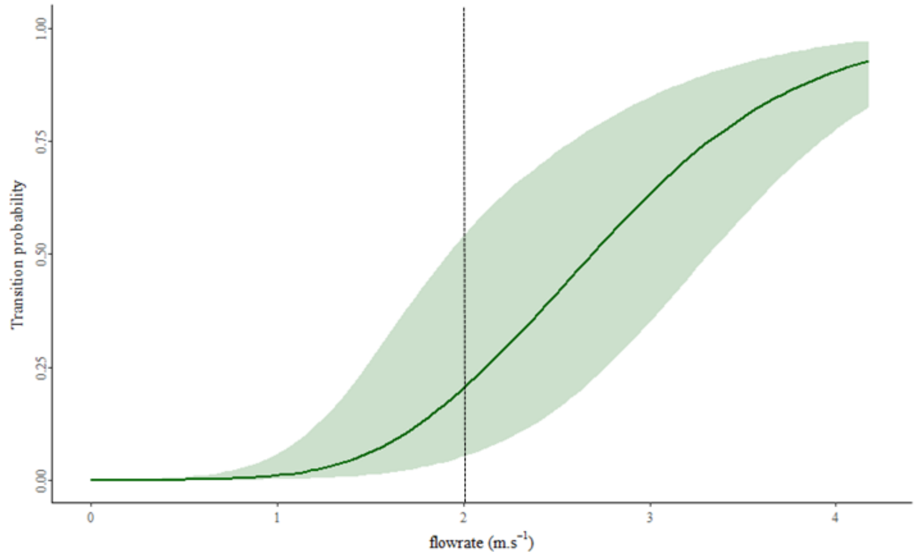


Figure 10 **Probability of transitioning from a known localised foraging state to a GeoTravel-HydroLocalised state.** Known foraging is assumed due to agreement of foraging type movement (localised) in both geo-spatial and hydro-spatial models. The figure shows the mean estimate (green line) and confidence intervals were calculated following the delta method for standard error determination in the package momentuHMM (McClintock & Michelot 2017).

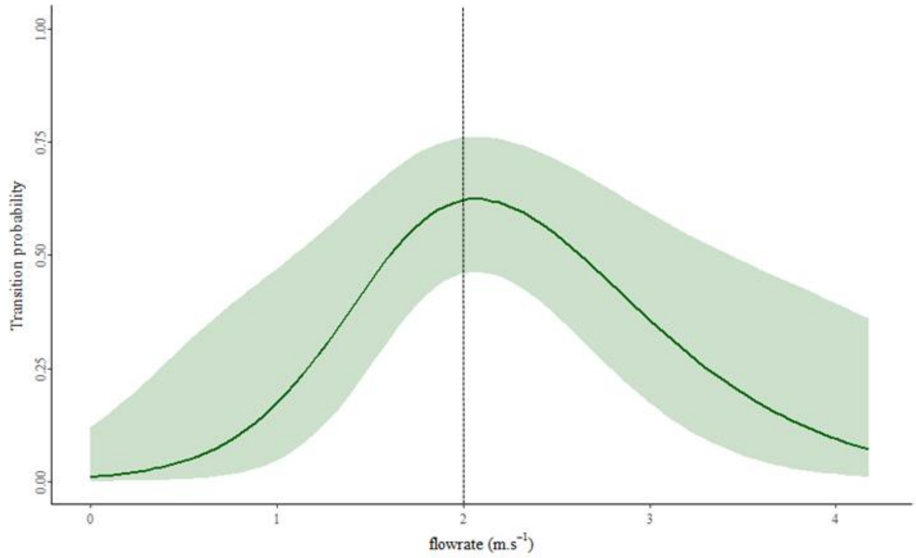


Figure 11 **Probability of transitioning from a known localised state to a GeoLocalised-HydroTravel state.** Known foraging is assumed due to agreement of localised foraging type movement (localised) in both geo-spatial and hydro-spatial models. The figure shows the mean estimate (green line) and confidence intervals were calculated following the delta method for standard error determination in the package momentuHMM (McClintock & Michelot 2017).

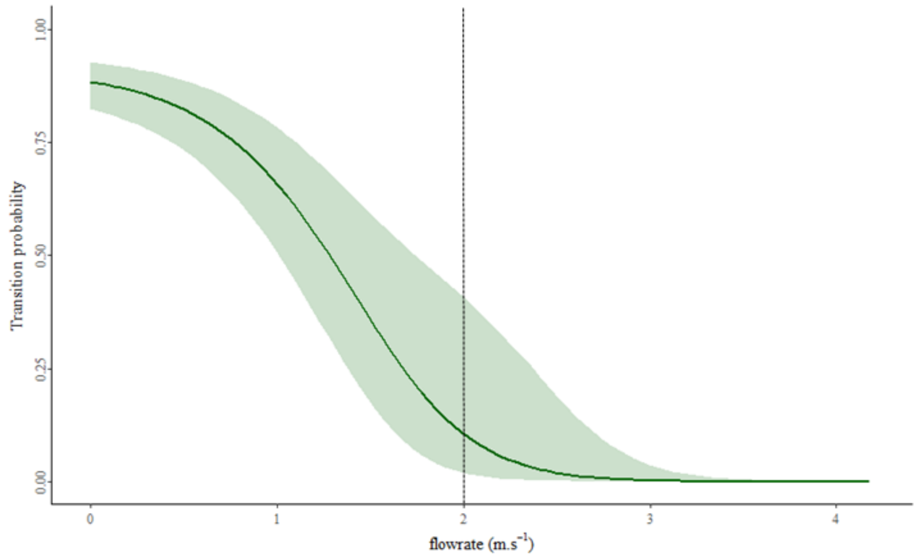


Figure 12 **Probability of remaining in a known localised state.** Known foraging is assumed due to agreement of localised foraging type movement in both geo-spatial and hydro-spatial models. Confidence intervals were calculated following the delta method for standard error determination in the package momentuHMM (McClintock & Michelot 2017).

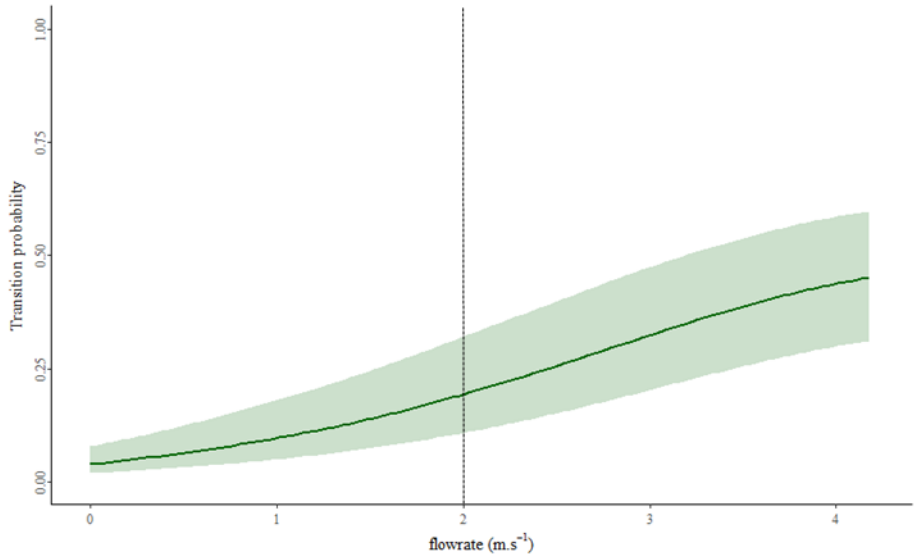


Figure 13 **Probability of transitioning from a known travelling state to a GeoTravel-HydroDispersed state.** Known travelling is assumed due to concurrence of travelling type movement in both geo-spatial and hydro-spatial models. Confidence intervals were calculated following the delta method for standard error determination in the package momentuHMM (McClintock & Michelot 2017).

2.4.3 Activity Budgets

The mean proportion of time spent foraging (classified as either in dispersed or localised states) as decoded by the Viterbi algorithm, differed by 6.4% between the geo- and hydro-space models. Across individuals, seals spent a mean of 52.1% (s.d. 11.2%) of their time foraging when estimated by the geo-spatial HMM compared to 57.5% (s.d. 14.9%) as estimated by the hydro-spatial HMM (Fig. 14). The proportion of locations that were assigned different states (travelling, localised, or dispersed foraging) in geo- and hydro-space was 37% (s.d. 11%). The difference as determined by a Bernoulli two-sample test for equality of proportions was significant between the geo- and hydro-space models ($\chi^2 = 145.1$, $p < 0.001$). When foraging locations (dispersed and localised) from both models were combined the mean proportion of time spent foraging across all seals was 71% (s.d. 9%). Locations where there was disagreement that the activity state was foraging between the geo- and hydro-space models occurred predominantly in areas of the Pentland Firth where tidal current speeds are highest (Fig. 15 and 16).

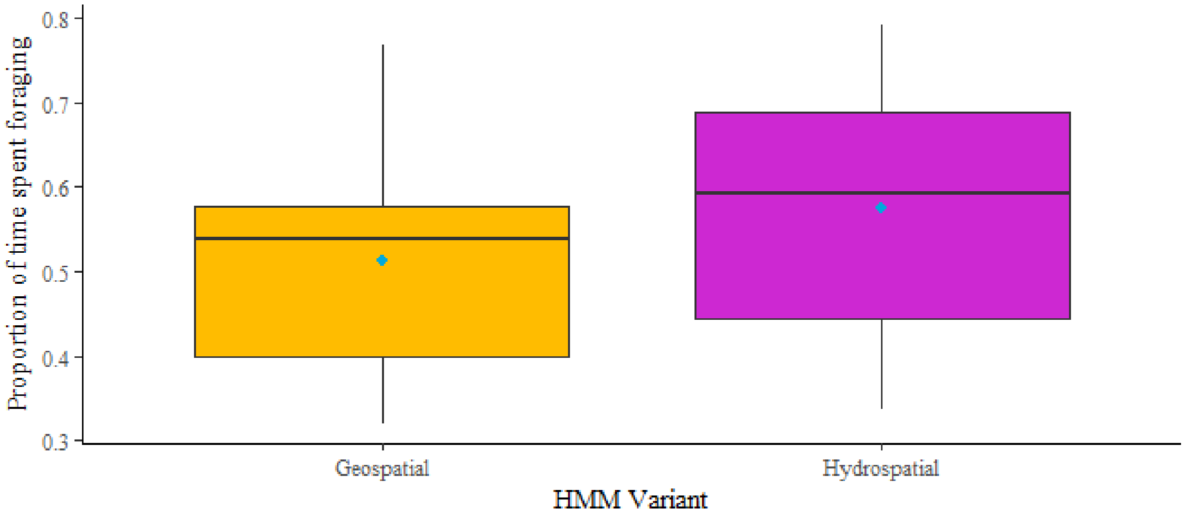


Figure 14 **Proportion of time spent foraging (dispersed or localised).** Boxplot of the estimated time spent in a foraging state in geo-spatial and hydro-spatial HMMs. Whiskers represent 95% confidence intervals; solid bars represent median value and blue dots represent means.

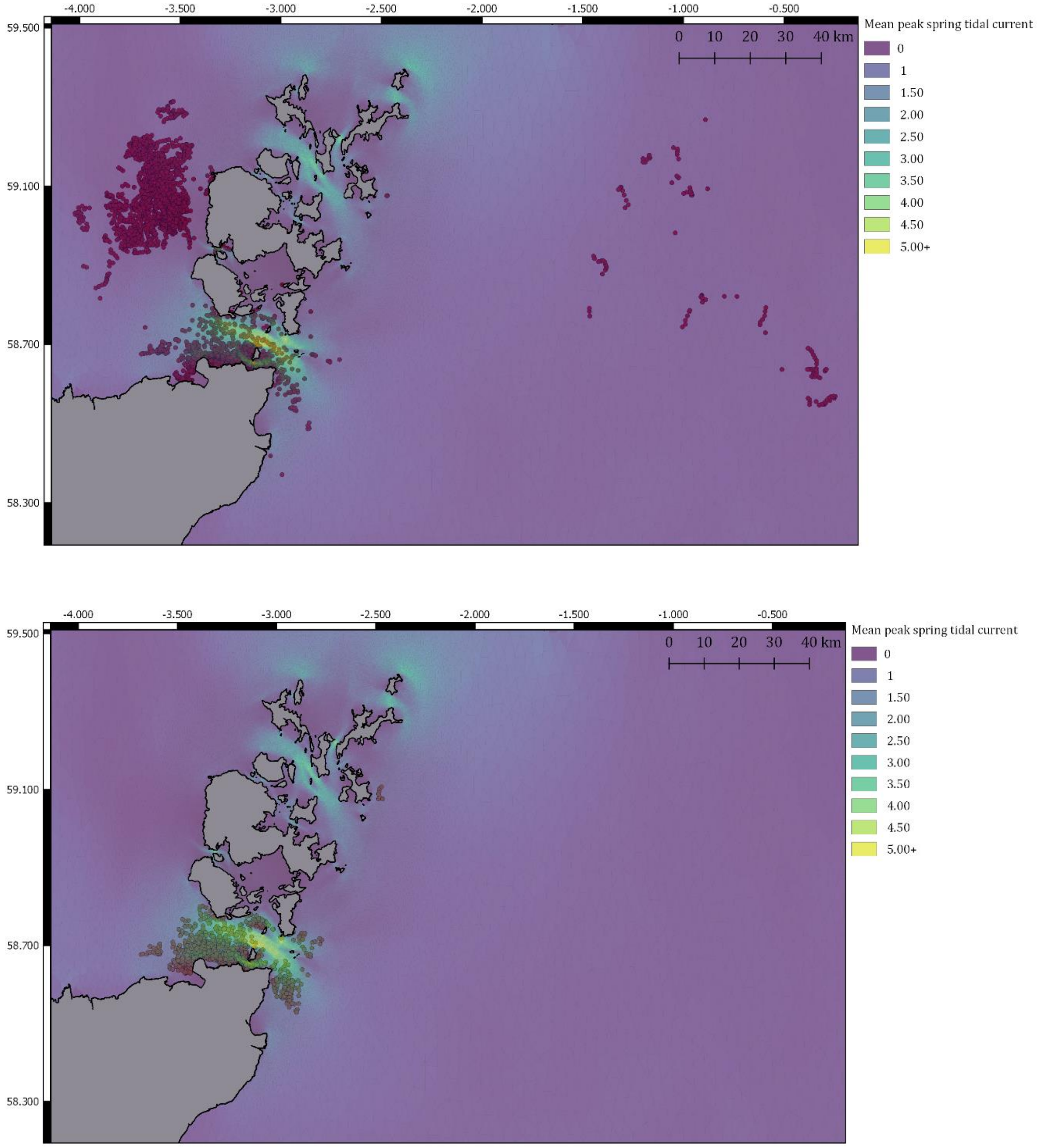
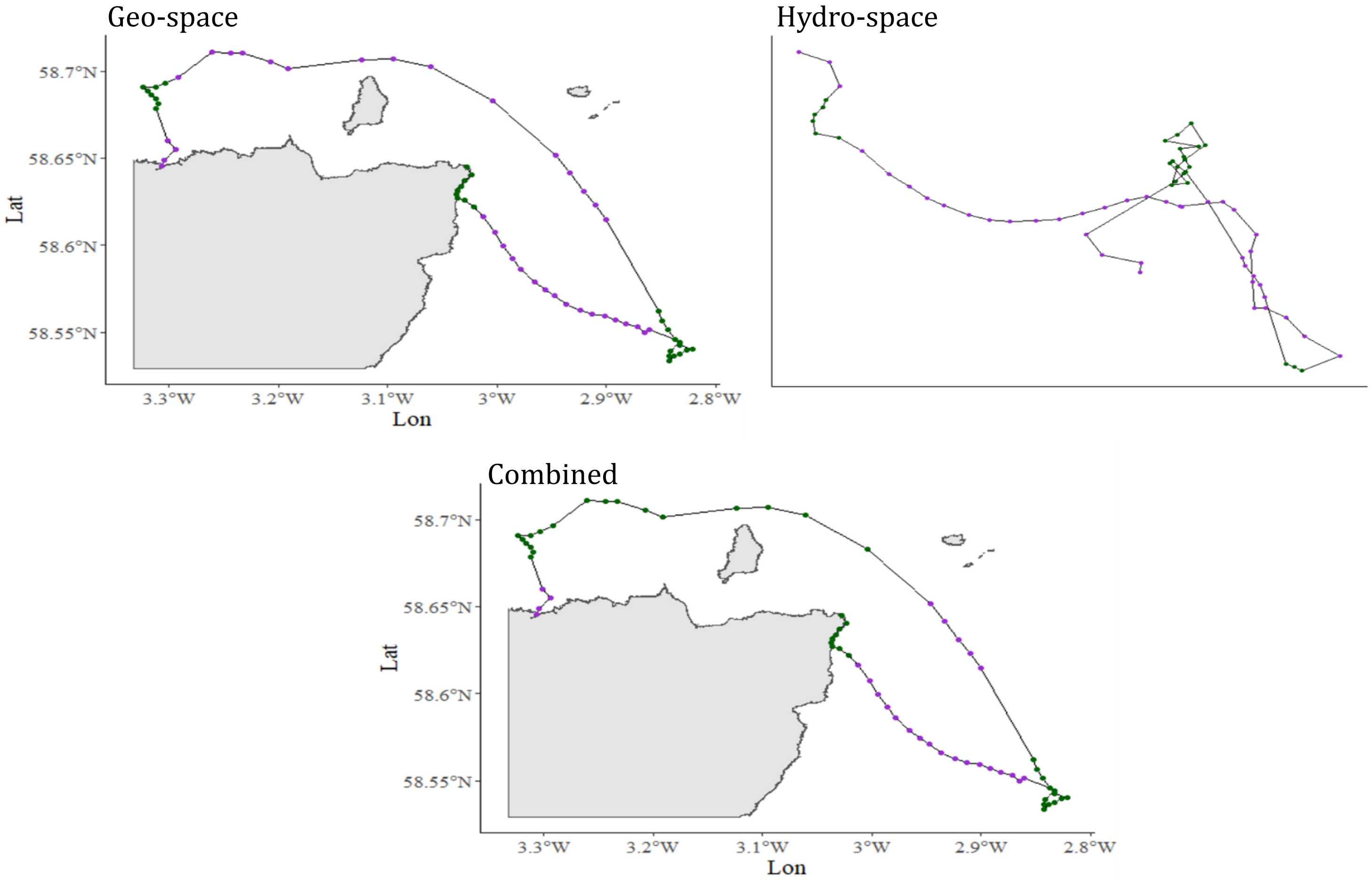


Figure 15 **Foraging locations in the geo-spatial and hydro-spatial models.** (top panel) all locations which were estimated as foraging (localised and dispersed) in both geo-spatial and hydro-spatial HMMs, and (bottom panel) all locations which were inferred as foraging in one model but not the other. Note that disparity occurs almost exclusively in energetic waters in the narrow channel between the mainland and Orkney. Locations are overlaid on a map of peak spring tidal current estimates from the Marine Scotland Scottish Shelf Model.


Geo-space

Hydro-space

Combined

Figure 16 **State assignations for an example trip.** Viterbi derived state-sequence is provided for the same trip shown in figure 5. Green points represent a localised foraging state and purple points represent a travel state. Geo-spatial (top left) and hydro-spatial (top right) state assignations are provided along with combined states (bottom) superimposed onto the geo-spatial track, assuming that both determinations of localised behaviour are informative (i.e. combining all localised states).

2.5 Discussion

This study has demonstrated that the behaviour of seals can be influenced by the underlying water movements in a tidally energetic environment, and that interpretation of foraging activity is highly dependent upon geo-spatial *and* hydro-spatial perspectives in movement data. Specifically, increased flow rates can mask discrete behaviours when only one perspective is considered due to the adjustments animals appear to make in order to remain in a foraging patch, or efficiently search for prey in energetically demanding conditions. Flow conditions also appear to significantly influence the transition between behavioural states, whereby seals either choose, or are forced to switch foraging tactics as a result of changes in tidal current magnitude.

Previous studies have highlighted the importance of accounting for environmental influences of movement trajectories (McConnell *et al.* 2002; Gaspar *et al.* 2006; Robinson *et al.* 2010; Gordine 2017). Further, some researchers have caveated their use of state-space models to identify foraging behaviour, emphasising the importance of understanding the underlying water movements (Dragon *et al.* 2012; McClintock & Michelot 2017). This work represents the first time where these issues have been addressed in a tidal stream environment.

While measured metrics such as diving and tri-axial acceleration have been used to refine state-space models of animal movement in the past, the present study represents a unique insight into the effects on extrinsic drivers of movement behaviour and activity derived using state-space models. It is also a novel example of how behaviour, inferred through HMMs, can be affected by environmental covariates. Specifically, the proportion of time spent foraging was significantly different between geo- and hydro-spatial models. This supports the use of the combined approach for activity budget determination for species foraging in dynamic ecosystems. Moreover, by assessing both the animals' geo-spatial movement as well as their swimming behaviour with respect to hydrodynamics, I have shown that seals can demonstrate significant plasticity in foraging patterns with probabilities of remaining in or transitioning to inferred foraging states changing markedly with increasing flow rates.

2.5.1 Activity budgets in geo-space and hydro-space

The formal comparison of HMMs highlighted that correcting geo-spatial movement trajectories to account for current vectors can lead to contrasting interpretations of movement. For example, seals that exhibit localised movements in geo-space during high current periods may in fact be moving significant distances through the water. In contrast, seals exhibiting little directional swimming during high current periods may exhibit highly directional movements in geo-space which would traditionally be interpreted as travelling. In other words, directional persistence can either become more or less pronounced in geo- and hydrospace as a result of incorporating tidal vectors.

Overall time spent putatively foraging was greatest when estimated through hydro-spatial movement; 52.1% (s.d. 11.2%) and 57.5% (s.d. 14.9%) for geo-space and hydrospace, respectively. While significant, considering this difference in isolation potentially masks a greater disparity; where and when foraging behaviour was predicted to occur. When overall numbers of time-steps exhibiting conflicting state assignations were compared, I observed a difference of 37%. There is, therefore, a potential misclassification rate of 37% when looking solely at geo-spatial movement in these types of habitat.

Given the importance of identifying foraging locations when looking to identify protected areas for conservation (Game *et al.* 2010; Grecian *et al.* 2012), this result could have significant importance for marine spatial planning. Foraging hotspots are considered the primary areas of interest when designating MPAs. Transit routes are less considered (Stokes *et al.* 2015), provided ample alternate options are available. However, if foraging locations for harbour seals in this habitat were based purely on geo-spatial movement patterns, conservation efforts could run the risk of misclassifying foraging areas as transit routes and consequently target only a proportion of the important at-sea areas. Previous studies of harbour seal distribution and movement behaviour in these energetic regions may warrant revisiting, should the inferences be taken as indicative of total foraging effort. By combining the inferences of the movement patterns in each perspective (geo- and hydro-space), we gain a further understanding of when and where seals may be performing discrete behaviours.

A study in a less energetic region of the UK previously found a difference in activity budgets between geo-spatial and hydro-spatial models of movement behaviour; however, this only described inferred hydro-spatial foraging not being detected in the geo-spatial model (Russell 2016). In the present study, the differences in the proportions of time spent foraging between geo-spatial and hydro-spatial HMMs, coupled with the large number of putative foraging locations that were estimated in one model and not the other (in both directions), are likely indicative of the different foraging tactics employed by individuals occupying highly energetic conditions.

A relatively frequent occurrence when the two models were combined was when seals in high currents appeared to swim rapidly in a directed fashion in hydro-space, indicative of travelling behaviour, but displayed localised movements in geo-space (GeoLocalised – HydroTravelling behaviour, Fig. 8 and 9). This may be indicative of foraging on geo-stationary prey patches. For example, at particular geographic locations there may be an increase in foraging opportunities as a function of flow speed. Prey species using currents to passively travel between sites may be funnelled through a small area, and/or, turbulent conditions peripheral to the main flow may aggregate relatively immotile prey (Sebens *et al.* 1998; Zamon 2001; Bailey & Thompson 2010). Alternatively, predictable, geostationary benthic prey patches may exist in certain high flow areas, which are not as directly affected by hydrodynamics. Seals may exploit these features by adopting a strategy of increased swim speed against the prevailing flow to avoid geographic displacement. This observation is analogous to feeding behaviour identified in harbour porpoises (*Phocoena phocoena*) in tidal races on the west coast of the UK, which swim into the current when foraging during peaks of tidal flow, and presumably take advantage of tidally concentrated prey patches (Pierpoint 2008). Certain benthic and pelagic foraging seabird species have also been observed to consistently orient themselves facing into tidal currents, surfacing in locations suggesting swimming against the prevailing flow, but often downstream (Holm & Burger 2002; Wade *et al.* 2013). Holm and Burger (2002) noted all 19 recorded flights of pigeon guillemots (*Cepphus columba*) occurred during either peak flood or ebb tides and resulted in individuals flying upstream of the current, starting a dive and surfacing again downstream. Similarly, Wade *et al*. (2002) observed that surface diving seabirds were significantly more likely to dive facing into a current than with it, often surfacing upstream of the pre-dive surface interval. The localised and dispersed states in the geo-spatial HMM showed turn angles centred around ±π rad, and possibly suggests a similar behaviour being employed by the seals, albeit seals cannot escape the prevailing flow as directly as flying birds. Foraging in high currents may result in this pattern if an individual was attempting to maintain position in geo-space and exploit a benthic foraging patch as it would likely be displaced from this location during descent and ascent phases, and when at the surface. Such behaviour would not be identified as foraging in hydro-spatial movement as the animal would appear to consistently swim unidirectionally against the current in order to maintain position and appear as though it were travelling. The prevalence of this disparity can be seen in figure 9 in the GeoLocalised – HydroTravel state. In reality, it may be that seals are forced to drift downstream while in the surface phase of a dive, swim upstream when close to the seabed (where flows are lower) and surface upstream of their previous diving location. Although this analysis provides insights into seal behaviour, it remains unclear whether seals here are utilising benthic or pelagic prey patches; however, as they spend a large proportion of time swimming against the prevailing current flow in an effort to maintain a location in geo-space, this suggests foraging given the energetic cost they are presumably incurring.

Another relatively frequent occurrence when the two models were combined was one in which geo-spatial travelling states were identified as localised foraging states in the hydro-spatial model (GeoTravel – HydroLocalised and GeoTravel – HydroDispersed states, Fig. 9). This is indicative of seals showing little directional movement within a water mass, resulting in movement behaviour that mirrored the current trajectory (Figs. 5 and 17). It also goes some way to explaining why the turn angle distributions for the hydro-spatial localised state were normally centred around 0 rather than uniformly distributed as the geo-spatial counterpart; if an animal was drifting with a current without performing much swimming, hydro-spatial turn angles would likely show a lesser degree of tortuosity. Therefore, in hydro-space, movements would be interpreted as resting or foraging behaviour i.e. slow horizontal speeds. In contrast, geo-spatial movements would be inferred as travelling. Such behavioural patterns may be a means of travelling or searching for benthic prey in an energetically efficient manner.

Alternatively, it could represent foraging on pelagic species which are also moving within the mobile water mass. In support of this, it has been demonstrated that fish assemblages peak during high flow periods (during both flooding and ebbing tidal phases), and vertical distributions of fish schools are consistently centred around mid-water in the inner sound of the Pentland Firth (Fraser *et al.* 2018). It is therefore possible that, during high flow periods, seals could benefit from reduced energetic costs by switching from foraging on geo-stationary, benthic prey, to foraging on pelagic species. This behaviour has been observed in other species. For example, Bennison *et al.* (2019) observed that in Atlantic puffins (*Fratercula arctica*); movement tracks showed no indication of area-restricted search behaviour (in geo-space) during entire foraging trips and foraging bouts appeared to be similar to that expected by planktonic advection by the prevailing tidal current.

Previous studies have used concurrent dive data to identify prolonged surface intervals and differentiate foraging behaviour from resting behaviour (McClintock *et al.* 2013; Bestley *et al.* 2015; Russell *et al.* 2015; McClintock *et al.* 2017). Although dive behaviour was not formally used in the current HMM analyses, the method by which haulouts were detected and removed is likely to have removed at-sea resting behaviour close to (<0.25km) haulout sites (see Methods) which is commonly observed in harbour seals

(McClintock *et al.* 2013; Ramasco, Biuw & Nilssen 2014; Russell *et al.* 2015). This combination of factors is likely to have reduced the misidentification of resting behaviour as foraging. However, this question is addressed in further detail in Chapter 3 of this thesis with a temporally resolved analysis of dive data.

2.5.2 Foraging behaviour as a function of tidally driven currents - remaining in a foraging state

While geo-spatial prey encounter rates may increase in areas of high tidal current, the ability to exploit this resource is only valuable to a predator if its own locomotory capabilities allow it to remain resident in geo-space. The maximum burst speed of a harbour seal is approximately 4 $m.s^{-1}$ (Williams & Kooyman 1986) but it is unlikely that seals can efficiently sustain swim speeds greater than 1.5 $m.s^{-1}$-2 $m.s^{-1}$ (Hind & Gurney 1997; Gallon *et al.* 2007) for prolonged periods; it is therefore likely that area restricted search behaviours would be less observed in geo-space as water speed increases above 1.5 $m.s^{-1}$. This may explain the peak in the probability of transitioning from a known localised foraging state to a state where the animal is localised in geo-space but traveling in hydro-space at speeds approaching 2 $m.s^{-1}$ (Fig. 12). At current speeds below the minimum cost of transport speed for an 87 kg harbour seal (~1.3 $m.s^{-1}$, mean mass for seals tagged in this study), it should be relatively cost-effective to forage at a benthic or pelagic prey patch. As current speeds increase above ~1.5 $m.s^{-1}$, oxygen consumption increases exponentially if the seal attempts to remain in the same geo-spatial location (Williams & Kooyman 1986; Thompson, Hiby & Fedak 1992). In theory, a seal would have to adjust its locomotory strategy to continue to exploit this patch by either swimming faster against the current (and incurring a greater energetic cost), or by utilising micro-scale hydrodynamic features such as eddies, or static, bathymetric objects to reduce apparent flow. Such strategies (Karman gaits) have been shown to be used by fish to maintain position in rivers (Liao *et al.* 2003; Liao 2007). The results from this study suggest this change in movement behaviour when current speeds increase. As current speeds exceed ~2m.s^{-1}, the probability of transitioning to geo-spatial travelling and hydro-spatial localised foraging increases significantly. This suggests that, in these flow rates they are probably adopting a drifting behaviour to allow assisted transport to either a) forage on dynamic prey resources rather than static benthic ones or b) use the current for passive transport from one patch to another. What is likely is a combination of both these strategies, given the potential entrainment of prey species in currents and the inferred foraging behaviour often observed after drifting periods cease (e.g. Fig. 17). To date, there has been little evidence of pinnipeds drifting in currents speeds greater than their maximum swimming speeds. Thompson (2012) noted juvenile grey seals drifting with currents and consistently diving to the seabed presumably foraging while moving passively along the horizontal plane. Campagna *et al.* (2006) and Della Penna *et al.* (2015) both recorded southern elephant seals (*Mirounga lenonina*) passively drifting with large scale currents and eddies. Given the inferred productivity in these regions and that associated dive behaviour suggested foraging patterns (Campagna *et al*. 2006), it is likely that this passive behaviour was also related to foraging. The drifting behaviour identified in the present study, with localised hydro-spatial movement, similarly indicates that little energy is being expended by the seal to move along the horizontal plane. However, there is a key difference between these two studies, in that harbour seals, unlike elephant seals, are not capable of swimming faster than all of the flow rates they are observed to experience. Drifting could therefore be seen to be forced rather than sought. However, given that the probability of transitioning to a drifting state continues to increase with increasing flow rate, it seems clear that seals do not often attempt to escape these currents (by swimming cross-current which would produce less directed geo-spatial movement) and so remaining entrained within them can be seen as somewhat preferential. With the likelihood that prey species will also be similarly entrained by currents it may follow that harbour seals use this to their advantage and forage while drifting. It is also possible the seals are allowing currents to transport them through environments and periodically diving to the bottom to search for suitable prey patches. However, given the dive behaviour presented in Chapter 3, this seems unlikely.

2.5.3 Foraging behaviour as a function of tidally driven currents – transitioning from travelling to foraging

The observed changes in the probability of transitioning into or remaining in a foraging state (whether geo-spatial or hydro-spatial) with increasing flow rate suggests that tidal currents are a significant driver of harbour seal at-sea behaviour. It is likely that this switch occurs as a bottom-up response to increasing prey densities resulting from bio-physical coupling with complex, temporally heterogenous hydrodynamic features (Zamon 2001; Zamon 2003). Indeed, the probability of switching from travelling to foraging (first in geo-space and then in hydro-space) continued to increase up to the maximum current speeds shown to be used by the seals. The relatively high density of seal usage within the Pentland Firth channel where strong currents are observed (Fig. 2) may explain this behaviour as being a response to an apparent bottleneck effect, concentrating tidally predictable prey sources which are responding to localised aggregations of zooplankton (Zamon 2001; Pierpoint 2008; Bailey & Thompson 2010). A study of Pacific harbour seals found an increased proportion of salmonid capture events during increasing flooding tides in a narrow channel when compared to other tidal phases which suggested a tidally mediated prey encounter rate (Zamon 2001). Similarly, Hastie *et al*. (2016) observed an increase in harbour seal presence during periods of peak flow (~2 hours before high water) in narrow channels on the west coast of Scotland, where flow speeds can reach in excess of 4 m.s^{-1}. The results presented in the present study suggest a similar pattern whereby individual seals preferentially switch to a foraging state when subjected to faster flowing currents, possibly to exploit prey species which are subject to the water movement which aggregates or disorientates them. However, given the probability of remaining in a specific geo-hydro foraging state also changes with increasing current strength, it is likely that multiple foraging tactics are used to forage in tidally dominated habitats.

Wilson (2014) found that diet composition for harbour seals within the Orkney management unit (which encompasses the Pentland Firth haulouts) shifted seasonally between being dominated by sandeels (*Ammodytes spp.*) during the spring and summer months and pelagic fish such as herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) in the autumn. Further, it was clear that seals within this management unit showed elevated variability in diet when compared to other populations around the UK. This supports the foraging plasticity observed here, both by the transition probabilities as well as the geographic locations of the different behavioural states.

2.5.4 Caveats

As primarily benthic foragers, harbour seals spend the bulk of their time foraging at depth, surfacing briefly to breathe and occasionally rest (Bjørge *et al.* 1995; Tollit *et al.* 1998; Russell *et al.* 2015). Consequently they minimise the amount of time spent exposed to surface drag (Thompson & Fedak 1993) and, if foraging on demersal species, are subjected to currents considerably less than maximum flow rates observed in mid-water (Vogel 1994). It may follow that the apparently high energetic demands of seals observed foraging in strong currents are being avoided by spending extended periods of time in flow speeds markedly different from the mean flow in the water column. This likelihood is further augmented by the fact that the transition from known foraging to a geo-spatial localised – hydro spatial travelling state continues to increase above the assumed minimum cost of transport speed for harbour seals in this study. This would not be identified in the model presented given the use of depth averaged currents to correct the geo-referenced location data. This issue is addressed in further analyses in Chapter 3.

The hydrodynamic model used to estimate current strength did not include contemporary meteorological forcing data to augment model predictions. While broad oceanographic processes are somewhat predictable, fine-scale features such as flow regimes and coherent structures in tidal streams are heavily subject to external forcing such as wind stress. Therefore, the flow speeds and directions experienced by the seals may have been subject to a degree of error. However, during development, the model underwent rigorous validation using ADCP data from multiple years and therefore, in lieu of extending the model with contemporaneous ADCP and meteorological data, I am confident the broad patterns of flow have been accurately captured. Further the temporal resolution of the raw seal data was far finer than that of the hydrodynamic model; ~3 minutes compared to hourly averages. This could yield significant mismatches in flow speed experienced by the seals as averages may encompass peaks or troughs in the tidal cycle and therefore under or overestimate the external forcing imposed on the individual, respectively.

The presence of small-scale oceanographic features such as eddies was also not resolved in the underlying hydrodynamic model and these could equally serve to help harbour seals exploit fast flowing currents by providing alterations in assisted trajectory. The rotational forces produced by eddies may allow seals to remain geo-stationary in currents without the need to expend energy, equal to the force of the current, swimming against it. While this may not change our interpretation of activity budgets, it would provide a potentially different explanation of the way in which seals are foraging. Future studies could seek to resolve this issue by using high resolution dive data and 3-dimensional current profiles to examine precisely how seals interact with tidal currents, however, this was outside the scope of the present study. In addition, accompanying acoustic doppler current profiling (ADCP) casts should be used in tandem with movement data collection to calibrate any flow models and alleviate the issue of assuming the hydrodynamic model predictions represent reality. Such data could then be used to robustly investigate how observed states differ in multiple dimensions, e.g., how dispersed and localised behaviours differ in terms of diving behaviour. Inclusion of multiple data streams which aid interpretation of locomotory activities such as tri-axial accelerometery, speed sensors and magnetometry could help extract additional behavioural states associated with foraging (Leos-Barajas *et al.* 2017b). This could provide further insight into the effects of water currents on the 3-d behaviour of diving predators and address a major source of error in 3-dimensional dive reconstruction (Shiomi *et al.* 2008; Iwata *et al.* 2015).

2.6 Conclusions

The extension of a commonly used method to infer behaviour from movement data with a high resolution hydrodynamic model has provided a novel perspective on the complexities of harbour seal at-sea behaviour. The use of this technique will aid future studies on animal movement where trajectories may be significantly affected by the movement of their surrounding environment. Here, harbour seal foraging behaviour was correlated with tidally energetic processes. Further, the apparent foraging movement parameters changed as a function of increasing flow rate suggesting a high degree of behavioural plasticity in seals and provides new insights into how behavioural strategies have developed in tidally energetic habitats.

Chapter 3

Plasticity in diving behaviour in a tidal stream environment suggests seals maximise efficiency in varying flow conditions

"I used to bullseye sandeels with my diving behaviour back home, those currents weren't much bigger than 2 m.s^{-1}"

3.1 Abstract

For air-breathing, diving predators, maximising efficiency at depth is a key component in determining individual fitness. With increasing spatial and temporal habitat heterogeneity comes an increasing need to develop multiple foraging strategies to account for difference drivers of movement and prey fields. Tidally energetic habitats present several challenges to the movement of predators in both the horizontal and vertical dimensions. However, they are often areas of predictable prey sources making them attractive if the predator can successfully navigate the pronounced flows. This study used location and dive data from animal-borne tags to quantify the diving behaviour of harbour seals (*Phoca vitulina*) in a tidal stream environment. Clustering of dives showed behavioural classifications which reflected those found from a horizontal movement analysis of the same individuals (Chp. 2). This indicated that changes in behaviour are displayed in both variations in horizontal and vertical movements. Animals appeared to descend faster and spend longer at depth with increasing current speeds. Further, diurnal patterns showed a shift towards benthic diving at night and pelagic foraging during the day with an additional, significant seasonal pattern in dive depth. Observed relationships between dive behaviour and hydrographic conditions highlight the importance of tidal currents for seals foraging in tidally energetic habitats and suggests that such habitats confer not only a series of significant challenges, but also a series of unique benefits to seals.

3.2 Introduction

A central question in ecology is how animals find and exploit food in dynamic and variably predictable habitats (Stephens & Krebs 1986). When studying air-breathing, marine predators this question presents some significant and unique challenges as foraging behaviour generally occurs underwater and can rarely be directly observed. However, information on movement patterns and depth use in these species is key to understanding their foraging behaviour at a range of two-dimensional and three-dimensional scales (e.g. Thompson & Miller 1990; Thompson *et al.* 1991a; Fossette *et al.* 2008).

The marine environment is characteristically heterogenous, both temporally and spatially. Flexible foraging tactics are therefore likely to be crucial for marine predators (Stephens & Krebs 1986); the availability of prey patches can vary with constantly changing environmental conditions (Johnson, Parker & Heard 2001; Launchbaugh & Howery 2005; Weimerskirch 2007; Furness & Greenwood 2013; Day *et al.* 2019) and predators may need to match this with adaptations to their foraging tactics and/or prey sources. Populations inhabiting temporally dynamic environments may therefore demonstrate generalist tendencies such as broad diet compositions and habitat preferences, while exhibiting a number of specialist behaviours to allow individuals to exploit a range of different prey sources (Gilmour *et al.* 2018) or foraging conditions. For example, recent studies have noted that marine predators are often observed foraging over long periods in areas of high tidal currents, where energetic demands of locomotion can be high if the desired orientation is against the prevailing flow (Wade *et al.* 2013; Hastie *et al.* 2016). Consequently, a variety of foraging tactics might be expected to occur given the differences in flow conditions over tidal cycles, especially when sustained flow speeds can exceed the burst speeds of the individuals observed. Analysing movement data with concurrent environmental data can therefore serve to disentangle complex behavioural ecology questions (Nathan *et al.* 2008; Dodge *et al.* 2013) which can have strong conservation implications when forecasting the effects of potential change in environmental conditions.

The depths at which air-breathing predators can forage is ultimately limited by the physiological constraints of diving (i.e. proximity to the surface and breath-hold capacity; Kooyman & Ponganis 1998). Dynamic environments potentially confer an additional challenge in that they're often moving at speeds greater than the animal's own swimming speeds. This aspect also makes the analyses of behaviour challenging given the highly variable nature of their movements; however, this also makes them particularly interesting when considering ecological questions which relate to bottom-up processes and when developing mechanistic approaches to understanding the marine environment.

Harbour seals (*Phoca vitulina*) are one of the most widely distributed phocids, ranging across northern temperate and polar waters in both the Atlantic and Pacific oceans (Bigg 1969; Thompson 1989). They are found in many tidally energetic areas across their largely coastal habitats (Zamon 2001; Jones *et al.* 2015; Jones *et al.* 2017). Significant research effort has been devoted to the assessment of their broad spatial distributions (Jones *et al.* 2015), population trends (Thompson, Lonergan & Duck 2005; Thompson *et al.* 2019), two-dimensional inferences of foraging behaviour (Thompson & Miller 1990; Thompson *et al.* 1991b; McClintock *et al.* 2013; Russell *et al.* 2015), and vital rates such as survival and fecundity (Cordes & Thompson 2014). However, there is a distinct paucity of information on the influence of static and dynamic environmental covariates on diving behaviour (Blanchet *et al.* 2015). Previous studies have shown that harbour seals exhibit a high proportion of benthic and demersal diving to depths of between 15 – 400 m (Bjørge *et al.* 1995; Tollit *et al.* 1998; Gjertz, Lydersen & Wiig 2001; Blanchet *et al.* 2015). However, foraging dives to mid-water depths have also been observed in some populations (Tollit *et al.* 1998; Wilson *et al.* 2014b; Blanchet *et al.* 2015). This variability is reflected by their varied diet (Bromaghin *et al.* 2013; Luxa 2013; Wilson & Hammond 2019) and the occurrence of mid-water foraging dives appears to occur in areas where prey availability is assumed to have a higher temporal and spatial variation (Wilson *et al.* 2014b; Blanchet *et al.* 2015; Wilson & Hammond 2019). Further, distinct seasonal trends in dive characteristics have been repeatedly observed and have been suggested to be linked to prey migration, meteorological and oceanographic variations, (Blanchet *et al.* 2015), age (Bowen, Boness & Iverson 1999), and breeding phenology (Wilson *et al.* 2014b).

Given the variation in water current strength (and direction) across the water column, it is possible that diving behaviour may be more variable in areas demonstrating a greater range of oceanographic conditions. Marked temporal variations in oceanographic conditions has also been suggested to influence variations in prey availability relative to water depth and may drive the observed variety in the diet of generalist predators (Andersen *et al.* 2013) as harbour seals have been suggested to be. However, to date, no studies have determined the effects of water movement on diving behaviour.

One of the most dynamic marine environments around the UK is the Pentland Firth, a channel between the north coast of Scotland and the Orkney Islands (Neill *et al.* 2017) which connects the North Sea and the North Atlantic and experiences relatively large tidal currents. Harbour seals are present here throughout the year and regularly use the most tidally-energetic areas of the region (Jones *et al.* 2017; Thompson *et al.* 2019). This study aims to quantify harbour seal diving behaviour and relate this to a range of static and dynamic environmental covariates to establish whether seals show exhibit changes in diving behaviour in response to environmental conditions on a range of temporal scales. Further, models of horizontal movement often suffer from a lack of empirical data to justify the assumptions of underlying behaviours. Diving behaviour can therefore help to elucidate and validate the underlying behavioural states associated with the observed processes, given our prior knowledge of seal foraging behaviour and diet composition. This chapter therefore also aims to understand the functional mechanisms underlying the diving behaviour by linking information on behavioural activity states based on horizontal movement (Chp. 2), dive behaviour, and a range of environmental co-variates.

3.3 Methods

A combination of GPS tags and time-depth recorders (TDRs) were used to 1) measure the diving behaviour of seals in a tidally energetic habitat, 2) relate these behaviours with behavioural state assumptions from the movement analysis in Chapter 2, and 3) quantify the effects of a range of temporal and spatial covariates on diving behaviour. The overall aim was to determine whether the plasticity in movement behaviour observed in Chapter 2 is reflected in seal diving data.

3.3.1 Telemetry Data

Fastloc® GPS/GSM tags (SMRU Instrumentation) were deployed on 14 harbour seals in 2011 and TDR/UHF tags (Pathtrack Ltd.) were deployed on 40 harbour seals over four deployments in 2016, 2017 and 2018 in the Pentland Firth, Scotland (Fig. 1). Seals were caught on, or close to, haul-out sites using tangle nets in the water or hoop-nets on land. All Seals were weighed and then anesthetised with intravenously administered Zoletil-$_{100}$® at a dose rate of 0.005 ml.kg^{-1} prior to further handling (Sharples *et al.* 2012). GPS tags were glued to the fur at the back of the neck and TDRs were glued to the fur at the apex of the back using Loctite 422™ cyanoacrylate adhesive. All capture and handling protocols were carried out under UK Home Office licences #60/4009 and #70/7806 in accordance with the Animals Scientific Procedures Act 1986.

Dive data were processed onboard the tags and transmitted in different formats for the two tags types. For the GPS/GSM tags, pressure values were recorded every 4 s and discrete dives were identified in-situ when the pressure sensor recorded a depth of ≥ 1.5 m for > 8 s. Depth traces for discrete dives were then abstracted to 11, regularly spaced, linearly interpolated points (inclusive of pre- and post-dive surface points) on-board the tag prior to transmission (Fedak, Lovell & Grant 2001).

TDR/UHF devices recorded depths at regular 10 second intervals throughout the lifespan of the tag. Continuous depth records were then transmitted to terrestrial, UHF receiving base-stations (see Chp. 2) whenever the animals hauled out. Post-processing was required to determine discrete dives in the UHF data. To ensure that data between tag types were broadly comparable, a bespoke algorithm was written in the programming language *R* to produce dive records emulating the format used by the GSM tags. Firstly, a zero offset correction of depth was applied using the R package *diveMove* (Luque 2007) due to the possible drift over time in pressure sensors (Luque & Fried 2011). Discrete dives were then classified when a depth record of >5 m was recorded for at least 10 seconds (i.e. 2 consecutive dive records). A larger dive-depth classification threshold was necessary given the comparatively reduced temporal resolution of the raw UHF data; using a 1.5 m threshold resulted in multiple dives being classified as single dives as the seal had time to record a depth value, surface and descend back to below threshold depth before the next depth value was recorded. This approach is highly conservative as multiple shallow dives could be discarded but it is necessary to ensure confidence in the final data-set by reducing the likelihood of including multi-dive metrics which would inflate certain estimates such as dive time, and proportion of time spent in discrete phases.

To make behavioural inferences, dives were separated into four distinct phases (surface, descent, bottom, and ascent). Descent and ascent phases were first extracted by fitting a 4th order polynomial to the dive depths (or inflection points for the GSM tags) and attributing a transit period to any vertical speeds exceeding a slope which equalled 0.3 $m.s^{-1}$ (Luque 2007; Jouma'a *et al.* 2016). This differs from previous methods of assigning dive phases whereby any period greater than 80% of the maximum dive depth is considered a bottom phase (e.g. Schreer, Kovacs & Hines 2001; Sala *et al.* 2011; Krause *et al.* 2016). Importantly, the method presented here allowed for multiple bottom phases in a single dive which may represent prey encounters during transit to and from the maximum dive depth. Any period outside of the assigned descent and ascent periods was determined as a bottom phase. For the UHF-TDR tags, surface phases were considered as the time between successive depth records shallower than 5 metres. This likely overestimates the time spent at the surface between dives as it discounts shallow dives above the threshold; however, the assumption considers that shallow dives and surface periods may satisfy a similar biological function through recovery from dives.

The metrics which were extracted from these dives (dive depth, proportion of the water column used, proportion of time in the bottom phase, descent rate, bottom-phase wiggliness, bottom-phase duration, dive duration and post-dive surface duration) and their definitions are provided in Table 1. All variables except bottom-phase wiggliness were calculated for both tag types; reduced resolution throughout the dive from the GSM tags due to pre-transmission data abstraction precluded the ability to robustly estimate fine-scale activity such as this. Consequently, only UHF-TDRs were used for the principle component analysis. To ensure that analyses of dive data were not confounded by male display dives during the breeding season (Van parijs *et al.* 1997; Van Parijs, Hastie & Thompson 1999), data collected during the pre-breeding and breeding periods were excluded; Julian day 152 (June 1st) to 243 (August 31st).

3.3.2 Environmental Data

To test the relative influence of tidal currents on diving behaviour, a series of other environmental variables were included in an analyses of individual dive metrics. Candidate independent variables were chosen based on a literature search of important drivers of phocid diving and foraging behaviour in shelf-sea and coastal ecosystems (Bjørge *et al.* 1995; Tollit *et al.* 1998; Gjertz, Lydersen & Wiig 2001; Beck, Bowen & Iverson 2003; Hastings *et al.* 2004; Jessopp, Cronin & Hart 2013; Photopoulou *et al.* 2014; Wilson *et al.* 2014b). To associate dive metrics with environmental covariate data, each dive was given a location based on adjacent GPS location fixes. The mid-point between dive start and end times was matched to a linearly interpolated track between successive GPS locations for the same animal, providing an estimated location for each discrete dive. If the mid-point of a dive was more than 10 minutes from the nearest GPS fix, it was excluded from further analyses.

Depth averaged tidal current data were extracted for each dive location from the Pentland Firth and Orkney Waters sub-domain of the Marine Scotland Scottish Shelf Model (Wolf *et al.* 2016). For details of the model and location matching protocols see Chapter 2. Bathymetry data were also assigned to each dive location using the European Marine Observation and Data Network (EMODnet) 1/16 * 1/16 arc minutes (~ 115 * 115 m) regular grid Digital Terrain Model (DTM) for European Waters (EMODnet 2016). Each bathymetric depth was converted to a temporally resolved value which accounted for tide height. Firstly, estimated bathymetric depth at lowest astronomical tide (LAT) values provided by the EMODNet DTM were converted to mean sea level using the Vertical Offshore Reference Frame (VORF) correction. Mean sea level was then corrected for each dive to account for sea level height change as a function of tide using temporally resolved tidal cycle prediction as estimated using the POLPRED tidal prediction model. The proportion of the water column used in each dive was then calculated as the maximum dive depth divided by the estimated bathymetric depth. After calculation, a proportion of dives (~6%) registered depth values that were below the estimated bathymetric depth. For these dives, proportion of the water column dived to was corrected to 1.

Diving behaviour has been shown to be correlated with target prey type and prey encounter rate (Sato *et al.* 2004; Le Bras *et al.* 2016); in the absence of concurrent, temporally resolved prey distribution data, sediment type has been used as a useful proxy for prey distribution (Aarts *et al.* 2008). Sediment data were downloaded from the Folk 5-Class Classification layer of the multiscale EMODnet Seabed Substrate data portal (http://www.emodnet.eu/seabed-habitats). Each dive was assigned to one of five categorical variables defined within the layer as; 1. mud to muddy sand, 2. sand, 3. coarse substrate, 4. mixed sediment and 5. rock and boulders.

Diurnal patterns in diving behaviour outside the breeding season have been noted in several pinniped species and is assumed to be a consequence of seasonal stratification and vertical prey distribution (Burns & Testa 1997; Bennett, McConnell & Fedak 2001; Hastings *et al.* 2004). A diurnal cycle variable was assigned to each dive as a binary vector being either 'Day' or 'Night'. Position in the local diurnal cycle was calculated using the R package '*suncalc' (Agafonkin & Thieurmel 2017)*. Any period after nautical dusk and before nautical dawn was determined 'Night' and therefore twilight periods of dusk and dawn were included within the 'Day' category. Crepuscular patterns were therefore not considered in the analysis.

3.3.3 Statistical analyses

3.3.3.1 Principal component analysis and dive clustering for HMM validation

Principal component analysis (PCA) allows the identification of statistically discrete groups within a data set based on the linear combinations of each of the measured metrics and a quantification of the extent to which these combinations explain the variance in the data (Jolliffe 2011). PCA aims to simplify the number of variables by combining the important terms and reducing the degrees of freedom. This is a particularly useful method to apply when attempting to identify many different groups within a dataset, allowing for a more interpretable combination of terms.

To categorise dives, a PCA was applied to the metrics (per dive) presented in Table 1. This effective reduction of explanatory variables provided a set of principle components for further analyses. The principle components were then incorporated in a cluster analysis using a set of Gaussian mixture distribution models with the R package '*mclust*' (Fraley *et al.* 2012). Each model, accounting for a different number of clusters, was fit using maximum likelihood estimation and was selected by assessment of the BIC scores. This has advantages over heuristic approaches as each data point can be assigned a probability of belonging to one of two or more clusters, partially addressing any uncertainty. The final model, based on highest BIC score, identified the clusters which best explained the variation in the principal component distributions, and consequently the dive types assignations. The model probabilistically assigned each dive to a cluster and the dive shapes were inspected visually to interpret the dive function based on known biological information on seal diving and foraging behaviour.

The dive clusters were used, in combination with behavioural state assignations, to validate inferences of state switching inferred from a Hidden Markov Model (see Chapter 2 for full description of model formulation). Behavioural states were derived from horizontal movement trajectories using geo-referenced data and inferred, hydro-referenced, locomotory behaviour. The aim of this two-dimensional model was to quantify movement in the context of tidal currents. It also served to assess the possible misclassification of foraging behaviour when only one perspective of movement was accounted for in an energetic system. To validate this, dive classifications were correlated with contemporaneous, HMM derived observed states. State assignations for individual time-steps were correlated to dive clusters if the interpolated GPS location underlying the discrete state fell within 15 minutes of any particular dive. If multiple dives fell within that 15-minute window, the closest dive was correlated to that time-step. Relative proportions of each dive cluster in particular observed states were compared and used to assess whether the interpretation of underlying behavioural states from the HMM are mirrored by the inferences made from dive behaviour. This method did result in some dives being used in more than 1 time-step; however, dive behaviour of phocids has repeatedly been noted to occur in bouts of similar function (e.g. Austin *et al.* 2006; Wilson *et al.* 2014b) and therefore this should not bias the interpretation.

The ultimate aims of the comparison between state-assignations are two-fold. Firstly, it allows assessment of the use of horizontal movement as a proxy for discrete behavioural states; if dive-records, which are associated with individual states, tend to be dominated by particular behaviours, it provides support that the model of horizontal movement has identified true behavioural distinctions. Secondly, discrete dive behaviours can be used to validate the underlying behavioural inferences made from the associated movement model.

Table 1 **Dive metrics included in PCA and cluster analysis.** All metrics are provided along with descriptions and derivation.

Dive Metric	Description	Source and Calculation
Dive Depth (m)	Maximum depth value registered (in metres) by the tag during a single dive	Tag derived. Taken as the maximum absolute value recorded by the pressure sensor.
Proportion of the water column	Proportion of the water column the maximum depth value during a single dive represents	The maximum dive depth divided the bathymetric depth. Bathymetric depth was taken as the LAT estimated form the EMODNet DTM corrected to MSL through VORF correction and adjusted for tidal height.
Proportion of time in bottom-phase	Proportion of time spent in the inferred bottom-phase of a dive	Individual dives divided into descent, bottom, ascent and surface periods through vertical speed threshold calculation through the R package *diveMOVE.* Bottom-phase was then divided by the total duration of the dive.
Descent Rate (m.s^{-1})	Speed with which the animal transited from the surface to the beginning of the inferred bottom-phase in a dive	Total distance between the surface and the depth of the first bottom-phase record divided by the time between the surface record and the first bottom-phase record.
Bottom-phase wiggliness index (m)	The degree of vertical sinuosity during the inferred bottom-phase of a dive	Absolute vertical distance travelled in the bottom-phase of the dive (Leos-Barajas *et al.* 2017a).
Bottom-phase duration (s)	The total amount of time spent in the inferred bottom-phase of the dive	Time-stamp of the final record in the inferred bottom-phase subtracted by the time-stamp of the first record in the inferred bottom-phase.
Dive Duration (s)	The time between end of the pre dive surface interval and beginning of the post dive surface interval	The time-stamp of the final record in the entire dive subtracted by the time-stamp of the first record in the dive.
Post-dive surface duration (s)	The amount of time spent at the surface after surfacing from a dive, before commencing the next dive	The time-stamp of the first record of the following dive subtracted by the time-stamp of the final record of the dive in question.

3.3.3.2 Dive Metric Modelling

Individual dive metrics (descent rate, proportion of the water column used, proportion of dive spent in the bottom-phase, and dive duration) were analysed as response variables, using generalised additive models (GAMs) within a generalised estimating equation (GEE) framework using the R packages '*splines*' and '*geepack*' (Halekoh, Højsgaard & Yan 2006). Errors were modelled as gamma distributions with an inverse link function for all models except for the response variables representing proportions. Proportional responses were modelled with a binomial error structure and logit link function. A GEE framework was chosen due to the inherent correlation associated with time-series data, which is likely to propagate through to the residuals, a violation of a key assumption of traditional GAMs(Wood 2017). Within a GEE framework, longitudinal data are grouped into panels, within which data are permitted to be correlated and between which are assumed to be independent of each other. Robust sandwich-based estimates of variance (Pirotta *et al.* 2011) inflate the standard errors around the estimates, ensuring that the presence of autocorrelation has been accounted for without directly modelling it. The *acf* function in the R package '*stats'* was used to assess temporal autocorrelation and the most relevant GEE panel size was determined to be individual seals. Coefficient estimates derived from GEE-based models for a given covariate are representative of a population-level response rather than a mean individual response. To ensure that these inferences could be generalised across individuals and the population, relative density plots of sample size for each covariate were produced (Appendix II).

Interactions between each of the continuous variables of bathymetric depth, current speed and Julian day, with the factor variable of diurnal period were tested in the models. Current speed and bathymetric depth terms were entered as cubic β-splines due to the assumption that the relationships with response variables could be nonlinear. Julian day was fit with a cyclic spline to ensure that the model represented the difference between day 365 and day 1 the same as all other sequential days. Basis functions for the cyclic splines were generated using a traditional, univariate GAM with

Julian Day as the response variable and the '*cc*' argument in the '*bs'* function from the R package '*splines*'.

Model selection was carried out using backwards hypothesis testing and model simplification. The significance of covariates was assessed using a Wald's Test and an assessment of p-values (Hardin & Hilbe 2012). Multiple ANOVAs were fitted for each of the final models using the '*getPvalues'* function in the package '*MRSea'* (Scott-Hayward *et al.* 2013a). In each ANOVA, a single covariate was included last in the calculation, to re-confirm covariate significance by assessing marginal terms. Spline terms were iteratively replaced with linear terms if non-significance was established, and models were re-tested. A traditional significance level (α = 0.05) was considered in all model selection steps. Finally, responses were predicted across the range of the predictor variables (rather than the range of values possible within the study area) to ensure no false inferences were made beyond the information provided by the telemetry data. Each prediction for a given variable kept all other variables constant at their median values. All predictions were generated on the response scale to ease interpretation of the marginal effects.

3.4 Results

A total of 97277 dives were recorded across 32 of the 54 tagged seals. The remaining tags transmitted less than 14 seal days of data each and were excluded from further analyses. A large proportion (0.79) of recorded dives were within the Pentland Firth, with animals rarely moving into waters >150 m deep (Fig. 1). Median maximum dive depths across individuals was 92.8 m (range: 58.6 m - 198.7 m) and median dive duration was 197 seconds (range: 71 seconds - 333 seconds).

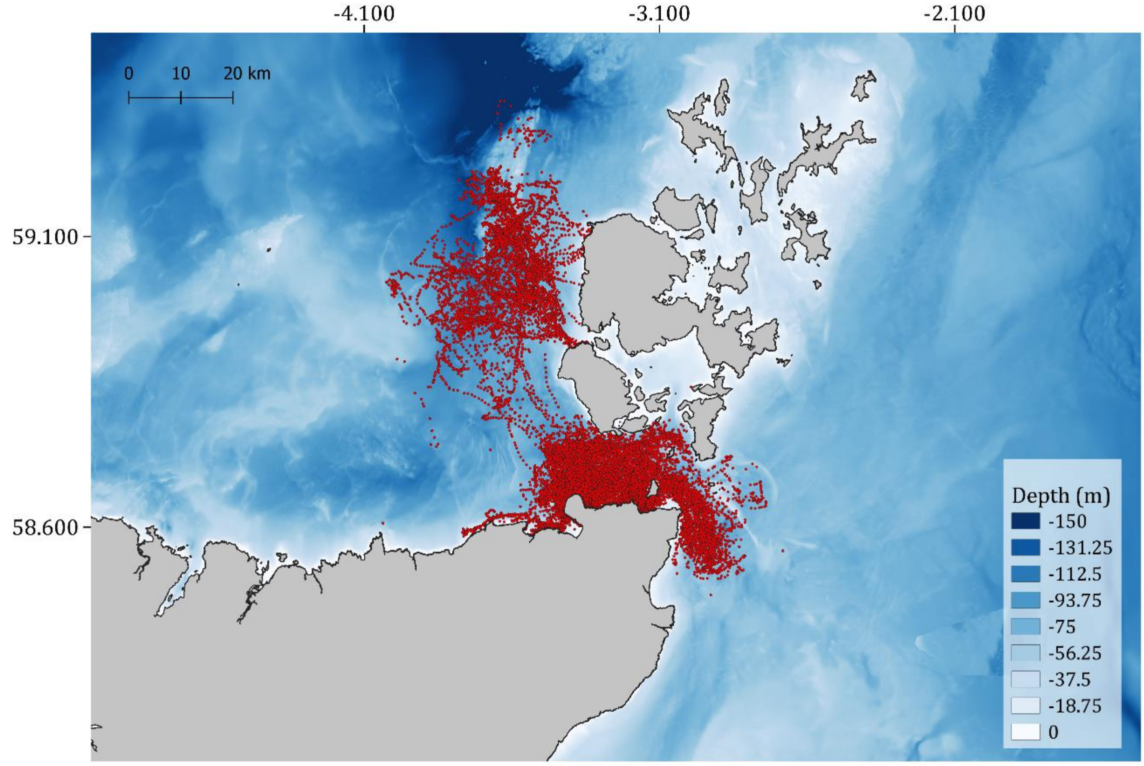


Figure 1 **Dive locations.** Red points indicate filtered dive locations; each location is within 15 minutes of a GPS fix. The underlying blue surface shows the bathymetric depth scale.

3.4.1 Dive Clustering

The principle component analysis identified 5 principle components from the eight dive metrics which explained ~94% of the variation in the data (Fig. 2). The contribution of dive metrics to each principle component can be found in Appendix II. Principle component 1 accounted for 46.8% of the variation in the data and was most strongly influenced by bottom phase wiggliness, total duration in bottom phase, proportion of the water column used and maximum dive depth. Principle component 2 accounted for 17.7% of the variation in the data and was most strongly influenced by descent rate, total duration in bottom phase of the dive and the total dive duration.

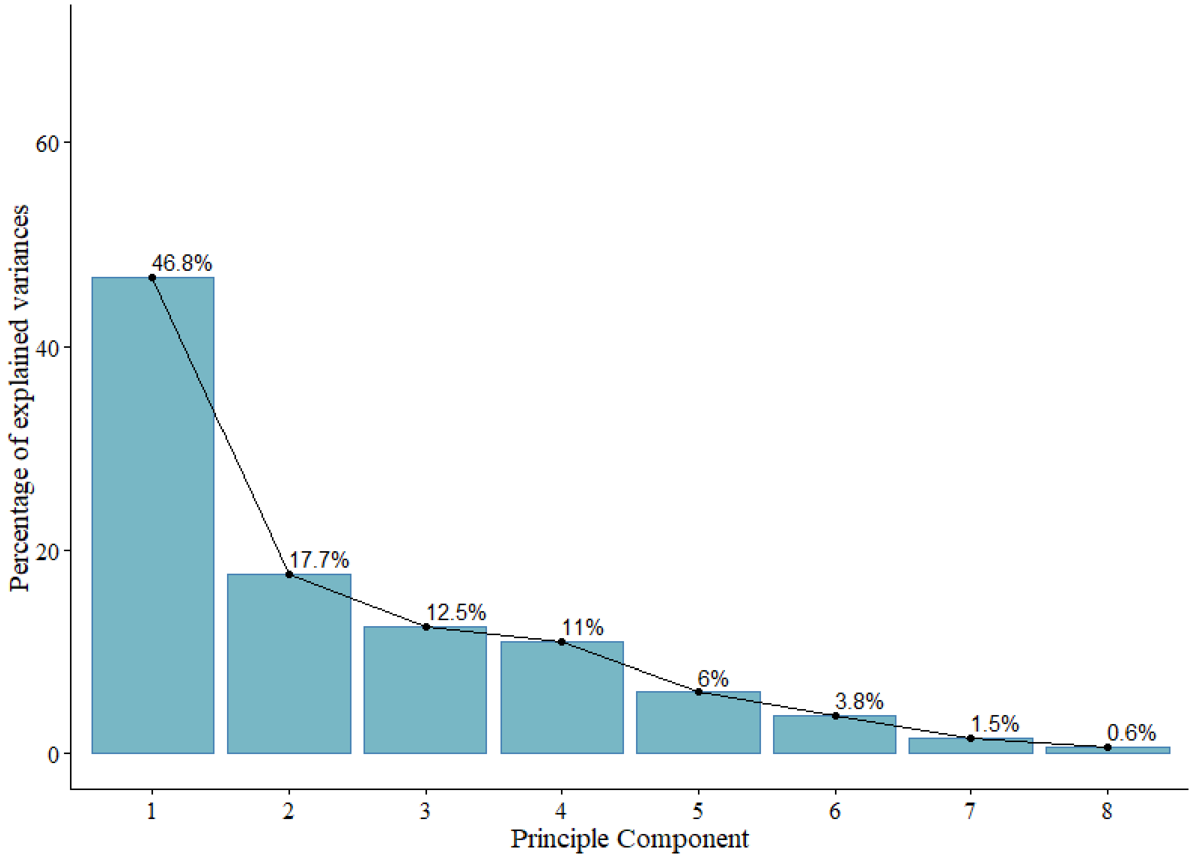


Figure 2 **Percentage of explained variance contributed by each individual principle component**. Significant figures have been rounded so cumulative explained variance only sums to 99.9 %.

Cluster analysis proceeded by computing and comparing BIC scores for 14 different model iterations, with each iteration sequentially adding clusters until the integrated likelihood was maximised. The optimal model identified five discrete clusters; each cluster represents an identifiably different general dive profile representing different ranges for each dive metrics (Fig. 3). Mean and standard deviations of the eight dive metrics were calculated for all clusters and sample time-depth plots were generated to assist in behavioural interpretation of each identified cluster (Table 2 and Fig. 3).

A centroid plot of the first 2 principle components associated with the cluster analysis demonstrates that discrete dive types could be easily distinguished and that behavioural modes can be robustly teased apart with the dive data (Fig. 4). The 95% range of all clusters overlapped with at least one other cluster's range except cluster 5 (V-shaped dives; Fig. 5); however, these two principle components only accounted for 64.5% of the variation in the data so further discrimination is not represented by this plot alone (see Appendix II for full suite of plots for every PC used in this analysis).

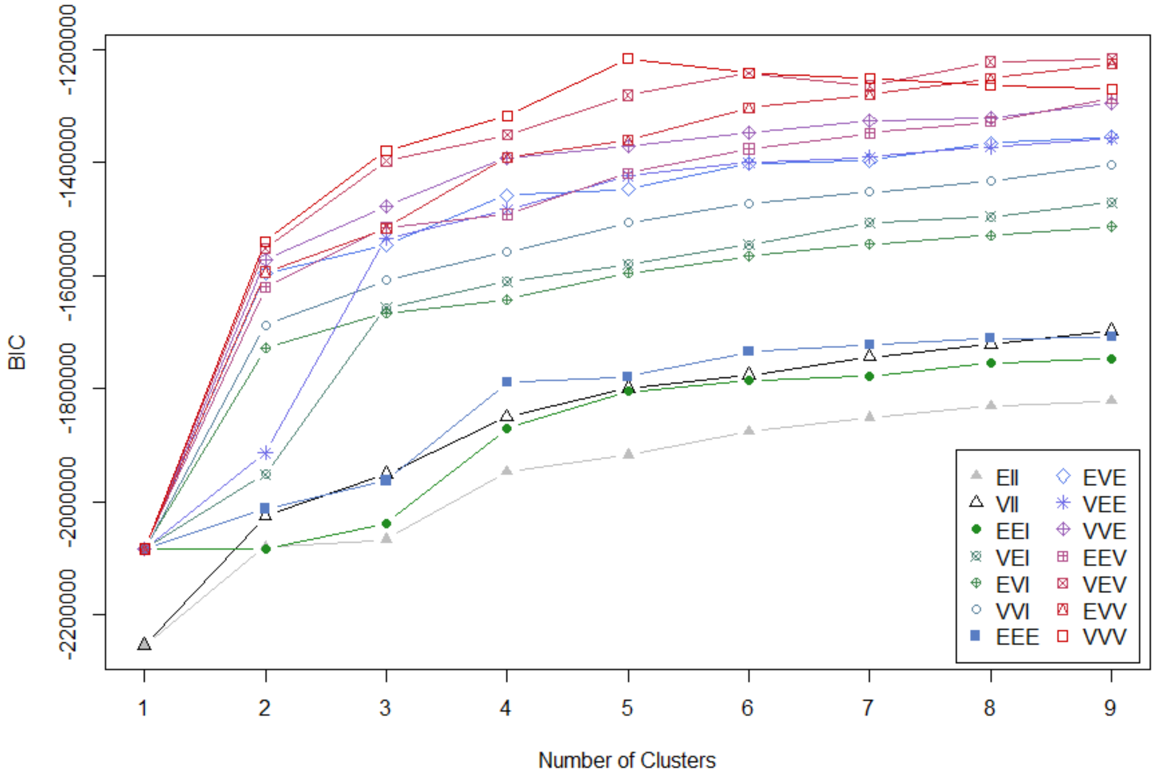


Figure 3 **BIC scores for each Gaussian mixed model iteration**. The 14 different models identify the volume, shape and orientation of the covariates as being either equal or variable. The full description of each model can be found in (Scrucca *et al.* 2016). Note the optimal model; VVV showing the maximised integrated likelihood being reached at 5 clusters.

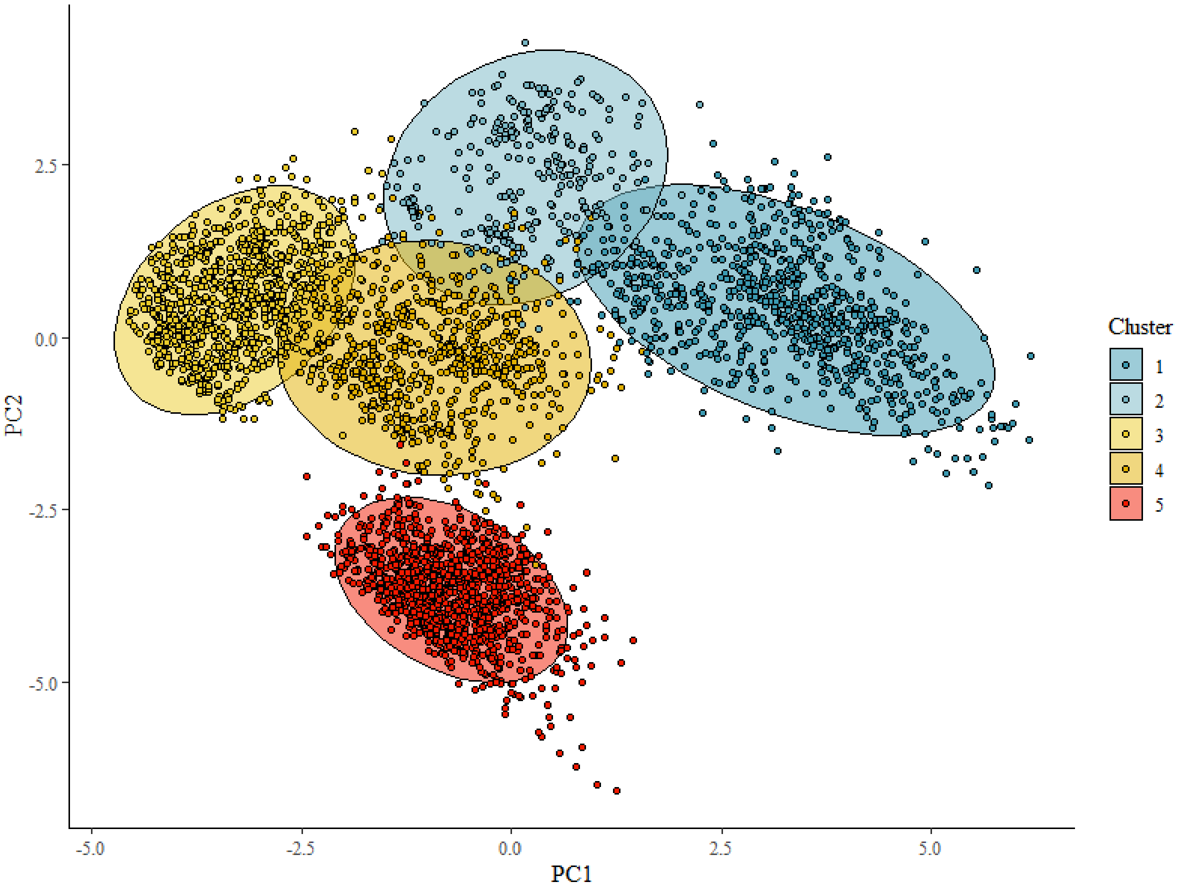


Figure 4 **Principle component 1 vs principle component 2.** Points represent a random sample of 5000 observations from the model data. Centroids represent where 95% of the model data are contained.

Figure 5 shows summarised metrics and an example of a time-depth profile from each cluster. Cluster 1 was characterised by deep, benthic/demersal dives with relatively flat bottom phases and fast descent rates; cluster 2 was characterised by shallow, flat bottomed dives with slow descent rates; cluster 3 was characterised by mid-water dives with high wiggliness during the bottom-phase; cluster 4 was characterised by deep, benthic/demersal dives with slower descent rates and highly wiggly bottom-phases; and cluster 5 were broadly v-shaped dives (Thompson *et al.* 1991a; Wilson *et al.* 1996), characterised by slow descent rates and very short bottom-phases (Fig 5).

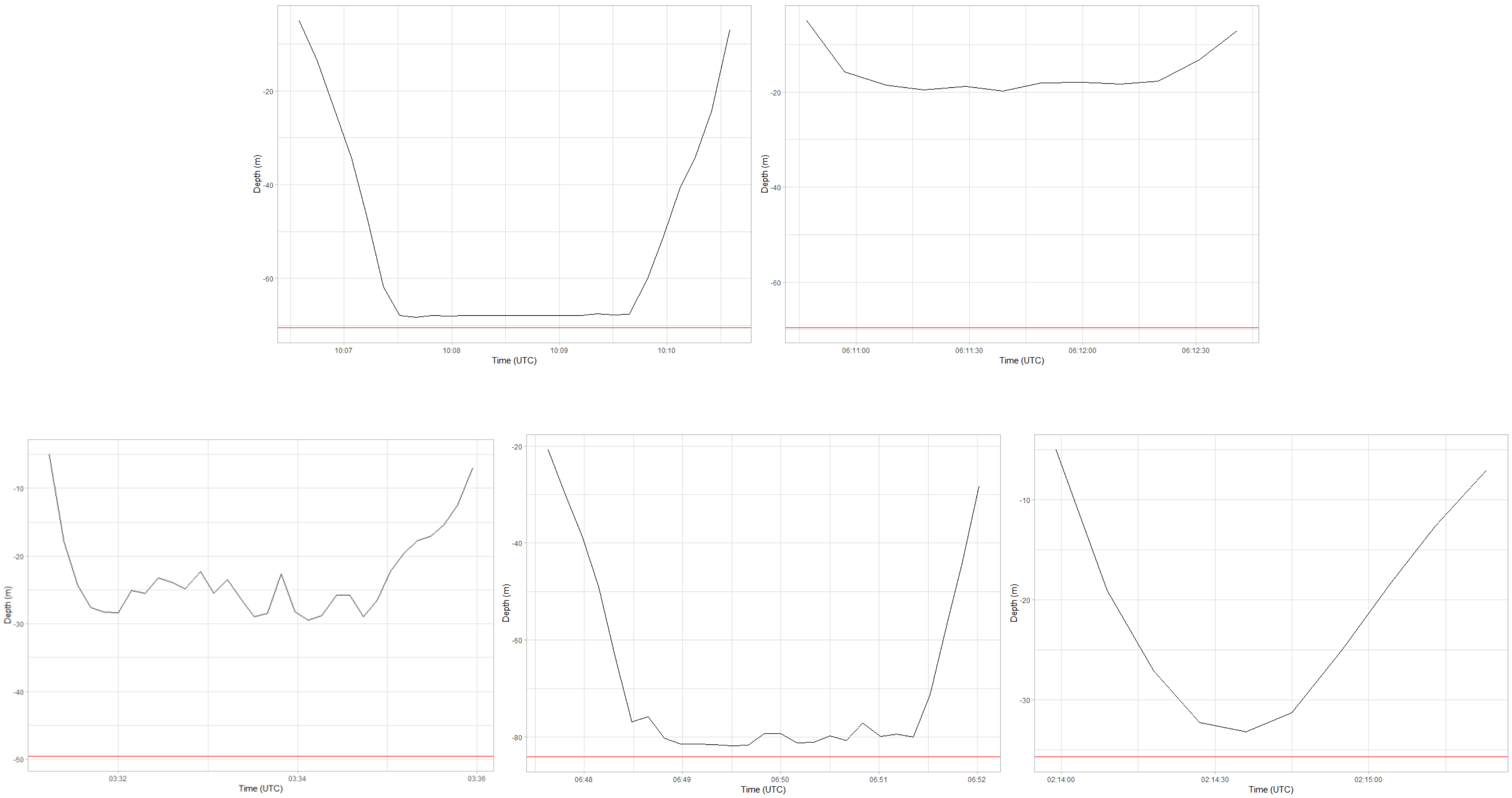


Figure 5 **Example time-depth profiles for each dive cluster**. Times are given in UTC and depth in metres below the surface. Associated mean and standard deviations for dive metrics can be found in figure. 4. From left-to-right and top-to-bottom: examples of dive clusters 1, 2, 3, 4 and 5 are presented.   Red lines indicate the bathymetric depth at the location of the dive.

3.4.2 HMM comparison

HMM derived states 1, 2, and 3 (geo-spatial dispersed states coupled with hydro-spatial dispersed, localised and travel states, respectively) all had relatively similar dive cluster proportions; between 61.3% - 66.42% of dives were comprised by a combination of dive clusters 1 and 4 in each of these states. Dive cluster 3 was the next most represented in states 1,2 and 3 followed by cluster 5. Dive cluster 2 represented <6% of the dive record in all three cases.

State 4 (Cross-current localised) was mostly represented by dive cluster 2 (36.75%). Clusters 1 and 3 were relatively evenly represented in this state (18.4% and 25.94%, respectively) with clusters 4 and 5 comprising a combination of <19%.

State 5 (Geo-Hydro localised) demonstrated a very similar pattern to states 1, 2 and 3, with clusters 1 and 4 comprising a combined total of 70.1%. However, cluster 3 contributed a smaller relative proportion of the dive record in this state compared to the first 3 states (3.72%).

State 6 (Swimming against the current) was the only state which did not have all dive clusters represented in the record; dive cluster 5 was absent from all time-steps predicted to be state 6. Seals were diving in a manner consistent with cluster 1 for 63.68% of the time, with cluster 4 being the next most represented at 28.46%. Dive clusters 2 and 3 represented <8% of the total record during time-steps predicted to be in state 6.

Cluster #	**Inferred qualitative description**	**Parameter**							
		Dive Depth (m)	***Proportion of water column***	***Proportion of time in bottom-phase***	***Descent Rate (m.s^{-1})***	***Bottom-phase wiggliness index***	***Bottom-phase duration***	***Dive duration (s)***	***Post-dive surface duration (s)***
1	Benthic Foraging on Static Prey	55.1 (19.72)	0.82 (0.18)	0.61 (0.19)	0.9 (0.48)	4.11 (1.65)	169.73 (48.85)	291.28 (126.12)	138.92 (58.26)
2	Shallow Travelling	14.71 (2.26)	0.4 (0.15)	0.5 (0.049)	0.48 (0.25)	5.75 (4.59)	15.34 (6.94)	31.45 (12.57)	92.94 (62.03)
3	Pelagic foraging	26.12 (8.53)	0.61 (0.21)	0.72 (0.1)	0.81 (0.41)	27.67 (8.68)	168.87 (66.94)	228.54 (70.76)	129.27 (60.95)
4	Benthic /Demersal Foraging on Pursuit Prey	56.17 (22.38)	0.91 (0.11)	0.58 (0.16)	1.25 (0.52)	14.94 (12.4)	145.54 (72.15)	242.19 (76.3)	99.49 (66.51)
5	Deep Travelling /Prospecting	40.37 (19.15)	0.77 (0.23)	0.11 (0.056)	0.62 (0.44)	0 (0)*	11.77 (4.11)	138.15 (70.0)	65.07 (57.47)

Table 2 **Mean and standard deviation of dive metrics for each discrete cluster**. Standard deviations are provided in brackets.

HMM derived state 8 (Drifting - directed) had 43.6% and 30.9% of dives identified as belonging to clusters 3 and 1, respectively. The remaining 3 clusters each contributed <11% to the total dive record for state 8.

Time-steps predicted to be state 7 (Cross-current travel) were represented by high (>20%) proportions of dive clusters 1, 2 and 3 with dive cluster 5 representing 17.26% of the dive record during this state. The Geo-Hydro travelling state (state 9) demonstrated the largest proportion of dive cluster 5 (36.05%) compared to all other states, with a similar proportion (33.28%) being represented by cluster 2. Dive cluster 1 represented ~19.15% of state 9 with clusters 3 and 4 representing a combined proportion of <12%.

3.4.3 Dive Metric Modelling

Results from model selection via backwards hypothesis testing are shown in Table 3 along with Wald's Chi-squared statistics, the associated degrees of freedom and P-values. Further, individual-based distribution plots aided interpretation of the spread of the data so qualitative inferences on individual behavioural traits could be made from the population-level estimates from the GAM-GEE based model predictions (Appendix II).

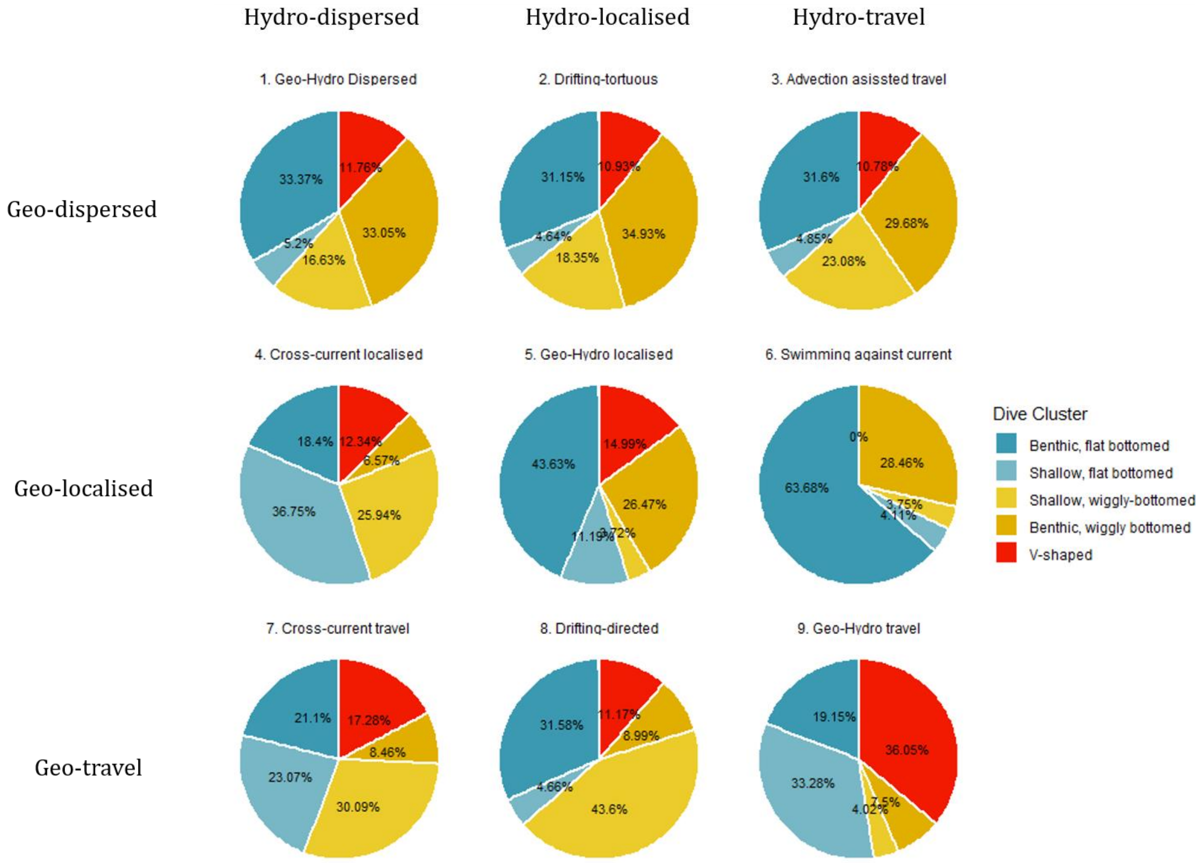


Figure 6 **Proportion of dive clusters represented by each HMM derived state**. State descriptions are presented above each pie chart and are the same state assignations as presented in Chapter 2. Rows separate geo-spatial states where the top row indicates all geo-spatial dispersed states, the second row indicates geo-spatial localised states and the bottom row indicates geo-spatial travelling states. Columns similarly separate hydro-spatial states into (left) dispersed, (centre) localised and (right) travelling states.

Variation in descent rate was best explained by current speed, bathymetric depth, benthic substrate and Julian day (Table 2). An additional interaction term with diurnal period was retained for bathymetric depth. Inspection of model predictions shows that, between current speeds of 0.4 – 1.7 m.s^{-1} (Fig. 7), descent rate increased markedly from ~0.5 to ~1.6 m.s^{-1} . The descent rate then decreased in current speeds up to 3 m.s^{-1}; beyond this, estimates of descent rate have wide confidence intervals, likely due to a lack of data and inferences must be treated with caution. Seals generally descended faster in deeper areas and during the winter months. Descent rate was also faster at night regardless of the bathymetric depth of the region. Descent rate was highest in areas characterised by sandy, coarse and mixed sediments with the lowest descent rates being estimated in rocky regions (Fig. 7).

The proportion of time spent in the bottom phase of dives varied with current speed, bathymetric depth and Julian day but to varying degrees (Fig. 8). Seals spent longer in the bottom phase of a dive in low to mid flow speeds (peak response at ~1 $m.s^{-1}$) and in 50 – 60 m deep water. The interaction with diurnal period suggested that seals spent longer in the bottom phase of dives at night, regardless of the bathymetric depth of the region. However, confidence intervals are relatively wide suggesting this result should be treated with caution. Mean bottom time was greatest during winter and spring months with the overall minima reached during summer (Fig. 8).

Predicted dive durations and bottom phase durations peaked at low to mid current strengths (Fig. 9). Mean dive duration was predicted to increase with increasing bathymetric depth reaching a maximum at depths around 50 m. Seals were predicted to dive for up to a minute longer during winter months compared to spring and early summer predictions. No diurnal interactions were retained in model selection for the response of dive duration (Fig. 9).

Seals utilised a smaller proportion of the water column at higher current speeds (Fig. 10) with peak water column usage observed in speeds of ~0.5 $m.s^{-1}$. Further, seals dived to a greater relative depth at night regardless of current speed. The proportion of the water column used decreased with increasing current speed during both the night and day; however, the magnitude of the decrease was greater during the day (Fig. 10).

Predicted proportion of the water column was greater during night than during the day, at all current speeds up to 3 m.s^{-1}, beyond which confidence intervals show high levels of uncertainty. The proportion of the water column used showed little variation in water depths up to 100 m, with a gradual decrease in dive depth in deeper areas. A seasonal shift to shallower relative depths was observed in autumn and winter months, with maximum water column usage being predicted in spring. A diurnal interaction was retained in model selection for the Julian day covariate, with seals diving to a greater proportion of the water column at night during spring and summer but shallower at night during autumn and winter. However, confidence intervals for this interaction suggest that the effect size for the interaction is extremely small. A significantly greater proportion of the water column was used in sandy and mixed sediments than in coarse sediment or rocky environments.

Table 2 **Table of $\chi 2$ and p values.** Shaded boxes indicate variables which were retained during model simplification. If interactions are retained, partial effects are not reported.

Response Variable	**Predictor Variable**						
	Current speed : Diurnal period	*Current speed*	*Bathymetric depth : Diurnal period*	*Bathymetric depth*	*Julian day : Diurnal period*	*Julian day*	*Sediment*
Descent rate	$\chi^2 = 0.66$, df = 3; p = 0.41	$\chi^2 = 18.6$; df = 3; p < 0.001	$\chi^2 = 7.87$, df = 3, p = 0.003	-	$\chi^2 = 0.76$, df = 4; p = 0.44	$\chi^2 = 12.9$; df = 4; p <0.001	$\chi^2 = 8.54$; df = 4; p = 0.0035
Dive duration	$\chi^2 = 2.89$; df = 3; p = 0.08	$\chi^2 = 9.86$; df = 3; p = 0.002	$\chi^2 = 1.72$; df = 3; p = 0.14	$\chi^2 = 8.42$; df = 3; p = 0.003	$\chi^2 = 0.49$; df = 4; p = 0.32	$\chi^2 = 4.9$; df = 4; p = 0.02	$\chi^2 = 4.37$; df = 4; p = 0.037
Proportion of time in bottom phase	$\chi^2 = 3.27$; df = 3; p = 0.07	$\chi^2 = 11.94$; df = 3; p < 0.001	$\chi^2 = 6.3$; df = 3; p = 0.014	-	$\chi^2 = 7.5$; df = 4; p = 0.006		$\chi^2 = 0.76$; df = 4; p = 0.38
Proportion of the water column	$\chi^2 = 11.77$; df = 3; p < 0.001	-	$\chi^2 = 0.17$; df = 3; p = 0.68	$\chi^2 = 8.08$; df = 4; p = 0.004	$\chi^2 = 5.78$; df = 4; p = 0.016	-	$\chi^2 = 4.04$; df = 4; p = 0.04

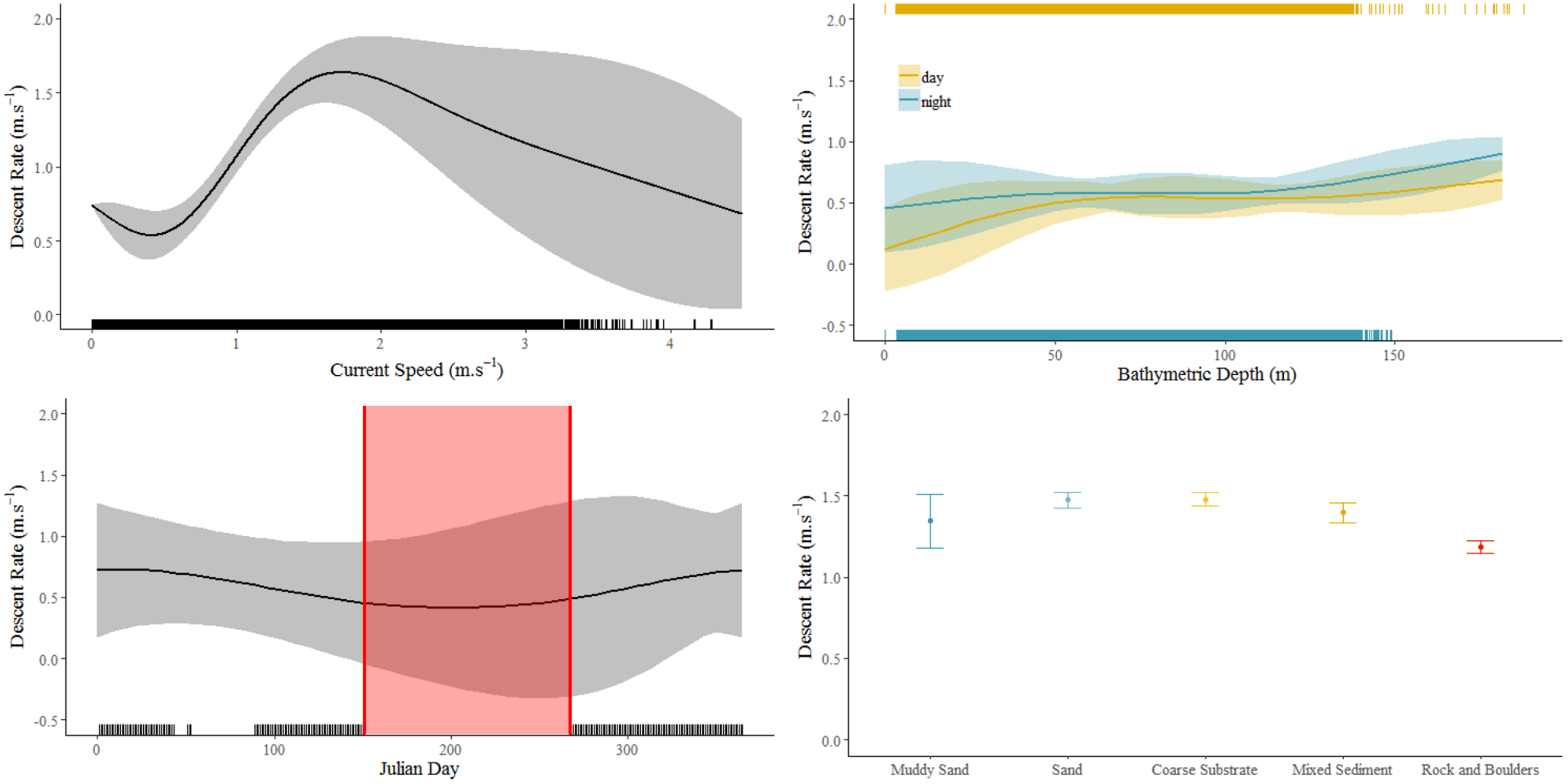


Figure 7 **Covariate effects on changes in descent rate.** Solid lines represent population mean estimates on the response scale. Grey shaded areas demonstrate uncertainty using GEE derived 95% confidence intervals. Red shading indicates periods of data removal. Mean effect estimates of the factorial variable of sediment type (bottom-right) are given by points with bars representing upper and lower GEE derived 95% confidence intervals. Rug plots demonstrate the spread of the observations and provide context for the uncertainty estimates.

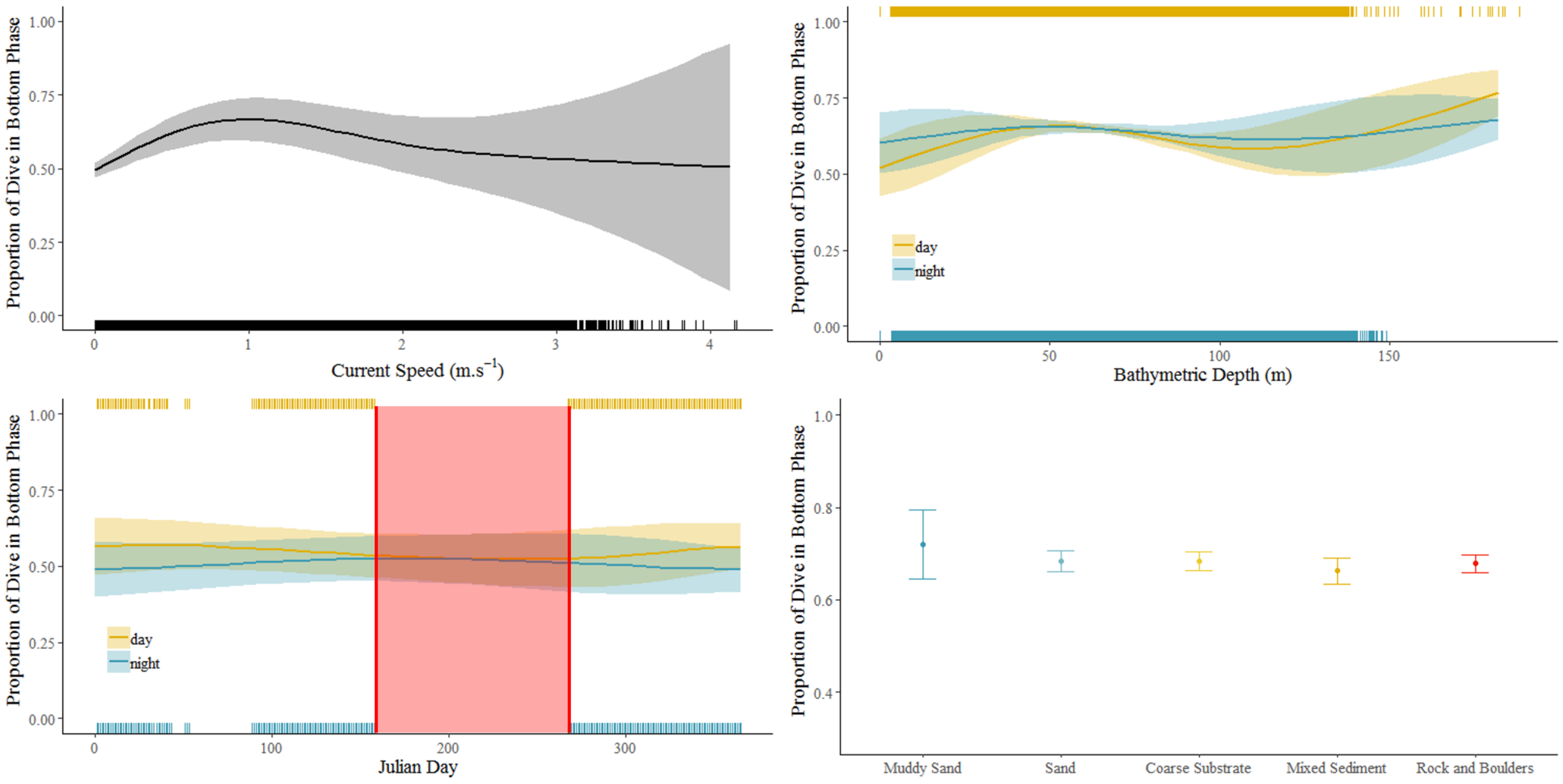


Figure 8 **Covariate effects on changes in proportion of time in the bottom phase of a dive.** Solid lines represent population mean estimates on the response scale. Grey shaded areas demonstrate uncertainty using GEE derived 95% confidence intervals. Red shading indicates periods of data removal. Mean effect estimates of the factorial variable of sediment type (bottom-right) are given by points with bars representing upper and lower GEE derived 95% confidence intervals. Rug plots demonstrate the spread of the observations and provide context for the uncertainty estimates.

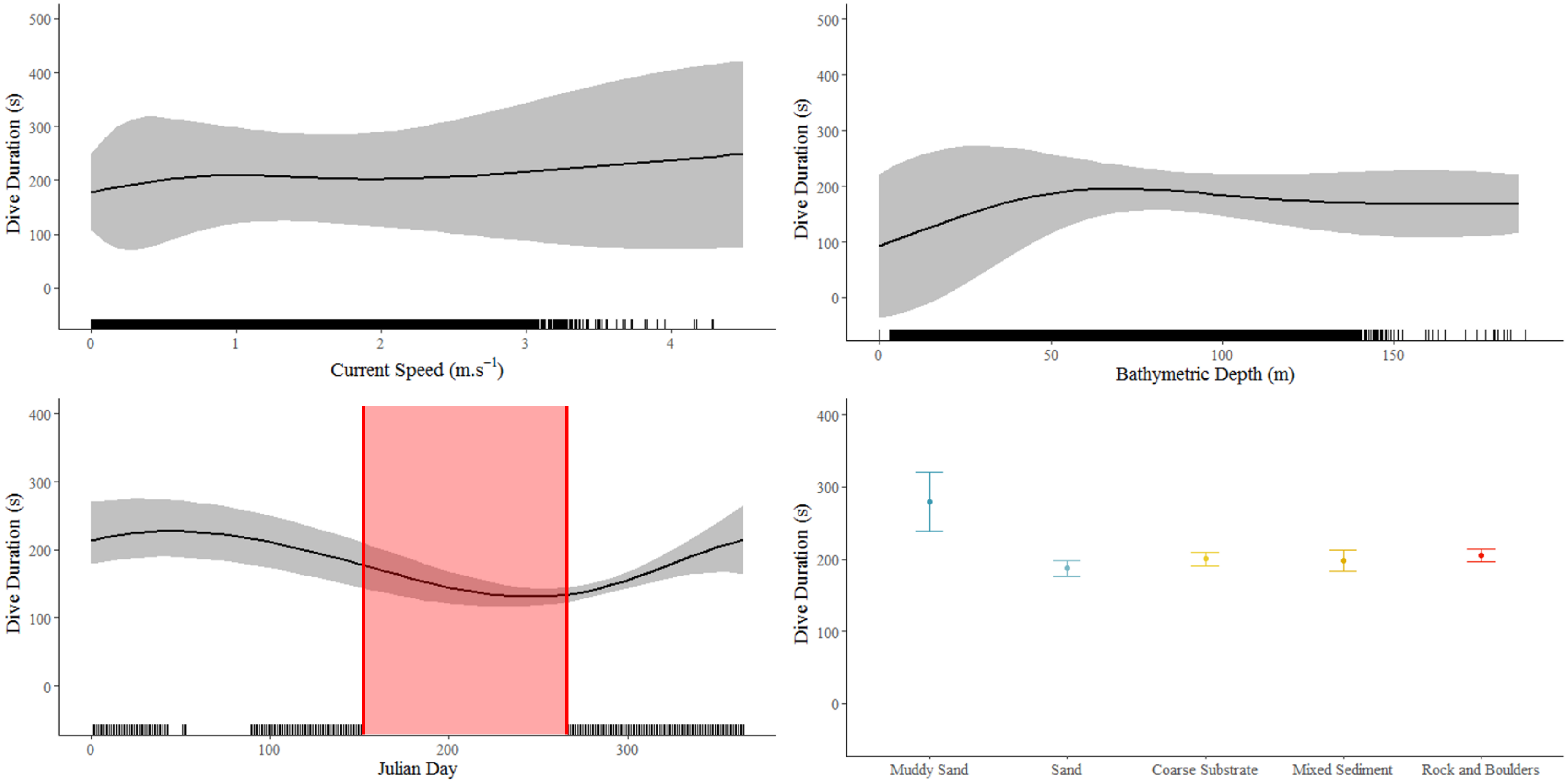


Figure 9 **Covariate effects on changes in dive duration.** Solid lines represent population mean estimates on the response scale. Grey shaded areas demonstrate uncertainty using GEE derived 95% confidence intervals. Red shading indicates periods of data removal. Mean effect estimates of the factorial variable of sediment type (bottom-right) are given by points with bars representing upper and lower GEE derived 95% confidence intervals. Rug plots demonstrate the spread of the observations and provide context for the uncertainty estimates.

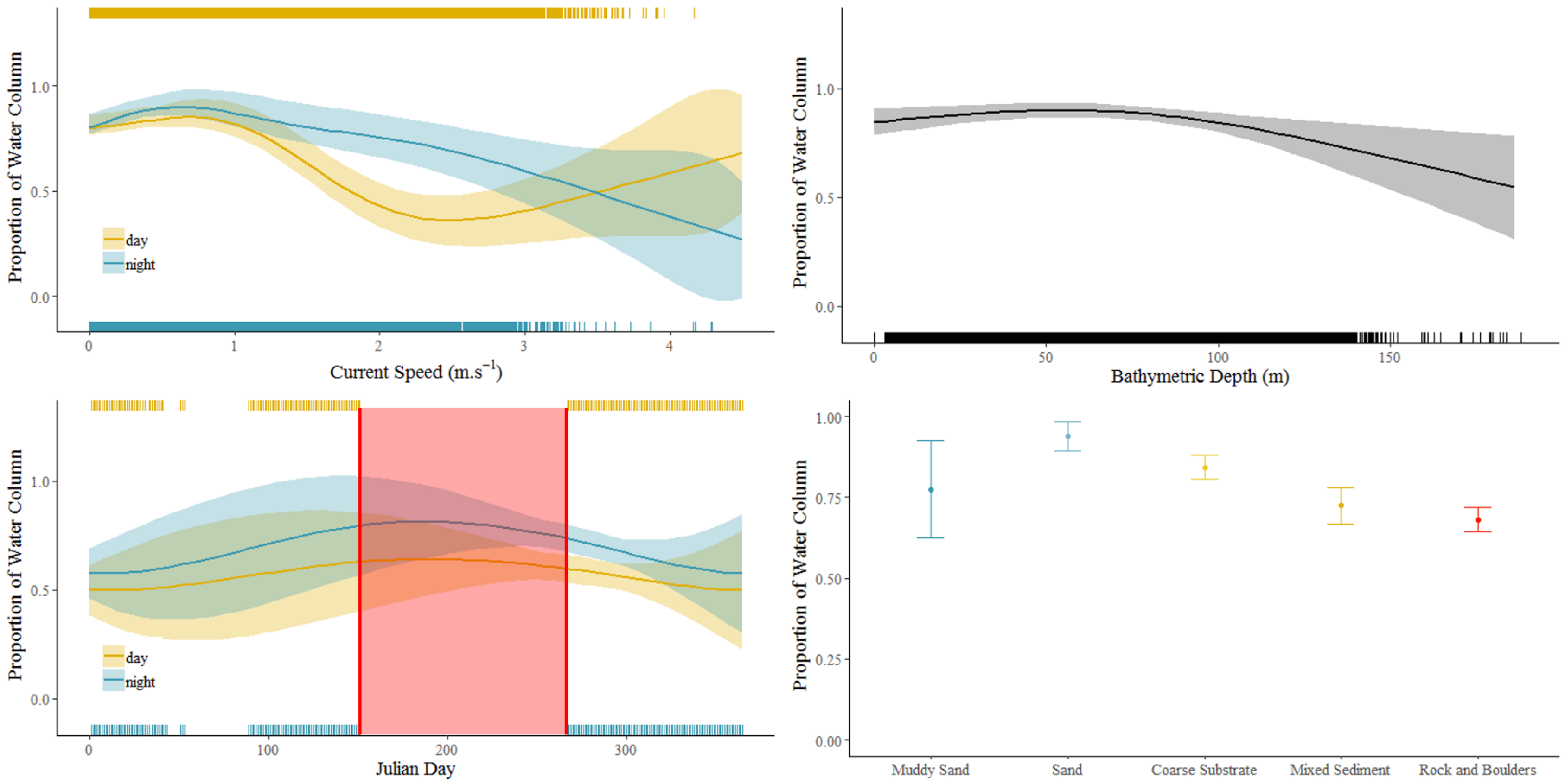


Figure 10 **Covariate effects on changes in proportion of the water column used.** Solid lines represent population mean estimates on the response scale. Grey shaded areas demonstrate uncertainty using GEE derived 95% confidence intervals. Red shading indicates periods of data removal. Mean effect estimates of the factorial variable of sediment type (bottom-right) are given by points with bars representing upper and lower GEE derived 95% confidence intervals. Note y-axis range spans values less than 0 and greater than 1 to include the insignificant confidence intervals in high flow rates. Rug plots demonstrate the spread of the observations and provide context for the uncertainty estimates.

3.5 Discussion

The results presented here show that harbour seals can exhibit a high degree of variability in dive behaviour in a temporally and spatially dynamic environment, and that a number of environmental covariates influence their diving behaviour. To my knowledge, this is the first study showing the relationships between the diving behaviour of harbour seals, or indeed any marine mammal, and hydrography in a tidal stream environment. Further, the results represent a first insight into harbour seal dive behaviour as it relates to dynamic habitat variables in the UK and suggest that seals may switch foraging tactics as a result of tidal flow.

Observed diving behaviour was compared with results of a discrete time HMM, which demonstrated transition probabilities that were representative of individual-level behavioural switching (Chp. 2). This comparison largely supported the inferences of foraging behaviour made from the horizontal movement data. It therefore seems reasonable to assume that behavioural switches occur frequently in response to changing environmental conditions, and that foraging plasticity is a common trait of harbour seals in this tidally energetic environment. The result also supports previous suggestions (Chp. 2) that harbour seals adjust their foraging tactics to successfully exploit variably energetic conditions as well as local, static environmental features. With many individuals occupying a wide range of hydrodynamic conditions across the study period, it is therefore proposed that these results demonstrate that seals adopt a generalist rather than specialist approach to foraging in this region. It was notable that all HMM derived states included multiple dive types which highlights these analyses, while useful is providing broad-scale inferences, are problematic for describing fine-scale harbour seal behaviour. However, the dive data cluster analyses was useful for quantifying and interpreting activity budgets and, in tandem with horizontal movement and environmental data, provided useful insights into the environmental drivers of behaviours.

Benthic diving was the most common dive-behaviour exhibited during the *known localised* state categorised by both geo-spatial and hydro-spatial movement in the HMM (geospatial localised - hydrospatial localised; state 5; Fig. 6). This supports the widely held assumption that such area-restricted search (ARS) behaviour is indicative of foraging (Kareiva & Odell 1987). When seals were geo-spatially stationary in increasing flow rates by swimming against a prevailing current (geo-spatial localised – hydro-spatially travelling), benthic dives also predominated. Concurrently, a significant increase in descent rate and proportion of time in the bottom phase of dives was observed. Within the water column, current strength generally peaks close to the surface (assuming no external forcing) and decreases to effectively 0 at the boundary between the water and the sea-bed (Brown 1999). It is therefore possible that seals avoid significant displacement during benthic foraging in increased tidal currents by reducing the amount of time spent in the highest flow rates during descent phases. In addition to assisting geo-spatial localised foraging, this tactic may also allow seals to exploit prey patches that are unavailable for less efficient benthic diving competitors such as seabirds (Waggitt *et al.* 2016).

Behavioural mechanisms to avoid high flow rates at the surface has also been noted in other species during migration (Metcalfe, Hunter & Buckley 2006; Campbell *et al.* 2010). However, given the regularity with which they display this behaviour, it seems likely that the apparent avoidance of high currents in the water column by seals is linked to foraging rather than as a means to assist travelling. Specifically, as central place foragers that do not tend to migrate large distances to breed and forage, harbour seals are able to haul-out regularly, presumably to rest between foraging bouts. This results in a larger proportion of their time at-sea dedicated to foraging when compared to migratory species or animals with larger home-ranges (Russell *et al.* 2015). Further, the association of benthic diving and fast descent rates with prolonged periods of swimming against the current to remain in a geostationary patch (state 6 in the HMM; Fig. 6) suggests a desire to remain local rather than travel.

Hydro-spatial localised behaviour was more apparent at current speeds greater than 1.7 ms^{-1} suggesting seals were drifting with the prevailing flow (Chp. 2). During hydro-spatial localised behavioural states where geo-spatial dispersed or travelling predominated, the dive cluster analysis showed a high proportion of mid-water dives with high levels of movement in the bottom-phase of the dives, lasting similar durations as benthic foraging dives. These changes in behavioural patterns during periods of increasing flow may demonstrate a switch from benthic to pelagic foraging. Seals appear to switch from an ARS pattern in geo-space to an ARS pattern in hydro-space, with foraging putatively remaining the primary driver. This hydro-spatial ARS behaviour appears analogous to that of elephant seals (*Mirounga leonina*) in the southern ocean demonstrating “quasi-planktonic” foraging bouts (Della Penna *et al.* 2015) and puffins (*Fratercula arctica*) in Ireland, which were shown to engage in no geo-spatial ARS movement but drift with the current and dive during passive horizontal transport (Bennison *et al* 2019). Similarly, harbour porpoises (*Phocoena phocoena*) have been more detectable using drifting acoustic recorders than moored recorders in energetic systems, suggesting their utilisation of currents while foraging by drifting or actively moving downstream (Benjamins *et al.* 2016); however, this is potentially confounded by lower detectability by static receivers which are more vulnerable to ambient flow noise during increased currents. In flow rates lower than the minimum cost of transport speed in harbour seals (~1.8 m.s-1 ; Thompson, Hiby & Fedak 1992; Gallon *et al.* 2007), water movement is unlikely to significantly affect the energetic costs of travelling and foraging; as such, seals may be more capable of remaining at a geo-stationary prey patch at flow speeds below this. This would make the exploitation of benthic prey patches in low currents efficient and diving pelagically whilst moving with a current may become a more energetically favourable strategy at higher currents.

The observed changes in diving behaviour with flow speed therefore suggest that prey switching occurs (from benthic to pelagic) as current speed increases. This is supported by results that show that, compared to other regions, harbour seals in this region have a relatively varied diet. Wilson and Hammond (2019) showed that both pelagic and benthic species were important components of harbour seal diet in the Pentland Firth and Orkney waters throughout the year. The authors also show that diet is more varied in this area than many other populations around the UK and that prey composition may be shifting more towards other pelagic and demersal species due to crashes in local sandeel populations (Frederiksen *et al.* 2004). The seasonal fluctuations in the proportion of the water column used supports these results in that benthic diving was more apparent in spring and summer months with a shift towards mid-water diving in autumn, though confidence intervals are relatively wide for these predictions. It is important to note that the diet analyses of Wilson and Hammond (2019) identified population level variability and it remained unclear whether this constituted a population of generalists or several specialists. Density plots of covariate representation (Appendix II) suggest that this population is likely made up of a mixture of both, with many individuals inhabiting multiple conditions and others preferring a narrower environmental range. It should also be noted that the summer and early autumn effects estimates should be treated with a great deal of caution in this present study. Data were abstracted to ensure breeding periods did not affect behavioural interpretations in early summer and deployments subsequent to the cessation of moulting periods did not begin until late September. Model predictions around these dates carry necessarily wide confidence intervals and should be interpreted with caution.

Descent rate and relative dive depth as a proportion of the water column decreases as depth-averaged current strength increases beyond ~1.7 m.s^{-1}, and seals switch to geo-spatial travelling or dispersed patterns (Chp. 2). However, confidence intervals around the estimates of descent rate are progressively wider above these values despite relatively large sample sizes up to ~3 m.s^{-1}. This increased variability in descent rates at these flow speeds suggests that descent rate may not be a constraint while seals drift with currents and hydro-spatially forage. Interestingly, the negative relationship between proportion of the water column and current speed differed between day and night. Significantly more benthic diving was predicted at higher current speeds at night and mid-water diving occurring more frequently during the day and at depth-averaged current-speeds exceeding 1 m.s^{-1}. Most previous studies investigating phocid diving in relation to diurnal patterns have noted a pronounced trend towards deeper diving during the day, suggesting a response to vertical migrations of prey (e.g. Bennett, McConnell & Fedak 2001; Photopoulou *et al.* 2014). However, these studies have tended to focus on habitats which exhibit clear vertical stratification in the water column and where diurnal vertical migration of motile plankton and nekton occurs. The area of the present study, being coastal and characteristically energetic, is likely to have a highly mixed water column, so vertical migration of primary production is reduced.

It is possible that there are a variety of sensory modalities required for different flow conditions and different prey types. During periods of low flow, the use of whiskers to detect fine-scale changes in surrounding water hydrodynamics (Murphy *et al.* 2017) may be favourable, and at high flow rates, where turbulence limits or preclude this, vision may by the primary sensory modality for foraging. In other words, the apparent switch from deep, benthic diving at night to pelagic diving during the day may therefore represent a switch from conditions where mystacial vibrissae innervation is the primary sense for prey location (Schulte-Pelkum *et al.* 2007) to a vision-based, pursuit hunting which requires light to locate moving prey. With more light closer to the surface, pursuit hunting would benefit from residency in the upper photic zone. Sensory modality may also explain why at higher flow rates, seals appeared to spend relatively more time at shallower depths relative to the bathymetric depth. Specifically, higher flows likely cause increasing turbulence and a larger boundary layer emanating from the water-substrate interface (Vogel 1994). Turbulent flow becomes more laminar as frictional forces dissipate in the upper water column. This would allow seals to employ the use of mystacial vibrissae by detecting hydrodynamic trails of forage fish (Schulte-Pelkum *et al*. 2007) without being masked by turbulent flow in the demersal region. Although this is potentially an oversimplification of a highly complex system, the overall patterns observed in the dive data do suggest that seal behaviour is affected by the interactions between current strength and the seabed, and that a combination of changes in prey distributions and availability likely drive the patterns observed.

Irrespective of season and daylight, dive depth was shallower in flow rates above 2m.s^{-1}. This may be a direct response to increases in the abundance of fish in the water column; for example, Williamson *et al* (2019) observed that the overall size of mid-water fish schools increases with increasing flow rate. Some predatory species have been observed frequently targeting fast flowing areas presumably due to this 'tidal coupling' relationship where prey species are aggregated and/or disorientated by the energetic conditions. These hydrodynamically influenced dive depths appear to support the tidal coupling hypothesis in that the seals spent significantly longer diving to pelagic depths in faster flow than during lower flow rates when they appeared to dive more benthically. Williamson *et al.* (2019) also noted that pelagic fish school area and frequency peaked during daylight periods which lends further support to the assertion that the seal dive behaviour here is related to prey switching; dive depths consistently showing shallower diving during daylight periods.

The results presented here suggest that foraging behaviour is influenced by diurnal cycles, tidal state, and season in this region, and that behaviour switching is likely a response to prey availability as well as environmental conditions. Given that foraging-like dive behaviour accounted for the highest percentage of all of the HMM derived states which were categorised as putative foraging also reinforces the assertion that hydro-spatial and geo-spatial movement patterns should both be considered when establishing a predators activity budget and foraging behaviour in dynamic environments.

It is important to highlight that there a number of caveats associated with this study; most notably foraging behaviour is inferred from the movement and dive data here and was not measured directly. A recurring theme in movement ecology in the realm of remote sensing is the reliance on statistical approaches and underlying assumptions of foraging ecology in order to make inferences about the function of specific movements (Patterson *et al.* 2008; Joo *et al.* 2013). Often researchers do not have the ability to directly observe animals to validate behavioural inferences based on movement and rely on ancillary data from other populations and/or pre-conceived biological theories. Given that the environment in this study presents unique challenges to seals it could be equally feasible that behavioural assumptions made from a different population are not applicable.

This study has attempted to address this issue by relating the identified movement patterns to previous, robust measurements of diet however the interpretations of the drivers of the diving patterns remain uncalibrated. Further studies might consider measuring the effect of environmental drivers on dive behaviours in the context of discrete dive clusters as well as extrinsic covariates, essentially coupling the 2 different analyses conducted in this study. This may help elucidate how 'foraging' dives and 'travelling' dives may differ in their fine-scale properties; however, this would reduce the sample size for each analysis, rendering it more challenging to decipher a signal in the data. Furthermore, foraging has been directly recorded in virtually every 'dive-shape' identified in harbour seals (Lesage, Hammill & Kovacs 1999) and therefore these distinctions may not robustly broaden our understanding of activity budgets. Researchers must therefore continue to observe these movements in finer scale to gain a better understanding of activity budgets and energetic balances to strengthen these inferences.

Current speeds presented are model derived and depth-averaged, and do not take account of external forcing such as wind and local atmospheric pressure. Further, the resolution of the model precludes the identification of fine-scale oceanographic features such as eddies and boils, and this may limit the power of such analyses to tease apart fine-scale behavioural strategies. As such, the significant relationships between diving behaviour and habitat covariates must be interpreted with these caveats in mind.

The use of two different tag types presented some challenges in data processing and the difference in raw-data resolution could have an impact of the robustness of dive metric estimation. If animals spend little time in the bottom-phase of a dive, such as the V-shaped dives identified in these data, decreasing data resolution may begin to mask the true maximum depth of dives or indeed bottom phase behaviours which indicate behavioural modes may be masked. For example, if a tag records a depth estimate every 10 seconds and during a v-shaped dive an animal descends (and ascends) at 1.5 $m.s^{-1}$ to a depth of 50 metres, if a depth record was taken at 40 metres during descent then the maximum depth of a dive would be recorded as 45 metres (the subsequent depth reading, during the ascent phase). This would represent a 10% error in estimated proportion of the water column used and could have pronounced implications for behavioural inference. In practice, the behavioural assignations used here would not have been severely affected as all V-shaped dives, regardless of dive depth were presumed to be indicative of travelling behaviour however it is an important consideration especially when considering behavioural implications and physiological limitations.

The present study was novel in that, for the first time, dive behaviour of seals was investigated in the context of complex hydrodynamics in a tidally energetic region. However, previous studies have speculated that finer-scale hydrodynamic features than presented here may influence foraging mechanisms of harbour seals. For example, Hastie *et al.* (2016) suggested that in a similarly energetic system, harbour seals may use micro-scale eddies to exploit the periphery of the prevailing flow and utilise adjacent, slower moving water to swim upstream while foraging. Similarly, Lieber *et al.* (2018) found the probability of harbour seal occurrence to increase with the presence of peripheral eddies and vertical shears using ADCP line transects. While the results presented here showed changes in diving behaviour with foraging in a tidal-stream, the association with micro-scale features was not possible given the scale of the hydrodynamic models available in the area. Further, the use of depth-averaged current data limits the analyses to horizontal current velocities over time, and ignores the fact that, as tidal state changes, average current may represent a different proportion of the maximum current speed in the water column.

3.6 Conclusions

The observed relationships between dive behaviour and hydrographic conditions highlight the importance of tidal currents for seals foraging in tidally energetic habitats, and suggests that such habitats confer not only a series of significant challenges, but also a series of unique benefits to seals. Useful future studies would be to use higher resolution tracking techniques such as sub-surface sonar (Hastie *et al.* 2019a; Hastie *et al.* 2019b) or high resolution biologging devices such as accelerometers, magnetometers and swim speed loggers (Wilson, Shepard & Liebsch 2008) to investigate the foraging tactics and mechanisms of seals in the context of their fine-scale vertical and horizontal movements. Further steps towards refinement of three-dimensional oceanographic models would also aid in the interpretation of these types of data and allow a more robust inference as to the conditions immediately surrounding moving seals. These techniques may aid in our interpretation of how seals might utilise micro-scale, tidally generated features and would help determine the mechanisms underlying the behavioural plasticity of foraging harbour seals.

Chapter 4

Harbour seals avoid tidal turbine arrays during operations

“That’s no moon; it’s an operational tidal turbine”

4.1 Abstract

The increasing global demand for energy coupled with the desire to reduce atmospheric carbon has fuelled the development of the renewable energy industry in recent years. Owing largely to their predictability, tidal currents provide one useful source of renewable energy which can be harnessed in a similar manner to wind. However, due to its relative infancy, data on the environmental impacts ranging from direct interactions with marine fauna to changes in physical oceanic properties, are largely lacking. Here, I present an analysis which quantifies the behavioural effects of the presence and operations of the world's largest operational tidal turbine array on a population of harbour seals (*Phoca vitulina*) in the north of Scotland. The results demonstrate that seals show overt avoidance responses to the operations of the turbine, with a significant decrease in predicted abundance (between 24% and 39%) within a range of ~2 km from the turbine array while they are generating power. I also show that, over the longer period of exposure to the presence of the turbines, no significant changes in distribution were observed indicating that during the study period, foraging sites were not obstructed by any apparent barrier effects or perceived threats. These results provide important information which can be used to update estimates of potential interactions and collision rates between harbour seals and tidal turbine arrays and demonstrates a robust analytical framework which can be employed in future studies to assess how arrays of increasing size and operational status can affect distributions of marine animals.

4.2 Introduction

The tidal energy industry is in its infancy compared to other renewable energy sources such as wind and solar farms. However, the spatial and temporal predictability of tidal currents make it an attractive choice, with several sites around the world being proposed for development. Tidal turbines are deployed subsea to extract energy from tidally-driven water currents with the majority of designs being horizontal-axis turbines with rotating blades; this has led to concerns about the potential impacts of turbines, through direct collisions between large animals (e.g. marine mammals) and turbine blades (Wilson *et al.* 2006; Dolman & Simmonds 2010; Hastie *et al.* 2017; Sparling, Lonergan & McConnell 2017; Fraser *et al.* 2018; Joy *et al.* 2018; Williamson *et al.* 2019).

Tidal turbine development sites are characterised by being relatively coastal with fast tidal currents; such energetic habitats are commonly a consequence of topographical features which force water through narrow channels, shallow water, or around headlands (Simpson & Sharples 2012). The predictable nature of these oceanographic features is also thought to provide foraging opportunities for marine predators (Uda 1958; Wolanski & Hamner 1988; Zamon 2001; Zamon 2003), and provide enhanced migratory and travelling efficiency when travelling with prevailing flow (Raya Rey *et al.* 2010). For example, harbour seals (*Phoca vitulina*) are a coastal marine mammal species which has been observed in high numbers at tidally energetic sites; observations of tidally mediated residency and foraging behaviour suggest the sites to be of particular importance to some populations (Zamon 2001; Hastie *et al.* 2016). This link has also been noted in several species of seabirds and cetaceans (Pierpoint 2008; Cox, Scott & Camphuysen 2013; Wade *et al.* 2013; Waggitt & Scott 2014; Benjamins *et al.* 2015; Cox *et al.* 2018). This has led to concerns that large scale turbine array installations may result in collisions with these species, or create perceptual or physical barriers to movement, restricting access through these areas. These restrictions may lead to increased transport costs, reduction in key foraging opportunities, or direct mortality (Chp. 5; Onoufriou *et al.* 2019) which has the potential to lead to population-level effects.

Studies to predict the potential impacts of tidal turbines on marine mammals have focussed primarily on the development and application of models to estimate species-specific rates of collision (Wilson *et al.* 2006; Band *et al.* 2016; Thompson *et al.* 2016). These models are underpinned by estimates of the abundance and distribution of animals in areas of proposed tidal energy developments. Abundance data are then scaled by estimates of rates of avoidance by individuals as a result of animals detecting the turbines and exhibiting behavioural avoidance responses (Hastie *et al.* 2017). This is often difficult due to lack of empirical data which results in most collision risk models simply calculating estimated encounter rates. Encounter rates are defined as the rate at which animals would strike a turbine if they did not respond to the presence or operations of the device; essentially assuming no change to observed, pre-installation movement processes. Recent studies have suggested that this assumption is invalid given the changes in distribution seen as a response to active single devices or simulated devices (Hastie *et al.* 2017; Sparling, Lonergan & McConnell 2017; Joy *et al.* 2018) but as yet, no information exists to inform the avoidance rate after turbine arrays are scaled up or how animals may evade the devices at close range. However, there is growing evidence that the installation of static anthropogenic structures may also increase biodiversity through bottom-up processes (Pickering & Whitmarsh 1997; Inger *et al.* 2009; Russell *et al.* 2014; Fraser *et al.* 2018; Williamson *et al.* 2019), potentially attracting animals to tidal turbines to forage. To date, there is an almost complete lack of data on how marine mammals respond to tidal turbine arrays.

As acoustically sensitive animals it is generally held that avoidance behaviour is likely to be triggered by aversive responses to the acoustic signal of the structures, be it during installation or operation. While closer range avoidance could be triggered by visual cues alone, the relatively high turbidity of coastal channels may render this difficult beyond a few 10s of metres. Harbour seals can detect sounds at frequencies of up to ~110 kHz at pressure levels as low as 140 dB re 1 μPa, however are particularly sensitive to frequencies between 0.1 – 50 kHz (Cunningham & Reichmuth 2016). The predominant narrowband acoustic components of operational tidal turbines have been established at tonal frequencies of 120 Hz, 750 Hz and 1.5 kHz, falling within the sensitivity range of harbour seals (Goetz *et al.* 2011). These frequencies are notably above the sensitivity threshold of harbour seals up to (and possibly further than) 1500 metres from the devices. However, outside slack water periods, pressure levels over 1,000 metres from the devices often fall below ambient noise due to increased flow, rendering it increasingly unlikely that harbour seals could detect them at these distances (Goetz, Hastie & Sparling 2011). Aversive responses are consequently more likely to occur closer to the devices (up to ~1,000 metres) where the turbines are perceptibly louder, or potentially a greater distances in the instances where flow noise is low but flow speed has reached levels sufficient for turbine operations. However, as has been demonstrated in previous studies, novelty and threat perception, in addition to received sound pressure level, are equally important factors to consider when assessing why a seal may respond to a sound source (Deecke, Slater & Ford 2002; Hastie *et al.* 2017).

Partly due to the limited numbers of operational tidal turbine arrays, studies investigating the avoidance or attraction of marine mammals to turbine arrays, and the consequent changes in density and distribution have been limited to measuring responses to controlled acoustic exposures or single test turbines (Hastie *et al.* 2017;

Sparling, Lonergan & McConnell 2017; Joy *et al.* 2018). These studies showed that marine mammals do exhibit avoidance responses to single devices. Hastie *et al.* (2017) found that harbour seal abundance decreased significantly up to 500 metres from a speaker playing tidal turbine sounds. Similarly, Sparling, Lonergan and McConnell (2017) showed that seals transited past a test turbine at greater distances during operational periods. This dataset was further analysed by Joy *et al.* (2018) who incorporated environmental covariates, as well as the operational status of the turbine, to demonstrate an overall reduction in usage within a 200 metre buffer of the turbine site; this led to assumed avoidance rates of ~68%. Although useful in understanding the potential collision risks associated with single turbines, to ensure that the industry develops in an environmentally sustainable manner, data on the responses by animals to operational arrays of turbines is urgently required.

The largest tidal turbine array in the world (as measured by power generation potential and device size) is located off the north coast of Scotland. This is also an area with a relatively large, but rapidly declining, population of harbour seals (Fig. 1; Thompson *et al.* 2019). Major haulout sites on the north coast of Scotland are all within 10 km of the turbine array and there is likely to be significant overlap between the seals' at sea distribution and the turbine array (Jones *et al.* 2017). This study therefore aims to describe the patterns of at-sea distribution by harbour seals around a turbine array and quantify distribution changes in response to turbine presence and operation. While uncertainty around close-range cannot be specifically addressed with the presented data, this analysis aims at characterising potential displacement or attraction which can ultimately help to refine estimates of collision rates by augmenting our understanding of how relative abundances will be affected.

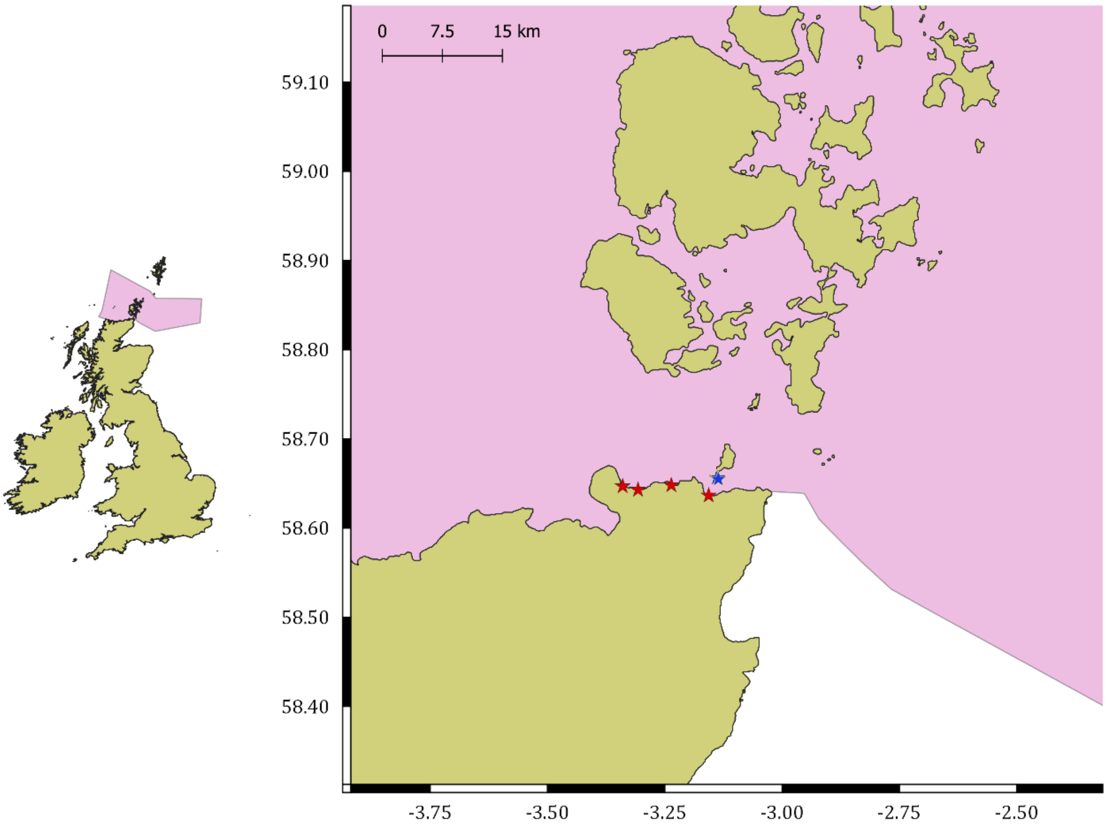


Figure 1 **North Coast and Orkney seal management unit.** The full UK map (left) shows the North Coast and Orkney UK Seal Management Unit delineated by the pink polygon. The Pentland Firth map (right) includes turbine locations indicated with blue stars and seal tagging locations indicated by red stars.

4.3 Methods

MeyGen Holdings Ltd. under the umbrella of SIMEC Atlantis Energy began installation of four 1.5 MW tidal turbines, three Andritz Hammerfest Hydro HS1500 turbines and one AR1500 turbine, in the inner sound of the Pentland Firth in January 2015 (Rajgor 2016). The installation of all four turbines was completed in February 2017 with full operations commencing in August 2017. The turbines were installed in a non-linear array between 96 and 286 metres apart. Each structure consists of six gravity-based, concrete ballast blocks as foundations (totalling 1,500 tonnes) anchoring each of the three turbine support structure legs, a nacelle, and rotors measuring 18 m in diameter. Given that the turbines are gravity based, the noise emitted during installation was relatively low compared to other installation techniques (e.g. pile-driving); therefore these periods were not considered as significant stressors and only the presence and operational periods were considered as potential drivers of distribution.

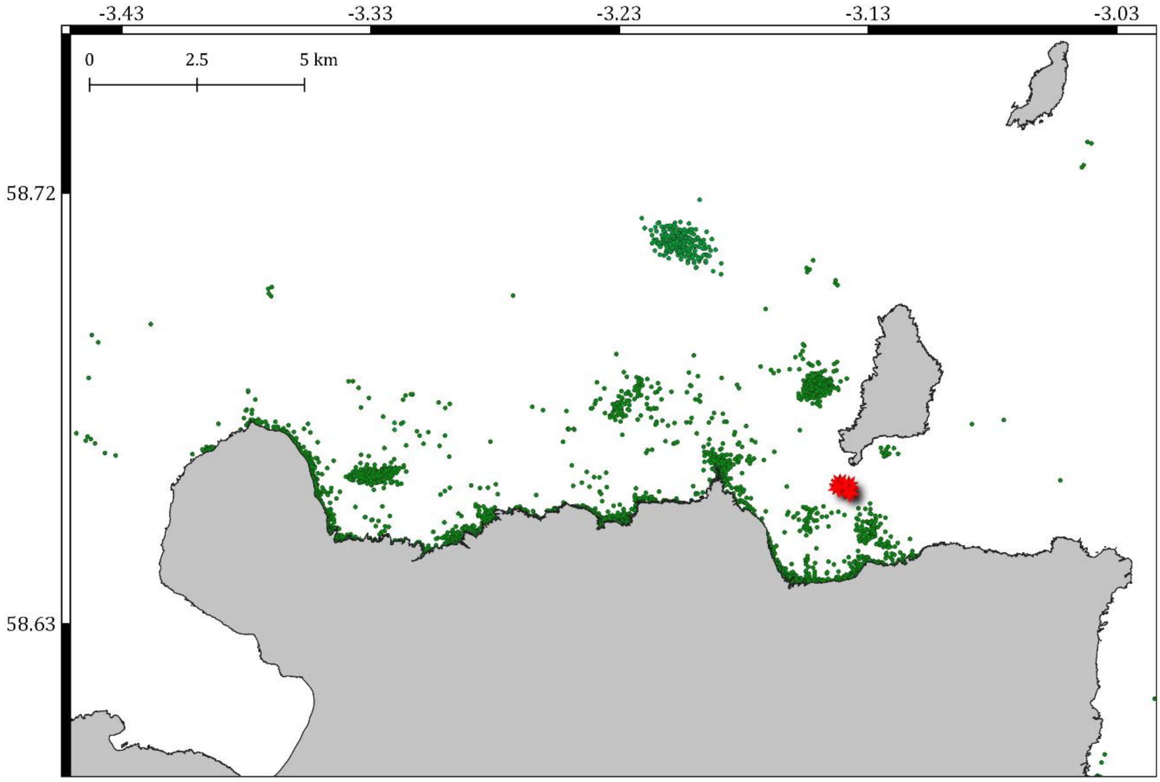
4.3.1 Telemetry data collection and processing

To measure the distribution of seals around the operational tidal turbine array, Fastloc® GPS/GSM tags (SMRU Instrumentation) were deployed on 14 harbour seals in 2011 and 2012, and Fastloc® GPS/UHF tags (Pathtrack Ltd.) were deployed on 40 harbour seals over 4 deployments in 2016, 2017 and 2018 (Chp. 2: Table 1, Fig. 2). For full details of tags, scheduling, and capture and handling protocols, see Chapter 2.

Given the potential for harbour seals to exhibit behavioural responses to the presence of turbines (Russell *et al.* 2014; Russell *et al.* 2016; Williamson *et al.* 2019) and/or to the operation of turbines (Hastie *et al.* 2017; Sparling, Lonergan & McConnell 2017; Joy *et al.* 2018), the data were analysed at two temporal scales. The first analysis compared the distribution of seals between periods when turbines were present or absent. Presence of turbines was assumed consistent from the final installation date and included periods when the turbines were generating and not generating. The second analysis only included data collected after the turbine installation date and compared distribution between periods when the turbines were generating and not generating electricity (see *section 4.3.2*).

Seal tracks were linearly interpolated to regularised 15-minute intervals to ensure data resolution was consistent between all individuals. A 15-minute interval was chosen as this represented a compromise between data-resolution differences between tag types (see Chp. 2 for details). Interpolated locations which fell within data gaps of >2 hours were determined to be unreliable and removed from the analysis. Further, data between May and September were removed to ensure that behavioural responses to the turbine array were not conflated with breeding and moulting phenology at this time of the year (Cordes & Thompson 2013).

Only return trips (trips with both a start and end haulout location within the Pentland Firth) were used in the analyses of distribution (Fig 2). Three individuals frequently used haulouts in Orkney and Shetland and foraged primarily outside the Pentland Firth, so were removed from the analyses. This effectively reduced the availability polygon used in the generation of pseudo-absences (see below) and ensured a suitably high-resolution prediction grid could be used to measure responses. All seal locations (and pseudo-absences) were assigned to one 500 m x 500 m grid-cell within the study site. These data were then used in the final analyses in which a use-availability framework was employed to assess the likelihood of animals using a particular site given a range of environmental or anthropogenic stimuli.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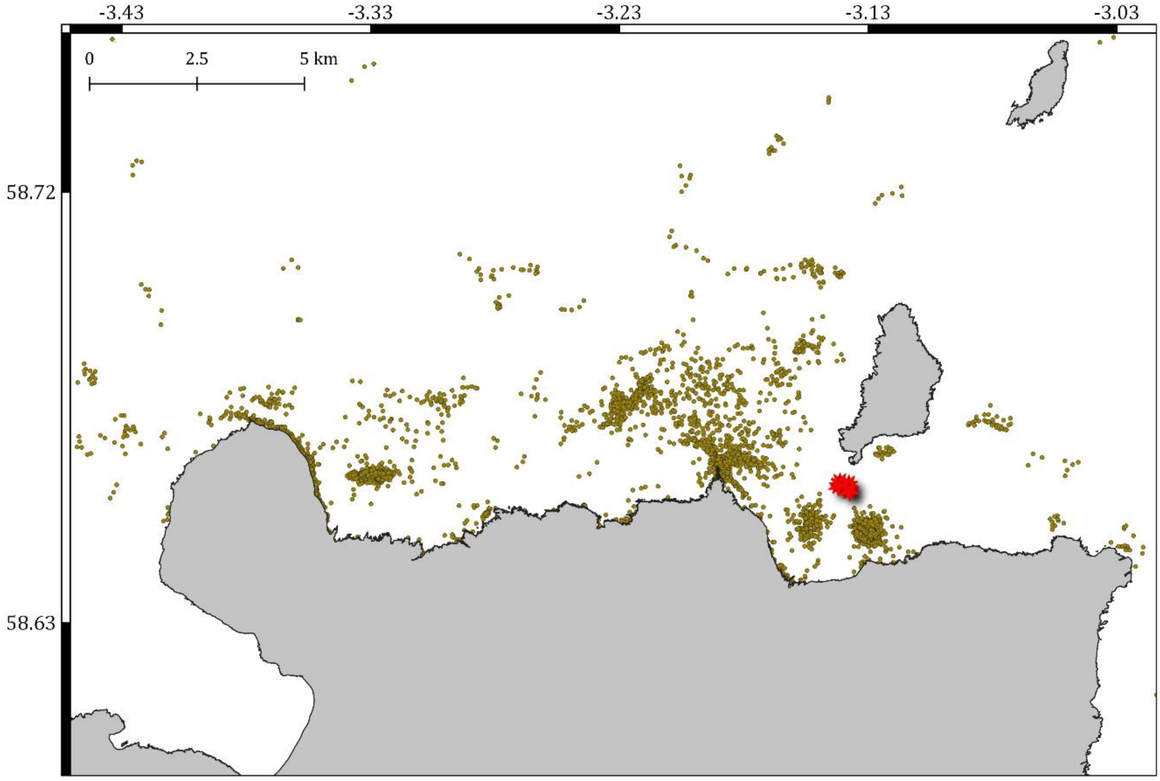
-3.33
-3.23
-3.13
-3.03
0
2.5
5 km
58.72
58.63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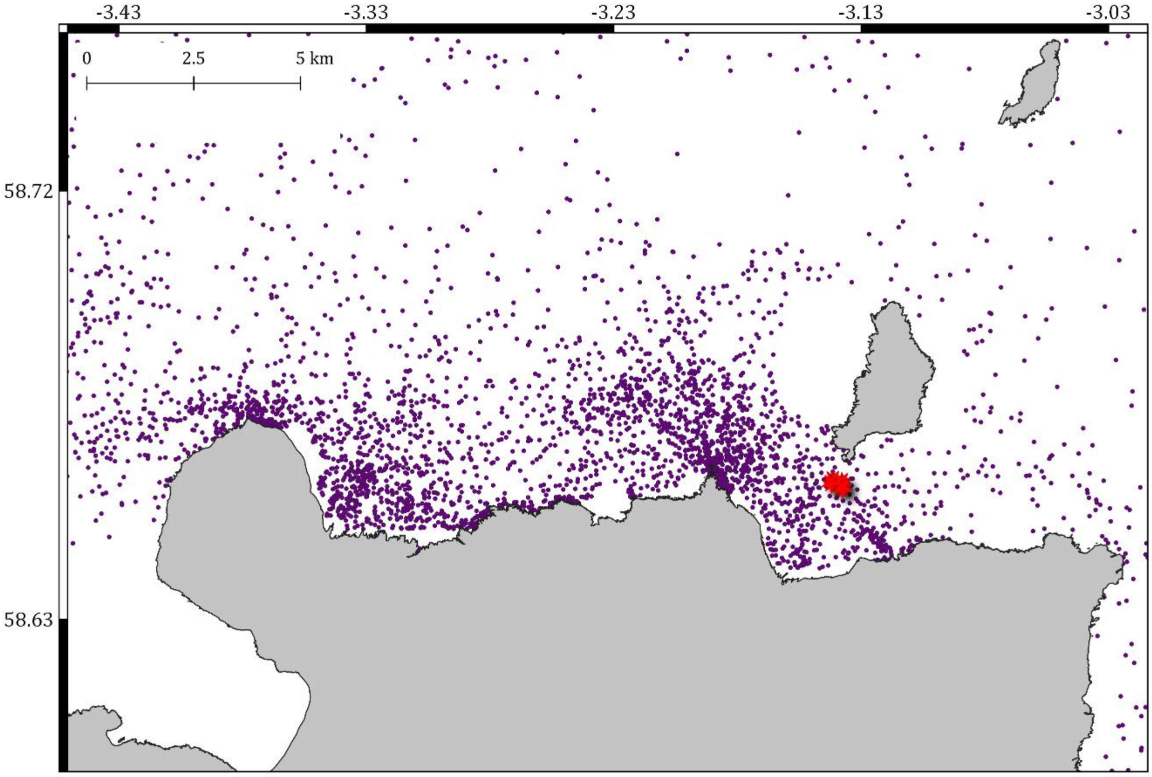

Figure 2 **All locations from return trips in the Pentland Firth by HMM derived behavioural state (chapter 2).** (top) All "Geo-Hydro foraging" locations, (middle) all "swimming against the current" and (bottom) all drifting with the current locations. Red stars represent turbine locations. Future references to the 'study site' in this chapter should be thought of as the rough extent of these maps.

4.3.2 Covariate data

Turbine operational data were provided by the turbine developers SIMEC Atlantis Energy Ltd. A continual time-series from 1st October 2017 to 1st January 2019 were provided at a 1-minute resolution detailing RPM of the turbine, and the power generation. A binary response variable of 'operating' or 'not operating' was assigned to each seal location based on the power generation data. A value of 5 kW was used as a threshold for operation; this was based on correlation plots which confirmed that a power generation threshold of 5 kW could be used to determine an acoustic output of the device. Accompanying passive acoustic monitoring mounted on the base of one of the turbines confirmed that peak noise generation of the device was achieved at an approximate power generation threshold of ~5 kW (Palmer *et al.* 2019; Fig.3). Source level was constant above this. Any seal locations associated with power generation values below this were considered to be in non-operational periods. The acoustic signal of the turbines showed a peak frequency at 20 KHz (Fig. 3). This frequency falls within the peak sensitivity of harbour seals (Cunningham & Reichmuth 2016) and therefore can be assumed to be detectable at close ranges. However, no maximum detectable range was assumed, and all seal locations were considered 'exposed' during periods of operation regardless of distance to the source. Non-operational periods included instances where the turbine was rotating but not generating electricity and therefore periods where the seals could detect the motion of the turbine if in visual range. However, due to the resolution of distribution being estimated in this study, this should not affect final estimates of avoidance as close-range evasion is not being considered.

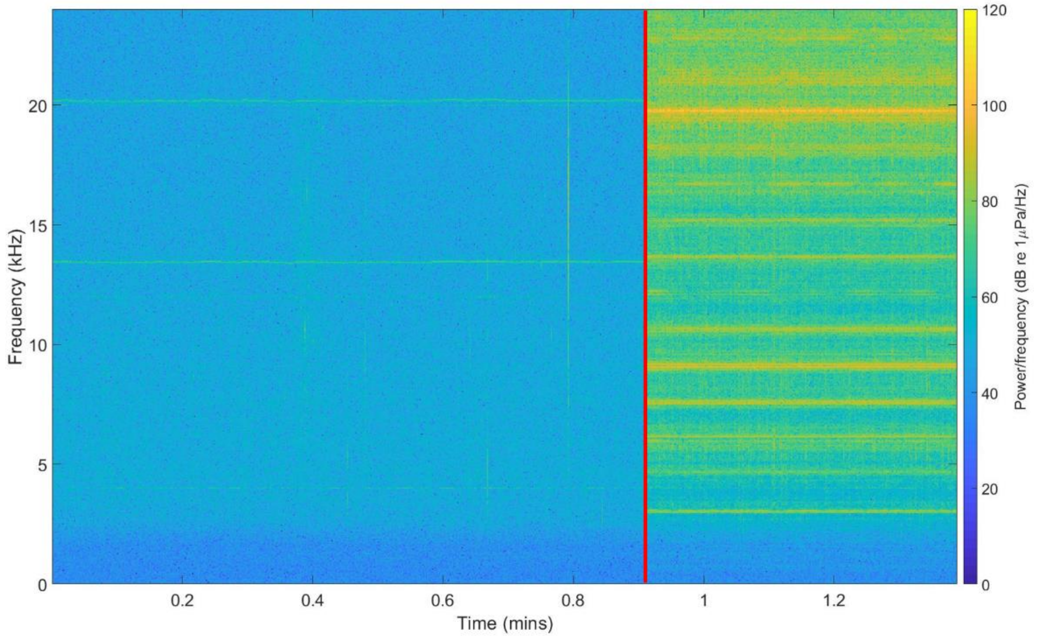

Figure 3 **Acoustic signature of the turbine power generation.** Spectrograms were used to determine the threshold at which the acoustic signal peaks. The red bar indicates the onset of power generation values exceeding ~5 kW.

Given the influence of tidal state on harbour seal behaviour at sea (Chp. 2), it was also included as a covariate for testing. Although the operational status (power extraction and rotor RPM) of a fully operational tidal turbine is expected to be highly colinear with tidal state, this turbine array was in a demonstration phase and there were numerous periods when the turbines were not operating (Fig. 4). Non-collinearity was confirmed using variance inflation factors calculated using the '*vif*' function in the R package '*car'.* This enabled tidal state to be tested in the same models as turbine operation, and to predict seal distributions as a function of both tidal state and turbine operational state. Tidal state information was extracted from the tidal prediction software POLPRED version 2.003 (National Oceanography Centre, Liverpool, UK). Given the relatively small study area and short trip distances of harbour seals, tidal state (low and high waters) were predicted for a single point at the centre of an availability polygon (see below for definition of availability polygon). The difference between the time stamp of the location and the nearest high water time was then calculated and a continuous variable of 'Time Around High Water' (-6 hours : 6 hours) was created to match seal locations to tidal state (Fig. 4).

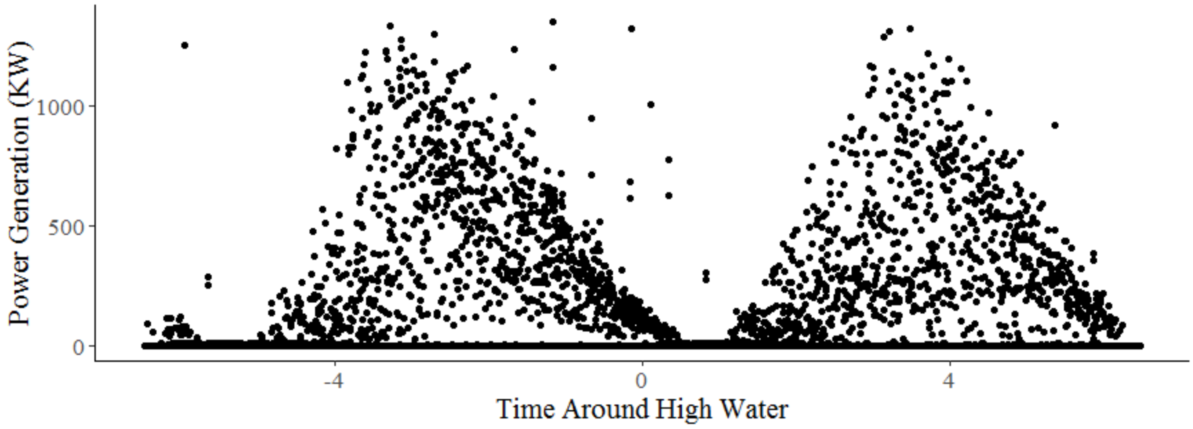

Figure 4 **Power generation by the turbine array**. Power generation as a function of tidal state.

4.3.3 Statistical Analysis

A use-availability design was used to analyse the seal location data to model population distribution as a function of both the accessibility and selection of areas (Matthiopoulos 2003). If all points in a given area are assumed to be equally available to an individual, then that individual's preference can be thought of as directly correlated to its distribution (Matthiopoulos 2003). However, harbour seals are central place foragers and are ultimately constrained by distance to suitable haulouts (Stephens & Krebs 1986; Bailey, Hammond & Thompson 2014) so this assumption of equal availability across all space is violated. Here, the geodesic distance between all seal locations and the haulouts of departure and return were calculated for each trip. Maximum distance travelled within each trip was then determined as the longest geodesic distance between a location and a haulout, A single availability polygon was then created based on this maximum distance regardless of whether it was the haulout of return or departure. In other words, the largest distance value of all trips across all individuals was used as the radius of the accessibility polygon. For each observed presence point, two temporally matched, randomly placed pseudo-absences were generated within the accessibility polygon. These pseudo-absences can be thought of as way of modelling telemetry tag data to resolve individual preference by including information about locations which were available but were not selected by the observed individuals.

Each model was fit using a binary response of 0=pseudo-absence and 1=presence as the dependant variable. Using this, the modelling exercise attempts to predict the likelihood of a seal being present in any given grid-cell as a function of the covariates described above. Complex Region Spatial Smothers (CReSS) were used to ensure smoothing around coastlines was carried out using geodesic distances rather than typical spatial smoothing algorithms such as thin-plate splines which employ Euclidean distances to measure point to point similarity (Scott-Hayward *et al.* 2014). CReSS smooths were employed in combination with Spatially Adaptive Local Smoothing Algorithms (SALSA) to select for the most appropriate number and location of knots. SALSA varies the position of knots from a starting point of even knot distribution in a smooth term, such as would be employed by a typical cubic β-spline in statistical packages such as '*mgcv*' (Wood 2015; Wood 2017). The algorithm then iteratively changes the knot positions and refits a model, conducting automated model selection using pre-defined selection criteria (e.g AIC). This algorithm has recently been adapted to specifically investigate the effects of anthropogenic structures on marine species distributions using survey data (Scott-Hayward *et al.* 2013b) and is appropriate for studies using telemetry data to assess changes in distributions using use-availability designs (Russell *et al.* 2016). Smooth terms were initially fit in a Generalised Additive Model (GAM) framework to establish appropriate knot locations. Traditional GAM inference assumes independence between model residuals and therefore fitting models to telemetry data often violates this assumption given the likelihood of sequential data points being heavily dependent on temporally adjacent observations (Pirotta *et al.* 2011). Final models were therefore re-fitted using Generalised Estimating Equations (GEE) to account for the inherent temporal autocorrelation in telemetry data. GEEs allow for entire time-series of data to be modelled in a regression analysis while explicitly accounting for residual auto-correlation (Pirotta *et al.* 2011; Hardin & Hilbe 2012). This approach require data to be split into discrete panels, between which independence is assumed but within which the autocorrelation is accounted for through robust, sandwich-based estimates of variance (Pirotta *et al.* 2011). Different panel criteria were tested for post-hoc through an assessment of autocorrelation function plots. Results suggested that individual seal was the most appropriate panel size for this analysis. However, only presences were included in the individual panels given that pseudo-absences were randomly generated and therefore likely to cause an underestimation of autocorrelation between data points if included. All pseudoabsences were included in separate panels before final models were run.

Model selection proceeded through a 2-stage process. Firstly, backwards, stepwise selection using quasi-likelihood information criterion (QIC) scores was conducted by iteratively removing covariates until no further improvement was noted. QIC is analogous to Akaike's Information Criterion (AIC) commonly used in logistic model selection but is adapted for use with models which are based on quasi-likelihood. A ΔQIC score of -2 between sequential models was considered an improvement (Burnham & Anderson 2002). Marginal p-values for each covariate from the minimal adequate model (i.e. the final selected model from the backwards, stepwise selection protocol using QIC) were then calculated using the '*getPvalues*' function in the R package '*MRSea*' (Scott-Hayward *et al.* 2013a). Using a p-value significance threshold of 0.05, non-significant covariates were removed, and significance was re-tested until all significant covariates were retained.

Model validation was conducted by comparing fitted versus observed values using the area under the curve (AUC) of the receiver operating characteristic (ROC) curve for each model to determine thresholds in the construction of confusion matrices (as per Pirotta *et al.* 2011). These allow the percentage of false-positives and false-negatives to be compared to true positives and negatives, and can therefore be used to assess relative model fit (Fielding & Bell 1997; Pirotta *et al.* 2011).

The exponent of the linear predictor from the final logistic model was used to generate predictions of distribution as per Beyer *et al.* (2010). A prediction grid comprised of 500 m x 500 m grid-cells was constructed and predictions for all retained covariate combinations were generated. Uncertainty around estimates were calculated through a parametric bootstrap process and presented as 95% confidence intervals. Final predictions were normalised to 100 to represent the percentage of the population (and percent changes between scenarios) to provide a biological context to prediction values. Grid-cell specific significance was finally determined based on whether the confidence intervals for any given cell spanned 0; a significant decrease was reported if upper and lower confidence intervals fell below 0 in that cell, and a significant increase was reported if both confidence intervals fell above 0.

4.4 Results

A total of 1,878 and 1,059 seal days of data were collected within the delineated study site (Fig. 2) for analysis of the effects of the presence and operation of the turbines, respectively. This included a total of 2,012 and 1,156 trips to sea within the study site, for the presence and operation analyses respectively. Overall patterns of movement were indicative of frequent transit behaviour rather than prolonged residency in the areas immediately surrounding the turbines.

Overall, model performances were good, and the confusion matrices indicated that 85% and 78% of predictions were correct with AUC scores of 0.69 and 0.81 for the effects of turbine presence and turbine operations, respectively (Table 1).

Table 1 **Model validation.** Performance checking for both turbine presence and turbine operations models, with 2 pseudo-absences per observed presence.

Model	*Turbine Presence*			*Turbine Operation*		
AUC	0.69			0.81		
Confusion Matrix		*Observed*			*Observed*	
	Predicted	1	0	*Predicted*	1	0
	1	13794	3175	1	9532	5612
	0	3655	31723	0	2477	18406
Total Observed		17449	34898		12009	24018
Confusion Matrix (%)		*Observed*			*Observed*	
	Predicted	1	0	*Predicted*	1	0
	1	79.05	9.10	1	79.37	23.37
	0	20.95	90.90	0	20.63	76.63

4.4.1 Effects of Turbine Presence

Seal distribution was strongly influenced by tidal states with marked differences in distributions between low and high water. The final model selected through QIC and marginal P-value only retained the smooth of tidal state and the interaction between location and the smooth of tidal state as explanatory covariates. Seal abundance was predicted to be greater in the western region of the study site during ebbing tide but showed a more dispersed pattern during the flood tide and high water (Fig. 5). Distribution across the site was highest around high water than any other state of tide (Fig. 5). Distribution around low water showed higher abundance in grid-cells close to haulout sites, compared to other states of the tide.

Presence of the turbine array did not significantly influence at-sea distribution (Table 2) but was retained in model selection using QIC criteria (Table 2). This result suggests that some difference was noted when predicting seal distributions between the two conditions but did not significantly affect the observed changes across the study period.

Table 2 **Turbine presence model selection**. Marginal p-values generated from repeated ANOVA tests for each covariate in the model including turbine presence as a covariate. Values in bold indicate term retention through ΔQICu and significance at the 0.05 level. Colons (:) indicate interaction terms. ΔQIC_u represents change from the full model including all covariates; 37908.62.

Covariate	*ΔQIC_u upon term removal*	*Marginal p-value*
Turbine presence	**+112.2**	0.062
s(Location (lat, lon))	**+262.5**	**<0.0001**
Tidal Phase	**+62**	**0.011**
Tidal Phase : s(Location (lat, lon))	**+330**	**0.02**
Turbine presence : s(Location (lat+lon))	-71	0.22

4.4.2 Effects of Turbine Operation

The model selected through QIC and marginal P-value assessment retained all covariates and interactions; importantly, both tidal state and turbine operation were retained as explanatory covariates. Further, the interaction terms between turbine operations and location, and between tidal phase and location were retained.

Inspection of the model predictions showed that seal presence decreased significantly up to 2 km from the centre of the turbine array during operational periods. Point estimates of percentage change in grid-cells within this area ranged between -24% and -39%; mean change in usage across all grid cells within 2 km of the turbine was -27.6% (mean 95% C.Is: -11% and - 77%).

Abundance also significantly increased within an area in the northern region of the study site during turbine operation. Further increases were predicted between 4 and 13 km from the centre of the turbine array; however, at these distances, increases were not significant (i.e. bootstrapped confidence intervals of usage change in these grid-cells spanned 0). Distribution predictions suggested similar tidally mediated distributions as the previous (turbine presence) model predictions; seal distribution was predicted to be greater in the western region of the study site during ebbing tide but showed a more dispersed pattern during flooding tide and high water (Fig. 5). Abundance across the site was highest around high water than any other state of tide (Fig. 5). Distribution around low water showed higher abundance in grid-cells close to haulout sites, compared to other states of the tide.

Table 3 **Turbine operations model selection.** Marginal p-values generated from repeated ANOVA tests for each covariate in the model including turbine operational status as a covariate. Bold values indicate term retention through ΔQICu and significance at the 0.05 level. Colons (:) indicate interaction terms. ΔQIC_u represents change from the full model including all covariates; 27845.62.

Covariate	*ΔQIC_u upon term removal*	*Marginal p-value*
Turbine operational status (on/off)	**+210**	**0.022**
s(Location (lat, lon))	**+311.1**	**<0.0001**
Tidal Phase	**+114**	**0.032**
Tidal Phase : s(Location (lat, lon))	**+75.7**	**0.029**
Turbine operational status: s(Location (lat+lon))	**+39.8**	**0.042**

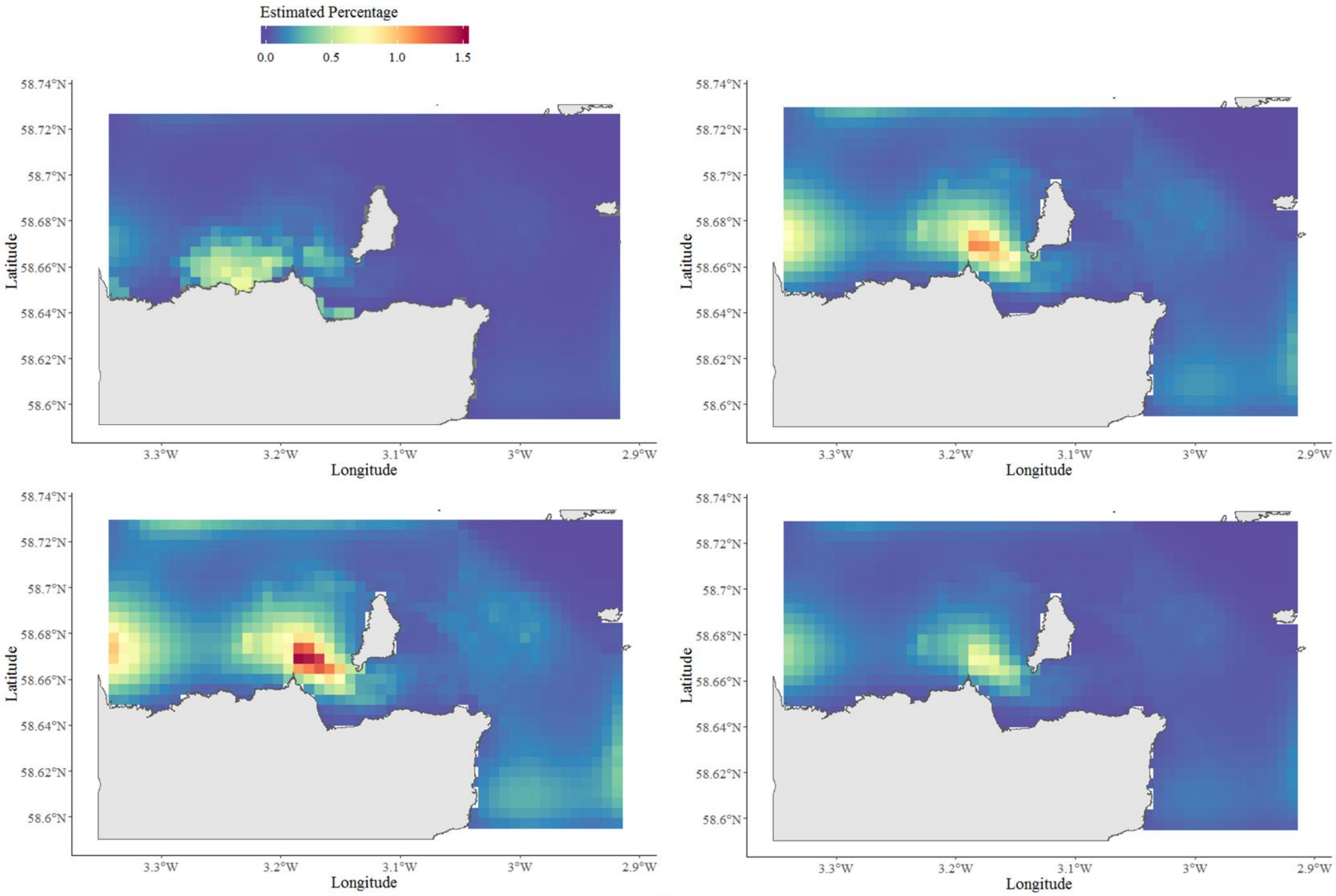

Figure 5 **Predicted distribution of seals in the inner Pentland Firth as a function of tidal phase**. (top left) Slack low water (top right), mid-water flood tide (bottom left), slack high water, and (bottom right) mid-water ebb tide. Scale bar represents the estimated percentage of the maximum at-sea population, per 500 m x 500 m grid-cell.

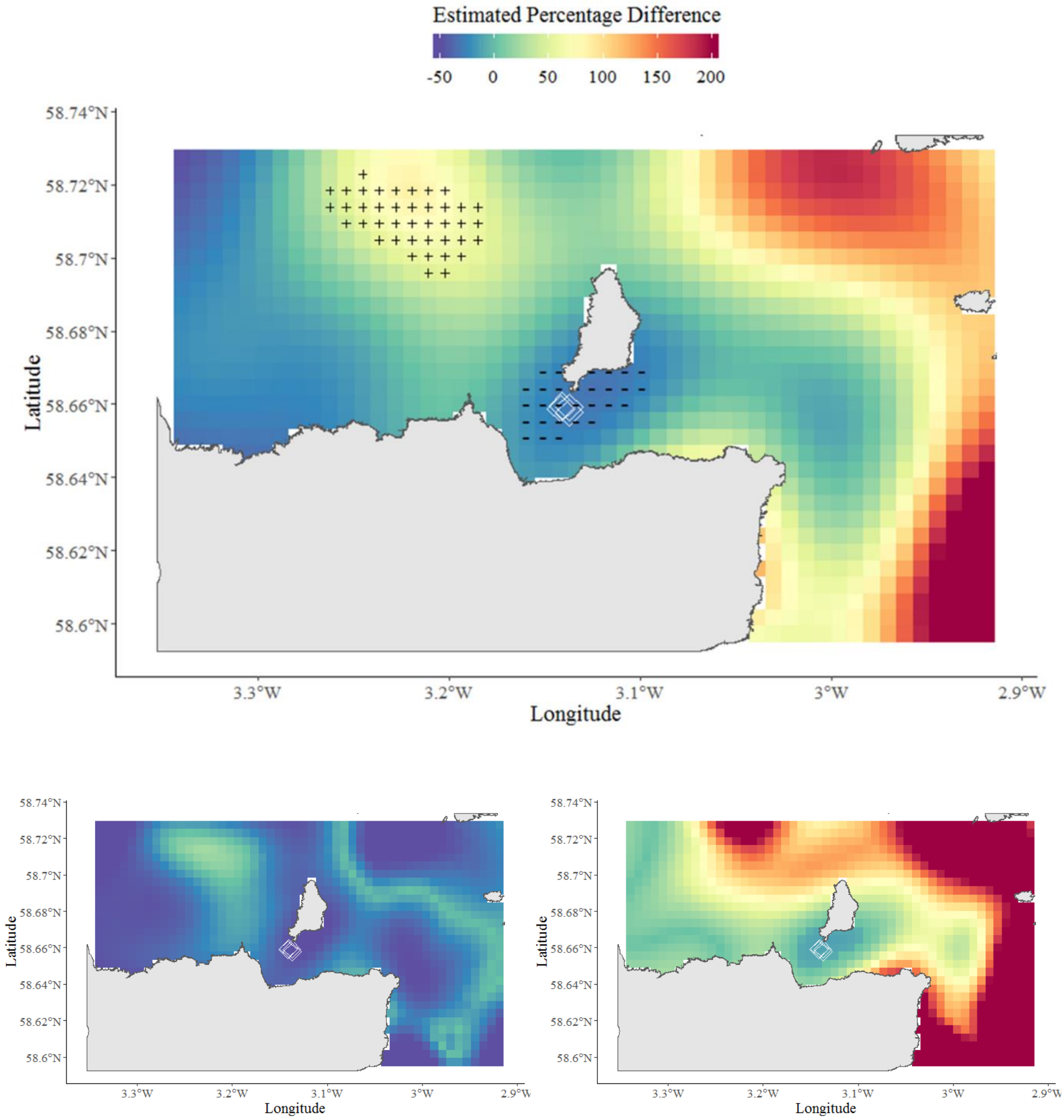

Figure 6 **Predicted changes in distribution between non-operational and operational periods in the inner Pentland Firth.** The scale represents the predicted percentage change in usage as a proportion of the at-sea population of harbour seals. The turbine locations are highlighted with white diamonds. Negative (-) and positive (+) symbols denote cells with a significant decrease or increase in abundance respectively. Significance was calculated through parametric bootstrapping and each grid cell was assessed to determine whether 95% confidence intervals spanned 0. Mean predictions (top), lower (bottom left) and upper (bottom right) confidence intervals around the mean are provided.

4.5 Discussion

The results presented here show, for the first time, that seals exhibit apparent responses to a commercial-scale tidal turbine array, with significant changes in their at-sea distributions relative to the array. Although there was no measurable impact of the presence of the array, seals exhibited a spatial response to the operation of the turbines; there was a significant decrease in seal abundance up to 2km of the array when the turbines were generating power.

A small but insignificant decrease between pre and post-installation periods was observed in grid-cells close to the turbine array. This suggests that the presence of the turbines did not elicit significant avoidance responses by seals. However, it is important to highlight that it is possible that the observed decreases are real, but the analyses suffered from a lack of statistical power. The turbines were not fully operational for the entirety of the post-installation period, meaning changes between these periods may be more difficult to resolve if seals only responded to the operations rather than presence. Further, the relatively small, pre-installation sample size may have hindered the ability of detecting a change. Over a longer period of exposure to the presence of the turbines, or a larger pre-installation sample size, a significant change in population distribution may have been apparent; however, it is unclear how effects may change with changing operational frequency and array size. Nevertheless, these results suggest that, over the time period of the study, seals are not significantly attracted to individual turbine structures for foraging as has been observed at offshore wind turbines (Russell *et al.* 2014; Russell *et al.* 2016). Given the lack of significant differences between pre and post installation distributions, it seems unlikely that foraging opportunities have been reduced by the turbines. It must be noted that the time period of this study is likely too short for epifaunal communities to fully establish to the point at which they become attractive for predators. However, it has been suggested that these tidal turbines are being used as refuges for pelagic fish species so seal prey abundance within the immediate vicinity of the turbines may be seen to be increasing, even in the absence of established epibenthic communities (Williamson *et al.* 2019). Regardless, this potential increase in prey density does not appear to have influenced the abundance of seals in the channel.

The result showing that abundance decreases significantly during operational periods up to 2 km away from the array is an important one and suggests turbine operation may be perceived as aversive by seals. This is markedly further than previous reports of harbour seal (Hastie *et al.* 2017; Sparling, Lonergan & McConnell 2017; Joy *et al.* 2018) responses to the sounds or operation of a single turbine. This supports previous hypotheses that the seals respond to an acoustic rather than visual cue, given that turbidity in such an energetic environment and the relatively fast attenuation of light in water likely precludes visual detection beyond a few tens of metres. Harbour seals are acoustically sensitive to frequencies between 1 and 120 KHz at received levels as low as 60 dB re 1μPa (Cunningham & Reichmuth 2016) and behavioural responses (i.e. avoidance) to anthropogenic sounds have been noted in several captive and wild studies of harbour seals (Hastie *et al.* 2014; Russell *et al.* 2016; Hastie *et al.* 2017). Although there is limited data on the acoustic output of the tidal turbine array in the current study, previous studies of the SeaGen turbine at Strangford Lough reported an estimated broadband RMS source level of 174 dB re 1μPa-m (Goetz *et al.* 2011; Robinson & Lepper 2013). Despite this relatively high level, during high flow conditions when the turbines were operating, all estimated 1/3 octave band received levels above 1kHz dropped below ambient conditions at a range of 190-210 m. Recent recordings using drifter buoys at the MeyGen turbine array suggest that the acoustic signal of one of the turbines remains above ambient levels up to ranges of approximately 2 km from the device (Rische & Wilson, *pers comm*). This suggests that during periods of power generation, the turbine is likely to be audible to seals at distances of up to 2 km and potentially explains the distance of the observed reduction in seal usage in the present study.

The observed reductions in abundance during operational phases have important applied and biological implications. Specifically, concerns about the potential negative effects to marine mammals mainly derive from the potential for collisions with turbine blades. The population level effects of these interactions are currently predicted using collision risk models which scale estimated animal density by an assumed avoidance rate to calculate the number of expected collisions in a given period (Wilson *et al*. 2006; Band *et al*. 2016). Using the Band Collision Risk model (2016) together with pre-installation density estimates consistent with this study and no avoidance rate, an estimate of 54 (25 – 96) collisions per year would be predicted (Band *et al.* 2016). Using the lower and upper confidence intervals of avoidance in the grid-cell containing the turbines (-49% and -11%) collisions would be reduced by between 6 - 27 seals per year. Although potentially positive, the reduction in collision risk during operational periods must be viewed alongside potentially persistent negative effects such as the obstruction of important foraging opportunities or transit routes. However, no significant change in overall distribution was observed between pre and post installation periods suggesting important foraging areas have not significantly changed as a result of exposure to turbines. This combination of factors suggests that, overall, a reduction in usage in this site is likely a beneficial response to turbine operations; foraging opportunities do not appear to be markedly reduced as the seals demonstrate a statistically similar distribution pattern overall, regardless of turbine presence and only appear to avoid the area when the turbine is operating reducing the potential for collisions.

Although these results are a significant step forward in terms of understanding the effects of tidal turbine arrays, making broader predictions from the results should be carried out with a degree of caution. For example, tidally energetic sites are, by their nature, highly heterogenous in their oceanography and geography, and differences between sites may be important in determining how animals in discrete populations will respond to these devices. For example, previous observations of harbour seal avoidance responses to tidal turbines and tidal turbine noise, have all been made in narrow channels (Kyle Rhea, Scotland and Strangford Lough, Northern Ireland) (Hastie *et al.* 2016; Hastie *et al.* 2017; Sparling, Lonergan & McConnell 2017; Joy *et al.* 2018)where turbines (or turbine sound sources) were either situated near intensively used areas or between haulouts and putative foraging sites. Conversely, baseline data for the Pentland Firth suggests that the inner sound where the turbines are installed is not an important foraging site which, even in the absence of devices, is used primarily as a transit route. Given this, the area to the north of the island of Stroma is also available to the animals to transit between haulouts and foraging sites to the northern and eastern regions of the Pentland Firth. Further, the at-sea usage hotspots presented here show some important at-sea areas >2 km to the west of the north-west turbines which would not require passage within audible range of the devices. If turbine arrays were perceived as barriers to movement, unlike areas such as Strangford Lough and Kyle Rhea, the seals here may have additional options for transit to foraging sites. It is therefore important to consider, not only the abundance of animals in an area but also the motivation that those animals have to be in the area when looking to predict avoidance responses in other areas.

The presented results appear compelling; however, there are several caveats and potential limitations in the study design and analytical framework which should be considered. For example, the use of pseudo-absences as control points assumes that the entire area of the study site is available to each individual, that this availability is temporally consistent, and that distance from haulout is the only feature which limits an animal's range or movement. This particular study area presents some potential issues which may violate this assumption. Specifically, tidal currents in some areas of the Pentland firth often reach speeds in excess of the maximum burst speed of a harbour seal (4 m.s-1; Williams & Kooyman 1986). It is therefore likely that there is spatial and temporal heterogeneity in availability across the study area as high current speeds will preclude the ability of the seals to swim against them potentially rendering areas inaccessible. While the addition of tidal state as a covariate in the models goes some way to accounting for this, considering these results an example of traditional 'habitat preference' is likely erroneous and one would be more suited to consider these results 'extrinsically forced seal distribution'. This distinction is important when developing concepts about the drivers of observed usage patterns in highly dynamic environments; seal movement must be considered a function of both preference and forcing, and future studies may seek to account for this by weighting absences according to more biologically relevant accessibility criteria.

The use of confusion matrices to validate model fit can be questionable for use-availability designs given the fact that this ultimately tests the ability of the model to detect true-absences when indeed the absences are randomly generated. Given the relative lack of non-likelihood based methods of assessing model fit (as is required for a GEE framework), final models were refit to a random subset of data with 2, 5, 7 and 10 pseudo-absences and confusion matrices were constructed for each to compare the relative fit between models covering increasing proportions of the available habitat. Little difference was noted between these values so final models were run using two pseudo-absences per presence point to maximise computational efficiency. Whilst absences remained randomly generated, this allowed for an assessment of how representative the models of the available habitat were by quantifying how many absences per presence point are necessary to gain a representative result in this particular study site (Keating & Cherry 2004; Manly *et al.* 2007; Aarts *et al.* 2008). This method of validation was also deemed reasonable in this scenario given the large number of individuals sampled, relative to the total population size and the study area; it has been suggested that larger scale studies are less prone to the problem of placing pseudo-absence points where animals (not observed) actually were (Aarts *et al.* 2008). Therefore, the assumption of pseudo-absences being representative of true absences is increasingly tractable when more individuals are sampled over the same time period.

In terms of future work, a key avenue of research to allow accurate predictions of the effects of tidal turbines is the fine-scale behaviour in close proximity to operating tidal turbines. The results presented here have shown the frequency of encounters between seals and turbines is likely to be reduced; however, individuals not exhibiting avoidance at the scales measured here may still be vulnerable to collision. Future studies should seek to track animals' three-dimensional movements at scales of metres around individual operating turbines. This could be achieved with sophisticated biologging devices or the employment of active acoustic monitoring systems such as sonar (Hastie *et al.* 2019a; Hastie *et al.* 2019b). Assessing the near-field environment to observe long-term, multi-species reactions in combination with this type of larger scale distribution analysis should help to resolve the multi-dimensional effects of the tidal energy industry and help understand the effects of such devices on trophic interactions in the surrounding area.

4.6 Conclusions

This study has shown that harbour seals respond to the operations of a tidal turbine array, with a reduction in abundance of up to 39% within a 2 km buffer zone of the turbine array. However, overall distribution does not appear to be affected by the presence of the turbines. This represents an important step in determining the environmental impact of such devices. Nevertheless, it is only with continued monitoring of local population trajectories, long-term movements of animals in response to prolonged exposure and increasing array sizes, and information on fine-scale behaviour around turbines, that the true long-term effects of tidal energy industry can be determined.

Chapter 5

Empirical determination of severe trauma in seals from collisions with tidal turbine blades

"I find your lack of injuries disturbing"

This chapter has been published as:

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5.1 Student's contributions

I, Joseph Onoufriou, conceived the study and, with significant assistance from Dr. Dave Thompson and Mr. Simon Moss, designed the methodology and conducted the trials for this chapter. With the assistance of Dr. Andrew Brownlow, I conducted the CT scanning and post-mortem analysis of all carcasses, digitised data and developed the scoring system for pathological indicators of mortality. In addition, I independently carried out all data analysis and writing. In summary, I was integrally involved in all aspects of conception, design, data collection, analysis and dissemination of this work.

5.2 Abstract

Tidal energy converters (turbines) are being developed in many countries as part of attempts to reduce reliance on hydrocarbon fuels. However, the moving blades of tidal turbines pose potential collision risks for marine animals. Accurate assessment of mortality risk as a result of collisions is essential for risk management during planning and consenting processes for marine energy developments. In the absence of information on the physical consequences of such collisions, predicting likely risks relies on theoretical collision risk models. The application of these at a population level usually assumes that all collisions result in mortality. This is unlikely and the approach therefore produces upwardly biased estimates of population consequences. In this study, I estimate the pathological consequences of direct collisions with tidal turbines using seal carcasses and physical models of tidal turbine blades. I quantify severe trauma at a range of impact speeds and to different areas of seal carcasses. A dose-response model was developed with associated uncertainty to determine an impact speed threshold of severe trauma to use in future collision risk models. Results showed that severe trauma was (a) restricted to the thoracic region, with no evidence of injury to the lumbar or cervical spine; (b) only observed in collision speeds in excess of 5.6 $m.s^{-1}$ (95% c.i. 4.4 to 6.6) and (c) affected by body condition with increasing blubber depth reducing the likelihood of severe trauma. Synthesis and applications: This study provides important information for policy makers and regulators looking to predict the potential impacts of tidal turbines on marine mammals. I demonstrate that the probability of severe trauma in seals due to collisions with turbine blades is highly dependent upon collision speed, and that the majority of predicted collisions are unlikely to cause fatal skeletal trauma. I recommend that collision risk models

incorporate appropriate mortality assumptions to ensure accurate estimates of the population consequences are produced in risk assessments for tidal turbine deployments.

5.3 Introduction

Over the past few decades, marine environments have experienced rapid industrialisation, with increases in marine transportation, oil and gas exploration and extraction, aquaculture and fisheries (Smith 2000). Many of these activities can lead to negative impacts such as vessel collisions (Vanderlaan & Taggart 2007) and fisheries gear entanglement and bycatch (Read, Drinker & Northridge 2006) which pose acute traumatic risks to marine mammals. In many cases, the nature and extent of human interactions can have important consequences for the demographics of affected populations and pose an existential threat to some species (Read, Drinker & Northridge 2006).

More recently, a number of novel technologies in the marine energy sector have emerged that have the potential to kill or injure marine species. For example, tidal stream energy extraction is being developed in several countries; this is typically carried out using large floating or seabed-mounted turbines that extract kinetic energy from tidally-driven, moving water (Boehlert & Gill 2010; Sparling, Lonergan & McConnell 2017). Proposed energy developments comprise large arrays of such turbines deployed in tidally energetic coastal environments (Boehlert & Gill 2010). Evidence also suggests that marine predators are attracted to tidally energetic regions (Alldredge & Hamner 1980; Wolanski & Hamner 1988). Further, static structures may increase primary productivity through artificial reefs which are known to attract top-predators (Todd *et al.* 2009; Russell *et al.* 2014). The likely spatial overlap between tidal turbines and marine mammals has led to concerns about potential impacts on these species. Rotor speeds are often relatively high, with tip speeds of up to 12 $m.s^{-1}$ (43 km/hour; Sparling, Lonergan & McConnell 2017), three times the collision speeds thought to kill large cetaceans during ship strikes (Vanderlaan & Taggart 2007). Although there is evidence to suggest that seals exhibit avoidance responses to the acoustic cues of tidal turbines (Hastie *et al.* 2017; Chapter 4; Sparling, Lonergan & McConnell 2017; Joy *et al.* 2018), estimated avoidance rates are not absolute and there remains a potential that collisions with rotating turbine blades may cause direct mortality.

The risk of collisions with marine mammals depends on the numbers of animals at the tidal sites, their natural behaviour and any behavioural responses to encountering turbines. At present there are no empirical data on collision rates between marine mammals and operating turbines, and no information on the physical consequences of such collisions. Predicting the impacts of tidal turbines on marine mammals therefore relies on theoretical collision-risk models (CRMs). These combine available information or assumptions about animal behaviour and the spatial and temporal patterns of animal abundance to estimate numbers of potential collisions between animals and turbines. Estimates can then be used to predict population consequences of proposed turbine deployments (e.g. Band, 2000; Wilson *et al.* 2006; Band, 2016).

Currently, CRMs require information on animal movement to estimate the number of times an animal would be predicted to encounter a turbine blade in the absence of close-range evasion responses. There are two CRMs widely used to quantify collisions between marine mammals and tidal turbines: 1) the Scottish Association for Marine Science (SAMS) Research Services Limited (SRSL) Encounter Rate Model (Wilson *et al.*

2006) which estimates the overall rate of collisions between animals and turbines using an adaptation to a predator-prey model by Gerritsen and Strickler (1977), and 2) the modified Band collision risk model (Band *et al.* 2016) which estimates the risk posed to individual seals during a nominal number of transits through a simulated turbine. There is, however, very few data to inform the potential for fine-scale avoidance behaviour (Wilson *et al.* 2014a; Bald *et al.* 2015), so estimates from these models are often un-realistic. Further, there is no data to inform how severity of collisions may vary over a tidal cycle and between individuals. In lieu of these data, estimates are still required in order to approximate the environmental impact of such devices, however these values carry with them a necessarily high degree of uncertainty.

To date, estimates of population level effects have been based on a precautionary assumption that all collisions result in death or permanent disablement of the animals involved (Wilson *et al.* 2006; Band *et al.* 2016). This assumption is unlikely to be true for all cases, and the models may therefore produce inaccurate predictions about the effects on populations of marine mammals. Further, although it may be reasonable to assume that high speed collisions will cause injury, turbine blade tip-speeds vary over a tidal cycle and are zero at low flow rates around slack tide. The speed of impact also varies along the turbine blade, increasing linearly along the length of the blade from zero at the root to a maximum speed at the blade tip.

Only two studies have explored the validity of the mortality assumption. Carlson *et al*. (2014) and Copping *et al.* (2017) used a range of skin and blubber morphometrics of killer whales (*Orcinus orca*) and harbour seals (*Phoca vitulina*) respectively to investigate the potential energy transfer from blade to individual. Although the authors present a range of severities and provide useful insight into how collisions can vary over a tidal cycle, the collisions were simulated and damage to the skeletal system and internal organs, and hence probability of mortality, was not directly measured.

In this study, I investigate the physical consequences of collisions between seal carcasses and a replica tidal turbine blade. I carried out a series of experimental trials to quantify the physical damage and assess the relationship between collision speed and the probability of inducing severe, traumatic injuries.

5.4 Materials and Methods

All experiments in this study were conducted using dead stranded or by-caught animals being opportunistically sampled and as such does not fall under Home-office regulation. Appropriate ethical approval was therefore provided by the University of St Andrews School Ethics Committee without the necessity to undergo assessment by the Animal Welfare and Ethical Review Board.

5.4.1 Experimental set-up

To determine the consequences of collisions between seals and tidal turbines a full-scale replica of the leading edge of a turbine blade tip section was constructed and fixed to the bow of a jet-drive boat to carry out a series of controlled collisions with seal carcasses (Fig. 1).

The 840mm long, straight edged replica was made from reinforced PVC blocks (Supplementary material) and had the same profile as the leading edge of the tip of an Andritz Hydro Hammerfest HS1000 (http://www.andritzhydrohammerfest.co.uk) turbine blade. The tip represents the part of the blade with the narrowest leading edge and therefore the most damaging point of contact. I took this approach to ensure that collisions represented the worst-case scenario and therefore produce conservative estimates of damage. The base of the blade was angled backwards ~5° from vertical to achieve a slight downward component of the impact to ensure that carcasses remained submerged throughout the collision while maintaining an angle of attack close to perpendicular to the motion of the blade. Perpendicular strike orientation was required to ensure maximum energy transfer to the strike location (Grear *et al.* 2018).

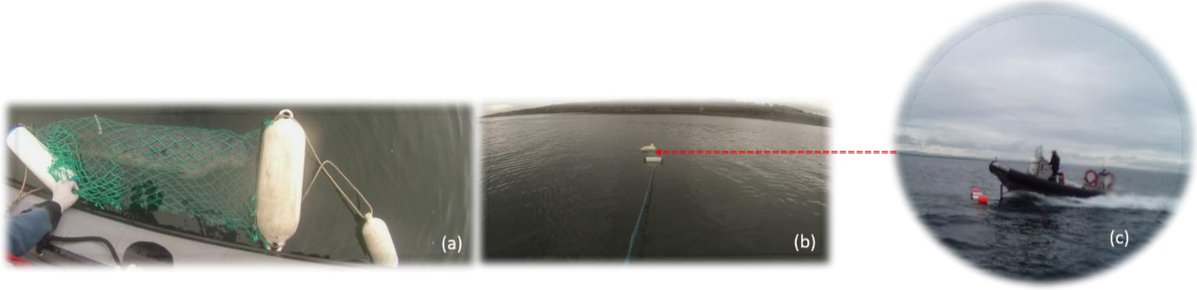

Figure 1 **Trial set-up.** (a) the seal carcass oriented in a coarse mesh, net bag attached at each end to flotation buoys. Note the dorsal surface of the seal carcass presented in the top of the photograph and the head-to-tail orientation following the length of the bag. (b) the seal carcass suspended on the surface of the water with a quick release line attached to one flotation buoy. (c) the vessel with the simulated turbine blade immediately prior to an impact. Note the vertical orientation of the model turbine blade on the keel of the boat and the perpendicular orientation of the boat with respect to the seal carcass.

Seal carcasses were collected for collision trials between 2014 and 2017. A total of nineteen carcasses, 12 males and 7 females, were collected; one juvenile and two adult grey seals (*Halichoerus grypus*) were collected as stranded carcasses, fifteen were juvenile grey seals by-caught in fishing nets in the south-west of England and one adult male harbour seal from the west coast of Scotland.

All carcasses were visually assessed at collection for obvious signs of pre-existing trauma, decomposition, or emaciation. Skeletal trauma was broadly assessed on site through palpation and tactile investigation before being collected and returned to laboratory conditions where further assessment could take place. Suitable carcasses were frozen at -20°C. No experimental bias was imposed on the carcass collection in that all carcasses which met the criteria of decomposition state were considered, regardless of age, sex or species.

Prior to the collision trial, each carcass was subjected to computed tomography (CT) scans to assess any pre-existing trauma. This provided a baseline from which resulting from the collision trials could be assessed. Morphometric data of length, girth and mass was also taken. All individuals which were used in the final trials were judged to be in good physical health and showed no signs of emaciation.

Collision trials took place during calm (Beaufort 0-2) weather in a sheltered bay on the east coast of Scotland. Carcasses were defrosted at ambient temperature for 10 days prior to collision trials in September 2016 and 2017 to ensure complete thawing of the soft tissue. In each trial the jet boat was driven at the carcass at a pre-determined speed. The boat was positioned accurately enough to successfully collide with a pre-determined target area on the carcass (Appendix III). Collision locations were confirmed with a downward facing, bow-mounted, high definition (720p) video recorder (Vivitar ™ Action Cam DVR782HD), recording at a frame rate of 30 fps. Collision trials were designed to cover a range of impact speeds which represented the expected tip speeds of operational tidal turbines (Sparling, Lonergan & McConnell 2017). During a trial, each carcass was subjected to multiple collisions. However, each collision location on that carcass was targeted only once as multiple strikes to the same location could compound effects by progressively weakening the skeleton; this assumes that collisions to discrete locations did not weaken other parts of the skeleton. Dorsal collisions were expected to give the highest likelihood of skeletal trauma given the exposure of the spine and its connection to the skull, rib-cage and pelvis. All carcasses were therefore targeted dorsally and the focal impact points were the skull, thoracic spine and pelvis. Perpendicular impacts were attempted in all cases to mimic the worst case scenario with maximal transfer of collision energy; fractures are more likely with a faster impact absorption as impact loading is a factor of both force and time over which the force is applied (King 2018). Further, established tissue deformation properties for seals suggest that angle of attack has a large impact on stress-strain curves, with frontal impacts producing the greatest deformation to blubber layers (Grear *et al*. 2018).

Preliminary trials with five carcasses were conducted with a different, curved turbine blade replica, attached to the keel of the jet boat. Details of these trials and conversion factors to allow direct comparison of results to the later trials are presented in the electronic supplementary material.

5.4.2 Injury assessment

Each carcass was subject to post-trial CT scans (Siemens SOMATOM Scope 16 slice spiral) to provide insight into skeletal trauma. Post-mortem analyses followed to confirm fractures, identify soft-tissue damage and measure mid-sternal blubber thickness. Each case was inspected for signs of soft tissue damage associated with blunt force trauma. Injury criteria are given in table 2. Key locations for assessment were integument, visceral organs, diaphragm and observations of musculature haemorrhage. Mid-sternal blubber thickness and stomach contents were recorded to assist in interpretation of ante-mortem condition.

Pathological features of severe trauma were identified, categorised by location and tallied to provide a quantification of the extent of injury. As this experiment was carried out on dead carcases which had undergone several freeze-thaw cycles, it was not possible to assess subtle indications of collision trauma, such as morbidity or delayed mortality. Necropsy assessment was therefore restricted to identifying traumatic pathologies considered severe enough to cause immediate or assured fatality.

5.4.3 Statistical Analysis

To assess the effect of turbine blade speed on the probability of inducing severe trauma in seals, I modelled the presence of pathological indicators of mortality using generalised linear models (GLM) with binomial errors and a logit-link function. Each collision was coded as 0 or 1 depending upon the absence or presence of one or more pathological indicators of severe trauma associated with that collision. I used this binary variable as our response and as such were testing the correlation between known, detectable fatality and select intrinsic and extrinsic covariates. This allowed us to determine the dose-response relationship (Harris *et al.* 2018) between impact speed and severe trauma in a probabilistic framework. Discrete pathological indicators of mortality (i.e. damage which would be indicative of mortality in a living seal) were assigned based on anatomical region; I assigned injuries to specific trials based on the strike location nearest to the injury in question. Multiple spinal injuries on one individual were considered discrete if they occurred in a different region of the spine; namely the cervical, thoracic, lumbar or sacral region. Rib fractures were included as one attribute regardless of the number of fractures occurring. If multiple rupture locations or traumatic lesions were observed on the same organ, this was considered a single discrete attribute. In cases where trauma could have been the result of another pathological attribute (e.g. hepatic herniation as a result of diaphragmatic rupture), causation was not assumed, and both attributes were considered discrete. None of the carcasses demonstrated any signs of external trauma and were visually indistinct from pre-trial condition; no lesions, cuts or external bruising was visible as a result of collision trials.

Candidate variables tested in the model were collision speed, blubber thickness, sex, strike count and strike location. Strike count was given as the number of strikes that particular trial constituted for that individual and therefore had a maximum value of 3. The inclusion of this variable tested whether multiple strikes affected the likelihood of the presence of pathological indicators of mortality. Mass was initially included but was removed due to collinearity with blubber thickness. Blubber thickness was considered a more relevant metric as it provides a better proxy for animal health and blubber should act as protection from impact (Pond 1978; Iverson 2009). An interaction term between speed and blubber thickness was included to assess whether the ability of speed to describe the pathology of a collision case could be affected by blubber thickness. Model selection was undertaken using backwards, stepwise selection and comparing Aikaike's Information Criterion (AIC) values. An improved fit was determined if AIC value reduced by 2 from the previous model (Burnham & Anderson 2002).

As an example of how the results could be used in practice, the tidal prediction software POLPRED was used to generate estimates of current speeds at ten minute intervals over a one month period in a site proposed for tidal energy extraction. These current data were used to generate estimates of the blade speed assuming that the turbine stalls at a current speed of 1 $m.s^{-1}$ and reaches a maximum tip speed of 12 $m.s^{-1}$ for current speeds of 2.5 $m.s^{-1}$ and higher as demonstrated by the SeaGen tidal turbine operating in Strangford Lough, Northern Ireland (Sparling, Lonergan & McConnell 2017). This distribution could then be taken as the proportion of theoretical collision speeds between randomly moving seals and tidal turbine blades across a tidal cycle. The increase in blade tip-speed from 0 $m.^{s-1}$ to $12 m.s^{-1}$ was assumed linear from the stall to maximum current speed as turbine rotation is directly driven by the current. These values were assumed consistent with typical tidal turbine operations (Sparling, Lonergan & McConnell 2017) and model predictions were correlated with these calculated, theoretical impact speeds to determine the proportion of cases which would confidently result in fatality. Finally, these proportions were combined with flow speed predictions for a proposed tidal turbine array site in Scotland. These were used to estimate the proportion of the turbine blade swept area which had speeds above a determined mortality probability from the dose-response model, across a tidal cycle.

All statistical modelling and subsequent analysis was performed in R (R Core Development Team 2016).

5.5 Results

5.5.1 Trials

A total of 28 collisions were carried out at speeds ranging from 2.1 $m.s^{-1}$ to 10.34 $m.s^{-1}$. Table 1 details the speed and location of each strike along with morphometric data of the carcasses.

Table 1 **Morphometrics of experimental subjects including speed and collision location for each collision trial.** * indicates the collision speeds which were calculated post-hoc after impact with a curved blade. See Appendix III for full details. All individuals were judged as sub-adults except for seals HgA, HgC and PvDV which were classed as adults. All individuals were grey seals except seal PvDV which was a harbour seal.

Seal ID	Sex	Mass	Blubber Depth	Trial Number	Collision Speed (m.s^{-1})	Collision Location
TA04	m	18	30	1	4.9	Thoracic Spine
				2	5.6	Head
				3	5.2	Lower Pelvis
HJ02	m	32	23	4	5.5	Sacral Spine
				5	5.5	Thoracic Spine
JG07	f	19	14	6	6.3	Thoracic Spine
JG06	f	22	19	7	6.5	Sacral Spine
TA03	f	20	19	8	6.1	Cervical Spine
				9	6.8	Pelvis
HJ01	f	32	19	10	8.2	Sacral Spine
HJ03	m	38	24	11	7.1	Thoracic Spine
				12	7.5	Cervical Spine
JG03	f	39	22	13	5.6	Sacral Spine
				14	5.3	Cervical Spine
PvDV	m	86	34	15	8.4	Thoracic Spine
				16	8	Pelvis
				17	8	Head
HJ05	m	42	16	18	9.26	Head
				19	9.26	Thoracic Spine
HJ08	m	25	23	20	10.19	Head
				21	10.07	Thoracic Spine
JG10	m	27	18	22	10.08	Thoracic Spine
				23	10.19	Pelvis
HJ07	m	46	18	24	10.03	Thoraco-cervical spine
				25	10.34	Cervical spine
				26	10.29	Thoracic Spine
HJ09	f	26	22	27	10.19	Thoracic Spine
				28	9.98	Pelvis
HgA	m	200	16	29	2.5*	Pelvis
				30	2.5*	Skull
				31	2.2*	Thoracic Spine
HgB	m	52.3	22	32	2.07*	Pelvis
				33	2.07*	Skull
				34	2.07*	Thoracic Spine
HgC	m	206	47	35	5.25*	Pelvis
				36	5.25*	Skull
				37	5.25*	Thoracic Spine
TA05	f	56.7	25	38	5.27	Pelvis
				39	5.27	Skull
				40	5.27	Thoracic Spine
TA07	m	48.7	24	41	5.27*	Pelvis
				42	5.27*	Skull
				43	5.27*	Thoracic Spine

5.5.2 CT scans, radiography and post-mortem analysis

Pre-trial CT scans confirmed the absence of fractures, severe muscle haemorrhage and large organ ruptures or herniation. Post-trial analyses of the cross-sectional scans of each seal carcass revealed several skeletal injuries. Damage to the spine was observed in eleven carcasses. Spinal injuries included fractures to the lateral spinous processes and, separation and fracture of vertebrae (Fig. 2) often associated with focal muscle maceration (Fig. 3, Table 2). Broken ribs were recorded in four cases (Fig. 4) and a fractured scapula in one case (Fig. 5). No damage was recorded to the pelvis, skull or mandible in any case, despite these locations being targeted during trials.

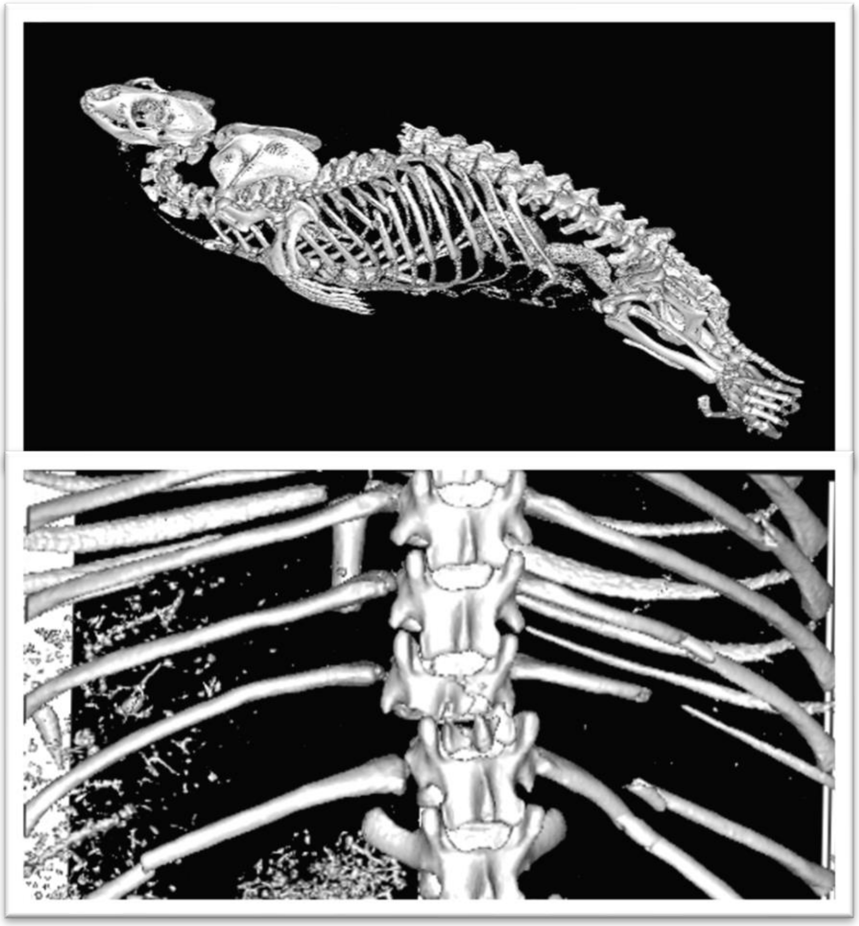

Figure 2 **CT Scans of thoracic injury.** Separation in the thoracic vertebra of seal PvDV (above) and separation in the thoracic vertebra with associated fracture of the lateral spinous process (below). Results of trial #15 in Table 1.

Figure 3 **Soft tissue damage associated with spinal fractures.** Maceration of axial musculature around spinal fractures of seal HJ02 (left) and HJ01 (right). Results from trials #5 and #10 respectively (Table 1).

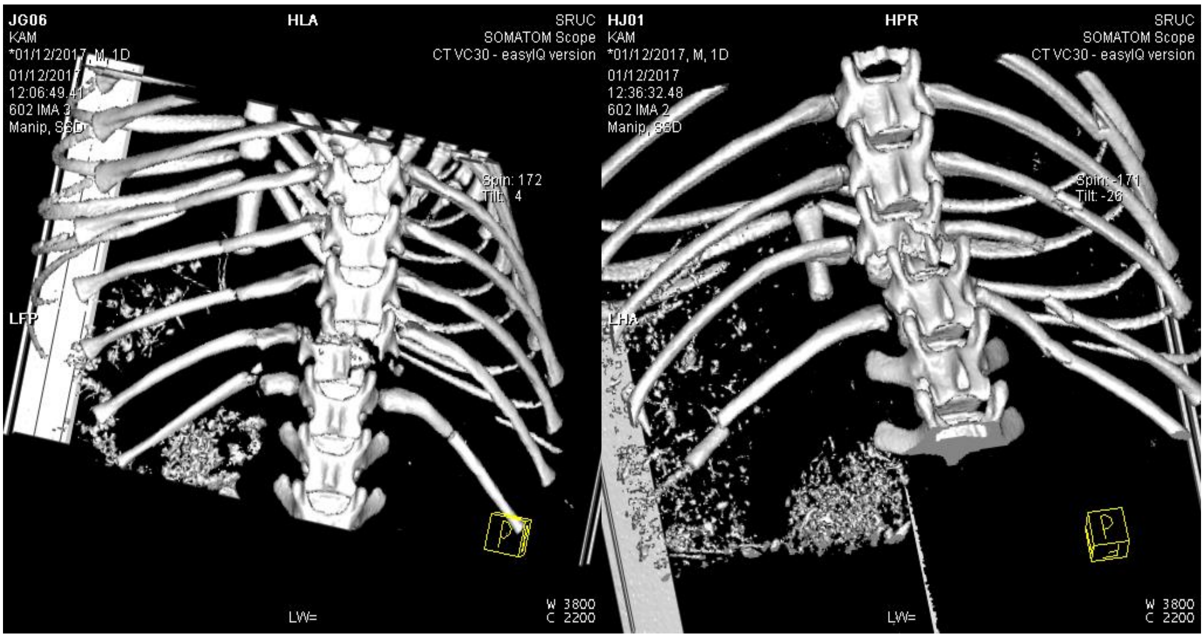

Figure 4 **CT Scans of injury to the rib-cage.** Fractured ribs of (left) seal JG06 and (right) HJ01. Results from trial #7 and #10 respectively (Table 1).

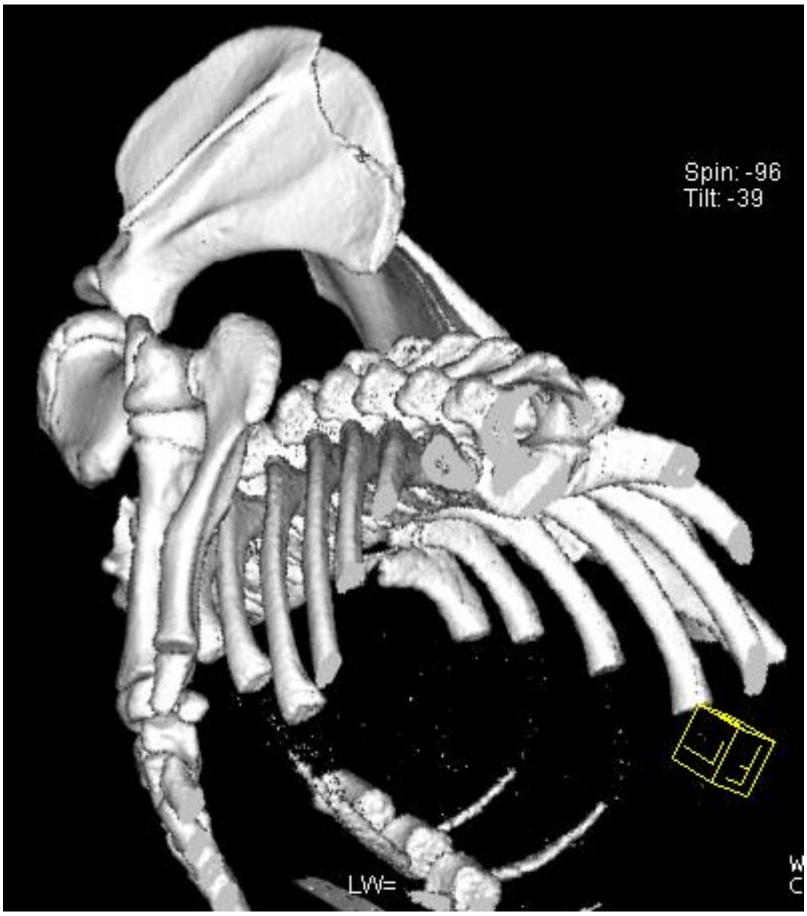

Figure 5 **Fractured left scapula of seal HJ03.** Results from trial #12 (Table 1).

Hepatic rupture was noted in four cases (Fig. 6), three of which were also associated with diaphragmatic rupture and herniation of abdominal organs into the thoracic cavity. Three additional cases demonstrated diaphragmatic rupture with no herniation. Pulmonary rupture was noted in two cases and cardiac rupture in one case. Liquefaction of the blubber layer was observed in the only harbour seal represented in the trials (Fig. 7). In addition, rupture of the thin mediastinum, a potentially sub-lethal indication of trauma, was noted in 5 cases.

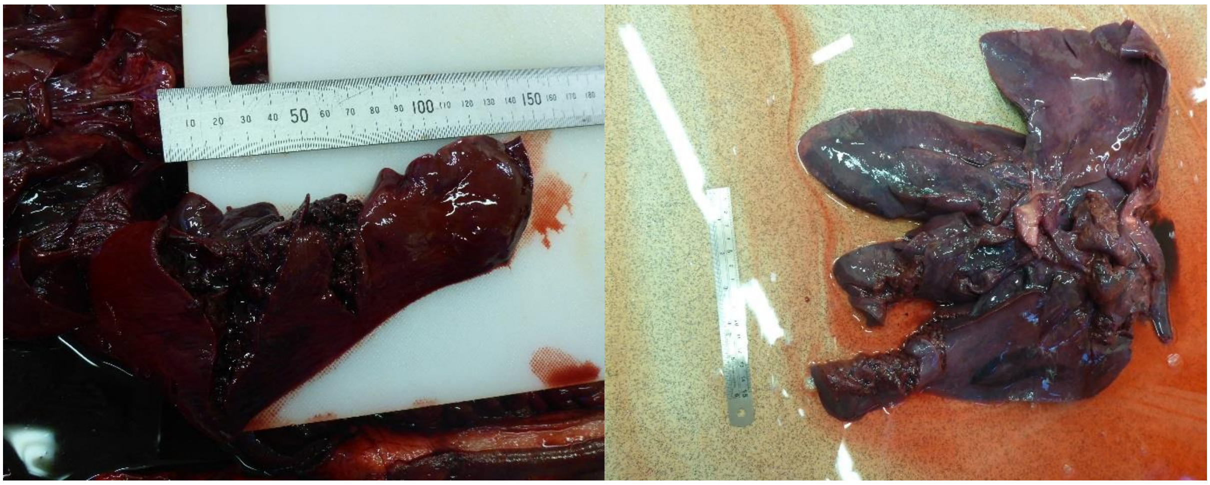

Figure 6 **Liver damage.** Ruptured liver of (left) seal HJ01 and (right) seal PvDV. Results from trial #10 and #16 respectively (Table 1).

Figure 7 **Liquefaction of the blubber layer of seal PvDV.** The adipose cell rupture extended ~21 mm into the blubber from the subcutis. Results from trial #15 (Table 1).

All seals were judged to have been in good physical condition prior to death with expected blubber reserves for their assumed age and varying degrees of food in the gastro-intestinal tract. Gross examinations revealed no evidence of underlying terminal disease or morbidity.

5.5.3 Dose-response relationship

The best fit binomial GLM retained the covariates speed of collision ($\beta = 1.23$, s.e. = 0.44, z = 2.76, $p<0.05$) and location of the strike (factor=Thoracic Spine, $\beta = 4.16$, s.e.=1.77, z=2.35, $p<0.05$) (Table 3). The interaction term between speed and location, and blubber depth did not improve model fit and were therefore removed from the final model. Random effects did not improve model fit and so were discarded from the final model.

Strike location explained a significant amount of the variation in the data; null deviance (21.9, 18 d.f) decreased to a residual deviance of 8.9, 15 d.f with the inclusion of strike location, blubber and speed as covariates. A second model was subsequently fit to data from strikes to the regions which demonstrated severe trauma (Thoracic spine). The best fit model through backwards stepwise selection retained the covariates of speed of collision ($\beta = 1.13$, s.e.= 0.35, z=3.23, $p<0.05$) and blubber depth ($\beta = -0.35$, s.e. = 0.15, z=-1.008, $p >0.05$, Table 3). Model predictions suggest that the probability of severe, fatal injury exceeds 0.5 at 5.1 $m.s^{-1}$ (95% CIs: upper=3.2 $m.s^{-1}$, lower=6.6 $m.s^{-1}$, Fig. 8). I evaluated the influence of each data point (*i*) using a graphical assessment of Cook's Distance (D_i). No Cook's Distances were noticeably different from the median, with no values above 0.5. This is generally considered indicative of no overt influence of any single data point (Chatterjee & Hadi 2015).

Table 2 **Pathological indicators of mortality.** Identification of presence (red) or absence (green) of broad pathological indicators of mortality for each seal carcass. Seals are arranged from slowest mean collision speed (top) to fastest (bottom).

Seal ID	**Mean Collision Speed (m.s^{-1})**	**Diaphragmatic Rupture**	**Spinal Fracture**	**Fractured Rib(s)**	**Liver Rupture**	**Liver Herniation**	**Pulmonary Rupture**	**Cardiac Rupture**
HgB	**2.1**	🟩	🟩	🟩	🟩	🟩	🟩	🟩
HgA	**2.4**	🟩	🟩	🟩	🟩	🟩	🟩	🟩
TA04	**5.2**	🟩	🟩	🟩	🟩	🟩	🟩	🟩
HgC	**5.25**	🟩	🟩	🟩	🟩	🟩	🟩	🟩
HJ02	**5.5**	🟩	🟩	🟩	🟩	🟩	🟩	🟩
JG03	**5.5**	🟩	🟥	🟩	🟩	🟩	🟩	🟩
JG07	**6.3**	🟩	🟥	🟩	🟩	🟩	🟩	🟩
JG06	**6.5**	🟩	🟥	🟥	🟩	🟩	🟩	🟩
TA03	**6.5**	🟩	🟩	🟥	🟩	🟩	🟩	🟩
HJ03	**7.3**	🟩	🟥	🟩	🟩	🟩	🟩	🟩
PvDV	**8.1**	🟥	🟥	🟥	🟥	🟥	🟥	🟥
HJ01	**8.2**	🟥	🟥	🟥	🟥	🟩	🟩	🟩
HJ05	**9.26**	🟥	🟥	🟥	🟥	🟩	🟩	🟩
JG10	**10**	🟩	🟥	🟩	🟩	🟩	🟥	🟩
HJ09	**10.1**	🟥	🟥	🟥	🟥	🟥	🟩	🟩
HJ08	**10.2**	🟥	🟥	🟥	🟩	🟥	🟩	🟩
HJ07	**10.2**	🟥	🟥	🟩	🟥	🟥	🟩	🟩

Probability of severe trauma resulting from collisions with the thoracic spine decreased with increasing blubber depth (Fig. 9) although the confidence intervals around the model predictions were high.

Table 3 **Backwards stepwise selection of model parameters using AIC.** Covariates are denoted by Sp (speed of collision), L (location of strike), Sx (Sex), Sc (strike count) and B (Axial blubber depth). A colon (:) denotes an interaction term between covariates. The first line of each section represents the maximal model with all covariates and interactions included, and therefore have a ΔAIC of 0. Grey shading indicates the best-fit model in that selection.

Model Data	Covariates	AIC	ΔAIC
All Locations	Sp:L+Sx+Sc+B	33.46	0
	Sp:L+Sc+B	28.66	-4.8
	Sp:L+B	24.45	-9.01
	Sp:L	22.52	-10.94
	Sp+L+B	22.87	-10.59
	Sp+L	20.98	-12.48
Thoracic Spine	Sp:B+Sx+Sc	24.92	0
	Sp:B+Sx	22.81	-2.11
	Sp:B	18.34	-6.58
	Sp+B	16.4	-8.52
	Sp	14.52	-10.4
	B	26.74	1.82

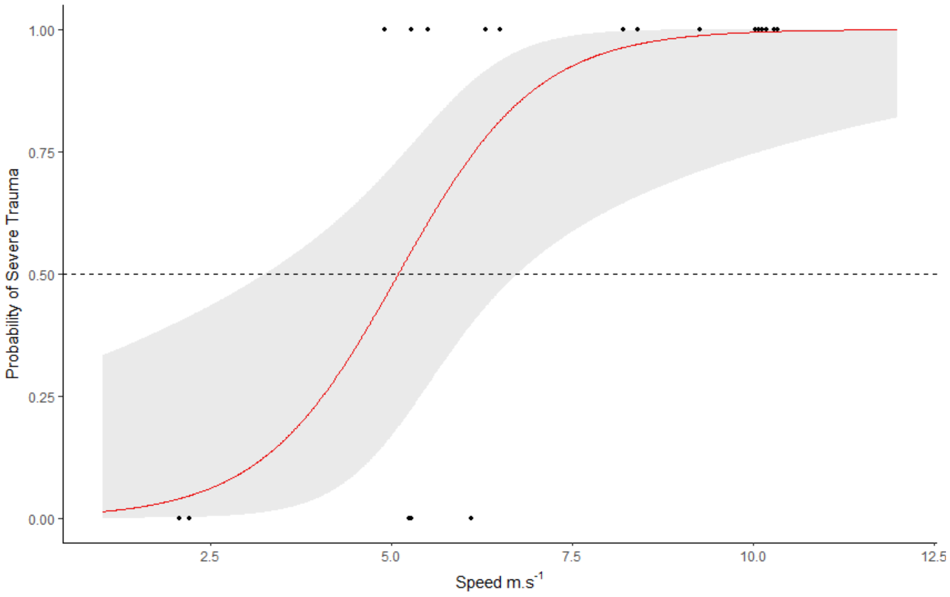

Figure 8 **Probability of severe trauma as a function of blade impact speed of collision.** Fitted values (red line) are given with associated bootstrapped 95% confidence intervals (grey shaded area). The horizontal black dashed line indicates the 50% probability of severe trauma. Probabilities are estimated using an assumed blubber depth of 21.5 mm; the mean mid-sternal blubber thickness of seals used in these trials.

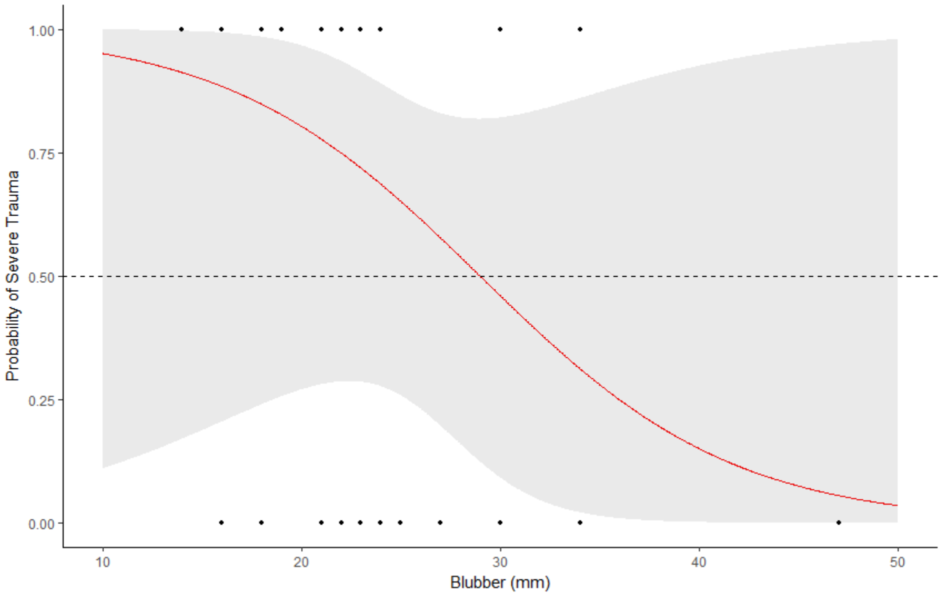

Figure 9 **Probability of severe trauma as a function of blubber depth.** Fitted values (red line) are given with associated bootstrapped 95% confidence intervals (grey shaded area). The horizontal black dashed line indicates the 50% probability of severe trauma. Probabilities were estimated using a constant collision speed of 6.7 m.s-1; the upper CI for a 50% probability of severe trauma from model predictions of the effect of collision speed to a carcass with a mid-sternal blubber thickness of 21.5 mm.

5.6 Discussion

This study provides the first empirical estimates of the likelihood of severe trauma to a marine mammal as a result of collisions with tidal turbine blades at a range of speeds. I have demonstrated that collision speed is an important predictor of physical trauma. I then predict that a large proportion of potential collisions would occur at speeds below those likely to result in severe skeletal injuries. Other potentially fatal injuries that were identified (e.g. cardiac rupture, liver herniation) only occurred at collisions speeds markedly higher than the threshold speeds for severe skeletal injuries (Table 2). However, given the limitations in reliably assessing more subtle trauma in carcases which have undergone freeze-thaw cycles, it should not be interpreted that collision speeds below these thresholds are benign.

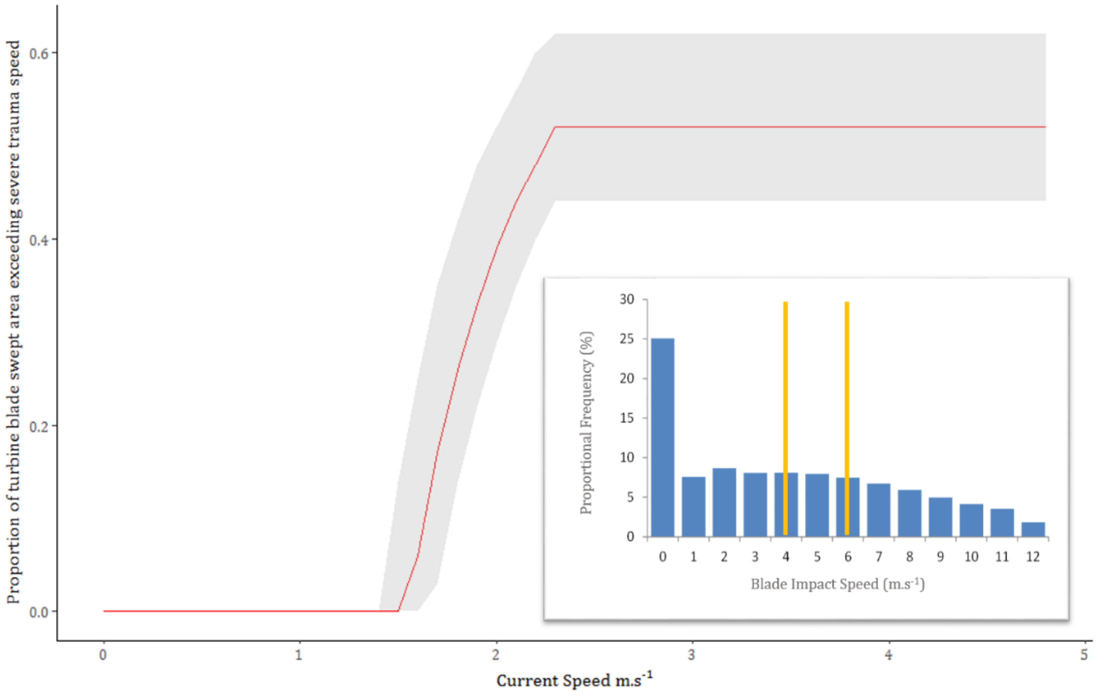

Figure 10 **Proportion of a blade swept area estimated to cause severe trauma.** The proportion is plotted as a function of current speed assuming a cut-in current speed of 1 m.s^{-1} and a constant blade tip speed in current speeds >2.3 m.s^{-1}, as demonstrated by the SeaGen device in Strangford Lough, Northern Ireland (Joy *et al.* 2018). The mean threshold for severe trauma is shown by the red line and bootstrapped 95% confidence intervals are shown by the grey shaded area. The panel plot shows a frequency distribution of blade impact speeds over a full lunar cycle. Yellow bars indicate 95% confidence intervals around the estimate of impact speed resulting in severe trauma.

Model predictions highlight physiological parameters as marginal predictors of the severity of collisions when compared to the energy imparted by a collision, and therefore the risk is reasonably constant across the range of likely sizes and body conditions of pinnipeds in UK waters. Given the paucity of data on the impacts of tidal turbines on the marine ecosystem, this study addresses a major uncertainty and provides regulators and industry with information to establish and refine mitigation measures to avoid potentially deleterious effects of the tidal industry.

The potential for collisions between marine predators and renewable energy devices has been theoretically assessed through a number of different approaches (Wilson *et al.* 2006; Grant, Trinder & Harding 2014; Band *et al.* 2016). However, limited by the paucity of information on the potential for mortality during collisions, most have tended towards cautionary approaches whereby mortality is assumed to be the only outcome of any collision event. Band *et al.* (2016) demonstrated that imposing a mortality threshold would have a significant effect on the resulting estimate of removal from local populations of seals. When compared to the frequency distribution of collision speeds at an example tidal array site, the model predictions suggest the impact speed threshold of severe skeletal trauma would result in at least 48% of predicted collisions being immediately fatal (Fig. 10). When interpreting these predictions, it is important to bear in mind that collisions were with the section of the blade with the narrowest and therefore most damaging part (the tip); this is due to the concentration of energy transfer through the skin and blubber layers. Further, they only encompassed strikes to the dorsal region of the seal carcasses and do not address a probable decrease in the likelihood of skeletal injury with strikes to the ventral surface. Therefore, the results should be interpreted with these caveats in mind.

Due to the current assumption in collision risk models that all collisions will be fatal, it can be concluded that previous mortality estimates derived from CRMs could justifiably be adjusted to account for the mortality threshold measured here. It is important to highlight that I do not conclude that 52% of the collisions were benign (discussed below), only that they did not result in the catastrophic trauma identified in this study. I do not suggest that all fatal injuries are covered under this framework but indicate which impact speeds would almost certainly result in severe trauma should they occur. The dose-response curve does not therefore indicate survival of all cases below the threshold, but rather highlight the number of cases which can confidently be assume to result in fatality. Furthermore, the results in this study pertain to phocids (primarily juvenile grey seals) and care should be taken when extrapolating out to other taxa and age-classes. CRMs estimate collisions under the assumption of randomly moving seals colliding with a tidal turbine blade and largely ignore the potential for a change in seal distribution across a tidal cycle (Thompson *et al.* 1997; Zamon 2001), the potential for close-range avoidance (Hastie *et al*. 2017), and the change in distribution due to the presence of tidal turbines (Sparling, Lonergan & McConnell 2017; Chapter 4). Nevertheless, this mortality threshold is likely to have a significant effect on collision estimates and subsequent assessments of the consequences for populations of seals.

From the tidal energy industry perspective, these results have important implications for both mitigation and consenting. It has been demonstrated that harbour seals show avoidance behaviours at scales of tens to hundreds of metres (Hastie *et al.* 2017; Sparling, Lonergan & McConnell 2017), but information on close range evasion of the rotating blades is currently lacking. Information on the consequences of interaction are therefore critical for estimating potential mortality risks. Our results suggest that for a turbine operating at a maximum tip-speed of 12 m.s^{-1}, the number of fatal collisions as previously predicted through collision risk models could be reduced by as much as 52%. However, caution must be taken when applying these corrections as this study only addressed immediately fatal injuries. Further work is needed to assess potential lethal effects of injuries due to slower collisions that were not apparent in this study.

Our results also suggest that the demographics of seal populations around an array site is an important factor to consider as intrinsic characteristics such as mass or blubber thickness influence an individual's ability to withstand blunt-force trauma. These results could be used to design mitigation or monitoring strategies around turbine sites which could be more cost-effective if they only needed to be enforced during periods where collisions will be fatal; studies have shown that seal presence in a tidal channel is influenced by tidal state (Zamon 2001; Hastie *et al.* 2016). Therefore, periods of exhaustive monitoring, and mitigative shutdown should seals be detected, could be imposed to reduce the likelihood of interactions during periods of high seal usage.

Quantification of collision consequences in the marine environment have been largely limited to ship strikes in large cetaceans and this bears little comparability to the physical attributes of smaller pinnipeds. However, there is literature detailing the relationship between automobile and sporting impact speeds, and injury in humans. (Watanabe *et al.* 2012) used modelled collisions between pedestrians and automobiles to demonstrate that impact speeds of 20 Km/h (5.5 $m.s^{-1}$) did not result in any severe injuries including skeletal fractures and soft tissue injuries to major organs or the brain. However, at higher speeds, mass of the subject and location of the strike became an important predictor of injury. This is broadly analogous to our findings that at speeds lower than 5.6 $m.s^{-1}$ collisions do not cause severe pathological injury regardless of intrinsic attributes or strike location. Further, I noted that at higher speeds blubber reserves offer a protective effect. This inference must be treated with caution however as the decline in probability of severe injury includes wide confidence intervals which span 0.5 at blubber depths above 20 mm. Theoretical models of interactions between larger marine mammals and tidal turbines have suggested that impacts may be benign across all scenarios. (Carlson *et al.* 2014) suggested adult southern resident killer whales would not succumb to any injuries caused by collision with the OpenHydro tidal turbine, a ducted, multi-blade turbine in Puget Sound, Washington, assuming collisions with the skull were worse case scenarios. As our results demonstrate that the probability of traumatic injuries decreases with increasing blubber thickness, it appears likely that size and/or condition is an important consideration when determining the outcome of a collision between a tidal turbine and a marine mammal.

Only carcasses which were known to be recently deceased were used in this study and I was careful to not over-interpret the consequences of collisions to soft-tissue due to the potential confounding of the freeze-thaw process. The freeze-thaw process can generate pathological artefacts which can be confused with the impact of trauma, such as pseudo-bruising of subcutis; the resemblance of haemorrhage in the thoracic cavity, pericardial sac and abdominal cavity; apparent subcapsular renal haemorrhage; pseudo-contusions of the brain; apparent haemorrhage from the nares; and blood-staining of the anterior ocular chamber (Roe, Gartrell & Hunter 2012). Consequently, many likely sequelae from collisions involving live animals could not be confidently evaluated in this experiment. Nonetheless, the assessment indicators chosen, of severe catastrophic trauma incompatible with life, were felt to provide robust upper bounds for quantifying the impact of blade collisions using cadavers. The freeze-thaw process is also known to have a significant impact on the structural rigidity and stress/strain features of soft tissue, particularly skin and blubber (Grear *et al.* 2018). The protective properties of blubber may be hindered by the freezing process, providing less resistance to direct impact . However, studies have shown there is limited evidence to suggest a significant structural change to blubber as a result of freezing (Grear *et al.* 2018) and regardless, this would render the presented results additionally conservative. An increased sample size using un-frozen carcasses for the empirical testing of the pathological consequences of collision to both the skeletal structure and soft-tissue, representing a wider range of demographics, species and fitness states would help resolve the relationship between animal size, collision speed and mortality.

Post-trial CT scans revealed no evidence of skull fractures. This contrasts with the human literature where collisions with a range of shapes have been shown to produce fractures at much lower speeds (Hodgson & Thomas 1973; Yoganandan *et al.* 1995;

Delye *et al.* 2007). This may be related to the differing skull thicknesses of humans compared to the seals in this study; mean frontal skull thickness of the seals here was 6.9 mm (±0.8) whereas adult human skulls have mean frontal thicknesses of between 5.7 mm and 6.3 mm respectively (Mahinda & Murty 2009). It has been demonstrated that frontal skull fracture in humans can be induced for energies of between 22-24 J (Delye *et al.* 2007) and at impact speeds as low as 2.73 $m.s^{-1}$ (Hodgson & Thomas 1973). I demonstrated that seal skulls are capable of withstanding collisions to the frontal region with a turbine blade at speeds of up to 10.1 $m.s^{-1}$. Deyle *et al.* (2007) suggested the disparity in forces required to fracture embalmed and non-embalmed skulls could be a result of energy absorption by the scalp. Seals have considerably thicker scalps than humans which may explain the higher resistance to frontal skull fracture as full compression of the tissue occurs at a higher impact energy. Energy will also be lost in these collisions through rotation of the head and therefore it is possible that a combination of morphology and increased spinal flexibility in seals may reduce the likelihood of skull fracture. Strike location on the skull is also likely to have an effect as resistance to fracture varies across the skull with strength, decreasing from the posterior skull to the lateral and frontal regions (Hodgson & Thomas 1973; Yoganandan & Pintar 2004). These results therefore likely exhibit the worst case scenario for skull fracture and give further justification for the lack of skull damage at the speeds presented.

The experimental procedure presented in this study was not able to assess the effects of traumatic brain injury (TBI), specifically concussion and axonal strain injuries. The combined effects of autolysis and the freeze-thaw process precluded the assessment of TBI due to possible mis-identification of traumatic injury (Roe, Gartrell & Hunter 2012). This presents a potential issue as cases of concussion considered mild in humans can cause symptoms that in seals (as a diving mammal) could lead to drowning. (Omaya & Hirsch 1971) demonstrated that the tolerance to concussion scales with the ratio of brain mass to head mass and that the reduction in this fraction in chimpanzees compared to humans and rhesus monkeys resulted in a higher tolerance to TBI. Coupled with a thicker scalp, animals with more 'padding' are more resistant to TBIs resulting from either angular or linear acceleration. It can therefore be assumed that due to their relatively large skulls and small brains, and the capacity for some cushioning from a thin blubber layer on the head, seals may be relatively more resistant to TBIs. Further, the location of the strike and the size of the animal's skull and scalp will have an effect on whether a TBI is sustained. However, this remains an area which requires further research and the results of this investigation should not be considered categorical evidence of severity of brain injuries, or indeed any soft tissue damage, as a result of collisions with tidal turbines.

In summary, this work has provided robust evidence that immediate, severe skeletal injury would occur during all collisions between seals and tidal turbine blades at impact speeds above 6.6 $m.s^{-1}$ with no pathological indicators of severe trauma detectable at collision speeds below 5.5 $m.s^{-1}$. A dose-response curve fitted to these data estimate a lower 95% confidence interval for severe trauma of 4.4 $m.s^{-1}$. In the worked example for a typical, horizontal axis tidal turbine, 48% of the potential collisions are estimated to be at speeds greater than this threshold. This has potentially major implications for regulators assessing the environmental risks associated with the tidal energy industry. These results can be adapted to suit different tidal regimes and turbine designs. Given that blade speed is a major factor in determining likelihood of severe injury, design considerations that reduce blade speed could avoid these problems. Additional work to determine the extent of soft tissue damage and potential concussion injuries would reduce the uncertainty surrounding these estimates.

Chapter 6

General Discussion

"When gone am I, the last of the tidal ecology researchers will you be. The [tidal] force runs strong in your family. Pass on what you have learned."

6.1 Introduction

The tidal cycle has a central role in shaping marine ecological processes, from governing species assemblages in littoral communities (Colman 1933) to driving the mixture of nutrients through the water column in shelf seas (Sharples, Moore & Abraham 2001). This has led to a wealth of research into the importance of large scale, tidally driven features to marine fauna. Much effort has been directed towards studying a range of trophic interactions in tidal currents (e.g. Gibson 2003) and mixing fronts (e.g. Begg & Reid 1997) and there is increasing evidence that some species spend large amounts of time travelling and foraging within tidal stream habitats (Benjamins *et al.* 2015). However, the relationships between these dynamic habitats and large predators remains relatively poorly understood; understanding how predators move and forage in them is key to understanding their importance. The overall aim of this thesis was to measure the movement and diving patterns of a large marine predator (harbour seals) in a tidally energetic area; these data were used quantify foraging behaviour and investigate the behavioural mechanisms that seals use to maximise forage successfully in strong tidal currents. Further, the data were used to determine the potential effects of marine renewable energy developments in tidal stream habitats for harbour seals.

Chapter 2 investigated how harbour seals move as a function of tidal current strength in a tidally energetic region off the coast of the UK. For this, I took the approach of considering their movements in relation to both hydro-space and geo-space. Using GPS tracking data from animal-borne tags, I employed discrete time Hidden Markov Models (HMM), to compare hydro-spatial and geo-spatial movement of seals and quantify how these different perspectives might influence our understanding of activity budgets. I then took the novel approach of combining the two different movement perspectives (geo-spatial and hydro-spatial) to infer how harbour seals adjust their foraging and travelling behaviour in response to variations in current flow. The results highlighted that, in energetic regions, this combined approach to behavioural classification is essential for quantifying foraging behaviour and identifying specific areas of importance. Further, I found there to be marked plasticity in the foraging behaviour of seals as a function of current strength. Seals were more likely to transit into foraging states with increasing current speeds. However, the specific movements which identified foraging behaviour varied; passive drifting was identified more in high flows, directed swimming against currents in mid-strength flows and small-scale area-restricted search movement (in both perspectives) at low flows. The results of this chapter highlight the highly variable nature of predator behaviour in tidal stream environments.

Horizontal movement in isolation can be a good indicator of behaviour for many species (Dragon *et al.* 2012; Bennison *et al.* 2018); however, for diving predators such as harbour seals, an understanding of the underwater, vertical movements in relation to water currents was required to quantify foraging. My aim in Chapter 3 was to categorise broad dive categories and consider these within the context of the HMM results outlined in Chapter 2. I then analysed a series of individual dive metrics to determine whether harbour seals adjust their diving behaviour to maximise foraging efficiency. Data on depth use were collected from depth records on GPS-GSM tags and individual time-depth recorders on the same cohort of seals used in Chapter 2. A data reduction approach, through principle component analysis and model-based clustering, revealed that inferences about foraging from the dive behaviour generally matched those made from the horizontal movement HMM. When conducting “typical” area-restricted search patterns in geo-space, seals spent a large proportion of time diving benthically, presumably foraging on benthic prey sources. When drifting with currents, seals appeared to spend large portions of time diving to mid-water depths, showing high degrees of activity in the bottom-phase of dives, indicating possible foraging on pelagic species. A fine-scale analysis of individual dives revealed that seals descended to maximum depths significantly faster in increasing currents; however, once current speeds rose above ~1.7 $m.s^{-1}$, diving became largely pelagic and descent rate appeared to vary markedly. Further, a seasonal and diurnal effect on diving behaviour was found. Seals were more likely to dive benthically in the spring and at night. Seasonal switches in dive patterns appear to reflect known diet composition of animals in this population (Wilson & Hammond 2019) and diurnal patterns also suggest a degree of switching in foraging behaviour which may be linked to prey switching or prey behaviour. This analysis revealed a degree of plasticity in harbour seal diving behaviour as a function of tidal currents similar to that observed in their horizontal movements (Chp. 2). The diving behaviour provided an important dimension to our understanding of harbour seal behaviour in tidal streams and suggests that tidally driven processes along with seasonal and diurnal heterogeneity play a role in driving behavioural dynamics.

Given the potential importance of tidally energetic habitats to marine industry, I looked to establish whether the installation and operation of a tidal turbine array led to significant changes in seal behaviour. Using the GPS tracking data from Chapter 2, I investigated whether a newly installed tidal energy array in the Pentland Firth affected the distribution of seals, at two temporal scales; as a function of a) the presence of the turbine array and b) the operations of the turbine array. Results showed that there was no significant change with respect to the presence of the turbines, but that there was a significant decrease in seal abundance up to 2 km away from the array during operations. This suggested that seals show an overt avoidance response to tidal turbines during power generation and the scale of the avoidance suggests this to be a response to the acoustic output of the devices. These results have important implications for the development of risk assessments for marine species in the vicinity of these devices.

Although the results show clear avoidance behaviour by seals at scales of 100s-1,000s m from the turbine array, they also suggest that a proportion of seals may move in close proximity to the turbines and potentially collide with turbine blades. Given this, I aimed to assess the possible physical consequences of collisions between seals and tidal turbine blades (Chp. 5). I took an experimental approach whereby I carried out a series of controlled collisions between seal carcasses and a model tidal turbine blade at various speeds in order to identify a threshold, above which mortality would be likely. Results suggested that collisions at speeds in excess of 5.6 $m.s^{-1}$ would likely result in fatality, regardless of where on the body the individual is struck. Further, the probability of fatality was affected by blubber layer thickness; there was a lower probability of fatality with thicker blubber layers. These results can be used as direct scalars of collision risk models for seals in that estimated collision rates can be scaled by the values provided by the resulting dose-response curves as well as the associated avoidance rates quantified in Chapter 4.

6.2 Harbour seal movements in energetic habitats

Data on animal movement can allow researchers to understand important individual, population, ecological, and global scale processes (Steinberg & Kareiva 1997; Patterson *et al.* 2008). Deliberate movement occurs as a result of a desire to satisfy a goal. Therefore, if the goal is known, inferences can be made as to the mechanisms and drivers of the movement process. Information on breeding and foraging cycles can aid the understanding of these goals. Outside of breeding seasons, predators can be seen to be primarily driven by the desire to gather energy, therefore movements can largely be indicative of the distribution of foraging resources, either as a function of searching or hunting (Costa 1991).

Optimal foraging theory suggests that individual fitness is governed by efficient foraging behaviour (Stephens & Krebs 1986), and therefore adaptable foraging tactics in regions of high variability would be advantageous. When variability is predictable (e.g. tidal cycles), the pattern of foraging plasticity should, in theory, be more apparent, given the ability of the animals to establish successful tactics over time (Irons 1998; Bradshaw *et al.* 2004; Weimerskirch 2007). If individuals can maintain successful foraging in a range of different environmental conditions, overall fitness should be greatly increased compared to individuals with a narrow range of foraging behaviours (Stephens & Krebs

1986). Consequently we might expect to see different results in individuals which have not yet developed consistent foraging tactics such as immatures (Carter *et al.* 2019).

Recently, our ability to collect data on animal movements with concurrent environmental measurements has led to several studies on the importance of environmental dynamics for predators. Information on the associations between marine predator foraging movements and oceanic features has highlighted how important oceanographic features are to understanding marine population fitness (Cox *et al.* 2018). Several studies have described the associations between large scale oceanographic features such as macro-scale frontal systems and currents, and seabirds (e.g. Durazo, Harrison & Hill 1998), pinnipeds (e.g. McConnell *et al.* 2002), turtles (e.g. Gaspar *et al.* 2012) and cetaceans (e.g. Reilly 1990). However, there were significant data gaps with regards to how smaller, coastal species interact with finer scale features such as tidal streams (Benjamins *et al.* 2015). To address this, I showed that, for harbour seals, strong tidal currents can be closely linked to foraging behaviour (Chp 2 and 3). As predicted by Stephen and Krebs (1986), a relatively high degree of foraging plasticity was observed in the heterogeneous environment, compared to other harbour seal studies (McClintock *et al.* 2013; Russell *et al.* 2015; Russell 2016); this suggests different foraging tactics may be employed by harbour seals in varying energetic environmental conditions. However, it is important to highlight that the use of a novel analytical method to identify behavioural changes may mean this degree of plasticity is exhibited in other populations but has not been explored. Harbour seals are often described as generalist predators (Bowen *et al.* 2002; Sharples, Arrizabalaga & Hammond 2009; Wilson & Hammond 2019) so a wide range of foraging behaviours would be a reasonable assumption. A useful next step in understanding this would be to apply the technique from Chapter 2 to other populations or areas to assess whether adaptive foraging behaviour is a common trait of harbour seals or whether this is driven by exceptionally dynamic conditions.

While robust inferences of movement behaviour can be made using observations of an individual's breeding/foraging state, other fundamental intrinsic parameters such as sex, age and size can have equally strong effects. Age and size were not tractable covariates to investigate in this thesis, as only breeding age individuals were targeted for tagging. Additionally, sex was not considered in the movement analyses of Chapters 2 and 3, and this may be a useful avenue for future research. Although phocid foraging behaviour has been shown to differ between sexes (e.g. Slip, Hindell & Burton 1994; Baechler, Beck & Bowen 2002; Carter *et al.* 2017), many of these differences are apparent in species exhibiting pronounced sexual dimorphism, possibly owing to differences in physiological capabilities as well as life-history constraints (Le Boeuf *et al.* 1993). Although sexual dimorphism is not pronounced in harbour seals, early iterations of the movement models in Chapter 2 included the covariate effect of sex on transition probabilities and found there to be a difference in the foraging patterns between males and females at particularly high flow rates (Fig. 1). Males were more likely to transit from a hydro-spatial foraging state to a hydro-spatial travelling state with increasing flow rate i.e. male seals were more likely to swim against the current in increasing flow rates than females; therefore, females were more likely to drift with currents. Further, females were not observed in depth averaged flow rates above 3 m.s^{-1} throughout the entire study period so all predictions of seal behaviour in flow rates above this are solely derived from the movement of male seals.

There is a general paucity of information on sex and size differences in body composition of harbour seals, and morphometrics gathered in this study indicate very little difference in body size between sexes (Chp. 2, Table 1). However, there remains an apparent signal which warrants further investigation. It was difficult to resolve the biological drivers of the identified differences but it is possible that they are driven by different life-history requirements resulting in different strategies, or that there are fundamental differences in physiological capabilities meaning females have a narrower range of foraging behaviours available to them. Indeed, proportion of lean to lipid mass (and ultimately strength) could be a constraint to an animal's ability to swim against prevailing currents. For example, grey seals males are seen to preferentially load lean mass before lipid mass as opposed to females which preferentially load lipid mass throughout non-breeding periods (Beck, Bowen & Iverson 2003). It is suggested that these differences are a function of sex-specific metabolic properties due to the differences in breeding requirements, and a consequent difference in perceived cost-benefit on certain behaviours (Kelso *et al.* 2012).

Differences in cost-benefit balances between sexes can manifest themselves in more or less risk-averse strategies resulting in differences in foraging tactics (Beck, Bowen & Iverson 2003; Beck *et al.* 2003). If rich but temporally heterogeneous foraging patches exist in areas of high tidal flow, and an individual's physiology gives it the capacity to counter the displacement effect more so than other conspecifics, it may make energetic sense to continually target that patch in the absence of competitors. However, a perceivable risk may exist whereby if resources happen to be low, the increased energetic expenditure of navigating strong currents would result in a vast drain on resources and have a detrimental effect on fitness. This could result in significantly reduced lipid reserves and a decreasing ability to successfully bring a pup to parturition. We therefore may expect to see males in strong currents more so than females, with females electing to forage in slower flow rates in order to minimise their metabolic rates. Analogous behaviour has been observed in diving grey seals pups where females spend longer in the bottom phases of dives and perform benthic dives more often than males (Carter *et al.* 2017). The suggested reason for this is that females have to load more lipid reserves and therefore target lower quality, more predictable prey than males, which elect to spend more time in pursuit foraging of larger fish in the water column. These cost-benefit trade-offs appear obvious even in early stages of phocid development (Kelso *et al.* 2012; Carter *et al.* 2017) and therefore suggest a possible avenue for the differences in behaviour demonstrated here.

The results from Chapters 2 and 3 highlight the significant variability in harbour seal foraging behaviour in energetic environments and provide a basis from which these intrinsic variables can be further investigated.

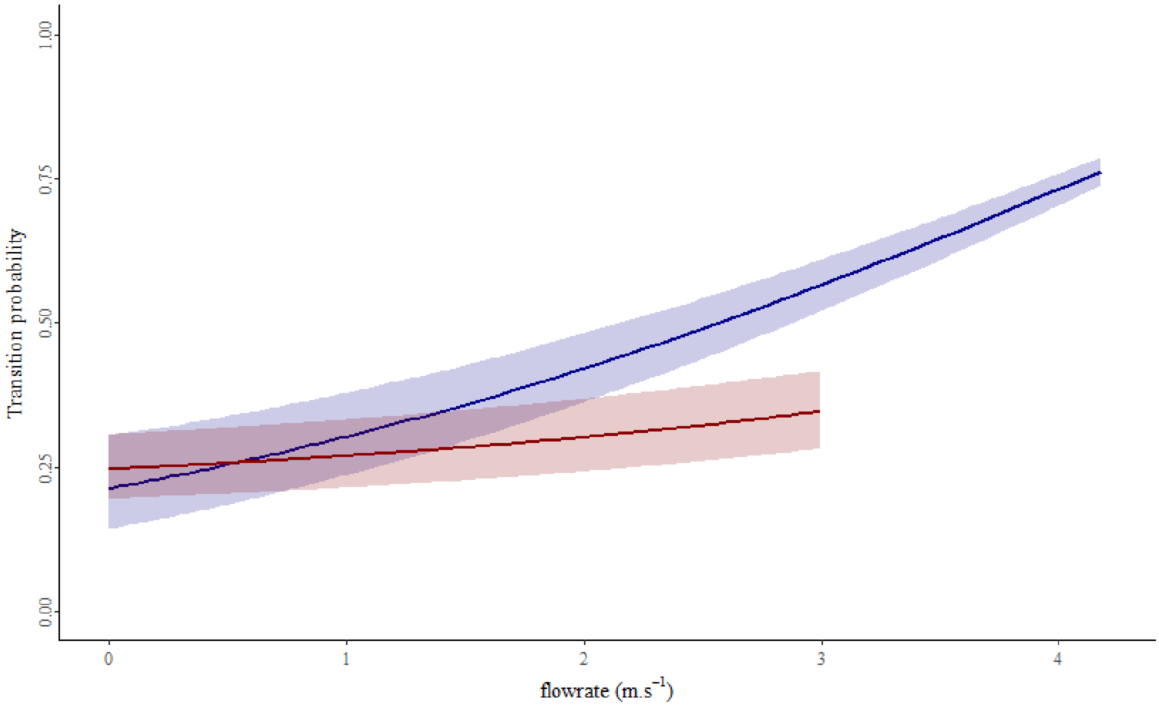

Figure 1 **The probability of transitioning from a localised to traveling state in a hydro-spatial only HMM.** The blue line represents the predicted male effect and the red line the predicted female effect on the transition probabilities. Shaded areas represent 95% confidence intervals.

The approaches in Chapters 2 and 3 revealed foraging behaviours, hitherto undocumented in harbour seals. I established how harbour seals move in both the horizontal and vertical planes, and how this is influenced by flow. However, to understand how populations may be affected by environmental change, a more holistic approach to identify patterns of space-use with regards to fixed and mobile habitat covariates is needed. The discrete behavioural states from these models could be extended to act as dependent variables in habitat models whereby distributions could be thought of as where animals perform specific behaviours rather than simply when they perform them. Largely, habitat models are used to identify areas of importance which can guide management and mitigation decisions. With robust estimates of when and where animals forage, areas of importance could be more accurately defined and marine spatial planning can be tailored to suit species specific needs. With associated knowledge of transit routes and foraging areas, habitat models delineated by underlying behavioural state could improve our ability to protect populations.

Misidentification or underrepresentation of foraging events can influence conservation efforts given how some researchers, interested in habitat selection, parametrise their models. It is a common practice to estimate habitat preference or selection through modelling inferred foraging locations rather than overall distribution (inclusive of all other behaviours) due to the relatively high assumed importance of foraging patches compared to all other areas (e.g. Doniol-Valcroze *et al.* 2012; Scales *et al.* 2016; Wege *et al.* 2019). If researchers only have access to 2-dimensional movement data, which is often the case, then establishing habitat selection models becomes an increasingly difficult task when animals spend prolonged periods of time in dynamic waters.

Given the mounting evidence that foraging marine animals are often attracted to ocean currents and eddies (Suryan *et al.* 2006; Bon *et al.* 2015; Della Penna *et al.* 2015; Grecian *et al.* 2016; Hastie *et al.* 2016; Hays 2017) the use of current correction appears a vital tool for conservation given the importance of robust identification of foraging locations. In the case of this study, 37% of the locations were classified as different behavioural states between geospatial and hydrospatial models, suggesting a potential misclassification rate of 37%. This could mean that up to 37% of foraging behaviour could be missed if hydrospatial movement was not considered. Consequently, important foraging areas might be misclassified as less important, producing erroneous or unrepresentative foraging distributions and having knock-on effects when used for conservation efforts in marine spatial planning. This is of concern in the current study given the recent, rapid decrease in local abundance and these results may be a key factor in producing more representative foraging distributions which could aid in the protection of the population.

Technological advances in marine biotelemetry have resulted in the increasing use of multi-channel data-loggers; data on geographical location (Thompson *et al.* 1991a), depth use (Le Boeuf *et al.* 1988), fine-scale movement (Shepard *et al.* 2008), acoustic environment (Johnson & Tyack 2003), temperature and salinity (Boehme *et al.* 2009) are now regularly collected on animal-borne devices. However, as resolution and breadth of data increases, tags can become prohibitively expensive and so many studies are still constrained to the collection of only one or two data streams. Time-stamped location data is usually favoured as without it, concurrent environmental conditions can be difficult (or impossible) to estimate and they can be used in isolation to make broad inferences about underlying behaviours and life-history stages (Carter *et al.* 2016). The presented evidence that horizontal movement and diving behaviour are inherently linked, in both geospace and hydrospace, coupled with the general acknowledgement that diving behaviour is a sound indicator of foraging (Le Boeuf *et al.* 1988), suggests that the method in chapter 2 could be used in isolation for researchers intending to study seal movement in dynamic systems, without the necessity for significant extra expenditure on fine-scale movement or depth tags. The method both validates previously held assumptions that horizontal movement metrics can be attributed to behavioural states reasonably well and provides a method by which this can be refined in a fast moving environment. Evidently, there are questions which could be answered on behaviour that would benefit from extra data streams, however in instances of archival data sources or limited funding, I have shown that tracking data in isolation can still be a very powerful tool for ecological research.

Associations between predators and fast flowing systems are widely believed to indicate elevated concentrations and disorientation of lower trophic level species; the so-called ‘tidal coupling hypothesis’ (e.g. Zamon 2003) . The bottom-up effect of predictable coherent structures in tidal streams creating equally predictable concentrations of zooplankton, is theorised to attract planktivorous fish species which in turns attracts piscivorous predators (Wolanski & Hamner 1988). The importance of tidal currents in harbour seal movement patterns presented in this thesis support this theory and suggest that harbour seals exploit various aspects of tidal coupling. As current strength increases seals were often observed swimming into the current, descending faster and often diving to the seabed. Further, in contrast to previous observations for several other taxa including pinnipeds (Hays 2003), seals were more likely to dive pelagically during the day and benthically at night. Interestingly, with increasing current strength, seals transitioned to diving depths in the upper parts of the water column. Although this occurred during the day and night, the onset of this pelagic diving began at lower current speeds during the day. Together, these analyses suggest three broad behavioural patterns: benthic and pelagic diving while swimming against currents, and pelagic diving while drifting with currents. These are indicative of prey switching as a result of the diel and seasonal fluctuations in prey abundance or availability.

Catch rates of pelagic species such as herring (*Clupea harengus*) and whiting (*Merlangius merlangus)* are relatively high in the areas immediately peripheral to the high energy channel of the Pentland Firth (Fig. 2; Heessen, Daan & Ellis 2015). Important spawning grounds for the Shetland, Orkney and Buchan Herring stock exist in these waters with nursery grounds immediately to the west (Ellis *et al.* 2011). This results in an increased abundance of adult herring in the coastal regions during the spawning season throughout Autumn which likely use tidal currents for selective stream transport over large distances (Blaxter & Batty 1990). Further, depth distributions suggest these species to peak in concentration at around 30-70 metres (Fig. 3) and show a diel pattern whereby fish are found in denser, deeper aggregations during the daytime (Heessen, Daan & Ellis 2015). Sandeel (*Ammodytidae spp.*) catch rates in Orkney waters and surrounding areas contribute significantly to the overall commercial take in the North Sea. Additionally, they have a pronounced diel cycle which reflects the pattern of seal diving observed in Chapter 3; adult fish emerge from the sediment in the morning, forage in the water column during daylight, and then burrow into the sediment again during darkness (Winslade 1974; Freeman, Mackinson & Flatt 2002). Further, they spend most of the winter season hibernating relatively deep in the substrate (Hassel *et al.* 2004).

In combination, these observations support the inference that the observed movement and diving behaviour is driven by primarily by sandeel availability. Specifically, harbour seals spent more time foraging at mid-water depths during the daytime, when sandeels are more likely to be foraging pelagically, and switched to benthic diving during hours of darkness, when sandeels burrow into the sediment (Winslade 1974). As current strength increases, it is less likely that seals can forage benthically given the reduced ability to maintain geostationary position. At high current speeds, pelagic foraging on sandeels (and other pelagic species such as herring) is therefore more likely during the day. Given that sandeels are likely incapable of withstanding flows above 1 $m.s^{-1}$ for any length of time (Johnsen *et al.* 2017), harbour seals should, in theory, be capable of expending relatively little energy by drifting with the current, foraging on schools of sandeels. This tactic appears analogous to foraging puffins in Ireland which were observed to drift with currents while foraging at pelagic depths (Bennison *et al.* 2019).

In the harbour seals studied here, the onset of pelagic foraging occurs at higher current speeds during darkness than during the day. Seals may be able to offset the energetic cost of maintaining geostationary movement by exploiting reliable prey patches consisting of benthic dwelling sandeels during the night. However, once current strength increases past a point where geostationary movement is too energetically demanding, seals may switch to pelagic foraging on species such as herring and whiting, which migrate towards the surface during darkness (Blaxter & Batty 1990). The seasonal component of diving behaviour identified in chapter 3, although showing interesting trends remains equivocal given the consistently wide confidence intervals around model predictions. However, the hibernation patterns of sandeels potentially render them less available to seals during the winter months. This, combined with the observation that adult herring come closer to the coast to spawn throughout autumn (Ellis *et al.* 2011), suggest that the increase in benthic diving during the spring, and the increase in pelagic diving during the autumn and winter, may be a genuine signal which warrants further investigation. In support of this, harbour seal diet in the UK has been shown to be dominated by sandeels, with a large seasonally important constituent of pelagic prey (predominantly herring) in the autumn and winter months in the north coast and Orkney management area (Wilson & Hammond 2019).

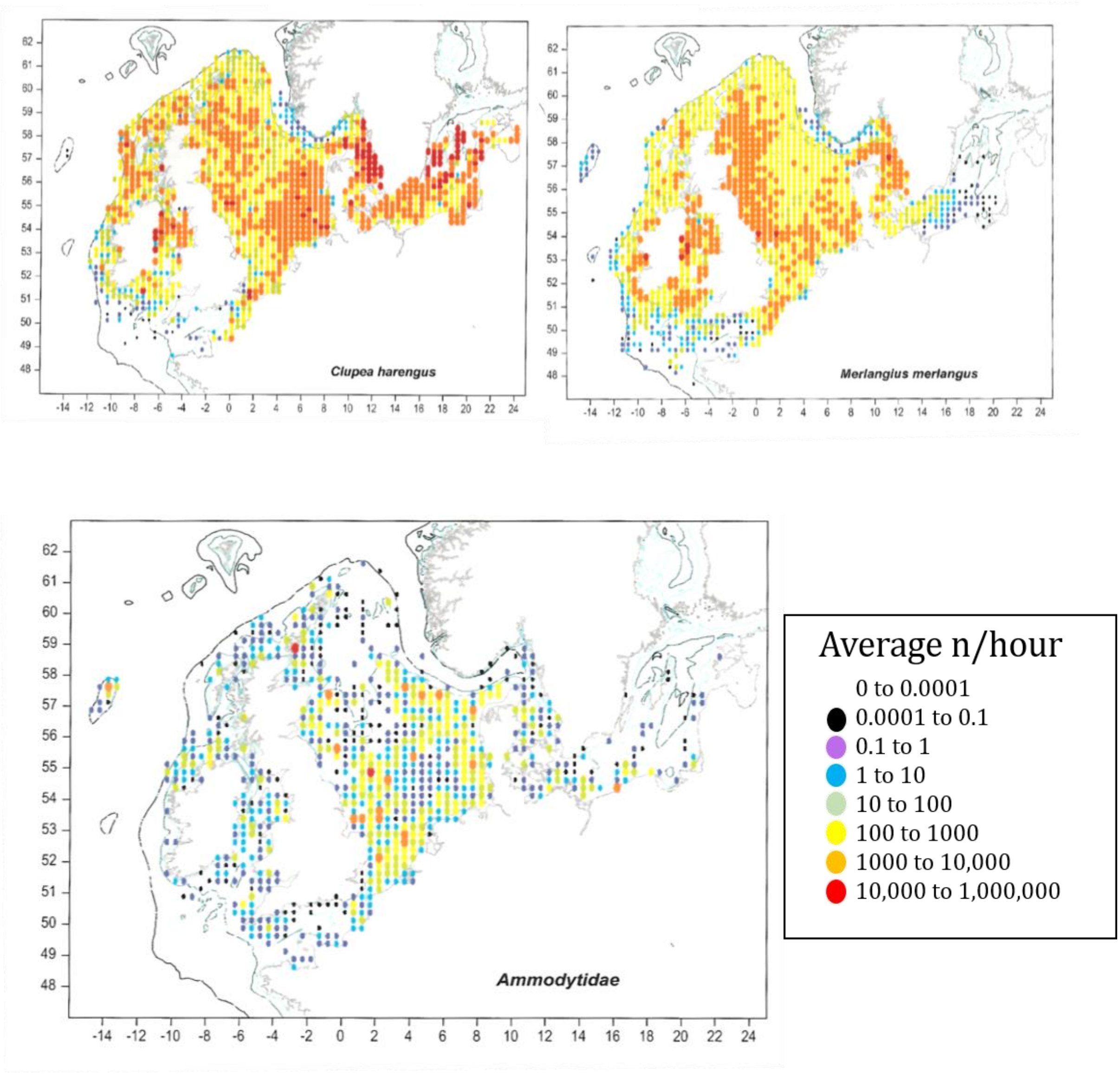

Figure 2 **Spatial distribution of important prey fish around the UK.** Herring (*Clupea harengus*; top left), Whiting (*Merlangius merlangus*; top right) and Sandeels (*Ammodytidae spp.*) distributions are given by catch rate. Figures from Heessen, Daan and Ellis (2015).

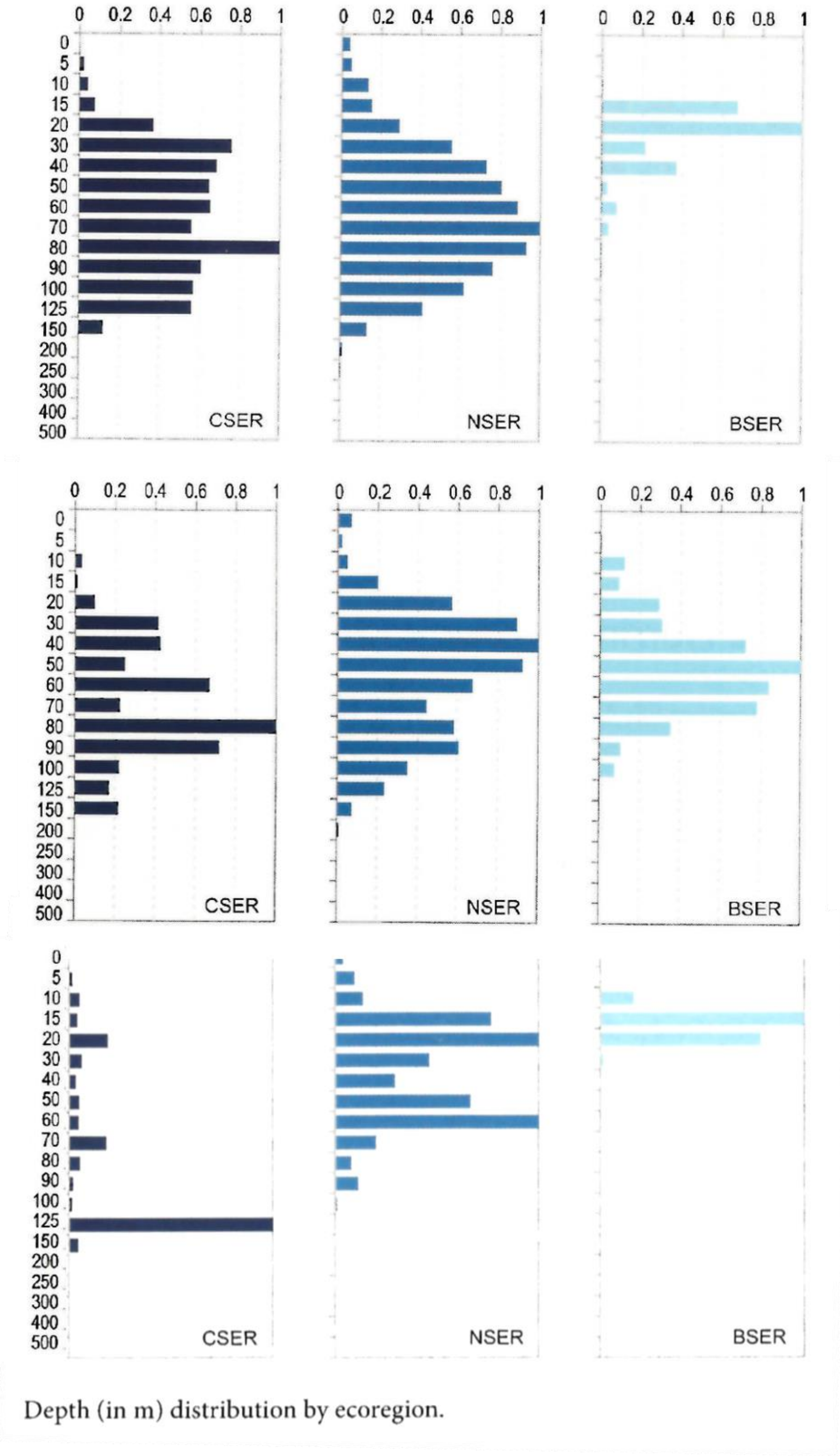

Figure 3 **Depth distribution of pelagic fish around the UK.** Whiting (top row) and Herring (bottom row) vertical distributions are given in binned depth bands of different sizes for the Celtic Sea (CESR), North Sea (NSER) and the Baltic Sea (BSER). Values represent total number caught at that depth divided by the total number of hauls at that depth, normalised to 1. Figures from (Heessen, Daan & Ellis 2015).

With the results in Chapter 2 and 3 suggesting that behavioural mechanisms underlying animal movements in tidally dominated regions should be considered from both a geo- and hydro-centric perspective, I have shown that harbour seals exhibit complex interactions with both geostationary and mobile habitat features. The differences between hydro-spatial and geo-spatial foraging identified here are specific to the study population in this thesis. However, it seems clear that water flow not only influences the movement behaviours of animals but can also significantly affect our interpretations of the function of those movements. This is not a new concept, and several previous studies have recommended taking hydro-referenced movement into account when establishing behavioural classifications of marine animals (McConnell *et al.* 2002; Gaspar *et al.* 2006; Horton *et al.* 2011; Bon *et al.* 2015; Dodge, Galuardi & Lutcavage 2015; Briscoe *et al.* 2016; Trudelle *et al.* 2016). Despite this, simplified, geo-centric approaches still prevail in movement ecology, even in systems which exhibit substantial flow.

The results have highlighted the potential issues of classical approaches of movement characterisation in mobile environments. If not utilised in future studies of energetic systems, researchers risk making false inferences or misinterpreting the relative importance of areas or habitat features. Researchers now have an evidence based, statistical study with which to refer and develop, and it will no longer be defensible to ignore the use of current correction in moving systems in instances where oceanographic data is available. I therefore believe the work will have a significant impact on movement ecology and lend vital, quantitative support to the notion that, as Gasper *et al.* (2006) stated, “neglecting ocean currents can lead us up the wrong track”.

6.3 Effects of the tidal energy industry

To understand the effects of a tidal energy installation on harbour seals I used the GPS data from Chapters 2 and 3 to explore the spatial distributions of seals as a function of both the presence and the operations of the turbines. I used a recently developed analytical package (Scott-Hayward *et al.* 2013b) which allowed inclusion of 2-D Spatially Adaptive Local Smoothing Algorithms (SALSA) in combination with generalised additive models (GAMs). GAMs were fit in a generalised estimating equations (GEEs) framework using Complex Regional Spatial Smoothers (CReSS). The results showed that there was a significant effect of the operations of the turbine on seal distribution, with an apparent avoidance response up to approximately 2km from the turbines. The models, which accounted for the effects of tidal state found in chapters 2 and 3, showed that, regardless of turbine presence or operations, tidal dynamics was a key driver of harbour seal distributions.

The response presented here supports previous studies on the effects of single tidal turbines (or their acoustic emissions) showing that harbour seals exhibit avoidance of them during operations (Hastie *et al.* 2017; Sparling, Lonergan & McConnell 2017; Joy *et al.* 2018). However, the avoidance response seen here was at a scale far greater than previously reported and this may be due to differences including numbers of turbines, turbine acoustic emissions, and habitat (Chp. 4). For example, previous avoidance of turbines by seals had been exclusively observed in the narrow channels of Strangford Lough, Northern Ireland (Sparling, Lonergan & McConnell 2017; Joy *et al.* 2018) and Kyle Rhea, Scotland (Hastie *et al.* 2017). These sites are close to harbour seal haulout sites and, particularly in the case of Strangford Lough, there is a pronounced bottleneck effect whereby seals are required to transit past the turbine (or sound source; Fig. 4) to foraging grounds. Conversely, the Pentland Firth represents a less enclosed region, with the channel where the turbines were installed being one of many transit routes between haulout sites and foraging patches (Fig. 5). Additionally, many putative foraging sites lie to the west of the turbines so seals would not necessarily need to transit past the turbines to forage.

The acoustic emissions of tidal turbines when operating are likely to be detectable by seals (Goetz *et al.* 2011; Palmer *et al.* 2019). If seals detect these and perceive them as a threat, it is possible that, rather than transit past the turbines, they may opt to avoid the channel altogether. This highlights the importance of geographical or environmental context when predicting responses in future. For example, in the case of Strangford Lough, seals avoided the turbine by transiting past it at the periphery of the channel. If the magnitude of the avoidance response was a linear function of the number of additional turbines installed, the ability to avoid them would become apparently reduced due to the reduced proportion of available channel to transit in. This could result in increased risk of collision, resulting in an overall population fitness reduction.

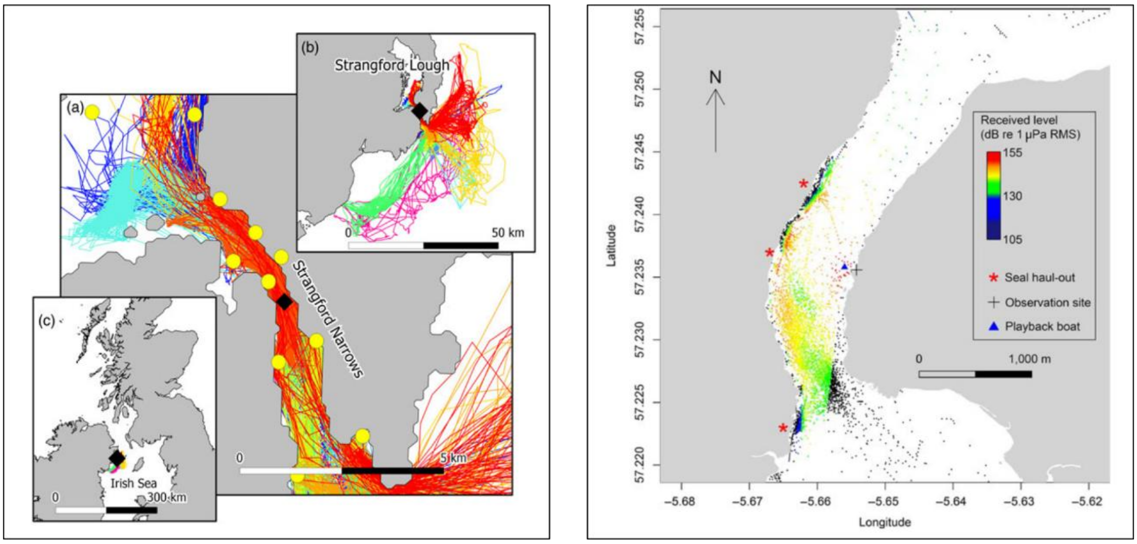

Figure 4 **Relative positions of transit routes and haulout sites in previous studies of the effects of tidal turbines on harbour seals**. Strangford Lough (left) is shown with associated haulout sites (yellow circles) and turbine site (black diamond). Kyle Rhea (right) is shown with haulout sites (red stars), turbine sound source (blue triangle) and seal location colour coded by estimated received levels. Figures taken from Sparling, Lonergan and McConnell (2017) and Hastie *et al.* (2017) respectively.

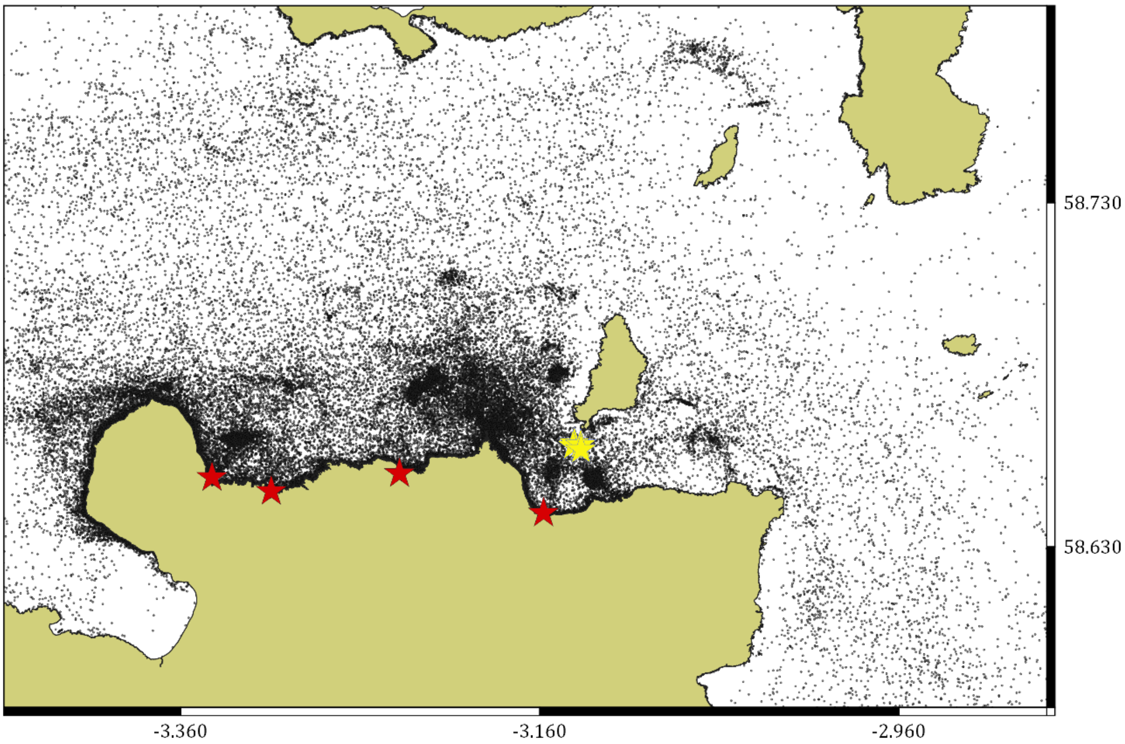

Figure 5 **Seal location data in the Pentland Firth in relation to tidal turbines and haulout sites.** Seal locations are represented by the black points, turbine locations by the yellow stars and regularly used haulout sites by the red stars.

Although the results in the thesis provide important information on avoidance patterns at scales of 100s-1,000s of metres, information on near field (metres) behaviour remains urgently required (Hastie *et al.* 2019a; Hastie *et al.* 2019b). I have shown that seals show a degree of avoidance to turbines when operational, and therefore at their most dangerous (Onoufriou *et al.* 2019). However, the resolution of GPS data precluded an analysis of avoidance behaviour at close ranges; therefore, the potential for a proportion of seals to collide with turbines remains.

The lack of technology capable of tracking seals underwater near the turbines at suitable scales currently precludes estimation of near-field evasion rates (Hastie *et al.* 2019a). The results from Chapter 5 are therefore intended to circumvent this knowledge gap by approaching the problem from a different angle; if seals do collide with turbines, how likely are they to be fatally injured? Based on the results from chapter 5, the potential for fatality as a result of a collision remains a valid concern as I showed that fatal interactions are likely to occur at collision speeds of ~5.6 $m.s^{-1}$ (well below the maximum operating tip speeds of tidal turbines). I recommend that future developments of collision risk models explicitly consider this threshold to help scale estimated collision rates by expected number of fatalities to more accurately quantify population level effects.

The major caveat throughout Chapter 5 was the lack of robust information on soft-tissue damage and concussion. Previously frozen carcasses do not demonstrate the same soft-tissue pathology as living tissue, therefore more subtle injuries may have been overlooked (Roe, Gartrell & Hunter 2012). Specifically, the differences between fresh and frozen tissue mainly reside in the breakdown of cell linings during the freezing process; this normally renders tissue more susceptible to tears or ruptures

(Roe, Gartrell & Hunter 2012; Grear *et al.* 2018). Given this, we would expect to see elevated soft-tissue damage in frozen and thawed carcasses subjected to collisions when compared to fresh carcasses. In fact, the results showed that all soft-tissue rupture identified in the pathological analyses was associated with skeletal damage, assumed certain to cause death in a wild seal. The assumption that these results are broadly applicable across all collisions therefore appears valid. It is thus suggested that future studies on the effects of interactions between seals (and other large marine fauna) and tidal turbines focus on the ability of animals to evade the devices at close range and resolve whether collisions are likely to occur at all, whether fatal or not.

The main barrier for consenting of tidal turbine arrays currently rests on uncertainty around economic viability and how installations may affect the local ecosystems, both on the long and short-term. The results from chapters 4 and 5 represent a significant step forward in both the understanding of marine mammal responses to novel, anthropogenic acoustic stimuli and the planning and consenting procedure for marine renewable energy developments. The fitness consequences of the demonstrated avoidance, both at the individual and population level, are clear in that reduced likelihood of inhabiting areas near turbines during operations results in reduced likelihood of harmful or fatal collisions. These distribution shifts also appear short-lived in so much as over the entire study period, no significant effect of turbine presence was observed, suggesting foraging areas have not yet been rendered perceptibly inaccessible. Therefore, reduction in foraging opportunities could be occurring during operational periods however, does not appear to be affecting where seals forage when the turbines are not operating. Compounded with the likelihood that a relatively small proportion of collisions will be fatal, compared to the previously held assumption that all collisions will result in fatality, these results should augment consenting procedures by reducing the uncertainty around environmental impact, especially in areas which overlap with threatened populations of marine animals. The quantification of the results from these chapters are directly translatable to currently used collision risk models, a key feature in consenting for tidal turbine arrays and, as demonstrated in section 6.4 (below), and can be used to provide evidence based estimates of collision rates in various operational scenarios. Furthermore, these results provide crucial evidence suggesting the overall impact of these devices for harbour seals is far less than the necessarily conservative estimates pre-dating this work (Wilson *et al.* 2006; Band *et al.* 2016; Jones *et al.* 2017) and can aid in the development of this renewable energy industry which could have a significant impact in reducing global carbon emissions in the coming decades. While this thesis should only be considered in the context of the turbine array in the Pentland Firth, the results from chapter 5 can be assumed uniform across test sites, assuming physical consistency across harbour seal populations. The results from chapter 4 also demonstrate a robust framework through which array developments at other sites can continually monitor their impact of the distribution and abundance of local marine mammal populations and serves as a guide as to how seals may respond to proposed arrays in the future.

6.4 Future Work

From ecology to engineering: updating collision risk model

Moving forward, a major challenge remains for applied marine mammal ecologists, policy makers and regulators, and industry engineers; how will increasing industrialisation of coastal waters affect local populations of animals? As a well-studied, semi-aquatic species, residing largely in accessible regions, the harbour seal population in the UK has one of the most robust population estimates of any marine mammal. We have detailed information on habitat preferences (e.g. Bailey, Hammond & Thompson 2014), movement behaviour (e.g. Russell *et al.* 2015), population size and trajectories (e.g. Thompson *et al.* 2019), and survival and fecundity rates (e.g. Cordes & Thompson 2014) for several discrete populations. They therefore represented the ideal model species to assess the impact of offshore renewables (among other potential stressors). Currently, the potential impacts of the tidal energy industry on seals are predicted using collision risk models. To provide a formal assessment of the influence of the thesis results on collision predictions, I have applied the mortality thresholds and spatial avoidance estimates to a commonly used collision risk model and quantify estimates of collision and mortality rates. This work is preliminary and is presented as an example to guide their use in future studies and applications.

I used the updated Band Collision Risk Model, which incorporates mortality scalars and horizontal and vertical density grids to produce model predictions (Band *et al.* 2016). The model uses an observed depth distributions across 10 metre depth bins and observed swim speed over ground of seals, derived from telemetry data (Thompson *et al.* 2016). Collision rates are calculated and summed across all turbine rotation speeds at different stages of tide. Using the spatial models from Chapter 4, I predicted absolute abundance of seals within the grid-cell containing the MeyGen-Atlantis Tidal Turbine Array (Chp. 4) for (a) absence of turbines entirely, during periods of flow (average of prediction values for all times except 1 hour either side of slack water), and (b) during operations. This was carried out by calculating model predictions as proportions of the whole prediction space and multiplying them by the population estimates (81 seals) for the entire north coast site (Thompson *et al.* 2019). This allowed a direct comparison of a method which uses baseline data and assumes no avoidance to a method which accounts for the observed changes in seal behaviour as a function of the turbines operating.

Assuming no avoidance (baseline data only) to the current four turbine array in the Pentland Firth, and a predicted density of 0.002 seals per 500 m^2 in the array region, collision rate was estimated at 54 $seals.year^{-1}$. Assuming a mortality probability of 1 (Band *et al.* 2016), this can be considered 54 $mortalities.year^{-1}$; however, using the mortality threshold derived in Chapter 5, this decreases to 38 $mortalities.year^{-1}$. Further, using the avoidance rates predicted during operation (Chp. 4), the estimated collision rate reduced to 21 $seals.year^{-1}$ which yielded a mortality rate of 14 $seals.year^{-1}$. Whilst 14 seals a year represents a significant proportion of a population already in decline (Thompson *et al.* 2019), this exercise highlights the importance of behavioural and physiological data to inform these models; here I estimated an overall reduction in mortality rate of ~55%. It has been shown in previous studies of bird flight in relation to operational wind farms that close range avoidance can occur at rates of up to 99% (Winkelman 1992; Painter, Little & Lawrence 1999; Madders 2004). If this rate is translatable to harbour seals in tidal turbines then these mortality rates may be scalable even further, reducing the likely fatality rate of these interactions to less than 1 $seal.year^{-1}$.

Understanding animal movement through holistic movement models

The advent of modern biologging techniques to provide ultra-high resolution data could offer a means by which we can further understand fine-scale behaviour of marine animals in dynamic habitats (Cooke *et al.* 2004). Several recent studies have shown that tools, such as accelerometers, can help resolve foraging behaviour more robustly and in higher resolution than data from more traditional tags (e.g. Fossette *et al.* 2008; Shepard *et al.* 2008; Naito *et al.* 2013; Volpov *et al.* 2015). These data have also been used as means of validating model based approaches to behavioural classification (e.g. Leos-Barajas *et al.* 2017a). Holistic bio-loggers which include multiple sensors such as accelerometers, magnetometers, speed sensors, hydrophones, CTDs, GPS, TDRs and even active sonar are now becoming more available (Goulet *et al.* 2019). Further, increasing complexity of mechanistic modelling frameworks is allowing the integration of multiple data-streams to quantify and understand animal behaviour at sub-second resolutions (Leos-Barajas *et al.* 2017b; McClintock *et al.* 2017). In combination with development of high spatial resolution hydrodynamic models, a similarly ever-growing field, drivers of seal foraging behaviour and the ways in which body movement and adjustments allow animals to exploit energetic environments could be determined.

This thesis presented a rudimentary, discrete time Hidden Markov Model to model seal movements in tidal flows. However, application of an extension to this framework, the Hierarchical Hidden Markov Model, would allow the inclusion of data streams of varying resolutions, such as accelerometery and dive data along with GPS locations to resolve the complexities of movement in flow (Langrock *et al.* 2012a). Further, the inclusion of intrinsic covariates could be included to aid interpretation of the potential physiological limitations of movement in these habitats. This approach would require the assumption that foraging behaviours are variable in regions of high flow, as shown by the results in Chapters 2 and 3. Thus a modelling framework incorporating different scales of movement in tidal flows, such as flipper stroking rates, body orientation, lunging, descent and ascent rates and bottom time in conjunction with environmental covariates could not only refine our understanding of activity budgets but would be useful in determining how animals adapt to life in high flow.

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Appendix I: Supplementary Material for Chapter 2

Extent of hydrodynamic model elements

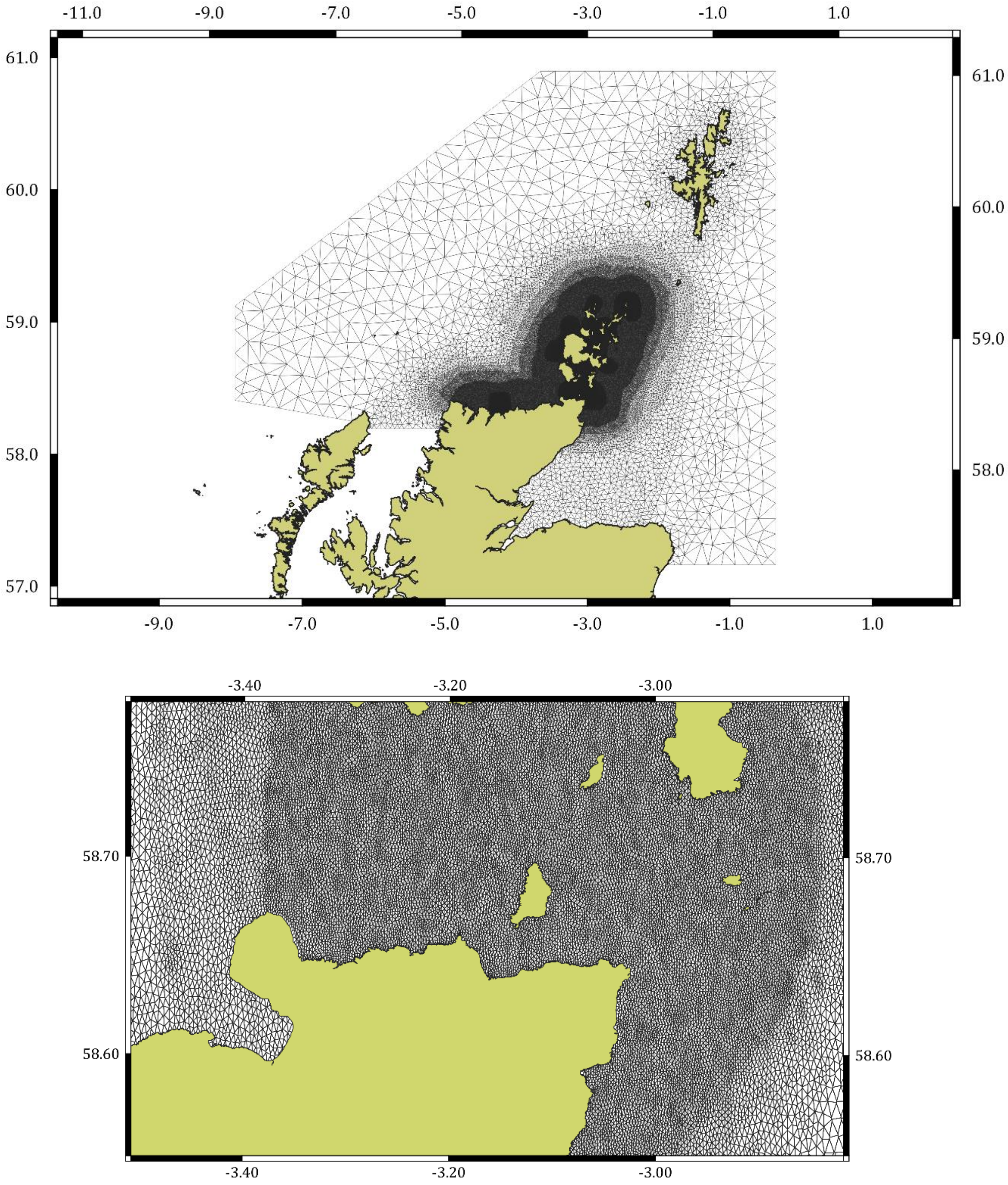

Fig A1.1 **Extent of model elements for the Pentland Firth and Orkney Waters sub-domain of the Scottish Shelf Model.** Plots show the entire horizontal range (above) and the inner Pentland Firth (below). Model elements get finer in resolution towards the inner Pentland Firth.

Daily distance travelled

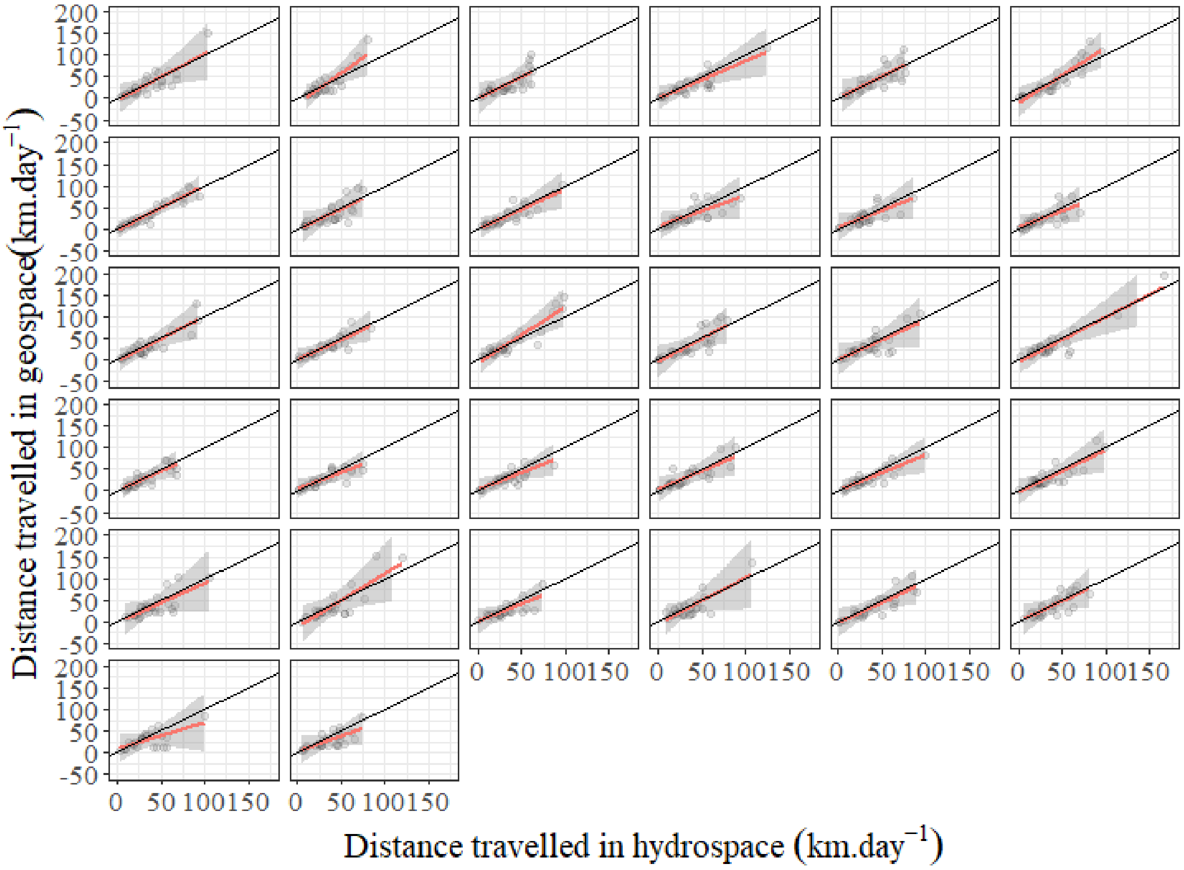

Figure A1.2 **Daily distance travelled in geo-space vs hydro-space.** Each point represents the total distance moved during each 24-hour period; data for all seals is provided. The red line and shading shows the mean estimate (± 95% CIs) from a linear regression between hydro- and geo-space distance. The dashed line indicates the y=x relationship. The trend indicates that, in general, animals travelled similar distances in geo and hydro-space however an overall slight skew towards further distances travelled in hydro-space was observed (overall R^2=0.79).

HMM Validation

HMM validation was undertaken by visual inspection of pseudo-residuals. Pseudo-residuals were near to normally distributed for the hydro-spatial step length and turn angle (Fig A1). Autocorrelation function (ACF) plots revealed a small degree of autocorrelation in pseudo-residuals however only to a lag of 13. Pseduo-residuals were near to normally distributed for turn angle in the geo-spatial HMM with a comparative right skew in step length pseudo-residual distribution when compared to the hydro-spatial HMM (Fig A2). ACF plots revealed no autocorrelation in turn angle but a small degree of periodical autocorrelation in step length pseudo-residuals. This suggests that a degree of variability within the data was not explained away by the fitted model and additional covariates or states may have resulted in a superior model fit for geo-spatial data. However, given the project goals and the limited biological interpretation of additional states, coupled with the addition of hydro-spatial information in the combined approach, the final model was deemed both a good fit and biologically interpretable, which is an essential compromise when fitting HMMs (Pohle *et al.* 2017).

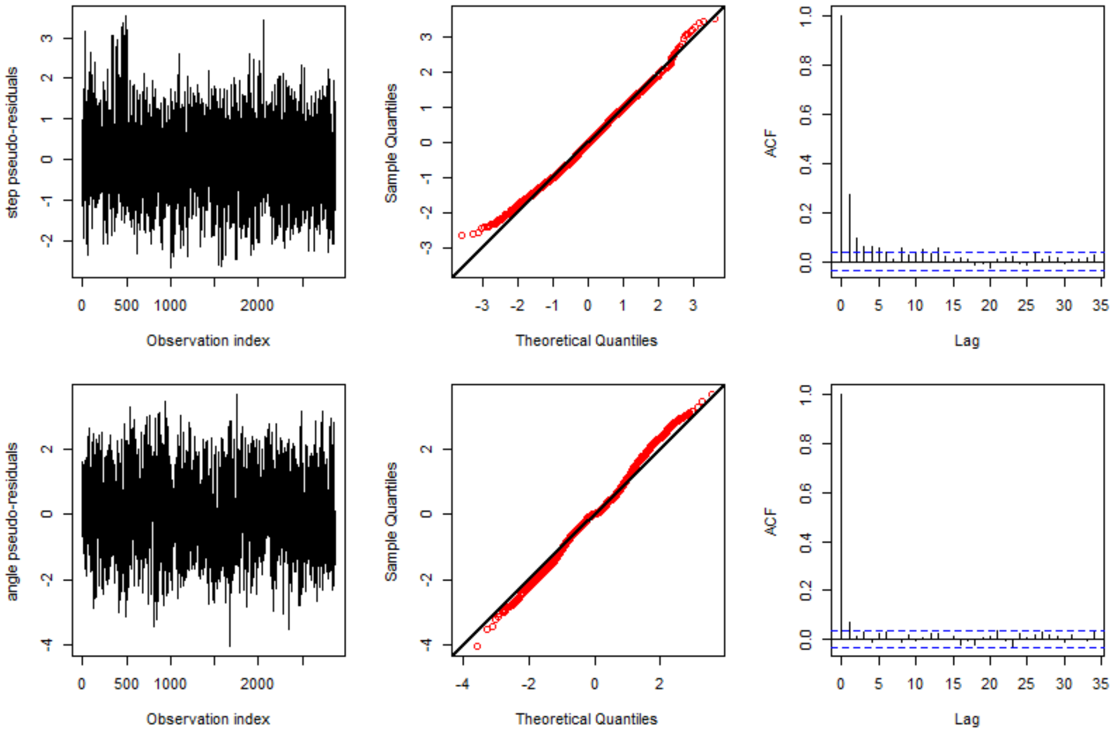

Figure A1.3 **Model pseudo-residuals for the hydro-spatial HMM.** Observation indices and qq-plots are provided to inform normality of residuals for step length Itop row) and turn angle (bottom row). Autocorrelation function plots are provided up to a lag of 35.

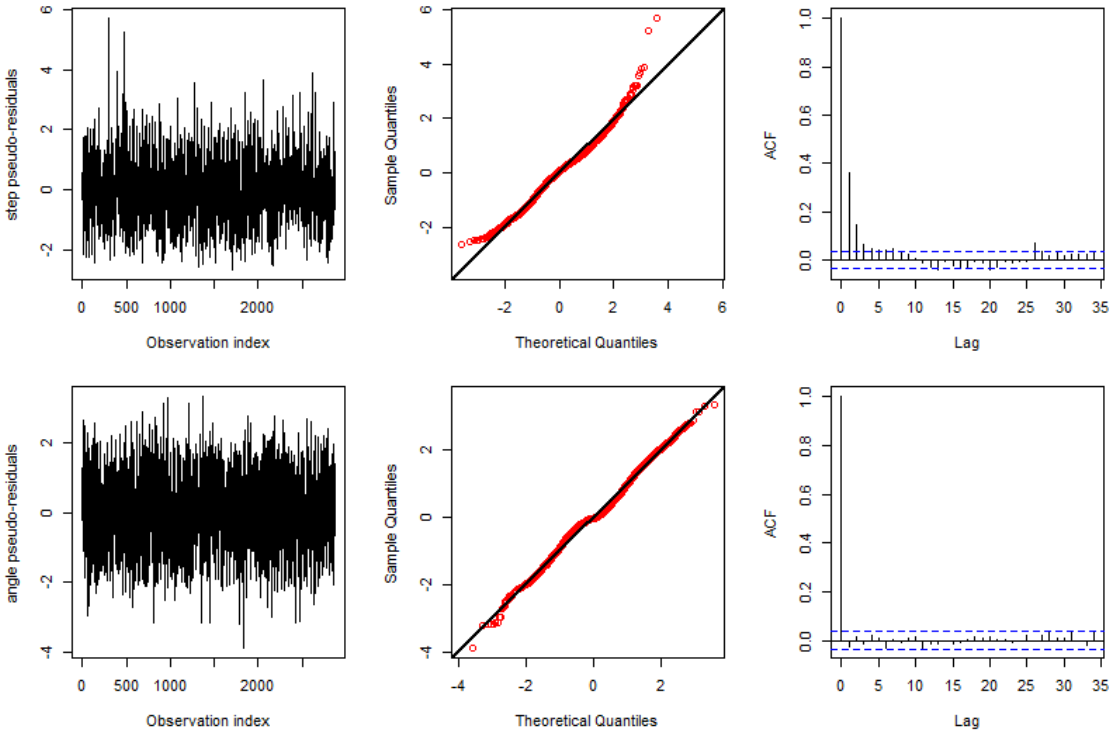

Figure A1.4 **Model pseudo-residuals for the geo-spatial HMM.** Observation indices and qq-plots are provided to inform normality of residuals for step length Itop row) and turn angle (bottom row). Autocorrelation function plots are provided up to a lag of 35.

Appendix II: Supplementary Material for Chapter 3

Supplementary figures for principle component analysis

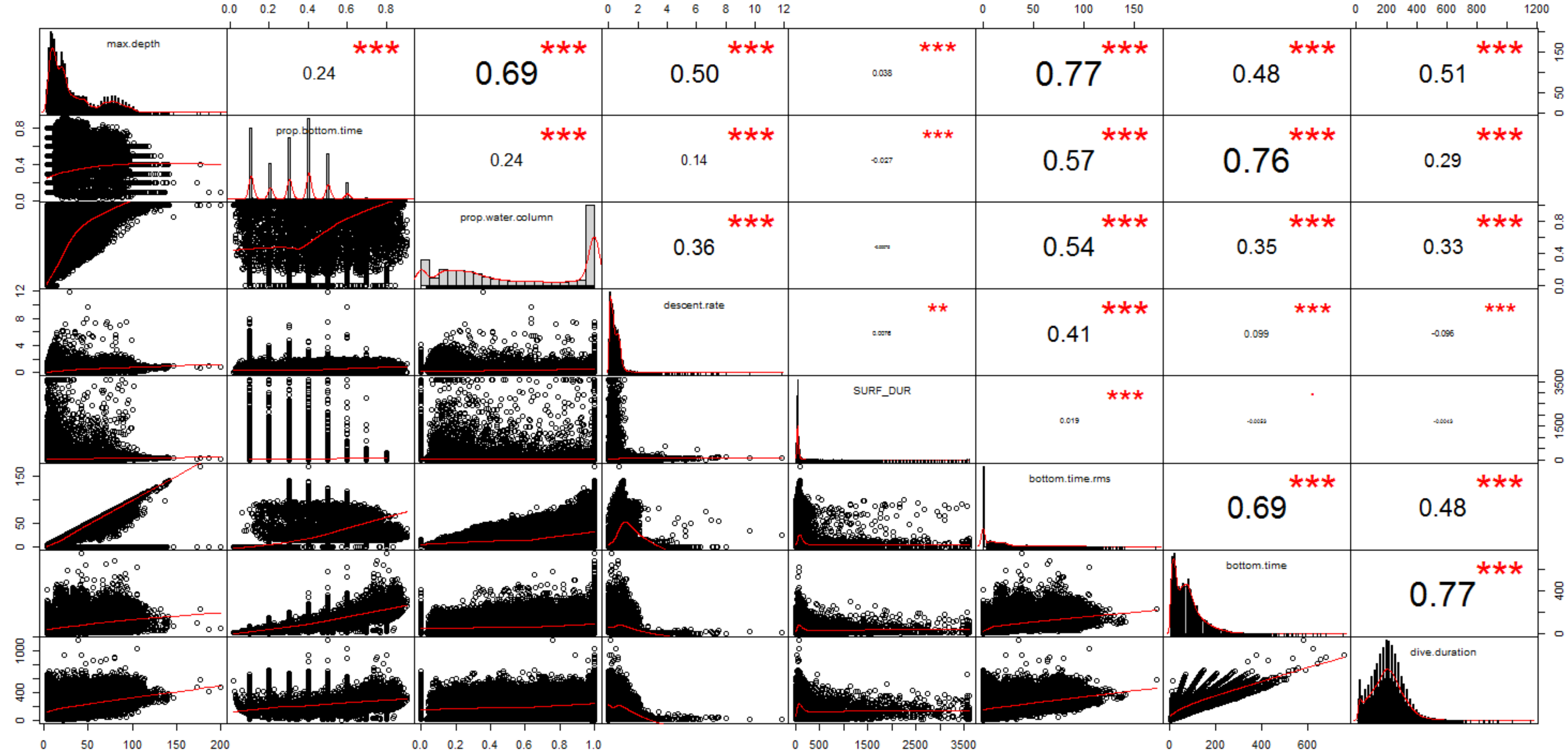

Figure A2.1 Correlation plot for all dive metrics used in principle component analysis. Values represent degree of correlation.

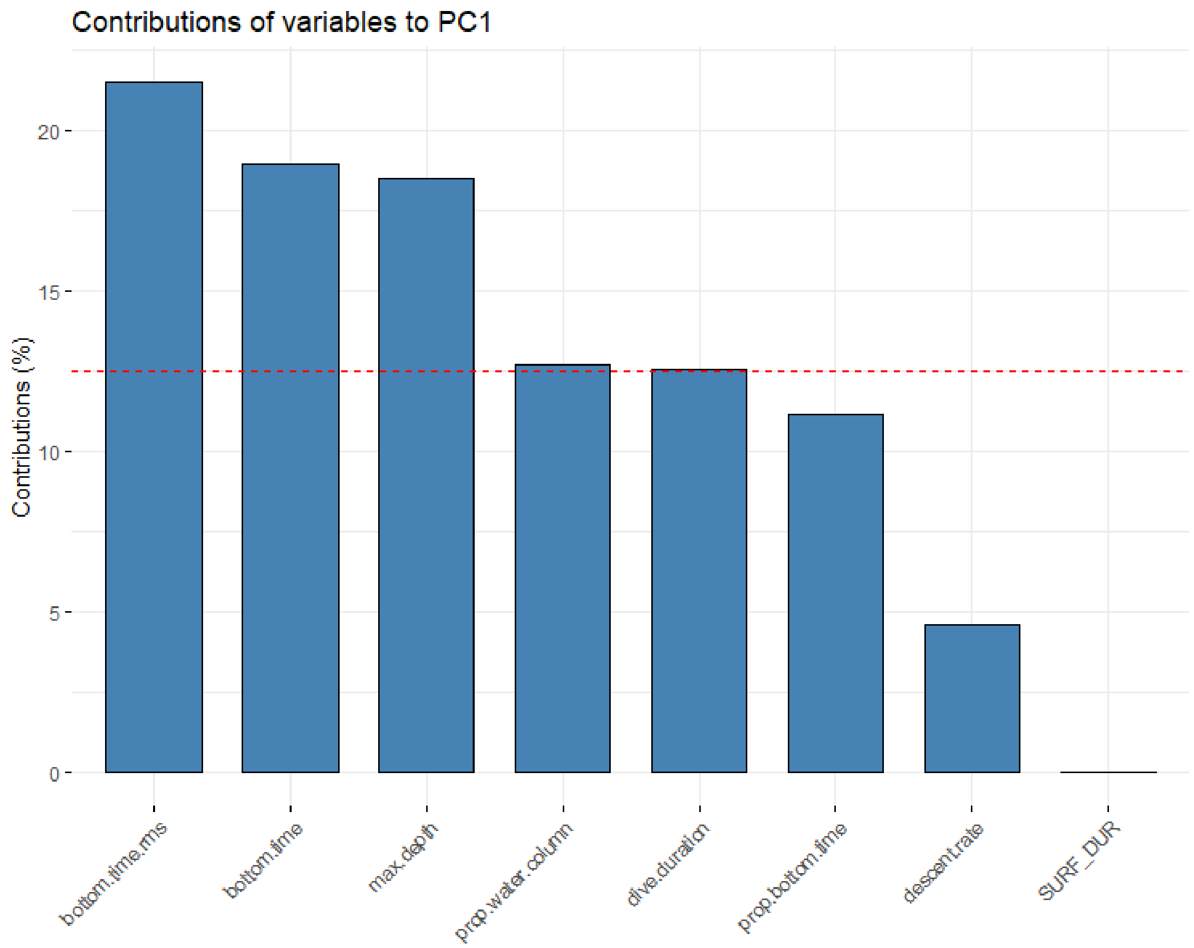

Figure A2.2 Histograms of contributions from each dive metric to principle component 1.

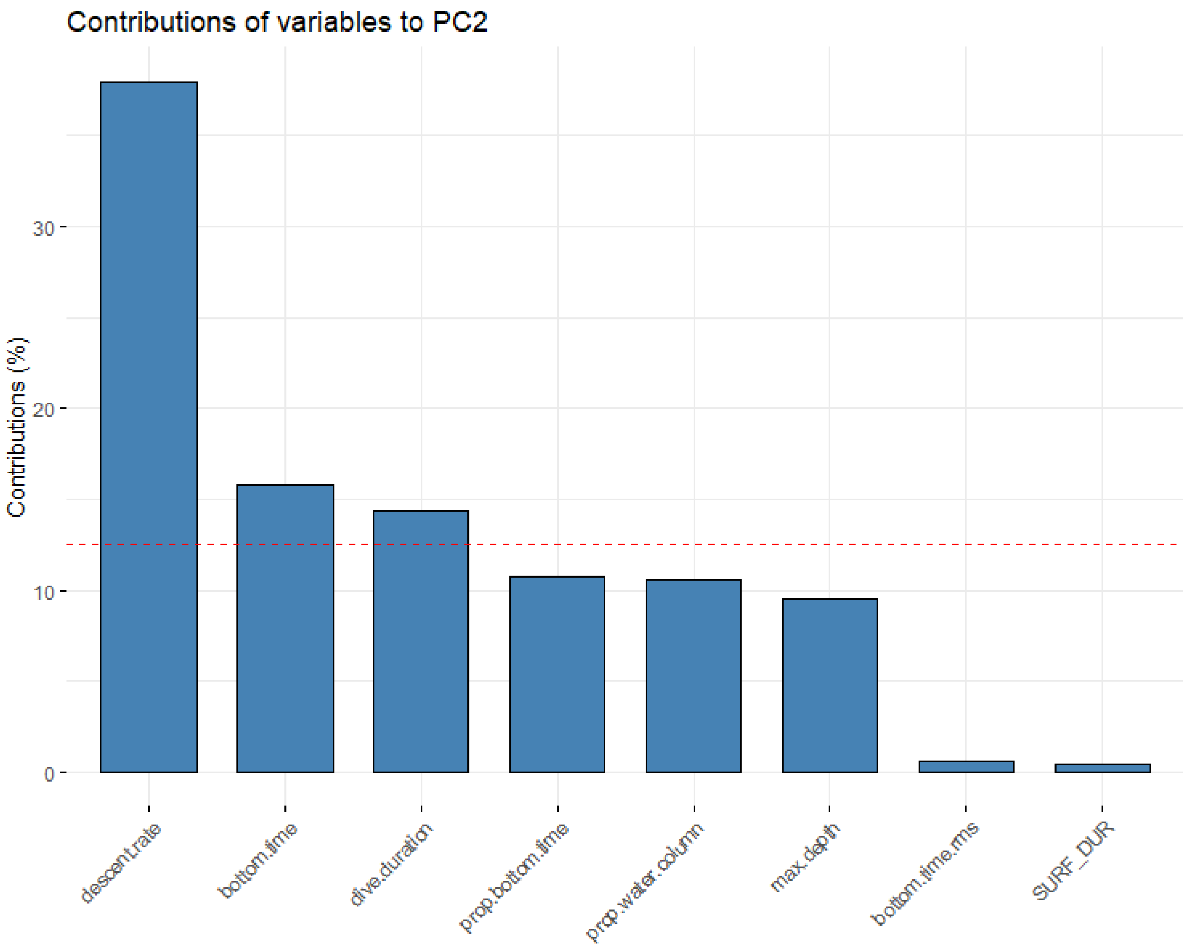

Figure A2.3 Histograms of contributions from each dive metric to principle component 2.

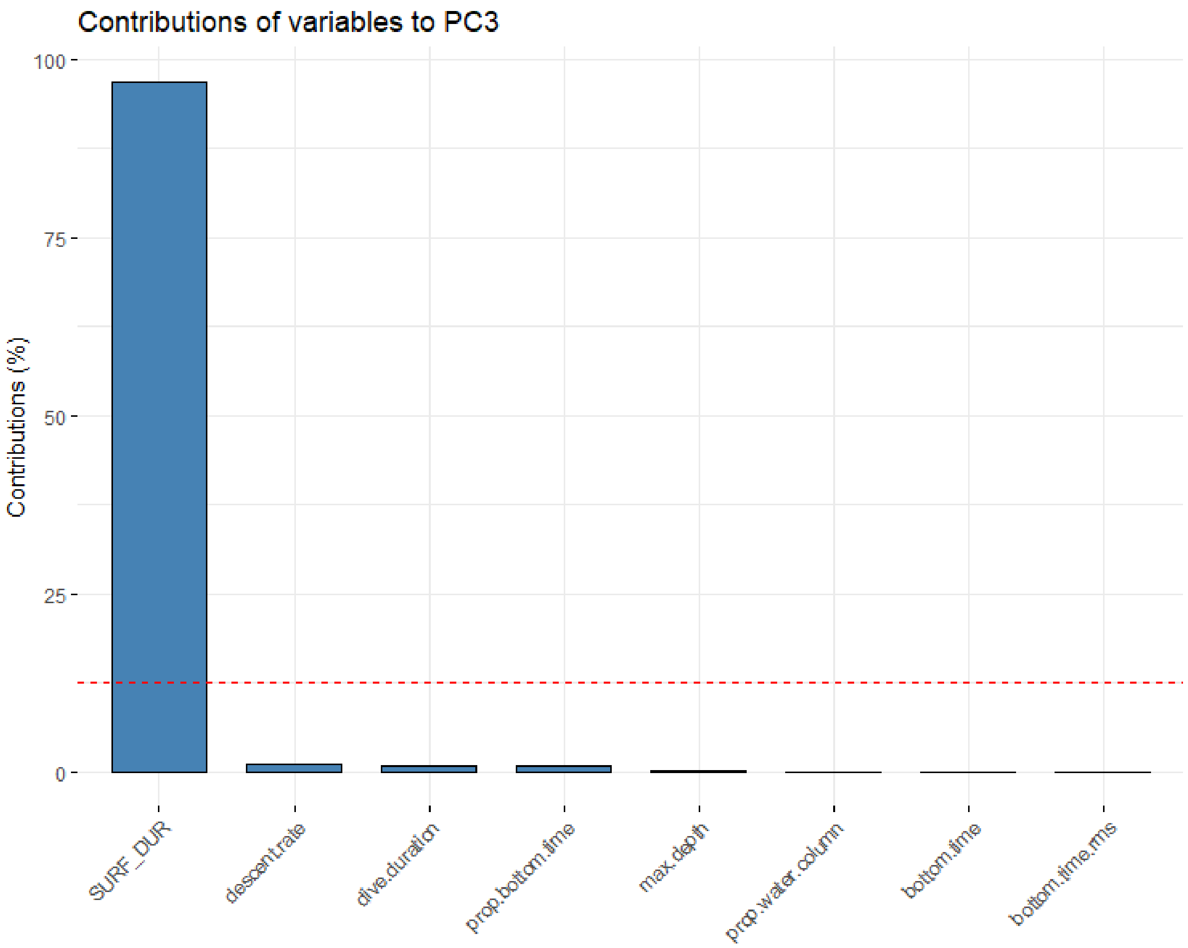

Figure A2.4 Histograms of contributions from each dive metric to principle component 3.

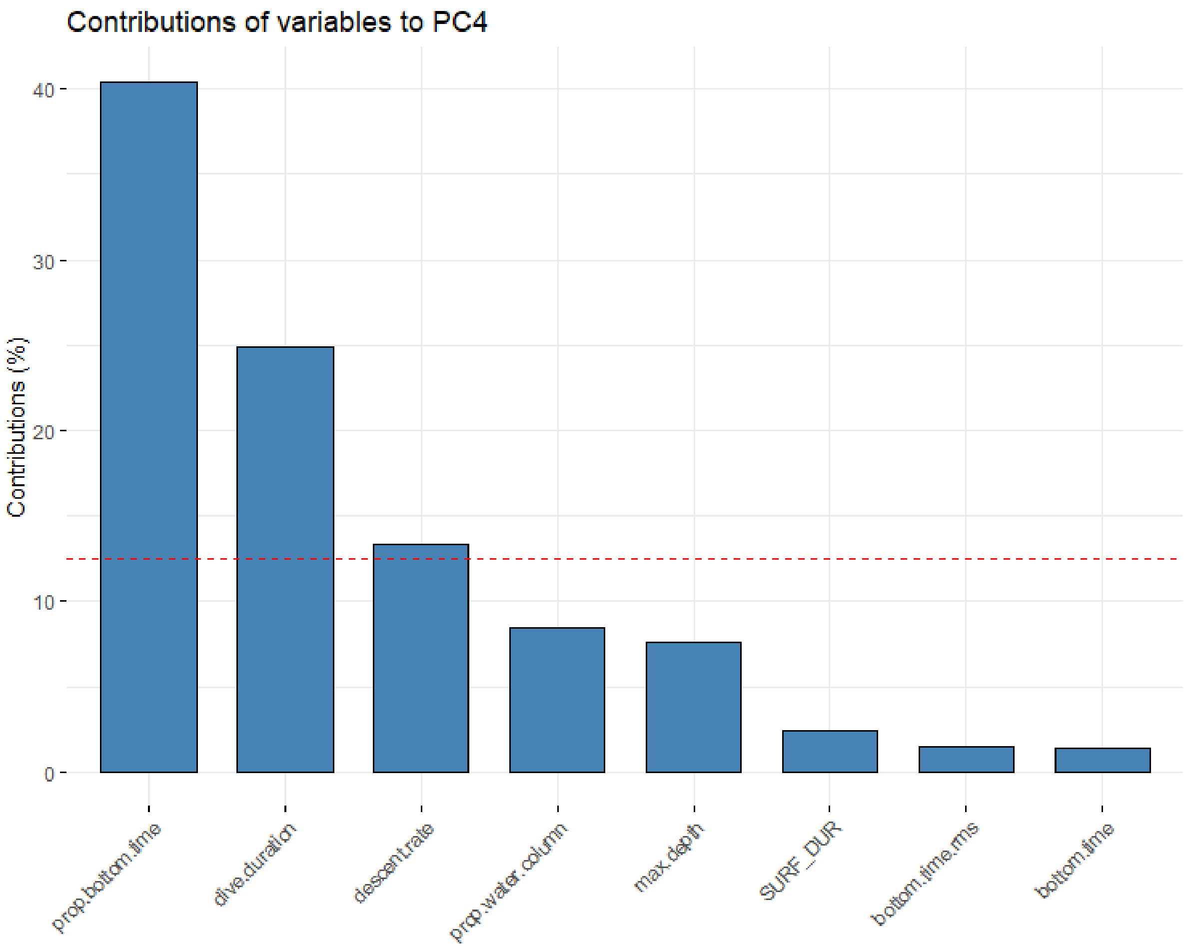

Figure A2.5 Histograms of contributions from each dive metric to principle component 4.

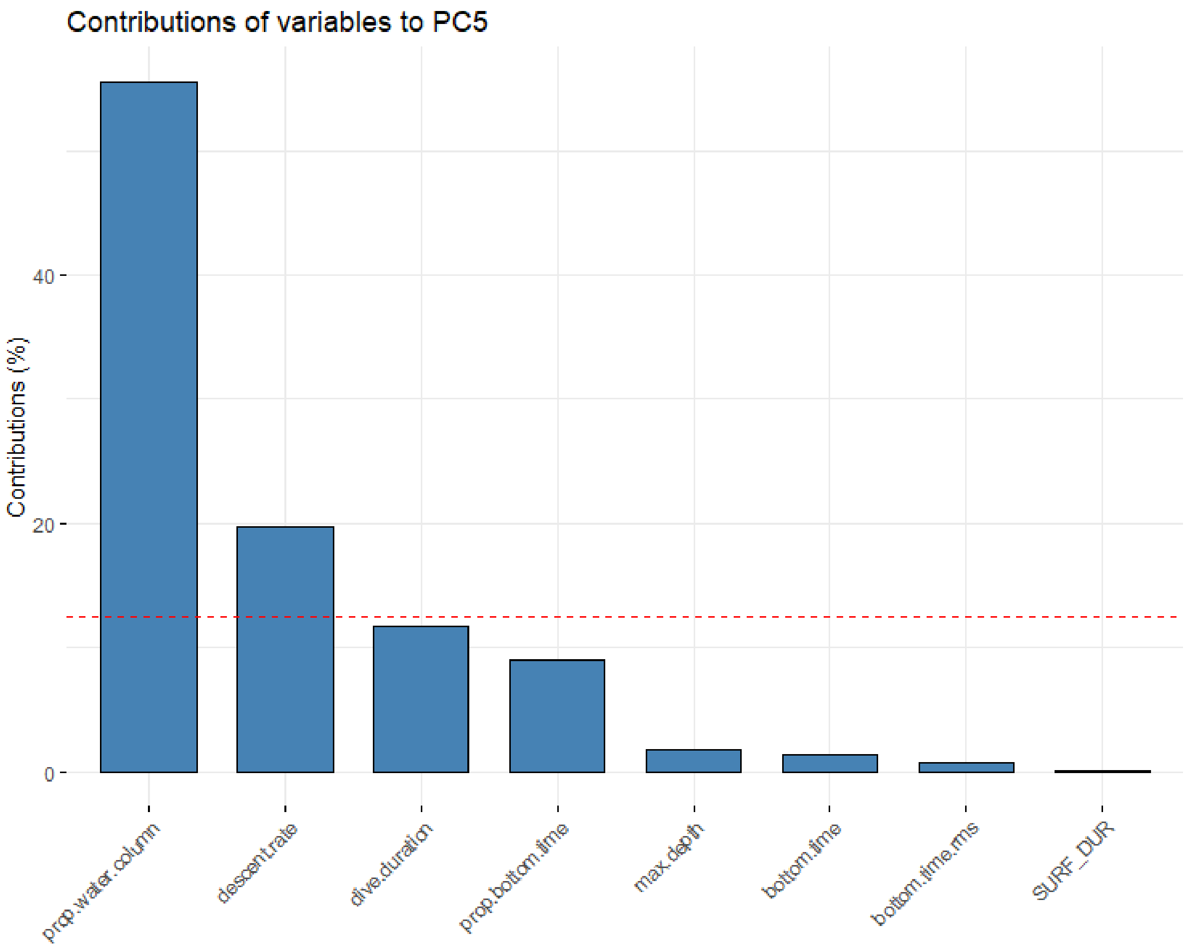

Figure A2.6 Histograms of contributions from each dive metric to principle component 5.

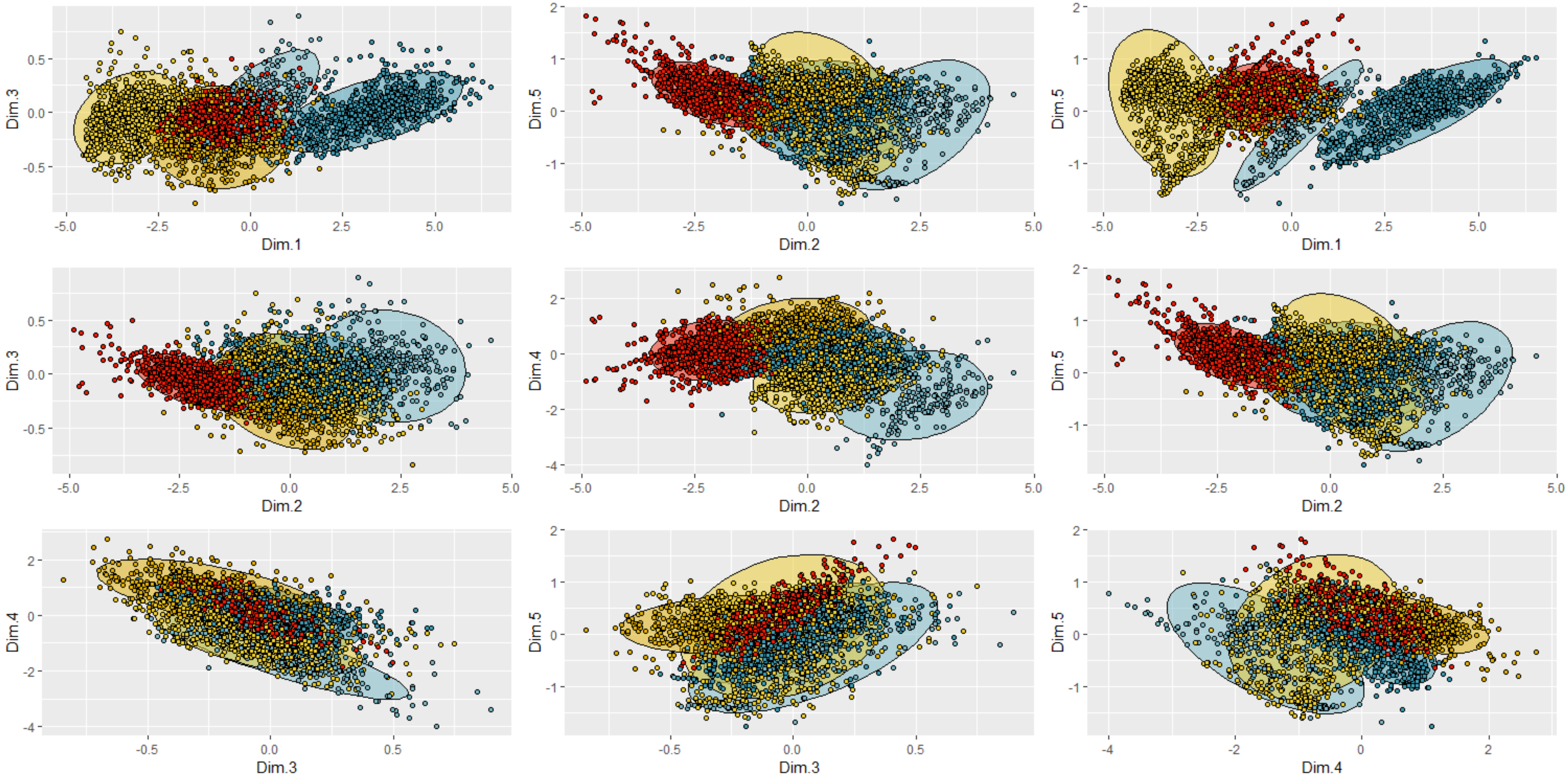

Figure A2.7 All principle component combination plots. Associated clusters for the random sample of 5000 dives are highlighted with different colours. Ellipses represent the 95% range of each cluster.

Density plots of covariate spread per individual

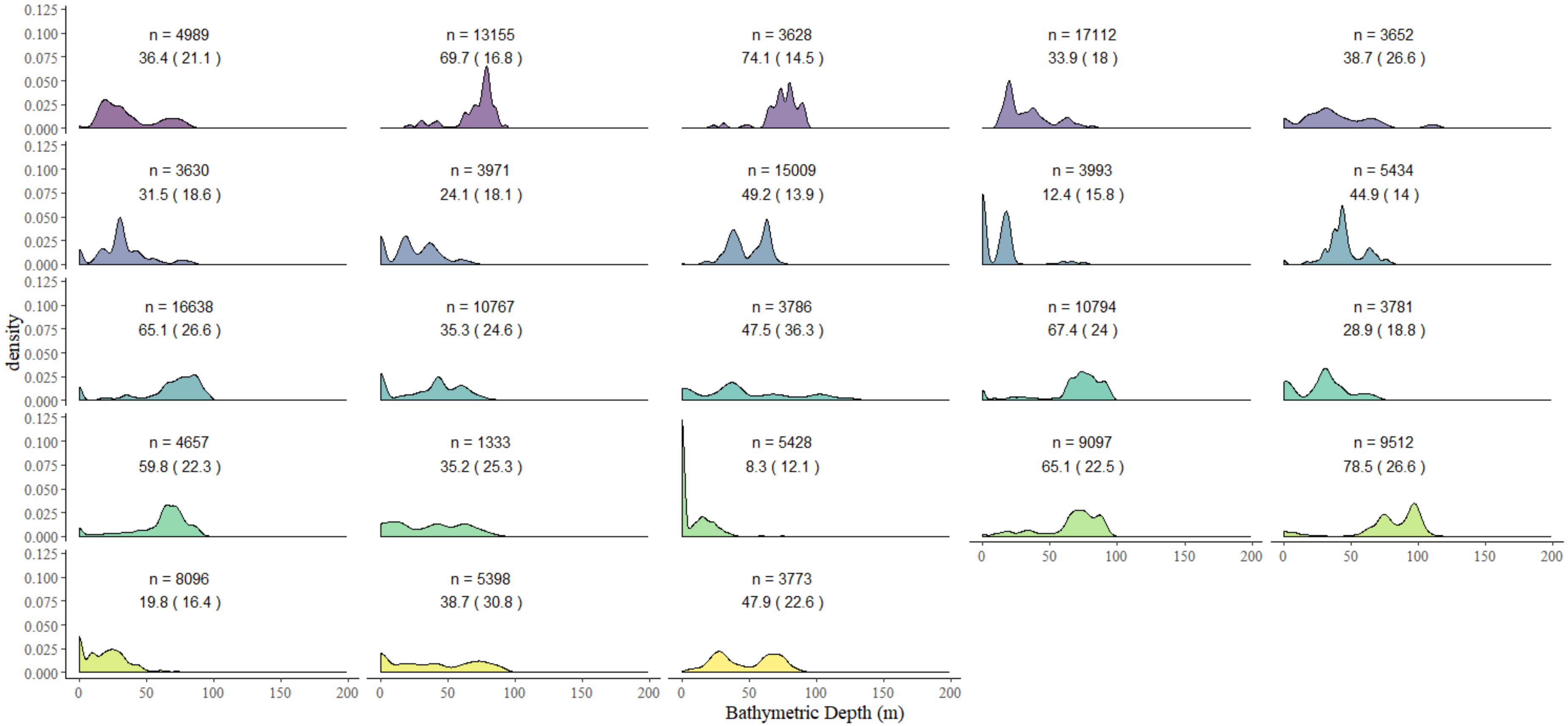

Figure A3.1 Density plots of bathymetric depth representation per individual. Sample size is given for each individual which represents the number of dives. Mean value of the covariate is also provided with the standard deviation in brackets.

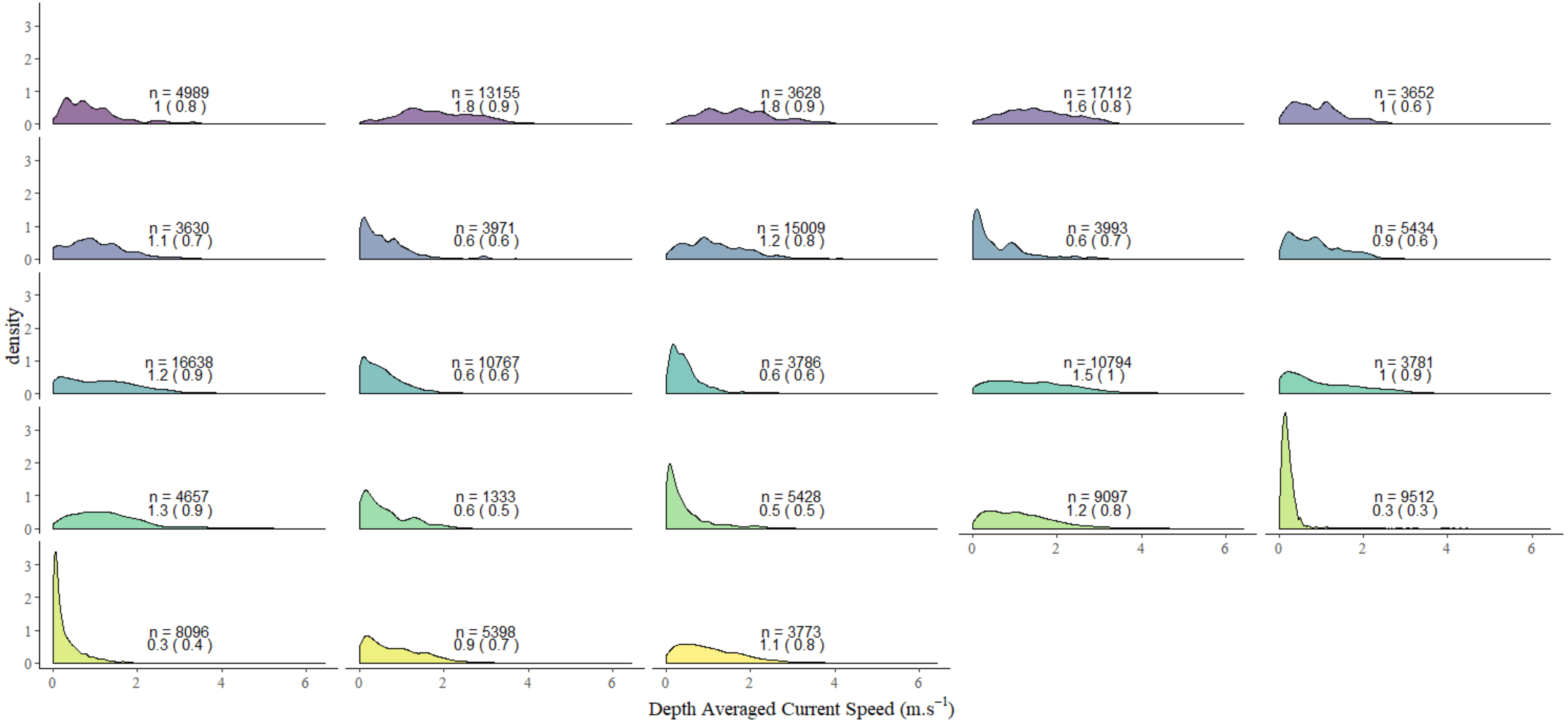

Figure A3.2 Density plots of current strength representation per individual. Sample size is given for each individual which represents the number of dives. Mean value of the covariate is also provided with the standard deviation in brackets.

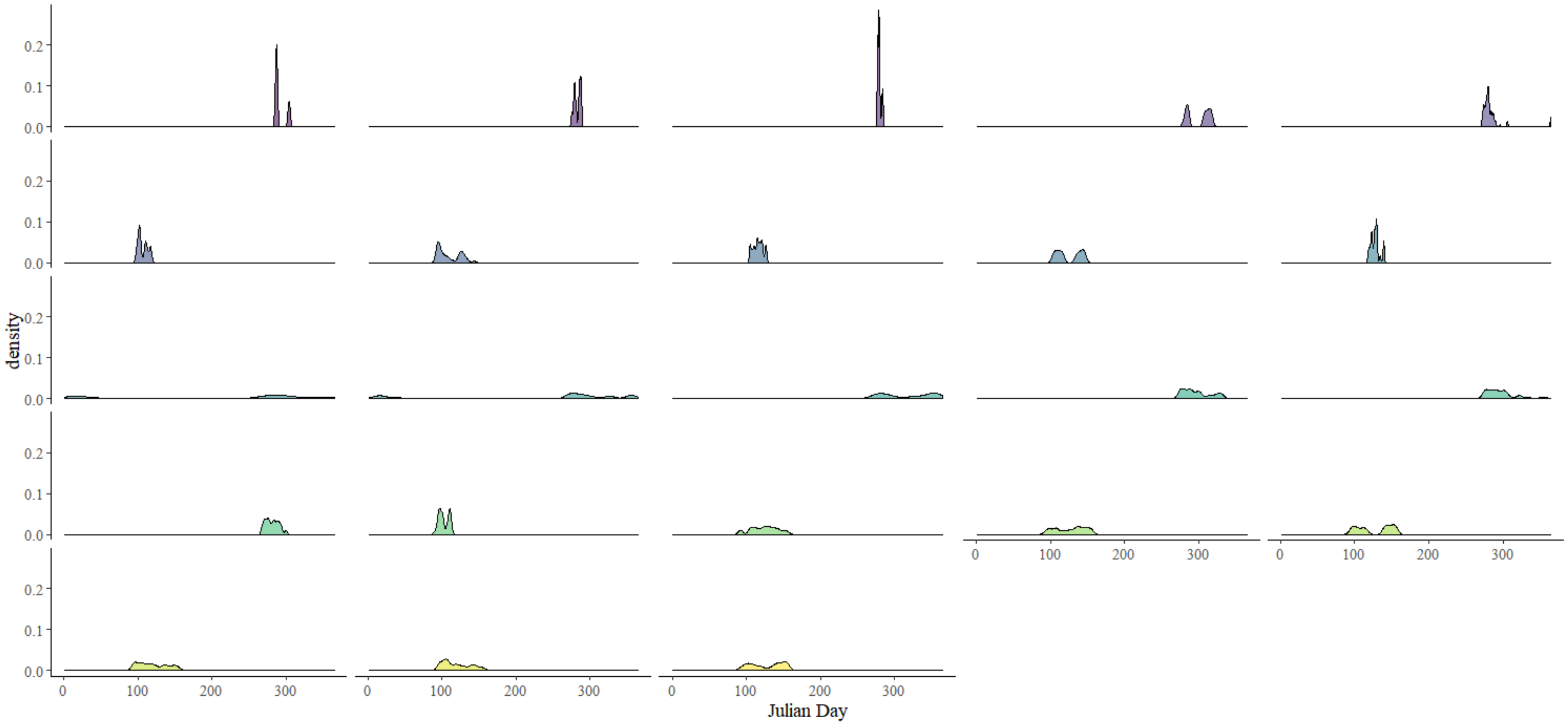

Figure A3.3 Density plots of Julian Day representation per individual. Sample size is given for each individual which represents the number of dives. Mean value of the covariate is also provided with the standard deviation in brackets. These plots effectively show the amount of data provided by each tag, through time.

Appendix III: Supplementary Material for Chapter 5

Experimental set-up for preliminary collision trials

Five seal carcasses were suspended either semi- or fully submerged just below the water surface with the use of buoys to account for the natural buoyancy of the carcasses (figure 1). The carcasses were tied at the neck, fore flippers and hind flippers to a horizontal line between two anchored buoys. Weights suspended from the anchor lines pulled the buoys apart and maintained the horizontal line under tension. The carcasses were held in a fixed position by strapping a buoy alongside the carcass and prevent rotation. The attachments were not rigid, so the carcass was able to move in response to the collisions, but the tension in the horizontal line provided some resistance to horizontal rotation (pivoting) and to horizontal displacement. The buoy strapped to the carcass added resistance to rotation and to horizontal displacement by increasing the surface area and hence increasing the drag forces acting on the body.

The turbine blade was simulated by fitting a profile similar to the leading edge of a tidal turbine blade to the keel of a high speed, jet propelled boat (figure 2). An initial design using a straight leading edge was constructed but abandoned because the leading edge protruded too far forward from the keel and therefore had the potential to produce large lateral forces at the high speeds required for the collisions. This posed potential safety concerns and would have prevented accurate positioning of the boat during high speed collision trials.

A replacement profile that protruded 40mm from the keel was moulded to follow the keel of the boat (Figure 3). Three lengths of PVC piping, arranged in a triangular structure, were fixed to the centre line of the hull (figures 3 and 4). Each 20mm diameter pipe was attached to the adjacent pipe with a polyethylene weld. The pipes were filled with a vulcanised silicon rubber for rigidity.

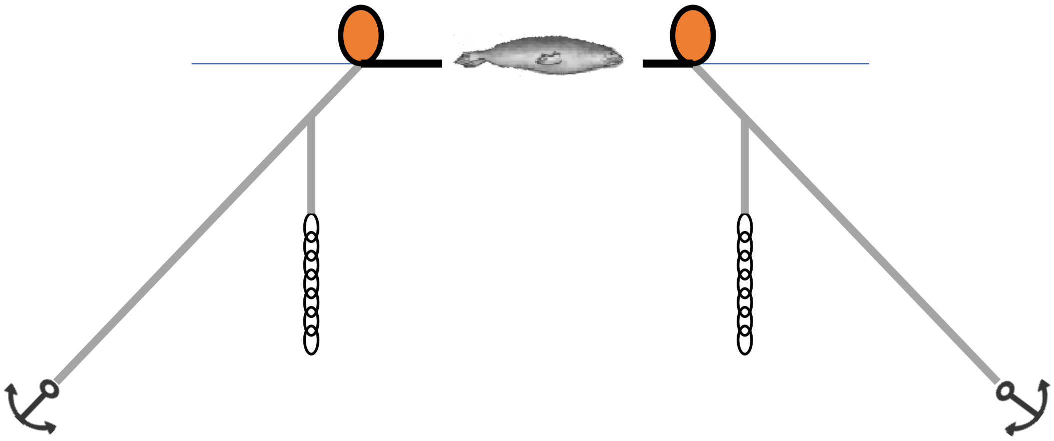

Figure A4.1 **Diagram of the experimental set-up.** Two orange buoys, weighted with chain and fixed in position at the surface with support anchors are connected by a 3 metre length of rope. The carcass under test is attached to this rope with further flotation buoys attached if the carcass displayed negative buoyancy.

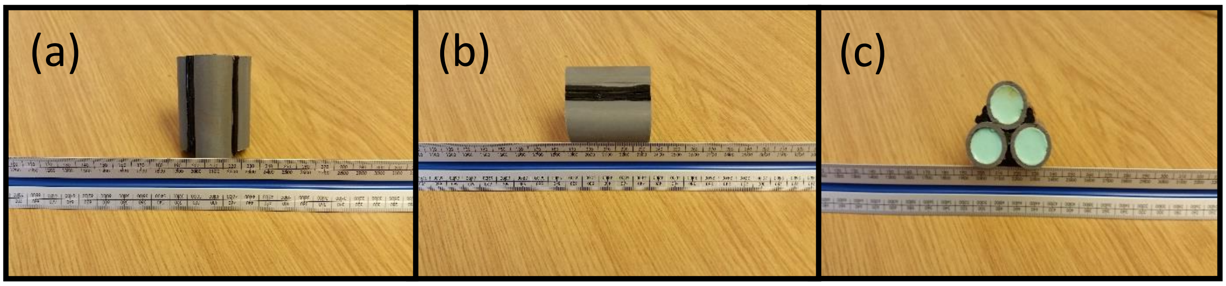

Figure A4.2 **An example length of the model turbine blade.** Perspectives are provided from (a) a head on view, (b) a side view and (c) a cross-sectional view.

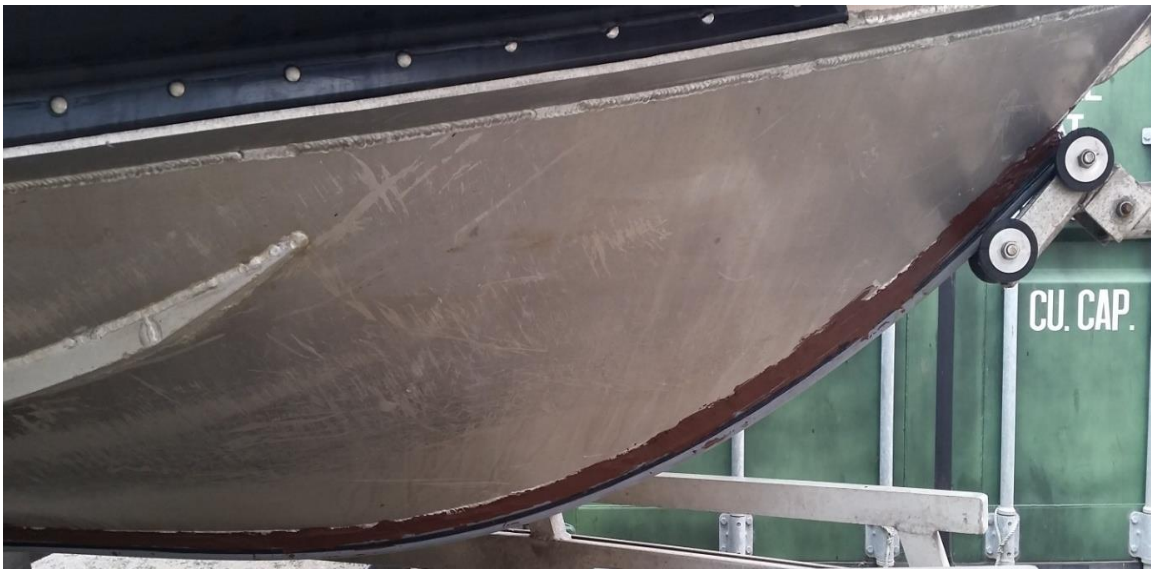

Figure A4.3: **The model turbine blade fixed to the boat hull at the mid-line.**

Collisions were inflicted on the head, torso (rib-cage and scapulae) and pelvis of each carcass by driving the jet boat at the target at known speeds. Trials were carried out in a large sheltered artificial harbour at Ardersier Point in the Inner Moray Firth. This site provided a sheltered, effectively enclosed area, 2 km x 0.25 km with no appreciable currents or wind driven waves in the inner harbour where the trials were conducted.

Photographs of the boat passing at known speeds (figure 4) were used to calculate angle of the blade at the impact point, assuming that the initial contact with the buoyed carcass was at 30cm above the surface. With the water surface acting as a flat, adjacent side to a right angle triangle, the impact angles for 3 $m.s^{-1}$ (6 kt), 6 $m.s^{-1}$ (12 kt), and 12 $m.s^{-1}$ (24 kt) were 43.7°, 33.9° and 28.2° respectively. We used these angles to calculate an effective collision speed for each trial, calculated as:

$$\text{Effective speed} = V \sin \alpha$$

Where alpha was the angle subtended by the blade at the water surface and V was the measured speed of the boat.

Table A4.1 shows the approach speeds, angles of attack and the resulting effective collision speeds imposed on the seal carcasses given the angle of attack. We were unable to account for the vertical movement of the boat due to small wavelets.

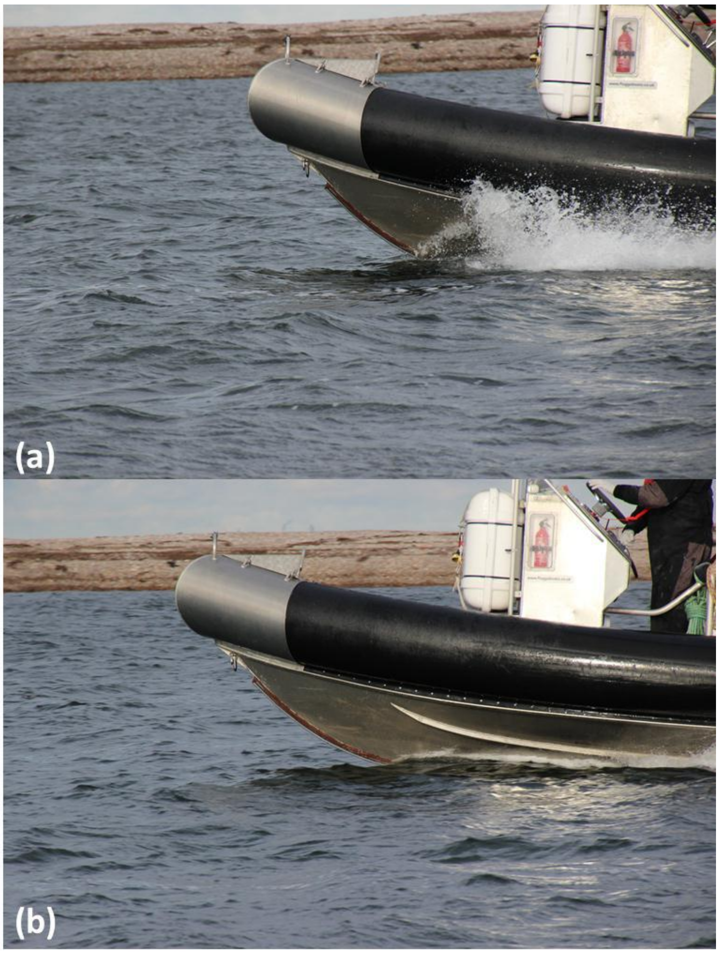

Figure A4.4 **A perpendicular perspective of the blade profile.** Profiles at (a) 6 knots, and (b) 24 knots. Note the elevation of the boat hull with relation to the water surface and the resulting angle of attack of the blade.

Table A4.1 **Adjusted displacement speeds at given angles of attack**. All values were calculated using trigonometric functions assuming the carcass was struck at the absolute centre of mass.

Boat Speed (m.s^{-1})	Angle of attack	Speed of displacement (m.s^{-1})
3	43.7°	2.07
6	33.9°	3.34
12	28.2°	5.67

Experimental set-up for subsequent trials

Collision trials took place during calm (Beaufort 0-2) weather in a sheltered bay on the east coast of Scotland. Carcasses were defrosted at ambient temperature for 10 days prior to collision trials in September 2016 and 2017 to ensure complete thawing of the soft tissue. Each individual was suspended immediately below the water surface inside a net bag which was buoyed at each end (Fig. 1, main text). The width of the net was sufficient to contain each seal carcass whilst being small enough to ensure that they did not rotate. The net was anchored at one end and the opposite end was tethered to a quick release system which separated upon impact. This ensured that the angle of attack was consistent throughout the trials, and the carcass was free to rotate or deform in response to the collisions. All collisions were carried out to the dorsal side of the carcass for consistency. The allowance of free rotation provided by the quick release mechanism resulted in no multiple strikes in the same trial as seals were free to rotate away from the trajectory of the blade after impact.