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Using a spatial overlap approach to estimate the risk of collisions between deep diving seabirds and tidal stream turbines: A review of potential methods and approaches ☆

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ABSTRACT

It is likely that there will be a substantial increase in the number of tidal stream turbines within the UK over the next decade. However, the ecological impacts upon marine top-predators, including seabirds, remain largely unknown. Although tidal stream turbines could have many direct and indirect impacts upon seabird populations, it is the risk of direct collisions between individuals and moving components that currently causes the most concern. Species such as Auks *Alcidae* sp., Cormorants *Phalacrocorax* sp. and Divers *Gavia* sp. almost certainly face higher risks than others. However, it is likely that they are not equally vulnerable. Part of predicting which are most vulnerable involves the estimation of spatial overlap between their foraging distributions and the location of tidal stream turbines. This paper reviews potential methods and approaches that should help to predict whether a population would: (1) exploit areas suitable for tidal stream turbines, (2) dive near tidal stream turbines within these areas, or (3) dive to depths where moving components are found? Answering these questions in a hierarchical manner (from 1 to 3) could help to predict the extent of spatial overlap for vulnerable populations. These approaches require a fundamental understanding of the mechanistic links between physical conditions, prey characteristics and foraging opportunities. Therefore, multi-disciplinary approaches incorporating methods usually associated with oceanographic and fisheries studies are needed to document physical conditions and prey characteristics over large and small spatial scales. Answering these questions also requires collaborative efforts and a strategic governance approach to collating the wide range of distributional, prey and physical datasets currently being collected.

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1. Introduction

The UK government has set targets to supply 20% of its energy requirements from renewable sources by 2020 (European Commission's Renewable Energy Directive (2009/28/EC)). However, it is recognised that land based energy resources including solar, wind and biomass often create conflicts over land use and ownership [1]. Therefore, alternative solutions are desirable. Fortunately the UK has large and exploitable offshore energy resources including wind, wave and tidal currents [2] and an increase in their use could go some way towards reaching these government targets. Currently the UK's marine renewable energy installations are dominated by wind turbines although it is acknowledged that diversification is necessary [3]. As a result, there is an interest in the development of installations to exploit tidal current energies, and it is likely that there will be a substantial increase in the number of tidal stream turbine installations within UK waters over the next decade [1].

The UK holds internationally important numbers of seabirds [4] and there is a legal obligation to consider the effects from tidal stream turbines upon these populations (The European Birds Directive; 2009/147/EC). Although the potential impacts on UK seabird populations are diverse in their nature and severity [5,6], it is the possibility of mortalities from collisions with moving components that often cause the most concern [7]. In this respect, tidal stream turbines differ from other marine renewable installations in that their moving components occur beneath the water surface. Therefore, only species that can dive to depths where moving components are found face collision risks. The depth at which moving components are found varies among currently active devices, although most are between 10 and 40 m from the water surface [5]. These depths are well within the maximum recorded diving ranges of several abundant species within the UK [5]. However, it is believed that Auks *Alcidae sp*, Cormorants *Phalacrocorax sp*. and Divers *Gavia sp.* are most vulnerable to collisions due to their tendency to consistently dive to depths where moving components are found, and also to exploit habitats suitable for tidal stream turbine installations [8]. Despite this it

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remains unknown whether direct collisions represent real and serious threats to these populations.

An important part of assessing collision risks may be estimating spatial overlap between the foraging distribution of vulnerable species and the locations of tidal stream turbines. Due to the diverse and synergistic manner of processes governing species foraging distribution [9–11], quantifying spatial overlap offers challenges. Therefore, pragmatic approaches are necessary. One approach is to divide the process of estimating spatial overlap into three different stages and spatial scales by asking whether a population would (1) exploit areas suitable for tidal stream turbines, (2) dive near tidal stream turbines within these areas, or (3) dive to depths where moving components are found? Answering these questions in a hierarchical manner (from 1 to 3) could help to predict the extent of spatial overlap for a range of species and identify those most vulnerable to collisions.

This paper reviews potential methods and approaches that should answer these three questions. It focuses exclusively on the species that are considered most vulnerable to collisions in the UK; they were Common Guillemots *Uria algaa,* Razorbills *Alca torda,* Atlantic Puffins *Fratercula arctica,* Black Guillemots *Cepphus grylle*, European Shags *Phalacrocorax aristotelis* and Great Cormorants *Phalacrocorax carbo.* Although Red Throated Divers *Gavia stellate*, Black Throated Divers *Gavia arctica* and Great Northern Divers *Gavia immer* are also considered vulnerable, there is little information on the foraging behaviour of these species. They were therefore omitted from any discussions, although many of the methods and approaches outlined here may well be applicable for these species. Throughout this paper, populations were considered to be groups of conspecifics that are present within a geographical region where tidal stream turbine installations are present or planned (~100 km). Areas within the regions where installations are present or planned are referred to as 'habitats' (1–10 km) and those immediately around tidal stream turbines as 'micro-habitats' (100 m).

2. Will populations exploit habitats suitable for tidal stream turbines (1–10 km)?

2.1. Tidal stream habitat and seabirds (1–10 km)

Tidal stream turbines require quite specific conditions. Mean spring peak tidal currents faster than 4–5 knots (2–2.5 ms^{-1}) and energy levels greater than 1 Nm^2 are needed for economically viable large scale (> 10 MW) projects [1]. These conditions are usually found in tidal passes between land masses and around headlands where topographical features cause currents to accelerate, providing the speeds and energy levels needed for sufficient energy returns [1]. In North America, large numbers of Auks and Cormorants have been recorded foraging within these habitats [11–14]. Within the UK, these habitats are limited in their spatial extent [15] and quantity, with only around 30 sites having the potential to provide economically efficient energy returns [16]. However, it cannot be assumed that they are not important foraging habitats on this basis alone. For example, most tidal resources are found in northern Scotland, Orkney and Shetland; the three regions that support the vast majority of breeding seabirds in the UK [4]. Moreover, seabird distribution maps based upon several decades of vessel surveys reveal high numbers of Auks and Cormorants within the regions where tidal passes are found [17]. Therefore, determining which of these populations exploit tidal passes is the first stage of predicting spatial overlap. However, it is also important to quantify what proportions of these populations may exploit these habitats. Seabirds are long-lived species with delayed maturity and low fecundity rates. As such, adult mortality rates have a significant influence on population dynamics [18] and predicting impacts depends upon estimating the number of potential mortalities among vulnerable species.

2.2. Seabird distributions (1–10 km)

At the habitat scale, strong and positive spatial relationships are often seen between a populations' foraging distribution and that of their preferred prey items [19–21]. High abundances of prey items are found in habitats characterised by high levels of primary production and/or accumulation of biological biomass and, as such, many foraging seabirds are also found within these habitats [11,22]. However, foraging distributions differ among populations, perhaps reflecting differences in their prey choice [23] and/or behaviours [24,25]. For example, Black guillemots and Cormorants usually exploit benthic prey [26,27] and could favour coastal habitats where the seabed is more accessible. For Cormorants, a need to dry out their wettable plumage between dives means that habitats also need to be near suitable roosting sites [28]. Atlantic Puffins, Common Guillemots and Razorbills usually exploit pelagic prey and may favour habitats where physical conditions help to accumulate zooplankton or fish, for example [11,24]. It must also be acknowledged that a populations' foraging distribution changes over time. This is sometimes explained by annual [29,30] or seasonal [31] changes in their preys' distribution or abundance. However, the main mechanisms are reproductive duties. During summer months seabirds must repeatedly commute between foraging habitats and terrestrial breeding colonies [32,33]. As a result, a populations' foraging distribution tends to be centred on the location of breeding colonies within the region [34].

2.3. Estimating spatial overlap (1–10 km)

Spatial overlap at the habitat scale most likely varies among populations and within populations over time. One way to estimate spatial overlap is to directly record foraging distributions over multiple years and seasons. However, even with large quantities of distributional data, robust estimates are difficult from these sources alone [35]. Moreover, the irregular changes in foraging distributions that are seen among seasons and years mean that future levels of spatial overlap cannot be accurately predicted from the past records. Therefore, there is a need to understand precisely how a populations' foraging distribution is shaped by the ecological and physical factors. This would allow predictions as to what scenarios (e.g. seasons, prey characteristics) could increase or decrease a populations' use of tidal passes.

One solution lies in spatial modelling approaches. Although encompassing a broad range of methods, most approaches are based upon resource selection functions (RSFs) [36]. RSF first uses statistical models to establish relationships between the presence or abundance of foraging individuals and a range of habitat characteristics. They then use these relationships to predict the chances of the presence (or the abundance) of foraging individuals within a habitat given its characteristics [36–38]. In addition to habitat characteristics, however, models must also consider ecological factors such as prey characteristics and the location of breeding colonies [39–41]. Thankfully, as RSF is based upon conventional statistics, they can accommodate multiple explanatory factors and also non-linear relationships such as functional responses [42,43]. By using spatial modelling approaches to understand relationships between foraging distributions and habitat characteristics, it is possible to start predicting which, and when, populations have the most spatial overlap at the habitat scale.

2.4. Distribution datasets (1–10 km)

Modelling approaches require datasets documenting when and where seabirds were foraging. In the UK, studies have collected such datasets at the habitat scale using several methods. In terms of collisions with tidal stream turbines, it is important that these methods differentiate between a populations' home range, which shall be defined as the area in which a population confines its activities [44], and their foraging distribution, which shall be defined as the area in which populations dive for prey items. This is because individuals flying through, but not diving within, a tidal pass do not face any collision risks. Three methods that are commonly used to record seabird distributions at the habitat scale are outlined below. Each method's advantages, disadvantages and ability to successfully differentiate between home ranges and foraging distributions are discussed.

2.4.1. Vessel surveys

Vessel surveys use onboard observers to record the species, abundance and behaviour of seabirds seen from the boat. Surveys can range from pre-planned cruises on scientific research vessels to opportunistic recordings from ferries or commercial vessels. However, a standardised method is adhered to meaning that datasets are comparable with one another [45,46]. Since the advent of the European Seabirds At Sea (ESAS) survey in 1979 (http://jncc.defra.gov.uk/page-1547), the results from vessel surveys have been stored in a central datasets managed in the UK by the Joint Nature Conservation Committee (JNCC). This provides circa 30 years of comparable datasets from UK waters. Observers note whether seabirds were flying, versus those sitting on the water [45], which provides reasonable ways to discriminate between foraging (sitting) and non-foraging (flying) Auks and Cormorants. Nevertheless, the need for good visibility [45] alongside logistical constraints associated with boatwork means that time at-sea is limited. As a result, spatial and temporal coverage is usually quite sparse. However, having large quantities of comparable survey results from several decades in a single database makes vessel surveys unique among the methods discussed here.

2.4.2. Aerial surveys

Modern aerial surveys use high-definition photography or videos mounted on an aircraft to take pictures or footage of the sea surface. The species, abundance and behaviour of seabirds are then determined after surveys by analysing these images [47]. As with vessel surveys, aerial surveys can identify whether seabirds were sitting on the water surface or flying, providing reasonable ways to discriminate between foraging (sitting) and non-foraging (flying) Auks and Cormorants. By using digital images and footage a permanent record of surveys is obtained which allows survey data to be reanalysed if necessary. This also reduces the effect of observer bias. However, as with vessel surveys, the need for good visibility alongside logistical constraints associated with this method means that time in the air is usually limited, reducing its spatial and temporal coverage. Aerial surveys also appear poor at detecting certain species such as Cormorants and Black Guillemots (Waggitt and Scott, unpublished data). There are many possible reasons for this ranging from their plumage colouration to a tendency for individuals to sit low in the water. Therefore, aerial surveys may only be suitable for certain species [47]. For these species, however, they could provide very accurate counts of foraging seabirds within the regions of interest [48].

2.4.3. GPS loggers

Within recent years GPS loggers attached directly onto seabirds have been used to record their at-sea movements [49,50]. Devices usually record individuals' locations every few minutes, providing particularly accurate information on their position in time and space. Although once limited to larger species, GPS loggers have now become light enough for species as small as Atlantic Puffins to be tracked [51] providing great flexibility in their application. When used in combination with analytical methods such as first passage time (FPT) [52] and fixed kernel density [53], or when deployed alongside with time-depth recorders (TDR) to record where individuals dived [54,55], they can identify most locations that an individual exploited during study periods. By then combining individual foraging distributions, it is possible to estimate a populations' foraging distribution. However, despite reductions in device costs, the number of seabirds tracked is small in comparison to the size of the populations being studied. As such, the foraging distributions recorded could be unrepresentative of the population as a whole, particularly when consistent differences occur between sexes [56,57], ages [58,59] and breeding colonies [60,61], or when individual specialisation is present [62–66]. The use of most GPS loggers is also restricted by the battery power, and individuals are usually only tracked over a few days or weeks. In many cases, their use is also restricted to breeding seasons when devices can be attached onto individuals at their nest site. Therefore, for the most part, foraging distributions are only recorded over several days during the breeding season (but see [67]). As a result, they often fail to detect shifts in foraging distributions between breeding and non-breeding seasons, or those seen within breeding seasons as reproductive duties [68–70] or prey characteristics [31] change. Although similar goelocator devices can record individuals foraging distributions over several months and years, they are not suitable alternatives due to their low spatial (200 km) and temporal accuracy (days) [71]. However, despite these drawbacks, GPS loggers can record an individual's foraging distribution to a high degree of accuracy over several days or weeks.

2.5. Habitat characteristics (1–10 km)

When using a spatial modelling approach to define a populations' preferred foraging habitat, suitable habitat characteristics need to be chosen. Most modelling studies are based solely upon the data available from satellite remote sensing methods such as bathymetry, chlorophyll *a* and sea surface temperature; perhaps due to their quantity, ease of accessibility and good spatiotemporal coverage [22,37,72–75]. However, subsurface conditions such as current speeds and similar oceanographic processes also need a consideration [24,76]. Due to an interest in marine renewable energies, there is likely to be a rapid increase in projects quantifying the subsurface characteristics of a region earmarked for installations around the UK. This could occur through either in situ measurements [77] or through oceanographic modelling approaches, where greater computing power alongside improved analytical software have culminated with increasingly accurate maps for a range of hydrodynamic processes over whole regions [78–83]. It is important, however, that models then combine these habitat characteristics with relevant ecological factors [39–41]. This includes prey distributions, abundance and quality. Such information can be obtained directly from fisheries surveys [84] or indirectly by using proxies such as conditions during critical stages of the annual cycle [85], or the timing of key oceanographic events [86,87], to estimate prey characteristics within the region of interest. Ecological conditions also include the location and sizes of breeding colonies, and in the UK this information is currently available from the JNCC Seabird 2000 database (http://jncc.defra.gov.uk/seabird2000).

3. Will populations dive in micro-habitats near tidal stream turbines (100 m)?

3.1. Tidal stream habitat and seabirds (100 m)

Tidal passes are not homogenous habitats and physical interactions between topography, bathymetry and strong currents create a range of hydrodynamic features such as areas of high turbulence, water boils, shears, fronts and convergences [12]. Changes in current speeds and directions over flood-ebb and spring-neap tidal cycles could also cause the location and extent of hydrodynamic features to change continuously. In conjunction with often complex bathymetry and topography, this creates high micro-habitat diversity at fine spatial and temporal scales. As a result, care is taken when choosing where to place tidal stream turbines within these habitats. The locations of devices are based mainly upon energy returns, ease of accessibility for installation and maintenance, and also cable access for providing energy to land-based substations [1]. Because of this, the distribution of tidal stream turbines in tidal passes has spatial structure, and installations do not occur evenly throughout these habitats. Therefore, it cannot be assumed that populations exploiting a tidal pass shall dive near tidal stream turbines. Predicting which populations could forage near tidal stream turbines requires an understanding of what factors drive their foraging distribution at the micro-habitat scale.

3.2. Seabird distributions (100 m)

In contrast to trends at habitat scales, studies generally reveal weak relationships between the foraging distribution of a population and that of their preferred prey items at the micro-habitat scale [19–21]. Although productive habitats contain high abundances of prey items, foraging opportunities therein appear limited in time and space [10]. It is becoming clear that the distribution of foraging seabirds at the micro-habitat scale depends not only upon the presence of prey items but also on the presence of conditions that enhance prey item availability [14,43]. As with processes at the habitat scale, these conditions seem to vary among species, possibly due to differences in their prey choice and/or behaviour [12,88]. The broadest differences may again occur between those exploiting benthic prey and those exploiting pelagic prey. Among the former, certain substrata or seabed types could increase prey availability to foraging individuals. For example, European Shags showed strong preferences for either sandy substrata or rocky areas supporting diverse invertebrate communities in the Firth of Forth, Scotland [27]. Those exploiting pelagic prey could require specific combinations of bathymetry, topography and hydrodynamics to force items towards the sea surface, into dense aggregations or restrict their movement; all of which would reduce energetic costs associated with deep dives and lengthy prey pursuit [11,14,43]. In addition to these broad differences, subtle variations could also occur among populations exploiting similar prey items. For example, three species of planktivorous Auks exploiting a tidal pass in North America favoured micro-habitats characterised by different hydrodynamic conditions [88]. These differences in micro-habitat selection could drive both temporal and spatial segregation among species exploiting tidal passes due to the highly heterogeneous nature of these habitats [12].

3.3. Estimating spatial overlap (100 m)

Several studies have already documented spatial and temporal segregation among species within tidal passes [12,14]. It therefore seems that spatial overlap at the micro-habitat scale varies among populations and within populations over short time periods; with individuals perhaps more vulnerable during certain tidal conditions. Design diversity [5,7] alongside issues concerning efficiency and accessibility (Section 2.1) means that the micro-habitat occupied or created near devices varies considerably among installations [89]. As a result, different populations could be vulnerable to different installations. Therefore, predicting spatial overlap at these scales requires comparisons between the micro-habitats favoured by vulnerable species and that found around each installation [89]. The micro-habitats around each installation are usually known by tidal stream turbine companies due to extensive monitoring before and after installations [1]. In contrast, species favoured micro-habitat have not been quantified beyond a few physical conditions such as tidal speeds [14] and visible surface features [12], conditions that may be shared by several micro-habitats within tidal passes. As tidal stream turbines could occupy very specific micro-habitats within tidal passes, the precise combination of physical features underlying a species favoured micro-habitat need to be quantified.

3.4. Distributional data (100 m)

At these scales, surveys recording seabirds foraging distributions need to cover as many different micro-habitats within a tidal pass as possible. This is best achieved by not only covering many different areas within these habitats, but also repeatedly sampling the same areas over entire tidal cycles to account for changes in either the location or presence of micro-habitats caused by variations in current speeds and directions [12,14,43]. They also need to discriminate between foraging and non-foraging individuals. Surveys fulfilling these criteria are scarce within the literature [12,14,90]; however, several methods are described below.

3.4.1. Vessel surveys

The presence of established methods with the ability to identify foraging individuals should make the execution of vessel surveys straightforward [45,46]. However, only one study has recorded fine-scale foraging distributions to the required criteria using these methods [43]. Perhaps the only caveat associated with these surveys is that some micro-habitats may be under-sampled due to constraints in ship manoeuvrability. Also foraging seabirds could swim away from the vessel as it approaches; something which may not be an issue when quantifying foraging distributions at the habitat scale but could cause problems at the micro-habitat scale.

3.4.2. Aerial surveys

Aerial surveys have several advantages over vessel surveys at the micro-habitat scale. Without the issue of ship manoeuvrability, all areas within a tidal pass can be equally sampled. Whole tidal passes can also be surveyed relatively quickly. Therefore, each area can be covered many more times during a tidal cycle, increasing the chances of detecting foraging events. Foraging seabirds are also unlikely to be disturbed by aircraft flying at altitude, removing problems associated with vessel surveys [47,48]. Despite these advantages, only one study has recorded fine-scale foraging distributions using aerial surveys [14]. Although detectability issues associated with Black Guillemots and Cormorants (Section 2.4.2) make aerial surveys unsuitable in some situations, they could provide accurate counts if vulnerable species in the tidal pass can be seen easily from an aircraft.

3.4.3. Shore surveys

As tidal passes are coastal habitats, shore surveys are also possible. These involve observers situated on high-ground alongside the tidal pass recording the species, abundance and behaviour of seabirds in distance bands, grids or seen associating with certain surface features [6]. Unlike vessel and aerial surveys, shore surveys can monitor whole tidal passes over prolonged periods spanning entire flood-ebb and spring-neap cycles, accounting for variations in the location, extent and presence of hydrodynamic features. Several studies have used shore surveys within tidal passes to document species fine-scale foraging distributions [12,14,90]. However, these surveys often suffer from detectability issues. In some cases, individuals furthest away from the observation point or on rough water surfaces are undercounted (Waggitt & Scott. unpublished data). These problems are exaggerated in large tidal passes spanning several kilometres. Although detectability issues concerning distance are well known [91], the issue of detectably in different surface conditions (other than sea state) has not yet been calibrated (Waggitt and Scott, unpublished data). Until this is rectified, these methods are perhaps best suited to small tidal passes where simultaneous surveys using observers situated in various locations could confirm that most foraging seabirds are being seen.

3.4.4. GPS tracking

As GPS loggers reveal individuals foraging distributions to a high degree of accuracy and do not suffer from the restrictions and detectability issues associated with vessel, aerial and shore surveys, they have several advantages over these methods. However, their use depends upon tagged individuals exploiting tidal passes during the study periods. As devices are attached at the nest site, it is unknown where individuals will forage during this time. For species usually foraging tens of kilometres from their nest sites such as Atlantic Puffins, Common Guillemots and Razorbills [33], these methods may be particularly inappropriate as it highly uncertain where tagged individuals will forage. However, for those usually foraging within a few kilometres of their nests, such as Black Guillemots and Cormorants [33], these methods could be more appropriate. By attaching devices onto individuals nesting alongside or near tidal passes, the chances of them exploiting these habitats are relatively high.

3.5. Micro-habitat characteristics (100 m)

To define species preferred micro-habitats, distributional datasets need to be accompanied with measurements of physical conditions and prey characteristics at fine spatial (~100 m) and temporal scales (minutes). Multi-disciplinary projects involving the simultaneous collection of fine-scale seabird distributions, physical conditions and prey characteristics provide the best means to achieve this. Although these approaches are rare at the micro-habitat scale [43] similar ones have been used regularly at the habitat scale [13,24,76]. Therefore, conducting them within a tidal pass may only require a novel use of established methods. In any case, projects must deploy oceanographic instruments to accurately quantify a range of physical conditions (e.g. currents, seabed properties, subsurface hydrodynamics and surface features) and also hydroacoustic sonar methods associated with fisheries sciences to record prey characteristics [92]. However, they could also benefit from physical datasets yielded from the vast quantities of surveying and research within these habitats over the recent years, such as in situ measurements and fine-scale oceanographic models [93–96].

4. Will populations dive to depths where moving components are found (< 100 m)?

4.1. Tidal stream habitat and seabirds (< 100 m)

Most tidal stream turbines have moving components upon or near the seabed [5,7] and only individuals diving to these depths face any risk of collisions. Both Auks and Cormorants all have the abilities to reach these depths [5]. However, individuals will dive to different depths in different scenarios, and those diving near tidal stream turbines will not necessarily reach depths where moving components are found. Therefore, the assumption of simple relationship between a species maximum diving depth, the depths of moving components and collision risks [5,7] needs to be improved. This requires an understanding of what factors could influence an individual's diving depth in micro-habitats where installations are found.

4.2. Seabirds distributions (< 100 m)

Although seabirds could spend considerable energy diving within high currents [97], this should not restrict their maximum diving depth within micro-habitats surrounding installations, as the maximum diving depths of vulnerable species far exceed the depths of installations [5]. Instead it seems likely their diving depths within these micro-habitats shall broadly reflect their preys' vertical distribution [98,99], e.g. individuals taking benthic prey shall dive to the seabed [63,100,101]. Among those taking pelagic prey, however, the situation is more complex, and their diving depths shall largely depend upon pelagic fish behaviour around tidal stream turbines. Although direct evidence is absent, it is widely assumed that pelagic fish will aggregate around tidal stream turbines whilst seeking refuge from strong currents or when foraging upon the invertebrate communities that could settle upon and around installations [102]. Despite this, their behaviour around installations could depend upon the prey species, the design of the device and also local hydrodynamics [6]. For example, in some cases interactions between high currents, installations and bathymetry could create areas of upward movement that force smaller pelagic fish towards the water surface [11,14,43]. The uncertainty is complicated further by the possibility that preys behaviour could change near foraging seabirds [103,104] or over tidal cycles due to changes in hydrodynamic conditions [14,43]. In short, the vertical distribution of pelagic fish, and therefore seabirds diving depths, probably varies among installations and also over time. It is also possible that species facing similar scenarios will show different diving behaviours. Common Guillemots and Razorbills exploiting Lesser Sandeels *Ammodytes marinus* and Sprats *Sprattus sprattus* in the Firth of Forth, UK, undertook deep and shallow dives respectively [105]. Atlantic Puffins could perform even shorter dives when exploiting Lesser Sandeels [106]. Identifying the underlying mechanisms offers challenges. However, it could reflect differences in prey selection. Single loading species such as Common Guillemots can only carry one prey item at a time and may undertake relatively deep and lengthy dives whilst selecting larger or nutritionally better prey. In contrast, multiple-loading species such as Razorbills and Atlantic Puffins that can carry several prey items at a time may be less particular about their choice of prey [105].

4.3. Estimating spatial overlap (< 100 m)

If populations seen diving near tidal stream turbines are exploiting benthic prey (Cormorants, Black Guillemots [8]) then high spatial overlap at these scales is inevitable given that individuals are diving to the seabed. However, if these populations

are exploiting pelagic prey (Atlantic Puffins, Common Guillemots, Razorbills [8]) then the situation becomes complex. For the most part, this reflects a limited knowledge of both prey characteristics and diving behaviour within tidal passes. It also reflects a poor understanding of predator–prey interactions at fine spatiotemporal scales [9]. Before estimating spatial overlap at these scales, this knowledge needs improving and several fundamental questions need to be addressed, such as: (1) how do pelagic prey behave in the different micro-habitats found within tidal passes, (2) how do seabird species vary their diving behaviour in response to changes in prey characteristics and hydrodynamic conditions, and (3) how do pelagic prey behave in the presence of diving seabirds?

4.4. Distributional data (< 100 m)

Few studies have recorded prey characteristics [14] or seabird dives [106] within tidal passes. This explains the poor knowledge of prey characteristics and seabird diving behaviour within these habitats. Below, several methods that could provide these data are discussed.

4.4.1. Hydroacoustics

As hydroacoustic sonar methods can record both prey behaviour [92] seabird dives [103,104,107] and predator–prey interactions [103,104] at fine spatiotemporal scales, a single deployment could provide much of the data needed to answer fundamental questions (Section 4.3). They also have several other benefits. Firstly, hydroacoustic sonar methods are unaffected by low light and high turbidity and therefore have advantages over others that can record underwater behaviours, such as video cameras. Secondly, they are also flexible in their application and can be deployed from vessels to target several micro-habitats within a survey [104], or from static moorings to monitor single micro-habitats over extended time periods [108–110]. Having said this, hydroacoustic methods do have some shortcomings when recording seabird dives as they cannot discriminate between species underwater. Moreover, the narrowness of sonar beams often makes collecting whole dive profiles difficult. However, having observers on vessels or alongside moorings during hydroacoustic sonar surveys can help to overcome identification problems [103,104,107] whereas estimating dive depths is often possible by using trails of air bubbles that persist behind diving seabirds to trace their movements [104]. Combining several sonar beams to increase the overall coverage could also overcome these issues.

4.4.2. GPS–TDR combinations

In addition to the development of GPS loggers (see Sections 2.4.3 and 3.4.4), there have also been developments in time-depth recorders (TDR) that record individuals' subsurface movements. When GPS loggers and TDR devices are used in combination, they have the ability to record the location, depths and durations of foraging dives [55]. As devices are attached directly onto individuals at the nest site, dive profiles can also be attributed to species. The major limitation is that these methods are most suitable for Black Guillemots and Cormorants that usually forage within a few kilometres of their nest sites (see Section 3.4.4). As these species generally exploit benthic prey items [8], their dive depths are perhaps more predictable than those exploiting pelagic prey [8]. Moreover, these methods are currently restricted to large species such as Cormorants [55] although reductions in device weight/size could make them suitable for smaller species in the near future.

4.5. Micro-habitat characteristics (< 100 m)

To answer key fundamental questions (Section 4.3), three-dimensional habitat characteristics at particularly fine spatial (< 10 m) and temporal scales (seconds) are required to define physical conditions at the precise time of seabird dives or preys presence. Ideally this requires in situ measurements during surveys as oceanographic models or predictions based upon existing datasets cannot account for stochastic variations occurring at these scales. In this respect, hydroacoustics methods have major advantages over GPS–TDR combinations in that oceanographic instruments deployed from either vessels or moorings can record physical conditions within these micro-habitats to the accuracy required to answer these questions. However, comparing pelagic prey characteristics and diving behaviours among different micro-habitats would still yield useful information. Therefore, oceanographical models and predictions based upon existing datasets could help to define the micro-habitat where preys behaviour or seabird dives were recorded.

5. Conclusions

With limited time to plan and licence installations, it is essential that the populations most vulnerable to collisions with tidal stream turbines are identified. Although it seems likely that Auks, Cormorants and Divers face the highest risks [8], variations among populations and over time seem likely. This variance can be attributed to various factors ranging from prey preferences to device design. However, the mechanistic links between physical conditions, prey availability and foraging opportunities could help to explain much of this variance. Therefore, predicting a populations' spatial overlap requires a fundamental understanding of these processes. Ultimately, particular conditions at the habitat and micro-habitat scale need to be associated with certain species or species assemblages. Particular conditions in the micro-habitats occupied by tidal stream turbines also need to be associated with certain diving behaviours or prey characteristics. Only with this knowledge can spatial overlap and collisions risks be estimated with a reasonable degree of accuracy. However, the level of confidence in these predictions will grow with increasing sample size. This not only includes collecting datasets over several seasons and years from the same locations, but also collecting and comparing datasets from many different locations. Therefore, data sharing among parties should be encouraged, and a strategic governance approach to collating the wide range of distributional, physical and prey datasets currently being collected could facilitate this.

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