



ARTICLE

Coastal and Marine Ecology

Tidal streams, fish, and seabirds: Understanding the linkages between mobile predators, prey, and hydrodynamics

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Abstract

Driven by the necessity to decarbonize energy sources, many countries are targeting tidal stream environments for power generation. However, these areas can act as foraging hotspots for marine top predators, such as seabirds. Thus, it is important to understand the ecological interactions influencing predator behavior and distribution in these areas, to determine the potential ecological implications of marine renewable devices. This study used concurrent observations of foraging seabirds, physical hydrodynamics, and prey presence across a tidal stream environment, before and after the installation of a commercial turbine array close to the island of Stroma, Scotland. There were three main findings: First, benthic foraging seabirds showed a clear preference for certain sections around Stroma where sandeels were detected, while pelagic foraging seabirds were seen all around Stroma. Second, there was a positive effect of water velocity on the number of pelagic foragers and common guillemots. Third, there was a positive effect of the presence of fish schools on the number of pelagic seabirds and common guillemots, in both the same and the previous transects. Thus, it is possible that seabirds target areas of predictable food sources during periods where prey might be easily accessed (e.g., periods of fast flows). Given the difference in the distribution between seabird categories, it is likely that marine renewable devices will impact each category differently. We conclude that any impact on sandbank locations, sandeels preferred habitat, due to the presence of tidal turbines is likely to alter the distribution of benthic foraging seabirds. For pelagic foraging seabirds and common guillemot, changes in prey presence and accessibility (depth and level of aggregation/disaggregation) will have a stronger effect on seabird presence. This study highlights the need to include concurrent physical and biological data when assessing the ecological impacts of tidal turbines.

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KEYWORDS

active acoustics, environmental impact, marine renewable energy, predator–prey interactions, velocity

INTRODUCTION

Driven by the necessity to decarbonize energy sources (Gielen et al., 2019), there is an increasing need to incorporate renewable energy resources into national energy policies worldwide. For example, a renewable energy target of at least 32% by 2030 was previously set by the European Union (EU), which was recently proposed to be increased to 40% (Directive [EU] 2018/2001). Marine renewable energy (MRE) sources, which include offshore wind, wave, and tidal, are an abundant and geographically diverse resource with the potential to supply up to 10% of EU's (Ocean Energy Forum, 2016) and 11% of UK (Coles et al., 2021) annual energy demand by 2050. Tidal stream energy, extracted from tidal currents in areas characterized by extremely fast currents ($>2 \text{ m s}^{-1}$) and a range of turbulent features (e.g., shear, jets, eddies, and boils), is becoming one of the preferred sources due to the predictable regular periodicity of tidal currents (Lewis et al., 2015).

Tidal stream environments are not only important from a renewable energy perspective, but also many seabird species are known to use these dynamic environments for foraging (Furness et al., 2012; Langton et al., 2011). In locations where seabird populations overlap with MRE deployments, one of the main concerns is collision risk, especially for seabirds that frequently dive to depths where tidal turbines will be positioned. Other concerns include disturbance (e.g., device noise and increased vessel activity in the areas) and displacement due to habitat modification (Copping & Hemery, 2020; Fox et al., 2018; Furness et al., 2012; Isaksson et al., 2020; Langton et al., 2011; Scott et al., 2014). However, the potential impacts of MRE devices are dependent on whether and how seabirds use the tidal stream environment. Thus, understanding foraging behavior and underlying factors influencing their site usage (e.g., habitat characteristics, prey) is vital.

In recent years, a stronger focus has been placed on understanding the ecological interactions influencing seabird behavior, with research indicating that seabird species respond differently to local physical processes and conditions, resulting in site-specific habitat-use patterns. For example, densities of foraging black guillemot (*Cephus grylle*) and European shag (*Phalacrocorax aristotelis*) were greatest during slack tide in Fall of Warness, UK (Waggitt et al., 2016), and in the Pentland Firth, UK (Johnston et al., 2021), while at Ramsey Sound, UK, and at the Isle of

May, UK, great cormorants (*Phalacrocorax carbo*) and European shags prefer to forage during the flood tide (Cole et al., 2019; Philpott, 2013). Auk species prefer periods of fast flow at Fall of Warness, UK (Atlantic puffin, *Fratercula arctica*; and common guillemot, *Uria aalge*; Waggitt et al., 2016) and in North America (e.g., pigeon guillemot, *Cephus columba*; and marbled and Kittlitz's murrelet, *Brachyramphus marmoratus* and *Brachyramphus brevirostris*; Drew et al., 2013; Holm & Burger, 2002).

Affinity with a particular tidal phase (known as the “tidal coupling hypothesis”; Zamon, 2003) was previously linked with enhanced prey availability (Fraser et al., 2018; Williamson et al., 2019). However, physical factors can only work to enhance prey availability when prey is present in sufficient abundance (Dänhardt & Becker, 2011), highlighting the need to include not only hydrodynamic variables but also prey densities when characterizing seabirds' habitat usage in tidal areas. Moreover, studies have shown that device structures and extraction of kinetic energy can lead to changes in prey behavior or availability due to changes in water movement and turbulence (Fraser et al., 2018; Williamson et al., 2019), which can lead to functional habitat loss.

In summary, to fully understand the effects of MRE, it is necessary to (1) understand how seabirds respond to hydrodynamics and prey distributions and (2) assess how these might change in the presence of MRE. In this study, seabirds, prey, and hydrodynamic data were collected simultaneously around the island of Stroma in a tidal channel in the north of Scotland (Pentland Firth, UK), pre (summer 2016) and post (summer 2018) deployment of a commercial-scale tidal turbine array by MeyGen Limited (MeyGen, 2015). The objectives were to (1) characterize the spatial and temporal variation of the different variables before and after array deployment, (2) investigate the effect of water velocity and prey presence on the number of seabirds, and (3) discuss the potential implications of the findings in the context of environmental impacts for management of the MRE industry.

METHODS**Data collection**

Data were collected around the island of Stroma, Pentland Firth, UK (Figure 1), an area characterized by exceptionally

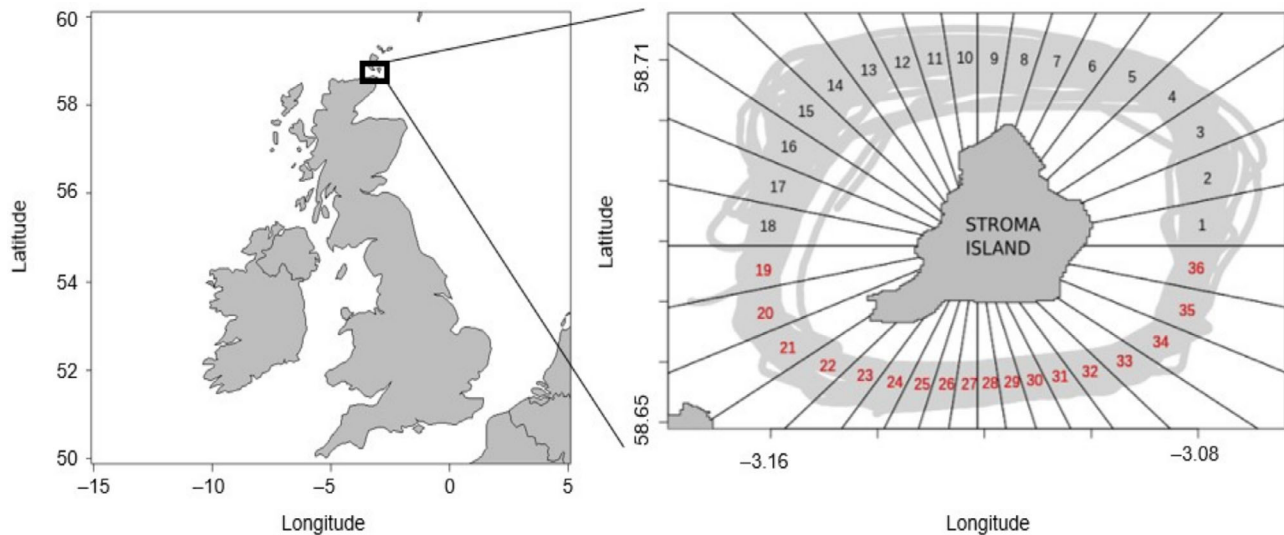


FIGURE 1 Map of the United Kingdom (left) highlighting the study area, island of Stroma (expanded, right) and survey transects (gray) and sections (1–36). Sections numbered 19–36 (in red) represented the Inner Sound. Note that section 23 is the location of the tidal turbine array deployed in 2017.

fast tidal currents that can exceed 5 m s^{-1} . A commercial array of four 1.5-MW tidal turbines was installed by MeyGen Limited (MeyGen, 2015) in 2017 in the Inner Sound immediately south of the island of Stroma (sections 19–36, Figure 1). The simultaneous collection of seabird and prey data was conducted using the Marine Scotland Science research vessel MRV *Scotia*, a vessel with an overall length of 68.6 m, which circled Stroma continuously between 22 and 25 June 2016 (before turbine deployment) and 20 and 25 July 2018 (after turbine deployment) with each circuit considered a transect. The direction of the circular vessel movement was always against the prevailing horizontal currents within the Inner Sound and with the current in the north of Stroma (sections 1–18, Figure 1). This survey design allowed for a reasonably consistent trajectory to be maintained at speeds suitable for recording foraging seabirds ($2.5\text{--}7.7 \text{ m s}^{-1}$; Camphuysen et al., 2004; Waggitt et al., 2016). Three-dimensional hydrodynamic models (Wolf et al., 2016) were used to determine the timing of changes in flow direction and used to turn the ship around, turning as close as possible in the same locations at the end of each of the 6 h of tidal flow direction (section 1 or 18, Figure 1). A total of 42 transects were conducted in 2016, and 71 in 2018, each lasting approximately 90 min.

Due to the variations in details of the exact route between transects, the total surveyed area was divided into observational units termed “sections.” Using the mean survey latitude and longitude of both years as the central point, each transect was split into arcs of 10° (Figure 1), using the R package “*circelize*” (Gu et al., 2014), with each section covering a mean distance

of approximately 543 m (± 275 SD), in 134 s (± 81 SD). Each section was sampled once per transect.

Seabird data processing

Seabirds were recorded visually based on standard strip-transect survey methodology (JNCC, 2004). Two teams of two observers (with the addition of a scribe in 2018) were stationed 10.6 m above sea level at the center of the vessel between 04:00 and 19:00 UTC each day with a 2-h alternating rotation period. Seabirds seen on the water surface were recorded once they were perpendicular to the ship and up to a maximum distance of 300 m so that locations of animals could be matched with all other physical data. Seabirds ahead of the ship were tracked using binoculars, and if they took flight or dived before passing perpendicular to the ship, they were recorded at the distance last seen on the water. Flying seabirds were not included in the analysis for the purpose of this study as they would not be actively foraging (Waggitt et al., 2016).

The species included in this study were Atlantic puffins (*F. arctica*), black guillemots (*C. grylle*), common guillemots (*U. aalge*), European shags (*P. aristotelis*), and razorbill (*Alca torda*) as they were previously identified as species most vulnerable to adverse effects from tidal turbines in Scottish waters (Furness et al., 2012). To provide a sufficient number of sightings for statistical analysis, these species were then split into categories based on their foraging strategies. Razorbills and puffins were categorized as “pelagic foraging seabirds,” as both species have similar foraging behaviors (Shoji et al., 2015),

preferring to forage in the upper layers of the water column despite their ability to perform deeper dives. In contrast, shags and black guillemots forage near the bottom in shallow waters and were categorized as “benthic foraging seabirds” (Howells et al., 2018; Johnston et al., 2018). Common guillemots can alter between pelagic and benthic foraging strategies (Chimienti et al., 2016) and were analyzed separately.

Fish data processing

Fisheries acoustics provides well-established techniques for determining the distribution and abundance of schooling fish species at high spatial and temporal resolution (Simmonds & MacLennan, 2007). Acoustic data were collected using a vessel-mounted Simrad EK60 multi-frequency echosounder (38, 120, and 200 kHz) to detect the presence of fish schools. The echosounder was configured to ping at all three frequencies simultaneously, every 1 s, with a pulse duration of 1.024 ms for each frequency. Echoview software (version 5.3) was used for all post-processing of EK60 acoustic data, which consisted of

volume backscattering strengths (S_v , in dB) at 0.2-m vertical resolution and a horizontal resolution ranging from 2.5 to 7.7 m (depending on vessel speed).

Turbulence detection

Preliminary visual inspection of the data showed areas of high backscatter near the surface (hereafter referred to as “turbulence interference”; Figure 2a) from entrained air resulting from breaking waves, boils, and turbulence in the upper layer (Fraser et al., 2017a). A number of echo signal processing methods were applied to filter these out. As surface turbulence had a stronger signal at 120 and 200 kHz, these two frequencies were summed and a threshold of -135 dB was applied, followed by a 7×7 median filter to remove remaining small areas of backscatter. Regions (echotrace boundaries) that were potential turbulent features were detected using the SHAPES algorithm in Echoview (Barange, 1994), using the detection parameters in Table 1.

Once these initial filters had been applied, regions were manually classified as surface turbulence or not

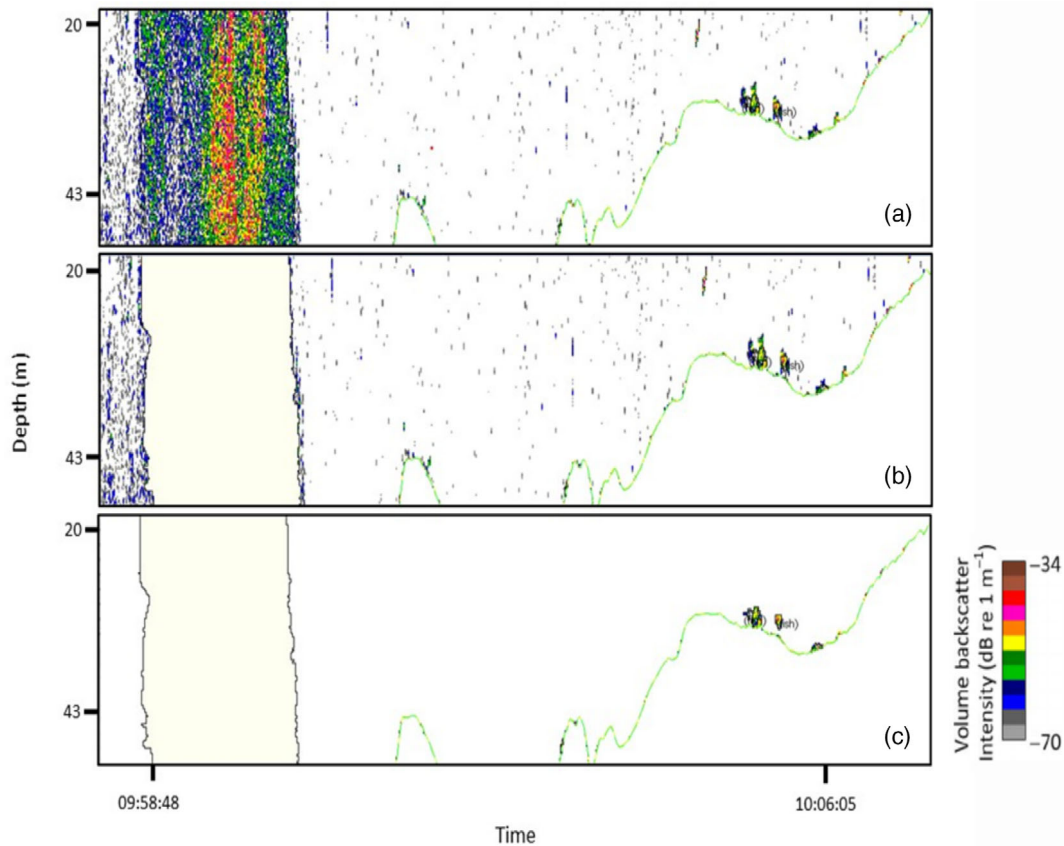


FIGURE 2 Example excerpt of EK60 data. (a) Raw data (200 kHz), (b) data after applying filter to remove turbulence (200 kHz), and (c) data after applying filter to detect fish schools only (200 kHz). Green line represents the best bottom candidate, calculated using the line picking algorithm in Echoview.

TABLE 1 Detection parameters used in SHAPES algorithm in Echoview (Barange, 1994) to detect surface turbulence and fish schools

Detection parameters (m)	Surface turbulence	Fish schools
Total school length	40	10
Total school height	2	1
Candidate school length	5	5
Candidate school height	1	1
Vertical-linking distance	0.5	2
Maximum horizontal linking	0.5	15

turbulence. The proportion of water column covered by turbulence interference per section per transect was calculated as the depth range covered by turbulence interference divided by bottom depth.

Fish school detection

Regions classified as surface turbulence were removed from the 38-, 120-, and 200-kHz echograms (Figure 2b) because there was no certainty regarding the presence of fish schools in these regions. Once turbulence was removed, the three frequencies were summed and a -200 -dB threshold was applied, followed by a 7×7 median filter to ensure that only objects that persisted on all frequencies were retained (e.g., fish schools). The thresholds used were selected based on the acoustic signatures of turbulence and fish targets of interest. Given that different fish species have different acoustic signatures (Horne, 2000), we recommend a close inspection of data before carefully selecting processing parameters (Fraser et al., 2017a). The resulting virtual echogram was used to mask the original 38-kHz echogram with a threshold of -70 dB applied (Figure 2c). The remaining echotraces on the masked 38-kHz echogram were detected using the SHAPES algorithm (Barange, 1994) using the detection parameters in Table 1 to identify regions that were potential fish schools (Fernandes, 2009).

As it is not possible to obtain physical fish samples by standard methods in these high-energy areas, fish were broadly classified as being with or without a swim bladder using the multifrequency echosounder data. Fish without a swim bladder reflect more acoustic energy at 120 and 200 kHz than at 38 kHz (Korneliussen, 2010), so fish schools with a difference in mean volume backscattering strength less than -2 dB between 38 and 120 kHz or between 38 and 200 kHz were classified as “fish schools without a swim bladder.” Given the acoustic

characteristics, shape and proximity to the bottom “fish schools without a swim bladder” observed in this study are most likely sandeels and will be referred to as such hereafter. The remaining individuals were classified as “non-sandeel schools.”

Once these initial filters had been applied, data were visually inspected to ensure that only fish schools, both small and large (school cross-sectional area ranged from 8 to 693 m² in 2016 and 12 to 5772 m²), were being classified (Fernandes, 2009), rather than entrained air or debris. Echotraces identified as fish schools that could not be visually distinguished from entrained air were excluded from further analysis.

The presence/absence of sandeel and non-sandeel schools per section and per transect was used as explanatory variables.

Water velocity

Water velocities were obtained from a high-resolution three-dimensional hydrodynamic model of the Pentland Firth and Orkney Waters (Wolf et al., 2016).

Statistical analysis

To ensure that the number of school absences was not inflated due to high turbulence interference coverage, data with more than 10% of the water column covered by turbulence were removed from any further analysis. This approach ensured that if present, fish schools can be detected in 90% of the water column; hence, the zeros in school presence/absence are likely true absences. A summary of the data not included in the model, including a total number of transects and presence/absence of schools excluded per section, can be found in Appendix S1: Table S1.

To estimate relationships between the numbers of seabirds (pelagic, benthic, and common guillemots) and year, velocity, and presence of schools, generalized additive mixed models (GAMMs) with negative binomial distributions (to account for any potential zero inflation and overdispersion) were used. Generalized additive mixed models were chosen as nonlinear relationships between variables were expected a priori based on preliminary data exploration. The presence of schools (both sandeels and non-sandeel schools) was included as a temporally lagged variable given that: (1) schools may be present but undetected in the current transect, in which case detection in the previous transect is a predictor of current presence; and/or (2) seabirds may display a lag response to school presence, targeting areas of expected prey

availability. The logarithm of the time spent in each section per transect was included in the models as an offset to account for differences in effort due to inevitable differences in speed over ground. The sensitivity of the results to the use of an offset for observation effort was checked using an alternative model formulation where the same variable was used as a regular spline term. Results were unaffected, and the estimated shape of the effect was approximately linear, confirming that the modeling assumption was reasonable. Section and transect were included in the model as random effects to account for any spatial and temporal variation not explained by the model variables (e.g., time of day, sediment type) or any spatial and/or temporal autocorrelation.

Restricted maximum likelihood (REML) was used for smoothness estimation. Automated variable selection was run by adding an additional penalty so that if a variable had no effect, its effect size would be shrunk toward zero (Marra & Wood, 2011). For each model, diagnostic tests were run to ensure that model assumptions were met (Wood, 2017). Statistical analysis was performed using the “mgcv” (Wood, 2017) package in “R” (version 3.6.1; R Development Core Team). Data and code (Couto et al., 2022) are available from Zenodo: <https://doi.org/10.5281/zenodo.6422030>.

RESULTS

Fish school presence

Potential sandeel schools were detected 40 and 39 times in 2016 and 2018, respectively. In both years, there was a clear spatial distribution, with the majority of schools observed at both the west and east southern edges of Stroma (sections 19–21 and 34–36, respectively) in both years (Figure 3a), with a mean presence of 4.5 schools per section in 2016 and 4.3 in 2018 in these sections and a mean presence of 0.42 and 0.39 schools in the remaining sections around Stroma. Sandeel schools are normally relatively stationary around their preferred habitats (van der Kooij et al., 2008); thus, we would expect them to be frequently present. There are two possible explanations for why we did not observe them in all transects: (1) It is almost impossible, in such highly energetic areas, to sample exactly the same locations within each transect and sandeel schools are extremely site-specific; and (2) it is possible sandeel schools have either partially buried themselves into the substrate (Winslade, 1974) or they have move closer to the surface (depth range <12 m) where they cannot be detected by the echosounder, but can still be available for benthic birds

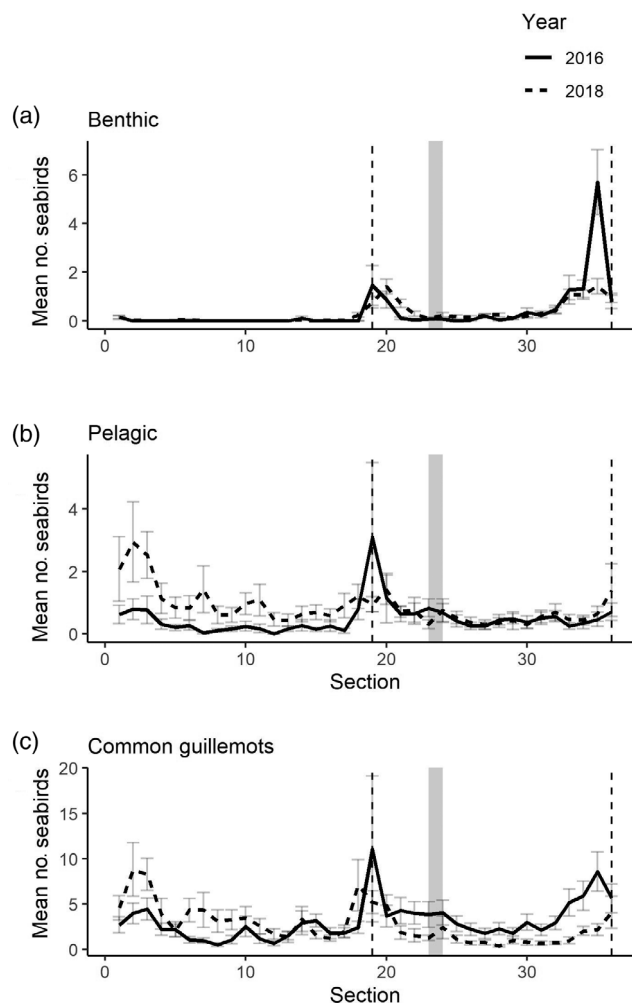


FIGURE 3 Mean number of (a) benthic foraging seabirds, (b) pelagic foraging seabirds, and (c) common guillemots per section for 2016 and 2018 with respective SE (lines). The area between dashed lines represents the Inner Sound (sections 19–36). Gray bar is location of tidal turbine array.

(Harris & Wanless, 1991). In the vicinity of the array (sections 23 and 24), no sandeel schools were detected in these sections in 2016 and only one was detected in 2018.

Non-sandeel schools were detected 18 times in 2016, with a mean detection of 0.5 schools per section, and in 2018, they were detected 139 times, with a mean detection of 3.8 schools per section (Figure 3b). For reference, previous studies in tidal stream areas showed an average rate of 1.10 schools per hour in a single location when sampling continuously for 15 days (Fraser et al., 2018; Williamson et al., 2019), as opposed to sampling multiple locations for an average of 2 min every 1 h 30.

Moreover, while schools were only seen sporadically in 2016, both in the north of Stroma (sections 1–19, mean detection of 0.6 schools per section) and in the Inner Sound (sections 20–36, mean detection of 0.3 schools per section), there was a clear preference for sections in the

north of Stroma in 2018, with a mean detection of 6.4 schools per section in sections 1–19 as opposed to a mean detection of 1.05 schools per section in the Inner Sound (Figure 3b). In the vicinity of the array (sections 23 and 24), no schools were detected in these sections in 2016 and only three were detected in 2018.

Water velocity

Overall differences in water velocity were detected, with a mean of $1.7 \pm 0.95 \text{ m s}^{-1}$ observed in 2016 when surveys were conducted close to the top of spring tides and a mean of $1.3 \pm 0.73 \text{ m s}^{-1}$ in 2018 when surveys were conducted closer to neap tides. Velocities in both years were on average $>1.5 \text{ m s}^{-1}$ in the north of Stroma (sections 1–18) and Inner Sound (sections 21–34) and $<1 \text{ m s}^{-1}$ at the eastern and western sides of Stroma (sections 19–21 and 34–36, Figure 3c).

Turbulence interference coverage

The proportion of water column covered by turbulence interference ($7 \pm 12\%$ observed in 2016 and $4 \pm 3\%$ in 2018) differed between years. Such differences were

particularly evident in the Inner Sound (sections 27–34, Figure 4d). Near the array (sections 23 and 24), mean turbulence coverage was $3 \pm 2\%$ in 2016 and $4 \pm 1\%$ in 2018.

Benthic foraging seabirds

Significantly higher numbers of benthic foraging seabirds were observed in 2018 (646) than in 2016 (443, Table 2). However, in both years, benthic foragers appeared to prefer particular sections around Stroma, with high numbers frequently observed in areas to the eastern and western sides of Stroma (sections 19–21 and 31–36, Figure 4a).

The model for benthic foraging seabirds, explaining 61.7% of the deviance (20.6% when random effects were excluded from the model, while smoothing parameters were kept fixed for the comparison), showed a negative relationship between the number of benthic foraging seabirds and water velocities between 1.5 and 3 m s^{-1} (Figure 5). Significantly more seabirds were observed when sandeel schools were present, both in the same transect and in the previous ones (Figure 5). The presence of non-sandeel schools had no significant effect on the number of benthic foragers (Figure 5).

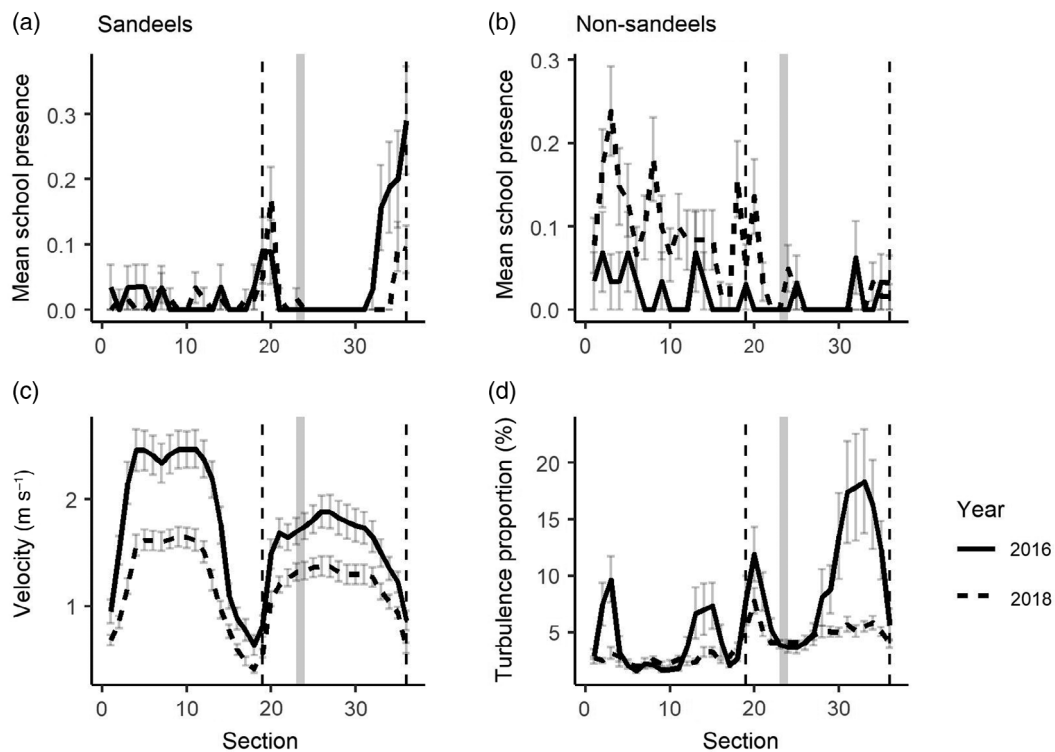


FIGURE 4 Average (a) presence of non-sandeel schools, (b) presence of sandeel schools, (c) water velocity, and (d) proportion of water column covered by turbulence per section for 2016 and 2018 with respective SE (lines). The area between dashed lines represents the Inner Sound (sections 19–36). Gray bar is location of tidal turbine array.

TABLE 2 Parametric coefficients included in the model (on the log scale)

Variable	Estimate	SE	<i>p</i>
Benthic foraging seabirds			
Intercept—2016	−8.09	0.40	<0.001
2018	1.99	0.27	<0.001
Pelagic foraging seabirds			
Intercept—2016	−4.798	0.3399	<0.001
2018	1.9343	0.4235	<0.001
Common guillemots			
Intercept—2016	−4.77	0.30	<0.001
2018	1.53	0.37	<0.001

Note: Significant variables appear in boldface.

Pelagic foraging seabirds

Significantly higher numbers of pelagic foraging seabirds were observed in 2018 (1958) than in 2016 (572; Table 2). However, contrary to benthic foraging seabirds, pelagic foraging seabirds were often seen all around Stroma, with a number of seabirds in each section varying over time.

The model for pelagic foraging seabirds, explaining 46% of the deviance (20.5% when random effects were excluded from the model while smoothing parameters were kept fixed for the comparison), showed a positive relationship between the number of pelagic foraging seabirds and water velocities between 1.5 and 3 m s^{−1} (Figure 6). Significantly more seabirds were observed when non-sandeel schools were present, both in the same transect and in the previous ones (Figure 6). The presence of sandeel schools had no significant effect on the number of pelagic foragers (Figure 6).

Guillemots

Significantly higher numbers of common guillemots were observed in 2018 (6256) than in 2016 (3759; Table 2), with a spatial distribution similar to pelagic foraging seabirds.

The model for common guillemots, explaining 48.8% of the deviance (17.6% when random effects were excluded from the model while smoothing parameters were kept fixed for the comparison), showed a positive relationship between number of common guillemots and water velocities between 1.5 and 3 m s^{−1} (Figure 7). Significantly more common guillemots were observed when non-sandeel schools were present, both in the same transect and in the previous ones (Figure 7). The presence of

sandeel schools had no significant effect on the number of common guillemots (Figure 7).

DISCUSSION

This study investigated a suite of physical and biological drivers of seabird use of high-energy tidal stream habitats, with data consisting of physical variables and prey species distribution collected simultaneously before and after the deployment of a tidal array. No differences in non-sandeel and sandeel schools, and the proportion of water columns covered by turbulence interference were observed before and after array installation in the vicinity of the devices.

There were three main findings: First, benthic foraging seabirds showed a clear preference for foraging within certain sections around Stroma, where sandeel schools were observed, while pelagic foraging seabirds were seen foraging all around Stroma, with numbers per section varying temporally. Second, a positive effect of water velocities between 1.5 and 3 m s^{−1} in the number of pelagic foragers and guillemots was observed. Third, there was a positive relationship between the presence of non-sandeel schools (both in the same transect and in the previous ones) and the number of pelagic seabirds and common guillemots. These findings are first discussed in an ecological context, addressing how the observed differences in seabird abundance and distribution between years could be related to velocity and prey, followed by the implications of these findings for MRE developments.

Benthic foraging seabirds

The spatial distribution of benthic foraging seabirds was similar between years, with greater numbers observed east and west of Stroma, coinciding with the sections where sandeel schools, one of the preferred prey species for both species (European shags and black guillemots; Howells et al., 2018; Johnston et al., 2018), were frequently observed. A recent study where European shag foraging locations in the Pentland Firth were identified using GPS data showed similar results, with east of Stroma being one of the preferred areas (Isaksson et al., 2021).

The positive effect of sandeels in the previous transect indicates that benthic foraging seabirds were responding not only to the current presence of prey but also to areas of expected prey availability. Previous studies showed that sandeels select habitats with higher proportions of coarse and medium sand (Holland et al., 2005; Wright et al., 2000). In this study, the sections where sandeel

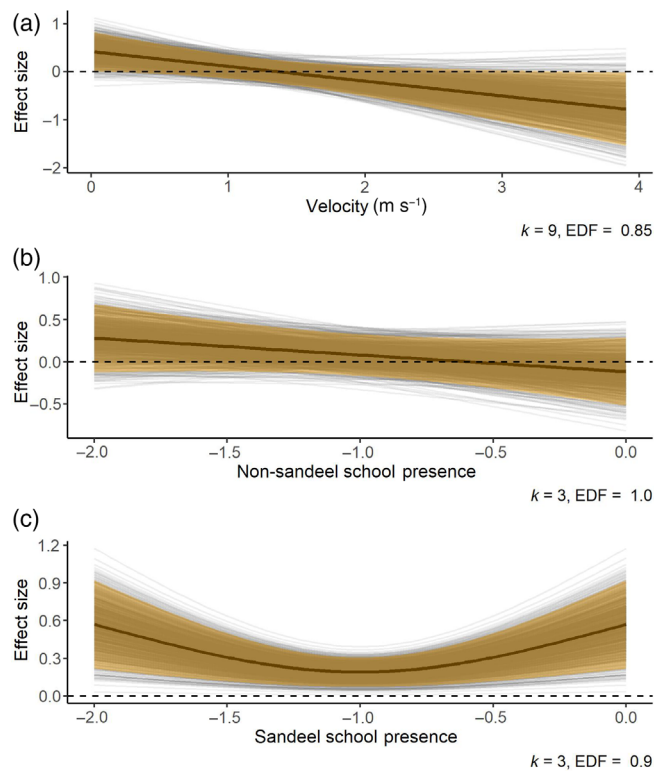


FIGURE 5 Relationships between benthic foraging seabirds (effect size on the log scale) and (a) velocity, (b) lagged presence of non-sandeel schools, and (c) lagged presence of sandeel schools. Solid black lines represent predicted relationships from the generalized additive mixed models (GAMMs), orange areas represent 95% CI, and dashed black horizontal lines show neutral effects of the respective variables. In all plots, the number of knots (k) and number of effective degrees of freedom (EDF) are included.

schools were observed fall within two known sandbanks (Chatzirodou et al., 2017).

Thus, it is possible that including sediment type in the models, coupled with the effect of the presence of sandeel schools, could potentially capture the full importance of sandeel presence on the behavior and distribution of benthic foraging seabirds. However, fine-scale information on sediment type was not available for this area.

A negative relationship between the number of benthic foragers and velocities higher than 1.5 m s^{-1} was also identified in this study. However, the sections where high numbers of benthic foragers were observed consistently had maximum velocities $<1.5 \text{ m s}^{-1}$. Other sections where velocities lower than 1.5 m s^{-1} were observed during times of slack tide, but with higher velocities during peak flow, attracted either far fewer birds or none. As such, it is entirely possible that the relationship with lower velocities depicted by the model is confounded with prey availability.

Nevertheless, similar relationships between benthic feeding seabirds and water velocity were previously

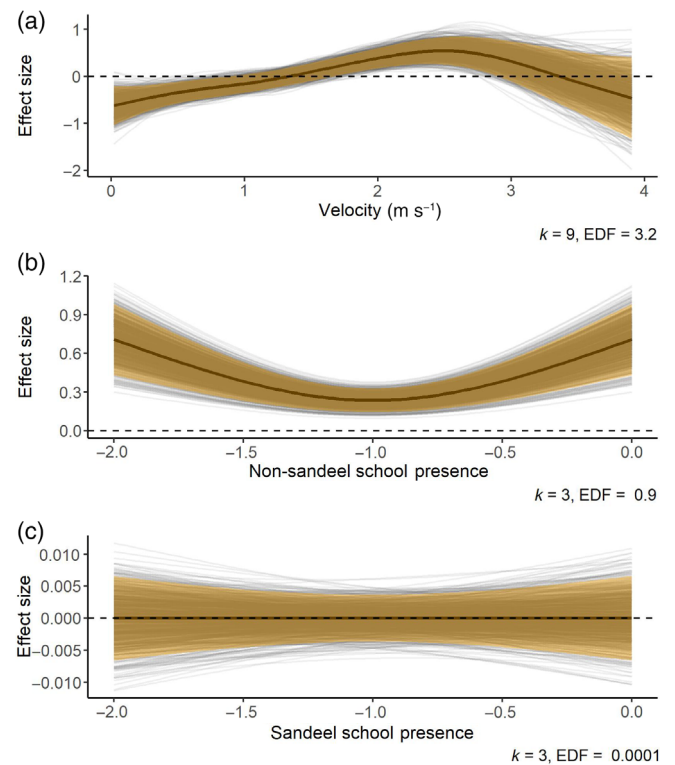


FIGURE 6 Relationships between pelagic foraging seabirds (effect size on the log scale) and (a) velocity, (b) lagged presence of non-sandeel schools, and (c) lagged presence of sandeel schools. Solid black lines represent predicted relationships from the generalized additive mixed models (GAMMs), orange areas represent 95% CI, and dashed black horizontal lines show neutral effects of the respective variables. In all plots, the number of knots (k) and number of effective degrees of freedom (EDF) are included.

observed for the study site (Johnston et al., 2021; Wade, 2005), and other tidal stream area within Scotland (Waggitt et al., 2016) and in Southeast Alaska (Drew et al., 2013). While fast water velocities and turbulence tend to bring schools closer to the surface, benthic feeding seabirds forage near the bottom and only infrequently benefit from concentrations of free-swimming prey in the water column (Drew et al., 2013). Thus, foraging in fast flow might increase energy expenditure (Heath & Gilchrist, 2010) without any gain.

Pelagic foraging seabirds and common guillemots

Contrary to benthic foraging seabirds, pelagic foraging seabirds and common guillemots were often found all around Stroma, with their numbers varying temporally and spatially. Given the significant relationship observed between the number of pelagic foraging seabirds and both velocity and presence of non-sandeel schools, spatial

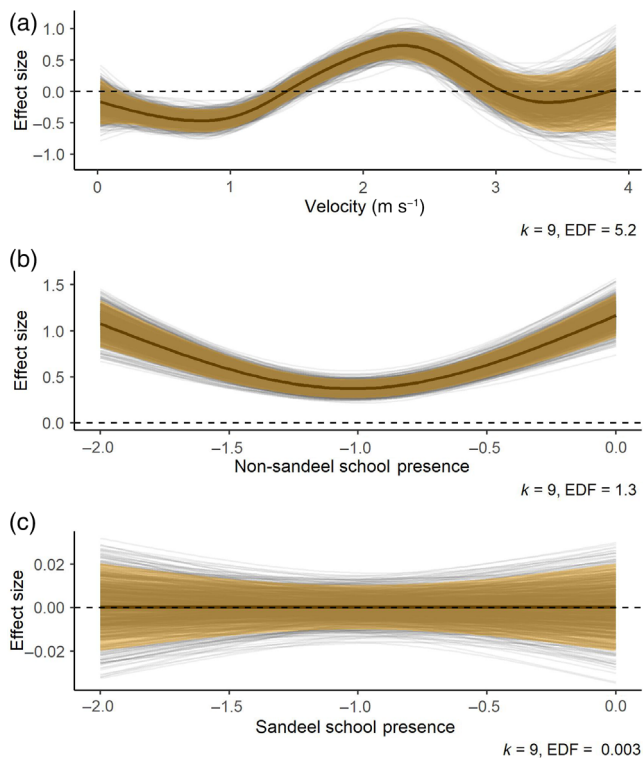


FIGURE 7 Relationships between common guillemots (effect size on the log scale) and (a) velocity, (b) lagged presence of non-sandeel schools, and (c) lagged presence of sandeel schools. Solid black lines represent predicted relationships from the generalized additive mixed models (GAMMs), orange areas represent 95% CI, and dashed black horizontal lines show neutral effects of the respective variables. In all plots, the number of knots (k) and number of effective degrees of freedom (EDF) are included.

and temporal changes in these variables might explain the variation observed in the numbers of pelagic foragers.

While previous studies showed that pelagic foraging seabirds tend to feed closer to the surface (Shoji et al., 2015), where fish schools cannot be detected by ship-mounted echosounders, and that seabirds often target single individuals rather than schools (Crook & Davoren, 2014; Enstipp et al., 2007), here we hypothesize that the presence of prey at depth translates into prey availability close to the surface, particularly during periods of fast flow. A recent study showed that during high current speeds ($1.8\text{--}2\text{ m s}^{-1}$), both dispersion and center of mass (mean distance of fish from the transducer weighted by their density) increased, suggesting fast flows result in fish being less aggregated and closer to the surface during periods of fast flow (Scherelis et al., 2020). Zamon (2003) studied tidal variation in the counts of mixed-species seabird flocks and relative abundance of fish schools and observed an increase in feeding activity during tidal flood phases ($>1\text{ m s}^{-1}$), when fishes became more dispersed in the water column, translating into

increased fish availability. The significant positive relationship between the number of pelagic seabirds and the presence of non-sandeel schools coupled with the significant positive effect of water velocity between 1.5 and 3 m s^{-1} seems to corroborate this hypothesis. Similar relationships between the number of pelagic seabirds and/or common guillemots were previously observed for the same area (Wade, 2005) and other tidal stream areas within Scotland (Waggitt et al., 2016).

In addition, a positive effect of non-sandeel schools in the previous transects was also observed. It was previously hypothesized that favorable foraging habitats would contain not only shallow but also prevalent prey (Waggitt et al., 2018). Thus, it is possible that seabirds target areas of predictable food sources during periods where prey might be easily accessed (e.g., periods of fast flows).

Therefore, this study indicates that spatial and temporal distribution and abundance of pelagic seabirds in tidal stream areas are influenced by a combination of prey presence and fast velocities that potentially increase prey catchability.

Effects of marine renewable devices on environmental variables and implications for seabirds

Previous studies showed that tidal turbines can alter the surrounding physical and biological environment, such as tidal currents, bed-shear stress, sediment transport, and fish school behavior (Fairley et al., 2015; Fraser et al., 2017b, 2018; Neill et al., 2012; O'Hara Murray & Gallego, 2017; Williamson et al., 2019). In this study, no differences in non-sandeel and sandeel schools were observed before and after array installation in the vicinity of the devices, despite the low proportion of the water column covered by turbulence in both years. Although proving a high spatial coverage, the sampling method used in this study had a low temporal coverage. Moreover, it is possible that fish school presence is masked by the devices and was removed from the data. Therefore, we suggest that further surveys are conducted before any conclusions are drawn, ideally using upward-facing active acoustic devices close to turbines to increase temporal coverage.

For benthic foraging seabirds

Our results showed that benthic foraging seabirds tend to aggregate at areas where sandeel schools may have been present, most likely around or near sandbanks. Although

it was previously considered that the presence of four 1.5-MW tidal turbines would only have minimal impact on the morphodynamics of the large sandbanks in this study region (Fairley et al., 2015), modeling studies have shown that if an array is located in the vicinity of a headland, it could lead to a considerable change in sandbanks over their lifetime (Neill et al., 2012, 2009). Thus, indirect effects on the surrounding habitat need to be taken into account when assessing the impact of tidal turbines on the distribution of benthic foraging seabirds.

For pelagic foraging seabirds

To generate commercially viable electricity from tidal stream resources, tidal turbines are normally deployed in areas with average flow velocities of at least 2 m s^{-1} and have a cut-in speed of around 1 m s^{-1} (Baston et al., 2014). Thus, based on the positive association of pelagic foraging seabirds with water velocities higher than 1.5 m s^{-1} observed in this study, we would expect that pelagic foraging seabirds could be at risk of collision with moving turbine blades.

Our results indicated that pelagic foraging seabirds and guillemots respond not only to velocities higher than 1.5 m s^{-1} but also to the presence of non-sandeel schools. Previous studies have shown that the presence of tidal turbines can act as a fish aggregating device, leading to an increase in the number of fish schools around turbines (Fraser et al., 2018; Viehman & Zydlewski, 2014; Williamson et al., 2019), which might lead to an increase in the number of foraging seabirds around the devices and therefore increase the risk of collision with moving parts. However, we hypothesize that prey presence on itself might not be the driving factor, but rather how available the prey is to seabirds. Previous studies have shown that large arrays may lead to significant changes in physical variables (De Dominicis et al., 2017), which might lead to changes in prey availability to seabirds that forage in the upper water column.

Overall, this study highlights the importance of understanding the impact of devices not only on predators but also on prey and including information both on prey and on hydrodynamics when designing monitoring plans, particularly when moving from small numbers of turbines to very large arrays.

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CONFLICT OF INTEREST


The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code (Couto et al., 2022) are available from Zenodo: <https://doi.org/10.5281/zenodo.6422030>.

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