Vertical migrations of fish schools determine overlap with a mobile tidal stream marine renewable energy device

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Abstract

1. Large increases in the generation of electricity using marine renewable energy (MRE) are planned, and assessment of the environmental impacts of novel MRE devices, such as kites, are urgently needed. A first step in this assessment is to quantify overlap in space and time between MRE devices and prey species of top predators such as small pelagic fish.

2. Here, we quantify how the distribution of fish schools overlaps with the operational depth (20–60 m) and tidal current speeds (≥1.2–2.4 m/s) used by tidal kites, and the physical processes driving overlap.

3. Fish schools undertake diel vertical migrations driven by the depth of light penetration into the water column, controlled by the supply of solar radiation and water column light absorption and scattering, which in turn depends on the cross-sectional area of suspended particulate matter (SPM). Fish schools were found shallower in the morning and evening and deeper in the middle of the day when solar radiation is greatest, with the deepest depths reached during predictable bimonthly periods of lower current speeds and lower cross-sectional area of SPM.

4. Potential kite operations overlap with fish schools for a mean of 5% of the time that schools are present (maximum for a day is 36%). This represents a mean of 6% of the potential kite operating time (maximum for a day is 44%). These were both highest during a new moon spring tide and transitions between neap and spring tides.

5. Synthesis and applications. Overlap of fish school depth distribution with tidal kite operation is reasonably predictable, and so the timing of operations could be adapted to avoid potential negative interactions. If all interaction between fish schools was to be avoided, the loss of operational time for tidal kites would be 6%. This information could also be used in planning the operating depths of marine renewable energy (MRE) devices to avoid or minimize overlap with fish schools and their predators by developers, and for environmental licencing and management authorities to gauge potential ecological impacts of different MRE device designs and operating characteristics.
INTRODUCTION

Most current large-scale developments in the marine sector such as oil and gas platforms and offshore wind farms are static and do not have submerged moving parts. A new aspect of tidal marine renewable energy (MRE) devices is that they have parts, or the entire structure itself, which move through the water and at speeds up to an order of magnitude greater than the prevailing currents. This presents a need to understand the potential spatial and temporal overlap between marine fauna, such as fish (Fraser, Williamson, Nikora, & Scott, 2018; Viehman & Zydlewski, 2015) and top predators such as diving seabirds and marine mammals (Williamson et al., 2017), and mobile MRE devices.

Amongst a growing number of MRE projects in Wales UK (Roche et al., 2016), Minesto have designed and are testing a utility scale 0.5 MW bottom-tethered tidal kite (Figure 1) in the ~85 m deep Holyhead Deep, UK (Figure 2), with other kite systems such as SeaQurrent also in development elsewhere. The Minesto kite has a 12 m wingspan that will fly in a figure of eight pattern potentially at up to ten times the current speed between approximately 20 and 60 m depth, with plans to install an 80 MW array of kites at the site (Figure 2). Understanding prey distributions of top predators and the processes driving prey presence is required to minimize potential negative interactions of top predators and associated prey with the tidal kites.

Despite most of the Irish Sea being tidally mixed year round, resulting in homogenous vertical distributions of phytoplankton, some groups of zooplankton undertake diel vertical migrations (DVM; Irigoien, Conway, & Harris, 2004; Scrope-Howe & Jones, 1986). Pelagic fish such as European sprat Sprattus sprattus, a zooplanktivorous forage fish, change their schooling behaviour and vertical distribution during the day, schooling deep during daylight, adopting shallower depth distributions after dawn and before dusk as they vertically migrate, and during darkness schools disperse (Nilsson, 2003; Solberg & Kaartvedt, 2017). Pelagic fish such as European sprat Sprattus sprattus, a zooplanktivorous forage fish, change their schooling behaviour and vertical distribution during the day, schooling deep during daylight, adopting shallower depth distributions after dawn and before dusk as they vertically migrate, and during darkness schools disperse (Nilsson, 2003; Solberg & Kaartvedt, 2017). In most species DVM is driven by light levels in the water column, Zooplanktivores need enough light to forage and maintain schools, but minimize predation risk by staying in as dark and deep water as possible (Bianchi & Mislan, 2016; Nilsson, 2003; Robison, 2003). Currently, there is insufficient understanding of the drivers of vertical distribution of fauna in coastal areas, and of how the high tidal current sites suitable for MRE development may influence DVM. For example, suspended particulate matter (SPM) controls turbidity by scattering and absorbing light (Granqvist & Mattila, 2004), and varies during the tidal cycle (Weeks, Simpson, & Bowers, 1993). Turbidity modifies DVM by reducing the depth of light irradiance (Lee, Kang, & Choi, 2015), which affects predation risk and other predator-prey interactions (Baptist & Leopold, 2010; De Robertis, Ryer, Veloz, & Brodeur, 2003; Kimbell & Morrell, 2015). The depth of light irradiance does not affect species equally due to reactive distance, defined as the maximum distance at which visual predators can detect prey (Vinyard & O’Brien, 1976). Reactive distance is more limiting for species that feed on larger and dispersed prey than species that feed on small common prey foraged for at close ranges (De Robertis & Handegard, 2013). Therefore, through these processes, tidally driven changes in SPM, particle size and cross-sectional area (contributing to turbidity) could control animal behaviour and vertical distributions in high current areas targeted for MRE development.

Understanding the distributions of prey for diving seabirds and marine mammals should help to improve predictions of MRE device-animal interactions. Marine mammals such as porpoise (Westgate, Head, Berggren, Koopman, & Gaskin, 1995) and foraging seabirds (Baptist & Leopold, 2010; Shoji et al., 2016) have been shown to change their diving behaviour diurnally, following prey availability,
and so during 24-hr periods MRE device–animal overlap may change due to diel and tidal cycles. Because environmental regulations can limit MRE operations when seabird and marine mammals are present, understanding these interactions is not only vital for minimizing environmental impacts, but also for assessing the economic viability of MRE operations.

The aim of the study was to determine how the vertical distribution of fish schools may overlap with a tidal kite, and how key interacting physical properties of the water column such as SPM, light penetration and tidal currents drive fish school behaviour.

2 | MATERIALS AND METHODS

2.1 | Study area

The study region is macrotidal, with a semidiurnal tide reaching up to 2.7 and 1.28 m/s for mean spring peak and mean neap peak velocities respectively in the West Anglesey Demonstration Zone for tidal energy (Piano et al., 2015). The Holyhead Deep, where our study took place, is a 70–90 m deep depression consisting of predominantly of mixed sediments surrounded by seabed of 40–50 m depth just over 8 km offshore (Figure 2). With spring tide peak velocities reaching just over 2 m/s, and depths of around 85 m in the leased seabed area of 9 km², it is suitable for a planned development of an 80 MW array of Minesto DG500 tidal kites.

2.2 | Behaviour of fish schools

2.2.1 | Long-term behaviour measurements

To study biological and physical processes at the site an instrumented seabed mooring system was deployed in the Holyhead Deep (Figure 2) from 1 October 2016 to 23 January 2017. To study the vertical distribution of fish schools and other marine fauna, an
upward looking four frequency (38, 67, 125, 200 kHz) factory calibrated ASL (ASL Environmental Sciences) Acoustic Zooplankton and Fish Profiler (AZFP) was deployed on the seabed at 85 m depth (Figure 2). Multiple frequencies allowed the categorization of targets in the water column based on their acoustic properties (Benoit-Bird & Lawson, 2016). The four frequencies pinged sequentially with a 3-s interval between the four pings from the 20 of October 2016 until the mooring was recovered on 23 January 2017.

2.2.2 | Ship based sampling

To understand the spatial extent and depth distribution of fish schools in the Holyhead Deep and the representativeness of the mooring point, we carried out vessel-based echosounder transect surveys (Figure 2) at a speed of 4 m/s using RV Prince Madog during the mooring deployment and recovery cruises. A hull mounted scientific single-beam-split-beam Simrad EK60 echosounder was used and calibrated following the methods of Demer et al. (2015). Two nominal frequencies of 38 and 120 kHz with simultaneous pinging, 512 µs pulse length and a 7 degree beam width were used. Aggregations and scattering layers observed with the EK60 were sampled using a modified 5 m² Oozeki mid-water trawl (Oozeki, Hu, Kubota, Sugisaki, & Kimura, 2004) with a 4.4 mm stretched mesh size (Figure 3). An ultra-short baseline underwater positioning beacon and depth logger were used to monitor trawl depth. Four trawls were taken on 5–6 October 2016 (during daylight), and six trawls were taken on 22–23 January 2017 (four during darkness and two during daylight). Fast swimming adult fish such as Atlantic mackerel and adult Atlantic herring likely avoided the mid-water trawl due to the small mouth opening (5 m²) and limited towing speed of 0.5 m/s (=1 knot) through the water.

2.2.3 | Processing of acoustic backscatter

Acoustic analysis of the seabed deployed AZFP backscatter focused on detecting and quantifying the depth distributions of swim bladdered fish schools and excluded fluid-like scatterers (krill etc.) and diffuse transient layers. Vessel mounted EK60 processing also focused on detecting schools only for understanding spatial distribution within the Holyhead Deep. Both AZFP and EK60 analysis was based on the methods of Fernandes (2009) using Echoview software (Echoview Software Pty Ltd; Figure 4; see Appendix S1).

2.3 | Drivers of fish school behaviour

2.3.1 | Seabed mooring

A LISST-100X (Laser in situ Scattering and Transmissometer-100X, Sequoia Scientific, Inc.) was deployed (Figure 2) to measure volume concentrations and size of SPM, set to log continuously in a burst mode, for 1 min, with 10-s intervals and 30 min between bursts, from 1 October 2016 to 25 January 2017. The LISST-100X was deployed on a taught line 8 m above the seabed. To measure current velocities a 300 kHz Teledyne RDI Workhorse Sentinel Acoustic Doppler Current Profiler (ADCP) was deployed 940 m north of the AZFP mooring (Figure 2). The distance between instruments prevented acoustic crosstalk whilst providing comparable data. The ADCP was configured in a burst mode, producing pings for 4 min every 10 min, with 5-s
ping intervals, in vertical depth bins of 40 cm from 1 October 2016 to 15 March 2017. Bursts were time averaged and hourly vertical current profiles calculated. Measurements closest to the instrument and the surface were removed via visual analysis due to interference at those boundaries. Current profiles were averaged over depth to calculate depth averaged current speeds (see Appendix S2).

### 2.3.2 Water column profiles

CTD (conductivity, temperature, depth) casts profiled the water column and collected water samples for calibration of LISST-100X data. This occurred every 30–60 min over a 24-hr period during the deployment (5–6 October 2016) and recovery (21–22 January 2017).
cruises to cover different tidal periods sufficiently. A LISST-100X was mounted on the CTD to characterize vertical profiles of SPM total volume concentration (TVC) and size (D50), with a LI-COR PAR (Photosynthetically Active Radiation) sensor to measure downward-travelling irradiance in the wavelength range 400–700 nm. The estimated relationship between the irradiance and LISST-100X profiles enabled the estimated relationship between SPM properties and light absorption for the site for the entire deployment period (see Section 2.3.4). The CTD and associated instruments were sampling at a frequency of 1 Hz.

2.3.3 Suspended particulate matter characteristics

Volume concentrations of SPM for 32 different size classes, ranging from 2.5 to 500 μm, were measured by the LISST-100X both on the seabed mooring and CTD. One-minute bursts of raw volume concentration measurements from the mooring were averaged over time, resulting in 30 min data intervals, from which daily averages for the sampling period were calculated. For measurements from the CTD mounted LISST-100X the downward section of the profile was used. The cross-sectional area of the particles was calculated as the volume of particles in each size class, divided by the mean diameter of the particles in that class. The cross-sectional area was then summed over the 32 classes to give the total cross-sectional area of particles, A (units m² per m³ of water of m⁻¹) for calculating the depth of light penetration (see Section 2.3.4).

2.3.4 Calculating irradiance depth

Due to the importance of light in affecting the depth distribution of pelagic fauna, we predicted how the depth of light penetration changed during the study period using a new method. LI-COR PAR profiles were used to calculate the diffuse attenuation coefficient $K_D$ for PAR, by regressing the natural logarithm of the down welling irradiance against the depth. The regression was carried out on measurements down to a depth of 10 m below the surface, or less if the irradiance was approaching the dark reading for the instrument. This gave 21 values of $K_D$ for the two cruises applying the above criteria, ranging from 0.29 to 0.62 m⁻¹ with a mean value of 0.41 m⁻¹. Assuming, in these waters, that the attenuation of light was mainly due to particles in suspension, the diffuse attenuation coefficient was plotted against total particle volume and total particle area ($A$). The relationship between $K_D$ and particle area can be expressed as:

$$K_D = 0.202 + 0.915 A$$

with $R^2$ for a linear regression of 0.91 and standard errors of slope and intercept 0.064 and 0.016 m⁻¹ respectively. The first value (0.202 m⁻¹) represents attenuation due to water and dissolved material and the second value (0.915) the attenuation produced by particles with an area of 1 m² in 1 m³ of water.

Equation 1 can be used to calculate the diffuse attenuation coefficient given the cross-sectional area of particles in suspension. The LISST 100X on the mooring was corrected to give the equivalent area of particles near the surface, by calculating the total area of particles in 10 m bins from the CTD profiles. For all profiles, the ratio of the average area of particles in the top bin to that in the bottom bin (the depth of the mooring), was 0.473. The near bed total particle area data was corrected using this ratio and $K_D$ was calculated with Equation 1.

Surface global irradiance (in units of MJ m⁻² hr⁻¹) from the meteorological station at Valley airport on Anglesey (30 km from the mooring site) was used to calculate the depth at which the irradiance reaches a ‘twilight’ value $E_0$, defined here as irradiance depth ($Z$), which can be calculated from the surface irradiance $E_0$ and the diffuse attenuation coefficient $K_D$, using:

$$Z = (-1/K_D) \log \left( \frac{E_0}{E_0} \right)$$

A value of $E_0 = 10$ MJ m⁻² hr⁻¹ was used in this calculation.

2.4 Patterns and relationships between fish school depths and physical properties

The described acoustic processing of the AZFP backscatter produced a depth and time for each detected school. These were averaged by hour to help account for inter-school variation in behaviour, to match the temporal resolution of environmental variables and allow observation of daily behavioural trends, and observe multiday to monthly patterns. To test for the effect of different tidal cycles with periods of 7 days (period between neap–spring tides), 14 days (neap to neap or spring to spring tides) and 29 days (N₂ harmonic lunar month of new moon to new moon) on fish school depth, time-series analysis using seasonal-trend decomposition by regression was conducted using the stR package (Dokumentov & Hyndman, 2018) in R (R Core Team, 2019).

2.5 MRE device overlap

The predicted proportion of hours that DVM fish schools are overlapped by kite flying operations during a day ($PO_{FS}$) was defined (Equation 3) as the ratio of the total number of hours fish schools (FS) are present in a day to the total hours that fish schools are within the kite operating envelope of 20–60 m depth and current velocity ($U$) 1.2–2.4 m/s.

$$P_{OFS} = \frac{\text{hours FS > 20 m & < 60 m & U > 1.2 m/s & < 2.4 m/s}}{\text{hours FS present}}$$

The predicted daily proportion of kite operation hours in a day overlapped by DVM fish schools ($PO_{FS}$) was defined (Equation 4) as the ratio of the total hours when the kite is operating as determined
by the current velocity, to the hours that fish schools are also present in the kite operating depth and kite operating current velocities (Equation 4).

\[
P_{0k} = \frac{\text{hours FS} > 20 \text{ m} \& < 60 \text{ m} \& U > 1.2 \text{ m/s} \& < 2.4 \text{ m/s}}{\text{hours } U > 1.2 \text{ m/s} \& < 2.4 \text{ m/s}} \tag{4}
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3 | RESULTS

3.1 | Composition of fish schools

Gas-filled scatterer aggregations in the water column detected using the EK60 vessel-based echosounder in October 2016 and January 2017 were mostly juvenile sprat S. sprattus and some whiting Merlangius merlangus according to the trawl samples (Figure 3; see Appendix S3).

3.2 | Behaviour of fish schools

Diel vertical migration (DVM) of schools were detected by both the bottom deployed AZFP and the vessel mounted EK60 echosounder. EK60 transect surveys showed that spatial distribution and relative density (nautical area scattering coefficient \(s_A\)) of swim bladdered fish schools undertaking DVM were random (Moran's I indexes for surveys \(p > .05\)) and temporally variable across the Holyhead Deep project area in both October 2016 and January 2017.

The bottom deployed AZFP showed schools of swim bladdered fish, that trawls indicated to be mainly composed of sprat, were present in all months of the study with 20,858 schools detected from 12:00 hr on 8 October 2016 to 12:00 hr on 20 January 2017. The mean hourly school height (bottom of school to top of school) was 1.28 m ± 0.51 (SD). These schools were not detected before 05:00 hr local time neither after 18:00 hr. Fish schools under -of 19.01 ± 8.5 m (SD) deepest hourly mean school depth was 49.67 m with a mean depth towards the surface and disperse in the evening (Figure 5). The descend from the surface in the morning, and then ascend back took DVM throughout the entire study. Schools would form and was 1.28 m ± 0.51 (SD) The mean hourly school height (bottom of school to top of school) was 1.28 m ± 0.51 (SD) from 12:00 hr on 8 October 2016 to 12:00 hr on 20 January 2017. The observed range in fish school depths between 10:00 hr and 14:00 hr each day did not show any correlation with the daily range in irradiance depth each day \((r_s -0.12)\) or current speed \((r_s -0.09)\).

Multiple linear regression produced significant relationships between median daily DVM fish school depth and daily maximum irradiance depth \((p < .001)\), daily median tidal current magnitude \((p < .001)\) and daily mean TVC of SPM \((p < .001)\). The model with these three predictor variables accounted for 78% (adjusted R\(^2\)) of the variation with assumptions of residual normality and homogeneity of variance and linearity met, with variance inflation factor analysis indicating acceptable predictor variable multicollinearity after the removal of median SPM D50 and mean solar radiation from the model. Separate linear regression models with only daily median D50 and daily maximum irradiance depth produced significant fits (both \(p < .001\)) explaining 63% and 60% of the variation in daily median DVM respectively, and 74% when both in the regression model. Median tidal magnitude only accounted for 41% of the variation when the only predictor variable included in the model \((p < .001)\).

Time-series analysis, using seasonal-trend decomposition by regression, of the mean daily DVM school depth indicates an overall trend of a deeper ~22 m depth distribution in October shifting to a ~15 m depth distribution in December and January, mainly shallowing during November. This analysis detected 14- and 29-day cycles that had similar importance for the observed school depths, with its influence diminishing during the study period, with unexplained variation dominating in January above the lunar cycles. The time-series analysis revealed similar trends in irradiance depth.

3.3 | Behaviour drivers

3.3.1 | Relationships between school depth and physical properties

Daily mean depth of DVM fish schools show a cyclical trend of reaching maximum and minimum depths every 2 weeks (Figure 6), with periods of significant \((r_s = 0.05)\) positive autocorrelation (max lag of 60 days) peaking at lags of 15 and 29 days. The daily median SPM size (D50) had significant positive peaks at 15, 29 and 44 days, median tidal current magnitude 15, 29, 45 and 59 days and maximum irradiance depth at 14 and between 27 and 31 days. Daily median SPM TVC had peaks in significant positive autocorrelation at 30 and 60 days. These same variables were significantly correlated (Spearman's Rank \(r_s, \alpha = 0.05\)) with the daily mean DVM fish school depth, with the maximum irradiance depth \((r_s 0.78)\) and SPM D50 (0.80) being positively correlated, median tidal current speed \((r_s -0.64)\) and SPM TVC \((r_s -0.58)\) being negatively correlated (Figure 7). The observed range in fish school depths between 10:00 hr and 14:00 hr each day did not show any correlation with the daily range in irradiance depth each day \((r_s -0.12)\) or current speed \((r_s -0.09)\).

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3.3.2 | SPM and tidal currents

Observed current speed showed a maximum of 2.19 m/s and a mean ± 1 SD of 0.92 ± 0.48 m/s (Figure 6). Strong tidal asymmetry can be seen between flood and ebb currents (Figure 5d). On a longer temporal scale, tidal currents show a spring-neap variation, during new moon and full moon phases tidal currents are greatest, representing spring tidal currents, and during first or third quarter phases they are smallest, representing neap tidal currents (Figure 6). Results show TVC and D50 are correlated to current speed (Figure 7) on tidal and spring-neap time-scales (Figure 6). Particle size is greatest when current speeds are at a minimum, during high water slack and low water (Figure 5) and during neap tides (Figure 6). On a spring-neap time-scale, TVC and current speed are positively correlated,
most likely due to a combination of advection and resuspension of local sediments (Figure 6). Median particle size presents an inverse relationship with current speed (Figure 7) with larger sizes for D50 occurring during neap tides, when current speeds are weakest (Figure 6).

### 3.4 | DVM fish school and MRE device overlap

When DVM fish schools were present, a mean daily proportion of time overlapping with potential kite operations (POFS) was 0.08 for both 8th–31st October and the whole of November, with December and 1st–20th January having a mean potential overlap of 0.02 (Figure 6c). The mean POFS for the study whole period was 0.05. Typically periods of overlap occurrence were 1–4 days in duration (Figure 6c), with the exception of a new moon spring tide (lower current speeds and fish remaining deeper than preceding and following full moon spring tides) at the end of October into November, when 10 consecutive days of overlap occurred, peaking with a day of 0.36 overlap. October (24 days sampled) and November (30 days sampled) had 10 and 11 days with overlap occurrence respectively. In contrast, December (31 days sampled) and January (20 days sampled) had 4 and 3 days where overlap occurred respectively (Figure 6c).

The mean daily proportion of kite operation hours in a day overlapped by DVM fish schools was 0.06 over the study period, with the
highest mean overlap for a single day being 0.44. When averaged over each month of the study period the mean daily proportion of total kite operating time overlapped by fish schools decreased from 0.10 (maximum for a day 0.40) and 0.09 (maximum for a day 0.44) over October and November respectively, to 0.02 in both December (maximum for a day 0.33) and January (maximum for a day 0.17).
This study observed fish schools (trawls indicate to be dominated by sprat) undertaking DVM in the Holyhead Deep. The depth reached by the schools varied, with greater depths reached every 2 weeks correlating (in descending order of correlation strength) with larger D50 values, deeper light penetration into the water column, lower daily tidal current speeds during neap tides and lower SPM concentrations. During the study period there was a trend of decreasing school depths from autumn into winter, with evidence that lunar cycles driving the tidal spring-neap cycle reduced in correlation with DVM in December and January when compared with October and September. This shallowing of fish schools with time, probably due to reduced solar radiation at the sea surface reducing the depth of light penetration, produced a reduction in the proportion of overlap between the fish schools and the DG500 tidal energy kite. Our findings have implications for management authorities and MRE device developers in assessing and potentially mitigating environmental impacts of marine
renewable projects, enabling a comparison of different MRE designs, operating depths and operating envelopes that may alter the duration of possible interactions with marine fauna.

The proportion of overlap calculated in this study is based on the DVM schools occurring between 20- and 60-m depth when the kite would be operational (based on current speed) only, and does not take into account the dimensions of the kite, the positive relationship between kite speed with tidal current speed, the dimensions and spacing of fish schools or any possible avoidance behaviour of fish schools. Therefore, the proportion calculated is a ‘worst case scenario’, which shows general trends and variations in magnitudes of potential overlap. In addition, the presence of DVM schools may be underestimated at dawn and dusk due to fish schools being close to the surface making detection less likely, especially when surface turbulence is present, which may inflate calculated POFS but have not an effect on POk.

Peaks in proportion of overlap between the kite and DVM fish schools did not occur during days when fish schools were migrating deepest, as might be expected. This was due to fish schools migrating deeper when turbidity was lower (lower TVC and larger D50) which occurs during neap tides with lower current velocities when the kite cut-in speed of 1.2 m/s is reached infrequently, and so the kite would not be operating for long periods. However, during the transition between neap tides to spring tides the fish schools were in the kite operating depth, despite migration depth becoming shallower, and the kite cut-in speed was now met more often resulting in overlap with kite operation and fish schools for longer periods of time. The longest period of overlap occurred for ten consecutive days at the end of October into the start of November, and was during a new moon spring tide when the schools were ‘shallow’ compared with a neap tide, but still migrating to average depths greater than 20 m when current speeds were >1.2 m/s for consistent periods of time. The low count of overlap days and proportion of overlap in December and January was driven by the DVM fish schools remaining shallower and not being present for as long each day as day length decreased. Due to the seasonal variation observed, caution should be given to extrapolating any results beyond the sampled time period. Fish have been shown to potentially modify their behaviour in the presence of marine renewable devices in other development areas (Fraser et al., 2018; Viehman & Zydelwski, 2015), and so work is currently underway to understand how schools may react to an operating tidal kite.

Diel vertical migrations of sprat schools has been observed in fjords (Knudsen, Hawkins, McAllen, & Sand, 2009) and the Baltic Sea (Nilsson, 2003), and here in an open marine coastal system of the Holyhead Deep. Due to the mixed water column in the Holyhead Deep, the ‘antipredation window’ (Clark & Levy, 1988) determined by the depth variation in light irradiance would appear a key driver of these vertical migrations, as opposed to temperature or dissolved oxygen levels influencing migratory behaviour in more sheltered and stratified systems (Solberg & Kaartvedt, 2017). This study has shown that the magnitude of fish school DVM can change in correlation with the spring-neap tidal cycle, due to its influence on irradiance depth in the water column.

Sprat schools may afford better protection during spring tides through the higher turbidity as the distance at which their predators can detect them, termed reactive distance, is reduced (De Robertis et al., 2003), while theirs is impacted less due to foraging on zooplankton prey at much closer ranges. However, the sprat are not migrating as deep during spring tides due to the restricted light penetration, which may increase the number of predator species that can reach them and the duration that predators can forage for, potentially overriding any survival advantage of higher turbidity. Neap tides will increase reactive distance for foraging sprat and their predators due to lower turbidity (lower TVC and larger D50, resulting a lower SPM cross-sectional area), but surface diving predators (visual, tactile and acoustic hunters) would need to reach greater depths with potentially higher energetic cost. An interesting question on the implications of our results on surface diving visual predators is whether reactive distance, mediated by the turbidity, is more important for predators foraging on sprat schools than the depth of prey during the day. Cormorants for example have short reactive distances of <1 m even in low turbidity water (White, Day, Butler, & Martin, 2007), and may benefit from shallow schools during turbid spring tides more than greater reactive distance when feeding on deeper prey during neap tides. In contrast, visibility may be more limiting for species that have greater reactive distances, and so forage more successfully during neap tides despite prey being deeper.

Gannets (Brierley & Fernandes, 2001) and Manx shearwater (Shoji et al., 2016) do not routinely dive to depths greater than 20 m, but are capable of reaching depths of 34 and 55 m respectively. Other species capable of diving between 20 and 60 m include the common guillemot, puffin and razorbill (Langton, Davies, & Scott, 2011). Common guillemots/murres Uria aalge were the most frequently sighted species of seabird in the Holyhead Deep in September 2016 (Jackson, 2017) and are known to feed on juvenile sprat and whiting (Anderson, Evans, Potts, Harris, & Wanless, 2014; Riordan & Birkhead, 2018). Common guillemots’ diving behaviour can follow the DVM of their prey (Regular, Davoren, Hedd, & Montecvecchi, 2010), and so the predicted proportion of overlap of fish school prey with the kite in this study could be similar and a proxy for the potential overlap between common guillemots and the tidal kite. However, if forging of diving visual predators focuses on the dawn and dusk descent and ascent phase (Dean et al., 2012; Garthe, Montecvecchi, & Davoren, 2007; Regular et al., 2010) then the implications of the school layer depth during the majority of the day would be diminished.

5 | CONCLUSIONS

We suggest that the depth of light penetration into the water column, calculated using a new method, may predictably determine the depth of DVM undertaken by sprat schools in the Holyhead Deep. Our results show that the depth of light penetration is influenced by the predictable, yet still seasonally variable, SPM dynamics. We show that these SPM properties are strongly influenced by the lunar cycle of tidal current speeds, which are highly relevant in areas of MRE.
development. Therefore, the temporal dynamics of SPM play an important role in determining potential overlap between MRE devices such as the DG500 kite and fish schools, and the predators potentially foraging on them. This finding shows that single or less than 7-day sampling campaigns can miss important behaviour of fish that may alter interaction predictions with MRE devices, and that changes to SPM dynamics from MRE developments may have ecosystem implications. As demonstrated in this study, understanding the behaviour of top predator’s prey species at MRE sites gives developers and environmental managers valuable information for predicting potential impacts, and comparing different MRE devices designs and operating characteristics. In addition, our findings have implications for understanding constraints on top predator foraging opportunities and use of high current areas.

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AUTHORS’ CONTRIBUTIONS
T.A.W. conceived the idea; T.A.W., S.E.J., J.G.H., B.S., B.P., A.G.D. and L.G. designed the methodology; T.A.W., S.E.J., B.P. and T.D.J. collected the data; T.A.W., S.E.J., and D.B. analysed the data; T.A.W. and S.E.J. led the writing of the manuscript with B.S. and J.G.H. contributing critically to the drafts; all authors gave final approval for publication.

DATA AVAILABILITY STATEMENT
Data available via figshare https://doi.org/10.6084/m9.fish are.11671740.v1 (Whitton et al., 2020).

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REFERENCES
Anderson, H. B., Evans, P. G. H., Potts, J. M., Harris, M. P., & Wanless, S. (2014). The diet of Common Guillemot Uria aalge chicks provides evidence of changing prey communities in the North Sea. *Ibis*, 156(1), 23–34. https://doi.org/10.1111/ibi.12099
Baptist, M. J., & Leopold, M. F. (2010). Prey capture success of Sandwich Terns Sterna sandvicensis varies non-linearly with water transparency. *Ibis*, 152(4), 815–825. https://doi.org/10.1111/j.1477-9299.2010.01054.x
Benoit-Bird, K. J., & Lawson, G. L. (2016). Ecological insights from pelagic habitats acquired using active acoustic techniques. *Annual Review of Marine Science*, 8(1), 463–490. https://doi.org/10.1146/annurev-marine-122414-034001
Bianchi, D., & Mislan, K. A. S. (2016). Global patterns of diel vertical migration times and velocities from acoustic data. *Limnology and Oceanography*, 61(1), 353–364. https://doi.org/10.1002/lno.10219
Brierley, A. S., & Fernandes, P. G. (2001). Diving depths of northern gannets: Acoustic observations of Sula bassana from an autonomous underwater vehicle. *The Auk*, 118(2), 529–534. https://doi.org/10.1642/0004-8083(2001)118[2][2]-529
Clark, C. W., & Levy, D. A. (1988). Diel vertical migrations by juvenile sockeye salmon and the antipredation window. *The American Naturalist*, 131(2), 271–290. https://doi.org/10.1086/284789
De Robertis, A., & Handegard, N. O. (2013). Fish avoidance of research vessels and the efficacy of noise-reduced vessels: A review. *ICES Journal of Marine Science*, 70(1), 34–45. https://doi.org/10.1093/icesjms/fss155
De Robertis, A., Ryer, C. H., Veloza, A., & Brodeur, R. D. (2003). Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 60(12), 1517–1526. https://doi.org/10.1139/f03-123
Dean, B., Freeman, R., Kirk, H., Leonard, K., Phillips, R. A., Perrins, C. M., & Guilford, T. (2012). Behavioural mapping of a pelagic seabird: Combining multiple sensors and a hidden Markov model reveals the distribution of at-sea behaviour. *Journal of the Royal Society Interface*, 10(78), 20120570. https://doi.org/10.1098/rsif.2012.0570
Demer, D. A., Berger, L., Bernasconi, M., Ethke, E., Boswell, K. M., Chu, D., ... Williamson, N. (2015). Calibration of acoustic instruments. *ICES cooperative research report No. 326*. Retrieved from http://ices.dk/sites/pub/PublicationReports/CooperativeResearchReport(CRR)/crr326/CRR326.pdf
Dokumentov, A., & Hyndman, R. J. (2018). stR: STR decomposition. R package version 0.4. Retrieved from https://cran.r-project.org/package=stR
Fernandes, P. G. (2009). Classification trees for species identification of fish-school echotraces. *ICES Journal of Marine Science*, 66(6), 1073–1080. https://doi.org/10.1093/icesjms/fsp060
Fraser, S., Williamson, B. J., Nikora, V., & Scott, B. E. (2018). Fish distributions in a tidal channel indicate the behavioural impact of a marine renewable energy installation. *Energy Reports*, 4, 65–69. https://doi.org/10.1016/j.egyr.2018.01.008
Garthe, S., Monteverci, W. A., & Davoren, G. K. (2007). Flight destinations and foraging behaviour of northern gannets (Sula bassana) preying on a small forage fish in a low-Arctic ecosystem. *Deep Sea Research Part II: Topical Studies in Oceanography*, 54(3–4), 311–320. https://doi.org/10.1016/j.dsr2.2006.11.008
Granquist, M., & Mattila, J. (2004). The effects of turbidity and light intensity on the consumption of mysids by juvenile perch (Perca fluviatilis L.). *Hydrobiologia*, 514, 93–101. https://doi.org/10.1023/B:hydr.0000018210.66762.3b
Irigoin, X., Conway, D., & Harris, R. (2004). Flexible diel vertical migration behaviour of zooplankton in the Irish Sea. *Marine Ecology Progress Series*, 267, 85–97. https://doi.org/10.3354/meps267085
Jackson, D. (2017). Minesto deep green ESAS survey summary: August to September 2016 and March to May 2017. Atlantic Ecology Report July 2017.
Kimbell, H. S., & Morrell, L. J. (2015). Turbidity weakens selection for assortment in body size in groups. *Behavioral Ecology*, arv183. https://doi.org/10.1093/beheco/arv183
Knudsen, F. R., Hawkins, A., McAllen, R., & Sand, O. (2009). Diel interactions between sprat and mackerel in a marine lough and their effects upon acoustic measurements of fish abundance. Fisheries Research, 100(2), 140–147. https://doi.org/10.1016/j.fishres.2009.06.015

Langton, R., Davies, I. M., & Scott, B. E. (2011). Seabird conservation and tidal stream and wave power generation: Information needs for predicting and managing potential impacts. Marine Policy, 35(5), 623–630. https://doi.org/10.1016/j.marpol.2011.02.002

Lee, H., Kang, D., & Choi, J. W. (2015). The effect of the suspended solid concentration on the daytime vertical distribution of Euphausia pacifica in the Yellow Sea. Korea. Fisheries Science, 81(5), 849–859. https://doi.org/10.1007/s12562-015-0904-5

Nilsson, L. (2003). Vertical migration and dispersion of sprat (Sprattus sprattus) and herring (Clupea harengus) schools at dusk in the Baltic Sea. Aquatic Living Resources, 16(3), 317–324. https://doi.org/10.1016/S0904-7079(03)00039-1

Oozei, Y., Hu, F., Kubota, H., Sugisaki, H., & Kimura, R. (2004). Newly designed quantitative frame trawl for sampling larval and juvenile pelagic fish. Fisheries Science, 70(2), 223–232. https://doi.org/10.1111/j.1444-2906.2003.00795.x

Piano, M., Lewis, M., Ward, S., Robins, P., Lewis, M., Davies, A. G., & Powell, B. (2015). Characterizing the tidal energy resource of the West Anglesey Demonstration Zone (UK), using TELEMAC-2D and field observations. In C. Moulinec & D. Emerson (Eds.), Proceedings of the XXII TELEMAC-MASCARET technical user conference October 15–16(pp. 195–203). Retrieved from https://henry.baw.de/bitstream/20.500.11970/104333/1_30_Piano_2015.pdf

R Core Team. (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing. Retrieved from https://www.r-project.org

Regular, P., Davoren, G., Hedde, A., & Montevecchi, W. (2010). Crepuscular foraging by a pursuit-diving seabird: Tactics of common murrens in response to the diel vertical migration of capelin. Marine Ecology Progress Series, 415, 295–304. https://doi.org/10.3354/meps08752

Riordan, J., & Birkhead, T. (2018). Changes in the diet composition of Common Guillemot Uria aalge chicks on Skomer Island, Wales, between 1973 and 2017. Ibis, 160(2), 470–474. https://doi.org/10.1111/1010-1268

Robison, B. H. (2003). What drives the diel vertical migrations of Antarctic midwater fish? Journal of the Marine Biological Association of the United Kingdom, 83(3), 639–642. https://doi.org/10.1017/S0025334403007586

Roche, R. C., Walker-Springett, K., Robins, P. E., Jones, J., Veneruso, G., Whitton, T. A., ... King, J. W. (2016). Research priorities for assessing potential impacts of emerging marine renewable energies: Insights from developments in Wales (UK). Renewable Energy, 99, 1327–1341. https://doi.org/10.1016/j.renene.2016.08.035

Scoope-Howe, S., & Jones, D. (1986). The vertical distribution of zooplankton in the western Irish Sea. Estuarine, Coastal and Shelf Science, 22(6), 785–802. Retrieved from http://www.sciencedirect.com/science/article/pii/027771486900995

Schoji, A., Dean, B., Kirk, H., Freeman, R., Perrins, C. M., & Guilford, T. (2016). The diving behaviour of the Manx Shearwater Puffinus puffinus. Ibis, 158(3), 598–606. https://doi.org/10.1111/ibi.12381

Solberg, I., & Kaartvedt, S. (2017). The diel vertical migration patterns and individual swimming behavior of overwintering sprat Sprattus sprattus. Progress in Oceanography, 151, 49–61. https://doi.org/10.1016/j.pocean.2016.11.003

Viehman, H. A., & Zydlewski, G. B. (2015). Fish interactions with a commercial-scale tidal energy device in the natural environment. Estuaries and Coasts, 38(1), 241–252. https://doi.org/10.1007/s12237-014-9767-8

Vinyard, G. L., & O’Brien, W. J. (1976). Effects of light and turbidity on the reactive distance of bluegill (Lepomis macrochirus). Journal of the Fisheries Research Board of Canada, 33(12), 2845–2849. https://doi.org/10.1139/f76-342

Weeks, A. R., Simpson, J. H., & Bowers, D. (1993). The relationship between concentrations of suspended particulate material and tidal processes in the Irish Sea. Continental Shelf Research, 13(12), 1325–1334. https://doi.org/10.1016/0278-4343(93)90086-D

Westgate, A. J., Head, A. J., Berggren, P., Koopman, H. N., & Gaskin, D. E. (1995). Diving behaviour of harbour porpoises, Phocoena phocoena. Canadian Journal of Fisheries and Aquatic Sciences, 52(5), 1064–1073. https://doi.org/10.1139/v95-104

White, C. R., Day, N., Butler, P. J., & Martin, G. R. (2007). Vision and foraging in cormorants: More like herons than hawks? PLoS ONE, 2(7), e639. https://doi.org/10.1371/journal.pone.0006639

Whitton, T. A., Jackson, S. E., Hiddink, J. G., Scouling, B., Bowers, D., Powell, B., & Davies, A. G. (2020). Data from: Vertical migrations of fish schools determine overlap with a mobile tidal stream marine renewable energy device. figshare. https://doi.org/10.6084/m9.figshare.11671740.v1

Williamson, B. J., Fraser, S., Blondel, P., Bell, P. S., Waggitt, J. J., & Scott, B. E. (2017). Multisensor acoustic tracking of fish and seabird behavior around tidal turbine structures in Scotland. IEEE Journal of Oceanic Engineering, 42(4), 948–965. https://doi.org/10.1109/JOE.2016.2637179

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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