Three-dimensional movements of harbour seals in a tidally energetic channel: application of a novel sonar tracking system

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Abstract

1. Understanding how marine predators utilize habitats requires that we consider their behaviour in three dimensions. Recent research has shown that marine mammals often make use of tidally energetic locations for foraging, yet data are generally limited to observations of animals at the water surface. Such areas are also of interest to the renewable energy industry for the deployment of tidal-stream energy turbines; this has led to concerns about potential impacts on marine mammals.
2. Methods for measuring animal movements underwater are limited; however, active sonar can image marine mammals and could potentially measure 3D movements in tidally energetic locations. Here, a dual 720 kHz sonar system was developed to investigate the 3D movements of harbour seals (*Phoca vitulina*) in a tidally-energetic channel.
3. Estimated mean depth (distance from the surface) of seals was 12.0 m (95% CIs = 11.6–12.4), and the majority of time was spent at the surface and at approximately 10–12 m distance from the surface. When expressed as distances from the sea bed, mean distance was 18.5 m (95% CIs = 18.0–18.9), and the majority of time was spent at 14 m from the sea bed.
4. Seal movements were generally in the same direction as the tidal flow with mean horizontal speeds of between 0.51 and 3.13 (95% CIs = 1.24–1.54) ms^{-1}. Mean vertical velocities (where a negative and positive value represents a descent and ascent respectively) for each seal track ranged between -1.76 and +0.88 (95% CIs = -0.23 – +0.03) ms^{-1}.
5. These results provide a basis for understanding how seals utilize a dynamic tidal environment and suggest that harbour seal behaviour can be markedly different to less tidally energetic habitats. The results also have important implications for the prediction of risk associated with interactions between diving seals and tidal turbines in these dynamic habitats.

KEYWORDS: behaviour, environmental impact assessment, new techniques, mammals, renewable energy.

Introduction

Many air-breathing marine predators such as marine mammals have evolved diving abilities allowing them to spend the majority of their time foraging below the surface, often at considerable depths. Understanding how these species utilize their underwater habitats therefore requires that we consider their distribution and behaviour in three dimensions (Davis et al., 1999; Harcourt, Hindell, Bell, & Waas, 2000; Hindell, Harcourt, Waas, & Thompson, 2002). Recent research has shown that marine mammals often make use of tidally energetic locations for foraging (for review see Benjamins et al., 2015; Hastie et al., 2016) yet data from these environments generally have been limited to observations of animals at the water surface with few studies measuring their behaviour underwater (Evers, Blight, Thompson, Onoufriou, & Hastie, 2017; Hastie et al., 2016; Hastie, Wilson, & Thompson, 2006).

Tidally energetic environments are also increasingly the focus of the renewable energy sector as countries strive to cut carbon emissions and reduce the effects of climate change (Callaghan, 2010); tidal stream energy extraction is typically carried out using subsurface turbines that extract energy from tidally-driven moving water. Although there are a wide range of different tidal turbine designs, the majority have large horizontal axis blades that rotate in a similar fashion to most wind turbines. The likely co-occurrence between marine mammals and tidal turbines has led to concerns about the potential for physical injury to marine mammals through direct contact with turbine blades (Wilson, Batty, Daunt, & Carter, 2007). However, at present there is a relative paucity of data on the 3D distributions and 'fine-scale' movements of marine mammals in tidally energetic habitats to quantify the true nature of the risks posed by operational tidal turbines.

Collecting data on the underwater behaviour of marine mammals can be challenging and available methods for measuring 3D movements underwater in high resolution are limited. This can be particularly challenging in dynamic habitats such as tidally energetic areas where the features of the habitat can be in constant flux. Technologies such as animal-borne telemetry systems have revolutionized our ability to observe and understand how marine mammals move underwater (McConnell, Fedak, Hooker, & Patterson, 2010) and can provide data on 3D movements at a very high resolution (Johnson & Tyack, 2003). However, when the focus is on how animals behave in spatially restricted habitats such as tidal rapids (e.g. Hastie et al., 2006), telemetry has its limitations. Specifically, most marine mammals are highly mobile and even if animals are tagged within an area of interest, it is uncertain whether they will remain within that area during the study. Further, the accuracy achieved by geo-referencing the 3D locations of animals using techniques such as accelerometery (Johnson & Tyack, 2003) is limited in areas with strong tidal currents due to the potential disconnect between animal orientation and movement through water, and their net movements over ground as a result of the effects of water movements.

However, there are several technologies that potentially allow direct observation of the underwater movements of marine mammals at specific areas of interest. Video technology has been used to only a limited extent to image marine mammals and record their behaviour underwater (e.g. Davis et al., 1999; Herzing, 1996; Ridoux et al., 1997; Simila & Ugarte, 1993). However, as light does not transmit well through water, such methods have only provided data at relatively short range (a few metres) and has only been carried out during daylight hours in waters with good visibility.

For species that vocalize predictably, passive acoustics have increasingly been used to estimate the positions of individuals in the horizontal (Clark, Ellison, & Beeman, 1985; Freitag & Tyack, 1993; Janik, Van Parijs, & Thompson, 2000; Jensen & Miller, 1999; Leaper, Chappell, & Gordon, 1992) and vertical planes (Hastie et al., 2006; Jensen & Miller, 1999; Møhl, Surlykke, & Miller, 1990; Watkins & Schevill, 1972, 1974, 1977). However, for species (such as seals) that vocalize infrequently or unpredictably, the use of passive acoustics is clearly not effective.

Active sonar has been used for many years to locate marine mammals underwater. For example, Lockyer (1977) reported information on sperm whale dive depths derived from whaling sonars. These devices were relatively crude "searchlight" sonars, with narrow transmit beams; the transducer was steered mechanically to point in different directions and the angular bearing to targets was provided by the orientation of the sonar head when the target is ensonified and returning the strongest echo. Recent research showed that a new generation of multi-beam sonar systems have the capacity to produce acoustic images of marine mammals with high spatial and temporal resolution and may provide a basis for monitoring the underwater movements in tidally energetic locations. For example, Nøttestad, Ferno, Mackinson, Pitcher, and Misund (2002) used a 95 kHz Simrad SA 950 multibeam sonar to measure the behaviour of fin whales (*Balaenoptera physalus*) foraging on herring schools, and Benoit-Bird & Au (2003) used a 200 kHz Kongsberg SM2000 to locate and track spinner dolphins in the water column in Hawaii. Further, West Indian manatee (*Trichechus manatus*) behaviour was measured in waters with very poor visibility (due to turbidity and sediment load) using a range of sonar systems (Gonzalez-Socoloske, Olievera-Gomez, & Ford, 2009; Gonzalez-Socoloske & Olivera-Gomez, 2012), and bottlenose dolphin (*Tursiops truncatus*) movements were tracked in high tidal flows using a 455 kHz Reson Seabat 6012 (Ridoux et al., 1997).

In the current study, we investigated the 3D movements of harbour seals (*Phoca vitulina*) in a narrow, tidally energetic channel off the west coast of Scotland. Previous studies have shown that this area is used by over 100 harbour seals during the summer months (Hastie et al., 2016). These seals showed a striking pattern in their distribution; all seals spent a high proportion of their time around the narrowest point of the channel during the flood tide (Hastie et al., 2016). Although information on the dive behaviour of the seals using animal-borne dive loggers and telemetry was reported in this previous study (Hastie et al., 2016), this was limited to rudimentary metrics (e.g. mean dive duration and max dive depth) and underwater locations were likely to be subject to a high degree of error as they were derived through linear interpolation between surface locations approximately 15 minutes apart. Here, we develop and calibrate a novel configuration of dual high frequency multibeam imaging sonars to measure the depths of diving seals. We then apply this to track the 3D movements of individual harbour seals in high resolution within the channel and discuss (a) how seals utilize this dynamic habitat, and (b) the implications of the results in understanding the potential impacts of tidal turbines.

Methods

Study area

The 3D movements of harbour seals were measured during the flood tide in a narrow, tidally energetic channel on the west coast of Scotland (Kyle Rhea: 57°14'8.10"N, 5°39'15.25"W) between the 10th and 11th June 2015. The channel runs from north to south, is approximately 4 km long, and is 450 m wide at its narrowest point (Figure 1). Water depths within the channel are less than 40 m. Tidal currents within the channel can exceed 4 ms^{-1} at peak flow (Wilson, Benjamins, & Elliott, 2013) with water moving from south to north during the flood tide and from north to sough during the ebb. Validation trials described below were carried out at a location approximately 4 km northwest of Kyle Rhea (57°15'56.97"N, 5°42'41.04"W); water depths here were approximately 60 m and the tidal currents were markedly lower than Kyle Rhea. Sea surface conditions during the study were generally good with only small ripples present (Beaufort scale = 0 - 1).

Figure 1 here

Calculating dive depth

Data were collected using two multibeam sonars (Tritech Gemini 720id, Tritech International Ltd, Aberdeen, UK) deployed from the side of a 7.5 m aluminium vessel and data were stored to external HDs using a laptop PC located in the cabin of the boat. The sonars were deployed using a custom-built sonar mount which allowed both the horizontal and vertical orientations of the sonars to be adjusted. In their normal orientation, each sonar covers a horizontal swathe of 120 degrees and a -3dB vertical swathe of approximately 20 degrees. A second sonar was then mounted alongside the first. It was orientated in the same horizontal angle but with a vertical angle offset of 17 degrees downwards. This provided a swathe where the two sonars overlapped and the seal could be detected on both sonars (Figure 2).

Figure 2 here

A model of the vertical beam pattern of the sonar was first established using the carcass of a grey seal (*Halichoerus grypus*) (approximately 1 m in length); this had been frozen within hours of death and was defrosted over 48 hours prior to the calibration tests. The seal was suspended underwater using a custom built harness and 50 m rope and was deployed from an inflatable boat. A lead weight of approximately 5 kg was suspended 1 m below the seal to act as ballast. An OpenTag depth logger (Loggerhead Instruments, FL, USA) (50 Hz sample rate) was attached to the seal to calibrate the depth estimates from the sonar. The inflatable boat manoeuvred to a range approximately 20-40 m from the sonar and the seal was raised and lowered through the sonar beams between the surface and the sea bed (40 m). The seal carcass was easily observed as a temporally persistent, highly localized pattern of high intensity pixels in the sonar images at depths of up to 33 m. The XY locations of the seal carcass and the relative peak intensity on each sonar was measured manually every second using the software SeaTec; it should be noted that engineering version of this software (Engineering version 1.18.10.36, Tritech International Ltd, Aberdeen, UK) was required to measure intensities. The vertical beam pattern of the sonars was measured by lowering and raising the seal vertically through the swathe of one of the sonars; the relationship between the measured intensity (as a proportion of the maximum sonar intensity) and both the angle of declination (degrees) and the range (m) from the sonar heads (measured using the depth of the OpenTag together with the measured distance to the target on the sonar) was modelled in a generalized linear model with Binomial errors and an logit link function. Using AIC for model selection, the best fit model of the patterns of intensity of the grey seal carcass when raised and lowered through the sonar swathes is described by Equation 1.

Equation 1

$$I_{seal} = I_{max} \times (1.598 - (0.7066 \times \alpha^2) - (0.0008 \times \log_{10} d))$$

Where:

I_{seal} is the intensity of the seal on the sonar;

I_{max} is the maximum intensity value reported by the sonar;

α is the vertical angle of the seal in degrees relative to the centre of the vertical beam of the sonar;

d is the range (m) of the seal from the sonar.

The XY locations of the seal were measured manually on the upper and lower sonars at one-second intervals using a marker tool in the sonar software. The peak intensity of the seal was also measured on each sonar at one second intervals and the ratio of intensities between the sonars was computed (Figure 2). The depth of the seals was then estimated by calculating the ratio of acoustic intensities measured on each sonar. The angle of declination of the seal from the water surface was calculated by comparing the measured intensity ratios to the expected ratios based on the modelled vertical beam patterns of the sonars (Figure 2). These angles, together with the ranges of the seal measured on the sonars, provided the information required to calculate the depth of the seal at one-second intervals. When the seal was only visible on one sonar image (e.g. when it was deeper than the lower limit of the upper sonar), the angle of declination was assumed to be a constant angle midway between the lowest detection angle of the two sonars (47 degrees).

The calculated depths were then divided into vertical tracks (where the seal was detected continuously on both sonars). As the sonars were mounted off the side of the boat, there was a risk that occasional rolling motion by the boat would lead to changes in the orientation of the sonars relative to the seal thus introducing apparent errors in measured depths. Each vertical track was therefore smoothed using a univariate penalized cubic regression spline smooth (with a Gaussian error distribution and log link function) implemented using the package 'mgcv' (Wood, 2006) in the statistical software R (R Core Team, 2012) to produce a series of modelled depths (± 95% CIs) for each track. Modelled depths were compared to those measured on the depth logger to estimate the accuracy of the method for predicting dive depth.

Three-dimensional movements of seals

Sixty-three seals were tracked within the tidal channel using the same boat-mounted dual sonar setup described in the Calculating dive depth section above. Data were collected between 30 and 120 minutes after low tide on the 10th June 2015, and between 153 and 190 minutes after low tide on the 11th June 2015. The boat operated in different parts of the channel but focused on areas previously identified as being of high use (Hastie et al., 2016). Effectively, the boat was repeatedly maneauvered to the southern end of the channel and allowed to drift passively with the tidal currents through the channel. Sonar data were collected continuously during the drifts and a constant visual watch was maintained for seals at the surface; the visual data were used primarily for seal species identification. It should be highlighted that the boat did not attempt to change course or speed when seals were sighted at the surface to avoid any potential depth estimate biases by focusing on tracking seals at the surface. All sonar and visual data collection were carried out under Home Office Animals (Scientific Procedures) Act licence number 70/7806.

The sonar data were reviewed post-hoc to identify seals; as described above, the seals were easily identified as highly localized patterns of temporally persistent, high intensity pixels in the sonar images (Figure 2). All seals detected on the sonar were assumed to be harbour seals; however, grey seals (*Halichoerus grypus*) and harbour porpoises (*Phocoena phocoena*) are relatively similar in size to harbour seals and are occasionally present in the study area. Although none were sighted at the surface during data collection, it is possible that a small proportion of the targets were of these other species. The XY locations of seals were measured at 1 s intervals manually using a marker tool in the sonar software and the depth of the seals was calculated using the intensity ratio method described above; however, the models to create the spline smooths of depth for seven of the seal tracks did not converge resulting in 56 seal tracks for the further analyses. Each seal track was geo-referenced in 3D within the channel using a combination of these XY locations and dive depth estimates, together with data from a GPS data logger on the boat, and the angle of orientation of the sonars provided by an OpenTag fixed to the top of the sonar mounting pole.

A series of summary movement metrics for each 3D seal track were computed; these included mean (± 95% CIs) horizontal speed over ground (ms^{-1}) and mean (± 95% CIs) vertical velocities (ms^{-1}). Further, the relative use of the water column was calculated for each track; this was expressed as the proportion of time spent in 2 m bins (distance from the surface and distance from the seabed), and as a proportion of the water column. Mean (± 95% CIs) values are presented for each bin across all tracks. For the distance from the sea bed and the proportion of the water column calculations, each seal location (calculated using the boat GPS logger and the range and bearing from the sonar) was plotted on high resolution (~2 m) gridded bathymetry data were obtained from Marine Scotland (http://aws2.caris.com/ukho/mapViewer/map.action). The bathymetry values were relative to Chart Datum and thus represent the lowest astronomical tide. Depth values relative to Mean Sea Level were derived by applying the United Kingdom Hydrographic Office Vertical Offshore Reference Frame (VORF) Lowest Astronomical Tide (LAT) correction (Iliffe, Ziebart, Turner, Talbot, & Lessnoff, 2013) for the study area to the bathymetric depths relative to Chart Datum. These depth values were then transformed to account for the depth variation over time caused by the tidal cycle. The National Oceanography Centre Hydrodynamics Dynamic Link Library (National Oceanography Centre, 2010) was used to generate estimates of the tide height relative to Mean Sea Level from the harmonics of the High Resolution UK Continental Shelf Model (CS20) which has a resolution of 1/60°lat by 1/40°lon (Proctor et al., 2004).

An important artefact of the sonar technique used here is that, due to the fact that shape of the ensonification volume from the sonars is effectively a circular disk sector (see Figure 1 in Parsons et al. (2017)), the range of depths that seals could be detected increases with range the sonar. There is therefore a potential bias towards detecting seals closer to the surface when they are relatively close to the sonar. To avoid this potential bias influencing the depth distributions, the proportion of time that seals spent in each depth bin were divided by the proportion of the volume of water column ensonified in each depth bin. For example, in the depth bin 0-2 m from the surface, approximately 100% of the water volume is ensonified, compared to approximately 81% in the depth bin 28-30 m from the surface. This weighting effectively increased the calculated proportions of time closer to the seabed to account for the overall lower volume of water being ensonified by the sonars and thus lower numbers of seals being available for detection.

Results

Three-dimensional tracking calibration

The results of the tracking calibration trials using the dual sonars and the seal carcass showed that the depth of the seal could be estimated accurately by measuring the ratio of intensities between the sonars and smoothing the depths using a cubic spline smoother. At ranges of between 27 and 40 m and for depths of between 0 and 35 m, mean error was +0.90 m (95% CIs = +0.62 – +1.17 m) and mean root-squared error was 2.38 m (95% CIs = 2.22 – 2.54 m). Mean error and mean root-squared error when the seal was detected on two sonars were +0.44 m

(95% CIs = +0.12 – +0.75) and 2.16 m (95% CIs = 2.01 – 2.32) respectively. Errors were comparatively higher when the seal was only detected on one sonar with a mean error and mean root-squared error of +1.65 m (95% CIs = +1.16 – +2.14) and 2.74 m (95% CIs = 2.41 – 3.07) respectively (Figure 3).

Figure 3 here

Three-dimensional movements of seals

The 3D movements of seals were successfully measured within the channel; fifty-six individual seal tracks ranging in duration from 7 to 99 s with a mean of 23.7 s (95% CIs = 19.5 – 27.9) were constructed (Figure 4). Estimated mean depth (distance from the surface) of all seals was 12.0 m (95% CIs = 11.6-12.4), and the majority of time was spent at the surface and at approximately 10-12 m distance from the surface (Figure 5). When dive depths were expressed as distances from the seabed, mean distance was 18.5 m (95% Cis = 18.0-18.9), and the majority of time was spent at approximately 14 m from the seabed. A relatively low proportion of time (mean = 0.02, 95% CIs = 0.00-0.04) was spent within 2 m of the seabed (Figure 5). When expressed as a proportion of the water column (where 0.00 is at the sea surface and 1.00 is at the seabed), mean depth was 0.39 (95% CIs = 0.38-0.40), and there were peaks in use at the surface and at 0.55 of the water column (Figure 5). The mean depth of the sea bed at the times and locations where seals were detected was 30.5 m and ranged from 13.6 to 35.7 m. It should be highlighted that a small proportion (~2%) of the seal depths were estimated to be at depths greater than the estimated seabed depth.

Figure 4 here

Figure 5 here

Horizontal speeds over the ground of the seals in the channel varied between 0.0 and 5.3 ms^{-1}; mean horizontal speeds for each seal track ranged from 0.51 to 3.13 ms^{-1} (95% CIs = 1.24 – 1.54) (Figure 6). The distribution of movement directions in the channel was variable; however, there was a clear peak in movements in a northerly direction (between 340° and 10°) (Figure 7). Mean vertical velocities (where negative and positive values represent a descent and ascent respectively) for each seal track ranged between -1.76 to +0.88 ms^{-1} (95% CIs = -0.23 – +0.03) ms^{-1} (Figure 7). When expressed as root-squared vertical velocities, mean values for each seal track varied between 0.00 and 4.7 ms^{-1} (95% CIs = 0.70 – 1.18).

Figure 6 here

Figure 7 here

Discussion

This paper presents the results of a study which used a new dual multibeam imaging sonar technique to measure the underwater movement behaviour of a mobile marine predator in a narrow, coastal channel subject to strong tidal currents. They show that, during the flood tide, harbour seals exhibited movements that were highly directed in the same general direction as the tidal flow (north) and that there were peaks in the use of the water column at the surface and towards the middle parts of the water column.

The results presented here illustrate that the novel dual sonar technique is an effective method of localizing seals within the water column, thus providing a means of tracking seals in three dimensions. The system used here was capable of tracking seals up to ranges of approximately

60 m from the sonar and to depths greater than 30 m. From this perspective, it should be highlighted that the seal used during the validation of the technique was relatively small (~1 m in length) and it seems reasonable to assume that larger seals are likely to present stronger targets and are therefore likely to be detectable at deeper depths.

Due to the challenges of maintaining the orientation of the boat in the relatively high water currents, it was not possible to track individual seals for extended periods (max duration = 99 s). It should also be highlighted that sonar vertical beam patterns across the entire monitoring range of the sonars (0 - 60 m) were modelled predictions based on measurements of a seal carcass within a limited part the range (~ 20 - 40 m range from the sonars). Although there are potential uncertainties in depth estimation for seals detected outside this range, the majority of wild seals here (90%) were tracked between this range (~ 20 - 40 m).

A critical but often overlooked factor when using active sonar to study the behaviour of marine mammals is that most marine mammals rely heavily on sound as a means of navigation and for detecting prey, and that the hearing and vocal ranges of many marine mammal species overlap with the transmission frequencies of many commercially available sonar systems (~12–150 kHz) (Richardson, Greene, Malme, & Thomson, 1995). Therefore, there is clear potential that the acoustic signals produced by some sonar systems could elicit behavioural responses in these species (Hastie, Donovan, Götz, & Janik, 2014). However, the fundamental frequency of the sonar used in the current study (720 kHz) was well above the effective hearing range of harbour seals (Cunningham & Reichmuth, 2016) and recordings indicate that low frequency components of the signal are relatively low in amplitude (Hastie, 2012); this suggests that the risk of this sonar system eliciting behavioural responses by harbour seals is relatively small.

Despite these caveats, with a mean error in depth estimation of approximately 2 m, the technique proved to be relatively accurate and showed little bias to either shallower or deeper estimates. The use of multibeam sonar to track seals in our study suggests that it represents an effective method for tracking diving animals in high resolution within a specific restricted area.

This represents an advantage over data provided by animal borne tags which is collected over the whole of an animal's home range, so that only a small proportion would come from the area of interest. It also proved highly successful in a tidally energetic location where reconstructing the 3D fine-scale tracks of animals from animal-borne GPS/dive loggers is likely to be subject to relatively large errors due to strong tidal currents (Shiomi et al., 2008). Further, although this study measured the underwater behaviour of harbour seals, the method is likely to be transferable to other marine mammal species and other large vertebrates. For example, a recent study used the same multibeam sonar to detect a range of shark species, including bull sharks (*Carcharhinus leucas*), great white sharks (*Carcharodon carcharias*), lemon sharks (*Negaprion brevirostris*), and sandbar sharks (*Carcharhinus plumbeus*) (Parsons et al., 2017), and it seems reasonable to assume that the dual sonar approach could be used to track the 3D behaviour of species like these underwater.

There is very little published information on the behaviour of seals in tidally energetic environments (Benjamins et al., 2015). However, Zamon (2001) studied the temporal and spatial patterns of harbour seals (*Phoca vitulina richardsi*) in relation to tidal phase in a tidal strait in San Juan Islands, Washington State. Counts of seals at the water surface were made from shore and were compared between different states of the tide. Results showed a clear tidal pattern in seal presence in the channel with highest counts during flood tides. Similarly, previous studies of tagged seals has shown that individual harbour seals spend a significant proportion of their time in the narrow channel studied here (Hastie et al., 2016). Furthermore, analysis of their spatial distribution within the channel revealed a striking pattern with the majority of the tagged seals spending a high proportion of their time close to its narrowest point during the flood tide (Hastie et al., 2016). Diving behaviour by seals in this previous study (Hastie et al., 2016) showed that all seals tagged with depth recorders made prolonged dives underwater in the tidal channel. However, this information was limited to rudimentary metrics such as dive duration or maximum dive depth, and the relatively low resolution of the data precluded a detailed analysis of their use of the water column (Hastie et al., 2016).

The dive depths measured in the current study are all relatively shallow and are well within the diving capabilities of harbour seals which have been recorded diving up to several hundred metres in some habitats (e.g. Eguchi & Harvey, 2005; Gjertz, Lydersen, & Wiig, 2001). Although there is little research into the diving behaviour of seals in tidally energetic locations, information on diving behaviour in other habitats has shown that harbour seals generally forage at or close to the sea floor (Bjorge, 1995; Bowen, Boness, & Iverson, 1999; Frost, Simpkins, & Lowry, 2001; Gjertz et al., 2001; Lesage, Hammill, & Kovacs, 1999; Tollit et al., 1998). From this perspective, the results of the current study appear markedly different to these previous results; harbour seals in the tidal channel here spent a relatively high proportion of their time around the middle of the water column with a low proportion of their time close to the sea bed.

When interpreting the dive data in the current study, it is important to have confidence that the detection probability of seals remained relatively constant throughout the water column. For example, previous research has shown that waves at the water surface can significantly corrupt the quality of the acoustic data to such an extent that they become unreliable for small target detection (Kozak & Salme, 2006). It is also possible that acoustic clutter associated with the sea bed may have influenced the detection of seals swimming close to the sea bed. However, the sea conditions during the current study were generally very good (Beaufort scale: 0-1) and the apparent decrease in use with increasing depth appeared to commence well above the sea bed (~14 m; Figure 5). Further, the observed proportion of time seals were tracked at the surface in the current study (mean = 0.17; Figure 5) is relatively similar to the proportion of time at the surface observed for tagged harbour seals previously in tidally energetic locations; Evers et al. (2017) report a mean of 0.18 and Hastie et al. (2016) report a mean of 0.27. This suggests that the overall pattern of time at depth has likely been captured in the current study. In support of the distinctive pattern observed here, one of the few other studies to measure seal diving behaviour in a tidally energetic environment (Evers et al., 2017) presents data on harbour and grey seal diving behaviour showing that both species exhibit a significant amount of mid-water swimming.

It is likely that the depth distribution of seals is governed to a large extent by the variation in prey availability with depth. Dietary evidence from previous studies around the UK indicate that harbour seals primarily forage close to the sea bed with benthic species such sandeels (*Ammodytidae* spp.), gadoids (whiting *Merlangius merlangus* and Atlantic cod *Gadus morhua*), flatfish (dab *Limanda limanda*, plaice *Pleuronectes platessa* and flounder *Platichthys flesus*) most commonly appearing in harbour seal diets (Pierce & Santos, 2003; Thompson et al., 1996; Tollit et al., 1998). In contrast, a previous study (Hastie et al., 2016) within the current study area reported frequent observations of seals feeding on Atlantic mackerel (*Scomber scombrus*); this was consistent with anecdotal observations made during the current study and suggests that the availability of this prey species in the channel may underpin the diving behaviour shown by the seals. Atlantic mackerel is a pelagic shoaling species that is generally not reported (Brown, Pierce, Hislop, & Santos, 2001; Thompson et al., 1996; Tollit et al., 1998) or occurs infrequently (Pierce & Santos, 2003) in the diet of harbour seals around the UK. It is a highly mobile species that makes relatively long migratory movements in dense schools in coastal waters (e.g. Walsh, Reid, & Turrell, 1995). During summer, they make northwards migrations along the west of Scotland (Reid, Turrell, Walsh, & Corten, 1997) and it seems plausible that mackerel move through the study area during the summer. The relatively shallow diving behaviour shown by the seals here could therefore reflect a higher abundance of this pelagic fish species towards the middle parts of the water column; future studies of seal diet composition using scat analysis (e.g. Tollit & Thompson, 1994) in the study area may help to test this theory. Although the behaviour of fish and the mechanisms underlying prey capture remain unknown, the results presented here provide an interesting insight into the routine diving depths of harbour seals in a tidally energetic habitat that is used intensively by seals (Hastie et al., 2016).

Seal movements in the channel were predominantly in a northerly direction (between 340° and 10°) and there was peak in the horizontal speed of movement of harbour seals between 1 and 1.5 ms^{-1}. It is important to highlight that the impact of water flows in tidally energetic areas can be important when interpreting seal movements. The movement of tracked animals reflects the summation of the movement of an individual plus the current vector (Hays et al., 2016). The flood tide (when the data were collected) in the study area generally flows from south to north with water movements that can exceed 4 ms^{-1} at peak flow (Wilson et al., 2013); given that the energetic cost of swimming harbour seals increases markedly at speeds greater than 1.5 ms^{-1} (Hind & Gurney, 1997) and the maximum burst speed for harbour seals is around 4 ms^{-1} (Williams & Kooyman, 1985), it is likely that the highly directed movements measured here (Figure 7) reflect seals being actively forced down the channel by the water flow. However, it should be noted that recent results of a study of seals tagged with GPS telemetry devices in this study area suggests that seals are capable of remaining within the channel during peak tidal flows (Hastie et al., 2016); it seems likely that by restricting the data collection to areas of the channel that were relatively deep with fast tidal currents, the full range of swimming directions were not captured in the current study. Disentangling the active movement of an animal from movement due to environmental flows is an important question in understanding how animals use dynamic environments but remains a challenge (Hays et al., 2016), particularly in highly dynamic tidal systems such as the one studied here.

The results presented here have important implications for understanding the potential impacts of industries operating in narrow coastal constrictions. By their nature, these areas are often associated with strong, tidally induced, water currents; this has led to the proposed installation of tidal turbines in many tidal sites (Jay, 2010; Toke, 2011) and their potential co-occurrence with marine mammals has led to concerns about the potential for physical injury through collisions (Wilson et al., 2007). From this applied perspective, the information gathered here is critical for assessing the potential impacts of tidal turbines, and the 3D movements in this channel have implications for industrial developments at this site and potentially other tidally energetic locations. Specifically, the results of the diving behaviour can be used to directly assess the relative overlap between diving seals and tidal turbines in the water column. When interpreting the results presented here with respect to this, overlap depends broadly on the depths at which tidal turbines are located, whether they are fixed to the sea bed or are surface floating, and the diameter of the blades, which will together influence the risk depths covered by the swept area of the turbine blades (Evers et al., 2017). In the current study, seals spent relatively little time within 12 m of the seabed, suggesting that for seabed mounted turbines with blades rotating within this distance from the sea bed, the risk of overlap may be relatively low. However, for seabed mounted turbines with blades that extend beyond this distance, or for surface floating turbines, the risk of overlap may be far greater. Overall, the proportion of time spent relative to either the sea surface or sea bed, can be used to estimate the density of animals within a zone of risk, and can be used to parameterize collision risk models (Evers et al., 2017).

From a conservation perspective, information on the relative risks associated with tidal turbines are particularly important when considering the potential impacts on harbour seal populations. This may be particularly important for populations in decline; for example, numbers of harbour seals have dramatically declined in several regions of the north and east of Scotland (Lonergan et al., 2007; Matthiopoulos et al., 2014; Thompson, Duck, Morris, & Russell, In review). Although the causes underlying these declines remain uncertain, potential drivers of the declines include changes in prey quality and/or availability, increasing grey seal population size which may be influencing harbour seal populations through direct predation or competition for prey resources, and the occurrence and exposure of seals to toxins from harmful algae (Matthiopoulos et al., 2014). Many of the regions exhibiting harbour seal population declines overlap with proposed tidal energy developments. In particular, counts of harbour seals in the Orkney Islands and the north coast of mainland Scotland declined by over 46% between 2001 and 2006 and continued to decline at over 10% per annum until 2016 (Thompson et al., In review). This is also an area identified as a key tidal energy resource and where tidal developments are in the advanced stages of planning (Lewis, Neill, Robins, &

Hashemi, 2015). Potential risks from turbines to this sensitive population are therefore relatively acute and accurate data to parameterize collision risk models such as those presented in the current study, are critical if the industry is to develop without having significant adverse effects.

In terms of wider conservation and industry relevance, it is therefore clearly important to understand how generalized these 3D movement patterns may be in other tidally energetic areas in order to quantify the true extent of collision risk and potential effects of the tidal power industry on harbour seal numbers. This requires that the techniques developed here are easily transferable to other sites proposed for tidal energy development. Given that the system can be deployed easily from a small vessel, it appears highly practical at most sites. However, there are a number of limitations that should be considered. Specifically, the maximum depth that seals were detected using the system was a ~35 m and although this would be sufficient to monitor the full water column in many of the existing tidal developments (Malinka, Gillespie, Macaulay, Joy, & Sparling, 2018; Sparling, Lonergan, & McConell, 2018), the industry is likely to exploit deeper water locations in future (Lewis et al., 2015).

The results of the study also show promise as a technique to track individual seals (and potentially other large species) around operational turbines once they have been deployed. For example, it may be possible to locate the dual sonars on a seabed mounted platform to the side of the turbine and effectively ensonify the turbine and the water column in both the upstream and downstream directions. Although likely dependent upon turbine design and location, this could effectively collect data on seal movements in three dimensions around the turbine, providing information on whether seals exhibit appropriate responsive movements to reduce the potential for collisions with tidal turbine blades. Information like this is critical if the tidal energy industry and marine mammals are to co-exist in the future and will be important for policy-makers developing guidance for the tidal industry.

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Figures

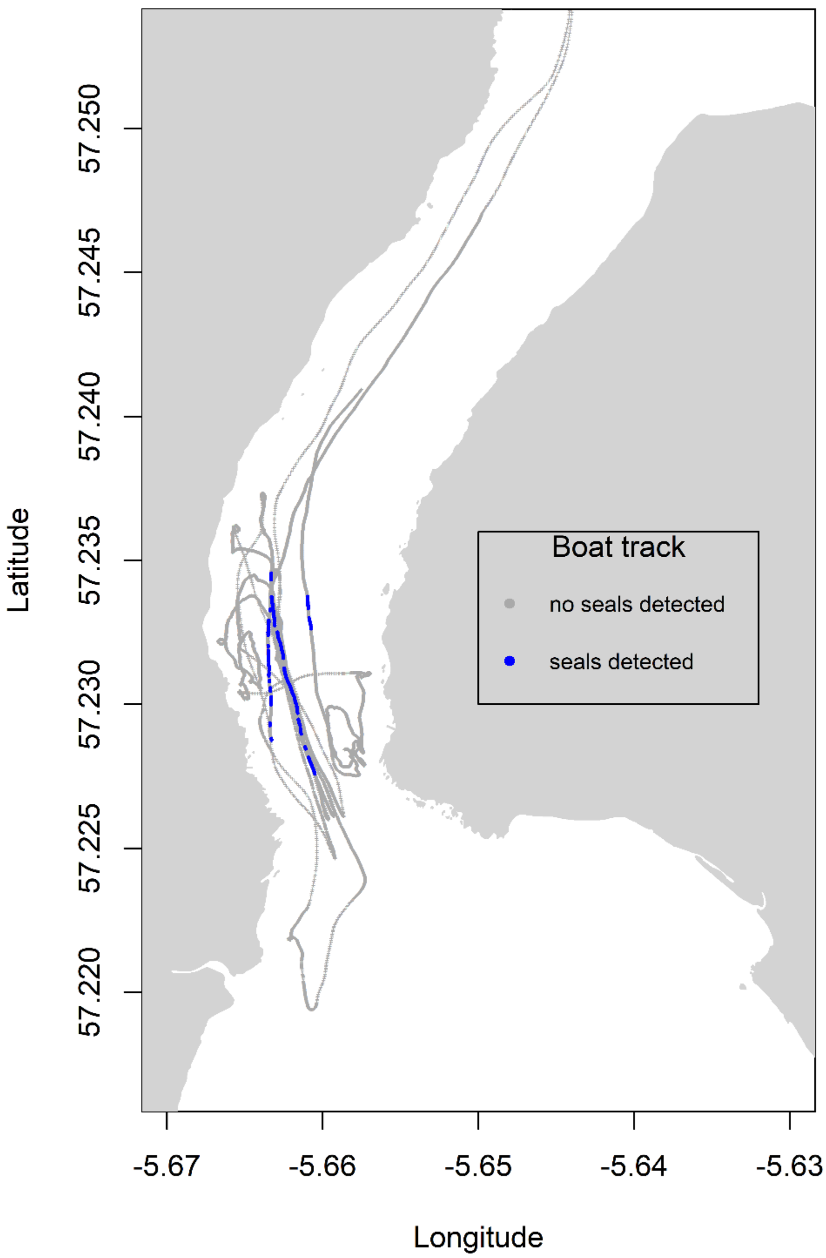

Figure 1: Map of the study area showing the track of the research boat, colour coded to show where seals were detected using the multibeam sonar (blue points) and where no seals were detected (grey points).

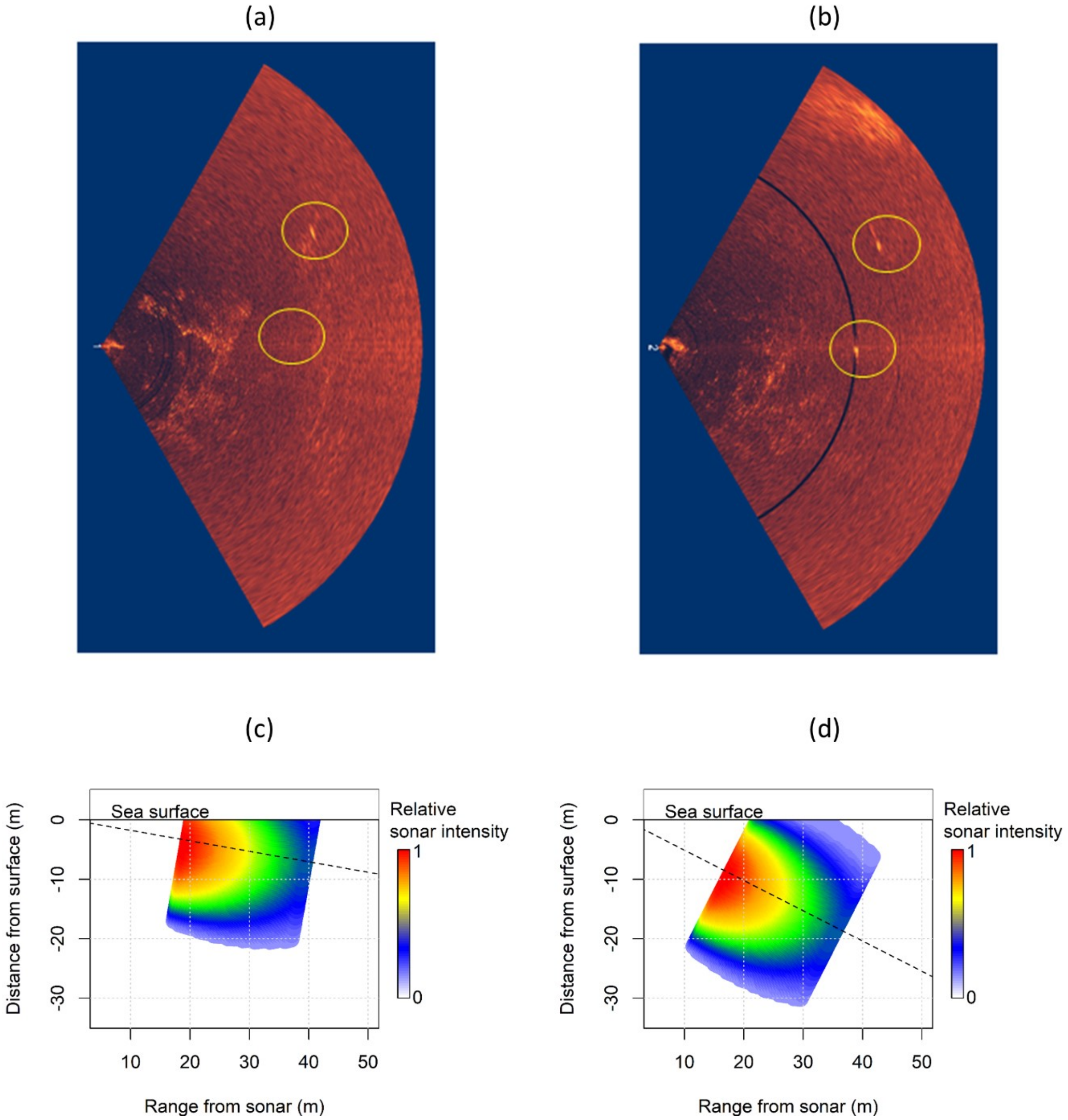

Figure 2: An example of the data used to calculate the depth of a seal using dual multibeam sonars mounted in a horizontal orientation but offset vertically. The upper panels show snapshots of sonar data collected within a narrow tidal channel off the west coast of Scotland on each of two multibeam sonars. Panel (a) shows an image from the sonar oriented vertically downwards from the sea surface by 10 degrees and panel (b) shows an image from the sonar oriented vertically downwards from the sea surface by 27 degrees. The lower panels (c) and (d) show the theoretical intensity of a seal measured between 20 and 40 m from the sonars mounted on the boat and oriented downwards by (c) 10 and (d) 27 degrees from the sea surface (the median line of peak intensity through the vertical beam for each sonar is shown by the dashed lines) from the sea surface; the vertical beam pattern was based on measurements of a seal carcass. In panel (a), a single harbour seal can be seen as a distinct target approximately 30 m from the sonar (highlighted by the yellow ring). In panel (b), the same seal can be seen, together with a second seal that is not apparent in panel (a); this indicates that the second seal is at a depth greater than the swathe of the sonar oriented downwards by 10 degrees from the sea surface.

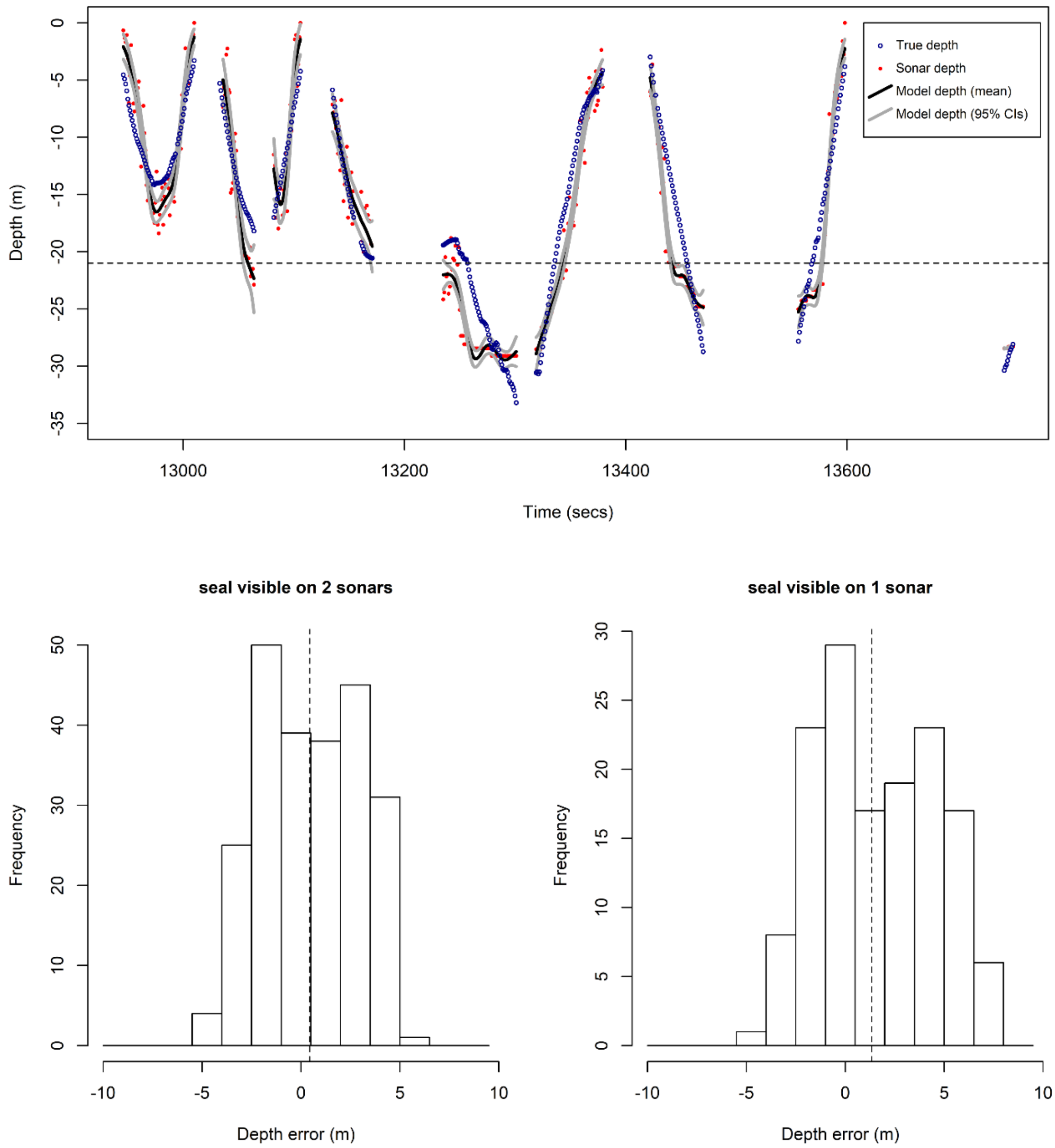

Figure 3: The upper panel shows the measured depths (using an OpenTag depth logger: blue points) of a grey seal carcass raised and lowered though the swathes of two 720 kHz multibeam imaging sonars; the raw estimated depths (using the ratio of intensities approach: red points) and modelled depths (black line) with 95% CIs (grey lines) made using a cubic spline smoother are also shown. The lower panels are histograms of the errors in depth estimation using the intensity ratio and cubic spline smoother approach; mean root-squared error (shown by the vertical line) when the seal was detected on both sonars was 2.16 m (95% CIs = 2.01 – 2.32) and was 2.74 m (95% CIs = 2.41 – 3.07) when the seal was only detected on one sonar.

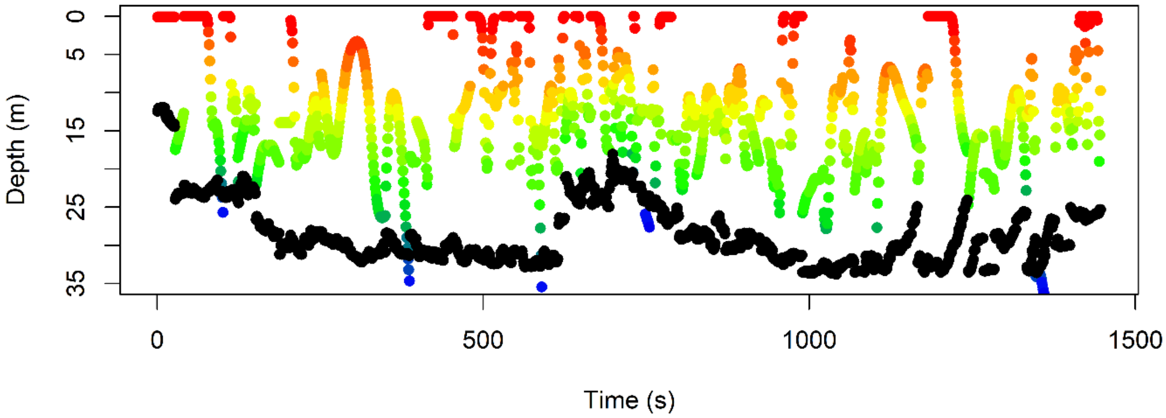

Figure 4: Estimated dive depths of the seals detected using the sonar system within a narrow tidal channel. The figure shows the modelled depths of the seals colour coded by the proportion of the water column (0.0 = red, 1.0 = blue) it was estimated at, and the seabed depth (black points) at the respective time and location of each seal. For illustrative purposes, all dive profiles have been spliced together to form a continuous series of dive and sea bed depths; as such, the time (s) along the x-axis does not represent the absolute time relative to the start of data collection.

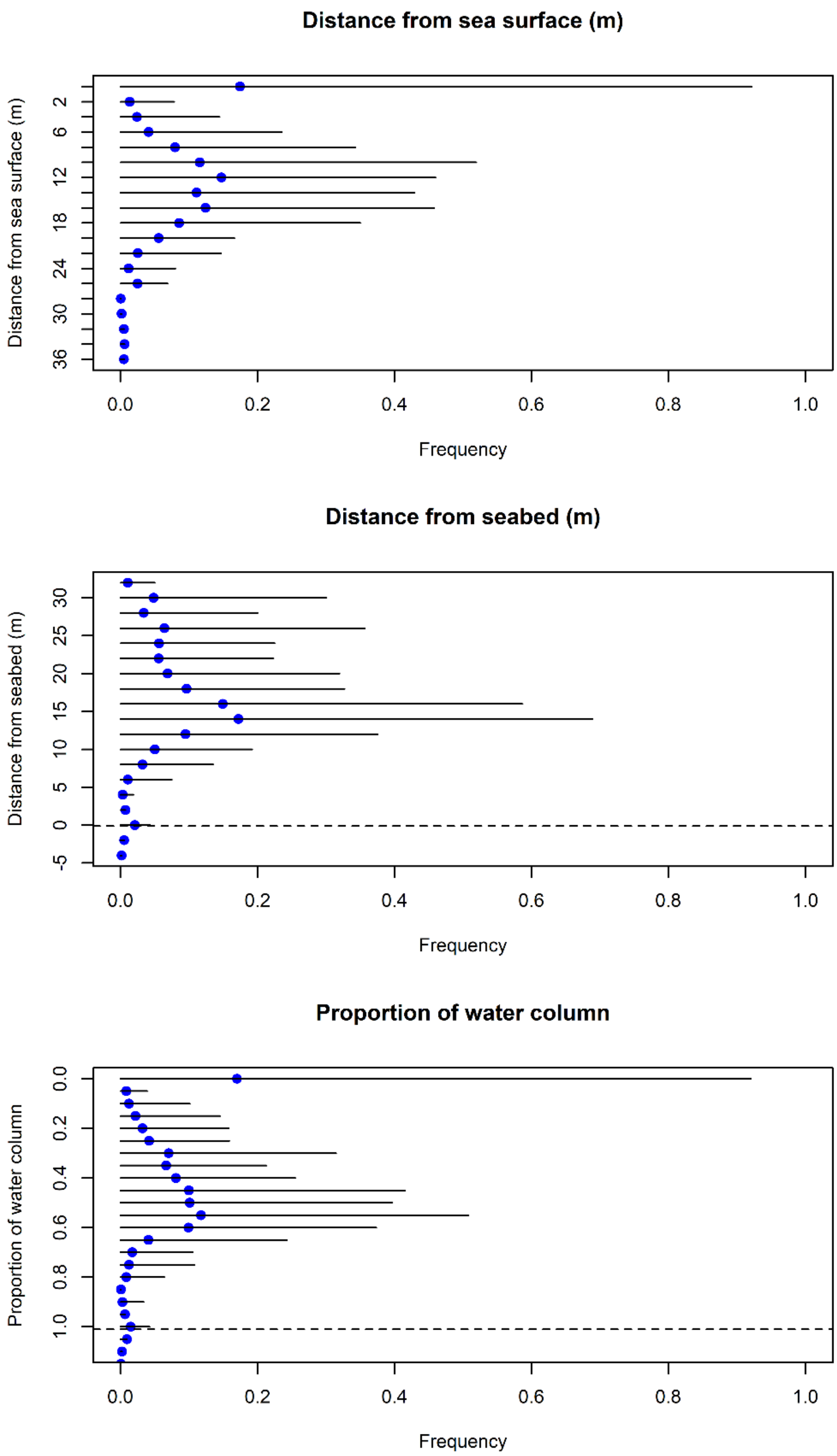

Figure 5: Distribution of the use of the water column by seals within a narrow tidal channel. The upper panel shows the use when expressed as depth from the surface (m) and shows peaks in use around the surface and at approximately 12 m distance from the surface. The middle panel shows the use when expressed as a distance from the seabed (shown by the dashed line) and shows the peak in use was at approximately 14 m from the seabed. The lower panel shows the use when expressed as a proportion of the water column [between the seabed (shown by the dashed line) and sea surface] and shows peaks in use at the surface and towards the middle parts of the water column.

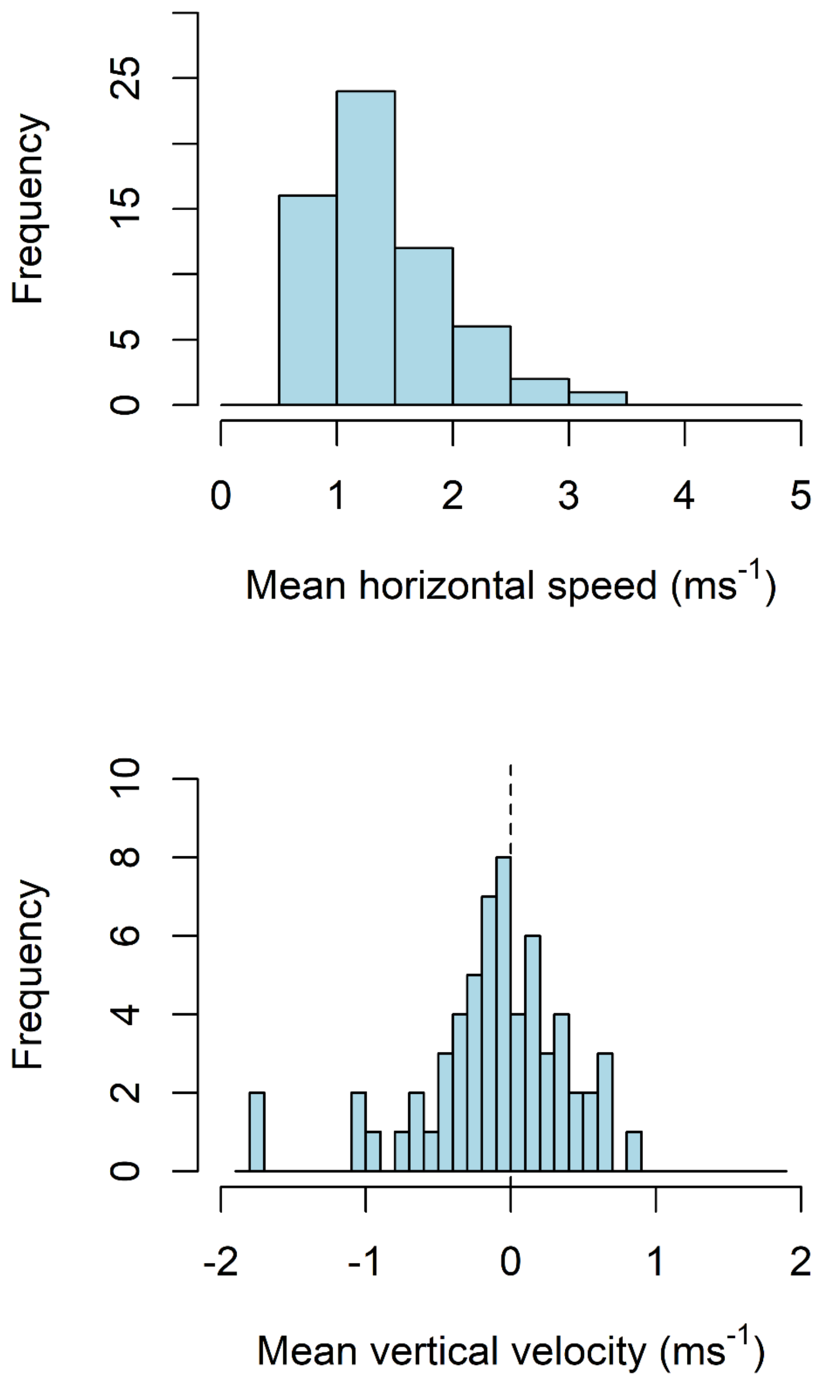

Figure 6: Distribution of median horizontal speeds over ground for each seal track (ms-1) within a narrow tidal channel (upper panel); the mean speeds show a clear peak between 1 and 1.5 ms-1. The lower panel shows the distribution of median vertical velocities of seals (ms-1) within a narrow tidal channel; the mean velocities ranged from -1.76 to +0.88 ms-1 (where a negative or positive value represents a descent or ascent respectively).

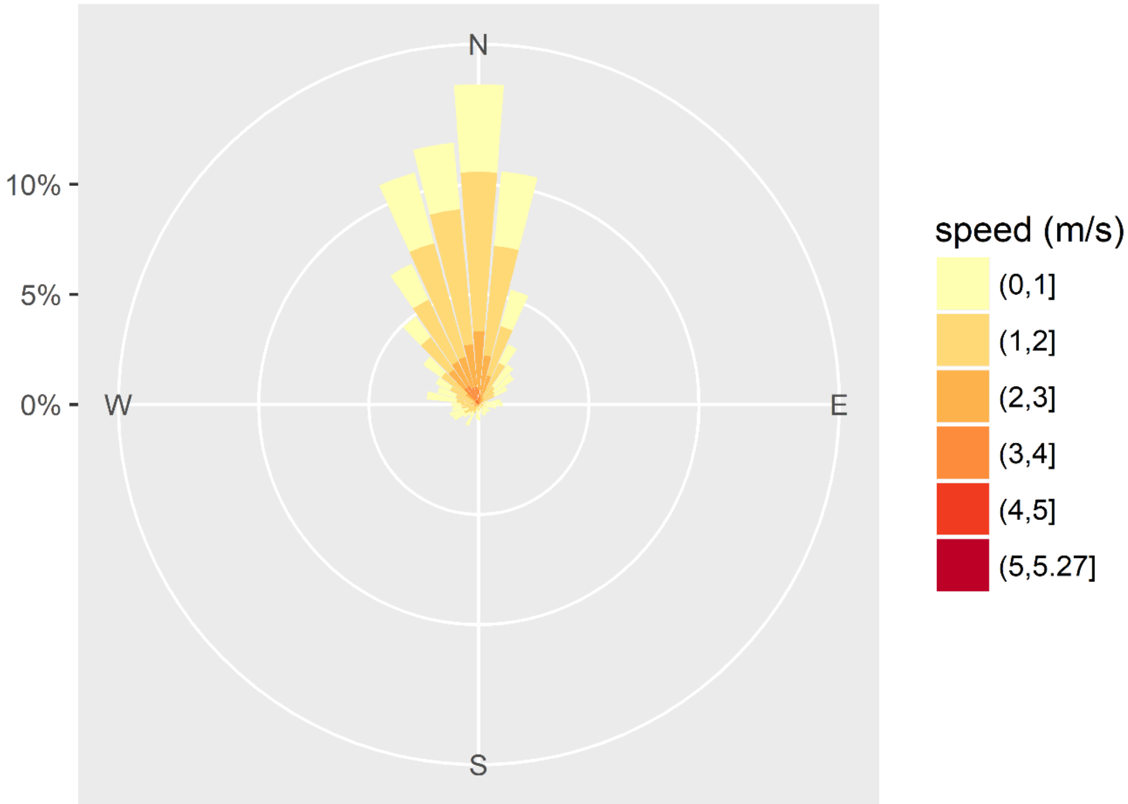

Figure 7: Distribution of the direction of movements of seals within the channel. The segments of the windrose show the proportion of time seals moved in a given direction; and the coloured bands indicate the proportions of movements of each speed. The figure shows a clear peak in the direction of movements between 340° and 10°.