Temporal patterns in habitat use by small cetaceans at an oceanographically dynamic marine renewable energy test site in the Celtic Sea

Cox, SL[1,2*]; Witt, MJ[3]; Embling, CB[1,4]; Godley, BJ[4]; Hosegood, PJ[2]; Miller PI[5]; Votier SC[3]; Ingram, SN[1]

[1]Marine Biology and Ecology Research Centre, Plymouth University, Plymouth, PL4 8AA, UK

[2]Marine Physics Research Group, Plymouth University, Plymouth, PL4 8AA, UK

[3]Environment and Sustainability Institute, University of Exeter, Penryn, TR10 9FE, UK

[4]Centre for Ecology and Conservation, College of Life Sciences, University of Exeter, Penryn, TR10 9FE, UK

[5]Plymouth Marine Laboratory, Prospect Place, Plymouth, PL1 3DH, UK

*Corresponding author: slcox417@gmail.com

Abstract

Shelf-seas are highly dynamic and oceanographically complex environments, which likely influences the spatio-temporal distributions of marine megafauna such as marine mammals. As such, understanding natural patterns in habitat use by these animals is essential when attempting to ascertain and assess the impacts of anthropogenically induced disturbances, such as those associated with marine renewable energy installations (MREIs). This study uses a five year (2009-2013) passive acoustics (CPOD) dataset to examine the use of an oceanographically dynamic marine renewable energy test site by small cetaceans, dolphins (unspecified delphinids) and harbour porpoises *Phocoena phocoena*, in the southern Celtic Sea. To be able to examine how temporal patterns in habitat use across the site related to oceanographic changes occurring over broad seasonal scales as well as those driven by fine scale (bi-weekly) localised processes (that may be masked by seasonal trends), separate analyses were conducted using (1) all daily animal detection rates spanning the entire five year dataset and (2) daily animal detection rates taken only during the summer months (defined as mid-June to mid-October) in 2010 (when continuous monitoring was carried out at multiple discrete locations across the site). In both instances, generalised additive mixed effects models (GAMMs) were used to link detection rates to a suite of environmental variables representative of the oceanography of the region. We show that increased harbour porpoise detection rates in the late winter/early spring (January-March) are associated with low sea surface temperatures (SST), whilst peaks in dolphin detection rates in the summer (July-September)

coincide with increased SSTs and the presence of a tidal-mixing front. Moreover, across the summer months of 2010, dolphin detection rates were found to respond to small scale changes in SST, possibly reflective of a preference for the stratified waters immediately offshore of the front. Together, these findings suggest that habitat use by small cetaceans within shelf-seas is temporally variable, species specific and likely driven by complex bottom-up processes. As such, the effective conservation management of shelf-seas requires that we understand the dynamic complexities of these systems and the species that inhabit them. In particular, we emphasise the need for a good understanding of the natural drivers of habitat use by marine megafauna before the potential impacts of anthropogenically induced disturbances, such as those associated with the construction, maintenance and operation of MREIs, can be assessed.

Keywords: Marine predator · Habitat use · Fronts · Passive acoustics · Marine megafauna · Marine mammals · Dolphins · Harbour porpoises *Phocoena phocoena* · Common dolphins *Delphinus delphis* · Oceanography · Marine renewable energy

1.0 Introduction

Mid to high latitude shelf-seas are frequently subjected to a multitude of anthropogenic pressures, many of which are impacting the abundances, behaviours and distributions of marine megafauna such as marine mammals (Pirotta et al. 2013, Pirotta, Brookes, et al. 2014, Lewison et al. 2014, McCauley et al. 2015). In recent years, marine renewable energy installations (MREIs) have received a lot of attention owing to the potential for these structures to disrupt and/or disturb the habitats of these animals (Gill 2005, Inger et al. 2009, Grecian et al. 2010, Witt et al. 2012). However, assessing and mitigating against the impacts of this may be confounded by the highly mobile nature of many marine megafauna alongside the dynamic structures of the systems they exploit (Scales, Miller, Hawkes, et al. 2014, Benjamins et al. 2015). As such, to be able to adequately inform regional marine planning procedures, a good understanding of the processes that drive spatio-temporal variability in habitat use by these animals is required (Shields et al. 2009, Scott et al. 2014, Waggitt & Scott 2014).

Mounting evidence suggests many marine megafauna concentrate in localised foraging regions (Hastie et al. 2004, Sydeman et al. 2006, Weimerskirch 2007), the situations of which are driven through bottom-up oceanographic processes that increase prey accessibility (Russell et al. 1999, Vlietstra et al. 2005, Embling et al. 2012). Many of these processes vary temporally in their occurrence, with concomitant consequences on the availability of the associated prey resources that attract marine megafauna (Van der Kooij et al. 2008, Embling et al. 2012, 2013, Cox et al. 2013). For example, regions of stratification (Hunt & Harrison 1990, Scott et al. 2010, Cox et al. 2013)

develop seasonally during the spring and summer, when increased solar irradiation heats surface waters sufficiently so as to overcome tidal and wind driven turbulent mixing (Pingree et al. 1976, Pingree & Griffiths 1978). This drives the formation of tidal-mixing fronts (Begg & Reid 1997, Durazo et al. 1998, Jahncke et al. 2005), which mark the transitional zones between resultant stratified offshore waters and permanently mixing inshore coastal waters (Simpson & Hunter 1974). The positions and strengths of these features may additionally alter over more localised scales with changes in turbulent mixing with the spring-neap tidal cycle and passing storm events (Nahas et al. 2005, Pisoni et al. 2015). As such, the use of oceanographically dynamic areas by marine megafauna may vary over both large (seasonal) and short (bi-weekly/weekly) temporal scales, which will influence exposure to localised anthropogenically induced disturbances. Moreover, failing to account for natural patterns in habitat use may obfuscate behavioural changes in response to such disturbances (e.g. the construction, maintenance and operation of many MREIs; Dolman & Simmonds 2010, Bailey et al. 2014).

Studies of marine megafauna are often limited by the logistics and constraints of data collection. In particular, a number of challenges exist when attempting to examine habitat use by small cetaceans such as dolphins and porpoises, which are not only highly mobile but also inconspicuous in their behaviours (e.g. spending long periods of time diving; Barlow et al. 2001, Sveegaard et al. 2011), and may be particularly vulnerable to disturbance from MREIs (Harwood & King 2014). However, these species are often extremely vocal enabling passive acoustic techniques to offer effective alternatives (Philpott et al. 2007, Pirotta, Brookes, et al. 2014, Pirotta, Thompson, et al. 2014) to labour intensive observational methods such as boat and land based surveying. Whilst the spatial coverage of these moored devices is often limited to within a few hundred metres of a deployment's location (dependent upon ambient noise levels), the ability to continuously log activity over temporal periods lasting several months makes these instruments particularly well suited to long term studies at point locations, such as those typical in MREI site assessments.

The overall aim of this study was to examine temporal patterns in the use of an offshore shelf-sea site in the southern Celtic Sea (Figure 1) by vocalising small cetaceans, harbour porpoises *Phocoena phocoena* and dolphins (unspecified delphinids). This site was selected for the study because (1) it is subject to seasonal stratification and the formation of a dynamic tidal-mixing front in the summer (Pingree 1975, Pingree & Griffiths 1978), and (2) it is the location of a pre-operational marine renewable wave energy test site. Daily detection rates of dolphins and harbour porpoises were obtained via a five year period of passive acoustic monitoring across the site, and examined in relation to a suite of environmental variables, sourced via a combination of satellite remote-sensing and numerical modelling. So as to be able to resolve how temporal patterns in

habitat use across the site relate to oceanographic changes occurring over broad seasonal scales as well as those driven by fine scale (bi-weekly) localised processes (that may be masked by seasonal trends), separate analyses were conducted using (1) all daily animal detection rates spanning the entire five year dataset and (2) daily animal detection rates taken only during the summer months (defined as mid-June to mid-October; Figure 2) in 2010 (when continuous monitoring was carried out at multiple discrete locations across the site; Figure 3).

2.0 Methods

2.1 Study site and species

The study site encompasses an area of roughly 12km by 3km ($\sim$40km^2), and is located in waters of between 40 and 50m depth around 25km offshore of the north Cornwall coast (Figure 1). The site is characterised by the presence of a dynamic tidal-mixing front during the summer months, the formation of which is driven by the thermal stratification of deeper offshore waters (Figure 2; Simpson & Hunter 1974). The location of this front varies through the summer, cycling the area in which the study site is located through periods when the water column is mixing or stratified (Figure 4; Cox 2016). The region experiences a semidiurnal tide. Currents flow in a predominantly east-northeast direction during the flood and west-southwest direction during the ebb (Cox 2016). Maximum current speeds range from around 0.5ms^{-1} during neap conditions to over 1.2ms^{-1} during spring conditions (Cox 2016).

Harbour porpoises are commonly observed within the surrounding region (Hammond et al. 2002, Leeney et al. 2008, 2011) alongside common dolphins *Delphinus delphis* (Hammond et al. 2002, Leeney et al. 2008, 2011), which have additionally been recorded on several occasions directly within the study site (Cox 2016). Regional sightings of Risso's dolphins *Grampus griseus* and bottlenose dolphins *Tursiops truncatus* are also known to occur, although these are generally less frequent (Leeney et al. 2011, Cox unpublished data) or concentrated in nearshore coastal areas away from the study site (Pikesley et al. 2012). Few known studies exist on the prey distributions and preferences of cetaceans in the Celtics Sea. Of the species linked to harbour porpoise and dolphin diets elsewhere, the region is known as a spawning ground for cod *Gadus morhua* and whiting *Merlangius merlangus* during spring, and sprat *Sprattus sprattus* during late spring/summer (Coull et al. 1998, Santos & Pierce 2003, Murphy et al. 2013). Additionally, the outer region of the continental shelf hosts spawning mackerel *Scomber scombrus* from May to August afterward of which, despite a mass population migration to northern North Sea feeding grounds, there is some limited evidence to suggest a partial movement into the waters around the South West of England in the summer/autumn (Coull et al. 1998, Iversen 2002, Jansen & Gislason 2013).

2.2 Passive acoustic monitoring

Acoustic loggers (CPODs, Chelonia Ltd, UK) were deployed (originally as part of a marine renewables impact assessment) across the study site, between September 2009 and December 2013. Devices were deployed at five discrete recording stations (Figure 1) separated by a distance of between three and four kilometres (omnidirectional detection ranges of CPODS are ~400m for harbour porpoise and ~500m-1km for dolphins; www.chelonia.co.uk, Philpott et al. 2007). Each device was positioned vertically in the water column, at mid-water depths of ~15m from the seabed, via a mooring system comprised of a single rope that ran between two surface buoys and was weighed down at the seabed by two anchor chains, each of which was positioned immediately below the location of a surface buoy, to create a U type profile. A device was attached to a line that rose from the centre of the portion of the submerged rope that ran parallel to the seabed between the two anchor chains

CPODs continuously monitor the 20-160 kHz frequency range for potential cetacean echolocation clicks. For each click detected they log the centre frequency, frequency trend, duration, intensity and bandwidth. Once recovered, data were downloaded and processed using version 1.054 of the custom CPOD software (www.chelonia.co.uk). This software differentiates between dolphin and porpoise clicks as well as other noise sources, such as sonar, using the Kerno classifier (Chelonia Ltd 2013a) that assigns a level of confidence for each detection classification as low, medium or high. To ensure data quality, our analyses only included click trains classified as medium or high, all of which were manually screened for false positives using the CPOD software (Chelonia Ltd 2013b).

Data were exported as detection positive hours per day (DPH; temporal scale chosen to minimise the influence of non-vocalising periods), separately for harbour porpoises and dolphins (unspecified delphinids as it is not currently possible to distinguish between associated species using CPODs). In addition to dolphin and harbour porpoise DPHs, details of the CPOD's operating performance were also exported as the percentage logging time lost per day (to provide information of times when the CPOD stopped operating due to an overload of noise from vessel traffic and/or tidally/weather generated turbulence) and the angle of the device in the water (that may vary with water current speeds), both of which can influence the detection capabilities of a device.

2.3 Environmental data

Dolphin and harbour porpoise DPHs were initially modelled against day of year (model parameter *DayOfYear*) to investigate how trends in occurrence varied seasonally. We then explored how these

temporal patterns were influenced by both broad scale and localised oceanographic processes by investigating relationships between cetacean DPHs and a suite of environmental parameters that characterised the bio-physical conditions across the five deployment stations. These included sea surface temperature (SST, model parameter *SST*), surface chlorophyll *Chlorophyll*, distance to closest front *Fdist*, across-site frontal activity *Gdens*, and relative position in the spring-neap cycle *SpringNeapCycle*.

2.3.1 Sea surface temperature (SST) and chlorophyll

SST was included to determine the influence of the regions seasonal warming and thermal stratification (approximated by an increase in surface waters) on cetacean habitat use. Moreover, a bi-weekly cycle of water mixing with the spring-neap cycle (Simpson & Sharples 2012) during the summer months (June-Oct) could alternate the five recording stations between periods when the water column was stratified (approximated by high surface temperatures) or mixing (approximated by comparatively lower surface temperatures) which may influence patterns in cetacean presence across the site (Figure 3). Surface chlorophyll was included to investigate links between marine predators and primary productivity (Louzao et al. 2006, Scott et al. 2010) that could be indicative of tight coupling between trophic levels.

SST, *SST*, was taken from advanced very high resolution radiometer (AVHRR) data, and surface chlorophyll-a, *Chlorophyll*, from Aqua-MODIS standard chlorophyll (OC3) data. These data were provided as weekly (seven day) composite maps with a spatial resolution of ~1.2km^2/pixel by the NERC Earth Observation Data Acquisition and Analysis Service (NEODAAS, Plymouth, UK). Data were sourced from the pixel corresponding to the location of each deployment station, and time matched using the central date of a seven day composite.

2.3.2 Front metrics

To determine the importance of the seasonally forming tidal-mixing front to small cetaceans in this area, composite front mapping techniques (Miller 2009, Scales, Miller, Embling, et al. 2014) were used to summarise thermal frontal activity across the five stations into two metrics: (1) front gradient intensity, *Gdens*, as a measure of the strength of frontal activity occurring directly at each of the five stations, and (2) distance to closest front, *Fdist*, as a measure of the distance between each of the five stations and the closest simplified front (Figure 3).

SST (converted from raw AVHRR infrared data) was mapped across the Celtic Sea at a spatial resolution of ~1.2km^2/pixel. Thermal fronts were then detected in each map using single image edge detection (SIED; Cayula & Cornillon 1992) with a temperature difference threshold of 0.4^{o}C

across the front (Miller 2009). *Gdens* was taken as the spatially smoothed average temperature gradient across all frontal pixels detected over a seven day period to give a continuous distribution of frontal intensity. A Gaussian filter with a width of five pixels was used for the spatial smoothing (Scales, Miller, Embling, et al. 2014). *Fdist* was taken as the distance from any point to the closest simplified front. Simplified fronts were defined using a clustering algorithm to identify continuous contours through the strongest frontal pixels on the spatially smoothed *Gdens* front map (Scales, Miller, Embling, et al. 2014). Data were sourced from the pixel corresponding to the location of each deployment station, and time matched using the central date of a seven day composite.

2.3.3 Relative position in the spring-neap cycle

Short term mixing events associated with spring conditions may influence patterns in cetaceans presence across the site (Embling et al. 2010, 2013). This may be due to the energetics associated with navigating turbulent environments (Embling et al. 2010) or because strong turbulent flows can influence prey availability (Embling et al. 2013). Additionally, during the summer months, changes in current strength may cycle the locations of the deployment stations through periods when the water column is stratified (more likely during neap conditions) or mixing (more likely during spring conditions; Pingree 1980, Cox 2016) which may influence the distributions of prey resources and, in turn, those of small cetaceans.

Offshore tidal elevation predictions were taken from the POLPRED offshore tidal computation software version 2.4.1.0 (National Oceanography Centre, Liverpool, UK) at 10 minute intervals continuously from January 2009 to January 2015 for a single central location of 50.36 N, 5.61 W. From these, daily changes in tidal height (daily tidal ranges) were calculated. A bespoke peak finding algorithm, written in MATLAB (2011b), was then used to identify complete neap-spring-neap cycles based on an oscillation of these daily tidal ranges. An index of relative position in the spring-neap cycle, *SpringNeapCycle*, was taken for each day as the time since the last neap tide (defined as a trough in the daily tidal ranges) divided by the total time between the neighbouring neap tides.

2.4 Statistical analysis

To investigate how trends in occurrence varied seasonally, DPH (response variable) was modelled, for dolphins and harbour porpoises separately, against *DayOfYear* (explanatory variable) using the entire five year dataset. We then explored how these temporal patterns were influenced by both broad scale (seasonal) and localised (bi-weekly/weekly) oceanographic processes by investigating relationships between dolphin and harbour porpoise DPHs and a suite of selected environmental

parameters (explanatory variables): *SST*, *Chlorophyll*, *Gdens*, *Fdist* and *SpringNeapCycle*. Because relationships with fine scale localised oceanographic processes may be masked by those occurring over large seasonal timescales, separate analyses were conducted using (1) the entire five year dataset and (2) daily animal detection rates taken only during the summer months (that ran from the 22nd June until the 20th October; Figure 2) in 2010 (when continuous monitoring at four out of five deployment stations across the site was achieved; Figure 3). The beginning of summer (22nd June) was defined as when SST measurements had increased and frontal activity (as indicated by the two front metrics) intensified (Figure 2). The end of summer (20th October) was defined as when SST began to cool and frontal activity decreased (Figure 2).

Across all analyses we used generalised additive mixed effects models (GAMMs) with a Poisson error structure and log link function, from the mgcv package (Wood 2015) in R version 3.1.2 (R Development Core Team 2014). Explanatory variables were fitted using cubic regression splines, or for *SpringNeapCycle* and *DayOfYear* cyclic splines, with a maximum of five knots. Although links between cetaceans DPHs and *SpringNeapCycle* may vary due to the specifics of a deployment stations location (e.g. bathymetric depth which may influence the intensity of short term mixing events and their associated impacts on prey distribution; Simpson & Hunter 1974), an interaction term could not be tested for between *SpringNeapCycle* and deployment station ID due to convergence issues. Scatterplots, histograms and boxplots of each explanatory variable were generated to check for extreme values and severe non-normality which would violate model assumptions (Zuur et al. 2010). To deal with a heavily skewed distribution, *Chlorophyll* was logged to give *LogChlorophyll*. As GAMMs are sensitive to collinearity between explanatory variables, which can lead to unreliable parameter estimates (Zuur et al. 2009), we tested the influence of each explanatory variable on dolphin and harbour porpoise DPHs in separate standalone models. This also minimised the number of data rows lost due to missing data values, the locations of which were often not consistent between variables (e.g. *SST* and *LogChlorophyll*).

High ambient click-like noise levels, caused by vessel traffic and/or strong water currents (attributable to large spring tides and passing weather events), can cause the CPOD to shut down temporarily to avoid overloading its memory with excessive noise recordings. Although this occurs at the scale of minutes (i.e. detection resumes at the onset of the next minute), prolonged noise events may cause the device to shut down for periods exceeding several minutes. As such, bias in detection rates may be introduced as a result of days when the CPOD was not fully operational. To minimise the effect of this we excluded those days when the time lost (i.e. the time the device shut down) across a day was not equal to zero. Across the entire year this resulted in the removal of 26.5% of recordings taken during spring conditions (*SpringNeapCycle* > 0.25 and < 0.75) and 17.8% of

recordings taken during neap conditions ($SpringNeapCycle \leq 0.25$ and ≥ 0.75) leaving a total of 770 and 801 recording days during spring and neap conditions respectively. Of the summer observations, 10.8% of recordings taken during spring conditions and 3.4% taken during neap conditions were excluded leaving 215 and 228 recording days during spring and neap conditions respectively.

To account for differences in detection capabilities between CPOD deployments (that may arise from inconsistencies in instrumentation, mooring configuration and/or location specifics; Thomsen et al. 2005), a random effect of deployment ID was incorporated across all analyses. Exploratory investigation of the data revealed the presence of distinct residual serial auto-correlation, and so a nested continuous temporal correlation structure was incorporated across all analyses. Several correlation structures were tested (e.g. exponential, rational quadratic, autoregressive) and the most appropriate selected through inspection of residual plots (Zuur et al. 2009). For the analysis conducted using the entire five year dataset, additional random effects of month and year were included to account for disparities in monitoring effort (Figure 3).

To ensure the data were not over-fitted, in addition to the use of *p*-values, conservative *k*-folds cross validation was used to compare between standalone models including and excluding each explanatory term/variable (Hastie et al. 2008, Cleasby et al. 2015). Data were divided into five continuous segments for each device deployment. Four subsets were then used as a training dataset to which each model was fitted both with and without the inclusion of the explanatory term/variable being tested. The coefficients from the fixed components of these models were then used to make predictions on the remaining, validation, data subset. This process was repeated until all data subsets had, in turn, been used as the validation dataset. A *k*-fold cross-validation (KCV) statistic was then calculated for each model as the sum of the total difference squared between the observed and predicted values of each validation dataset. An explanatory term/variable was retained if its inclusion decreased the KCV statistic and it had a *p*-value < 0.05 (as estimated by the model fitted using the entirety of the dataset).

Models were evaluated by plotting normalised residuals against all tested explanatory variables, month, year, angle of device, station ID, CPOD ID and deployment ID to check for any patterns indicative of a violation of model assumptions. Fitted versus predicted values were inspected to check for satisfactory model fit and auto correlation (ACF) plots were generated to check that residual temporal auto-correlation had been accounted for (see supplementary materials S1; Zuur et al. 2009). The deviance explained by the inclusion of an explanatory variable in the fixed

component of the model was taken as the percentage reduction in residual deviance from a null (intercept only) fixed model component (i.e. random effects between models were maintained).

3.0 Results

Passive acoustic monitoring was carried out at a minimum of one of the five deployment locations continuously from September 2009 to December 2013, excluding four gaps of greater than a month between (1) January to March, 2010, (2) January to March, 2012, (3) May to July, 2012, and (4) November, 2012 to February, 2013 (Figures 2 & 5). This yielded a total of 2023 days (48,552 hours) of data, on 1062 unique dates. Dolphin and harbour porpoise presence was recorded on 20.7% and 81.1% of these days respectively (Figure 5).

3.1 Seasonal variation in the occurrence of small cetaceans across the entire year

Dolphin detection rates ranged from 0 to 8 DPH and peaked during the summer, between July and September, across all years ($p < 0.001$, Table 1, Figures 5 & 6). During these months DPH were several times higher those observed during the remainder of the year (e.g. ~0.8 vs 0.1 DPH in August and March respectively; Figure 6). DPH increased linearly with *Gdens* ($p < 0.01$, Table 2, Figure 7) and *SST* ($p < 0.001$, Table 2, Figure 7) which explained 2% and 15.6% of deviance respectively. DPH was negatively correlated with *Fdist* ($p = 0.01$, Table 2, Figure 7) which explained 3.6% of deviance.

Harbour porpoise detection rates ranged from 0 to 24 DPH and were generally higher than those observed for dolphins across the entire year (predicted DPH ranging from one to eleven vs zero to one respectively; Figures 5 & 6). DPH peaked from late December to early March ($p < 0.001$, Table 1, Figures 5 & 6), and was negatively correlated with *SST* ($p < 0.001$, Table 2, Figure 8) which explained 14.4% of deviance. DPH varied significantly with *SpringNeapCycle* ($p < 0.001$, Table 2) although the deviance explained was low (1%). DPH were increased during neap conditions (Figure 8). This relationship was consistent between deployment stations.

3.2 Cetacean responses to fine-scale fluctuations in oceanographic conditions across the site

Detection rates of both species varied, both temporally and spatially (between monitoring stations), across the summer of 2010 (Figure 5). Dolphin DPH increased, by almost double, when *SST* was increased ($p = 0.01$, Table 2, Figure 9) which explained 6.6% of deviance. Variations in harbour porpoise DPH were not explained by any of the environmental variables.

4.0 Discussion

Our study provides new insight toward the temporal use by small cetaceans of a dynamic shelf-sea site subject to thermal stratification and the manifestation of a tidal-mixing front across the summer months. Using a longitudinal dataset of continuous acoustic detections of cetaceans across the site we showed a clear seasonal pattern in the use of the area that differed between species/groups. Increased harbour porpoise detection rates in the late winter/early spring (January-March) were associated with lower SSTs. In contrast, dolphin detection rates peaked in the summer (July-September) and coincided with increased SST and high frontal activity. Moreover, across the summer months of 2010, dolphin detection rates were found to respond to localised changes in SST. Together these findings suggest that habitat use by small cetaceans within shelf-seas is temporally variable, species specific and possibly driven by complex bottom-up processes. This has important implications for the methods used to assess the potential impacts of MREI construction and operation.

4.1 Species specific seasonal fluctuations in habitat use and links to physical oceanography

Seasonality in site use by small cetaceans has been identified across a number of regions (Skov & Thomsen 2008, Simon et al. 2010, Sveegaard et al. 2011). For example, in the Baltic Sea, populations of harbour porpoises are known to move between key sites (Sveegaard et al. 2011), the use of which varies between the summer and winter months (Sveegaard et al. 2012). Our results support such observations and show that at our study site off the north Cornwall coast, the occurrence and rate of both dolphin and harbour porpoise detections are also seasonally dependent. The high energetic demands of these species requires them to spend a high proportion of their time foraging (Williams et al. 2001, Lockyer et al. 2003), and this has been demonstrated in links between areas of high use and frequent foraging activity (Hastie et al. 2004). As such, temporal changes in their distributional patterns are likely to reflect those of their preferred prey which may, in turn, be driven bottom-up by dynamic oceanographic processes.

Harbour porpoises are particular known to feed frequently due to their small size and high energetic requirements, which together reduce their ability to withstand periods of starvation (Kastelein et al. 1997). As such, porpoises are often opportunistic in their foraging strategies and feed on a diversity of both pelagic and demersal fish (Santos & Pierce 2003, Santos et al. 2004). This flexibility means a wide variety of habitats may be suitable for foraging, and that harbour porpoises were present in the area for at least one to two DPH throughout most of the year (detections were recorded on 81% of days; Figures 4 & 5) reflects this. However, elsewhere peaks in porpoise site use are thought to correspond to periods when demersal fish are present suggesting these prey types are preferred (Sveegaard et al. 2012). Peaks in the use of our study site during early spring, when cod and

whiting are known to spawn in the region (Coull et al. 1998), support this and suggest that the tidal-mixing front and the warmer stratified waters of its offshore side are not particularly important habitats for harbour porpoises in this area despite some limited evidence of linkages to these habitats elsewhere (Weir & O'Brien 2000). Avoidance of, or competitive exclusion by, other species feeding at these features (e.g. dolphins and specifically bottlenose dolphins; Spitz et al. 2006, MacLeod et al. 2007) may partially influence this, although given harbour porpoises were generally still present, for at least one to three DPH (Figures 5 & 6), on the days when dolphins were detected suggests the effect of this is not substantial. Indeed, the inclusion of presence of other species as an explanatory variable in the entire dataset harbour porpoise analysis was not found to be a significant predictor of variation in harbour porpoise DPH.

In contrast to patterns in harbour porpoise site use, dolphins (most likely common dolphins, which are thought the most prevalent species present in the region; Cox unpublished data) were found almost exclusively during summer (on 21% of days across the year occurring primarily from June to October), when frontal activity and SSTs were high, reflective in part of the thermal preferences of the predominant species expected (Lambert et al. 2011). Common dolphins are known to use a number of active and highly cooperative foraging behaviours, and when a selection of prey resources are available, are thought to preferentially target energy rich pelagic fish such as mackerel (Meynier et al. 2008). These mid-trophic level species are particularly well suited to front associated habitats, where enhanced levels of zooplankton are thought to attract the smaller forage fish they feed on (Sims & Quayle 1998, Russell et al. 1999, Wall et al. 2009). As such, the suitability of an area for dolphins may be driven, bottom up, by the influence the seasonal presence of frontal features has on the timing of the use of a specific region by their prey (Kaltenberg et al. 2010). Our observations alongside those made in Wales (Goold 1998), where changes from high to low dolphin abundances between September and December were attributed to the presence and break-up of a corresponding front, support this.

4.2 Dolphin responses to localised changes in oceanographic conditions during the summer

A large-scale seasonal change in dolphin site use with frontal activity was not reflected in the analysis that included data solely from the summer months of 2010. This may be a result of the limited spatio-temporal resolution of the front metrics (weekly composites with some degree of smoothing may not be sufficient to adequately capture the dynamic characteristics of these features at localised scales), or because regional changes in prey densities that coincide with, but are not definitively driven by, frontal activity mean dolphins may not track the exact position of the front in this region. Alternatively, the prey resources that marine megafauna exploit around fronts might

not occur directly at the surface signatures of these features and instead be associated with transient processes occurring within a surrounding buffer zone. The tidal-mixing front within our survey region is highly dynamic and shifts laterally upwards of 10km over a time period spanning several days (Figure 3), which has been shown to coincide with bi-weekly peaks in sub-surface primary productivity that are thought to be related to periods of episodic water mixing and stratification with the spring-neap cycle (Cox 2016). These peaks in productivity have been linked to the fine-scale summer distributions of common dolphins in the region (Cox 2016), and are generally found within the thermocline of waters with high SSTs on the stratified side of a front (Franks 1992). Whilst surface chlorophyll measurements obtained via satellite remote-sensing would not have detected these patches of sub-surface productivity, it was found that the occurrence of dolphin detections increased both when SST was increased.

4.3 The influence of tidal currents at an offshore shelf-sea site

Harbour porpoises showed a weak but statistically significant response to position in the spring-neap cycle, with site use peaking during neap conditions (although note that device shut down during extreme mixing events hindered our ability to examine the importance of large spring tides). Generally, associations between cetaceans and specific tidal conditions have been reported in topographically complex regions that either concentrate (e.g. narrow channels; Pierpoint 2008) or interrupt (e.g. headlands, islands and offshore banks; Johnston et al. 2005, Bailey & Thompson 2010, Embling et al. 2012, Jones et al. 2014) current flows in a manner that increases prey availability. However, given our study region is located in a relatively smooth area where tidal flow occurs in parallel with, rather than against, the topographic gradient, mechanistic links with marine megafauna likely differ. Whilst the area may cycle through periods of mixing and stratification with the spring-neap cycle during the summer, the relationship between harbour porpoises and position in the spring neap cycle broke down when only data from the summer months of 2010 were included in analyses. As such, differences in site use between neap and spring conditions, when there are peak current speeds of $0.5ms^{-1}$ versus $1.2ms^{-1}$ respectively, could be related to the energetics involved with navigating more turbulent waters which may be particularly pertinent for harbour porpoises due to their high energetic requirements and small size (Embling et al. 2010).

4.4 Implications for managing marine renewable energy installations (MREIs)

Current best guidelines to assess the potential impacts of MREIs recommend approaches based upon BACI (Before, After, Control, Incident; Carstensen et al. 2006) or gradient (Dahne et al. 2013) designs (Bailey et al. 2014). For these to prove successful, natural patterns in habitat use, that may mask the detection of an impact, need to be delineated (Hewitt et al. 2001, Maclean et al. 2014).

However, the surveying strategies best suited to achieving this are not always clear (REF), although generally site characterisation prior to the introduction of a MREI is required (REF). Findings from this study suggest that site use by harbour porpoises and dolphins in shelf-seas can be highly variable, both through time and in response to dynamic oceanographic processes. As such, we highlight a need for baseline data monitoring conducted over spatio-temporal scales that reflect those of heterogeneity in cetacean site use and environmental variability.

Temporal variability in cetacean presence across the site varied in response to seasonal environmental changes. However, the restricted spatial extent of the deployment stations (~40km^2) in this study (Figure 1) meant we were unable to definitively determine if observed patterns in site use by dolphins were unique to the area and linked to the manifestation of the front, or related to broader regional trends that occur seasonally. To resolve this, ideally a control site would have been situated out with the vicinity of the frontal feature. However, if it is established that correlations between environmental covariates are consistent across years (i.e. temporal trends in *SST*, *Fdist*, and *Gdens* are the same year on year; see supplementary material S2 for correlation plots of explanatory variables used in statistical analyses of this study), changes in the use of a site following the introduction of, for example a MREI, can more confidently be linked to this event provided these correlations/temporal trends are maintained.

Results from our 2010 summer only analyses suggested that in addition to understanding broad seasonal trends in site use, to be able to accurately quantify how the abundances and distributions of cetaceans may be impacted by the introduction and operation of an MREI, an understanding of localised patterns in site use is required. For example, detection rates of dolphins were found to vary dependent upon small fluctuations in SSTs, which varied across the site (Figure 4). This appeared to be related to a cycle of mixing and stratification that accompanied the presence of a dynamic tidal mixing front (Cox 2016). The positioning of the deployment stations relative to this front meant that the ratio of time each station spent in the cool waters on the mixing side of the front compared to the warm waters of its stratified side differed (Figure 4). At the extremities of these, station four experienced mean temperatures across the season of 14.3 ±0.06^{o}C (± standard error) which were 0.7^{o}C lower than those of station one (15.0 ±0.08^{o}C). The impact of these discrepancies in oceanographic conditions meant mean detection rates across the season varied considerably between the two sites: site one averaged 0.61 ±0.08 DPH across the season whilst site four averaged 0.07 ±0.02 DPH, which was almost a tenfold difference. These deployment stations were separated by a distance of ~10km and so this highlights a need for fine-scale baseline monitoring to ensure that the locations at which monitoring devices are deployed are representative of patterns in cetacean use of a site.

As such, the spatio-temporal comparability of BACI control sites alongside point locations along gradient designs should be carefully considered and evaluated with regards to natural patterns in habitat use, particularly in areas where, for example, favourable features, such as tidal-mixing fronts, manifest that are dynamic in their occurrence. In some cases, the impacts of disturbance may be more pronounced at certain times (e.g. certain months and tidal conditions as shown here), whilst the proposed spatial situations of some developments may coincide with foraging hotspot locations (e.g. particular offshore banks and tidal-mixing fronts; Durazo et al. 1998, Stevick et al. 2008). As such, we emphasise the need for a good understanding of the natural drivers of habitat use by marine predators before it can determined how the expansion of anthropogenic activities, such as MREIs, will impact their populations and the ecosystems they occupy.

4.5 Conclusions

This study presents evidence that the use of a dynamic shelf-sea site by small cetaceans is temporally variable over both short (days to weeks) and long (seasonal) timespans. Patterns in habitat use were species specific and coincided with particular oceanographic conditions including changes in SST, frontal activity and tidal currents. Combined, these findings demonstrate that understanding habitat use by mobile marine predators in shelf-sea environments requires a detailed knowledge (at appropriate spatio-temporal scales) of the dynamic complexities of these systems alongside the biology of the species that inhabit them.

5.0 Acknowledgements

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1 **Tables**

2 Table 1. Results from temporal models fitted using the entire five year dataset. The influence of

3 year day *DayOfYear* on dolphin and harbour porpoise detection rates was tested for as a standalone

4 term in models that included a random effect of year and month, alongside deployment ID with a

5 nested continuous auto-regressive temporal correlation structure. The models intercept (standard

6 errors in brackets), estimated degrees of freedom (E.df), parameter coefficient (standard errors in

7 brackets), deviance explained (dev. exp.) and *p*-value are shown. The change in the *k*-folds cross

8 validation (KCV) statistic on the inclusion of each term in the model is also indicated.

	Intercept	E.df.	Coefficient	Dev. exp.	*P*-value	Δ KCV
Dolphins (unspecified delphinids)	-1.31 (0.18)	1	-1.28 (0.52)	3.6%	0.014	-10.7
Harbour porpoises	-1.45 (0.17)	1	0.82 (0.31)	2.1%	0.009	-10.2

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1   Table 2. Results from environmental models fitted using the entire five year dataset. From top to

2   bottom: (a) dolphins (unspecified delphinids) and (b) harbour porpoises *Phocoena phocoena*. Each

3   explanatory variable was tested for as a standalone term in separate models that included random

4   effects of month and year, alongside deployment ID with a nested continuous auto-regressive

5   temporal correlation structure. The models intercept (standard errors in brackets), estimated

6   degrees of freedom (E.df), parameter coefficient (standard errors in brackets), deviance explained

7   (dev. exp.) and *p*-value are shown. The change in the *k*-folds cross validation (KCV) statistic on the

8   inclusion of each term in the model is also indicated.

Environmental variable	Intercept	E.df.	Coefficient	Dev. exp.	*P*-value	Δ KCV
(a) Dolphin species						
Fdist	-1.31 (0.18)	1	-1.28 (0.52)	3.6%	0.014	-10.7
Gdens	-1.45 (0.17)	1	0.82 (0.31)	2.1%	0.009	-10.2
SST	-1.38 (0.18)	1	2.88 (0.40)	15.6%	< 0.001	-58.5
(b) Harbour porpoise						
SST	0.91 (0.10)	2.8	-1.02 (0.30)	14.4%	< 0.001	-1857
SpringNeapCycle	1.05 (0.14)	2.1	NA	1.02%	< 0.001	-66.2

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1 Table 3. Results from 2010 summer (22nd of June to 20th October) only models for dolphins

2 (unspecified delphinids). Each explanatory variable was tested for as a standalone term in separate

3 models that included a random effect of deployment ID with a nested continuous auto-regressive

4 temporal correlation structure. The models intercept (standard errors in brackets), estimated

5 degrees of freedom (E.df), parameter coefficient (standard errors in brackets), deviance explained

6 (dev. exp.) and *p*-value are shown. The change in the *k*-folds cross validation (KCV) statistic on the

7 inclusion of each term in the model is also indicated.

Environmental variable	Intercept	E.df.	Coefficient	Dev. exp.	*P*-value	Δ KCV
SST	-1.25 (0.33)	1.5	1.22 (0.43)	6.59%	0.011	-5.5

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Figure captions
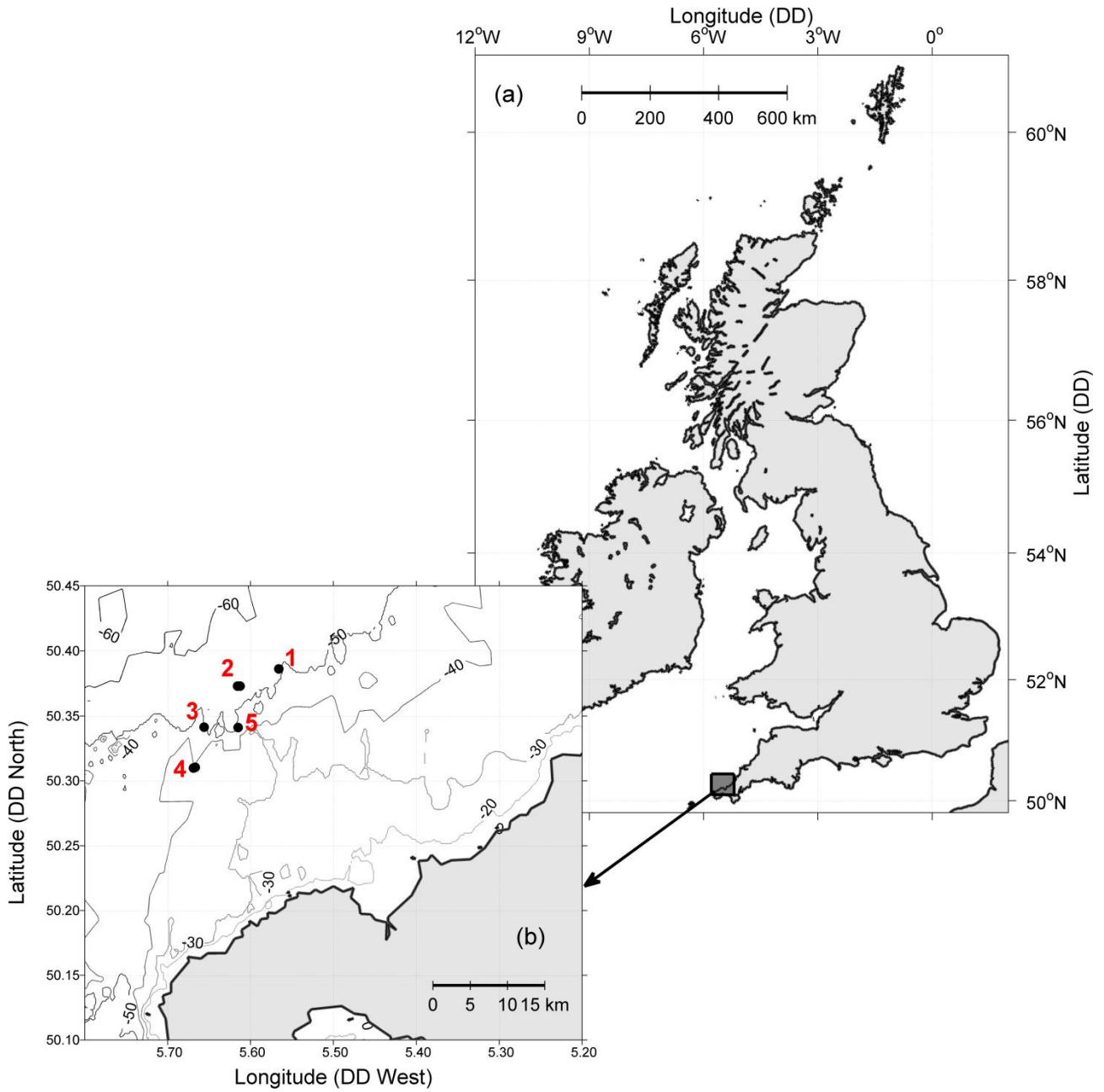
Figure 1. The deployment site. The deployment site: (a) in the context of the UK, and (b) with the positions of the CPODs (black filled circles) and bathymetric contours up to the coastline.
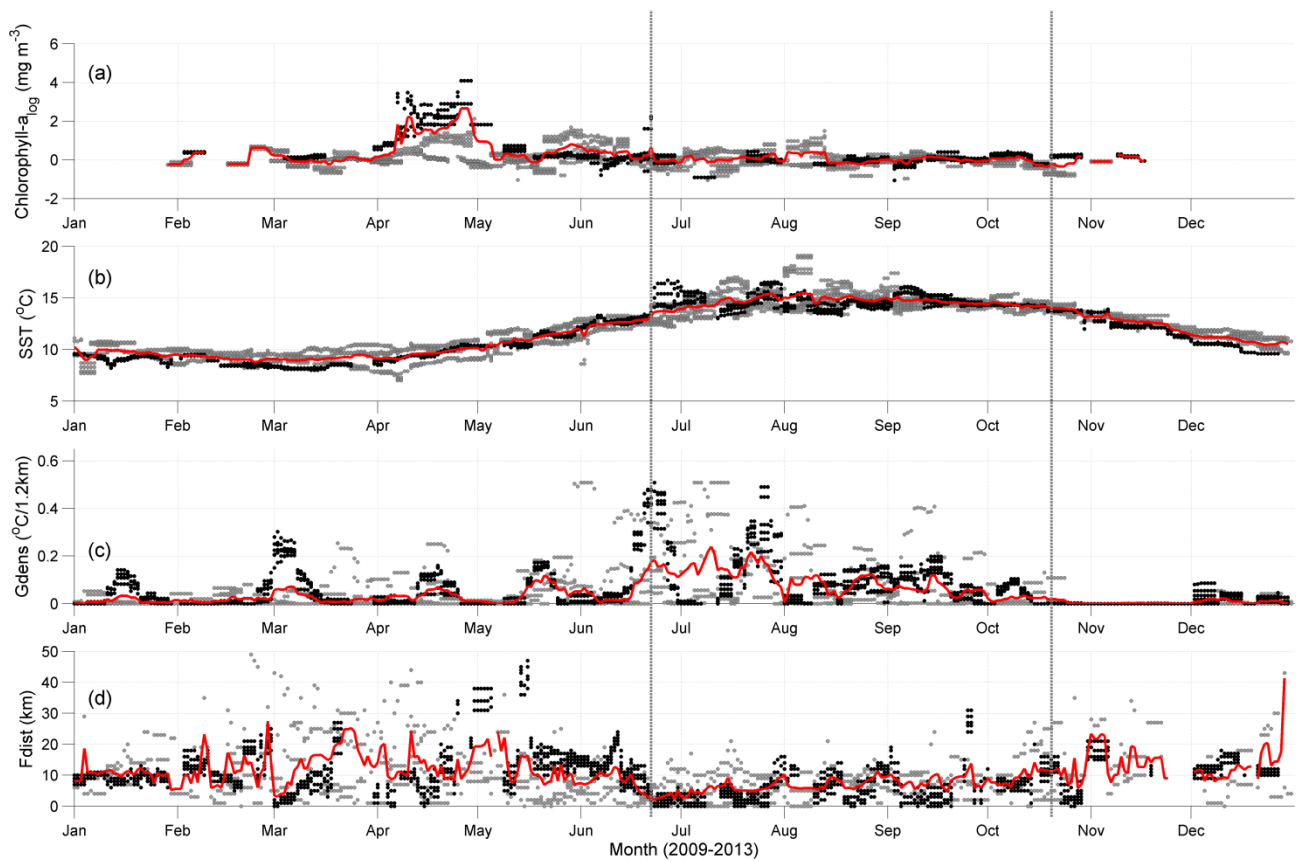
Figure 2. Variation in environmental conditions across the five deployment stations and years. Variation in environmental conditions averaged across the five sites and years is shown in red (raw values are plotted in light grey, and those from 2010 in black). From top to bottom: (a) surface chlorophyll-a *Chlorophyll*, (b) sea surface temperature *SST*, (c) front gradient *Gdens* and (d) distance to closet front *Fdist*. Seasonal variation is noted, with warmer temperatures and increased frontal activity during the summer months between June and October (marked with a dashed line). A peak in surface chlorophyll-*a* in late April indicates the occurrence of the annual spring bloom.
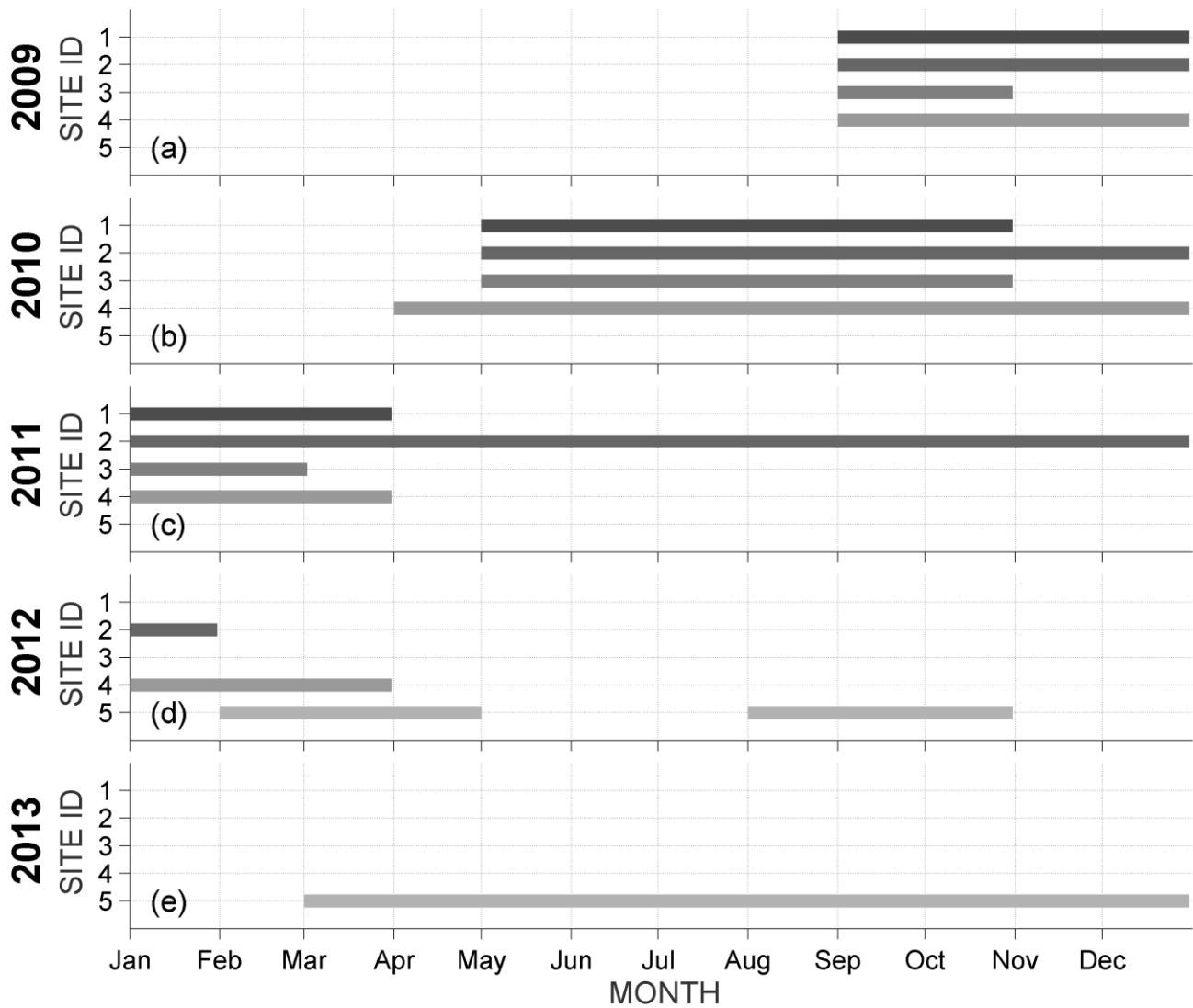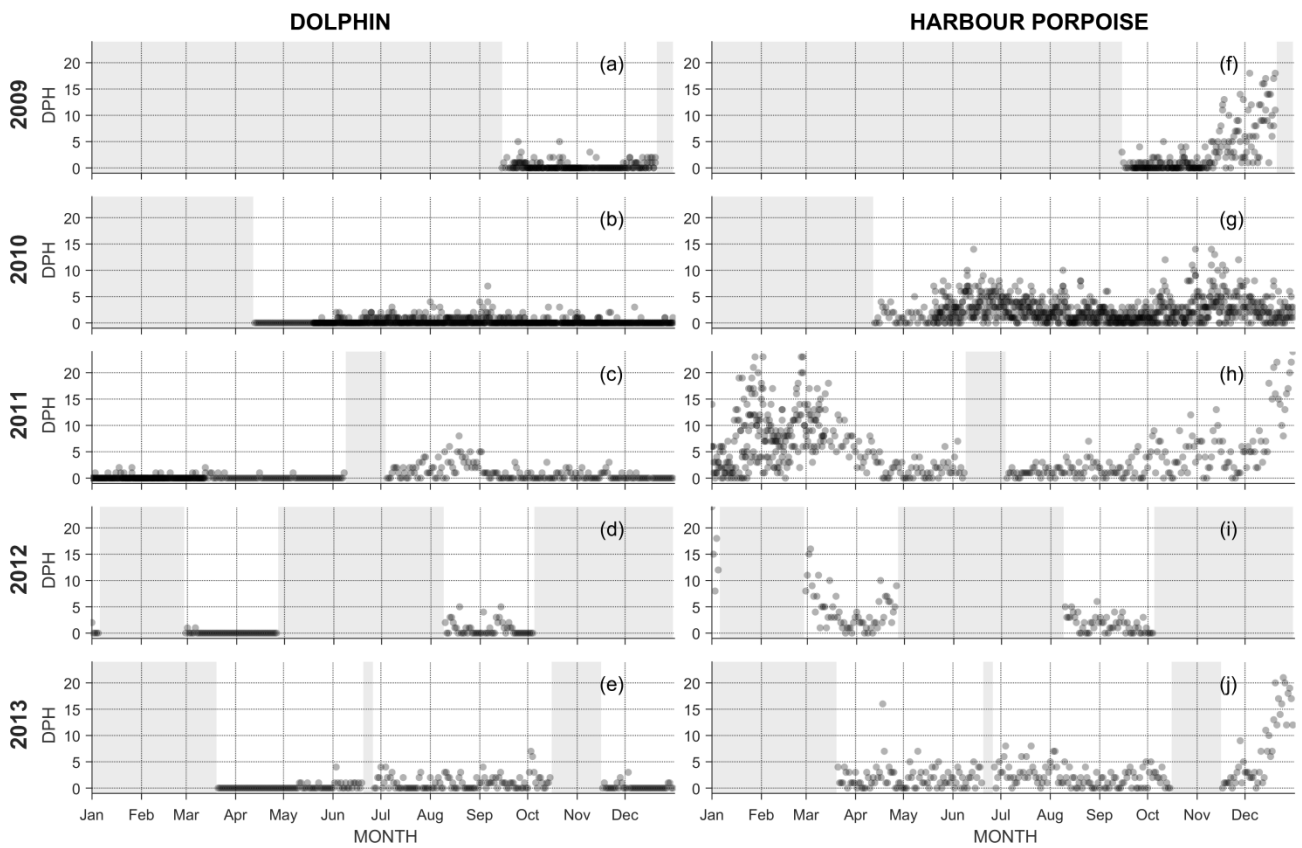
Figure 3. Across summer environmental variability in 2010. Across summer environmental variability in 2010 for (from top to bottom): sea surface temperature *SST* (a:c), Chl-a *Chlorophyll* (d:f), front gradient *Gdens* (g:i) and distance to closest front *Fdist* (j:l). Locations of CPOD deployment sites are shown by black dots with white outlines. Each column corresponds to a different date as indicated: 17th July (a, d, g & j), 1st August (b, e, h & k) and 14th August (c, f, i & l). A cycle of SST warming (approximate for thermal stratification) and cooling (approximate for water mixing) is noted between dates, and as such variation in the position and intensity of the front is evident.

Figure 4. Across summer environmental variability in 2010. Across summer environmental variability in 2010 for (from top to bottom): sea surface temperature *SST* (a:c), Chl-a *Chlorophyll* (d:f), front gradient *Gdens* (g:i) and distance to closest front *Fdist* (j:l). Locations of CPOD deployment sites are shown by black dots with white outlines. Each column corresponds to a different date as indicated: 17th July (a, d, g & j), 1st August (b, e, h & k) and 14th August (c, f, i & l). A cycle of SST warming (approximate for thermal stratification) and cooling (approximate for water mixing) is noted between dates, and as such variation in the position and intensity of the front is evident.

Figure 5. Patterns in the occurrence of dolphins (unspecified delphinids) and harbour porpoises *Phocoena phocoena*. Detection positive hours per day (DPH) of dolphins (a:e) and harbour porpoises *Phocoena phocoena* (f:j) across all device deployments. From top to bottom: 2009 (a & f), 2010 (b & g), 2011 (c & h), 2012 (d & i) and 2013 (e & j). Dolphin occurrence peaks in summer from around July to September, whilst, in contrast, peak detection rates of harbour porpoises occur from late December to March.
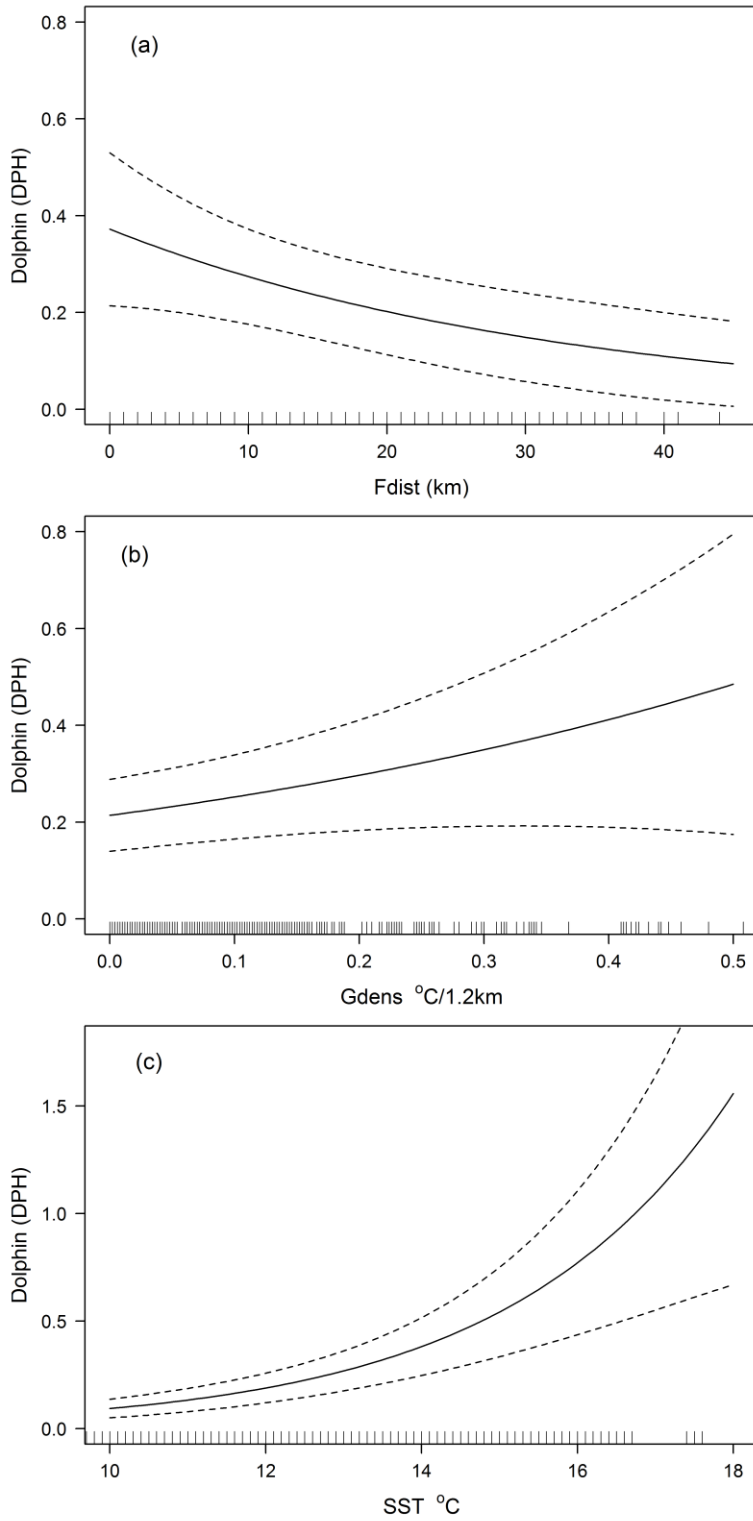
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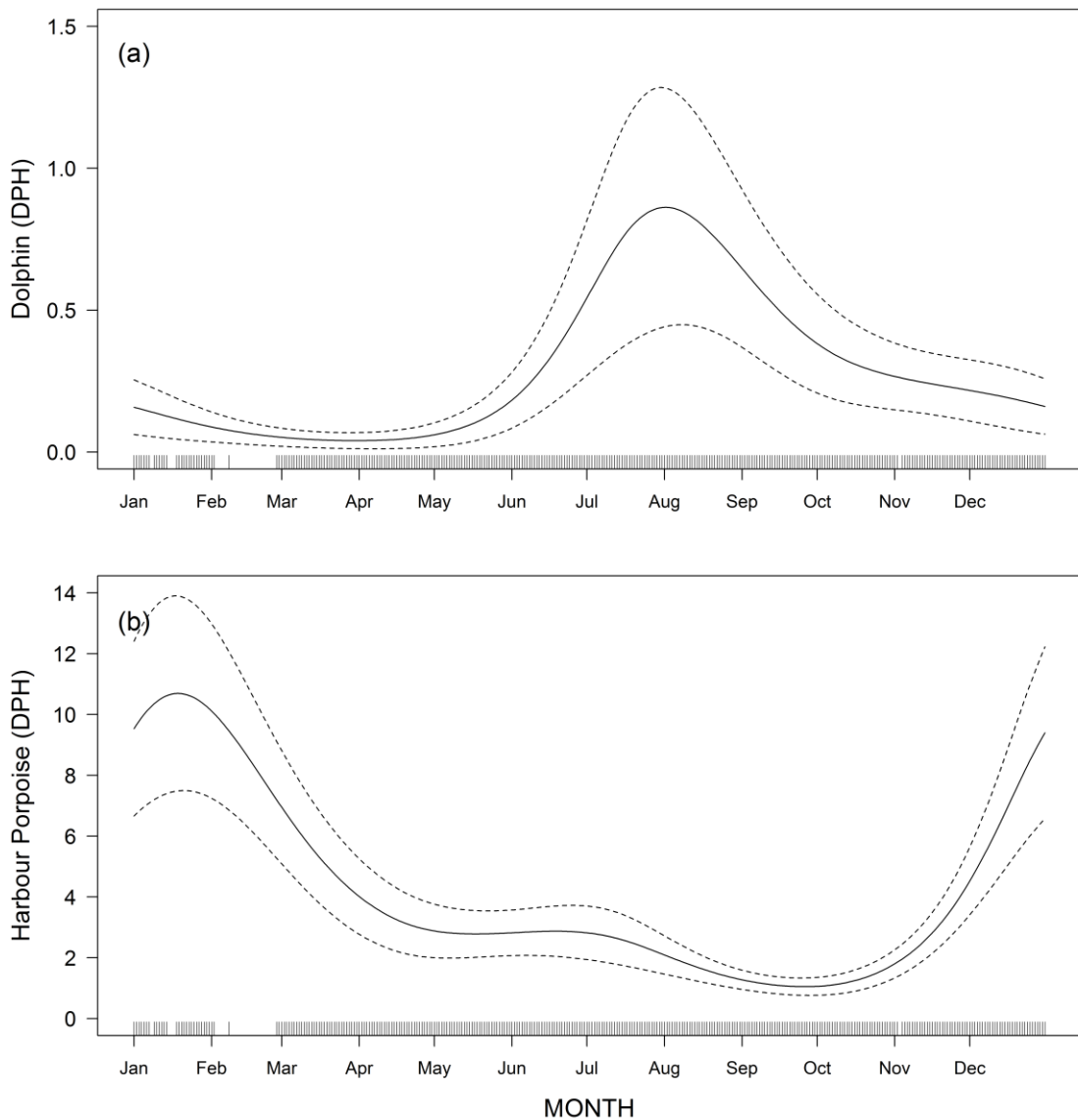
Figure 6. Results from temporal models fitted using the entire five year dataset. Predicted daily DPH for (a) dolphins and (b) harbour porpoises *Phocoena phocoena*. Dolphin occurrence peaks in summer from June to October, whilst, in contrast, harbour porpoise occurrence peaks from December to March.
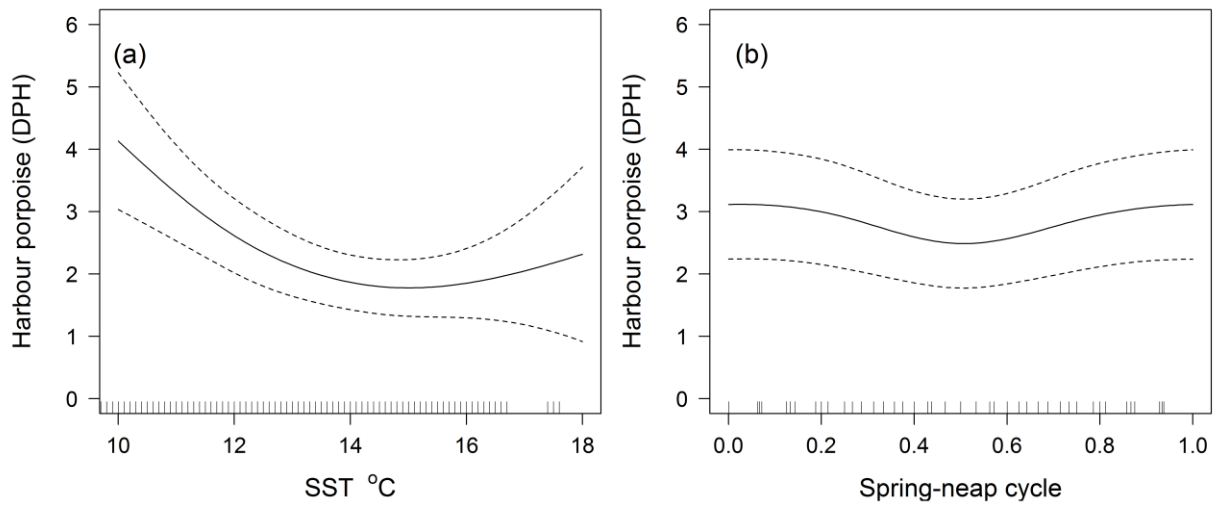
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Figure 7. Predicated dolphin (unspecified delphinids) detection positive hours per day (DPH) for the entire year models. From top to bottom: (a) distance to closest front *Fdist*, (b) cross-front gradient *Gdens* and (c) sea surface temperature *SST*.

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Figure 8. Predicted harbour porpoise *Phocoena phocoena* detection positive hours per day (DPH) for the entire year models. From left to right: (a) sea surface temperature *SST*, and (b) relative time in the spring-neap cycle *SpringNeapCycle*.
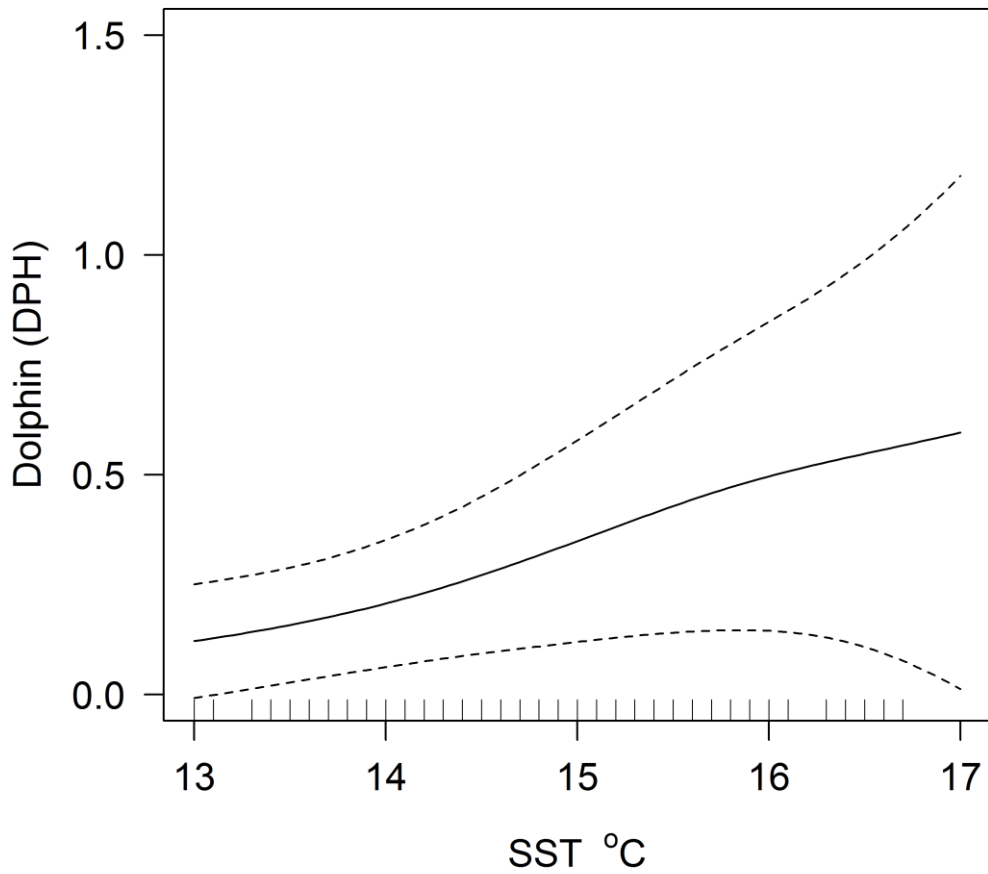
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Figure 9. Predicated dolphin (unspecified delphinids) detection positive hours per day (DPH). DPH in relation to sea surface temperature *SST*. Based on the summer only analysis.

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