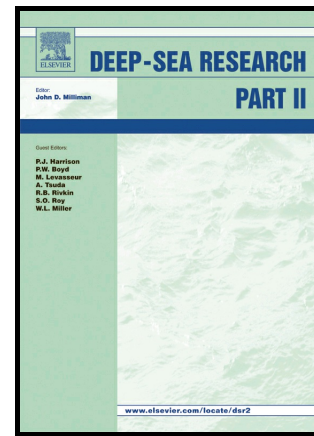# Author's Accepted Manuscript

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

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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 (C-POD) 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 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 and position in the spring-neap cycle, 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 et al. 2014a, 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 the impact of this may be confounded by the highly mobile nature of many marine megafauna alongside the dynamic structures of the systems they exploit (Scales et al. 2014b, 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 distributions of marine megafauna across oceanographically dynamic areas may vary over both large (seasonal) and short (bi-weekly/weekly) temporal scales, and failing to account for these natural patterns in habitat use may obfuscate behavioural changes in response to anthropogenically induced 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 et al. 2014a, 2014b) 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. Temporal patterns in habitat use across the site may 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). As such, separate

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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 40m 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 (by upwards of 10km), 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). Risso's dolphins *Grampus griseus* and bottlenose dolphins *Tursiops truncatus* are also known to occur in the region, although sightings are generally less frequent (Leeney et al. 2011) 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 after 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 (C-PODs, 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 C-PODS 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

C-PODs 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 C-POD 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 C-POD 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 C-PODs). In addition to dolphin and harbour porpoise DPHs, details of the C-POD's operating performance were also exported as the percentage logging time lost per day (to provide information of times when the C-POD 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 temporal patterns were influenced by both broad scale and localised oceanographic processes by investigating relationships between cetacean DPHs and a suite of environmental variables that

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characterised the bio-physical conditions across the five deployment stations. These included sea surface temperature (SST, model parameter *SST*), surface chlorophyll-a concentration *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-a

SST was included to determine the influence of the seasonal warming and thermal stratification (approximated by an increase in surface waters) of the region 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 4). Surface chlorophyll-a concentration (mg m^{-3}) 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 et al. 2014a) 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 4).

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°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

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of frontal intensity. A Gaussian filter with a width of five pixels was used for the spatial smoothing (Scales et al. 2014a). *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 et al. 2014a). 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 cetacean 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 impact the availability and distribution of prey (Yousif & Aglen 1999, 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 temporal patterns in site use 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. Because links between cetaceans DPHs and *SpringNeapCycle* may vary due to the specifics of a deployment station's location (e.g. discrepancies in bathymetric depth may influence the intensity of short term mixing events and their associated impacts on prey distribution; Simpson & Hunter 1974), an interaction term was tested for between *SpringNeapCycle* and station ID *StationID*. 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 (log[*Chlorophyll* + 1]) 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 C-POD 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 C-POD 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* ≤ 0.25 and ≥ 0.75) leaving a total of 770 and 801 recording days during spring and neap conditions respectively. Of the summer

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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 C-POD 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 dependent upon convergence and inspection of residual plots (Zuur et al. 2009). For the analyses 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, C-POD ID and deployment ID to check for any patterns indicative of a violation of model assumptions (Zuur et al. 2009). Fitted versus predicted values were inspected to check for satisfactory model fit (Potts & Elith 2006). 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).

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3.0 Results

Passive acoustic monitoring was carried out at a minimum of one of the five deployment stations continuously from September 2009 to December 2013, excluding four gaps of greater than a month between (1) January to March, 2010, (2) January to February, 2012, (3) May to July, 2012, and (4) November, 2012 to February, 2013 (Figures 3 & 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 than those observed during the remainder of the year (e.g. predicted values of ~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* ($p = 0.002$, Table 2, Figure 7) which explained 4.2% 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). It could not be tested if this relationship varied between deployment stations due to model convergence issues on the addition of the interaction term.

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 3, Figure 9) which explained 6.6% of deviance. DPH also varied with position in the spring-neap cycle, although this relationship was only evident at deployment station two where detection rates increased following peak neap conditions ($p = 0.01$; Table 3, Figure 9, supplementary materials S2). The deviance explained by this parameter was 2.81%. Variations in harbour porpoise DPH were not explained by any of the environmental parameters.

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 small scale changes in SST and position in the spring-neap cycle. 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 MREIs.

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 5 & 6) 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 analyses using the entire dataset 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 primary productivity sustain large numbers of zooplankton which 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 more localised analyses 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 (which could not be resolved due to the restricted spatial extent of deployment

stations; ~12km by 3km). Alternatively, at localised spatio-temporal scales, the prey resources that marine megafauna exploit around fronts might not occur directly at a feature's surface signature and instead be associated with transient processes occurring within a surrounding buffer zone, which may weaken links over finer scales. Indeed, the fine-scale summer distributions of common dolphins around the area's tidal-mixing front have been linked to ephemeral peaks in sub-surface productivity that occur within the thermocline of waters with high SSTs on the front's stratified side (Franks 1992, Cox 2016). The lateral extent of this stratification may alter in response to turbulent mixing with position in the spring-neap cycle, and possibly expand further inshore across the site during neap conditions (Cox 2016). Whilst surface chlorophyll measurements obtained via satellite remote-sensing would not have detected these periods of sub-surface productivity, it was found that the occurrence of dolphin detections increased both when SST was increased and during neap conditions, indicating a preference for times when the area was likely stratified. The latter of these relationships was only observed at station two suggesting that, relative to position in the spring neap cycle, the movement of the front and corresponding stratification of waters across the site is not consistent between stations (i.e. the waters around some stations may spend more (or less) time stratified, dependent on their position relative to the front; Figures 2 & 4).

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

Both species 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 influence 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) strong current flows (> 2ms^{-1}) in a manner that increases prey availability. Our findings suggest that in a relatively homogenous topographic area with comparatively weak tidal flows (between 0.5 and 1.2ms^{-1}), changes in tidal currents can also impact the behaviours and distributions of marine megafauna, although mechanistic links likely differ. Here, relationships between small cetaceans and position in the spring-neap cycle may be due to changes in productivity in response to the stratification of the site (which, bottom-up, likely influences the fine-scale distributions of pelagic prey - as outlined above). Alternatively, some demersal fish species (e.g. cod, that harbour porpoise are thought to feed on) may perform localised, short-term migrations from shallow to deep waters during spring conditions to avoid periods of increased current flows (whilst current flows are not as strong as those observed in nearshore coastal regions, they more than doubled during spring conditions ; Yousif & Aglen 1999). In some

instances, individual cetaceans themselves may avoid the area during these times (Embling et al. 2010), due to the energetics associated with navigating more turbulent waters, which may be particularly pertinent to harbour porpoises due to their high energetic requirements and small size.

4.4 Implications for managing marine renewable energy installations (MREIs)

The environmental impact assessment (EIA) process which most MREI developments need to follow in Europe typically requires an evaluation of baseline conditions, which includes quantifying the nearby spatio-temporal distributions of small cetaceans (which are protected under the European Union Habitat Directive), prior to the introduction of a MREI (Dolman & Simmonds 2010, Bailey et al. 2014). However, currently there is no clear guidance on how this should be achieved, despite the critical role site characterisation plays in determining natural patterns in environmental variability and habitat use, that may otherwise obfuscate cetacean responses to disturbance (Hewitt et al. 2001, Maclean et al. 2014). Whilst approaches based upon BACI (Before, After, Control, Incident; Carstensen et al. 2006) or gradient (Dahne et al. 2013) designs are typically recommended (Bailey et al. 2014), little information towards the appropriate spatio-temporal scales or timespans over which these should be conducted is provided (Leeney et al. 2014, Maclean et al. 2014). 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 monitoring conducted over spatio-temporal scales that reflect those of heterogeneity in cetacean site use and environmental variability.

Cetacean presence across the site varied over a number of temporal scales. Broad seasonal trends appeared to stem from an annually occurring cycle of warming and stratification across the site suggesting that at least a complete year of data is required to capture this variability. Ideally monitoring would be conducted across multiple years to evaluate the stability of these patterns through time. Assessing the consistency of correlations between underlying environmental covariates that drive these processes may aid in this (i.e. are temporal trends in *SST*, *Fdist*, and *Gdens*, the same year on year; see supplementary materials S3 for correlation plots through time of explanatory variables used in the statistical analyses of this study), particularly where bio-physical oceanographic conditions can be measured via satellite remote-sensing, the data outputs of which are often readily accessible via public domains. Patterns in cetacean presence were also found to respond to localised changes in bio-physical conditions, namely in relation to position in the spring-neap cycle (which was also likely related to small scale fluctuations in SST across the summer). This suggests that, whilst monitoring needs to be of a sufficient length so as to pick up on broad scale seasonal trends, it also needs to be of high enough resolution so as to avoid potential bias

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stemming from fine-scale variations in site-use. Passive acoustics appear to be a good tool for this as demonstrated here. Aerial-, boat- and land- based surveying are other monitoring methods commonly recommended for use in EIAs (Dolman & Simmonds 2010, Leeney et al. 2014), although their applicability may be limited in some situations due to access/weather constraints alongside the cost and effort associated with manually surveying at regular intervals over a variety of bio-physical conditions.

Patterns in site use may also vary spatially (Table 3, Figure 9), which needs to be carefully considered during the design stages of assessment programs. This is particularly pertinent when designating the locations of 'impact' and 'control' sites during BACI surveying, or monitoring point locations along gradient designs, which need to be of adequate comparability following the introduction of an MREI, and representative of cetacean site use. For example, despite a separation distance between stations one and four of only ~10km, mean daily detection rates at site one were almost tenfold higher than those at station four (0.61 ±0.08 (standard error) versus 0.07 ±0.02 DPH respectively) which reflected a 0.7°C difference in average seasonal temperatures (15.0 ±0.08°C versus 14.3 ±0.06°C at stations one and four respectively; detection rates of dolphins from our 2010 summer only analyses were found to vary dependent upon small fluctuations in SST across the site). As such, baseline monitoring should be carried out at multiple, strategically placed locations following prior investigation of site specific dynamics to ensure comparability/representability requirements are met. Data outputs from oceanographic modelling and remote sensing can aid in this (e.g. the heterogeneous distribution of SSTs between stations can be identified via the remotely sensed information in Figure 4). In combination with temporal requirements (outlined above), at highly dynamic locations this may result in a need for monitoring arrays of relatively high spatio-temporal resolution.

4.5 Conclusions

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

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5.0 Acknowledgements

References

Bailey H, Brookes KL, Thompson PM (2014) Assessing environmental impacts of offshore wind farms: Lessons learned and recommendations for the future. Aquat Biosyst 10:1–13

Bailey H, Thompson P (2010) Effect of oceanographic features on fine-scale foraging movements of bottlenose dolphins. Mar Ecol Prog Ser 418:223–233

Barlow J, Gerrodette T, Forcada J (2001) Factors affecting perpendicular sighting distances on shipboard line-transect surveys for cetaceans. J Cetacean Res Manag 3:201–212

Begg GS, Reid JB (1997) Spatial variation in seabird density at a shallow sea tidal mixing front in the Irish Sea. ICES J Mar Sci 54:552–565

Benjamins S, Dale A, Hastie GD, Waggitt JJ, Lea MA, Scott BE, Wilson B (2015) Confusion reigns? A review of marine megafauna interactions with tidal-stream environments. Oceanogr Mar Biol Annu Rev 53:1–54

Carstensen J, Henriksen OD, Teilmann J (2006) Impacts of offshore wind farm construction on harbour porpoises: Acoustic monitoring of echolocation activity using porpoise detectors (T-PODs). Mar Ecol Prog Ser 321:295–308

Cayula J-F, Cornillon P (1992) Edge detection algorithm for SST images. J Atmospheric Ocean Technol 9:67–80

Chelonia Ltd (2013a) C-POD.exe: A guide for users.

Chelonia Ltd (2013b) C-POD: Validating cetacean detections.

Cleasby IR, Wakefield ED, Bodey TW, Davies RD, Patrick SC, Newton J, Votier SC, Bearhop S, Hamer KC (2015) Sexual segregation in a wide-raning marine predator is a consequence of habitat selection. Mar Ecol Prog Ser 518:1–12

Coull KA, Johnston R, Rogers SI (1998) Fisheries sensitivity maps in British waters. UKOOA Ltd.

Cox SL (2016) The role of physical oceanography on the distributions and foraging behaviours of marine mammals and seabirds in shelf-seas. PhD, Plymouth University, Plymouth

Cox SL, Scott BE, Camphuysen CJ (2013) Combined spatial and temporal processes identify links between pelagic prey species and seabirds. Mar Ecol Prog Ser 479:203–221

Dahne M, Gilles A, Lucke K, Peschko V, Adler S, Krugel K, Sundermeyer J, Siebert U (2013) Effects of pile-driving on harbour porpoises (*Phocoena phocoena*) at the first offshore wind farm in Germany. Environ Res Lett 8:025002

Dolman S, Simmonds M (2010) Towards best environmental practice for cetacean conservation in developing Scotland's marine renewable energy. Mar Policy 34:1021–1027

Durazo R, Harrison NM, Hill AE (1998) Seabird observations at a tidal mixing front in the Irish Sea. Estuar Coast Shelf Sci 47:153–164

Embling CB, Gillibrand PA, Gordon J, J S, Stevick PT, Hammond PS (2010) Using habitat models to identify suitable sites for marine protected areas for harbour porpoises (*Phocoena phocoena*). Biol Conserv 143:267–279

Embling CB, Illian J, Armstrong E, Van der Kooij J, Sharples J, Camphuysen CJ, Scott BE (2012) Investigating fine-scale spatio-temporal predator-prey patterns in dynamic marine ecosystems: A functional data analysis approach. J Appl Ecol 49:481–492

Embling CB, Sharples J, Armstrong E, Palmer MR, Scott BE (2013) Fish behaviour in response to tidal variability and internal waves over a shelf sea bank. Prog Oceanogr 117:106–117

Franks PJS (1992) Phytoplankton blooms at fronts: Patterns, scales and physical forcing mechanisms. Rev Aquat Sci 6:121–137

Gill AB (2005) Offshore renewable energy: ecological implications of generating electricity in the coastal zone. J Appl Ecol 42:605–615

Goold JC (1998) Acoustic assessment of populations of common dolphin off the west Wales coast, with perspectives from satellite infrared imagery. J Mar Biol Assoc U K 78:1353–1364

Grecian WJ, Inger R, Attrill MJ, Bearhop S, Godley BJ, Witt MJ, Votier SC (2010) Potential impacts of wave-powered marine renewable energy installations on marine birds. Ibis 152:683–697

Hammond PS, Berggren P, Benke H, Borchers DL, Collet A, Heide-Jorgensen MP, Heimlich S, Hiby AR, Leopold MF, Oien N (2002) Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent waters. J Appl Ecol 39:361–376

Harwood J, King S (2014) The sensitivity of UK marine mammal populations to marine renewables developments. SMRU Marine, St Andrews

Hastie T, Tibshirani R, Friedman J (2008) The elements of statistical learning: Data mining, inference and prediction, 2nd edn. Springer

Hastie GD, Wilson B, Wilson LJ, Parsons KM, Thompson PM (2004) Functional mechanisms underlying cetacean distribution patterns: Hotspots for bottlenose dolphins are linked to forgaing. Mar Biol 144:397–403

Hewitt JE, Thrush SE, Cummings VJ (2001) Assessing environmental impacts: effects of spatial and temporal variability at likely impact scales. Ecol Appl 11:1502–1516

Hunt GL, Harrison NM (1990) Foraging habitat and prey taken by least auklets at King Island, Alaska. Mar Ecol Prog Ser 65:141–150

Inger R, Attrill MJ, Bearhop S, Broderick AC, Grecian WJ, Hodgson DJ, Mills C, Sheehan, E., Votier SC, Witt MJ, Godley BJ (2009) Marine renewable energy: Potential benefits to biodiversity? An urgent call for research. J Appl Ecol 46:1145–1153

Iversen SA (2002) Changes in the perception of the migration pattern of Northeast Atlantic mackerel during the last 100 years. ICES Mar Sci Symp 215:382–390

Jahncke J, Coyle KO, Zeeman SI, Kachel NB, Hunt GL (2005) Distribution of forgaing shearwaters relative to inner front of SE Bering Sea. Mar Ecol Prog Ser 305:219–233

Jansen T, Gislason H (2013) Population structure of Atlantic mackerel (*Scomber scombrus*). PLoS ONE 8:e64744

Johnston DW, Westgate AJ, Read AJ (2005) Effects of fine-scale oceanographic features on the distribution and movements of harbour porpoises *Phocoena phocoena* in the Bay of Fundy. Mar Ecol Prog Ser 295:279–293

Jones AR, Hosegood P, Wynn RB, De Boer MN, Butler-Cowdry S, Embling CB (2014) Fine-scale hydrodynamics influence the spatio-temporal distribution of harbour porpoises at a coastal hotspot. Prog Oceanogr 128:30–48

Kaltenberg AM, Emmett RL, Benoit-Bird KJ (2010) Timing of forage fish seasonal appearance in the Columbia River plume and link to ocean conditions. Mar Ecol Prog Ser 419:171–184

Kastelein RA, Hardeman J, Boer H (1997) Food consumption and body weight of harbour porpoises (*Phocoena phocoena*). In: Read AJ, Wiepkema PR, Nacntigall PE (eds) The biology of the harbour porpoise. De Spil Publishers, Woerden, The Netherlands, p 217–233

Lambert E, MacLeod CD, Hall K, Brereton T, Dunn TE, Wall D, Jepson PD, Deaville R, Pierce GJ (2011) Quantifying likely cetacean range shifts in response to global climatic change: Implications for conservation strategies in a changing world. Endanger Species Res 15:205–222

Leeney RH, Amies R, Broderick AC, Witt MJ, Loveridge J, Doyle J, Godley BJ (2008) Spatio-temporal analysis of cetacean strandings and bycatch in a UK fisheries hotspot. Biodivers Conserv 17:2323–2338

Leeney RH, Greaves D, Conley D, O'Hagan AM (2014) Environmental Impact Assessments for wave energy developments - Learning from existing activities and informing future research priorities. Ocean Coast Manag 99:14–22

Leeney RH, Witt MJ, Broderick AC, Buchanan J, Jarvis DS, Richardson PB, Godley BJ (2011) Marine megavertebrates of Cornwall and the Isles of Scilly: Relative abundance and distribution. J Mar Biol Assoc U K 92:1–11

Lewison RL, Crowder LB, Wallace BP, Moore JE, Cox T, Zydelis R, McDonald S, Dimatteo A, Dunn DC, Kot CY, Bjorkland R, Kelez S, Soykan C, Stewart KR, Sims M, Boustany A, Read AJ, Halpin P, Nichols WJ, Safina C (2014) Global patterns of marine mammal, seabird, and sea turtle bycatch reveal taxa-specific and cumulative megafauna hotspots. Proc Natl Acad Sci 111:5271–5276

Lockyer C, Desportes G, Hansen K, Labberté S, Siebert U (2003) Monitoring grotwth and energy utilisation of the harbour porpoise (*Phocoena phocoena*) in human care. NAMMCO Sci Publ 5:107–120

Louzao M, Hyrenbach KD, Arcos JM, Abello P, Sola LG de, Oro D (2006) Oceanographic habitat of an endangered Mediterranean procellariiform: Implications for marine protected areas. Ecol Appl 16:1683–1695

18

Maclean IMD, Inger R, Benson D, Booth CG, Embling CB, Grecian WJ, Heymans JJ, Plummer KE, Shackshaft M, Sparling C, Wilson C, Wright LJ, Bradbury G, Christen N, Godley BJ, Jackson A, McCluskie A, Nichols-Lee R, Bearhop S (2014) Resolving issues with environmental impact assessment of marine renewable energy installations. Front Mar Sci 1

MacLeod R, MacLeod CD, Learmonth JA, Jepson PD, Reid RJ, Deaville R, Pierce GJ (2007) Mass-dependent predation risk and lethal dolphin-porpoise interactions. Proc R Soc Biol Sci B 274:2587–2593

McCauley DJ, Pinsky ML, Palumbi SR, Estes JA, Joyce FH, Warner RR (2015) Marine defaunation: Animal loss in the global ocean. Science 347:12556411–12556417

Meynier L, Pusineri C, Spitz J, Santos MB, Pierce GJ, Ridoux V (2008) Intraspecific dietary variation in the short-beaked common dolphin *Delphinus delphis* in the Bay of Biscay: Importance of fat fish. Mar Ecol Prog Ser 354:277–287

Miller P (2009) Composite front maps for improved visibility of dynamics sea-surface features on cloudy SeaWiFS and AVHRR data. J Mar Syst 78:327–336

Murphy S, Pinn EH, Jepson PD (2013) The short-beaked common dolphin (*Delphinus delphis*) in the North-East Atlantic: Distribution, ecology, management and conservation status. Oceanogr Mar Biol Annu Rev 51:193–280

Nahas EL, Pattiaratchi CB, Ivey GN (2005) Processes controlling the positions of frontal systems in Shark Bay, Western Australia. Estuar Coast Shelf Sci 65:463–474

Philpott E, Englund A, Ingram S, Rogan E (2007) Using T-PODs to investigate the echolocation of coastal bottlenose dolphins. J Mar Biol Assoc UK 87:11–17

Pierpoint C (2008) Harbour porpoise (*Phocoena phocoena*) foraging strategy at a high energy, near-shore site in south-west Wales, UK. J Mar Biol Assoc U K 88:1167–1173

Pikesley SK, Witt MJ, Hardy T, Loveridge J, Loveridge J, Williams R, Godley BJ (2012) Cetacean sightings and strandings: Evidence for spatial and temporal trends. J Mar Biol Assoc U K 92:1809–1820

Pingree RD (1975) The advance and retreat of the thermocline on the continental shelf. J Mar Biol Assoc UK 55:965–974

Pingree RD (1980) Chapter 13: Physical oceanography of the Celtic Sea and English Channel. In: Banner FT, Collins MB, Massie KS (eds) The north-west European shelf seas: The sea bed and the sea in motion II. Physical and chemical oceanography, and physical resources. Elsevier Ltd., p 415–465

Pingree RD, Griffiths DK (1978) Tidal fronts on the shelf seas around the British Isles. J Geophys Res 83:4615–4622

Pingree RD, Holligan PM, Mardell GT, Head RN (1976) The influence of physical stability on spring, summer and autumn phytoplankton blooms in the Celtic Sea. J Mar Biol Assoc UK 56:845–873

Pirotta E, Brookes KL, Graham IM, Thompson PM (2014a) Variation in harbour porpoise activity in response to seismic survey noise. Biol Lett 10

Pirotta E, Laesser BE, Hardaker A, Riddoch N, Marcoux M (2013) Dredging displaces bottlenose dolphins from an urbanising foraging patch. Mar Pollut Bull 74:396–402

Pirotta E, Thompson PM, Miller PI, Brookes KL, Cheney B, Barton TR, Graham IM, Lusseau D (2014b) Scale-dependent foraging ecology of a marine top predator modelled using passive acoustic data. Funct Ecol 28:206–217

Pisoni JP, Rivas AK, Piola AR (2015) On the variability of tidal fronts on a macrotidal continental shelf, Northern Patagonia, Argentina. Deep-Sea Res II 119:61–68

Potts JM, Elith J (2006) Comparing species abundance models. Ecol Model 199:153–163

Russell RW, Harrison NM, Hunt GL (1999) Foraging at a front: Hydrography, zooplankton, and avian planktivory in the northern Bering Sea. Mar Ecol Prog Ser 182:77–93

Santos MB, Pierce GJ (2003) The diet of harbour porpoise (*Phocoena phocoena*) in the Northeast Atlantic. Oceanogr Mar Biol 41:355–390

Santos MB, Pierce GJ, Learmonth JA, Reid RJ, Ross HM, Patterson IAP, Reid DG, Beare D (2004) Variability in the diet of harbour porpoises (*Phocoena phocoena*) in Scottish waters 1992-2003. Mar Mammal Sci 20:1–27

Scales KL, Miller PI, Embling CB, Ingram SN, Pirotta E, Votier SC (2014a) Mesoscale fronts as foraging habitats: Composite front mapping reveals oceanographic drivers of habitat use for a pelagic seabird. J R Soc Interface 11:20140679

Scales KL, Miller PI, Hawkes LA, Ingram SN, Sims DW, Votier SC (2014b) On the front line: Frontal zones as priority at-sea conservation areas for mobile marine vertebrates. J Appl Ecol 51:1575–1583

Scott BE, Langton R, Philpott E, Waggitt JJ (2014) Seabirds and marine renewables: Are we asking the right questions? In: Shields MA, Payne AIL (eds) Marine Renewable Energy Technology and Environmental Interactions. Springer, Netherlands, p 81–92

Scott BE, Sharples J, Ross ON, Wang J, Pierce GJ, Camphuysen CJ (2010) Sub-surface hotspots in shallow seas: Fine-scale limited locations of top predator foraging habitat indicated by tidal mixing and sub-surface chlorophyll. Mar Ecol Prog Ser 408:207–226

Shields MA, Dillon LJ, Woolf DK, Ford AT (2009) Strategic priorities for assessing ecological impacts of marine renewable energy devices in the Pentland Firth (Scotland, UK). Mar Policy 33:635–642

Simon M, Nuuttila H, Reyes-Zamudio MM, Ugarte F, Verfub U, Evans PGH (2010) Passive acoustic monitoring of bottlenose dolphin and harbour porpoise, in Cardigan Bay, Wales, with implications for habitat use and partitioning. J Mar Biol Assoc U K 90:1539–1545

Simpson JH, Hunter JR (1974) Fronts in the Irish Sea. Nature 250:404–406

Simpson JH, Sharples J (2012) Introduction to the physical and biological oceanography of shelf seas. Cambridge University Press

Sims DW, Quayle VA (1998) Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. Nature 393:460–464

Skov H, Thomsen F (2008) Resolving fine-scale spatio-temporal dynamics in the harbour porpoise *Phocoena phocoena*. Mar Ecol Prog Ser 373:173–186

Spitz J, Rousseau Y, Ridoux V (2006) Diet overlap between harbour porpoise and bottlenose dolphin: An argument in favour of interference competition for food? Estuar Coast Shelf Sci 70:259–270

Stevick PT, Incze LS, Kraus SD, Rosen S, Wolff N, Baukus A (2008) Trophic relationships and oceanography on and around a small offshore bank. Mar Ecol Prog Ser 363:15–28

Sveegaard S, Andreasen H, Mouritsen KN, Jeppesen JP, Teilmann J, Kinze CC (2012) Correlation between the seasonal distribution of harbour porpoise and their prey in the Sound, Baltic Sea. Mar Biol 159:1029–1037

Sveegaard S, Teilmann J, Tougaard J, Dietz R, Mouritsen KN, Desportes G, Siebert U (2011) High-density areas for harbor porpoises (*Phocoena phocoena*)identified by satellite tracking. Mar Mammal Sci 27:230–246

Sydeman WJ, Brodeur RD, Grimes CB, Bychkov AS, McKinnell S (2006) Marine habitat "hotspots" and their use by migratory species and top predators in the North Pacific Ocean: Introduction. Deep-Sea Res II 53:247–249

Thomsen F, Elk N van, Brock V, Piper W (2005) On the performance of automated porpoise-click-detectors in experiments with captive harbour porpoises (*Phocoena phcoena*). J Acoust Soc Am 118:37–40

Van der Kooij J, Scott BE, MacKinson S (2008) The effects of environmental factors on daytime sandeel distribution and abundance on the Dogger Bank. J Sea Res 60:201–209

Vlietstra L, Coyle KO, Kachel NB, Hunt GL (2005) Tidal front affects the size of prey used by a top marine predator, the short-tailed shearwater (*Puffinus tenuirostris*). Fish Oceanogr 14:196–211

Waggitt JJ, Scott BE (2014) Using a spatial overlap approach to estimate the rick of collisions between deep diving seabirds and tidal stream turbines: A review of potential methods and approaches. Mar Policy 44:90–97

Wall CC, Muller-Karger FE, Roffer MA (2009) Linkages between environmental conditions and recreational king mackerel (*Scomberomorus cavalla*) catch off west-central Florida. Fish Oceanogr 18:185–199

Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? Deep-Sea Res Part II 54:211–223

Weir CR, O'Brien SH (2000) Association of the harbour porpoise (*Phocoena phocoena*) with the Western Irish sea front. In: Proceedings of the fourteenth annual conference of the European cetacean society. Cork, Ireland, p 61–65

Williams TM, Haun J, Davis RW, Fuiman LA, Kohin S (2001) A killer appetite: Metabolic consequences of carnivory in marine mammals. Comp Biochem Physiol Part A 129:785–796

Witt MJ, Sheenan EV, Bearhop S, Broderick AC, Conley DC, Cotterell SP, Crow E, Grecian WJ, Halsband C, Hodgson DJ, Hosegood P, Inger R, Miller PI, Sims DW, Thompson RC,

21

Vanstaen K, Votier SC, Attrill MJ, Godley BJ (2012) Assessing wave energy effects on biodiversity: The Wave Hub experience. Philos Trans R Soc 370:502–529

Wood S (2015) MGCV: Mixed GAM computation vehicle with GCV/AIC/REML smoothness estimation.

Yousif A, Aglen A (1999) Availability of pelagic distributed cod (*Gadus morhua* L.) to bottom trawls in the Barents Sea. Fish Res 44:47–57

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1:3–14

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer

Table captions

Table 1. Results from temporal analyses conducted using the entire five year dataset. Day of year *DayOfYear* was modelled, as a standalone term, against the detection rates (DPH) of dolphins (unspecified delphinids) and harbour porpoises *Phocoena phocoena* separately. Each model's intercept (standard errors in brackets), estimated degrees of freedom (E.df), parameter coefficient (standard errors in brackets), deviance explained (dev. exp.) and *p*-value are shown. The change in the *k*-folds cross validation (KCV) statistic on the inclusion of *DayOfYear* in the model is also indicated.

Table 2. Results from analyses conducted using the entire five year dataset for (a) dolphins (unspecified delphinids) and (b) harbour porpoises *Phocoena phocoena*. Each environmental parameter was tested for as a standalone term in separate models. Each model's intercept (standard errors in brackets), estimated degrees of freedom (E.df), parameter coefficient (standard errors in brackets), deviance explained (dev. exp.) and *p*-value are shown. The change in the *k*-folds cross validation (KCV) statistic on the inclusion of each term in the model is also indicated.

Table 3. Results for dolphins (unspecified delphinids) from analyses conducted using data from the summer (22nd of June to 20th October) of 2010 only. Each environmental parameter was tested for as a standalone term in separate models. Each model's intercept (standard errors in brackets), estimated degrees of freedom (E.df), parameter coefficient (standard errors in brackets), deviance explained (dev. exp.) and *p*-value are shown. The change in the *k*-folds cross validation (KCV) statistic on the inclusion of each term in the model is also indicated.

Figure captions

Figure 1. The study site (a) in the context of the UK, and (b) with bathymetric contours and the position of each deployment station (black filled circles with station IDs indicated in red).

Figure 2. Bio-physical oceanographic conditions observed at each the deployment stations over the five years (plotted in light grey with those from the year 2010 highlighted in black). Daily averages (across sites/year) are shown in red. From top to bottom: (a) log surface chlorophyll-a *LogChlorophyll*, (b) sea surface temperature *SST*, (c) front gradient *Gdens* and (d) distance to closet front *Fdist*. Seasonal fluctuations in the bio-physical conditions experienced across the site are noted. Warmer temperatures and increased frontal activity correspond to the summer months of June through to October (the extents of which are indicated by the vertical dashed lines). A peak in surface chlorophyll-a in late April indicates the occurrence of the annual spring bloom.

Figure 3. Deployment dates of passive acoustic monitoring across the five stations. Passive acoustic monitoring was carried out at a minimum of one of the five deployment stations continuously from September 2009 to December 2013, excluding four gaps of greater than a month between (1) January to March, 2010, (2) January to February, 2012, (3) May to July, 2012, and (4) November, 2012 to February, 2013. Monitoring was only achieved across the majority (four out of five) of stations in the summer of 2010 and spring of 2011. Note that C-PODs were rotated between deployment stations during the five year period (i.e. one deployment station did not have a set C-POD device that was consistent across the five years).

Figure 4. Bio-physical conditions experienced across the site during the summer of 2010. From top to bottom: sea surface temperature (SST) *SST* (a:c), log surface chlorophyll-a *LogChlorophyll* (d:f), front gradient *Gdens* (g:i) and distance to closest front *Fdist* (j:l). The locations of deployment stations are marked 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 across the deployment stations between dates, which coincides with variation in the position and intensity of the front.

Figure 5. Dolphin (unspecified delphinids; a:e) and harbour porpoise *Phocoena phocoena* (f:j) detections rates from each of the five deployment stations across each of the five years. Detection rates are presented on a square root scale as square root detection positive hours per day (DPH) + 1 ($\sqrt{(DPH + 1)}$) to aid legibility (note a $\sqrt{(DPH + 1)}$ value of 1 equates to 0 DPH and a value of 4 to 15 DPH). From top to bottom: 2009 (a & f), 2010 (b & g), 2011 (c & h), 2012 (d & i) and 2013 (e

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& j). Periods of no data are shaded grey. Dolphin detection rates peak in summer from around July to September across all years in which sufficient data are available to make comparisons. In contrast, peak detection rates of harbour porpoises occur from late December to March.

Figure 6. Results from temporal models fitted using the entire five year dataset. Predicted daily DPH for (a) dolphins (unspecified delphinids), and (b) harbour porpoises *Phocoena phocoena*. Dolphin detection rates peaks in the summer between July to September, whilst, in contrast, peaks in harbour porpoise detections rates occur between December to March.

Figure 7. Predicated dolphin (unspecified delphinids) detection positive hours per day (DPH) from models fitted using the entire dataset. From top to bottom: (a) distance to closest front *Fdist*, (b) cross-front gradient *Gdens* and (c) sea surface temperature *SST*.

Figure 8. Predicted harbour porpoise *Phocoena phocoena* detection positive hours per day (DPH) from models fitted using the entire dataset. From left to right: (a) sea surface temperature *SST*, and (b) relative time in the spring-neap cycle *SpringNeapCycle*.

Figure 9. Predicated dolphin (unspecified delphinids) detection positive hours per day (DPH) from models fitted using data from only the summer months (22nd of June to 20th October) of 2010. From left to right: (a) sea surface temperature *SST* and (b) *SpringNeapCycle* at deployment station two. See supplementary materials S2 for plots of *SpringNeapCycle* smoothers from the other deployment stations.
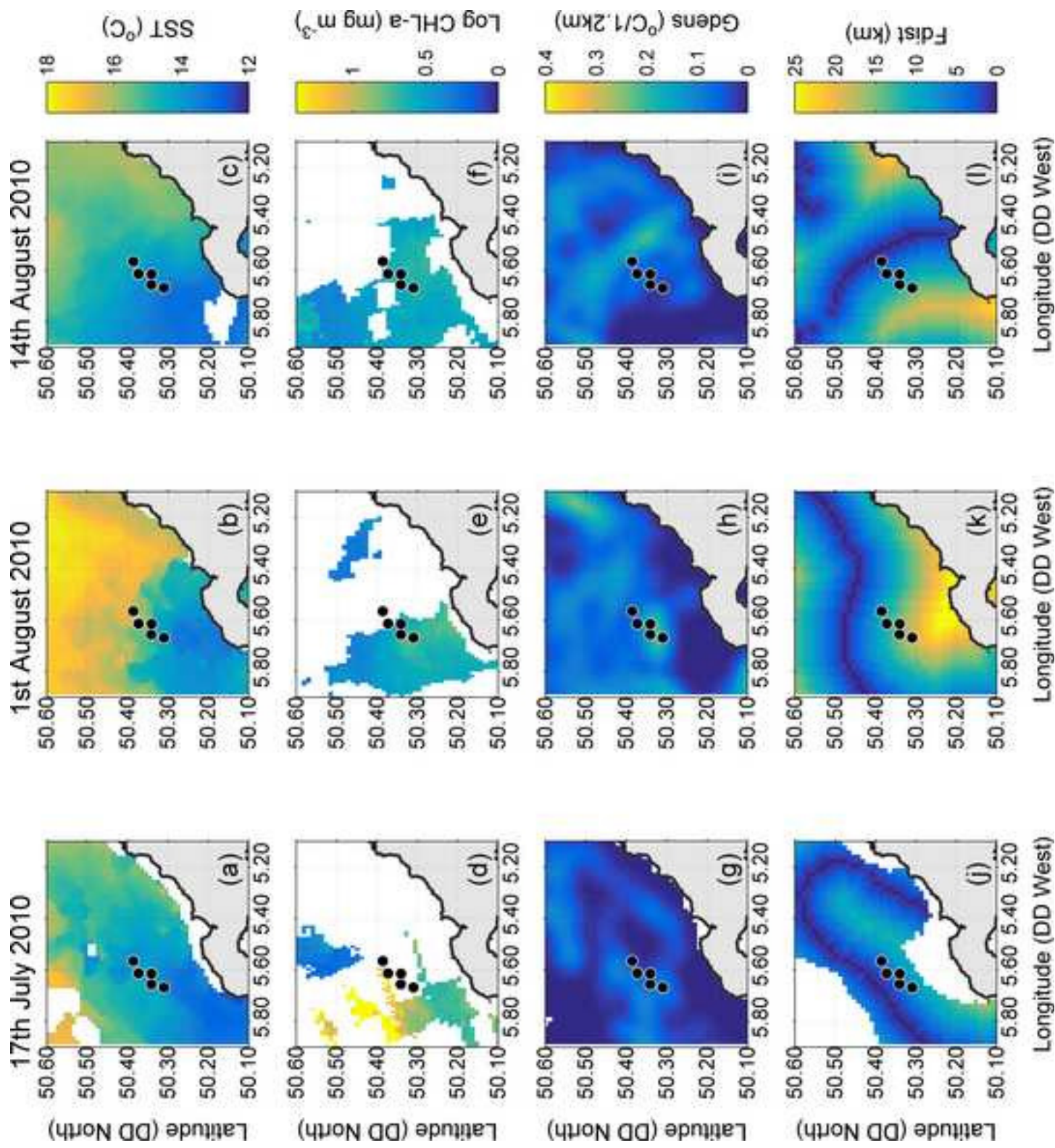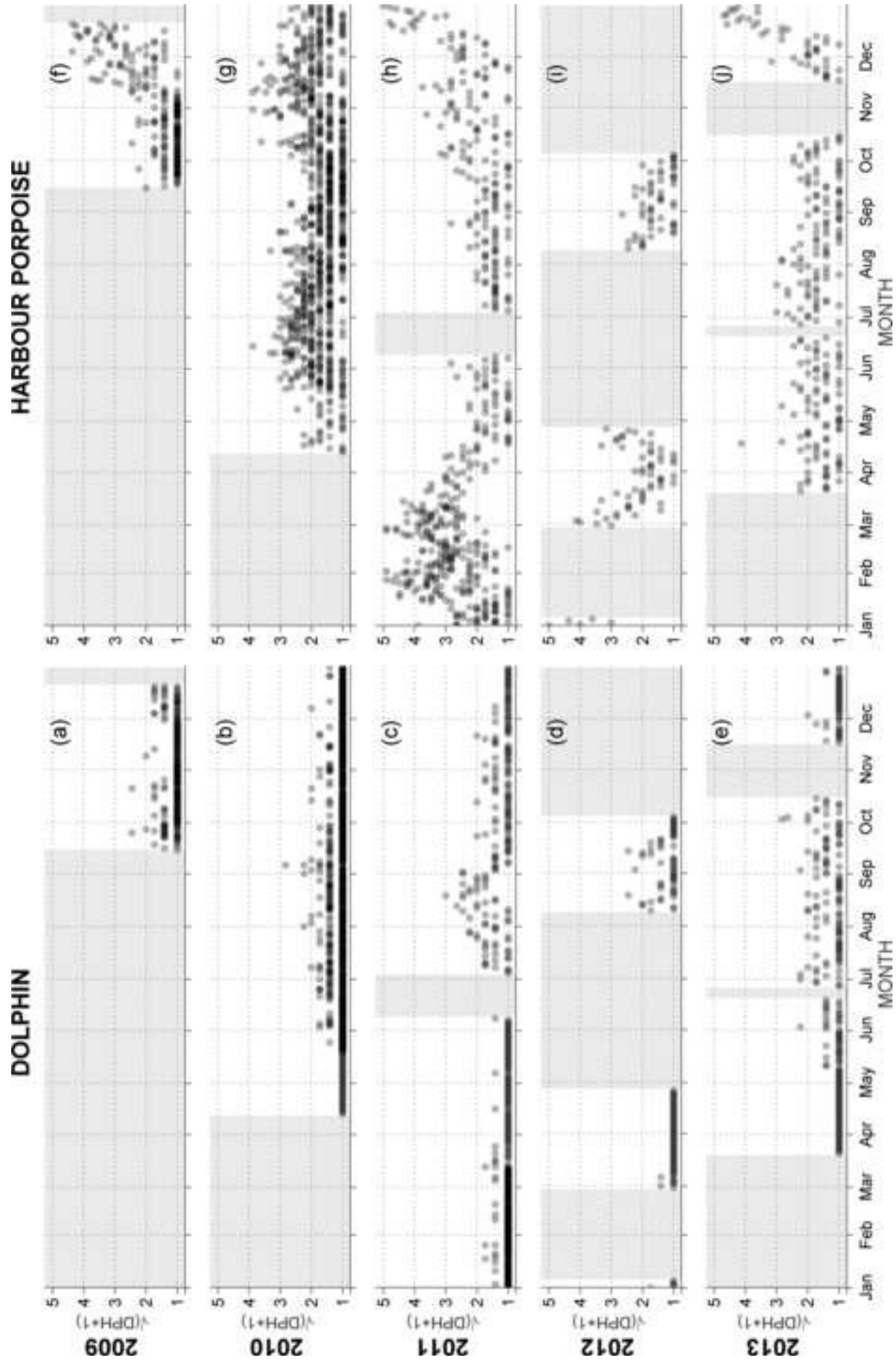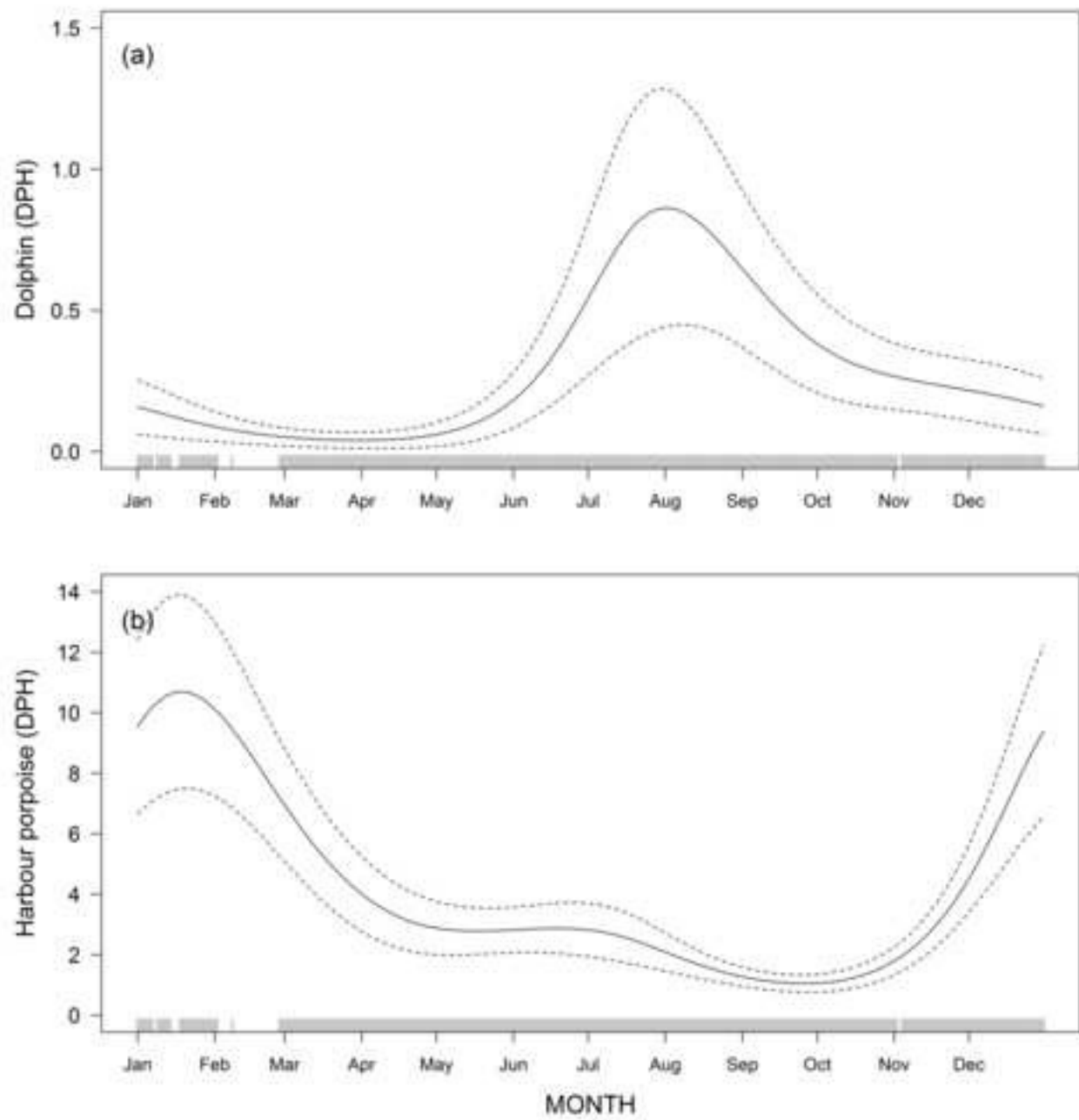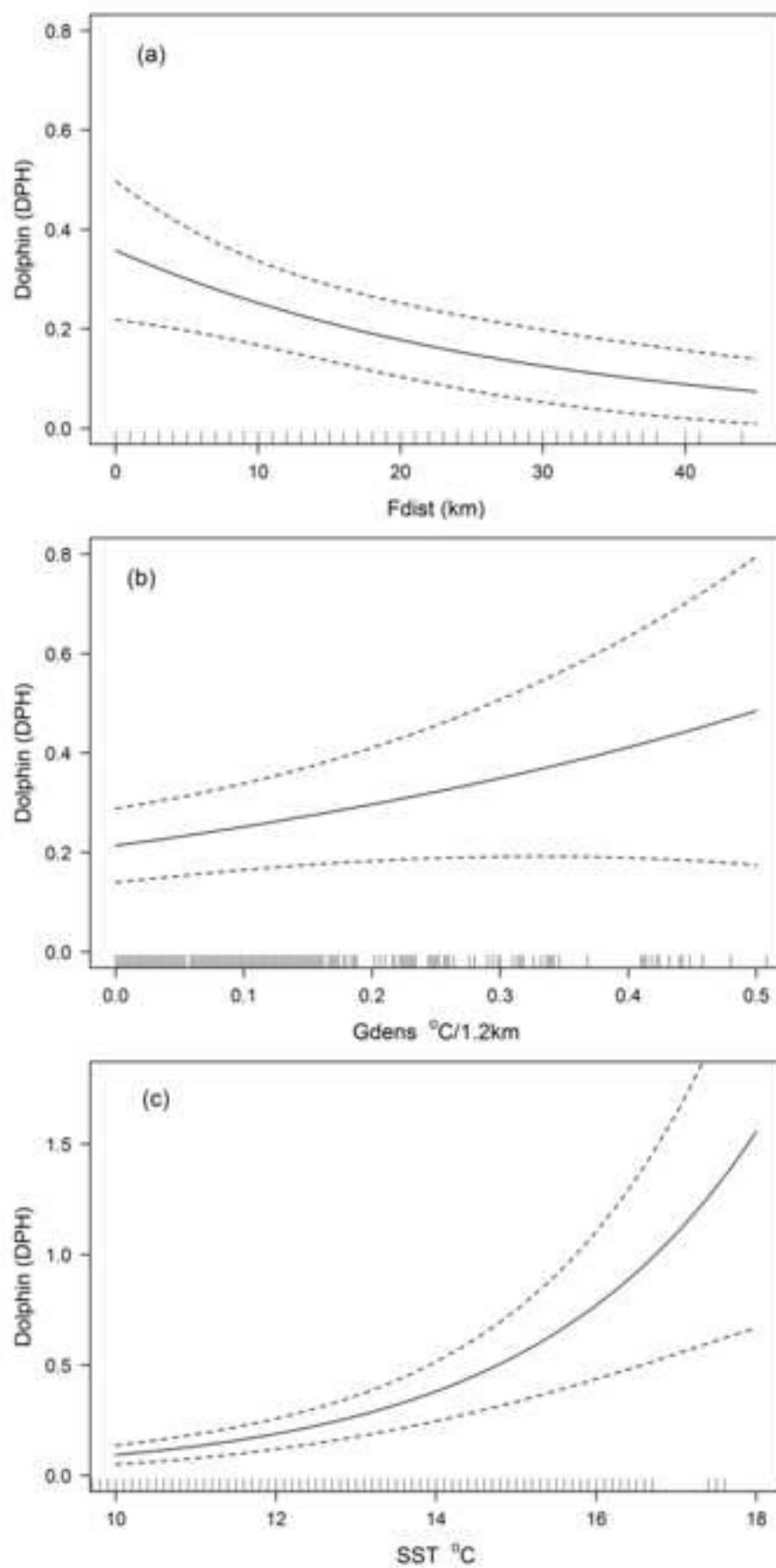
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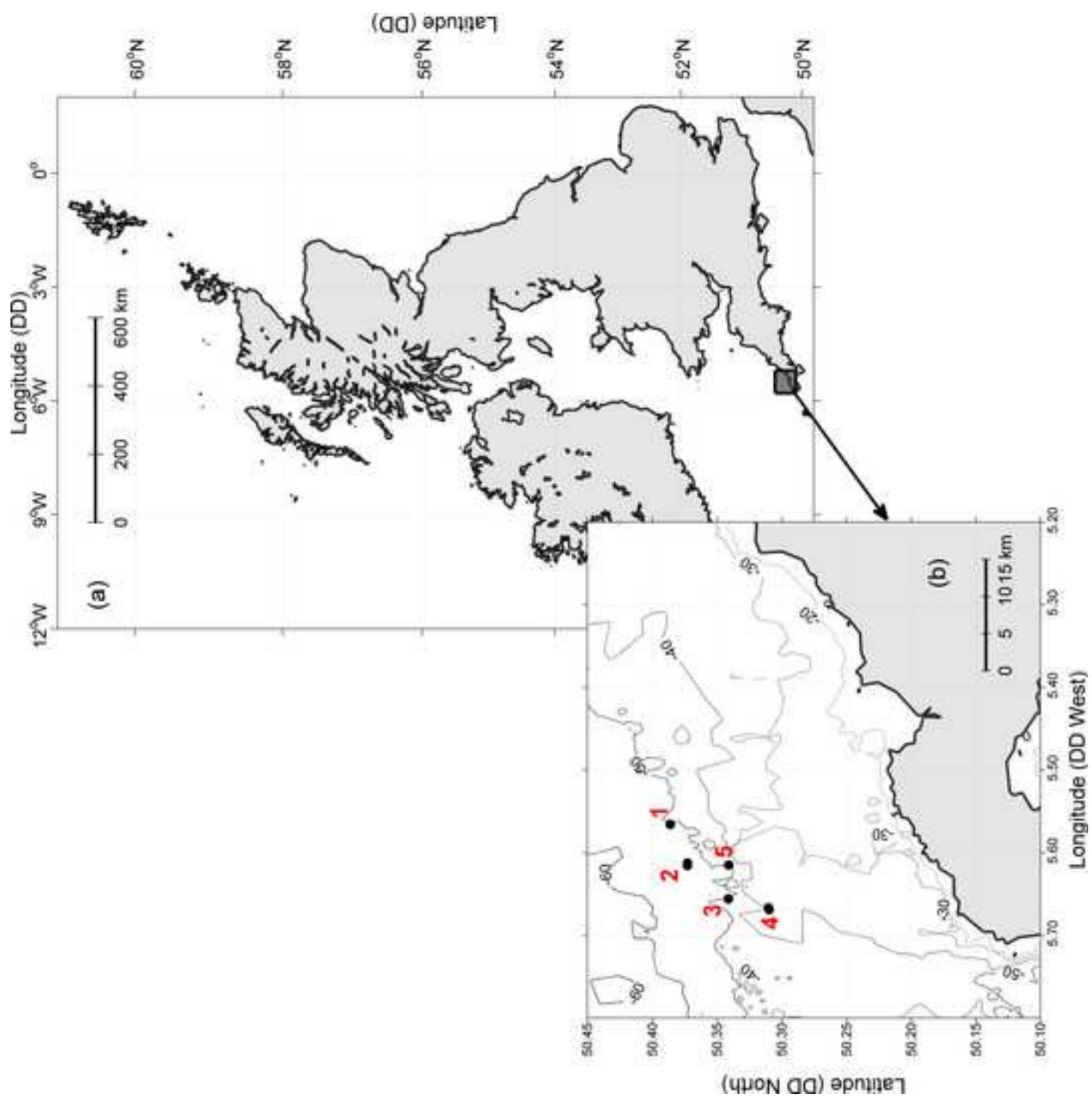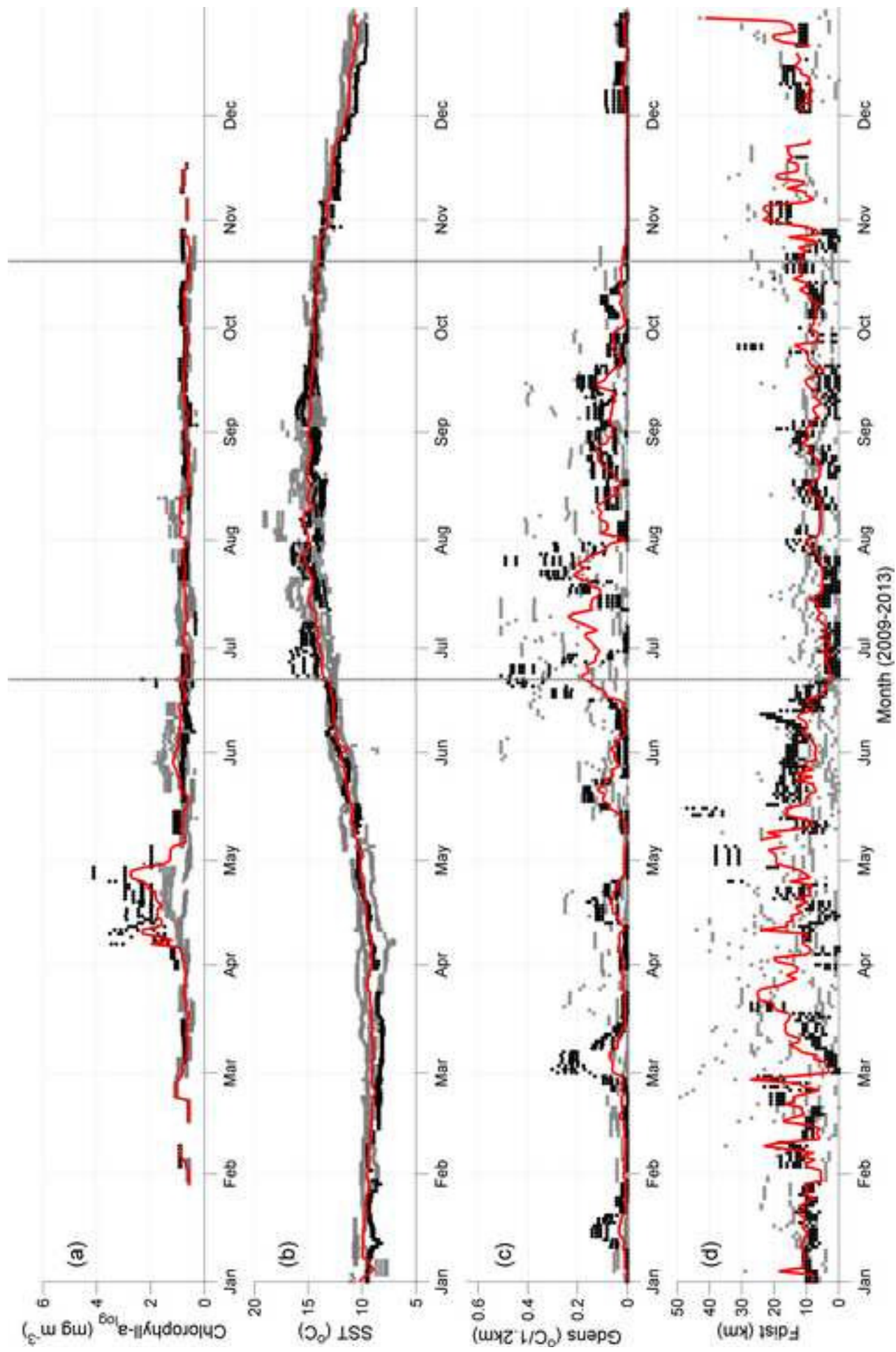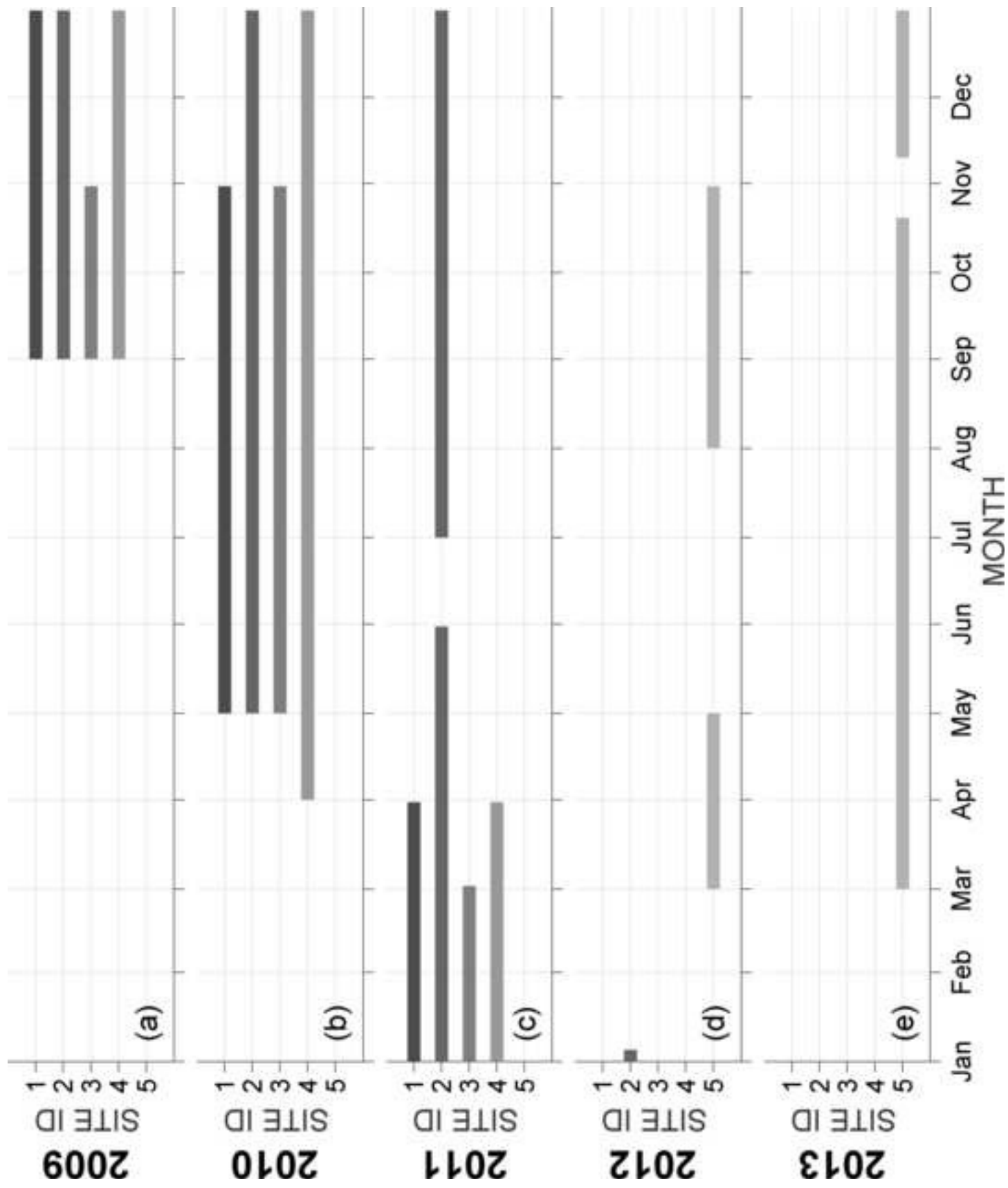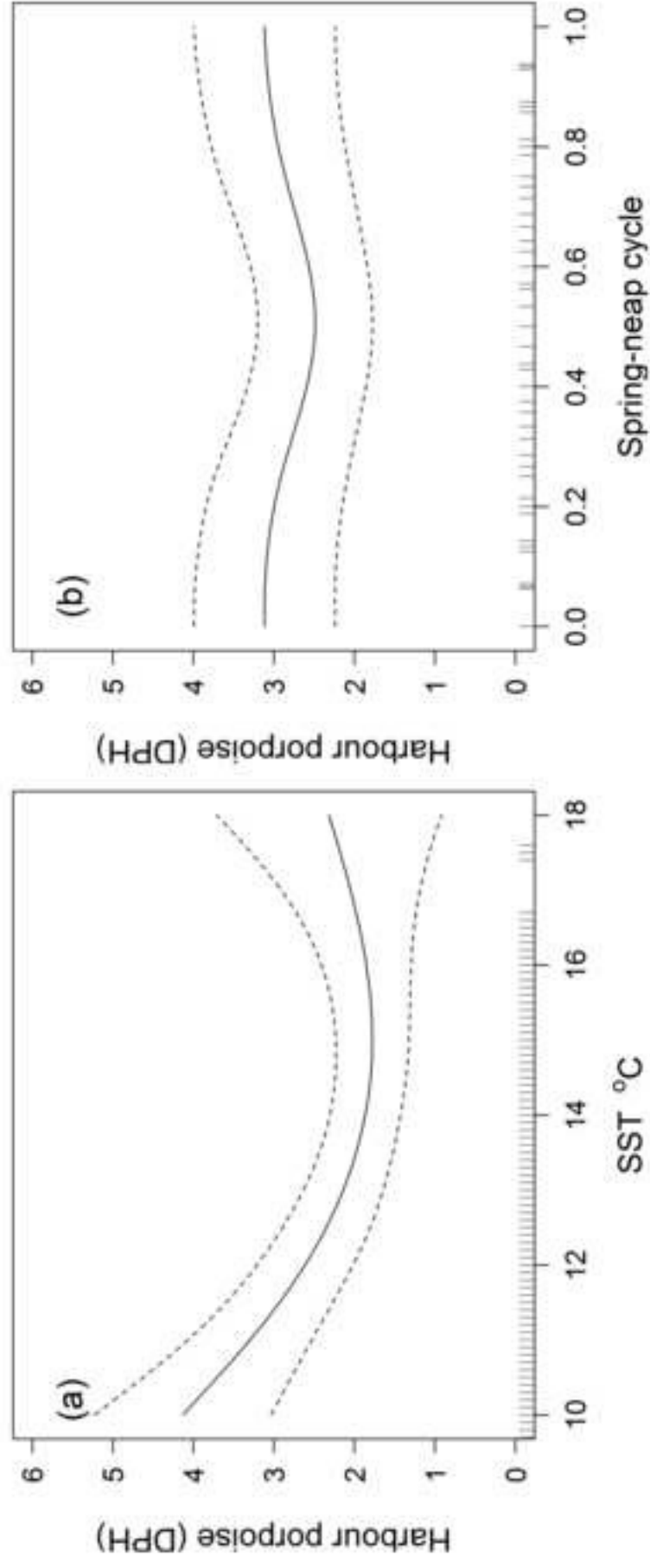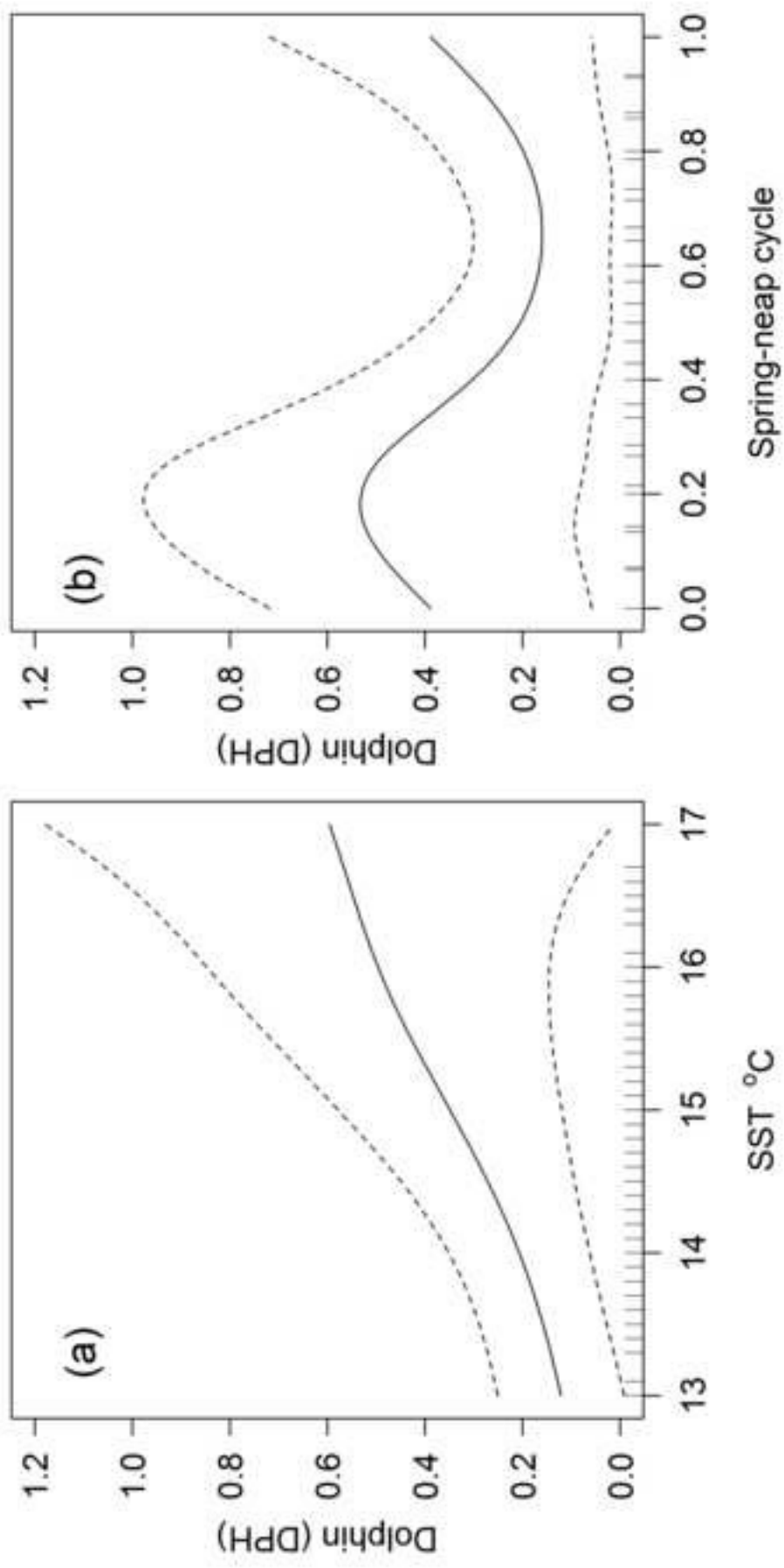
	Intercept	E.df.	Coefficient	Dev. exp.	*P*-value	Δ KCV
Dolphins (unspecified delphinids)	-1.32 (0.19)	2.82	–	15.3%	< 0.001	-59.2
Harbour porpoises	0.93 (0.08)	2.91	–	26.4%	< 0.001	-5107.9

Environmental parameter	Intercept	E.df.	Coefficient	Dev. exp.	*P*-value	Δ KCV
(a) Dolphin species						
Fdist	-1.37 (0.17)	1	-1.49 (0.49)	4.2%	0.002	-14.5
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	-1857.0
SpringNeapCycle	1.05 (0.14)	2.1	–	1.0%	< 0.001	-66.2

Environmental variable	Intercept	E.df.	Coefficient	Dev. exp.	*P*-value	Δ KCV
SST	-1.25 (0.33)	1.5	1.22 (0.43)	6.6%	0.011	-5.5
SpringNeapCycle:StationID	-1.23 (0.37)	–	–	2.81%	–	-2.1
- *Station 1*	–	0.36	–	–	0.303	–
- *Station 2*	–	1.69	–	–	0.013	–
- *Station 3*	–	0.00	–	–	0.735	–
- *Station 4*	–	0.00	–	–	0.395	–