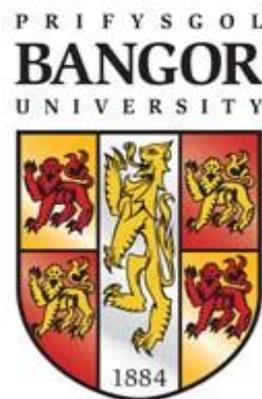


A photo-ID study of the Risso's dolphin
(*Grampus griseus*) in Welsh coastal waters and
the use of Maxent modelling to examine the
environmental determinants of spatial and
temporal distribution in the Irish Sea

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DECLARATION

This work has not previously been accepted in substance for any degree and is not being currently submitted for any degree.

This dissertation is being submitted in partial fulfilment of the requirement of the M.Sc. in Marine Biology.

The dissertation is the result of my own independent work / investigation, except where otherwise stated.

Other sources are acknowledged by footnotes giving explicit references and a bibliography is appended.

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Abstract

The Irish Sea is considered to be an area containing important habitat for the Risso's dolphin (*Grampus griseus*), and a number of distribution hotspots have been identified over the years. The creation of a photo-ID catalogue and database enabled the identification of 144 individuals in Welsh waters, from which it was estimated that a minimum of 162 individuals were encountered from 2003 to 2014. The 32 mother-calf pairings observed suggest the importance of Welsh waters for mating and parturition. Site fidelity in terms of re-sighting rates was relatively low (12.5%), similar to that which has previously been observed around Bardsey Island. An examination of home ranges by looking for matches between this catalogue and that of five other organisations from around the British Isles, showed individuals to occupy varying ranges. The most individuals (15) matched with the Whale and Dolphin Conservation (WDC) catalogue, indicating mostly localised home ranges, but evidence for large-scale migrations was also found with 2 matches with the Hebridean Whale and Dolphin Trust's (HWDT) catalogue. These results suggest that the Risso's dolphins seen in Welsh waters are part of an open population. In order to gain a better understanding of the drivers of their distribution, sightings data were analysed with respect to environmental variables: habitat type, energy, bathymetry, slope, oceanic thermal fronts, salinity, sea surface temperature and chlorophyll α concentration. Using Maxent species distribution modelling, the most important environmental variables found to determine habitat suitability were bathymetry, chlorophyll α concentration and salinity. These factors affect primary production and prey abundance either directly or indirectly by influencing oceanographic features including upwellings, fronts and gyres. Chlorophyll α concentration and salinity are also particularly important in the fine scale determination of prey aggregations. Slope was found to be the least important factor affecting distribution. In accordance with high sightings densities and predicted habitat suitability, the coastal waters around the Isle of Man, Anglesey, Bardsey Island and west Pembrokeshire are the areas identified to be the most important to Risso's dolphins. These areas should therefore be the focus of any future conservation and management strategies in the Irish Sea, to ensure the long-term protection and viability of the population.

List of Abbreviations

EMODNET	European Marine Observation and Data Network
GIS	Geographical Information System
GLM	Generalised Linear Model
HWDT	Hebridean Whale and Dolphin Trust
IWDG	Irish Whale and Dolphin Group
MWDW	Manx Whale and Dolphin Watch
SAC	Special Area of Conservation
SDM	Species Distribution Model
SST	Sea Surface Temperature
SWF	Sea Watch Foundation
WDC	Whale and Dolphin Conservation

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1. INTRODUCTION

Modern field studies of cetaceans began in the 1980s, and since then the knowledge of most species has dramatically advanced. In UK waters there are fifteen cetacean species considered to be residents or annual visitors and the Risso's dolphin (*Grampus griseus*) (Cuvier, 1812) is one of these species (Evans *et al.*, 2003). The Irish Sea is considered to be an important area for Risso's dolphin populations as it contains many distribution hotspots, concentrated around the Isle of Man, Bardsey Island and the Llŷn Peninsula in North Wales and west of Pembrokeshire (Baines and Evans, 2012; de Boer *et al.*, 2013). Data on the species are primarily collected by the Sea Watch Foundation (SWF) and Whale and Dolphin Conservation (WDC), however the status of the British population remains relatively unknown (Evans, 2008; Wharam and Simmonds, 2008).

1.1. Biology

Risso's dolphins are marine mammals of the order Cetacea and belong to the suborder Odontoceti or toothed whales. They are members of the family of true dolphins, the Delphinidae and are the only member of their genus (Rice, 1998; Baird, 2009). They can be recognised by a robust, torpedo-shaped body, blunt rounded head with no beak and large, broad melon with a distinctive vertical groove from the tip of the rostrum to the blowhole (Baird and Stacey, 1991). The dorsal fin is a distinct falcate shape (Walker and Cresswell, 2008) and centrally located on the back, as in most Delphinidae, and the pectoral fin, or flipper, is long and sickle-shaped, extending to approximately 17% of the body length. The species has a narrow tail stock and the tail fluke has a median notch and concave trailing edge (Evans, 2008; Jefferson *et al.*, 2008).

As neonates, Risso's dolphins are grey in colouration but become chocolate brown as juveniles. Skin pigmentation may then lighten as they mature, particularly along the leading edge of the dorsal fin (Evans, 2008). Some adults are completely white (Bearzi *et al.*, 2011), although they often remain dark around the fluke and the distal half of the pectoral fins (Baird and Stacey, 1991; Walker and Cresswell, 2008). As they mature, individuals may also accumulate scars on the surface of the body, which are primarily as a result of intraspecific interactions (Hartman *et al.*, 2008; Evans, 2008).

When born, neonates are typically 1.10 to 1.66m long, being 1.35m on average (Baird and Stacey, 1991). Adults are usually between 3.3 to 3.8m in length, with males often growing slightly larger than females, and they have an approximate maximum length of 4m and weight of 500kg (Evans, 2008). Individuals will reach physical maturity at around 2.30m, followed by sexual maturity at between 2.60 to 2.84m at 8 to 10 years in females and 2.62 to 2.97m at 10 to 12 years in males (Reeves *et al.*, 2002; Amano and Miyazaki, 2004; Raduán *et al.*, 2007; Baird, 2009). Despite the slight differences observed in size and age at maturity with sex, the species is not considered to exhibit sexual dimorphism (Hartman *et al.*, 2008). The average life expectancy is estimated to be around 20 years (Baird and Stacey, 1991), but reproductive females have been identified as old as 38 years (Evans, 2008; Bearzi *et al.*, 2011).

1.1.1. Reproduction

The life history of Risso's dolphins is relatively undocumented compared to other cetacean species, with many aspects of the reproductive strategy e.g. lactation period, not being fully understood (Evans, 2008). What knowledge there is has been largely based on worldwide sighting and stranding events. From the necropsies of 23 females stranded in Japan it was estimated that gestation time is between 13 and 14 months (Baird and Stacey, 1991). Based on sightings, it would appear that calves are born throughout the year (Baird and Stacey, 1991) but the timing appears to vary with geographic location: records in the UK suggest that the majority of births occur between March and July (Evans *et al.*, 2003; Evans, 2008). It is then thought that approximately 2-4 years elapse before the next pregnancy (Amano and Miyazaki, 2004).

1.1.2. Diet and feeding

The diet of a Risso's dolphin is almost exclusively teuthophagic, meaning it primarily preys on cephalopods (Cañadas *et al.*, 2002; Wharam and Simmonds, 2008), consisting of neritic, epipelagic, mesopelagic and bathypelagic cephalopods found in the oceanic waters above the steep continental shelf (Gaspari, 2004), although some small fish and pelagic tunicates may also be eaten (Würtz *et al.*, 1992; Baird, 2002; Azzelino *et al.*, 2008; Baird, 2009; Evans, 2013). Like many odontocetes, they use echolocation in the detection of their prey, and their dentition is specifically adapted for this kind of prey, typically having two to seven pairs of teeth in the lower jaw but no teeth in the upper jaw with the exception of

occasional small vestigial teeth (Reeves *et al.*, 2002; Evans, 2008; Wharam and Simmonds, 2008).

In the UK, stomach contents analysis of five Risso's dolphins from British waters found that the primary prey species was the curled octopus, *Eledone cirrhosa*, followed by the cuttlefish, *Sepia officinalis*, the veined squid, *Loligo forbesi* and the flying squid, *Todarodes sagittatus* (Clark and Pascoe, 1985; Zonfrillo *et al.*, 1988; Santos *et al.*, 1994). There do, however, appear to be regional variations in dietary preferences (Evans, 2013), and there have also been large seasonal variations in prey type observed (Bloch *et al.*, 2012) and resource partitioning between subgroups (Würtz *et al.*, 1992).

The species appears to be a primarily nocturnal feeder, only feeding during approximately 5% of the day, which allows it to take advantage of its prey's circadian vertical migrations towards surface waters (Bearzi *et al.*, 2011). This is potentially the most advantageous time to feed as up to 70% of their prey items are thought to be luminous or have photophores, which also suggests there may be a visual component to feeding (Peddemors, 1999). Groups of Risso's dolphins have been known to exhibit co-operative behaviour whilst feeding, swimming at regular intervals in echelon formation in order to improve the efficiency of foraging. Group diving behaviour has also been observed (Nuno and Pereira, 2008).

1.1.3. Behaviour

Risso's dolphins are gregarious in nature, typically forming groups of between 2 and 50 individuals (Kruse *et al.*, 1999). In UK waters, they are most commonly observed in groups of 6-12 individuals, with groups of up to 20 also being relatively common. Larger groups are seen much less frequently, but 100-200 individuals are occasionally observed together, and these tend to be temporary aggregations composed of several smaller groups, thought to be related to feeding activities or long-distance migrations (Evans, 1992, 2008). Risso's dolphins exhibit the typical surface behaviours associated with cetaceans including porpoising, breaching, spyhopping and tail-slapping (Kruse *et al.*, 1999; Evans, 2008; Baird, 2009). The most common activity is travelling, usually swimming at slow speeds of 2 to 12km/h (Kruse *et al.*, 1999; Evans, 2008; Walker and Cresswell, 2008). They are also known for their aggressive behaviour and intraspecific encounters are assumed to be the

primary cause of the distinctive white scarring often observed on adult individuals as a result of raking from teeth (Hartman *et al.*, 2008; Evans, 2008; Bearzi *et al.*, 2011).

1.2. Distribution

Risso's dolphins have a global distribution, but are found primarily between 60°N and 60°S (Figure 1.2.1.) (Leatherwood *et al.*, 1980; Baird and Stacey, 1991; Reid *et al.*, 2003; Evans, 2008). They are also often observed outside this range e.g. in Norwegian and Faroese waters (Bloch *et al.*, 2012). There is some uncertainty as to whether Risso's exhibit a broad, circum-global range or whether they are limited to continental margins (Jefferson *et al.*, 2014).



Figure 1.2.1. The extent of the expected global distribution (yellow) of Risso's dolphin extant populations (extracted from Taylor *et al.*, 2012)

The waters they inhabit are usually tropical and temperate warm waters ranging from 4.5°C to 28°C (Leatherwood *et al.*, 1980; Evans *et al.*, 2003; Bloch *et al.*, 2012), although they have occasionally been observed where temperatures fall below 10°C (Baird and Stacy, 1991; Evans, 2008; Walker and Cresswell, 2008). They exhibit a preference for steep continental shelf edge and upper continental slope habitats (Wells *et al.*, 2009). In northern European seas this preference has been seen to change seasonally with Risso's being observed around the continental shelf edge more during the winter and migrating inshore to

continental slope near shore waters during the summer (Leatherwood *et al.*, 1980; Reid *et al.*, 2003; Evans *et al.*, 2003; Evans, 2008; de Boer *et al.*, 2013).

Typically they are found in deep waters of between 400 and 1000m (Baird and Stacey, 1991), but in the UK they exhibit a preference for shallower waters of 50-100m (Evans *et al.*, 2003). Around the UK, major populations are estimated to occur mainly in the Hebridean region, Celtic Sea, western English Channel and the Irish Sea (NW and SW Wales and the Isle of Man) but they are uncommon in the North Sea (Figure 1.2.2.). In Wales the distribution is relatively localised, concentrated in a wide band which encompasses west Pembrokeshire, the western Llŷn Peninsula and Anglesey (Baines and Evans, 2012).

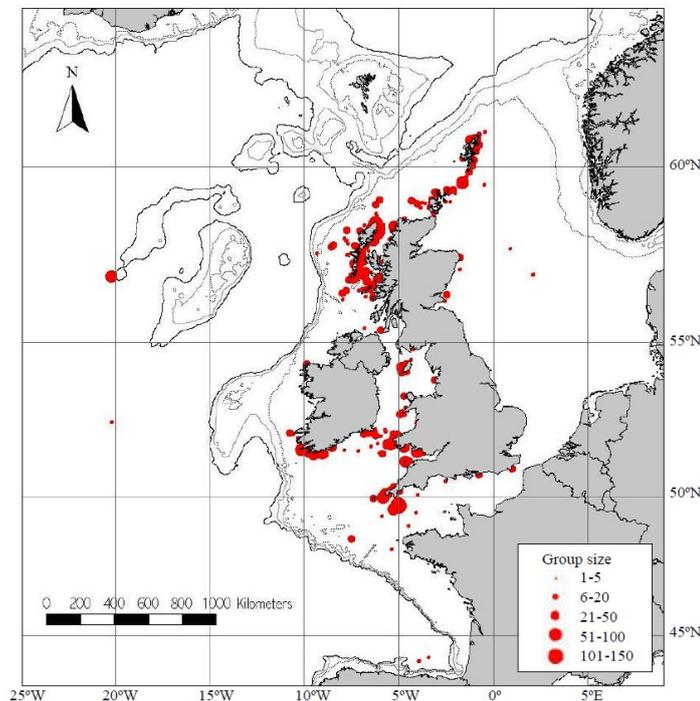


Figure 1.2.2. Map of the Sea Watch Foundation Risso's dolphin sightings around the UK. The size of the red marker indicates the size of the group observed (extracted from Evans *et al.*, 2003)

1.3. Photo-Identification

Photo-identification is a mark-recapture technique frequently used to identify individuals through the use of photographs taken at sighting events (Hammond *et al.*, 1990; de Boer *et al.*, 2013). It is considered an essential monitoring tool, helping to estimate the size and longevity of a population, identify the extent of distribution ranges and site fidelity, and

observe behaviours and patterns of association within populations. The technique is widely used as it is much less invasive than traditional mark-recapture techniques which involve direct contact and artificial marking e.g. tagging, and it is relatively inexpensive (Stewman *et al.*, 2006). Whilst this process is applied to a variety of terrestrial and marine species, it is most frequently applied to cetacean species due to their distinctive markings which render individuals unique and distinguishable, and their elusive nature which makes tagging difficult (Würsig and Jefferson, 1974; Gowans and Whitehead, 2001).

1.3.1. Identification

Cetaceans can be identified by a number of unique morphological characteristics including the shape of the dorsal fin, distinctive markings, pigmentation or lesions on the body, dorsal fin and fluke and the presence of scars (Figure 1.3.1.) (Hartman *et al.*, 2008). Depigmentation is a particularly useful feature to analyse for identification as Risso's dolphins are likely to have white scarring from intraspecific interactions or from interactions with cephalopod prey, and this scarring persists with stability for long periods of time (Casacci and Gannier, 2000; Bearzi *et al.*, 2011). The key features of an individual are then used to compare it to other individuals to find matches and re-sightings. Identified individuals are typically entered into a database and/or catalogue to allow re-sightings to be determined (Hartman *et al.*, 2008).



Figure 1.3.1. An example of dorsal fin photographs used for identification purposes, showing key identification features that can be used to distinguish between individuals including different dorsal fin shapes and scars, nicks, teeth rakes and pigmentation (extracted from de Boer *et al.*, 2013)

There are, however, problems with this process as the appearance of naturally occurring markings can change over time so it may be difficult to re-identify some individuals over long sampling intervals. Furthermore, some individuals are much more easily identifiable or exhibit certain behaviours that mean they will be overrepresented in a catalogue (Gowans and Whitehead, 2001).

1.3.2. Photographic assessment

To assist with the identification process, photographs are often graded on either one or a number of scales which refer to the quality, degree of pigmentation and the markings on the individual, with several different systems being used (Casacci and Gannier, 2000; Gowans and Whitehead, 2001; Hartman *et al.*, 2008). The purpose of this is to eliminate poor quality photos from the identification process and to create categories which group individuals to assist with identification (Stevick *et al.*, 2001).

Studies often use grading systems to assess the photographic quality such as that used by Gowans and Whitehead (2001) for the northern bottlenose whale (*Hyperoodon ampullatus*). This system uses black and white negatives to grade the photographic quality on a scale of Q1 to Q6, with Q6 being the best, based on the focus, exposure, angle of the fin and how much of the fin fills the frame. This index is independent of the markings so is not biased towards individuals with more distinctive markings. Photographic quality is considered to be important when identifying individuals, with Stevick *et al.* (2001) finding a significant relationship between quality and the number of errors occurring in identification, as well as the overrepresentation of those individuals with more distinctive features. Therefore, selectivity with the quality of photographs can help to reduce the rate of error and eliminate bias from overrepresentation.

Unique characteristics of a fin may also be categorised with a varying degree of detail. Pigmentation has been described on a variety of scales: Hartman *et al.* (2008) categorised photographs based on the degree of scarification on a scale of 1 to 6 based on the black skin to white scars ratio on the dorsal fin (Figure 1.3.2.), whereas Casacci and Gannier (2000) defined it on a 1 to 5 scale from black (no marks) to white (covered in marks). Casacci and Gannier (2000) went further with the photographic assessment to assign a coding based on the fin shape and angle of markings, and then located the position of these markings by dividing the body into nine areas to allow for a more precise description.

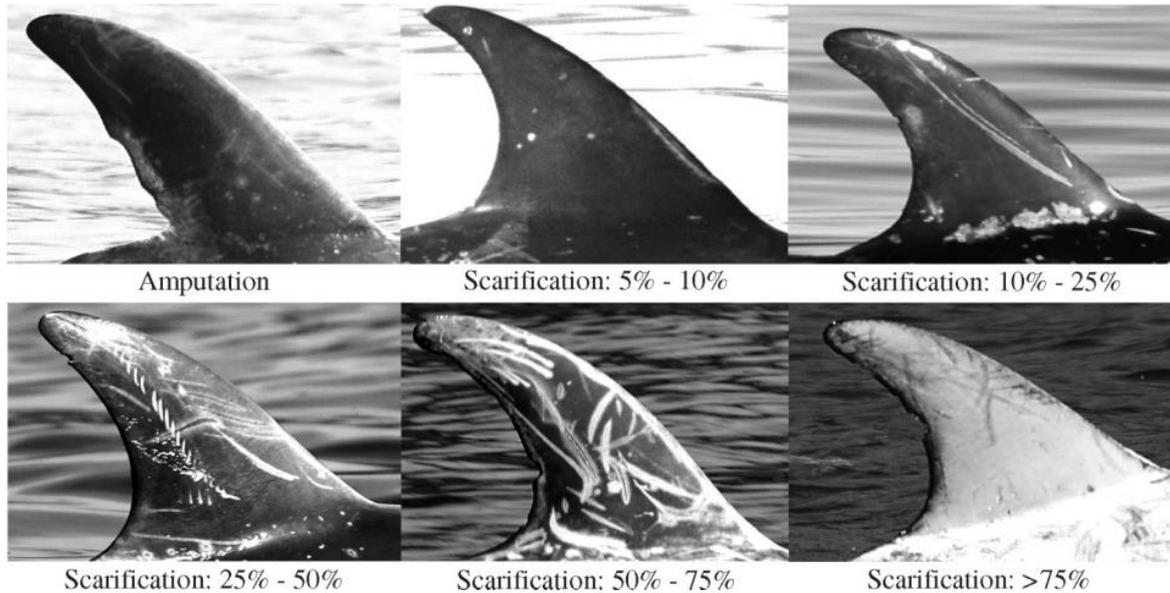


Figure 1.3.2. Categories of dorsal fin scarification used by Hartman *et al.* (2008)

1.3.3. Identification software

With the development of new technologies, the use of computer-assisted dorsal fin matching programs is becoming more common. These programs, such as DARWIN (Eckerd College Dolphin Research Group, Eckerd College, Florida) FinScan (Duke University, North Carolina), FinEx and FinMatch (both EuroPhlukes Initiative, Leiden University, The Netherlands) use traces of the fin or fluke outlines to calculate a dorsal ratio, which is then compared to all existing photos in the catalogue. They create a ranked list of the possible matches, with confidence limits for the nearest match to assist with the decision, thereby speeding up the process and increasing the efficiency of identification (Hillman *et al.*, 2002; Vermeulen *et al.*, 2008; Stewman and Debure, 2011). However, the matches identified by software should not be considered as definitive. They are less reliable when there are few distinguishing features for the matching process, and can therefore produce false positives. Consequently, it is always recommended that matches are checked by one or more observers before they are accepted, although this does have the potential disadvantage of introducing subjectivity to the analysis (Araabi *et al.*, 2000).

1.3.4. Site fidelity and home ranges

The tendency of returning to a previously occupied area is commonly referred to as site fidelity (Switzer, 1993). In cetaceans, site fidelity is often determined through photo-ID studies as wide-scale movement patterns can be established through the re-sighting of

individuals (Würsig and Jefferson, 1974; Leatherwood *et al.*, 1980). Strong site fidelity is considered to be indicative of a resident individual or population (Hartman *et al.*, 2008), although it may simply reflect the repeated return to an area, which may have a seasonal component.

Research indicates that Risso's dolphins exhibit site fidelity, with studies recording the same individuals in Pembrokeshire, Bardsey Island, Anglesey, and the Isle of Man (Baines and Evans, 2012). This suggests that the individuals seen in North Wales and the rest of the Irish Sea may be part of the same population. Identifying frequently visited areas and understanding the drivers of this distribution is essential for identifying potentially critical habitats for the population. The site fidelity of individuals is suggested to vary both seasonally and temporally, and there is evidence of Risso's dolphins performing inshore summer migrations, although the distances and locations of these migrations is not currently well known (Leatherwood *et al.*, 1980; Casacci and Gannier, 2000; Evans *et al.*, 2003; Hartman *et al.*, 2008; de Boer *et al.*, 2013).

Individual home ranges can also be determined through the use of photo-ID. A home range describes the area travelled by an individual to find prey, mate and care for young (Flores and Bazzalo, 2004; Rayment *et al.*, 2009). Individuals do not generally use all areas of their home range with equal intensity and a long-term concentration in certain areas is expected where environmental factors make the habitat most suitable (Samuel *et al.*, 1985). Understanding home ranges is also important for identifying critical habitats and has implications in population management (Rayment *et al.*, 2009).

1.4. Environmental factors affecting distribution

As highly mobile marine mammals, most cetaceans exhibit large-scale migrations and increased site fidelity at areas where they aggregate to feed, socialise, mate or calve. This distribution is influenced by their oceanic environment which experiences complex spatial and temporal heterogeneity (Hastie *et al.*, 2005; Pittman and Costa, 2009). As environmental determinants are dynamic in nature, there appears to be a degree of variation between species and regions (Hastie *et al.*, 2005).

Prey availability is an important determinant of distribution: cetaceans exploit regions with predictably high primary productivity and associated concentrations of prey. Aggregations are thought to be associated with oceanographic features including bathymetry, bathymetric gradients, water mass boundaries and upwelling regions (Hyrenbach *et al.*, 2000) as well as factors such as sea surface temperature (SST) and salinity (Bearzi *et al.*, 2011).

Risso's dolphins have been known to inhabit areas with well-defined physiographic characteristics (Azzelino *et al.*, 2008). Bathymetry has proved to be significantly related to distribution (Gómez de Segura *et al.*, 2008): bathymetric features can improve foraging opportunities by causing localised production, concentrating prey and making it accessible (Hyrenbach *et al.*, 2000). Preferences would also be expected for the depths at which their primary prey species, cephalopods, are found. This is predicted to be at approximately 50 to 300m (de Boer *et al.*, 2014), and around the UK Risso's dolphins have been shown to prefer waters of 50 to 100m (Evans *et al.*, 2003).

Risso's dolphins typically occupy the steep continental shelf edge and upper continental slope habitats. These are thought to be highly productive areas which means the species can be supported in higher densities (Yen *et al.*, 2004; Wells *et al.*, 2009). The bottom gradient has also been found to be an influential factor, with some studies finding them to prefer relatively steep bottom gradients (Baumgartner, 1997; Cañadas *et al.*, 2002; Azzelino *et al.*, 2008).

Risso's dolphins are thought to be found at higher densities where the temperature is more stable with few fluctuations (Kruse, 1989), with some studies finding a positive relationship between distribution and SST (Hastie *et al.*, 2005). Whilst they have a wide range of temperature tolerance (Evans *et al.*, 2003; Bloch *et al.*, 2012) it is thought that changes in SST cause seasonal patterns of distribution. These changes alter prey abundance (Bearzi *et al.*, 2011) as a result of changes in primary productivity (Takao *et al.*, 2012), which is often analysed using chlorophyll α concentration as a proxy (Friedland *et al.*, 2012).

Oceanic thermal fronts occur at the boundary between two water masses that differ in temperature (Miller and Christodoulou, 2014), and are also seen as a proxy for productivity. They support elevated production and retention of phytoplankton and zooplankton where the water masses converge, which results in a high abundance and diversity of pelagic

predators (Hyrenbach *et al.*, 2000; Miller, 2012; Miller and Christodoulou, 2014). The locations of fronts are also thought to be indicative of migratory routes of pelagic species (Hyrenbach *et al.*, 2000), with the seasonality of fronts contributing to the seasonality of distribution (Gannier and Praca, 2006).

Fronts occur frequently in UK shelf seas (Miller and Christodoulou, 2014), and many pelagic biodiversity hotspots have been found to be related to fronts, including the Isle of Man, which experiences high numbers of cetaceans and basking sharks. The upwelling and downwelling regions that occur at fronts cause concentrations of nutrients and primary productivity which in turn attract species at a higher trophic level as there are reliable prey concentrations (Gannier and Praca, 2006; Anderwald *et al.*, 2011, 2012; Baines and Evans, 2012; Miller and Christodoulou, 2014). The location of fronts has proved important in the conservation of pelagic marine species: Miller and Christodoulou's (2014) study of fronts was used in the planning and location of a number of Marine Protected Areas (MPAs) and was an important contributing factor to the recommendation of at least 11 of the 46 Marine Conservation Zones (MCZs) around the UK. These results have provided confidence for the use of long-term remote sensing of fronts as a proxy for pelagic biodiversity (Miller, 2012; Miller and Christodoulou, 2014).

Tidal stratification has been found to be an important indicator of cetacean presence and abundance as previous studies in the Bardsey Island region found that Risso's dolphins were more common when water was well mixed, with a stable salinity gradient. Here, they were sighted more frequently when the tidal stratification was approximately $2.7\text{m}^{-2}\text{s}^3$ which represents the location of tidal fronts where permanently mixed water is separated from seasonally-stratified water (de Boer *et al.*, 2014). Both the Celtic Sea and Irish Sea are well mixed (Miller and Christodoulou, 2014), which makes them potentially suitable for Risso's dolphins (Kruse, 1989), with strong tidal currents, which create a higher energy environment, thought to be more dominant in inshore waters (de Boer *et al.*, 2014). It is, however, difficult to quantify some of these factors and determine their relative influences on the distribution of Risso's dolphins due to their spatial and temporal variation. As a result there are still gaps in the current knowledge in this area (Azzelino *et al.*, 2008).

1.5. Species distribution modelling

Analysing the relationship between any species and its environment has long been an important issue in ecology (Guisan and Zimmermann, 2000). Species distribution models (SDMs) are widely used in biogeography, biology and ecology to estimate these relationships and have evolved with the development of statistical techniques and GIS tools, with multiple methods now available (Elith *et al.*, 2011). They work on the principle that the potential spatial distribution of a species can be predicted by relating the locations of their presence and/or absence to predictor variables that are known for these locations. Consequently, they are of particular importance for conservation management (Guisan and Zimmermann, 2000; Phillips *et al.*, 2004).

Where presence and absence data are available, general-purpose statistical methods can be used for modelling (Phillips *et al.*, 2006). These include logistic linear regression, generalised linear modelling (GLM), generalised additive modelling (GAM), neural networks, ordination and classification models and Bayesian models, or a combination of these techniques (Guisan and Zimmermann, 2000). In recent years, these multivariate models have evolved to include generalised mixed models and general estimating equations (GEE's), to account for issues such as spatio-temporal autocorrelation and zero inflation. Modelling using presence-absence data is most effective when the data have been sampled in a systematic manner (Hastie and Fithian, 2013).

The distribution of a species is however often only indicated by presence data. This is particularly true for cetaceans as many locations are not surveyed systematically or receive very little survey effort, leading to a lack of definitive absence data. Alternatively, if absence data are available, they can be of questionable reliability as they are difficult to assess in the field (Guisan and Zimmermann, 2000; Graham *et al.*, 2004). To address this issue, the maximum-entropy (Maxent) approach to species distribution modelling was introduced. Maxent modelling estimates the target distribution by finding the distribution of maximum-entropy, or most uniform distribution (Baldwin, 2009), using the presence-only data as the location of the species and the environmental variables to predict suitable areas of habitat (Phillips *et al.*, 2004), and is therefore considered to be a potentially valuable technique (Graham *et al.*, 2004).

1.6. Aims and objectives

The first aim of this research is to construct a photo-ID catalogue of Risso's dolphins observed in Welsh coastal waters from 2007 to 2014 using mark-recapture in order to identify individuals and repeat sightings. Matches with other catalogues will then be determined to allow site fidelity and home range sizes to be estimated.

The second aim is to determine the effects of environmental factors on the distribution of Risso's dolphins in the Irish and Celtic Seas. A predictive habitat SDM will be created using sightings data and available environmental data to determine potentially suitable sites for Risso's dolphins around the UK on a spatial, seasonal and inter-annual basis. This model will be used to identify key areas of habitat that are important to Risso's dolphins to assist with the conservation and management of the species.

1.7. Hypotheses

The hypotheses that this project will address are:

- 1) The dorsal fin and flank markings will enable individual Risso's dolphins to be identified.
- 2) Individuals will exhibit different degrees of site fidelity and occupy varying home ranges.
- 3) The spatial and temporal patterns of distribution of Risso's dolphins will be dictated by environmental factors.

2. METHODOLOGY

This project consisted of two major areas of study: the use of photo-identification to identify individuals and determine site fidelity and home ranges, and the analysis of environmental variables to examine the key determinants of distribution and enable the prediction of suitable areas of habitat using species distribution modelling. Understanding regions frequented by Risso's dolphins and areas with suitable habitat is important as it has implications for conservation management (de Boer *et al.*, 2013).

2.1. Study area

The overall study focused upon Risso's dolphins in the waters around the British Isles, with particular emphasis on the Irish Sea. The photo-identification and site fidelity study was conducted using all images collected by the Sea Watch Foundation (SWF) from 2007 to 2014 in Welsh coastal waters, and home ranges were examined in the Irish and Celtic Seas and Hebridean waters (Figure 2.1.1.).

Data were collected for the environmental factors under consideration from the Irish Sea and Celtic Sea for analysis (Figure 2.1.1.). These were selected as studies have shown that there are a number of locations within this area where high densities of Risso's dolphins are seen, e.g. around the Isle of Man and Bardsey Island, North Wales (Baines and Evans, 2012; de Boer *et al.*, 2013). SDMs were then expanded from this area in order to enable the prediction of potential areas of suitable habitat for Risso's dolphins around coast of the British Isles.

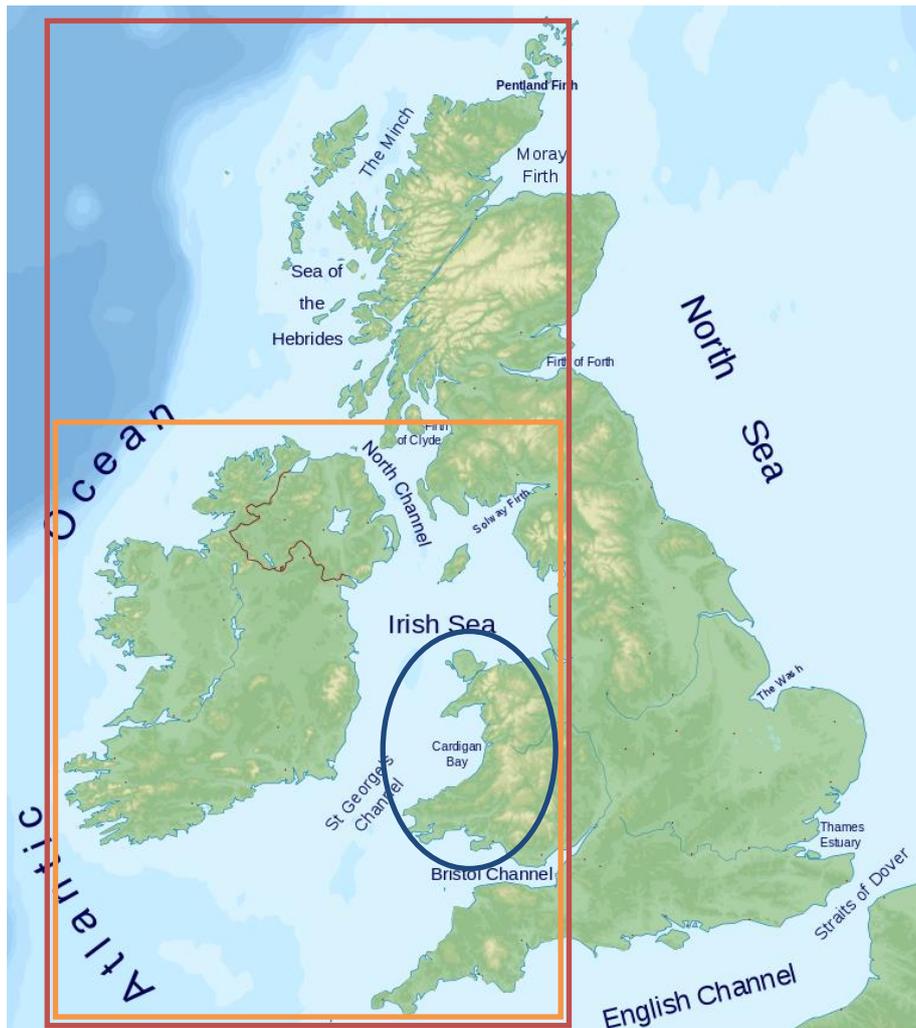


Figure 2.1.1. *The study areas selected for photo-identification and site fidelity (blue oval), home ranges (red square), environmental variables (orange square) and species distribution modelling (British Isles)*

2.2. Photo-identification

In order to produce a photo-identification catalogue, 1529 images taken between 2003 and 2014 were supplied by the SWF. There were 88 sightings in Welsh waters during this period but photographs were only available from 30 of these. All photographs from 2003 to 2005 resulted from sightings in Cardigan Bay and from 2007 to 2014 they were all taken in the North Wales region. There were no images available for 2006.

Prior to identification, all photographs underwent quality control. The scale used to rate the photographic quality was based on that used by Gowans and Whitehead (2001) with the main difference being that original digital images were used instead of black and white

negatives. This was considered to be an appropriate scale to use as it considers a number of parameters: the focus of the image, exposure, angle of the fin and the proportion of the image filled by the fin. Prior to identification all the images were assigned a quality rating (Q value) on a scale of 1 to 6 based on these parameters (Table 2.2.1.). Images were of varying quality for a variety of reasons including the photographers' level of experience with cetacean photo-ID, the quality of camera equipment, the distance away from the Risso's dolphins and the weather conditions on the day. Only photographs rated Q4 and above were taken forward to be identified: this decision was based on a photo-ID study of white sharks which concluded that only photographs of Q4 or higher were of adequate quality to allow individuals to be recognised and 'recaptures' made between sightings (Towner *et al.*, 2013). Of the 1529 photographs, 1214 were graded Q4 and above and kept for identification. Some images contained multiple fins so were retained for all fins present that were of Q4 and above, and all low quality fins in the photographs were ignored during the ID process.

Table 2.2.1. The scale used during photographic assessment to determine the quality of Risso's dolphin dorsal fin images, based on the descriptions by Gowans and Whitehead (2001)

Quality rating	Description
Q1	<i>Very distant, poor focus and very little flank showing, fin not square on</i>
Q2	<i>Very distant photograph with little flank showing</i>
Q3	<i>Distant photograph with little flank showing</i>
Q4	<i>Distant photograph with most of the flank showing</i>
Q5	<i>Close with good representation of the flank</i>
Q6	<i>Close photograph with most of the flank showing, well focussed and exposed image, fin square on to camera</i>

The individuals in the photographs graded Q4 and above then needed to be identified: to assist with the identification process, these photographs were entered into DARWIN 2.22 dorsal fin ID software. Whilst this software is more frequently applied to bottlenose dolphins, it was considered appropriate to use as Risso's dolphins share several characteristics with bottlenose dolphins, with large, distinctive dorsal fins and are also known to exhibit intraspecific aggressive behaviour, similar to bottlenose dolphins, which

results in their dorsal fins often becoming damaged over time, giving many individuals unique fin features (Stewman *et al.*, 2006; Evans, 2008; Bearzi *et al.*, 2011). However, pigmentation is also an important factor in Risso's identification due to their change of colouration with maturity (Evans, 2008). This is something DARWIN does not take into account, so visual observation was also used to help determine the identity of each individual.

Photographs were uploaded individually to the software. Prior to matching, photographs were then modified to improve the clarity of the image. Photographs were magnified or cropped at high resolution if the fin was taken at a distance, and if several dolphins were present in the frame it was entered and cropped multiple times to frame each individual. If necessary, the contrast was also enhanced to allow any pigmentation to be seen more clearly, although no pigmentation grading system was used. All right facing images were then flipped as DARWIN will only match fins when they are swimming to the left. Each fin shape was then traced to create an outline showing the position of key features including the base of the leading and trailing edges of the fin, the position of the tip and any prominent nicks or notches on the leading and trailing edges of the fin. The software then compared this trace to any existing photographs in its database and used a ranking system to determine how closely the trace matched that of the individuals already in the database: the 69 individuals already in the SWF database and catalogue were entered first so that matches to known individuals could also be made (Stewman and Debure, 2011).

Using the shape of the dorsal fin as a basis for ID to rank images with similar outlines, visual identification then took place in order to determine whether DARWIN had suggested a correct match or if the individual was new to the database and had not yet been identified. As part of this process individuals were examined using other morphological characteristics including distinctive markings, scarring, pigmentation and lesions (Hartman *et al.*, 2008). This was particularly important when considering individuals with no distinctive nicks or dorsal fin shape as these were often similar looking and therefore harder to identify.

All photographs were either matched to an existing individual or given a new unique identification number. All individuals seen after 2007, when serious data collection began for Risso's dolphins in the area, were numbered in the same format as those already entered in the catalogue. These were given a three digit number which referred to the year in which

the dolphin was first observed, starting at 001 to represent 2007 and continuing for each consecutive year, followed by a two-digit number represented an individual ID number, starting from 01 in each year. Individuals observed prior to 2007 could not be numbered in exactly the same way, so were instead given a four digit number which was the year they were first seen in, and then an individual ID number as before. A simple lettering system was used to grade the degree of marking on each individual: ‘W’ indicated a well-marked individual with distinctive nicks or missing sections of the fin, ‘S’ indicated an individual that was slightly-marked with more subtle nicks in the fin outline and ‘L’ and ‘R’ indicated an individual that was photographed from the left or right side respectively that had unique markings on the dorsal fin side and flank, but had no distinctive fin shape, meaning an individual’s left and right side could not be reliably be matched (Figure 2.2.2.). As an example, the first individual seen for the first time in 2009 with distinctive marking would be given the ID number 003_01W.

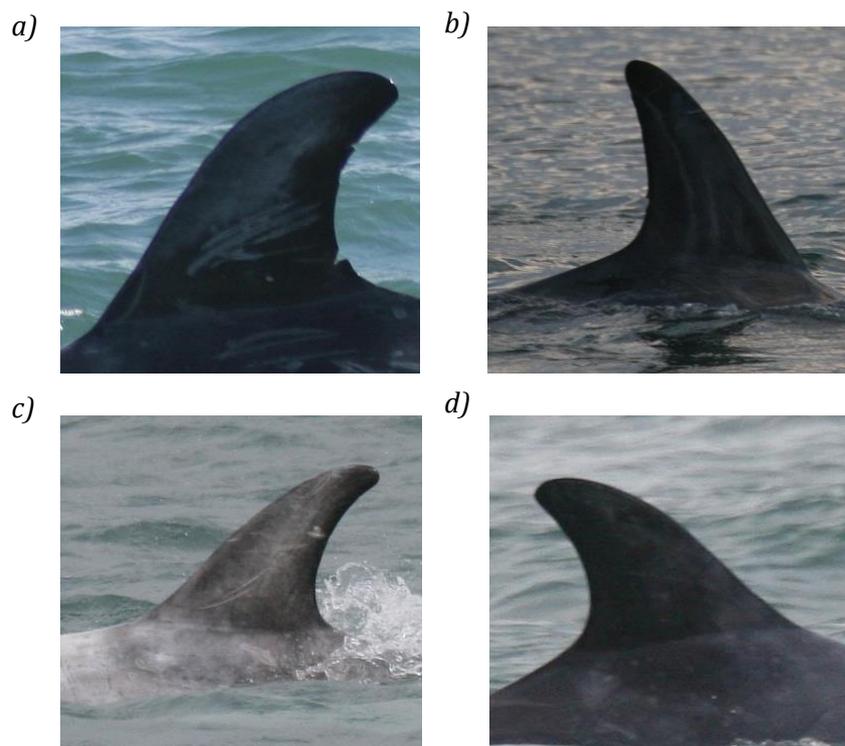


Figure 2.2.2. *Examples of individuals in the Sea Watch Foundation catalogue that were categorised as a) well-marked (W), b) slightly-marked (S), c) left (L) and d) right (R) based on dorsal fin characteristics*

Ancillary information was also entered into the SWF database. This included the date of the sighting from which each individual was first identified, whilst the marking and

orientation of the fin were also entered into a separate column. The sex of the individual was entered, whether it was known or unknown, and the method used for determination, for example, if the same individual was present with a calf on multiple occasions it was assumed to be female.

The numbers of well-marked, slightly-marked, left and right individuals were calculated and used to determine the minimum and maximum number of individuals identified over the study period. It was determined that there was neither the data nor current knowledge to apply a mark-recapture analysis to estimate the population size, so in the absence of being able to use this technique, an estimate was made of the minimum number of different individuals encountered during the study period. In order to calculate this, the mean proportion of the individuals observed that had some degree of identifying mark on the dorsal fin was calculated by dividing the number of identified individuals in each sighting by the best estimate of the number of individuals that were observed. The best estimate of the group size was however only available for 13 out of the 30 photographed sightings, so the calculation could only be performed using these data. The minimum number of individuals encountered could then be calculated by adding the number of dolphins that could be identified from both sides with the higher number of left and right fins, multiplying by 100, then dividing this by the proportion of marked individuals:

$$\frac{('W'+ 'S'+ 'L' \text{ or } 'R') \times 100}{\text{proportion estimated to be marked}}$$

2.2.1. Site fidelity

The number of individuals sighted on 2 or more occasions was determined by examining the matches within the SWF catalogue. This information was then used to estimate site fidelity by calculating a re-sightings rate as used by de Boer *et al.* (2014). Site fidelity was calculated as the percentage of the estimated number of individuals re-sighted from 2003 to 2014.

2.2.2. Home ranges

Once the SWF catalogue was up to date and individuals in Welsh waters had been identified, attempts were made to match these with individuals recorded in other Risso's dolphin catalogues compiled for other areas around the UK and Ireland to examine home ranges. The organisations which provided access to their catalogues were: Whale and Dolphin Conservation (WDC) - Bardsey Island, from 1997 to 2007; Manx Whale and

Dolphin Watch (MWDW) - Isle of Man from 2009, 10 and 13; the Hebridean whale and Dolphin Trust (HWDT) - Hebrides from 2005 to 2014; Marine Discovery, Cornwall from 2009 to 2011 and the Irish Whale and Dolphin Group (IWDG), Republic of Ireland from 2005 to 2012.

Once matches had been identified, a table was created to show the number of matches between the SWF catalogue and those of the five other organisations in order to identify which areas were most commonly frequented by the Risso's dolphins seen in Welsh waters. This information was used to determine the approximate spatial distribution over time and examine home ranges by creating a table to show the years and locations each matched individual was observed in (Leatherwood *et al.*, 1980; Hartman *et al.*, 2008; de Boer *et al.*, 2013).

2.3. Sightings data

The data regarding the sighting of Risso's dolphins were obtained from the SWF sightings database. Data were extracted for all months of each year from 2007 to 2013, and these encounters were also entered into the photo-ID database. The number of sighting events and the number of individuals seen in each month for all years were calculated in order to determine the total number of sightings and individuals and to examine seasonal and temporal patterns in occurrence. The number of sightings and individuals per month for the seven year period were then used to calculate the mean number of individuals seen at each sighting to allow a seasonal and temporal analysis to be made of the changes to group size. It should however be noted that the sightings data were not corrected for effort, so were analysed as raw values rather than sightings or individuals per unit effort.

The latitude and longitude of each sighting were then used to plot the sightings information as a point layer using ArcMap 10.1, with Mercator equal area projection, to determine the distribution of sightings within the study area. The best estimate of the number of individuals seen at each of the sightings was plotted to show the areas of highest density and a graduated colour scale was used to indicate the group size.

2.4. Environmental variables

Eight environmental variables which *a priori* knowledge suggested may be important factors in determining the distribution of Risso's dolphins were examined: habitat type, combined wave and tidal energy, bathymetry, slope, oceanic thermal fronts, salinity, SST and chlorophyll α concentration (Cañadas *et al.*, 2002; Azzelino *et al.*, 2008; Bearzi *et al.*, 2011; Baines & Evans, 2012; de Boer *et al.*, 2014). Data were obtained for each of these variables for the area -12 to -0.5°W and 60 to 49°N with the exception of oceanic fronts which were only available for a region of the Irish Sea from -7 to -2.2°W and 54.5 to 51°N. All variables were added separately to the layer of sightings data using the same projection as mentioned previously, looking at only the Irish and Celtic Seas, to determine the conditions under which Risso's dolphins had been observed, with the exception of SST and chlorophyll α which were analysed as time series from 2007 to 2013.

Habitat type, combined wave and tidal energy and bathymetry data were obtained from the European Marine Observation and Data Network (EMODNET). The habitat type and energy data were acquired from the EMODNET EUSeaMap pilot portal for broad scale modelled seabed habitat. These data were in a polygon format, containing multiple layers of data which were selected in order to plot the desired environmental variable. The habitat type was mapped using the 'Grouped' layer which assigned each cell to a habitat type which was considered to be a simplified classification of the EUNIS habitat codes applied to all EUSeaMap regions. It used a combination of biological zones, substrate type and depth to assign these habitats. All abyssal habitats were removed from the layer as the area of interest did not extend beyond the bathyal classification. The combined wave and tidal energy was mapped using the 'combenergy' layer which assigned each cell an energy of 'high', 'medium' and 'low' where for wave energy, 'high' > 1160 Nm⁻², 'medium' = 130-1160 Nm⁻² and 'low' = 0-130 Nm⁻², and for tidal energy, 'high' > 1200 Nm⁻², 'medium' = 210-1200 Nm⁻² and 'low' = 0-210 Nm⁻². The bathymetric data were sourced from the EMODNET Hydrography mapping portal at a cell size of 0.00416667km². These data were then used to calculate the slope of the area in ArcMap 10.1 using the Slope tool. The slope was determined as the percentage change in gradient from each cell in the raster surface to its neighbour with a z factor of 1 to determine the steepest downhill descent from that cell: when the change in angle was 45°, the rise in percentage was equal to 100 and as the slope angle approached 90° the percentage rise approached infinity.

Data regarding oceanic thermal fronts were obtained from Miller *et al.*, (2010) who used data from the Advanced Very High Resolution Radiometer (AVHRR) archive collected from 1998 to 2008 in the Irish Sea. The maximum spatial resolution of the data was 1.1km, which was considered sufficient for the detection of all scales of fronts that might have relevance to pelagic diversity. These data showed the frequency of front occurrence during each of the four seasons: only data for the summer season were used as the Celtic Sea front is present for 90-100% of that season compared to 50% in spring, 40% in autumn and absent in winter. These data were plotted along with the sightings that occurred during this season (June, July and August) over the seven year period to determine if the location of a front affected the species distribution.

Salinity, SST and chlorophyll α concentration, data were obtained from satellite observations from MyOcean. As salinity was not determined to be highly variable over the period studied, it was averaged over the seven year period to create one image to compare with the sightings data.

Two locations that *a priori* knowledge suggested were potential hotspots for Risso's dolphins (Baines and Evans, 2012; de Boer *et al.*, 2013) were selected for SST and chlorophyll α time series: the waters around the Isle of Man and the waters around Anglesey and the Llŷn Peninsula in North Wales. An area spanning from -5.1 to -4.0°W and 53.8 to 54.5°N was created around the Isle of Man and from -5 to -4.1°W and 52.6 to 53.7°N around the North Wales coast, and the number of individuals within this area was calculated for each month from 2007 to 2013 (Figure 2.4.1.). An average monthly SST and Chlorophyll α concentration were then calculated for these areas and plotted as a time series to determine if the number of individuals seen was affected by these variables both seasonally and temporally.



Figure 2.4.1. The areas selected for time series analysis using sea surface temperature and chlorophyll α data around the Isle of Man (red box) and North Wales (purple box)

2.5. Maxent species distribution modelling

In order to estimate the relationship between the distribution of Risso's dolphins and the environmental variables under consideration, species distribution modelling was performed. Maxent distribution modelling was selected, whereby the target probability distribution of a species is estimated based on the probability distribution of the maximum entropy. This approach was appropriate for use as, although presence-absence data were available for the study area (Baines & Evans, 2012), using presence only to indicate the occurrence of the species allowed the utilisation of more sightings data, thus boosting sample sizes for these analyses. It works effectively with both the continuous and categorical variables present in the data set (Phillips *et al.*, 2004, 2006; Elith *et al.*, 2011). It is considered to be a highly valuable method of modelling (Graham *et al.*, 2004), despite not being as mature as other SDM methods like GLMs (Phillips *et al.*, 2006), and has important implications for determining potential areas of suitable habitats in relation to the conservation of a species (Phillips *et al.*, 2004; de Boer *et al.*, 2014).

Modelling was completed using Maxent version 3.3.3k. The data used to represent presence in the model were the known locations of Risso's sightings from the SWF

database. The environmental variables selected were all those previously discussed, with the exception of oceanic fronts as those data covered too small an extent. Salinity, SST and chlorophyll α were examined as seven-year averages in the main model, and separately as yearly and monthly averages to determine the seasonal and inter-annual changes in habitat suitability. The full extent of the sourced environmental data (12 to 0°W and 60 to 49°N) was used for modelling to enable suitable locations for Risso's dolphins to be predicted for areas where surveying had not taken place.

These data, however, had to be manipulated in ArcMap 10.1 before the model could be run. All variable rasters had to be of the exact same cell size and extent (Phillips, 2011), so the rasters were adjusted to a cell size of 0.005 km⁻² using bilinear interpolation, as this was the highest resolution of any variable, and were clipped to the extent of 12 to 0°W and 60 to 49°N. Maxent also requires all files to be in ASCII format so all clipped rasters were then converted into ASCII files in ArcMap 10.1 before being inputted to the model.

The majority of the default parameters of the Maxent programme were used with the exception of the random test percentage. In this model it was set to 25%: this allows a certain percentage of the presence data to be used as test data which are then withheld and used to evaluate the model's performance which is important in reducing bias in the model (Phillips *et al.*, 2006).

The model produced a map in the form of a continuous raster, with violet squares to indicate the sightings used as test locations and white squares to indicate the sites used for training locations. The colours were shown on a logarithmic scale of 0 to 1 to allow the changes to be seen more clearly. Warmer colours (red) indicated areas predicted to have highly suitable environmental conditions, whilst colder colours (dark blue) indicated areas where predicted conditions were unsuitable and therefore less likely to have Risso's dolphins present (Phillips, 2011).

Additional outputs were also selected so that response curves and jackknife testing to measure variable importance were also produced. Response curves were produced for each variable in the model to show how each affected the Maxent prediction. These comprised a graph which showed how the predicted probability of habitat suitability in terms of the logistic prediction of presence (y axis) changed as the specified metrics for each

environmental variable (x axis) also changed. These could be produced as the model was exponential, therefore meaning that the probability allocated to each cell was proportional to the exponential of the selected combination of variables (Baldwin, 2009).

The jackknife tests of variable importance were performed to estimate the variables with important individual effects (Elith *et al.*, 2010). This method works by running the model, excluding one variable at a time, which allows information to be produced regarding the performance of each variable in the model in terms of its importance in explaining the species distribution and the unique information it provides (Baldwin, 2009). This alternative way of estimating the variable importance was selected rather than a table to show the analysis of percentage contributions as the values from the table were only heuristically defined as they were dependent on the coding Maxent used. Therefore, multiple runs of the same model may have resulted in different percentage contribution values, depending on the algorithm the model used (Phillips, 2011).

3. RESULTS

3.1. Photo-identification

1214 photographs that were classified Q4 and above and suitable for identification. From these, a minimum of 144 different individuals were estimated to have been identified from sightings in Welsh waters from 2003 to 2014 (Table 3.1.1.). This figure was based on the number of well-marked and slightly-marked individuals seen during each year plus the number of right side individuals as this was the higher of the left and right counts. The maximum number of individuals that could have been observed if all left and right fins belonged to different individuals was 209, but it was decided that the minimum estimate was more likely to be accurate as, in all years except 2013, the difference between the left and right fin counts was between 0 and 2 individuals, so it was assumed that the majority of left and right sides belonged to a single individual.

There were more left and right individuals identified, with approximately 56.25% having no distinguishing fin outline, compared to 43.75% with a unique identifiable fin shape. At least 12 well/slightly-marked and 25 left and right individuals (25.7% of the population) were thought to be female due to the presence of a calf in one or more photographs. On a seasonal basis, female-calf pairings were observed from July to October, with 16 of these occurring in October. On an annual basis, they were seen during 6 of the 11 years, with the greatest number (16) occurring in 2009. Only 1 individual was categorised as definitely being male. The most sighting events with associated photos for ID occurred in 2009, which was also the year when the most new individuals were identified.

Table 3.1.1. The number of individuals in the Sea Watch Foundation catalogue identified as well-marked, slightly-marked, left and right individuals based on dorsal fin characteristics, and the number of photographed sightings from 2003 to 2014

Year	Well-marked	Slightly-marked	Left	Right	Minimum estimate	Maximum estimate	No. of sighting events
2003	2	1	1	2	5	6	2
2004	0	1	1	3	4	5	2
2005	0	2	12	10	14	24	3
2006	0	0	0	0	0	0	0
2007	5	9	8	9	23	31	3
2008	8	7	0	1	16	16	3
2009	6	3	27	27	36	63	7
2010	1	7	7	9	17	24	1
2011	1	3	4	3	8	11	2
2012	1	0	1	0	2	2	1
2013	1	4	1	12	17	18	1
2014	1	0	3	5	6	9	5
Total	26	37	65	81	144	209	30

From the 13 best estimates of the group size available, 130 out of 146 dolphins observed were identified, resulting in 89% of individuals being marked. An estimate for the minimum number of different individuals encountered during the study period was then made. The number of right sides was used for this calculation as this was the higher of the two left and right counts. The number encountered was estimated at 162 Risso's dolphins:

$$\frac{(26+37+81) \times 100}{89} = 161.80.$$

3.2. Site fidelity

During the study period, 18 individuals in the SWF Welsh catalogue were re-sighted, representing 12.5% of the individuals seen, based on the minimum estimate of the number of individuals: 15 on two occasions and 3 on three occasions. Of those re-captured, the most were well-marked (6) and slightly-marked (6), and very few were those without a distinctive fin shape, with 3 right and 3 left. The most re-sightings occurred in 2008 when 8 individuals were re-sighted within that year. Individual 001_22L had the longest period between first and last sighting, from 2007 to 2014. No re-captures occurred in 2003, 2005, 2012 or 2013 (Table 3.2.1.).

Table 3.2.1. The individuals from the Sea Watch Foundation catalogue identified in two or more sightings, from 2003 to 2014. Ticks indicate the number of times an individual was identified in each year

ID	2003	2004	2005	2007	2008	2009	2010	2011	2012	2013	2014
001_07R				✓		✓					
001_13L				✓				✓			
001_22L				✓			✓				✓
002_01W					✓✓						
002_03S					✓✓						
002_04S					✓✓						
002_07W					✓✓						
002_08W					✓✓	✓					
002_09W					✓	✓					
002_10S					✓✓						
002_12S					✓✓						
002_13S					✓		✓				
002_14S					✓	✓					
002_15W					✓✓	✓					
004_01W							✓	✓			
004_12L							✓	✓			
004_22R		✓					✓				
008_02R											✓✓

3.3. Home ranges

The examination of home ranges using the five catalogues covering different regions found a total of 23 matches with the SWF catalogue (Table 3.3.1.), equating to 16.1% re-sighted around the British Isles. Matches indicated that the home range of the dolphins identified in the SWF catalogue is relatively small, with the most individuals (15) being matched with the WDC Bardsey Island catalogue, and a small number of matches were also made with the MWDW catalogue in the Isle of Man. Only 2 matches were made with the HWDT catalogue. These were the furthest matches made, equating to travelling a distance of approximately 550km. No matches were made between the catalogues of SWF and Marine Discovery or IWDG.

Table 3.3.1. The number of individuals from the Sea Watch Foundation catalogue that were matched with the Risso’s dolphin catalogues of Marine Discovery, the Irish Whale and Dolphin Group, the Hebridean Whale and Dolphin Trust, Manx Whale and Dolphin Watch and Whale and Dolphin Conservation (Bardsey Island)

Catalogue	No. of individuals matched
Marine Discovery	0
IWDG	0
HWDT	2
MWDW	6
WDC	15
Total	23

From the matching results, it can be seen that three of the individuals re-sighted by the SWF on two occasions were matched with other catalogues: two were seen twice more around Bardsey Island and the third individual was seen once around the Isle of Man. The two individuals that were re-sighted in the Hebrides were observed two years apart in Welsh waters both in the same year within four days of each other but approximately 190km apart. The individual identified over the longest time period was 002_07W which was first seen in waters around Bardsey Island in 1997 at the start of the catalogue, and then again in 2002. It then appeared six years later in the SWF catalogue where it was observed twice in 2008, giving a total of 11 years between the first and last sightings.

Table 3.3.2. The individuals from the Sea Watch Foundation catalogue matched with each catalogue, and the years and locations of matches

SWF no	SWF dates		Catalogue matched with	Year matched		Location
2004_03R	2004		WDC	2005		Bardsey Island
001_01S	2007		WDC	2007		Bardsey Island
001_02S	2007		WDC	2007		Bardsey Island
001_04S	2007		MWDW	2009		Isle of Man
001_05W	2007		WDC	2007		Bardsey Island
001_08W	2007		WDC	2007		Bardsey Island
001_10S	2007		MWDW	2009		Isle of Man
001_18W	2007		MWDW	2009		Isle of Man
001_19R	2007		WDC	2005		Bardsey Island
002_05W	2007		WDC	2001	2006	Bardsey Island
002_07W	2008	2008	WDC	1997	2002	Bardsey Island
002_11S	2008		MWDW	2009		Isle of Man
002_14S	2008	2009	WDC	2001	2006	Bardsey Island
003_01W	2009		HWDT	2013		Kallin harbour, Grimsay
003_09R	2009		WDC	2005		Bardsey Island
003_18S	2009		MWDW	2009		Isle of Man
003_56R	2009		WDC	2005		Bardsey Island
004_01W	2010	2011	MWDW	2009		Isle of Man
004_07R	2010		WDC	2004		Bardsey Island
004_08S	2010		WDC	2007		Bardsey Island
004_13L	2010		WDC	2005		Bardsey Island
005_02W	2011		HWDT	2013		Butt of Lewis, Hebrides
005_02W	2011		WDC	2002		Bardsey Island

A map was also created to provide a visual representation of the approximate locations where a number of the Risso's dolphins were observed (Figure 3.3.1.). This shows that the home ranges of each individual were highly variable with one individual appearing to stay around the North Wales coast (002_05W), and another which was seen to travel from North Wales at least as far as the Isle of Man (004_01W). The two individuals (003_01W and 005_02W) which showed the longest migrations were also mapped to show the extent of their home range.



Figure 3.3.1. A map of the British Isles to show the extent of the predicted home ranges of four individuals: 002_05W (yellow stars), 003_01W (blue stars), 004_01W (red stars) and 005_02W (orange stars)

3.4. Sightings data

Between 2007 and 2013 there were 473 sightings of Risso's dolphins within the Irish and Celtic Seas, in which a total of 2740 dolphins were observed. These sightings were recorded from a mixture of dedicated vessel surveys, platforms of opportunity and land-based watches.

A clear seasonal pattern was observed in the number of sightings observed in this area (Table 3.4.1.). There were very few sightings in the first and last two months of each year, with the number of sightings increasing towards the middle of the year. The maximum number of sightings over the period studied occurred in the month of May (90), although no sightings were reported in May 2009. The subsequent months of June, July and August also showed a high number of sightings, suggesting the greatest presence of Risso's dolphins happens in the late spring and summer months. The inter-annual changes did not appear to follow such a distinct pattern (Table 3.4.1.). The greatest number of sightings (95) occurred in 2009, and the fewest (47) in 2012, and there was a degree of inter-annual variation. The data suggested that years with higher numbers of sightings (e.g. over 60), may be followed by a lower number of sightings (e.g. below 60), in subsequent years: 2007 and 2009 were both years with high sighting numbers which were followed by one and three years of low sightings respectively.

Table 3.4.1. The number of Risso's dolphin sightings for each individual month from 2007 to 2013, recorded as the frequency of sightings across the study area

	2007	2008	2009	2010	2011	2012	2013	Total
January	0	0	0	1	0	0	1	2
February	0	0	0	0	2	1	0	3
March	1	0	11	2	3	5	1	23
April	8	8	9	5	2	1	1	34
May	33	14	6	10	0	9	18	90
June	8	5	32	10	4	6	18	83
July	12	2	9	6	19	8	28	84
August	6	12	9	14	17	8	6	72
September	4	9	17	4	6	5	5	50
October	6	6	2	1	2	3	6	26
November	0	0	0	1	0	0	2	3
December	0	1	0	1	0	1	0	3
Total	78	57	95	55	55	47	86	473

Seasonal patterns were also observed in the number of individuals seen, exhibiting a very similar pattern to the number of sightings. Very few individuals were present in the first and last two months of each year, with peaks observed in the middle of the year (Table 3.4.2.). The greatest number of individuals was seen in June (638), and the fewest in February (7), whilst more than 300 individuals were seen per month between May and September. On an annual basis, the most individuals were seen in 2013 (640) and the fewest in 2008 (268), with no obvious inter-annual pattern.

Table 3.4.2. The estimated number of Risso’s dolphins observed for each individual month from 2007 to 2013, recorded as the frequency of observed individuals across the study area

	2007	2008	2009	2010	2011	2012	2013	Total
January	0	0	0	9	0	0	3	12
February	0	0	0	0	6	1	0	7
March	2	0	16	11	10	16	4	59
April	22	18	18	14	20	5	27	124
May	147	49	41	40	0	33	141	451
June	33	27	256	80	12	104	126	638
July	38	24	56	62	94	37	195	506
August	37	66	31	80	126	63	53	456
September	27	54	131	26	42	23	21	324
October	20	24	2	14	5	10	59	134
November	0	0	0	5	0	0	11	16
December	0	6	0	1	0	6	0	13
Total	326	268	551	342	315	298	640	2740

Group size was highly variable over the seven year period (Figure 3.4.1.). Evans (1992, 2008) suggests that Risso’s are most commonly observed in groups of between 6 and 12 individuals. In this study, the mean group size was calculated to be within this range during 23 months, but was below this range for 37 months. The expected size was exceeded in June, July, August and September during 4 years, and was highest in April 2013 when the mean group size was 27.

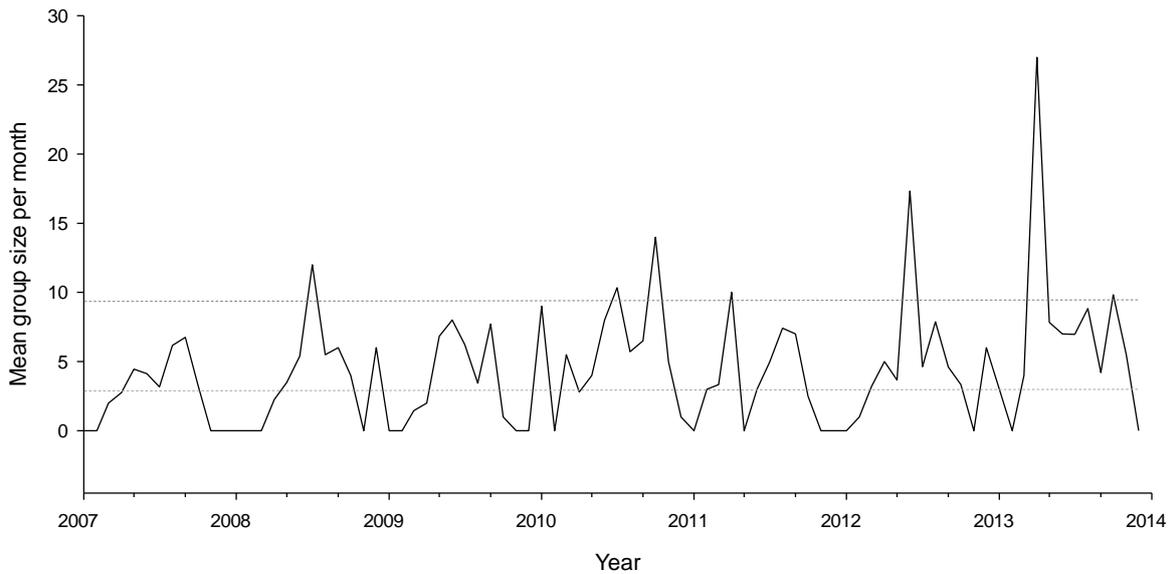


Figure 3.4.1. A time series of the mean group size of Risso's dolphin per month from 2007 to 2013

3.5. Environmental variables

The sightings data showed that over the seven year period, sightings were concentrated mostly around the Isle of Man, the north-west and south-west Welsh coasts and the south coast of the Republic of Ireland. The majority of sightings were concentrated in inshore waters around these coasts. These sightings data were then plotted in conjunction with each of the environmental variable layers (Figures 3.5.1-3.5.6).

3.5.1. Habitat type

Around the Isle of Man and the east coast of the Republic of Ireland, the most common habitat types over which Risso's dolphins were sighted were shallow coarse or mixed sediment and shallow sands (Figure 3.5.1.). These were also the dominant habitat types around the Welsh and Cornish coasts, although here dolphins were also frequently observed over shallow aphotic rock or biogenic reef. The preferred habitat type around the south and west coasts of Ireland was shallow seabed. Risso's dolphins were also observed on the shelf habitats, although more infrequently, but were not observed on shelf rock or biogenic reef. No dolphins were reported in any of the bathyal habitats.

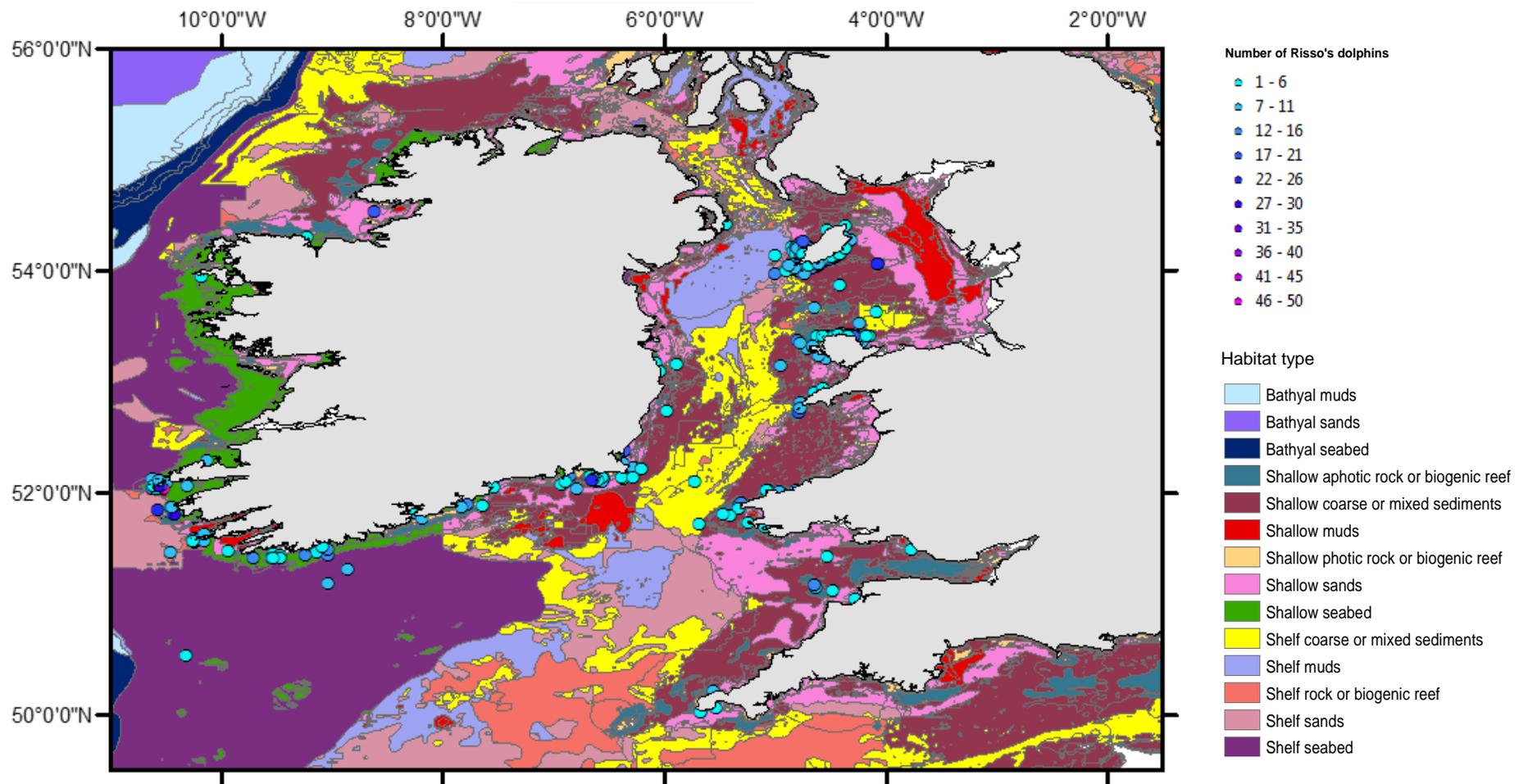


Figure 3.5.1. The location of Risso's dolphin sightings from 2007 to 2013 in association with the habitat types of the study area

3.5.2. Combined wave and tidal energy

Of the three combined energy levels, Risso's dolphins were observed predominantly in high energy waters (Figure 3.5.2.), suggesting a preference for areas of high wave and tidal energy. These areas were mainly located in coastal areas. Areas of moderate energy had the next highest density of sightings, and encompassed nearly all sightings occurring offshore. Only four sightings occurred in waters classified as low energy, which suggests this condition is not beneficial.

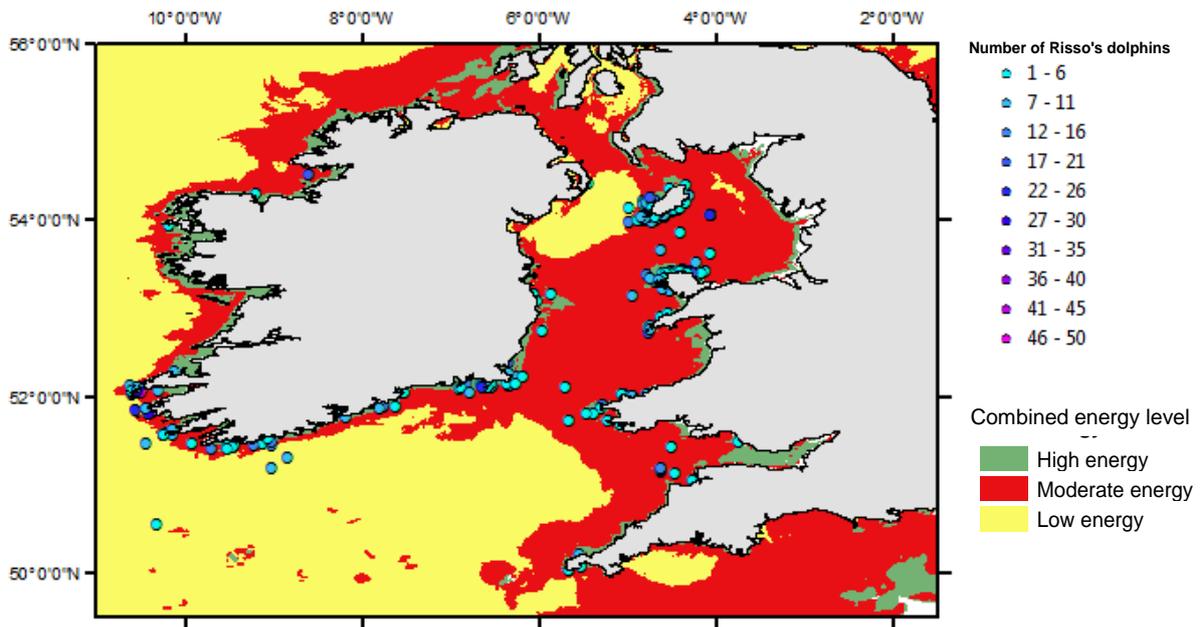


Figure 3.5.2. The location of Risso's dolphin sightings from 2007 to 2013 in association with the combined wave and tidal energy of the study area

3.5.3. Bathymetry

When examining the relationship between sightings and bathymetry, it can be seen that Risso's dolphins exhibited a preference for shallow waters (Figure 3.5.3.), with the majority seen in coastal waters where the depth was between 10-50m. Sightings were made less frequently between 50-150m, further offshore, and only a few were seen in depths exceeding 150m. The dolphins observed within these depth ranges were typically in small groups of 1-6 individuals. No dolphins were observed at depths deeper than 450m, indicating a preference in this region for shallower, continental slope waters.

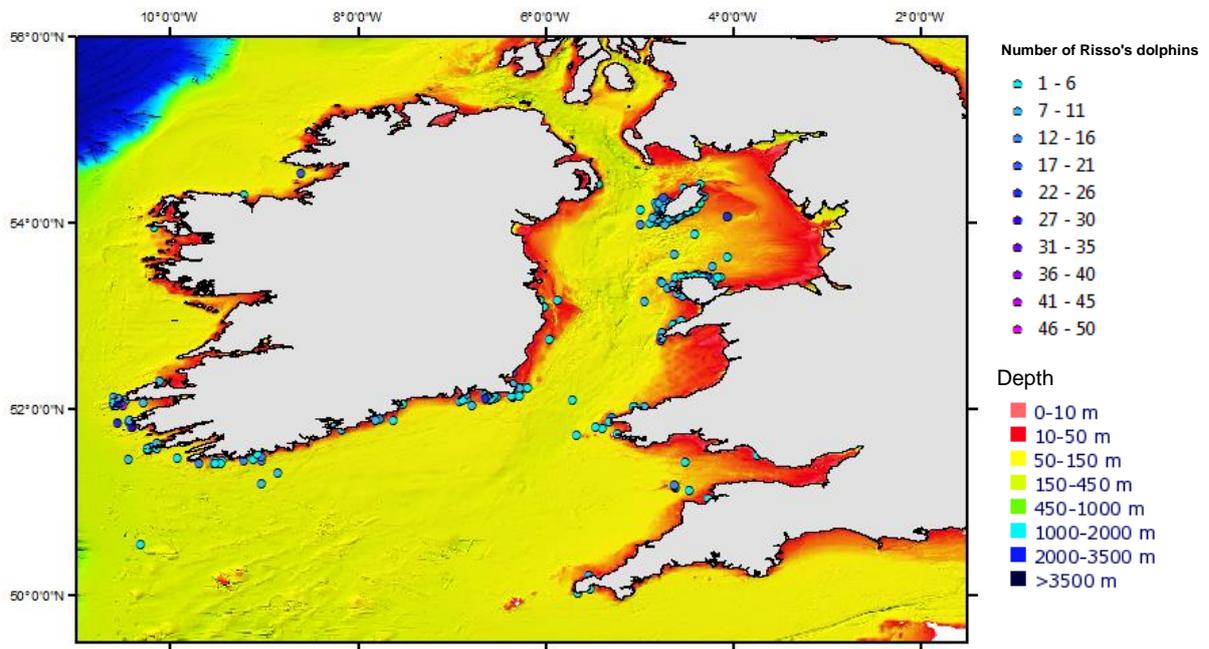


Figure 3.5.3. The location of Risso's dolphin sightings from 2007 to 2013 in association with the bathymetry of the study area

3.5.4. Slope

The calculated percentage change in slope shows that there is very little change in slope in the majority of the study area (Figure 3.5.4). In the areas where sightings occurred the slope was generally very low, being less than 1.5% or 0.675° , indicating that Risso's dolphins have a preference for areas where the topography is shallow. The maximum slope was 23.656% which equates to an approximate 10.6° change between cells, but this area of highest slope was located to the north-west of Ireland where no sightings were reported.

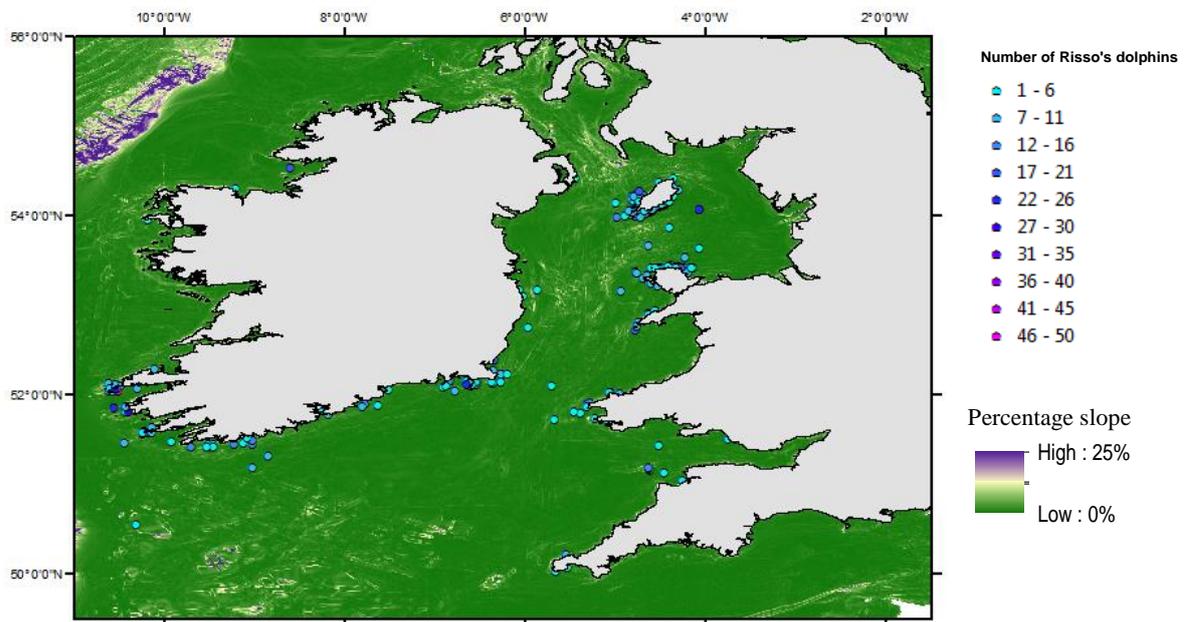


Figure 3.5.4. The location of Risso's dolphin sightings from 2007 to 2013 in association with the topography of the seabed of the study area

3.5.5. Salinity

On average, salinity is lower in the Irish Sea than in the Celtic Sea (Figure 3.5.5). Risso's dolphin sightings are distributed throughout the salinity range, indicating that their distribution may not be significantly affected by salinity. There is, however, a higher density of sightings in the areas at the lower end of the salinity scale which could be indicative of a preference towards slightly lower salinity conditions. The range in salinity is only 1.34, and this may be too small for any patterns to be observed.

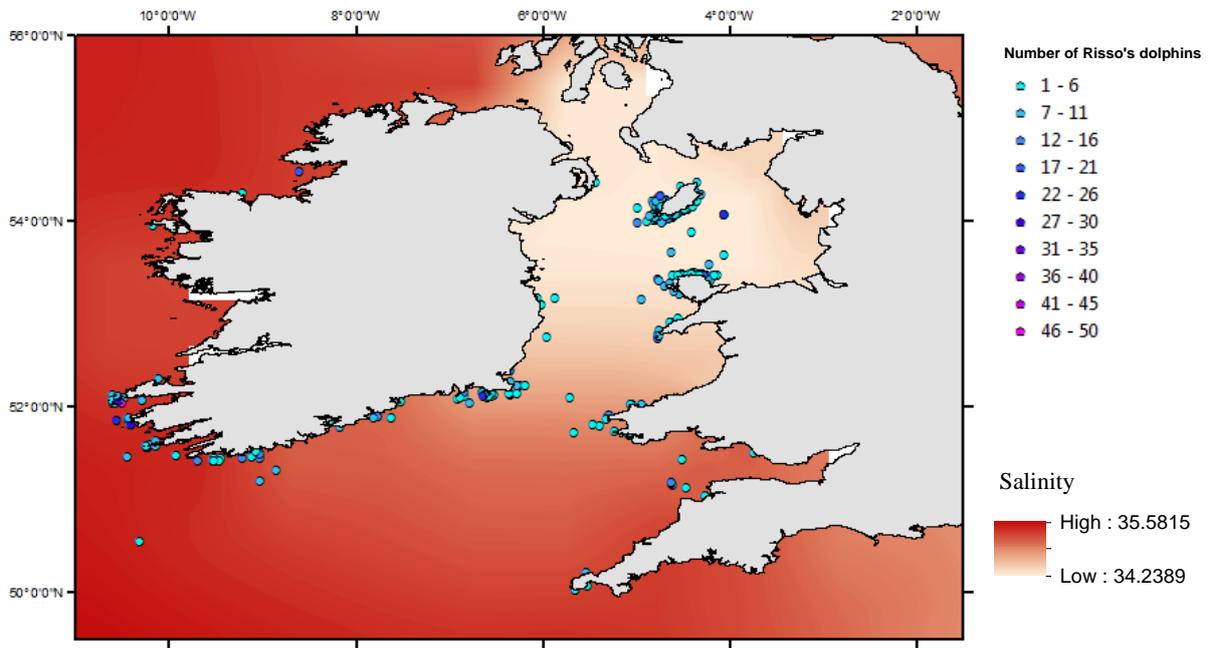


Figure 3.5.5. The location of Risso's dolphin sightings from 2007 to 2013 in association with the mean salinity (2007-2013) of the study area

3.5.6. Thermal fronts

There is a very high probability (80.8-101.2%) of a front occurring at the boundary between the Irish and Celtic Seas, with two sightings coinciding with the location of this front (Figure 3.5.6.). There is also high frontal probability running parallel to the coast of the Republic of Ireland and North Wales and from the south of the Isle of Man to the Northern Irish coast, where a number of sightings were concentrated. Data were not available at distances close to the shore so it cannot be conclusively determined whether the inshore sightings are occurring along fronts.

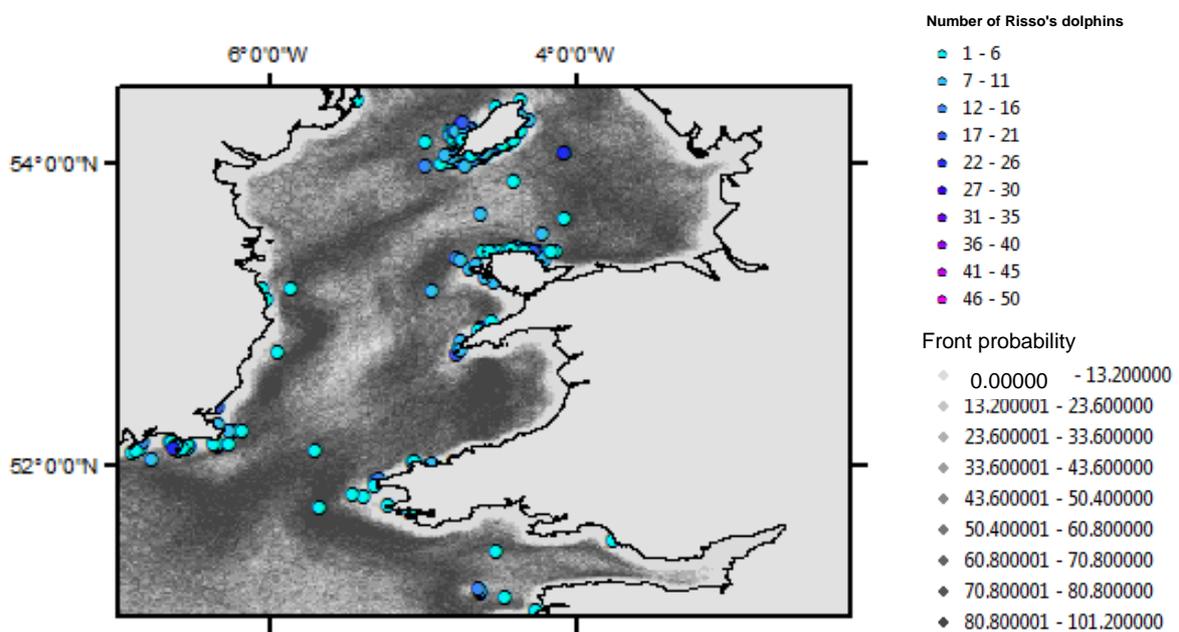


Figure 3.5.6. The location of Risso's dolphin sightings from 2007 to 2013 in association with the probability of summer oceanic thermal fronts with summer (June-August). Darker colours represent a higher frontal probability

3.5.7. Time series – SST and Chlorophyll α concentration

The Isle of Man box contained 261 (55%) of the 473 sighting events from 2007 to 2013, during which time a total of 1366 dolphins were observed. In this area, the highest number of individuals was seen in May 2007 (Figure 3.5.7.). There were four months when particularly high average numbers were observed (May to August), and 2007, 2009, 2012 and 2013 all recorded a peak number of individuals above two hundred.

A clear seasonal cycle in SST was observed, with the lowest temperatures recorded during the winter months and the highest temperatures in the summer months, the highest being in August. Minimal inter-annual variation was observed (Figure 3.5.7.). The peak in numbers of individuals most frequently occurred prior to the peak in SST, in five of the seven years, occurring 1, 2 and 3 months earlier. The peaks also coincided in 2 years, but were never observed in the months following the August SST peak.

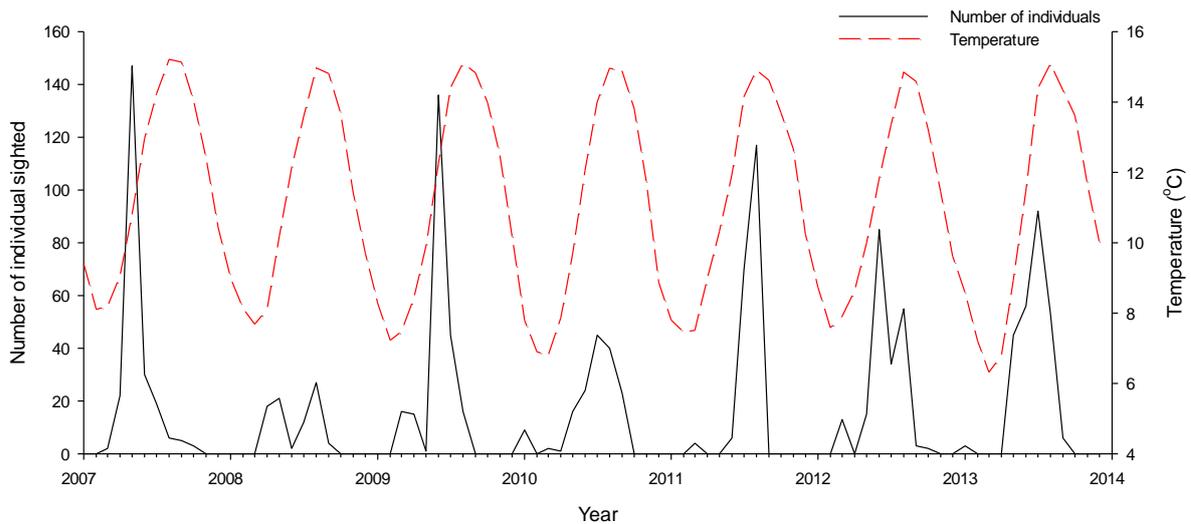


Figure 3.5.7. Time series showing the variation in mean monthly sea surface temperature ($^{\circ}\text{C}$) and the number of individuals seen in the designated Isle of Man box from 2007 to 2013

In all years, with the exception of 2010 and 2011, two peaks in chlorophyll α concentration were observed (Figure 3.5.8.). The first peak, when present, occurred in January, and the second peak between April and May. Risso's dolphin numbers appeared to be unaffected by the first bloom whilst the peak number of individuals occurred one to four months after peaks in chlorophyll α . There were gaps in the data in 2013, so no reliable conclusions

could be drawn regarding the relationship between the number of individuals and chlorophyll α concentration in that year.

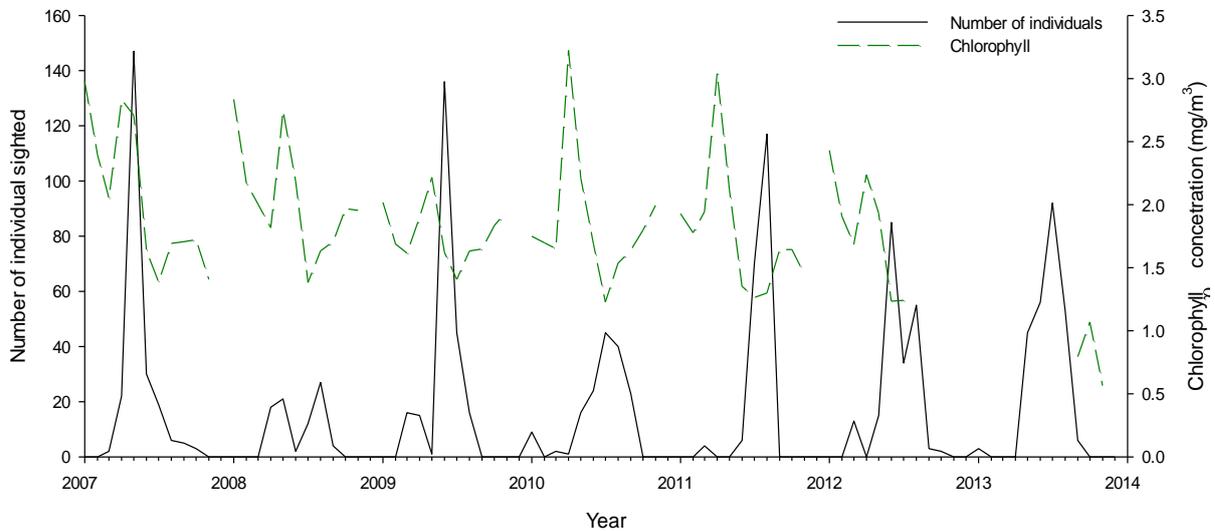


Figure 3.5.8. Time series showing the variation in the mean monthly chlorophyll α concentration (mg/m^3) and the number of individuals seen in the designated Isle of Man box from 2007 to 2013

In the Welsh box, 69 of the 473 sighting events from 2007 to 2013 occurred, during which time a total of 415 dolphins were observed. In this region, the highest number of individuals was seen in September 2009. From a seasonal perspective, most individuals were seen between July and September, whilst on an annual basis the number of individuals was substantially higher in 2008, 2009 and 2013 than any of the other years.

A very similar seasonal cycle in SST to the Isle of Man was also observed, with minimal inter-annual variation (Figure 3.5.9.). However, the peak in individuals most frequently occurred following the peak in SST, one month after in four years and two months after in one year. The peaks coincided in 1 year, and in 2011 the largest number of individuals was seen in the month prior to the peak in SST.

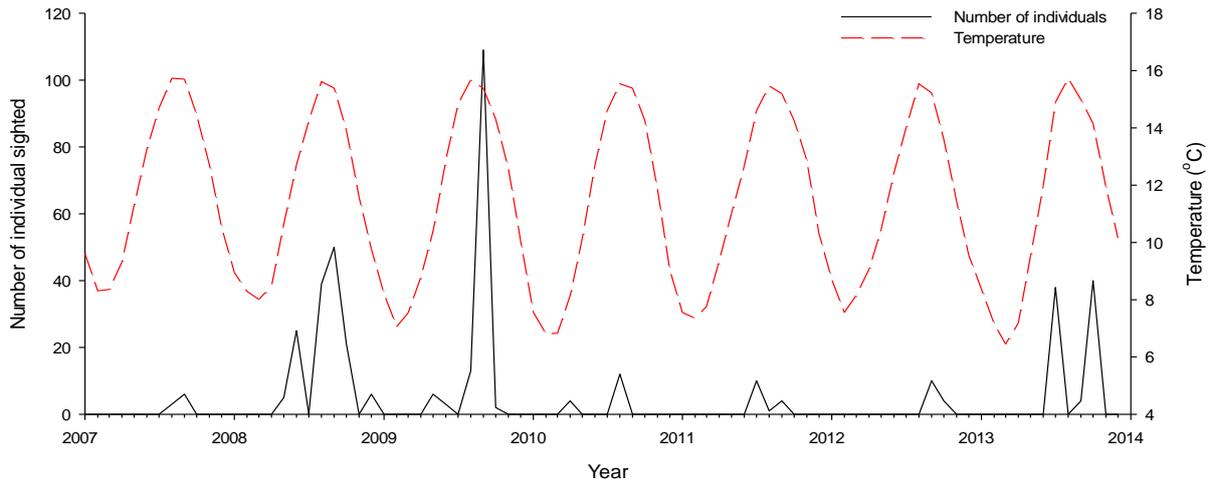


Figure 3.5.9. Time series showing the variation in mean monthly sea surface temperature ($^{\circ}\text{C}$) and the number of individuals seen in the designated North Wales box from 2007 to 2013

The peak in chlorophyll α concentration occurred in January or February in all years (Figure 3.5.10.). Clear second peaks occurred in April 2008 and 2009, and in all other years the chlorophyll α concentration appeared to decline from the first peak through to August/September and then began to increase again at a similar time to the highest density of dolphins. Again, environmental data from 2013 were insufficient to determine if any relationship was present in that year.

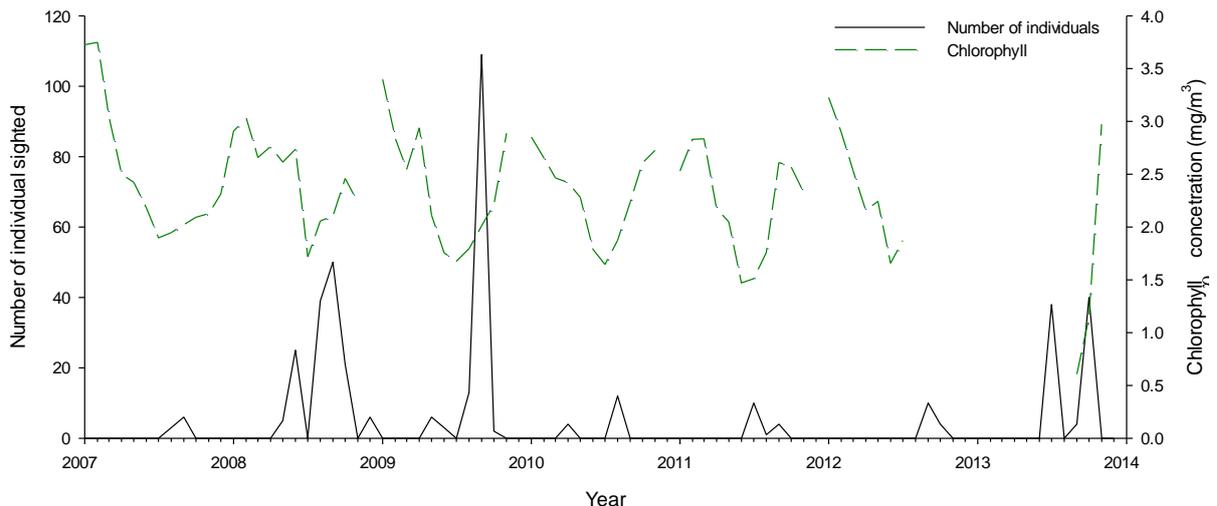


Figure 3.5.10. Time series showing the variation in the mean monthly chlorophyll α concentration (mg/m^3) and the number of individuals seen in the designated North Wales region from 2007 to 2013

It was also noticed that the number of individuals seen in the Isle of Man box was greater slightly earlier in the year (May to August), than in the Welsh box (July to September), and for a longer period of time. The numbers of individuals seen around the Isle of Man was substantially higher than in North Wales. The SST for both areas was very similar, ranging from approximately 6°C to 16°C. The peaks in chlorophyll α concentration were mostly higher during the winter months in North Wales, above 3.0mg/m³ in four years as opposed to only two years in the Isle of Man, but spring peaks were either weaker in North Wales or absent.

3.6. Maxent species distribution modelling

3.6.1. Environmental variables

A Maxent model was run to predict the probability of habitat suitability using seven of the selected environmental variables (habitat type, combined wave and tidal energy, bathymetry, slope, mean salinity, mean chlorophyll α concentration and mean SST) (Figure 3.6.1.). This model indicated a high predicted probability of presence in the coastal waters around the Isle of Man, particularly to the south and west, where the orange colouration indicated a probability of between 0.85 and 0.92. Conditions were also shown to be well-suited to Risso's dolphins around the coast of Ireland, typically with a probability of around 0.77, with the exception of the north-east coast of Ireland, whilst on the east side suitable habitat extended into the Irish Sea. The probability was high around the majority of the Welsh coast, being greatest in north-west Anglesey (0.85), and predicted high suitability (0.69) also extended into the Cardigan Bay area.

In the centre of the Irish Sea there were a number of small areas where there was a low to medium predicted probability (0.23-0.46). In the waters between the Isle of Man and the coast of northwest England an area of high probability (0.77) was observed which appeared to encircle an area of low probability (0.31). The probability of presence appeared to decline quite sharply as distance from the coast increased, suggesting that inshore locations typically exhibited environmental conditions better suited to Risso's dolphins.

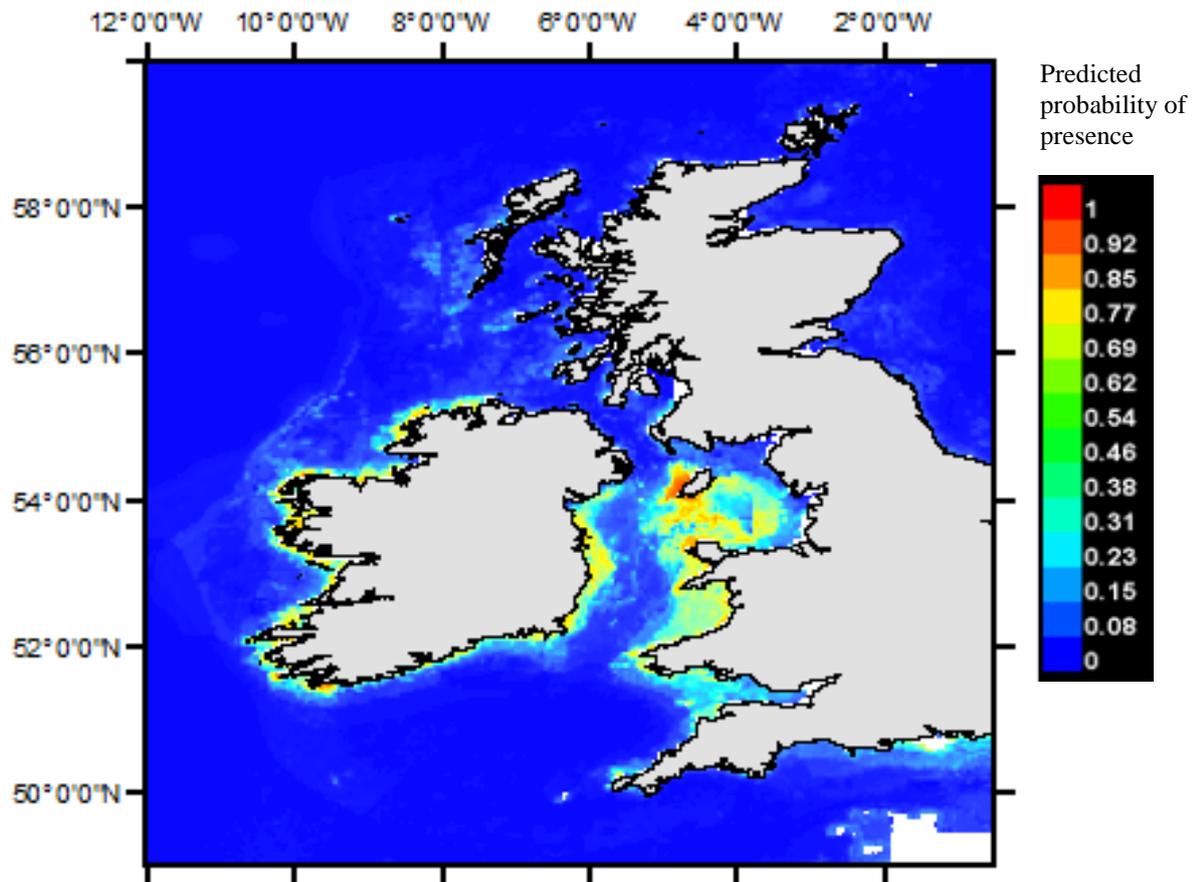


Figure 3.6.1. Maxent model showing predicted probability of habitat suitability during the period 2007 to 2013 based on seven environmental variables: habitat type, combined wave and tidal energy, bathymetry, slope, mean salinity, mean sea surface temperature and mean chlorophyll α concentration. Red represents the highest predicted probability of presence (1), and dark blue represents the lowest predicted probability of presence (0)

The jackknife test of variable contribution showed that the environmental variable with the highest gain when used in isolation was bathymetry, with a regularised training gain of approximately 1.25, followed by chlorophyll α concentration (1.1) (Figure 3.6.2.). Salinity was also determined to be important (0.95), and the impacts of energy and habitat type were very similar, both being around 0.85. SST had a lower training gain of 0.70, but was the environmental variable that decreased the gain the most when it was omitted, which therefore suggested it was the variable with the most information that was not present in the other variables. Slope was considered to be the least important contributor to the model, with a gain of < 0.1 . Analysis using the jackknife test of test gain and area under the curve (AUC) showed similar levels of importance in all variables, but there were a number of

differences: test gain showed salinity to be the second most important variable, with habitat type being more important than energy, whilst using AUC showed habitat type to be the third most important variable, with salinity and energy being of equal importance (Appendix 1).

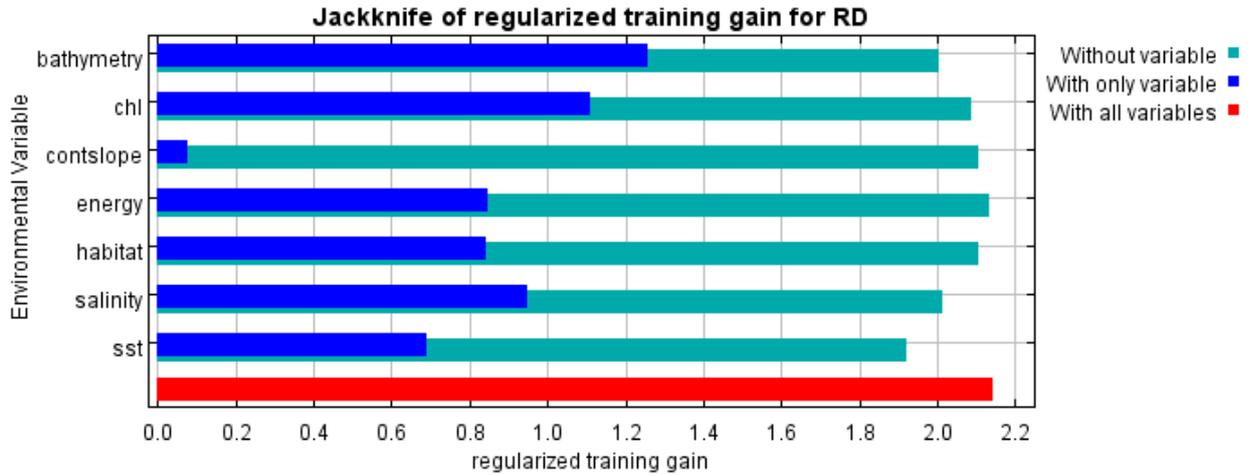


Figure 3.6.2. Jackknife test of regularised training gain from Maxent model of all environmental variables. Dark blue bar represent the use of the variable in isolation and the light blue bar with that particular variable omitted. Red represents the total gain.

The response curves (Appendix 2) suggested an ecological niche for each modelled environmental determinant. The response curve for habitat type showed that logistic prediction was much higher for five habitat types than in all others: shallow aphotic rock/biogenic reef, shallow seabed, shallow photic rock/biogenic reef, shallow sands and shallow coarse/mixed sediments were all predicted at approximately 0.5 and above, indicating a preference for shallow habitats with a variety of sediment types. Shallow seabed had the highest logistic prediction of approximately 0.85, whilst all abyssal and bathyal habitats were only 0.5. The energy response curve had the highest logistic prediction (>0.70) under high energy conditions, and the lowest under low energy conditions (<0.05). Logistic prediction peaked at >0.70 at approximately 50m depth. Beyond 50m, the decline in logistic prediction was rapid, with no predicted presence occurring beyond approximately 244m, indicating the preference for shallower waters previously suggested. Optimum salinity conditions were predicted to be 34.24, resulting in a <0.90 predicted probability. Logistic predictions slowly declined until salinity exceeded 34.8 when predicted presence declined more dramatically. The response curve for SST showed low logistic prediction below 0.1 at temperatures below 11 °C and above 12.5°C. Between these two temperatures, the logistic prediction increased dramatically, with an

optimum SST of 11.13°C resulting in a 0.78 probability of presence. Whilst slope was not considered to be an important contributor to determining distribution, it was predicted that habitat with a slope of 0-0.2% decline was most suitable.

3.6.2. Seasonal variation

The trends in habitat suitability were seen to vary on a monthly basis (Figure 3.6.3.). In March and April, the areas considered to have suitable environmental conditions based on salinity, SST, and chlorophyll α concentration were quite widespread, with no defined boundaries between suitable and unsuitable areas, but the predicted probability of presence did not exceed 0.77. In May the suitable areas were most concentrated around the Isle of Man, with >0.92 probability, with a further strip of suitable habitat offshore between the Isle of Man and Anglesey. Some medium levels of suitability were also seen off the Atlantic coast of Ireland, a trend which was also observed in the next two months. From June to September, the strip of suitable habitat in the Irish Sea moved south towards Anglesey, with probabilities >0.92 in June and August, and the probability also increased around the east coast of the Republic of Ireland. In October, the areas of suitable habitat again became more widespread, with areas of >0.77 predicted presence in Cardigan Bay, the Lancashire coastline, and also around the south coast of England and the Isle of Wight. The results therefore suggested that the area of highest predicted presence shifted from higher latitudes (around the Isle of Man) in late spring, to lower latitudes (North Wales/Anglesey) in late summer. The area of low suitability (<0.23) within the area of high suitability (>0.77) to the east of the Isle of Man was again observed strongly during May, June and August.

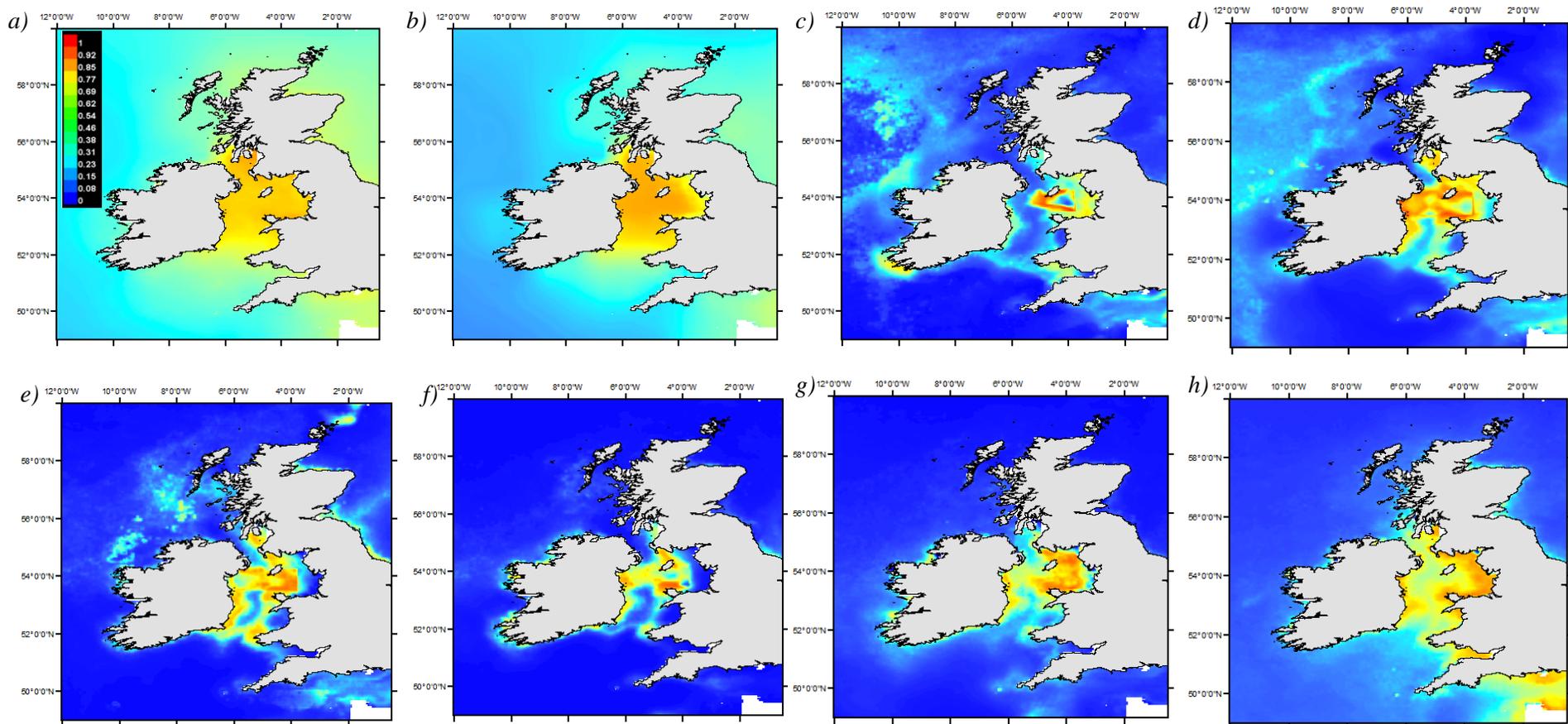


Figure 3.6.3. Maxent model showing predicted probability of habitat suitability using mean monthly salinity, sea surface temperature and chlorophyll *a* concentration in a) March, b) April, c) May, d) June, e) July, f) August, g) September and h) October. Red represents the highest predicted probability of presence (1), and dark blue represents the lowest predicted probability of presence (0)

The jackknife test showed that the variable contributing the most to the model varied seasonally (Appendix 3). From March to September, salinity was considered to be the most important variable: in all months except June, SST was the least important. October was the only month during which chlorophyll α concentration was of greatest importance to the model, and again SST was the least important.

The response curves (Appendix 4a) of salinity showed very similar suitable conditions during March to June. The greatest logistic prediction occurred when the salinity was between 34.0 and 34.2, and then increased to between 34.2 and 34.4 from July to October, suggesting conditions suitable at slightly higher salinities later in the year. The logistic predicted presence of SST (Appendix 4b) responded in a very similar way in March and April, with most dolphins being seen in waters of 5.7°C and 6.75°C respectively and the probability increased rapidly as temperature increased: the opposite trend was seen in October. May and June also had similar responses, with a plateau in predicted presence greater than 0.55 for a 1.5°C range. July's response curve was the only month that exhibited two peaks: one of 0.85 probability at 11.6°C and one of 0.66 at approximately 14°C. In August and September, the peak probability occurred at 15.0°C to 15.5°C, and declined above and below these temperatures. The temperature with highest predicted presence was lowest at the start of the year and increased through to October. The response curve of chlorophyll α concentration was the most variable (Appendix 4c). Monthly predicted presence occurred at the highest chlorophyll α concentration in May, when the probability was >0.80 from 10 to 54mg/m³, and lowest during July when the probability was 0.73 at 1.9mg/m³. The response curves from April, and June to October were similar to that of a bell-shaped curve, and in March, May and June showed an exponential increase reaching a plateau.

3.6.3. Inter-annual variation

The model results showed changes in habitat suitability over time from 2007 to 2012 using the variables of mean annual salinity chlorophyll α concentration, and SST (Figure 3.6.4.). Although the areas of most suitable habitat varied on an inter-annual basis, there was always high predicted probability (>0.77) around the coast of the Isle of Man. This high probability was particularly prevalent in 2008 and 2011 when there was an area of predicted probability above 0.92 on the south-west coast of the Isle of Man. In 2009, 2010 and 2012, the area of low predicted probability previously seen was visible, most clearly in 2009, suggesting that the environmental conditions in this area were making it less suitable for Risso's dolphins. In addition, during 2007 and 2010, the extent of the suitable areas of habitat was at its greatest, predicting that the coast to the south and east of England had up to a 0.54 probability.

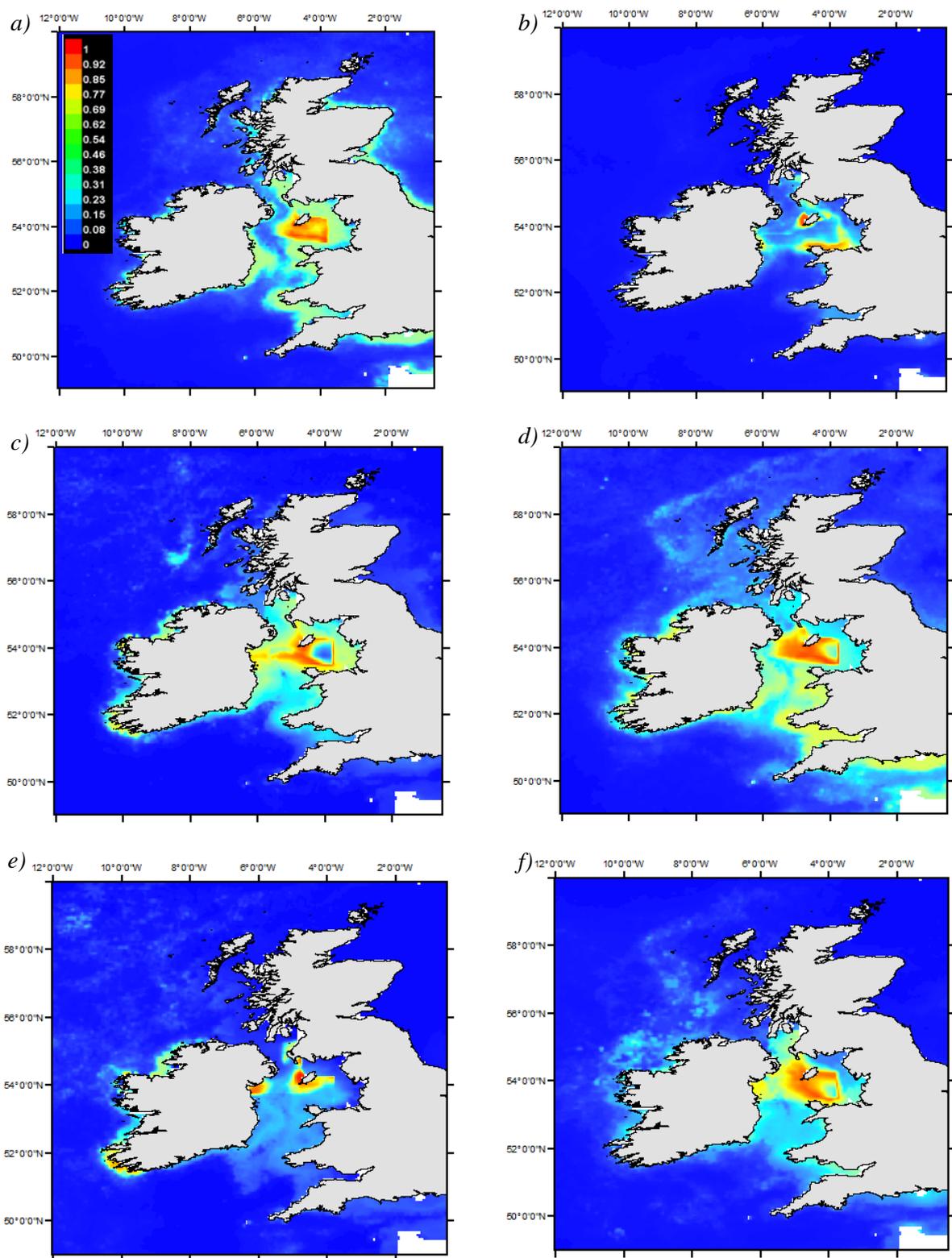


Figure 3.6.4. Maxent model showing predicted probability of habitat suitability using mean annual salinity, sea surface temperature and chlorophyll α concentration a) 2007, b) 2008, c) 2009, d) 2010, e) 2011 and f) 2012. Red represents the highest predicted probability of presence (1), and dark blue represents the lowest predicted probability of presence (0)

The jackknife test of variable contribution of regularised training gain showed that in all years, salinity was the variable with the highest contribution to the model (Appendix 5). Salinity also decreased the gain the most when it was omitted, therefore indicating it contained the most information not represented in the other variables.

The response curves showed that the highest logistic predicted salinity was very similar in all years (Appendix 6a), estimated at between 34.23 and 34.26 in all years, with 2011 having the highest maximum. At these salinities there was >0.90 probability of presence of Risso's dolphins. The response curves indicated there was more inter-annual variation in the SST (Appendix 6b) conditions with highest logistic predicted probability, ranging from approximately 10.77 to 11.625: the minimum and maximum temperatures with the highest predicted presence occurred in 2010 and 2007 respectively. In all years the predicted probability was low at the lowest temperatures, then increased to a peak of >0.65 at an intermediate temperature then declined again as the temperature increased further. The response curves for chlorophyll α concentration were the most varied over the six years (Appendix 6c); 2012 was particularly different in shape, with a plateau reached in predicted probability, but this may have been due to missing environmental data in that year, meaning annual averages were calculated using less data. The highest probability of presence was predicted to occur at chlorophyll α concentrations of between 1.75 and 3.75mg/m³. Chlorophyll α had the lowest logistic prediction in 2012 of approximately 0.67 and the highest in 2008 of 0.85.

4. DISCUSSION

4.1. Photo-identification

Photo-identification using dorsal fin and flank markings proved to be a successful method for enabling the identification of individual Risso's dolphins observed in Welsh waters. DARWIN was considered a suitable program for assisting with the matching of fins as this software made few errors in the rankings, and it helped in reducing any human error which could have occurred from matching by eye alone (Towner *et al.*, 2013).

Between 2003 and 2014, an estimated 144 individuals were identified in Welsh waters from 30 sighting events, with the minimum number of different individuals encountered during the study period estimated at 162. This estimated population size was higher than was calculated around Bardsey Island (121) from 1997-2007 (de Boer *et al.*, 2013), which is to be expected as Bardsey Island falls within Welsh waters. The estimate for Welsh waters was the best that could be made in the absence of sufficient data and current knowledge to apply a mark-recapture analysis to determine the population (Evans *et al.*, 2003).

In Wales, the number of left (65) and right (81) individuals identified was similar. De Boer *et al.* (2013) suggest that the majority of left and right sides would match to one individual rather than being from different animals. This would result in a relatively reliable estimate of the number of individuals that could only be identified from one side observed during the time period. This assumption, however, may not be particularly reliable, as there has been little supporting evidence of this.

The regular presence of females and calves throughout the study period, collectively accounting for approximately half of the individuals observed, shows that breeding is occurring within the population. Groups often consisted of multiple female-calf pairs which could be indicative of nursery groups, such as the group seen near Bardsey Island during 2010. This suggests that the study area may contain sites important for breeding and raising young. The exact location where breeding takes place in the study area has not yet been determined. Based on previous sightings in the UK it is considered that calves are born between March and July (Evans *et al.*, 2003; Evans, 2008), however, in this study, females and calves were only observed between July and October, with October showing the highest number. This could suggest that births take place slightly later in Welsh waters than in other areas around the UK, although it is difficult to conclude exactly when these

calves were born. Despite observing foetal folds on many of the calves, these features cannot be used to conclusively determine the timing of births as they can remain for approximately 3 months. Only one individual was identified as a definite male as the genital area was seen, but the gender of the rest of the individuals could not be determined as there was either no calf in association or no view of the genitals during sightings.

4.2. Site fidelity

Site fidelity of Risso's dolphins in Wales was low, measured at 12.5% in terms of re-sighting rates. This rate is comparable to studies in the north-western Mediterranean where re-sighting rates of 9.2-15.7% were calculated (David and Di Méglío, 1999), and 18.6% in a study focusing specifically on Bardsey Island. Much higher re-sighting rates have been observed in other regions including the Azores where the re-sighting rate was 63%: this is indicative of strong site fidelity (Hartman *et al.*, 2008). The relatively low re-sighting rate in the SWF catalogue suggests that site fidelity is not particularly strong and that the Risso's dolphins seen in Welsh waters may exhibit large scale movement patterns (de Boer *et al.*, 2013). It is likely, however, that site fidelity may have been underestimated as photographs were only available for 33% of the sightings documented in Welsh waters.

Whilst site fidelity appears to be weak, the results do show some evidence of seasonal and long-term site fidelity, as found by David and Di Méglío (1999). Seasonal fidelity was suggested as eight individuals were re-sighted during the same season in 2008 and two in 2014. Whilst only having three photographed sightings available for 2008, this year had the highest number of re-sightings, indicating site fidelity was stronger at this time. Long-term fidelity may occur as four individuals were re-sighted in the same area in successive years. The longest gap between the sighting of the same individual was six years: this does not, however, mean that individual was not present in Welsh waters during this period, just that it was not identified in any of the 30 sightings for which photographs were available. Individuals were still able to be identified after not being re-sighted in the photo-ID study for a number of years. Markings and scarring can persist for long periods which allows individuals to be recognised after many years, although they may acquire new markings over the years (Casacci and Gannier, 2000; Bearzi *et al.*, 2011), as can be seen when examining how individuals re-sighted in the SWF catalogue have changed in appearance over time (Figure 4.2.1.). Of the individuals re-sighted, the majority had some kind of

identifying fin shape: this result may be biased towards the well-marked and slightly-marked individuals as these were easier to identify, even when the quality of photograph was not as good. Recaptures between left and right fins may have been missed whereby an individual's left and right sides which had not been attributed to the same individual were seen on separate occasions.



Figure 4.2.1. An example from the Sea Watch Foundation catalogue to show how an individual can be recognised over time through the persistence of identifying markings. Individual 001_22L was observed in a) 2007 and again in b) 2010, but with the addition of markings to the trailing edge of the left side of the dorsal fin

Interestingly, only one of the 35 individuals seen prior to 2007 in the Cardigan Bay area matched with the individuals seen in North Wales: 004_22R was seen in 2004 in Cardigan Bay and then six years later in North Wales. This result may suggest that there is little mixing between the individuals observed in the two areas, but, more recent photographs of any individuals observed in Cardigan Bay would be needed to determine this as they were only available for seven sightings collectively from 2003 to 2005.

4.3. Home ranges

The individuals matched with other catalogues appeared to have relatively localised movement patterns, with their typical home range incorporating the coastal waters around North Wales, including Bardsey Island, and extending northwards at least as far as the Isle of Man. Individual 002_07W showed a localised home range persisting over 11 years, first

being sighted by WDC in 1997 and again in 2002 around Bardsey Island, then twice by SWF in 2008 on the north and then north-east coast of Anglesey. However, sightings are too infrequent to determine whether, during the long periods of time when this individual was not observed, it remained resident in Welsh coastal waters or migrated.

The results also showed evidence that long-distance migrations may be undertaken by a small number of individuals, with two matches being made with sightings in Scotland. These individuals were seen in separate sighting events in 2009 and 2011 in North Wales, and were then seen in two different events in Scotland in 2013 only four days apart. The Scottish sightings occurred within approximately 190km of each other in coastal waters near the Butt of Lewis and Kallin Harbour which are both located on islands in the Outer Hebrides.

No matches were obtained between the SWF catalogue and that of IWDG (Ireland) and Marine Discovery (Cornwall), but it is still possible that the dolphins seen in Welsh waters may also travel to regions covered by these catalogues. In 2009, an individual photographed by Marine Discovery was matched to one identified by WDC in 2006, approximately 320km further north, and this was the first time a Risso's dolphin from the Irish Sea had been matched to a different location (de Boer, 2009). The matches with the HWDT provide further evidence for extended home ranges and large-scale migrations outside the Irish Sea and suggest the Risso's dolphins in Welsh waters are part of an open population (de Boer *et al.*, 2013).

4.4. Sightings

Evans *et al.*, (2003) noted that Risso's dolphins in the UK were most commonly seen during May to September with numbers peaking from July to September. This pattern was also observed in the Irish Sea and in Irish coastal waters with both the number of sightings and individuals being highest from May to September. In this study, a very similar pattern was seen, with the number of sighting from May to August being particularly high (all over 70 sightings from 2007 to 2013 collectively), and September was also high (over 50). This observed pattern may be due to the inshore-offshore movements that occur seasonally, with Risso's dolphins migrating to coastal waters in the summer (Evans, 1980; Leatherwood *et al.*, 1980; Casacci and Gannier, 2000; Hartman *et al.*, 2008; de Boer *et al.*, 2013).

4.3.1. Group size

The main factors thought to influence the size of a group are the dispersion of food and the need to find a mate or protect young. Foraging benefits are likely to increase with group size if prey shows a clumped distribution and there is sufficient in a prey patch to sustain a number of animals. Large pods also often form for the benefit of social interaction and support. Females and calves may form large aggregations for protection to increase calf survival rates. For females, both foraging and reproductive needs have a positive influence on the optimum pod size, whilst male pods are more variable in size as there is a trade-off between the two factors (Hartman *et al.*, 2008). A large group size may be beneficial for males to help them outcompete other male pods for preferred foraging grounds or for access to a mate, although such groups are usually temporary and unstable (Connor *et al.*, 1992).

The most common group size for Risso's dolphins around the British Isles is between 6-12 individuals (Evans, 2008), but the average monthly group size observed was generally less than six. Small pods of this size may have been driven by male reproductive requirements (Hartman *et al.*, 2008). The largest group size recorded was in June 2009 when 50 individuals were observed off the south-west Irish coast, and large groups of around this size have also been sighted off Bardsey Island: these were potentially temporary aggregations comprising multiple smaller groups (Evans, 1980, 1992, 2008; Sea Watch unpublished data), formed either for feeding or the protection of calves. Group size can influence the probability of detection, as greater numbers are easier to detect (de Boer *et al.*, 2014), therefore it is possible that there were small groups or single individuals that were not detected during surveys.

4.5. Environmental variables

Environmental variables may act as proxies for Risso's dolphin prey and are thought to influence cetacean distribution by affecting the aggregation of prey species (Baumgartner, 1997; Cañadas *et al.*, 2002; MacLeod *et al.*, 2013). One of the prey species that is considered to be favoured by Risso's dolphins around the British Isles is the cephalopod *E. cirrhosa*, as it has often been found in the stomach contents of stranded Risso's in Wales, Scotland and southern England (Clarke and Pascoe, 1985; Santos *et al.*, 1994;

Atkinson and Gill, 1996), although they do also consume a variety of other cephalopod species (Evans and Hintner, 2010; Evans, 2013).

For cetaceans including Risso's dolphins which have a teuthophageous diet, physiography is thought to play an indirect role in determining distribution. It is influenced by mechanisms including topographically induced up-welling of nutrients, increased primary production and aggregations of zooplankton as a result of surface water convergence or enhanced secondary production (Cañadas *et al.*, 2002). Dynamic variables are thought to influence distribution in a more direct manner, with oceanographic features such as oceanic fronts and mesoscale features (Yen *et al.*, 2004) often being associated with dense prey aggregations (Hyrenbach *et al.*, 2000).

4.5.1. Physiography

Risso's dolphins are often found in association with regions of well-defined physiographical characteristics (Azzelino *et al.*, 2008). Bathymetry has a strong influence on the species (Gómez de Segura *et al.*, 2008), and was found to be the most important variable tested affecting distribution in this study: previous research has suggested bathymetrically-induced circulation enhances feeding opportunities and consequently is responsible for affecting the distribution and localised abundance of many pelagic cetacean species (Kruse, 1989). Around the British Isles it is predicted that Risso's dolphins will be found mainly on the continental shelf at around 50-100m isobaths (Evans *et al.*, 2003; Evans, 2008), and the optimum predicted depth that was estimated by the model was at the lower end of this range i.e. at 50m. This is shallower than typically observed in other regions (Evans *et al.*, 2003; Evans, 2008) where they are associated with deeper waters often around 1000m (Baird and Stacey, 1991; Baumgartner, 1997; Casacci and Gannier, 2000; Cañadas *et al.*, 2002). It is likely that the shallow bathymetric preference observed in this study could persist over time as cetaceans have been found to display long-term bathymetric associations (Yen *et al.*, 2004).

Bathymetric features can result in localised primary production which in turn concentrates prey aggregations (Hyrenbach *et al.*, 2000). Their primary prey species are most commonly found at depths between 50 and 300m, the lower end of this range being the depth of water in which most Risso's dolphins were observed in this study, and the upper end being very similar to the upper limit of Risso's dolphin distribution. Previous effort

has been made by MacLeod *et al.* (2013) to correlate the occurrence of Risso's dolphins with a model-based estimate of *E. cirrhosa* distribution, but no relationship was found. The spatial resolution may not have been sufficient for any relationship to be observed as Risso's dolphins can exploit very small areas of prey less than 10m in size when foraging in small groups, a size below the level of detection of most studies. Their study was however focused on Scotland, with the Irish Sea area being highly data deficient (MacLeod *et al.*, 2013), so repeating the analysis, concentrating on the Irish Sea and Irish coastal waters at a finer scale resolution, could produce different results. Around Bardsey Island, it has been suggested that the localised complex topography and deep ocean trenches create areas of upwelling with increased productivity that Risso's dolphins exploit (Wharam and Simmonds, 2008).

As identified in previous studies, Risso's dolphins were found to have strong associations with habitat type (Yen *et al.*, 2004). The predominant habitat types confirmed a preference for shallow water, as this was the habitats in which Risso's dolphins were most commonly observed: these had varying substrate types of coarse/mixed sediment, sands and aphotic rock or biogenic reef, suggesting that substrate type is not as influential a factor as the depth at which that substrate is found. To determine the functional mechanisms behind the choice of habitat type, this should be examined in association with behavioural mechanisms which may reflect sub-surface activities such as foraging (Hastie *et al.*, 2004), since substrate type has been found to influence the location of prey (Santos and Pierce, 2003).

In this study, Risso's dolphins were associated mostly with shallow coastal waters where the percentage change in slope was minimal throughout the majority of the area (0.675°), meaning it is an area of shallow slope. Slope was not found to be a significant variable, contributing less than 0.1 to the model. This result is different to that suggested in the literature where Risso's dolphins are usually found to be associated with the steep upper continental slopes as these are areas of well-defined physiographical characteristics and highly productive areas where a wide variety of cephalopod prey is available (Würtz *et al.*, 1992; Cañadas *et al.*, 2002; Azzelino *et al.*, 2008; Wells *et al.*, 2009; de Boer *et al.*, 2014). Research in the Mediterranean found Risso's dolphins to prefer areas of slope greater than 2.29° (Praca and Gannier, 2008), which is significantly larger than that estimated in this study.

4.5.2. Dynamic variables

Dynamic variables are those which are constantly changing over spatial and temporal scales, and these factors are potentially the most important in affecting the fine scale distribution of this species (de Boer *et al.*, 2014). Species distributions may respond to these spatial and temporal changes, resulting in a general redistribution of Risso's dolphins from year to year. It has, however, also been observed that regions of particularly high density do persist over time (Baines and Evans, 2012; Paxton *et al.*, 2014).

4.5.2.1. Oceanographic variables

Areas of higher combined wave and tidal energy were found to coincide with the highest densities of Risso's dolphin sightings, indicating a preference for high energy environments. The majority of these environments were coastal where tidal regimes are naturally more dominant. Energy was also found to be the fourth most important contributor to the overall model. Being located in one of the two regions of highest density, Bardsey Island is influenced by strong tidal streams, eddies and currents, so is a high-energy environment. It is therefore likely to be a hotspot for Risso's dolphin activity as the environmental conditions concentrate prey species (de Boer *et al.*, 2014). Both the relatively high number of sightings and predictive modelling results indicated this could be the case.

Evidence suggests that frontal features enhance primary productivity and provide predictable concentrations of prey (Simard *et al.*, 2002), and cetaceans have been thought to migrate with these fronts in order to take advantage of these aggregations (Hyrenbach *et al.*, 2000). The seasonality of fronts is thought to affect the seasonality of cetacean distribution (Gannier and Praca, 2006), and they may be indicators of the location of migration routes (Hyrenbach *et al.*, 2000).

From the data analysed, the Celtic Sea front can be seen clearly in the results, and a high frontal probability can also be seen in the area of the western Irish Sea front, although perhaps not as strongly. In the Irish Sea, tidally driven water movements are the dominant contributor to the physical oceanography (Robinson, 1978). Tidal mixing fronts form at the boundary of the Irish and Celtic Sea and in the western Irish Sea they form between the south coast of the Isle of Man and the Irish coast north of Dublin where areas of highly stratified slack water meet fast moving mixed water. These regions are suitable for frontal

formation as they are areas of continental shelf which experience high tidal dissipation with a large seasonal heat exchange (Reid *et al.*, 2003; Simpson *et al.*, 2009). The temperature and salinity distributions within the Irish Sea are thought to be predominantly controlled by tidal mixing (Robinson, 1978).

Whilst these frontal regions are likely to be highly productive during the summer, there were very few sightings recorded there. Baines and Evans (2012) showed that effort was relatively high around the Celtic front, with some areas having more than 100km of vessel effort, so the low density observed in this region is likely to be accurate. Conversely, there was little to no effort in the majority of the area covered by the western Irish Sea front, so the low density shown here could be due to lack of effort or presence. Fewer recorded sightings may be because highly productive frontal systems are often created near the shelf break (Baumgartner, 1997), but Risso's dolphins in the UK are found in coastal and continental shelf regions. Fronts are also responsible for creating a stratified environment as there is a separation of cooler fresh shelf water and warmer, more saline slope waters, but it has been shown that Risso's prefer a well-mixed environment with a stable salinity gradient (de Boer *et al.*, 2014). They may therefore, not make effective use of the productivity of frontal systems, and this might explain why the highest density of sightings still occurred inshore where frontal probability was low.

The patch of very low habitat suitability seen to the east of the Isle of Man in some of the models may result from its situation in an area categorised as offshore waters of transitional stability by Kennington and Rowlands (2006) where waters are regularly stratified, although this stratification is usually weak or intermittent. Risso's dolphins have been found to be more common when water is well mixed and separated from seasonally stratified water (de Boer *et al.*, 2014), so this preference could explain why this area is thought to be unsuitable for them.

The western Irish gyre, a cyclonic near-surface gyre (Hill *et al.*, 1997) where density-driven currents flow counter-clockwise between north Wales, the Isle of Man, and Ireland (Tilstone *et al.*, 2005; Robins *et al.*, 2013) is located in the study area. It has a strongly seasonal occurrence, being found only in spring and summer each year when stratification and weak tidal currents are present (Hill *et al.*, 1997; Robins *et al.*, 2013). The boundaries of gyres can often create a barrier to the transport of primary productivity (Robins *et al.*,

2013) and can result in areas of low productivity (Polovina *et al.*, 2008). However, the presence of the gyre does not appear to have a strong effect on the seasonal predictions of presence during spring and summer, with presence being relatively high during this time with the exception of May when the prediction of habitat suitability is very low.

4.5.2.2. Oceanographic variables

Salinity, SST and chlorophyll α concentration are also factors which have been associated with prey aggregations (Bearzi *et al.*, 2011). These are particularly important in determining the fine scale distribution of the species (de Boer *et al.*, 2014) as they are frequently changing on fine spatial and temporal scales, as well as vertically through the water column (Cullen, 1982).

The salinity of the Irish Sea is considered to be relatively high due to the influences of oceanic water from the south (Reid *et al.*, 2003), but it was found that salinity was marginally lower in the Irish Sea than in the surrounding waters. Areas of highest productivity often occur under conditions of lower salinity, which corresponds with the areas of highest habitat suitability in the majority of models. This may explain why more Risso's dolphins were observed in the slightly less saline Irish Sea than in surrounding waters. Salinity can sometimes be used to identify different water masses (Forney, 2000), but no features could be clearly identified from the results.

In the overall model, salinity was considered to be the third most important variable in determining distribution, with habitat being most suitable at salinities of around 34.2. In both the seasonal and inter-annual models, salinity was found to be the most important variable in the determining of distribution in seven of the eight months, despite seasonal variations in surface salinity being very small, and for all years examined, where larger variation is thought to occur (Reid *et al.*, 2003). Salinity has also been found to be an important variable in determining the distribution of other cetacean species including humpback whales (*Megaptera novaeangliae*) and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) in California (Tynan *et al.*, 2005), with strong salinity gradients supporting high primary productivity (Viddi *et al.*, 2010).

Changes in SST have been known to contribute to the seasonal changes in cetacean distribution as these cause resultant changes in prey abundance (Bearzi *et al.*, 2011). Both

time series showed that peaks in temperature were associated with peaks in the number of individuals observed, which may be due to the high level of seasonality in coastal waters (Felce *et al.*, 2013).

However, SST did not substantially contribute to the importance of the overall model, and was found to be the least important variable in all seasonal and inter-annual models. The results found a very low probability (<0.1) of presence below 11°C, with optimum conditions at 11.13°C. Whilst it is suggested that Risso's dolphins are rarely seen below 10°C (Wells *et al.*, 2009), they have a wide range of thermal tolerance (Evans *et al.*, 2003; Bloch *et al.*, 2012), being found in waters ranging from 4.5 to 28°C (Leatherwood *et al.*, 1980; Evans *et al.*, 2003; Bloch *et al.*, 2012) which may explain why this variable was not of particular significance to distribution.

Chlorophyll α , as a proxy for primary production, was found to be the second most important predictor in the overall Risso's dolphin habitat model. This may be because it is a highly patchy variable over both spatial and temporal levels as the scale and onset of oceanic plankton blooms have been known to show considerable variation from year to year (OSPAR, 2000): variables that exhibit patchiness may result in patchy distribution, which can be seen in the model predictions. Chlorophyll α has also been found to be an important variable in the occurrence of cetacean species including humpback whales (Tynan *et al.*, 2005).

Although chlorophyll α was generally considered to be more important than salinity, the seasonal modelling indicated that it was of greatest importance only during October, being second to salinity in all other months, and also second in all inter-annual models. This may be due to the changing timings of the spring plankton bloom both seasonally and inter-annually which shift the timing of optimal chlorophyll α conditions and, therefore, when primary production will be greatest (OSPAR, 2000).

4.4.3. Model predictions

Evans (2008) found that the major populations around the British Isles are observed predominantly on the Atlantic seaboard and in the northern North Sea (Figure 4.5.1.). They are seen most regularly around the Hebrides, and also the Northern Isles, the West coast of Ireland and have a patchy distribution in the Irish Sea, particular around the Isle of Man, North Wales and the St George's Channel (Evans *et al.*, 2003; Reid *et al.*, 2003). The

Maxent model which predicted suitable habitat based on all environmental variables examined agreed to some extent with the distribution described by Evans (2008), predicting that habitat is suitable around the west coast of Ireland and between the Isle of Man and North Wales. Based on the environmental variables selected there were, however, no areas of high predicted suitability around the Hebrides and very few around the Northern Isles, which would coincide with the high density areas observed by Evans (2008). It is possible that the concentration of sightings in the Irish Sea, Celtic Sea and Irish Coastal waters in the model has resulted in bias, but sightings from outside this area were also included, and, as the model is created purely by presence data, it should not have been affected by absence. As previously discussed, minimal mixing was found between Wales and these areas: the conditions that make the habitat suitable for Risso's dolphins in the Irish Sea and West Ireland coast may differ from the conditions which are suitable to those individuals that are part of a different population/subpopulation in Scotland.

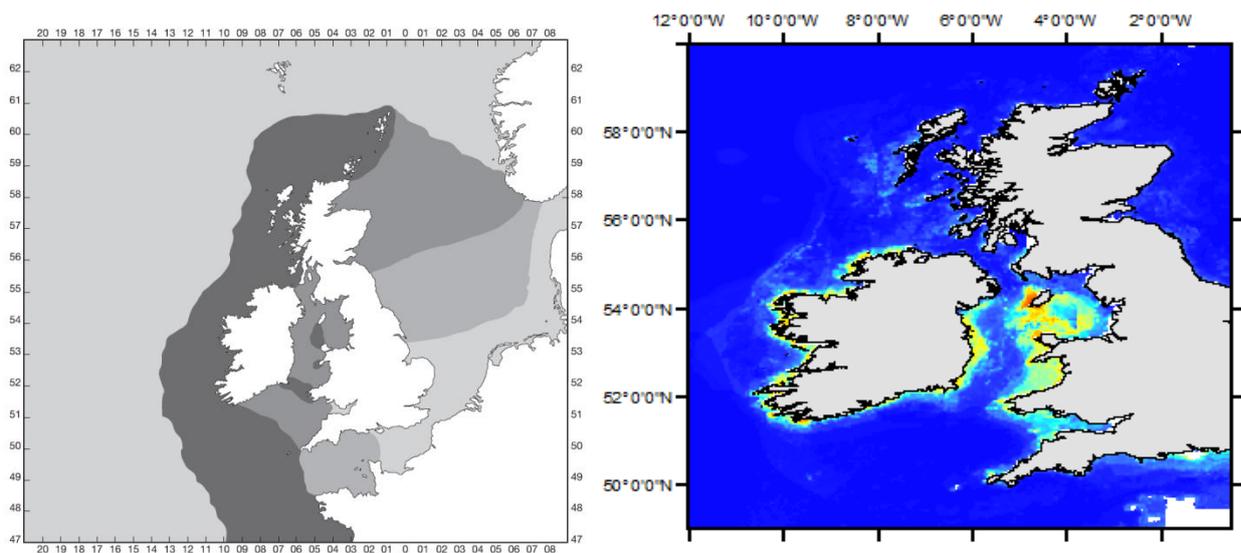


Figure 4.5.1. A comparison of the estimated Risso's dolphin distribution around the British Isles as used by Evans (2008) (darker colours indicate a higher density) with the Maxent model predicted habitat suitability using seven environmental variables (warmer colours indicate higher density)

The results of this research show that there were a number of sightings outside the predicted habitat range. These outliers may be as a result of groups travelling between major feeding grounds or temporary diversions from these feeding areas for trophic reasons. They may also be sightings of individuals that are engaged in mating or calving activities away from the regions they typically inhabit (Casacci and Gannier, 2000).

A further point of interest is that seasonal modelling showed that suitable habitat occurred at higher latitudes around the Isle of Man during May and June, and then moved southwards towards North Wales from July to October. A similar pattern is echoed in the time series, where it was noticed that, whereas more individuals were seen around the Isle of Man, the peak in numbers of individuals occurred earlier in the year (May to August), than in North Wales (July to October), although the specific reasons behind this change in distribution was not shown.

4.6. Management

Risso's dolphins are currently classified by the IUCN Red List as a species of least concern from data assessed in 2008, having previously been data deficient (Taylor *et al.*, 2012). Some international protection exists (Evans, 1999), for example, in Europe, they are protected by Annex IV of the EU Habitats Directive (1992) which protects all cetacean species, and in the UK, they are protected under the Wildlife and Countryside Act of 1981 and the Wildlife Order in Northern Ireland (1985). They are also encompassed by the Agreement on the Conservation of Small Cetaceans in Baltic and North Seas (ASCOBANS) applied in 1992, but this is not legislation (Evans *et al.*, 2003). However, the majority of the ruling does not specifically target Risso's dolphins. Largely, legislation relates more generally to cetaceans or they are covered incidentally by protected areas: Bardsey Island and its surrounding waters, where the density of sightings is relatively high, has been designated as a Special Area of Conservation (SAC) by the EU Habitats Directive, although this designation was only implemented for bottlenose dolphins (de Boer, 2009).

Understanding the distribution of Risso's dolphins and the key drivers of their distribution patterns is important as this knowledge can be used to implement effective conservation strategies (de Boer *et al.*, 2014) and predict the effect that any management may have on the species (Fourcade *et al.*, 2014). Areas that are known to support significant Risso's dolphin aggregations or are of predicted higher density should be considered as locations for future protective measures, and this study has confirmed the regular presence of Risso's dolphins in the Irish Sea and along the Atlantic coast of Ireland.

In 2008, WDC produced a Conservation Plan which aims to define the conservation needs of Risso's dolphins in waters west of the UK, based on the EU Habitats Directive, by determining the potential threats and areas of critical habitat to identify the necessary

management strategies and research action needed to ensure the long-term viability of the population. For a mobile species it is always difficult to determine the extent of a critical habitat, but for the Irish Sea the modelling and sightings information both suggest that the most important areas of habitat are located in the coastal waters of the Isle of Man and North Wales, and also potentially the West Pembrokeshire area, so conservation efforts in the Irish Sea should be focused on these coastal regions. It is however difficult to implement the correct protective measures for a population for which there is currently no definitive abundance estimate (Wharam and Simmonds, 2008), particularly as research suggests the number of individuals may be constantly changing as it is considered to be an open population (de Boer *et al.*, 2013).

Conservation strategies should also be developed on a regional basis as the model results did not suggest that density was likely to be high in Scotland, whereas studies have previously observed large numbers there, particularly in the Hebrides and North Minches (Atkinson *et al.*, 1999 Evans *et al.*, 2003, Paxton *et al.*, 2014). As mentioned previously, the few individual matches between SWF and HWDT suggest a lack of mixing between the two regions covered by these catalogues. A possible reason for this could be that their distribution may be affected by different environmental factors or the importance of these factors may differ, which could indicate the need for different conservation priorities. Maintaining a favourable conservation status is important as the species has a low intrinsic growth rate which means that, if species density declines, the time frame for population recovery is likely to be longer than one generation (Wharam and Simmonds, 2008). This could be achieved by introducing legislation specific to Risso's dolphins and through the designation of protected areas in the potential hotspots identified in this study.

4.7. Limitations and improvements

4.7.1. Sightings

Effort data are often used in cetacean studies to estimate the density of a particular species in relation to the time spent and the size of the area surveyed. Studies have shown that incorporating effort data is important in the analysis of cetacean distribution, particularly for the examination of long-term trends (Evans *et al.*, 2003; Baines and Evans, 2012), as survey effort has been shown to vary dramatically on both a spatial and temporal scale (Paxton *et al.*, 2014).

SWF records effort for the majority of sightings in their database as the distance travelled (for vessel & aerial surveys) and the time in minutes elapsed from the start to end of the dedicated search (for land watches), so the number of sightings or individuals can be calculated per kilometre travelled or hour of observation for a particular species as sightings per unit effort (SPUE) (Evans *et al.*, 2003; Reid *et al.*, 2003; Baines and Evans, 2012). The type of effort is scored along a scale of intensity from 1 to 7, ranging from casual watching that is not part of a dedicated watch to dedicated surveys by experienced observers using line transects (Evans *et al.*, 2003). Effort could not, however, be incorporated in this study due to time constraints, although Baines and Evans (2012) have done so for the species for the entire Irish Sea region in four year increments (Figure 4.7.1.). Useful comparisons can be made using this, as it shows that, in general, effort is highest in coastal regions. For example, the middle of the Irish Sea, with the exception of two strips joining North Anglesey and west Pembrokeshire respectively to the Irish coastline which coincide with ferry routes, had very little or no survey effort, which could explain why no sightings were reported for this area. Areas with high survey effort often coincided with high densities, but this was not always the case as effort was high in Cardigan Bay but sightings were low.

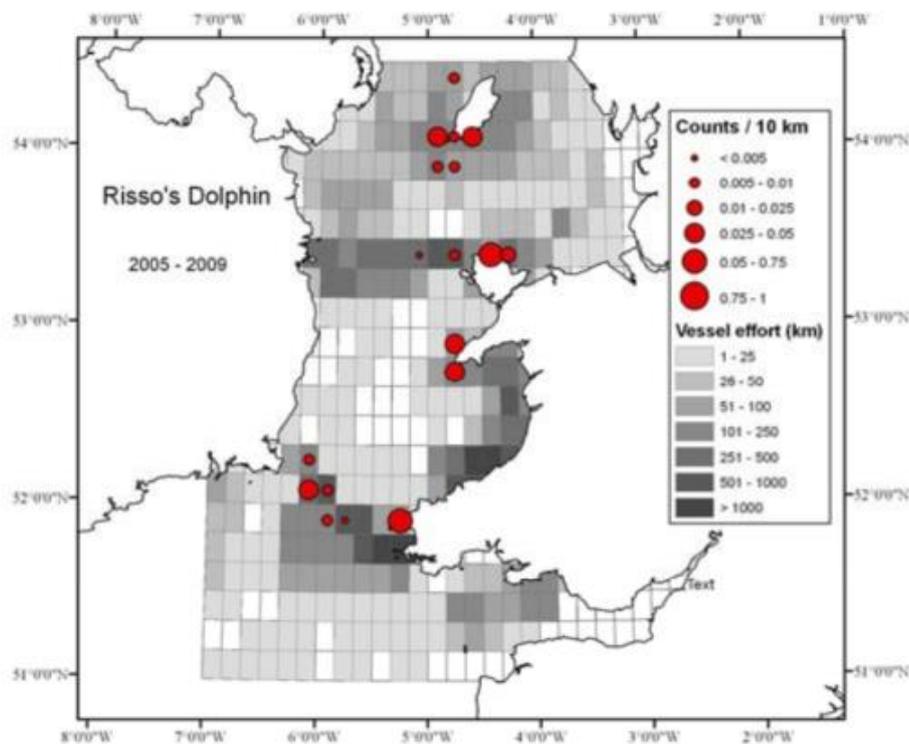


Figure 4.7.1. The mean density of Risso's dolphins in the Irish Sea with the associated vessel effort from 2005-2007 (extracted from Baines and Evans, 2012)

Bias from presence only data may occur for a number of reasons. Typically, effort is not evenly spatially distributed: in the Irish Sea, effort has been much greater around Wales than off the Irish coasts (Evans *et al.*, 2003), so the conclusions regarding the areas of lowest Risso's dolphin density may be due to a lack of survey effort rather than a lack of presence. It is also possible that effort was temporally biased as, in the UK, effort is particularly variable on a seasonal level, with a distinct lack of effort occurring during autumn and winter (Baines and Evans, 2012; Paxton *et al.*, 2014), generally due to adverse sea conditions. Consequently, the spring/summer peaks observed might be due to better effort instead of more individuals being present. Poor weather conditions could be further responsible for affecting results as they restrict the amount of field data that can be collected and the probability of visual detection decreases as the sea state and swell increase (Reid *et al.*, 2003).

In the continuation of this study, survey effort should be incorporated into any analysis to reduce bias and increase the robustness of conclusions drawn. It would also be advantageous to increase effort where there is currently very little, particularly in areas further offshore, to determine if the preference for coastal waters observed in this study is correct. Conditions permitting, a regular programme of survey effort should be instigated to provide an even coverage of surveys over the year to allow a more thorough analysis of seasonal patterns, as well as allowing the results to be examined on a finer scale.

However, the SWF Risso's dolphin sightings adjusted for effort for the whole of the British Isles and for the Irish Sea, (Evans *et al.*, 2003; Baines and Evans, 2012) showed a very similar seasonal pattern to that found in this study where the data was not adjusted for effort (Figure 4.7.2.), with most sightings and numbers of individuals between May and September. Therefore, based on the similarity with these studies, it is likely that not adjusting for effort has not significantly affected the patterns observed and resultant conclusions drawn regarding seasonal and inter-annual patterns of density.

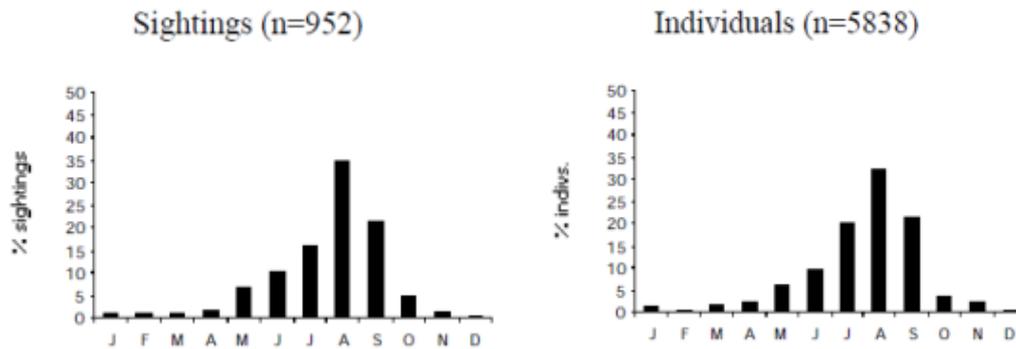


Figure 4.7.2. The Sea Watch Foundation effort-related seasonal distribution of sightings and number of individuals of Risso's dolphins in the UK (Evans *et al.*, 2003)

Variable survey conditions could also potentially influence the sightings results, as sightings were taken from a variety of platforms, and the speed, eye height and experience of observers can all affect the detectability of cetaceans (Evans & Hammond, 2004; Paxton *et al.*, 2014). Whilst survey methods are relatively consistent across the organisations, the type of survey vessels used and therefore platform height will vary. Furthermore, standardised sightings databases and catalogue formats across all organisations involved in data sharing would make direct comparisons and analysis over a larger study area easier.

4.6.2. Photo-identification

DARWIN was the software selected for use in identification, but there are other programs available which could be considered for use including FinScan and FinMatch and FinEx, which use similar principles to determine matches between cetaceans (Hillman *et al.*, 2002; Stewman and Debure, 2011). These could prove to be more accurate or useful to the study, so future research should consider if an alternative option might be more appropriate. DARWIN helped make identification more reliable, but it is still possible that errors occurred as photo-ID is a very subjective process resulting in the potential to have over or underestimated the number of individuals seen during the study period. To avoid this problem, matches made within the SWF catalogue should be confirmed by multiple identifiers to improve the validity of any matches made. This should also be applied in the classification of fin markings, to reduce the chance of duplication of individuals in the catalogue when future sightings are entered.

Problems may have arisen in the matching process, both for the analysis of site fidelity and home ranges. More marked individuals may have been matched because they had more easily recognisable features, and it is likely that more matches were missed between left and right individuals with more subtle identifying features and no distinctive fin outline. Problems with the re-sightings of these individuals may also have occurred if the left and right side of the same individual was photographed on separate occasions. As quality control was used to remove all poor quality photographs from the identification process, it is possible that new individuals were removed and not included in the catalogue, resulting in an underestimate of the number of individuals seen, or individuals that occurred in multiple sightings being missed, resulting in a lower estimate of the re-sighting rate. Having additional photographs could also improve the calculation of the re-sighting rate which would help to determine if site fidelity is indeed low within Wales. It could also provide a better idea of the timing and location of births which could be useful in identifying important nursery areas.

Calves were very difficult to identify in recaptures due to the long periods between photographs. Most had very indistinctly marked fins as calves, so if they were re-captured as a sub-adult or adult it is likely they would have been catalogued as a new individual. However, out of the 37 mother and calf pairs, only one female was observed on multiple occasions, so it is unlikely that this error occurred very often. More regular sighting with photographs could facilitate the tracking of the development of an individual calf's distinguishing characteristics over years to reduce misidentification.

Only approximately one third of sightings in Wales resulted in photographs for identification, and in some years there were no photographs available (2006) or only photographs from a single event (2010), which has the potential to bias the results. Ideally, photographs should be available from all sightings which would enable a more accurate estimate of the number of individuals to be made. The 68 sightings with no photographs may have contained the same 144 individuals already identified or completely new individuals, although it is most likely they would show a mix of both. The minimum number of individuals encountered (162) fell inbetween the estimated minimum and maximum numbers identified, so this is likely to be accurate. It should however, be taken into account that this value was calculated based on the mean proportion of marked individuals which could only be estimated from the 13 sightings where group sizes were

available. It was limited by data availability, so may not be truly representative of the proportion of marked individual over all the sightings. Future analysis should aim to include information regarding group sizes of all photographed sightings so that this estimate can be improved. Limited sightings information corresponding to photographs may also mean that there were actually slightly more sightings than the data analysed suggests and that the exact location and home ranges of individuals could not be fully determined.

4.6.3. Maxent species distribution modelling

The use of Maxent SDM modelling means that, based on the habitat characteristics, predictions can be made for those areas with little or no effort (Becker *et al.*, 2012), thereby reducing the potential of incorrect conclusions being drawn as a result of not taking effort into account in this study. However, the presence only data used to train the model may have been geographically biased due to unequal sampling effort across the study area which has the potential to be a source of inaccuracy and result in incorrect predictions. There may have been areas suitable for Risso's dolphins that were poorly represented in the survey data and others which were overrepresented due to locally high sampling effort. There are methods which can be applied to try and correct for bias, but these vary greatly depending on the species and type and intensity of bias (Fourcade *et al.*, 2014).

Maxent requires that all environmental variables used are of the same cell size and extent (Phillips, 2011). Since all variables were of differing resolutions, bilinear interpolation was used in order to achieve the identical extents for each. Although this produced a high resolution model, it resulted in a less precise dataset which may have caused some slight skewing of the model output. Cutting all variables to the same extent also meant that the amount of coastal information was reduced. Since Risso's dolphins in the UK are a primarily coastal, relatively shallow water species (Evans *et al.*, 2003), it is likely that the missing extent will have altered the relative importance of some of the coastal habitat. To improve this, higher resolution data covering a greater extent should be acquired for all variables to reduce bias in the model.

Problems may have arisen as a large amount data from satellites was missing as they are affected by extensive cloud cover or close proximity to coastal regions (Zhang *et al.*, 2008). This resulted in some months having to be removed from analysis, or averages and totals

being calculated based on very little data which may have skewed the salinity, SST and chlorophyll α results. The use of remote sensing data is further limited as it is only able to provide an indication of the surface value of the desired variable, because it only records the top layer of the euphotic zone (Smith, 1981), and therefore does not take into account any vertical changes in variables (Cullen, 1982). The analysis could also be improved by examining some of the variables in more detail, particularly habitat type and energy, since it is better to use continuous variables in the model, and to examine the effect of fronts on a wider scale.

The preferred niche of a species cannot be wholly determined using SDM as these models only consider a subset of the potential explanatory variables of distribution (Warren, 2012). There are additional variables e.g. tidal state, not included, which could be of high importance to the determination of distribution, therefore meaning that the results of the model may be placing too much emphasis on certain variables and relationships. Habitat modelling using a more extensive range of environmental variables to confirm the location of critical habitats would therefore be recommended (Wharam and Simmonds, 2008).

Examining Risso's dolphin presence in association with other cetacean species could prove useful as concentrations have been known to be found in association with bottlenose dolphins (*Tursiops truncatus*), short-finned pilot whales (*Globicephala macrorhynchus*) and common dolphins (*Delphinus delphis*) (Baird and Stacey, 1991). They have also been shown to exhibit different distribution and habitat use patterns to other cetaceans: Risso's dolphins and harbour porpoise (*Phocoena phocoena*) are often spatially segregated around Bardsey Island (de Boer *et al.*, 2014). Niche separation may occur due to competition for resources, and it could potentially be for a similar reason that few Risso's were observed in Cardigan Bay despite the predicted suitable conditions, as this area has a high density of bottlenose dolphins which Risso's dolphins would have to compete with. It may also simply be because species have different ecological needs, and examining community ecological variables and prey availability in the model could prove useful in determining the reason for any separation that occurs (Praca and Gannier, 2008). Furthermore, this study did not consider the potential anthropogenic impacts on the species distribution, for example, fisheries interactions, bycatch, boat traffic and gas embolisms as a result of noise pollution could also have been important drivers in their distribution. The majority of

evidence for anthropogenic threats comes from examining stranded individuals (Jepson *et al.*, 2003; Evans and Hintner, 2010).

It should also be remembered that the results of the model are only predictive and do not definitively show the actual distribution of Risso's dolphins. The suitability of West Scottish waters is, in most cases, shown to be low whereas studies have shown high densities (Atkinson *et al.*, 1999; Reid *et al.*, 2003; Evans *et al.*, 2003; Evans, 2008), and conversely, some of the seasonal and inter-annual models suggest areas around the south coast of England around the Isle of Wight to have suitable habitat, but there is presently little evidence of Risso's dolphins in these areas. Studies should therefore be expanded to survey in areas that the model indicates could contain suitable habitat that are not currently being investigated to assist with the evaluation of the model. Expanding the area of sightings used for modelling to include all waters around the British Isles would result in a more conclusive study and therefore improve model predictions. Statistical analysis of the model results would also be useful to evaluate its reliability, but this was outside the scope of this study.

Factors such as SST, salinity and chlorophyll α concentration are dynamic variables and therefore constantly changing, so modelling over a larger temporal scale cannot reflect the changing dynamics of the system at high resolution (Redfern *et al.*, 2006). Ideally predictions should be made on a finer temporal scale as this would be more useful to research. Predictions of habitat suitability were however constrained both seasonally and inter-annually by data availability.

4.7. Future study

The continued study of Risso's dolphins is important as there are still large gaps in our knowledge of the species, both in general and more specifically in the UK (Wharam and Simmonds, 2008; Evans, 2013). There are currently no estimates available of global population size (Taylor *et al.*, 2012) or trends (Baird, 2009), and little effort has been made to estimate the entire UK population due to a lack of current data (Evans *et al.*, 2003), leaving the overall status of the species uncertain (Bearzi *et al.*, 2011).

In the future, the continued collection of sightings data and conduction of photo-ID studies of Risso's dolphins would be beneficial as this would increase the sample size. As a result, an increased number of individuals could be identified and more re-captures confirmed which would improve the study of site fidelity. Expanding the study within this area could also potentially augment the understanding of home ranges and wide-scale movements, and allow any seasonal and inter-annual patterns to be seen more clearly. It is currently unknown whether Risso's dolphins are present in the locations observed all year round in coastal waters, or if they are present all year but further offshore, or are only seasonally present.

A more in-depth study examining the relationship between predator and prey distribution would be advised, as whilst the MacLeod *et al.* (2013) study found no correlation, prey availability is considered to be a key driver in the distribution of any cetacean species (Baumgartner, 1997; Boran *et al.*, 2001; Cañadas *et al.*, 2002). Expanding this study by incorporating a wider range of environmental variables into the model, e.g. thermocline and halocline depth, as well as examining the social structure, interactions and behaviour of Risso's dolphins, could also provide valuable information (Hartman *et al.*, 2008).

Continuing the current collaborative work and data sharing between the SWF and other cetacean organisations in the UK will help improve knowledge of the species (Wharam and Simmonds, 2008; Chen *et al.*, 2013). This would also increase the potential for finding matches between catalogues which would again help improve the understanding of site fidelity and the extent of home ranges. Ultimately, a longer time period of study is needed to identify trends and confirm if the findings of this research are correct.

5. CONCLUSION

Risso's dolphins were found to be regularly present in Welsh waters, as suggested by previous research. Using photo-ID, it was estimated that a minimum of 162 individuals were encountered from 2003 to 2014. The regular presence of calves indicated that the area is important for mating and parturition, which has implications for management. This study found that site fidelity was relatively low (12.5% in terms of re-sighting rates) within Welsh waters, but more photographic evidence is needed to confirm this. Home ranges were predominantly localised, with most individuals matched having a home range spanning from North Wales to the Isle of Man, although there was also evidence that large-scale migrations may occur.

The use of sightings information determined that the highest relative abundances of Risso's dolphins in the Irish Sea occur along the east, south and west coast of the Isle of Man, on the North-west Wales coast around Anglesey and the Llŷn Peninsula, and west of Pembrokeshire. Maxent modelling confirmed the habitat suitability of these areas and, of the variables examined, bathymetry was determined to have the most important influence on the distribution of Risso's dolphins around the UK. It is however likely that combinations of environmental variables, including some not considered in this study, is responsible for driving the distribution patterns. Understanding the key areas of high density and the determinants of this distribution is invaluable when discussing future management plans and conservation initiatives.

It is important that the study of Risso's dolphins continues in the UK to provide extended datasets for ongoing analysis. Long-term environmental changes may result in corresponding changes in the distribution and geographical range of Risso's dolphins. Continued observation of the species is essential to monitor any such variations and enable a swift response with appropriate management strategies to ensure the populations in both Welsh and UK coastal waters remain viable.

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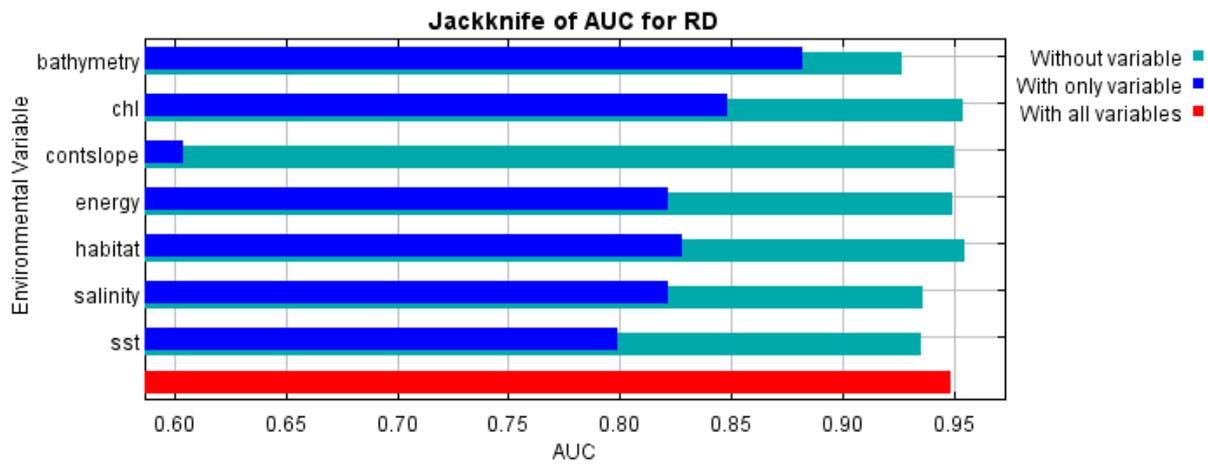
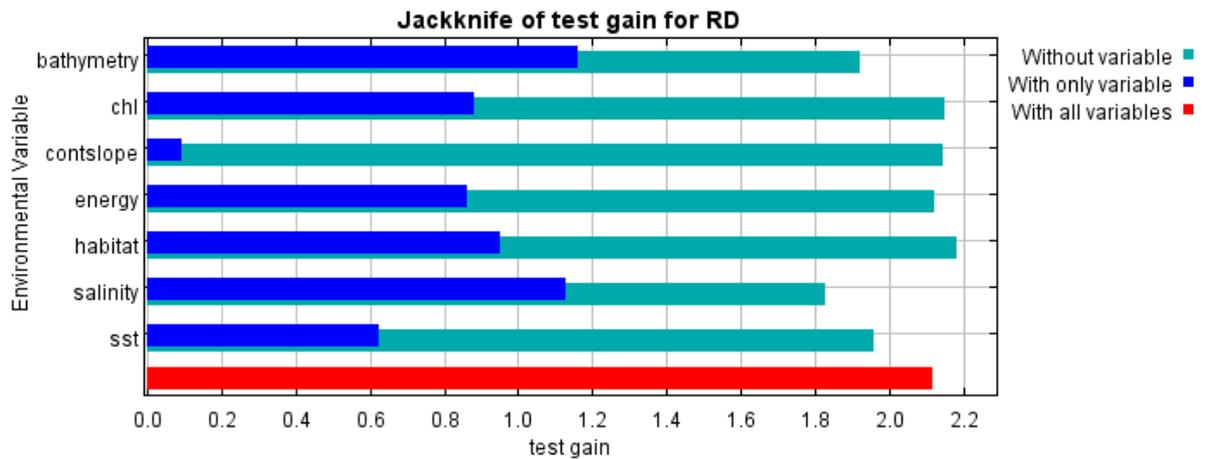
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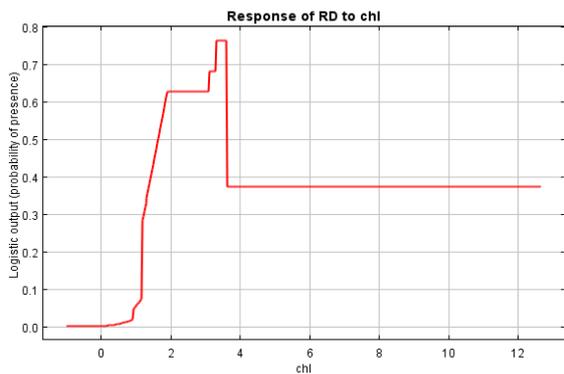
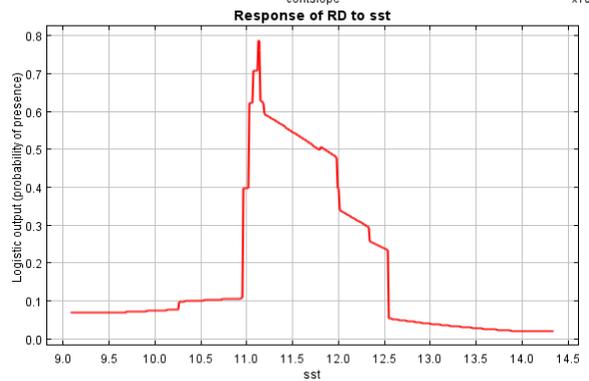
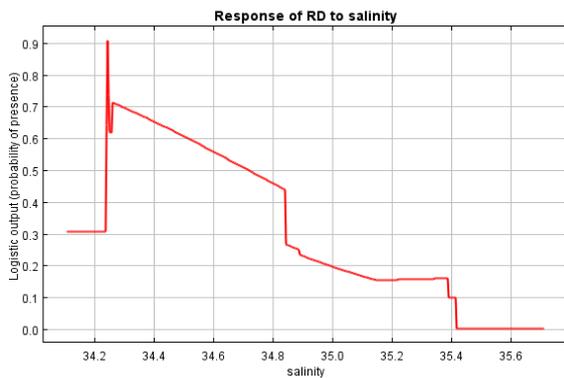
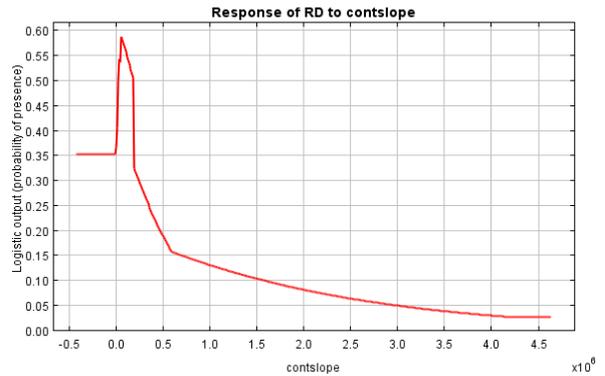
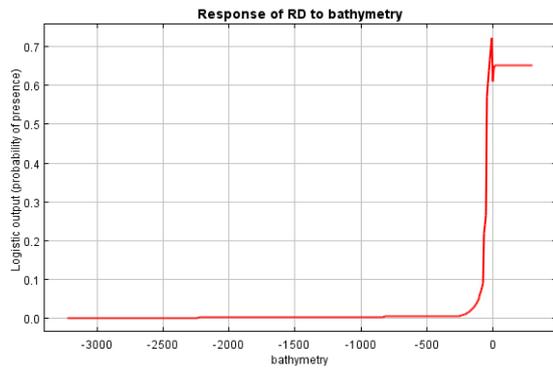
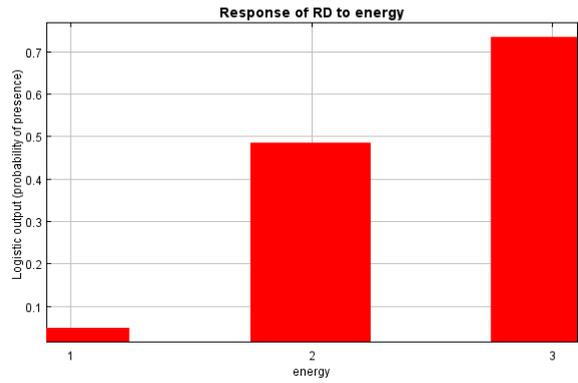
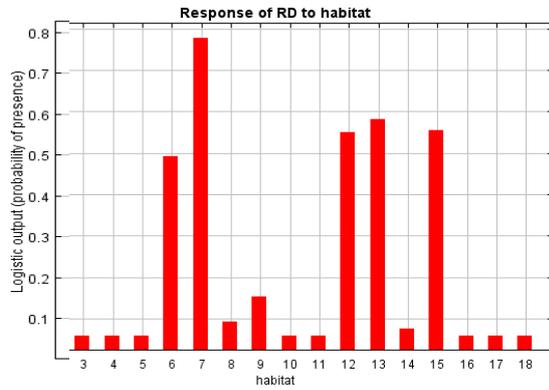
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Appendices

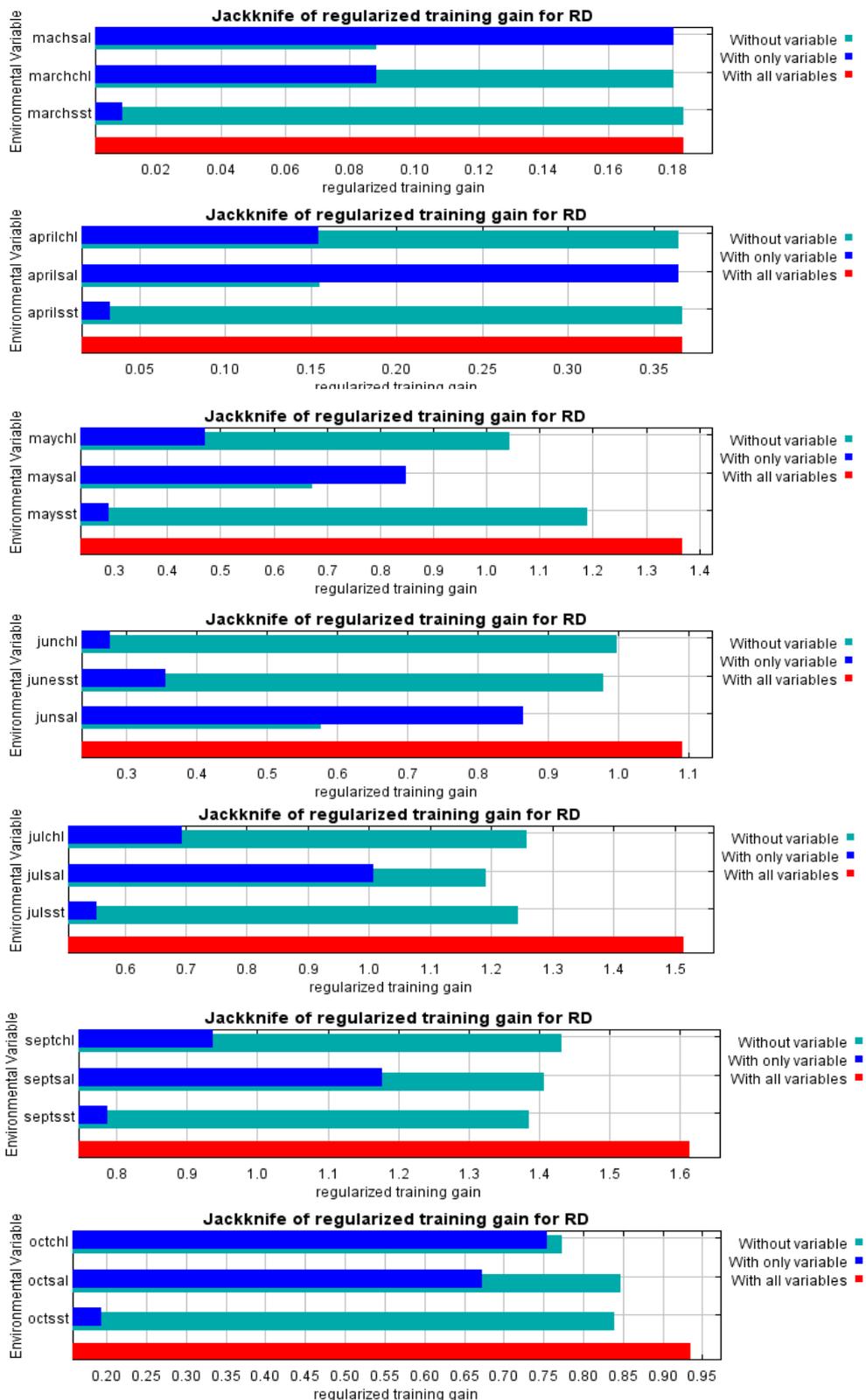
Appendix 1: Jackknife variable contribution predictions for the Maxent model of all environmental variables, using 25% test data. Dark blue bars represent the use of the variable in isolation and the light blue bar with that particular variable omitted. Red represents the total gain



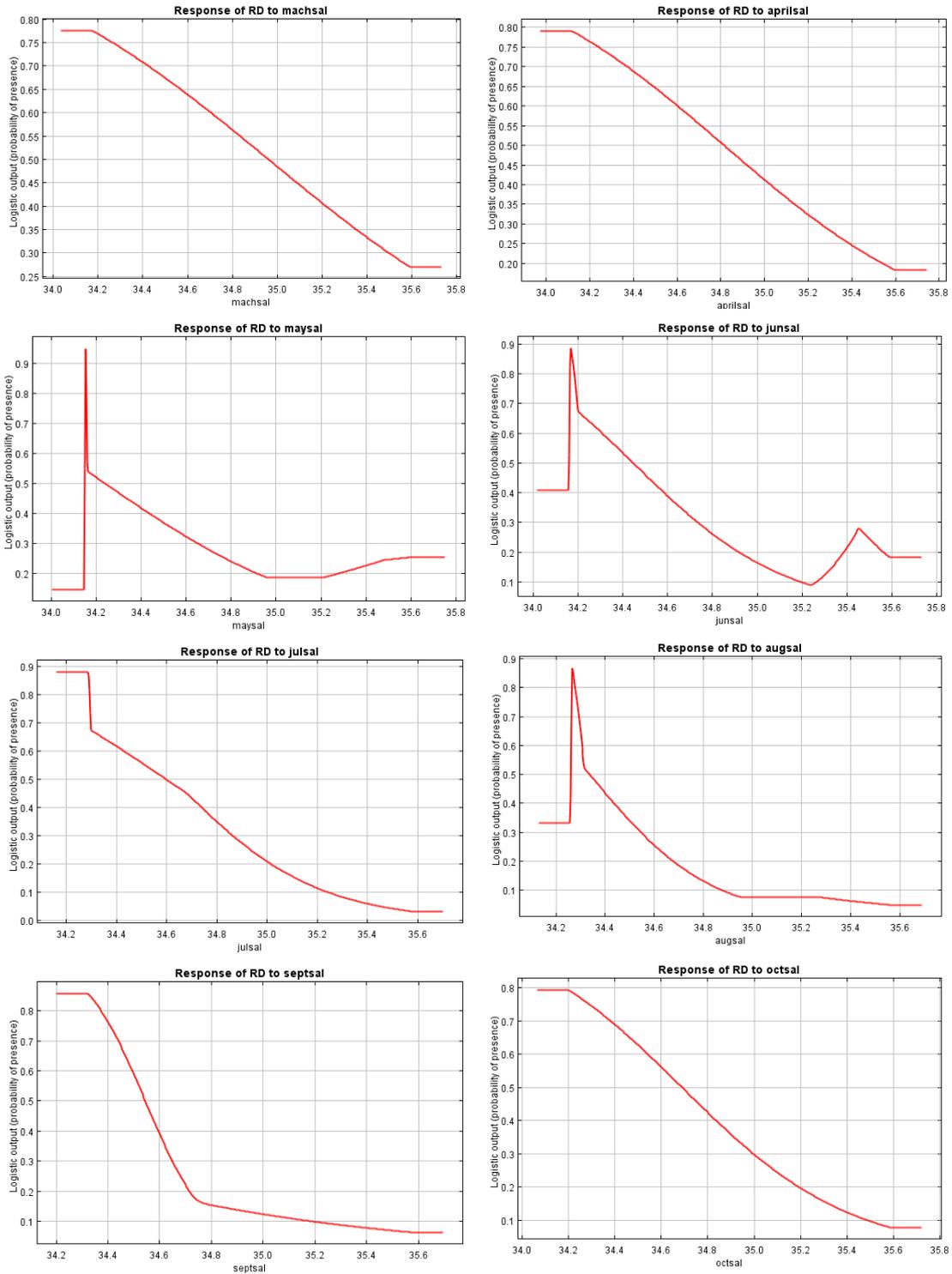
Appendix 2: Response curves of variables used to run the overall environmental variables model, and created using only the corresponding variable. The plots reflect the dependence of predicted suitability both on the selected variable and on dependencies induced by correlations between the selected variable and other variables.



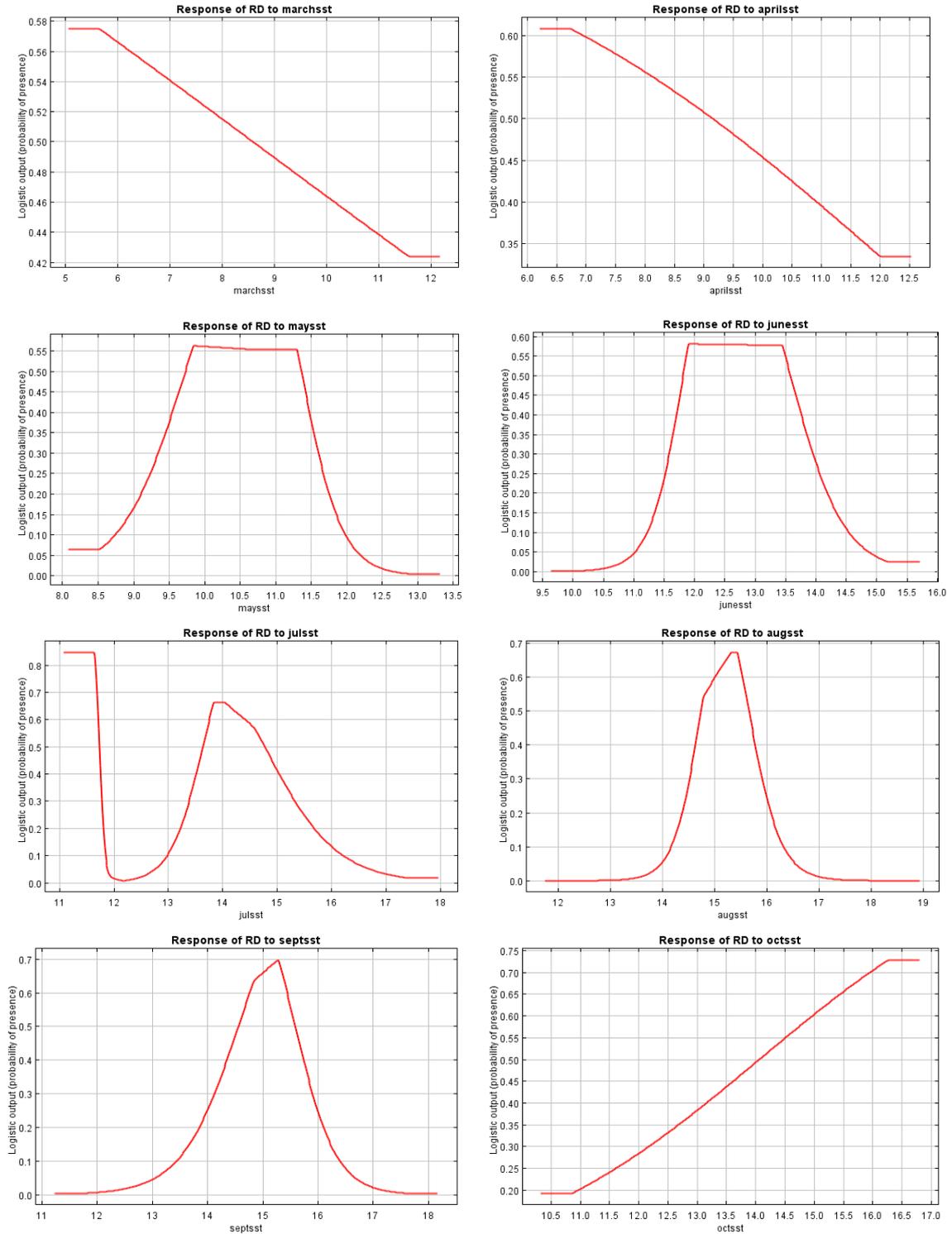
Appendix 3: Jackknife variable contribution predictions for the seasonal Maxent model, using 25% test data. Dark blue bar represents the use of the variable in isolation and the light blue bar with that particular variable omitted. Red represents the total gain.



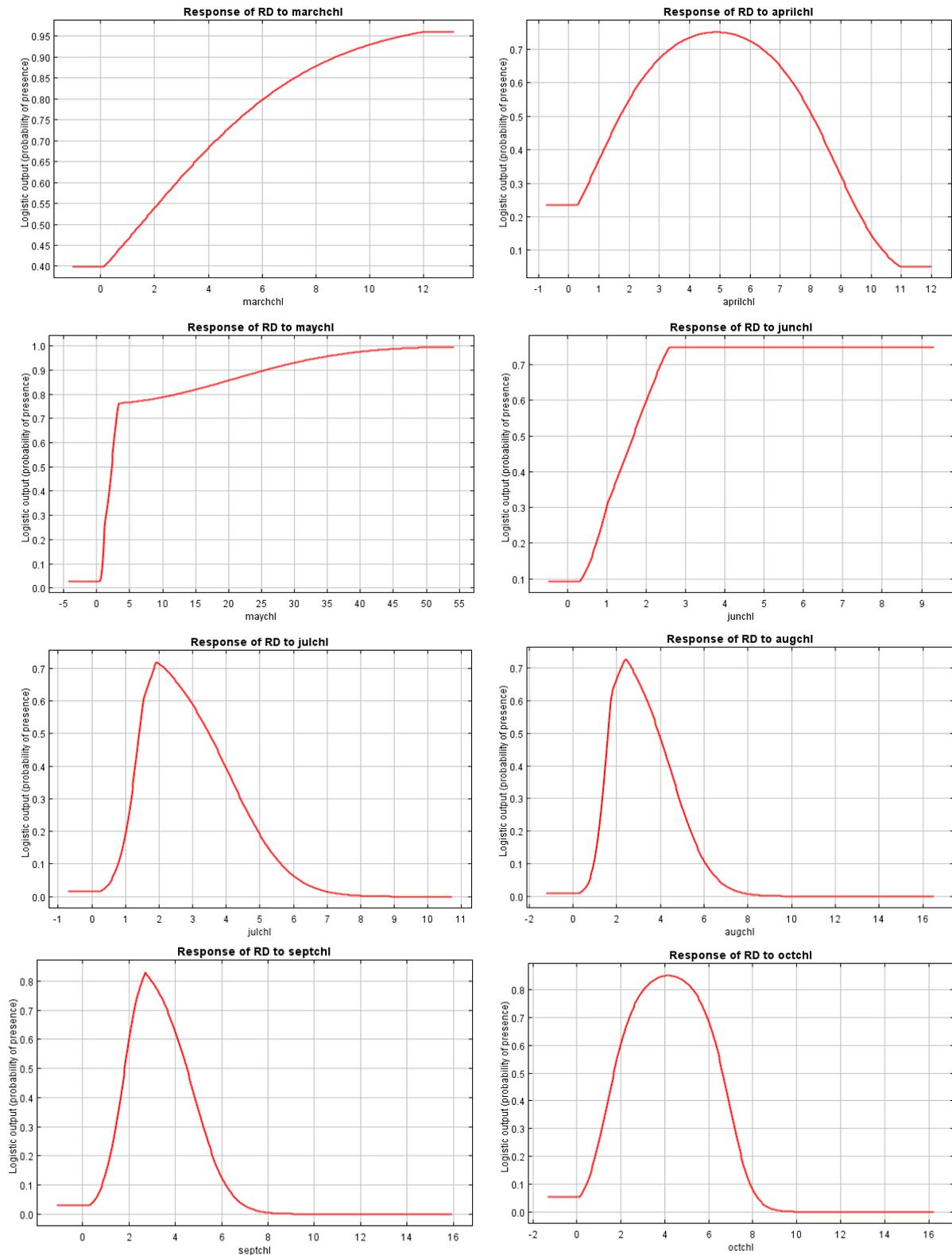
Appendix 4a: Seasonal response curves of salinity from March to October, created using only the corresponding variable. The plots reflect the dependence of predicted suitability both on the selected variable and on dependencies induced by correlations between the selected variable and other variables.



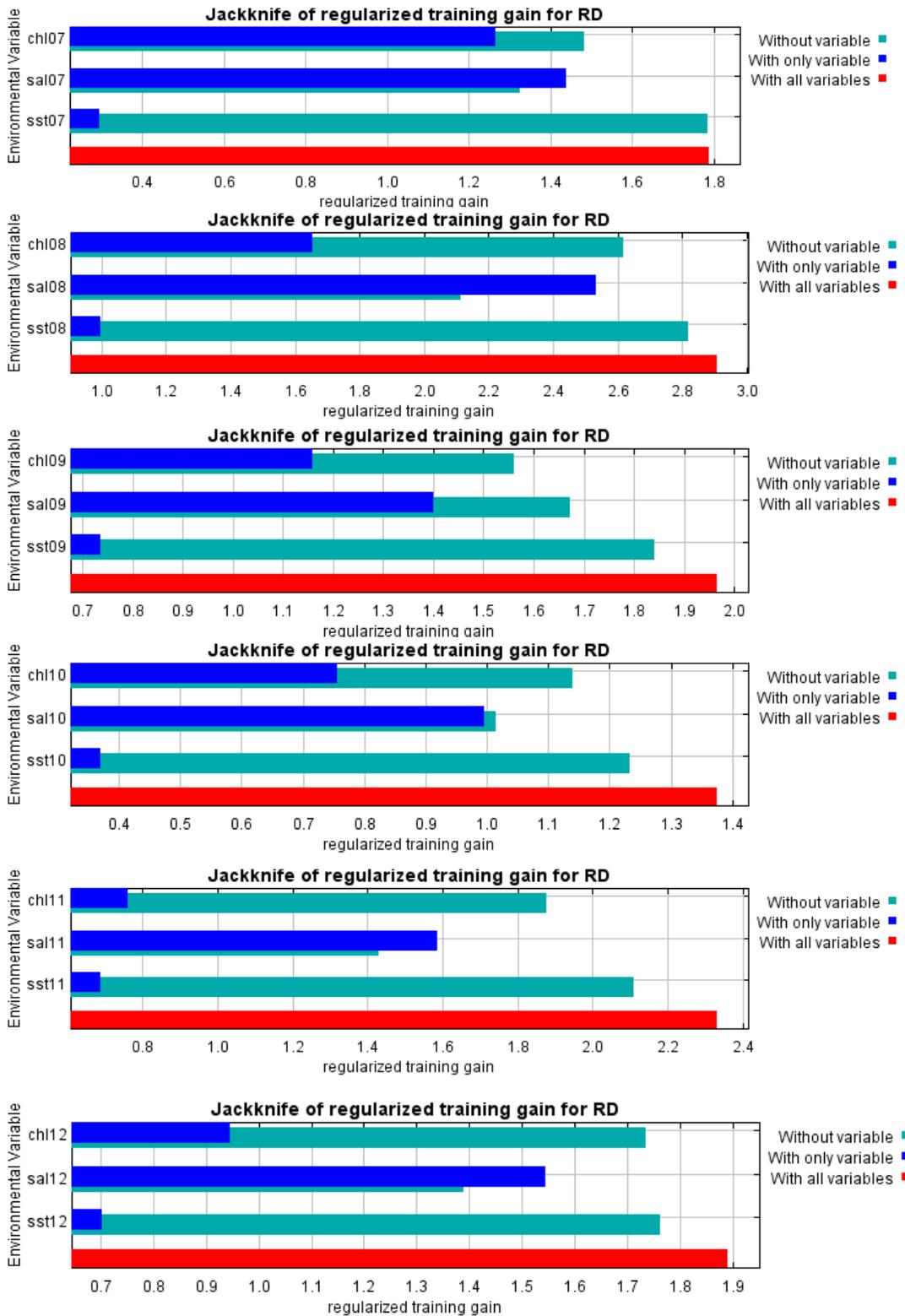
Appendix 4b: Seasonal response curves of SST from March to October, created using only the corresponding variable. The plots reflect the dependence of predicted suitability both on the selected variable and on dependencies induced by correlations between the selected variable and other variables.



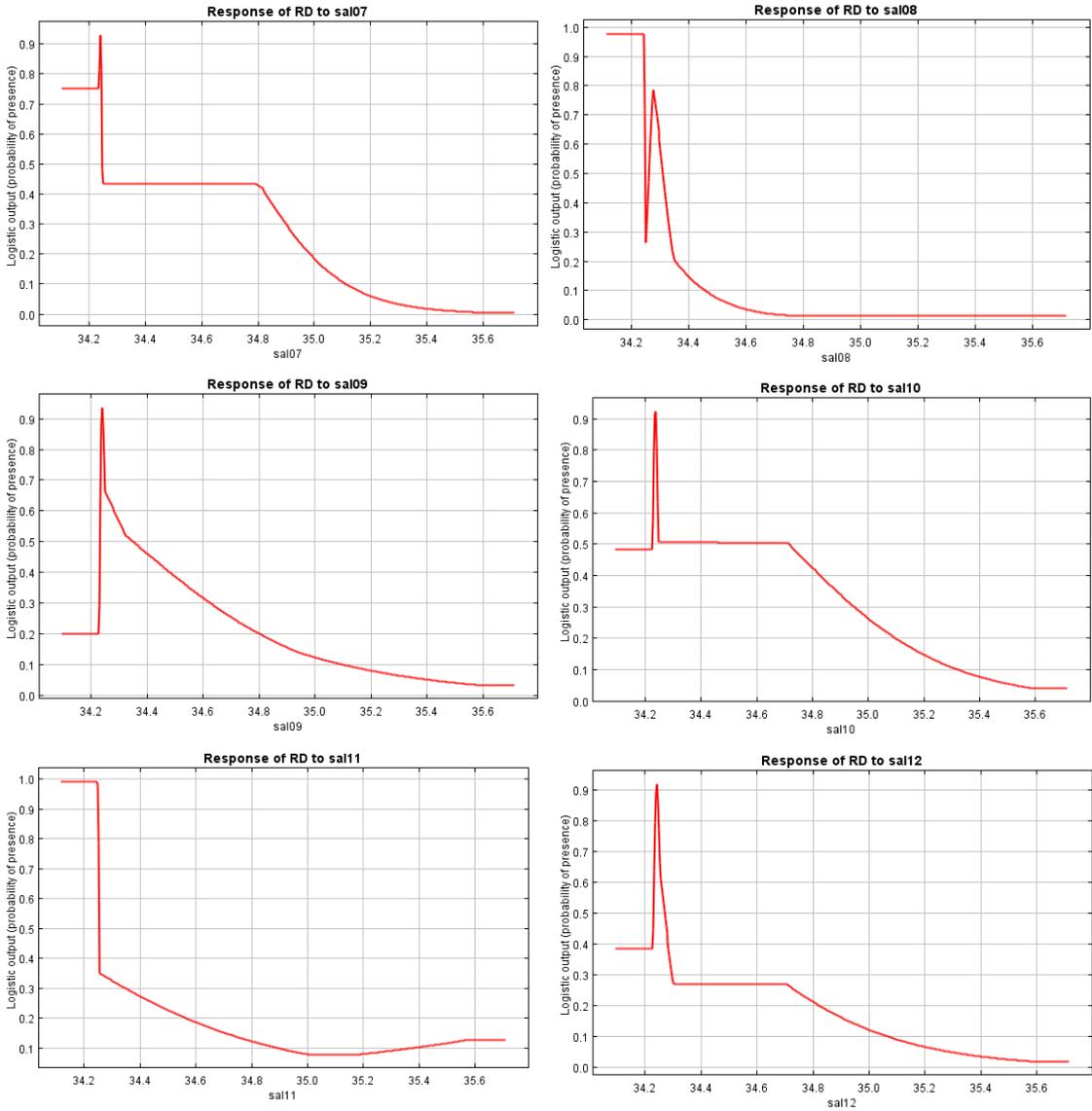
Appendix 4c: Seasonal response curves of chlorophyll α concentration from March to October, created using only the corresponding variable. The plots reflect the dependence of predicted suitability both on the selected variable and on dependencies induced by correlations between the selected variable and other variables.



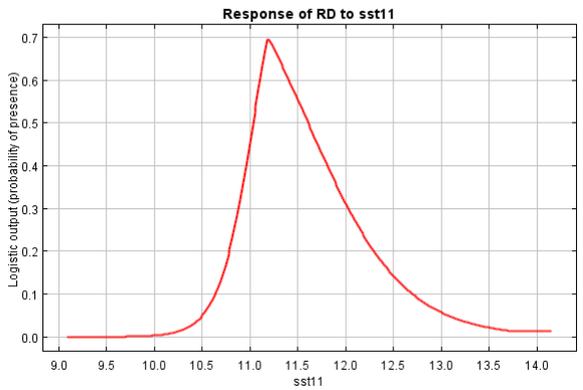
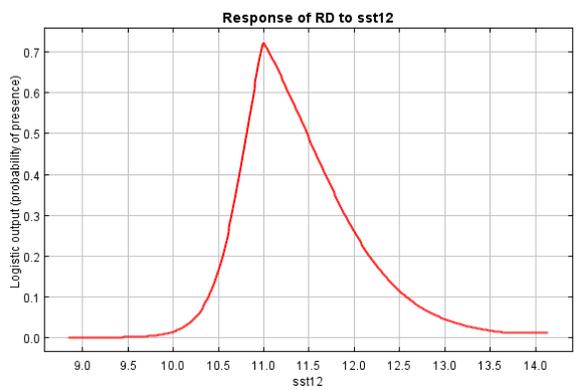
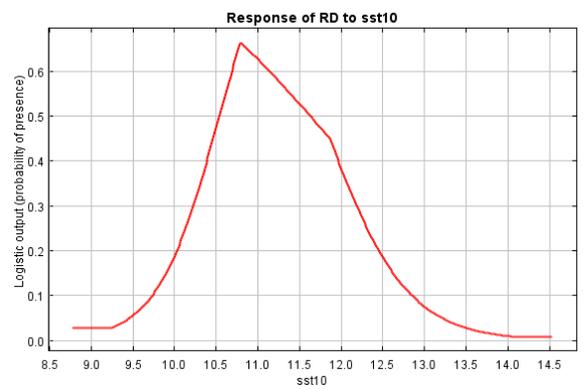
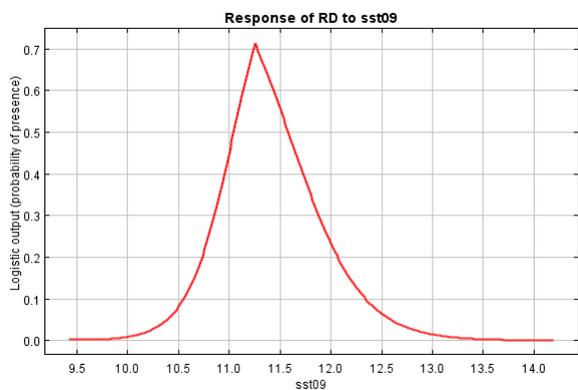
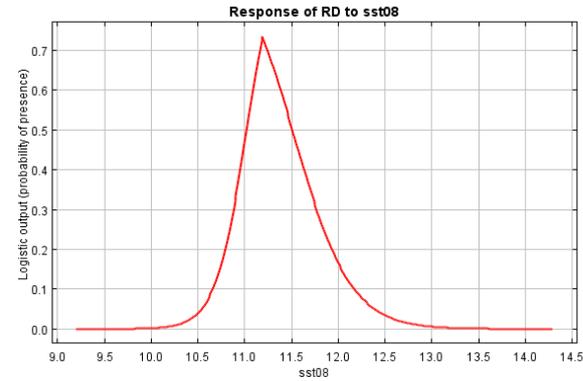
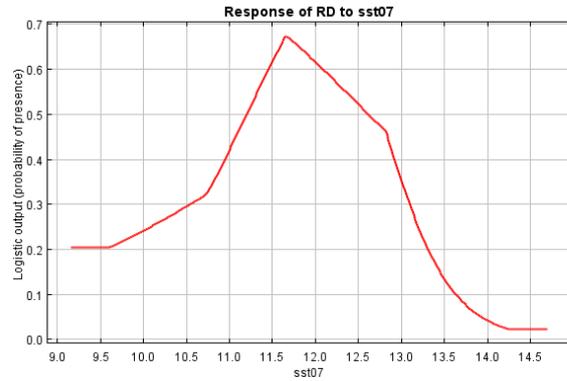
Appendix 5: Jackknife variable contribution predictions for the inter-annual Maxent model, using 25% test data. Dark blue bars represent the use of the variable in isolation and the light blue bar with that particular variable omitted. Red represents the total gain.



Appendix 6a: Response curves of salinity from 2007 to 2012, created using only the corresponding variable. The plots reflect the dependence of predicted suitability both on the selected variable and on dependencies induced by correlations between the selected variable and other variables.



Appendix 6b: Response curves of sea surface temperature from 2007 to 2012, created using only the corresponding variable. The plots reflect the dependence of predicted suitability both on the selected variable and on dependencies induced by correlations between the selected variable and other variables.



Appendix 6c: Response curves of chlorophyll α concentration from 2007 to 2012, created using only the corresponding variable. The plots reflect the dependence of predicted suitability both on the selected variable and on dependencies induced by correlations between the selected variable and other variables.

