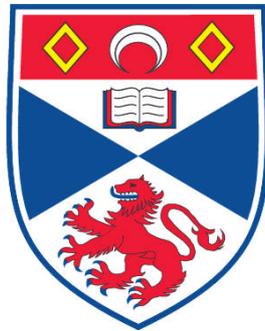


**VARIATION IN HABITAT PREFERENCE AND
DISTRIBUTION OF HARBOUR PORPOISES WEST OF
SCOTLAND**

Cormac G. Booth

**A Thesis Submitted for the Degree of PhD
at the
University of St. Andrews**



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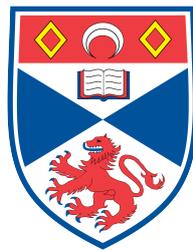
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**Variation in habitat preference and
distribution of harbour porpoises west
of Scotland**

Cormac G. Booth

**A thesis submitted to the University of St Andrews
for the degree of Doctor of Philosophy**

**Scottish Oceans Institute
Sea Mammal Research Unit
School of Biology**



**Submitted:
March 1st 2010**

I, Cormac Booth, hereby certify that this thesis, which is approximately 66,000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

I was admitted as a research student in October 2006 and as a candidate for the degree of Doctor of Philosophy in the School of Biology in March 2010; the higher study for which this is a record was carried out in the University of St Andrews between 2006 and 2010.

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Harbour porpoise surfacing on a calm day in the Inner Sound, west Scotland

“It’s easy to think that as a result of the extinction of the dodo, we are now sadder and wiser, but there’s a lot of evidence to suggest that we are merely sadder and better informed...”

- Douglas Adams

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Abstract

The waters off the west coast of Scotland have one of the highest densities of harbour porpoise (*Phocoena phocoena*) in Europe. Harbour porpoise are listed under Annex II of the EU Habitats Directive, requiring the designation of Special Areas of Conservation (SACs) for the species' protection and conservation.

The main aim of this thesis is to identify habitat preferences for harbour porpoise, and key regions that embody these preferences, which could therefore be suitable as SACs; and to determine how harbour porpoise use these regions over time and space. Designed visual and acoustic line-transect surveys were conducted between 2003 and 2008. Generalised Estimating Equations (GEEs) were used to determine relationships between the relative density of harbour porpoise and temporally and spatially variable oceanographic covariates.

Predictive models showed that depth, slope, distance to land and spring tidal range were all important in explaining porpoise distribution. There were also significant temporal variations in habitat use. However, whilst some variation was observed among years and months, consistent preferences for water depths between 50 and 150 m and highly sloped regions were observed across the temporal models. Predicted surfaces revealed a consistent inshore distribution for the species throughout the west coast of Scotland. Regional models revealed similar habitat preferences to the full-extent models, and indicated that the Small Isles and Sound of Jura were the most consistently important regions for harbour porpoise, and that these regions could be suitable as SACs.

The impacts of seal scarers on distribution and habitat use were also investigated, and there were indications that these devices have the potential to displace harbour porpoise.

These results should be considered in the assessment of sites for SAC designation, and in implementing appropriate conservation measures for harbour porpoise.

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Chapter 1

General Introduction

1.0 Background

A common approach in attempting to conserve the marine environment is the designation of sites as marine protected areas (MPAs) (Agardy 1994; Agardy 2000; Cañadas et al. 2003; Faucher and Weilgart 1992; Hooker et al. 1999; Hoyt 2005; Hyrenbach et al. 2000; Notarbartolo-di-Sciara 2008; Notarbartolo-Di-Sciara et al. 2008). However, there are questions as to whether this is the most suitable method for protecting species (Boersma and Parrish 1999; Hoyt 2005; Kelleher and Kenchington 1992). In many cases it may not be necessary to designate an area for protection in order to minimise a threat or pressure on a species (Cañadas et al. 2005; Notarbartolo-di-Sciara 2008). For example, measures to reduce by-catch of cetaceans in fishing gear can be implemented without need for an MPA (Evans 2008).

However, despite some concerns over their efficiency in achieving conservation goals, the establishment of MPAs is considered an important conservation tool by many international regulatory bodies (e.g. The OSPAR Convention 1992; The EU Habitats Directive 1992; ACCOBAMS 1996; ASCOBANS 2006; EU 2007).

In the United Kingdom, harbour porpoise (*Phocoena phocoena*), grey seals (*Halichoerus grypus*), harbour seals (*Phoca vitulina*), otters (*Lutra lutra*) and bottlenose dolphin (*Tursiops truncatus*) are listed on Annex II of the European Union's Habitats Directive which declares that for species or habitats listed, Special Areas of Conservation (SAC) must be established (EU Habitats Directive 92/43/EEC 1992). An SAC is defined as a "site(s) of Community importance where necessary measures are applied to maintain, or restore, to favourable conservation status, the habitats or populations of the species for which the site is designated". Such sites will only be considered when there is a clear area that represents the "physical or biological factors essential to [a species] life and reproduction" (EU Habitats Directive 92/43/EEC 1992). SACs have been established for all species listed above, with the exception of the harbour porpoise. The identification of suitable areas is problematic for this highly mobile species and consequently only a small number of sites have been proposed as suitable as SACs for the species, and none have yet been established. To address this matter, an

ad hoc experts workshop was convened by the European Commission in 2007 and they published guidelines on the designation of SACs for harbour porpoises (EU 2007; Pinn 2009). These new guidelines indicated that it would be possible to “*identify areas representing crucial factors for the life cycle of this species*” and that these factors would be identifiable on the basis of:

- 1) The continuous or regular presence of the species (subject to seasonal variation).
- 2) Good population density (in relation to neighbouring areas).
- 3) A high ratio of young to adults during certain periods of the year.

In a recent study on the west of Scotland (using some of the data analysed in this thesis - §1.5), a series of suitable sites for designation as SACs for harbour porpoise were suggested by Embling et al. (2010) based on the above guidelines. The majority of surveys in this region in the Embling et al. (2010) study were conducted in spring, summer and autumn, but sightings of harbour porpoises have been made in every month of the year on the west coast of Scotland (Reid et al. 2003), indicating a year round presence (thus meeting criterion 1). The west of Scotland has one of the highest densities of harbour porpoises in Europe (SCANS-II 2008)(meeting criterion 2). Aerial surveys as part of the SCANS-II program identified that 10% of all sightings made in good/moderate conditions included a calf (SCANS-II, unpublished). This percentage is higher than recorded throughout much of the North Sea (Hammond et al. 1995; Siebert et al. 2006; Weir et al. 2007) but lower than recorded in a small-scale survey in the eastern North Sea (Sonntag et al. 1999). Pinn (2009) suggests that a high ratio would be >60% of sightings including a calf. Consequently it is not clear whether 10% would represent a ‘high ratio of young to adults’. The west coast of Scotland appears to fulfil 2 – and possibly all 3 of these criteria and would therefore appear to be a strong candidate region within which to investigate further for suitable SAC sites.

One increasingly common method for identifying important regions suitable for protection is predictive habitat modelling. This has been used successfully for a range of species including: fish (Furness 1984; Mouton et al. 2007), squid (Sanchez et al. 2008), seabirds (Louzao et al. 2009; Rayner et al. 2007), and marine mammals (Bailey and Thompson 2009; Cañadas and Hammond 2008; Cañadas et al. 2005; Embling 2007; Embling et al. 2010; Gao and Gaskin 1998; Gregr and Trites 2001; Gridley 2005; Hastie et al. 2005; Ingram and Rogan 2002; Ingram et al. 2007; MacLeod et al. 2007a; Rayment et al. 2010; Tynan et al. 2005) and it has also been used successfully to define sites as marine protected areas (MPAs) for a number of cetacean species (Cañadas et al. 2005; Hooker et al. 1999; Notarbartolo-di-Sciara 2008; Panigada et al. 2008). Typically, for pragmatic reasons, MPAs have fixed geographic boundaries that relate to the environmental features important to a species (Agardy 1994). Such features can

be grouped into three types according to Hyrenbach et al. (2000): (i) static bathymetric (e.g. submarine canyons, reefs, banks and seamounts), (ii) persistent hydrographic (e.g. currents and frontal systems) and (iii) ephemeral hydrographic (e.g. upwelling regions). Also, because habitat modelling methods are evolving this means that MPA conservation goals can be updated as new modelling techniques are devised or more detection and/or explanatory data are collected and incorporated into re-fitted models, potentially improving MPA efficacy (Cañadas et al. 2005).

1.1 Predictive modelling for MPAs

1.1.1 Issues of scale in ecology

It is essential that appropriate spatial and temporal scales be used in habitat models in order to capture the processes that explain a species' distribution across an area (Redfern et al. 2008; Scott et al. 2002). In modelling, spatial scales can be considered in two ways: extent and grain. Extent refers to the overall geographic area being studied whilst the grain refers to the resolution at which relationships are being investigated (Wiens 1989). Because many of the processes that best explain the distribution of a species exist over different spatial and temporal scales it may not be possible to capture all of the processes in a single analysis. The data collection methods used are subject to a trade-off between precision and spatial coverage (Redfern et al. 2006). In distribution models, the relationships between species distribution and the associated environmental processes are usually dependent on both the extent and the grain selected and it is necessary for an appropriate scale to be chosen based on the goals of the study (Osborne and Suárez-Seoane 2002; Scott et al. 2002). Seal and harbour porpoise habitat preferences in the Moray Firth SAC (designated for the bottlenose dolphin found there) were shown to change depending on the grain used in analysis, however this is not always the case; bottlenose dolphin preferences appeared robust across different grain sizes (Bailey and Thompson 2009). Sometimes patterns are consistent irrespective of both the extent and grain used in modelling analysis (Redfern et al. 2008).

1.1.2 Extrinsic & Intrinsic factors

Both 'extrinsic' (i.e. biotic and abiotic) and 'intrinsic' factors (e.g. foraging strategies, reproductive status, inter- and intra-specific interactions) will influence a species' distribution. Extrinsic factors can both directly and indirectly shape the distribution of a species (Araujo and Guisan 2006; Austin 2002; Guisan et al. 2002; Guisan and Thuiller 2005; Randin et al. 2006).

It is likely that the distribution of cetacean species is most strongly affected by the abundance and distribution of its prey (Gaskin 1982; Selzer and Payne 1988). However, such direct data are often scarce and difficult to obtain, especially at a temporal or spatial scale appropriate for the

study in question. This is particularly true in the case of data on prey distribution (Santos and Pierce 2003). Obtaining direct prey species data is especially problematic when the species of interest is an opportunistic feeder and may be switching between prey species depending on its availability. Fisheries catch data may be useful in some places, but these data are often unreliable and at an inappropriately coarse scale. However, when no direct data are available it is possible to use ‘indirect’ factors, which serve as proxies for the ‘direct’ factors driving distribution. For example, the water depth, bottom sediment characteristics and/or current speed of an area could be important in determining the distribution of a prey species and so influence the distribution of its predators. The advantage of the use of indirect datasets is that they are often more easily measured than direct variables, e.g. bathymetric and tidal datasets are often available at a range of extents and grains. Consequently, indirect factors have been used extensively in cetacean predictive models (Bailey and Thompson 2009; Cañadas and Hammond 2008; Cañadas et al. 2002; Embling et al. 2010; Hastie et al. 2005; Panigada et al. 2008).

1.1.3 Autocorrelation

In cetacean survey datasets, autocorrelation occurs in the data when cetacean observations measured at neighbouring locations or times are more similar (positive autocorrelation) or less similar (negative autocorrelation) than randomly associated pairs of observations (Legendre 1993; Redfern et al. 2006). Positive spatial and temporal autocorrelation is common in ecological data as observations tend to be close together in space and time (Lennon 2000). In visual and acoustic line-transect surveys this can happen because animals are detected at several sequential sampling points along a continuous survey trackline. Spatial autocorrelation is particularly common when a species is associated with a variable that occurs in some definable spatial pattern. For example, if predators are taking advantage of a patchy prey resource, then they are more likely to be observed close together in time and space (Redfern et al. 2008). The main consequence of autocorrelation being unaccounted for in modelling efforts is that it can result in model ‘overfit’. This is the underestimation of model standard errors and can cause more variables than necessary to be retained in models, leading to potentially misleading models (Lennon 2000).

There are a number of methods for dealing with autocorrelation in data, many of which involve subsetting the dataset, or removing data before they are modelled. However, these approaches reduce the sample size on which predictive models are built. Increasing the grain size in the analysis can also be used to reduce autocorrelation. However, the limitation of this method is that it may also involve subsampling the data but also removes consideration of biologically significant patterns that operate at a finer scale than the chosen grain. This may lead to

important processes being missed by models. An increasingly popular method of dealing with spatial and temporal autocorrelation is to include a measure of autocorrelation in habitat models. This feature is incorporated in Generalised Linear Mixed Models (GLMMs), Generalised Additive Mixed Models (GAMMs) and Generalised Estimating Equations (GEEs). For example, in GEEs the assumption of independence is replaced with a working correlation structure which allows for the accounting of autocorrelation within models (Ballinger 2004; Hardin and Hilbe 2002). This method has been shown to improve model selection results in cetacean distribution models, over a GAM unadjusted for autocorrelation (Panigada et al. 2008).

1.1.4 The use of predictive modelling in this study

The main aim of this thesis was to identify consistently important regions for harbour porpoise to be suitable as SACs for the species. Models were constructed at a range of temporal and spatial scales using visual and acoustic line-transect survey data collected across the west of Scotland. Consequently, the data were spatially and temporally autocorrelated (as line transect survey data are not independent). This was accounted for at the modelling stage by using GAMs with GEEs used to ensure robust model selection. Direct prey data at appropriate temporal and spatial resolution were not available; however, indirect variables were used as proxies to identify important regions for harbour porpoise. The observed relationships between explanatory variables (static and dynamic oceanographic covariates) and harbour porpoises detection rates are discussed here as habitat preferences. The idea of ‘preference’ has its own connotation in behavioural studies but in this study, it is used as an umbrella term to explain where animals are most commonly detected.

1.2 Study Species: Harbour Porpoise

1.2.1 General Biology

The west coast of Scotland is an area of high biological productivity and it supports a rich biodiversity of marine species. There are records of 24 marine mammal species being sighted in the region. The most commonly recorded species are harbour porpoise, harbour seal, grey seal, minke whale (*Balaenoptera acutorostrata*), bottlenose dolphin and common dolphin (*Delphinus delphis*). Risso's dolphins (*Grampus griseus*) and killer whales (*Orcinus orca*) are also frequently sighted there (Shrimpton and Parsons 2000).

The harbour porpoise is a small odontocete, which is widely distributed throughout both the Atlantic and Pacific temperate and sub-arctic regions of the Northern Hemisphere (Donovan

and Bjørge 1995). A distinct population is also present in the Black Sea (Bjørge and Tolley 2002). The harbour porpoise is the most studied of the six species in the Family Phocoenidae, most of which are exclusive to coastal regions (Reeves et al. 2002). The harbour porpoise is the most common cetacean species on the west coast of Scotland and has been sighted there in every month of the year (Evans et al. 2003; Reid et al. 2003). Harbour porpoises are found mainly in inshore waters (Embling et al. 2010; Marubini et al. 2009) and the west coast of Scotland has one of the highest densities of porpoises in Europe (SCANS-II 2008).

Harbour porpoises have short, stocky bodies averaging 160 cm in length and 60 kg in weight in females and 145 cm and 50 kg in males (Bjørge and Tolley 2002). They are dark grey dorsally with a small triangular fin and have a white underbelly. Their surfacings are generally inconspicuous, characterised by a gentle, forward rolling behaviour. The bodyform of harbour porpoises serves as an adaptation to help limit heat loss in the cold climates they usually inhabit (McLellan et al. 2002, cited in Bjørge & Tolley, 2002). They carry limited fat stores and little energy reserves and consequently are forced to stay close to food sources and to feed regularly (Kastelein et al. 1997; Koopman 1998). Female harbour porpoises are 'income breeders' (Read 2001), that is they balance the costs of pregnancy and lactation by increasing their energy intake rather than depending on fat stores.

1.2.2 Diet

Porpoises are primarily piscivorous, preying heavily on small pelagic schooling and demersal fish species. They are opportunistic feeders and primary prey species are thought to vary considerably both spatially and temporally, and depending on the developmental stage of the animal (Bjørge 2003; Børjesson et al. 2003; Das et al. 2003; Gannon et al. 1998; ICES 2007; Santos and Pierce 2003; Santos et al. 2005; Santos et al. 2004). The majority of studies on diet around northwest Europe have focused on the North Sea, Orkney and Shetland and Danish waters (Herr et al. 2009; Santos and Pierce 2003; Santos et al. 2004). The main species in their diet are: whiting (*Merlangius merlangus*), cod (*Gadus morhua*), herring (*Clupea harengus*), mackerel (*Scomber scombrus*), capelin (*Mallotus villosus*), sole (*Solea solea*) and sandeels (*Ammodytes spp.*), though cephalopods and crustaceans have also been recorded in porpoise stomach contents. The only study of porpoise diet west coast of Scotland determined (from a small sample size collected from 1992 - 2003) that juvenile whiting dominated the diet, followed by haddock (*Melanogrammus aeglefinus*), saithe/pollock (*Pollachius pollachius*), sepiolid species (Santos et al. 2004). Sandeels, contributed a small percentage to the total diet (Santos et al. 2004). In the absence of detailed diet data in the region, inferences could perhaps be made based on the diet of other top predators in the region. A study on the diet of grey seals west of Scotland found it consisted

mostly of gadoids, herring and sandeels but the proportion that each contributed to the total diet varied considerably with region, season and year (Hammond and Harris 2006). More generally, it has been suggested that harbour porpoises may feed on a range of prey throughout the water column, both near the surface and also diving deep to take advantage of bottom dwelling species (Bjørge and Tolley 2002).

1.2.3 Life History

Harbour porpoises breed between June and August around the Atlantic and most neonate calves are observed in June and July indicating a seasonal reproductive period (Lockyer 1994; Lockyer 2003; Read 2001; Read and Hohn 1995; Read and Tolley 1997). Gestation lasts between 10 - 11 months and calves are 65 – 70 cm in length and 5 kg in weight at birth. Around the UK, animals reach sexual maturity at approximately 3 – 4 years of age and the reproductive interval is > 1 indicating that females produce a calf almost every year (Lockyer 1995). The maximum age recorded for the species is 24 years (Lockyer 2003). Little is known about the locations of breeding sites around Europe if indeed preferred breeding locations exist at all in this species.

Harbour porpoise are generally solitary animals, with the majority of sightings consisting of just one or two animals. Larger aggregations do occur, with group size generally increasing in summer and autumn (pers. obs.). Porpoise social behaviour is generally poorly understood, but there is evidence to suggest animals communicate with one another by varying click rate (Clausen et al. in press).

1.2.4 Distribution and Habitat Use

Harbour porpoise are a continental shelf species often found close to the coast. In many studies, porpoise habitat use has been linked to static bathymetric features such as depth and slope (likely as proxies for biologically significant phenomena). In the Bay of Fundy, animals were associated with areas characterised by a shoreward penetration of channels > 80 m in depth (Gaskin and Watson 1985; Watts and Gaskin 1985). Telemetry studies conducted in same region indicated that animals were transiting with reference to a 92 m depth contour as $> 55\%$ of tracking locations were made in water depths between 90 and 180 metres (Read and Westgate 1997). During surveys in the northeast Pacific, most porpoise sightings were made in waters between 100 – 200 m depth (Raum-Suryan and Harvey 1998). Studies in west Scotland have revealed similar preference for regions with water depths between 50 – 150 m (MacLeod et al. 2007a; Marubini et al. 2009). Additionally, in those studies, distance to land was retained in the final models with more porpoises being found closer inshore.

Hydrographic features have also been suggested as important, though many of these relationships varied between sites. Position in the daily tidal cycle has been important in a number of studies, but the exact relationship appears to differ. Peak harbour porpoise occurrence has been linked to all phases of tide: the slack (Embling et al. 2010), the ebb (Pierpoint 2008) and the flood tides (Calderan 2003; Johnston et al. 2005; Sekiguchi 1995). These studies suggested that the association with tidal variables was an indication of preference for productive regions such as areas of island wakes, which generate predictable fronts, eddies and rips in which prey aggregate (Johnston et al. 2005; Mann and Lazier 2006; Zamon 2003). Weir and O'Brien (2000) found that porpoises were associated with a tidal front in the Irish sea, with the majority of sightings occurring on the mixing side of the frontal zone.

As discussed previously, this study follows on from a study by Embling (2007), and uses some of the data collected during that study. Embling et al. (2010) showed that the models based on sightings data, maximum tidal current and position in the spring-neap tidal cycle were important with highest detections in areas with low tidal currents at spring tides. In Embling (2007) models based on acoustic detections of harbour porpoises percentage mud in the sediment and spring tidal range were important. These results indicate that features that are more dynamic were important predictors of relative density.

Studies of harbour porpoise diving behaviour have revealed animals can routinely dive to depths of 73 – 99 m and are capable of diving to over 200 m and have a maximum observed swimming speed of 4.3 m s^{-1} (Otani et al. 2001; Otani et al. 1998; Westgate et al. 1995). Studies of porpoise movements using satellite telemetry methods indicate that animals tend to occupy small core areas or focal regions for short periods while utilising a much larger area over which they range (Johnston et al. 2005; Read and Westgate 1997). These core areas have been calculated at 122 – 415 km^2 , while the total range 'available' to animals ranged over areas between 4,728 and 22,103 km^2 (Johnston et al. 2005). Similar patterns have been observed in the North Sea and Danish waters (ranges of $\sim 400 - 1600 \text{ km}^2$) (Teilmann et al. 2004). Read and Westgate (1997) estimated that porpoise home ranges in the Bay of Fundy and Gulf of Maine may be in excess of $\sim 50,000 \text{ km}^2$.

1.2.5 Passive Acoustic Monitoring for harbour porpoises

Harbour porpoises produce characteristic, narrowband, high-frequency clicks with peak frequencies at 115 – 145 kHz (Goodson and Sturtivant 1996). Studies of captive animals have reported clicks with a maximum source level (SL) of 172 dB re $1 \mu\text{Pa}$ pp @ 1m and more recent

work on free-ranging animals indicate higher source levels varying from 178 – 205 dB re 1 μ Pa @ 1m pp with a mean SL of 191 dB re 1 μ Pa pp @ 1m (Villadsgaard et al. 2007). Animals have been found to increase the source levels of clicks when further from their echolocation targets (Atem et al. 2009). Animals vocalise almost constantly and click rates increase as animals near a target (Clausen et al. in press; Kastelein et al. 2008; Verfuß et al. 2005; Verfuß et al. 2009).

Passive acoustic monitoring (PAM) is being used as an effective technique for monitoring cetacean species and provides a useful complement to visual surveys (Boisseau et al. 2007; CODA 2009; Embling 2007; Gillespie et al. 2005; Gordon et al. 2003; Hastie et al. 2005; Leaper et al. 2000; SCANS-II 2008). One of the disadvantages of visual surveys for harbour porpoises is that because they are small in size, often solitary and have cryptic surfacing behaviour, visual detection rates can be affected by survey conditions. Palka (1996) determined that visual detection rates for harbour porpoises decreased by up to 20% from Beaufort 0 to Beaufort 1 and by up to 75% between Beaufort 0 and Beaufort 3. The advantage of PAM techniques is that they allow for detection of species in most sea state conditions, at night and during poor sighting conditions. In surveying for harbour porpoises, the evidence for the efficacy of PAM methods is compelling as acoustic detection rates can be eight times higher than visual detection rates for the species (Gillespie et al. 2005). An additional advantage of PAM methods is that systems can be automated, requiring fewer people than visual surveys to maintain, and removing some of the potential for human error.

Because porpoise clicks are ultrasonic, it is necessary to use specialised equipment in order to detect animal vocalisations. Chappell et al. (1996) first described a system which used analogue filters and envelope tracing in three frequency bands, one at 100-150 kHz and two lower frequency control bands. Automatic triggers were used to detect clicks and the information was fed into a computer. The system has been updated by digitising the trigger outputs and using real time detection software to extract porpoise clicks (Gillespie and Chappell 2002). An additional aspect of the updated system was that it used two hydrophones (separated by a known distance) allowing the bearings of clicks to be calculated by comparing the time of arrival of clicks at each hydrophone. This system, called *Porpoise Detector* has been used in a number of successful surveys for harbour porpoises in the Baltic Sea (Gillespie et al. 2005); off the west coast of Africa (Boisseau et al. 2007) and off the west coast of Scotland (Embling 2007). The porpoise detection data collected between 2004 - 2005 by Embling (2007) were also used in this study.

A newer acoustic detection system (called *Rainbow Click*), which supersedes *Porpoise Detector*, has been developed. This system utilises the complete, raw high frequency signal and provides real time signal processing (Gillespie et al. in prep.). This improvement allows for a more detailed analysis of clicks detected, providing better information on species classification and group size estimation (Gillespie et al. in prep). This system was used in the SCANS II and CODA surveys (CODA 2009; SCANS-II 2008) and was used in conjunction with visual surveys in this study between 2006 and 2008.

A constraint when using PAM to detect harbour porpoise is that the high frequency sound of porpoise clicks attenuates quickly in water (Urick 1983) and consequently animals cannot be detected over long distances. Animals are rarely detected over 250 m from the hydrophone and the effective half strip width during SCANS survey was 208m (Gillespie et al. in prep). An additional issue impacting detection is that porpoise clicks are highly directional: Au et al. (1999b) recorded a 3 dB beam width of 16° - meaning animals will be more likely to be detected when orientated towards the hydrophone (Gillespie et al. in prep).

1.2.6 Status and Threats

The biggest threat to harbour porpoise populations in European waters is entanglement in bottom-set gillnets (ICES 2009), but this fishing practice is uncommon on the west coast of Scotland and consequently there is little or no by-catch in this region (CEC 2002). However, a number of anthropogenic activities do occur west of Scotland that may impact harbour porpoises. One source is from anthropogenic noise from loud, underwater sound sources deployed to deter seals from fish farm cages. These devices have been shown to exclude harbour porpoises from important habitats in Canada and their use is widespread throughout the west of Scotland (Gordon and Northridge 2002). Other noise sources, e.g. from boat traffic (both recreational and fishing vessels) and the installation and operation of marine renewable energy facilities may also impact porpoises and are described in §1.4. A source of natural porpoise mortality around the UK is from bottlenose dolphins, which has been reported around the UK (MacLeod et al. 2007b; Ross and Wilson 1996), though not west of Scotland. Killer whales around Scotland have been observed feeding on marine mammal species, most commonly seals (Bolt et al. 2009), but violent interactions between killer whales and harbour porpoises have also been observed on the west coast of Scotland, resulting in porpoise mortality (Fairbairns, pers. comm., Foote, pers. comm.). The populations of killer whales and bottlenose dolphins off the west of Scotland are very small (Foote et al. 2009; Foote et al. in press; SNH in press) and the harbour porpoise population is estimated to be 12,100 (CV = 0.43) (SCANS-II 2008).. While

predation rates of harbour porpoise west of Scotland are likely low, it is possible that a perceived predation risk may also impact their distribution.

Predators can have a direct impact on prey species at a population level by providing a source of mortality. However, they may also have a non-lethal impact on populations. Prey species may alter their behaviour in a trade-off of profitable foraging grounds for increased safety. Increased vigilance may also be exhibited at a cost of foraging efficiency. It has been suggested that the perceived risk of predation may actually be more important than mortality at a population level (Altendorf et al. 2001; Brown 1992, 1999; Kotler et al. 2002; Laundre et al. 2001). In cetaceans, predation risk has been found (along with prey availability) to impact habitat use at multiple scales (Acevedo-Gutierrez 2002; Heithaus and Dill 2002; Heithaus and Dill 2006; Nordstrom 2002; Wirsing et al. 2007a, b). Bottlenose dolphins were observed to stay away from high-productivity, high-predation risk shallow-water regions when tiger sharks (*Galeocerdo cuvier*) were present in the area, in favour of lower productivity but safer deeper water regions (Heithaus and Dill 2006). The extent to which the interactions with killer whales or bottlenose dolphins would represent a significant pressure on harbour porpoises west of Scotland in this region, given how low the predation rates are is unclear, but the predation rate does not need to be high in order for predation risk to be a significant factor (Altendorf et al. 2001; Brown 1992, 1999; Brown et al. 1999; Laundre et al. 2001).

1.3 Study Site

The west coast of Scotland encompasses the coastal islands and bodies of water between the mainland and the Outer Hebridean island chain from Lewis in the north to Barra Head in the south (Figure 1.1). The region comprises complex coastlines and topography and a range of physical processes influence the coastal marine environment (Ellett 1979; Ellett and Edwards 1983; Gillibrand et al. 2003; Inall et al. 2009; McKay et al. 1986). The topography varies markedly, consisting of a large number of islands, sea lochs, sounds and passages. A number of narrow, glacially deepened trenches provide steep slopes and deep channels > 100 m in depth. Some geographic variation exists; the northern region is characterised by deep water, with steep sided-fjords and few areas <50 m in depth, whereas the south consists of more extensive areas with water <50 m in depth, but still with a number of deeper, steep-sided channels especially close to the coast (Ellett and Edwards 1983)(Figure 1.2 a).

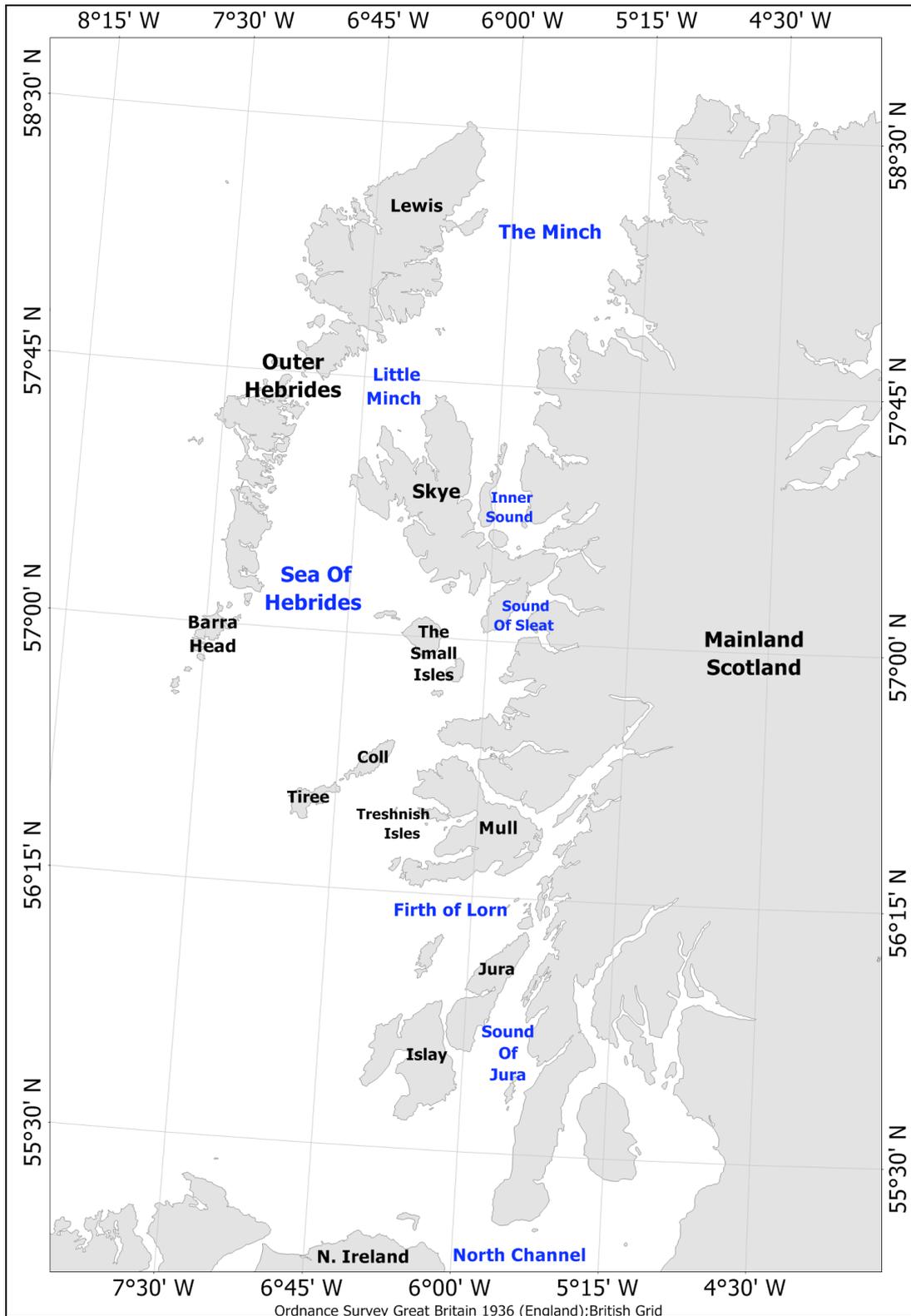


Figure 1.1 - The west coast of Scotland (with specific regions labelled - land masses in black; marine areas labelled in blue).

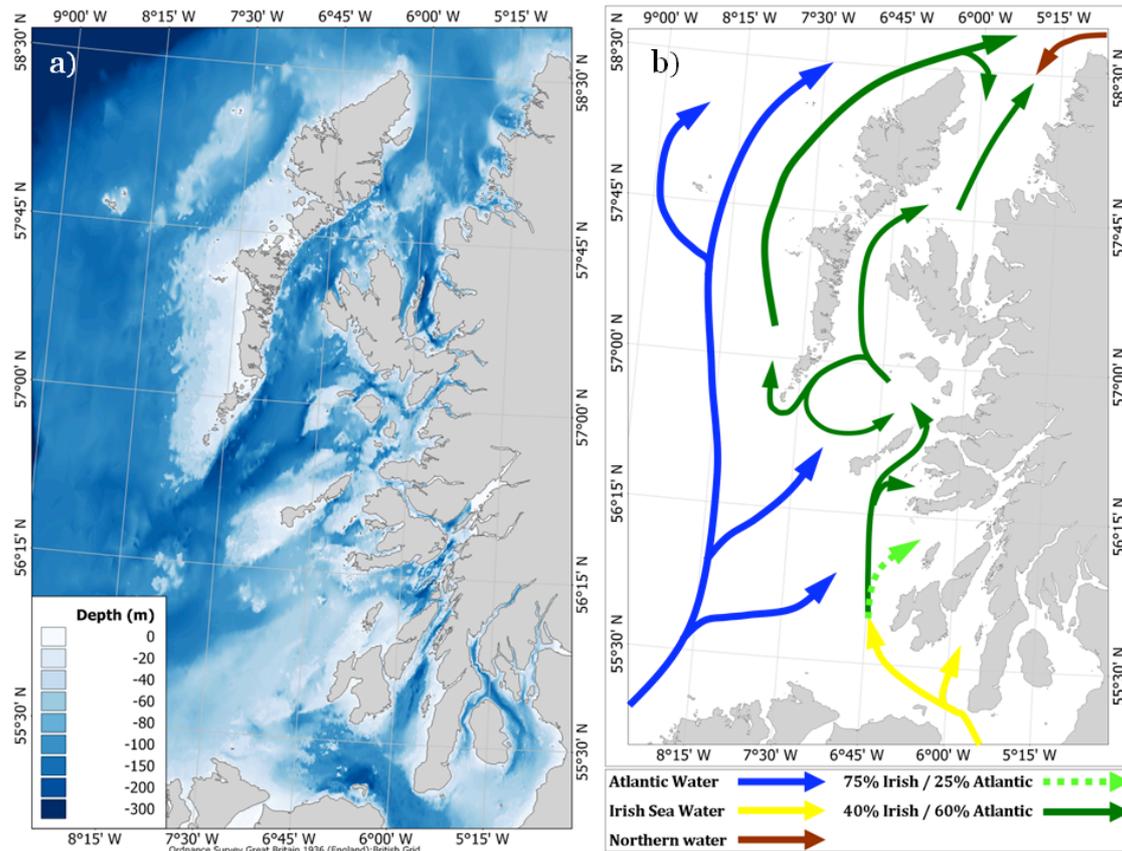


Figure 1.2 – (a) Bathymetry on the west of Scotland (sourced from EDINA); (b) Circulation patterns off the west coast of Scotland, showing the main current influges (solid blue, yellow and red arrows) and the extent of mixing in each current stream (green solid and dotted lines). The legend shows details of the degree of mixing. Adapted from McKay et al. (1986) with data from Proctor and Davies (1996).

Topographic features cause increased surface and bottom turbulence, tidal eddies and rips. Water circulation in the region is driven by three main water masses: two tidal flows from the south and freshwater runoff from land. A tidal mass of water flows north from the Atlantic along the west coast of Ireland until it reaches Scotland. In the North Channel of the Irish Sea, a second tidal water mass (the Scottish Coastal Current) brings high salinity water with a high nutrient-load into the region (Simpson et al. 1979). Where these two currents meet, the Islay Front develops and because these two tidal water masses are 180° out of phase and so they cancel each other out, tidal range in the Sound of Jura is minimal (Simpson et al. 1979). The Atlantic water also moves further north driving a cyclonic circulation in the Sea of Hebrides (Gillibrand et al. 2003) and to a lesser extent the currents and mixing continues in the Minch (McKay et al. 1986)(Figure 1.2b). Tidal currents also enter the region from the north, moving round Cape Wrath and into the Minch (Proctor and Davies 1996). Freshwater runoff from the mainland generates a positive east-to-west gradient in salinity. The strength of this gradient appears to vary significantly with season but is not >1.5 ppm (Gillibrand et al. 2003). A weak north-south gradient also exists but this is always <1.0 ppm.

Throughout the region, seasonal variations in conditions occur. Primary among these are shifts in sea surface temperature (coldest in spring; warmest in late summer/autumn). Furthermore a north-south gradient of 1 to 2 °C exists in spring and summer, but is generally absent in autumn (Gillibrand et al. 2003). High spring chlorophyll-a levels are present in coastal regions, in the Sea of Hebrides and in the Little Minch in the spring and levels peak in summer. There is also evidence for plankton blooms along the northwest Scotland mainland coast in autumn (Gillibrand et al. 2003).

1.4 Harbour porpoises and anthropogenic noise

Marine mammals produce a variety of sounds for communicating with conspecifics, individual recognition (Janik 2009a; Janik and Slater 1999), mate selection (Handel et al. 2009; Janik 2009b), and mother-calf bonding (Sayigh et al. 1990). Odontocete species use echolocation sounds for orientation, navigation and prey detection and all cetaceans possess highly sophisticated underwater hearing systems with a high auditory sensitivity over a wide range of frequencies (Nedwell et al. 2004; Richardson et al. 1995). It is likely that species also use this specialised auditory system to passively find prey (Burros and Myrberg 1987; Gannon et al. 2005). Their heightened auditory sensitivity and reliance on the use of sound makes marine mammal species very sensitive to the impacts of a noisy environment.

A wide range of human activities introduce sound into the marine environment including: commercial shipping, oil and gas exploration, marine renewable energy installations, military operations, academic research, fishing activities, marine recreational pursuits and coastal development (MMC 2007). In the case of harbour porpoises west of Scotland, concerns have been raised in relation to noise from fishing and recreational vessel noise, military sonar, future marine renewable energy installations and acoustic devices used on fish farms (Embling 2007; Parsons et al. 2000a; Parsons et al. 2000b; Shrimpton and Parsons 2000).

The Scottish Government has set a target that 40% of energy will be generated from renewable sources by 2020 and consequently over the last decade there has been an increase in coastal marine renewable energy (MRE) development around Scotland. These developments are focused on wind, wave or tidal energy and a number of sites on the west coast of Scotland have been identified as appropriate for MRE development (Scottish_Government 2009a). There is a wide range of potential impacts of such developments on the marine environment, many of which are poorly understood (for a review of these, see NERC 2009). The main issues likely to

impact harbour porpoises are: pile driving (Carstensen et al. 2006; Madsen et al. 2006; Tougaard et al. 2009; Tougaard and Eriksen 2006), risk of collision (Carter 2007) and behavioural responses to installations (e.g. avoidance/attraction) and increased boat traffic, due to maintenance (NERC 2009). Harbour porpoise have been impacted by pile driving noise, with a number of studies recording reduced occurrence during pile driving (as part of a wind farm installation) compared with pre-pile driving. Harbour porpoise distribution has been affected out to 15 km and 21 km from pile driving source (in Tougaard et al. 2003 and ; Tougaard et al. 2009 respectively). The potential for collision or behavioural reactions to MRE installations remains poorly understood (Carter 2007).

Commercial shipping, fisheries and recreational vessel traffic may also impact marine mammal species (Currey et al. 2009; Gerstein et al. 2005; Lusseau and Bejder 2007; Nowacek et al. 2001; Parks et al. 2007; Parks et al. 2009; Williams et al. 2009). Studies on a range of delphinid species have shown that repeated disturbance by small-vessel traffic cause short-term avoidance behaviours, which can lead to changes in activity budget and foraging ecology (which may impact energetic budget) and habitat exclusion (Bejder et al. 2006). Killer whales in Canada were observed to spend more time travelling and less time foraging when boats were present than when vessel traffic was low (Lusseau et al. 2009). Changes in respiration rates and swimming speeds have also been observed (Williams et al. 2009). Changes in bottlenose dolphin behaviour has been reported in response to interaction with tourism boats and animals tended to avoid regions with high tourism boat traffic (Lusseau and Bejder 2007). Vessel noise and increases in background noise (caused by the cavitation noise from high-speed small vessels) are thought to impact the communication ranges of pilot whales and bottlenose dolphins (Jensen et al. 2009). It is unclear whether harbour porpoises are impacted by the presence of vessel traffic west of Scotland in similar ways to those described here for other cetacean species. Tourism vessel density is low in the region, though repeat exposures to other anthropogenic noise sources may have an impact on animals. In general, it is very difficult to glean behavioural information only from harbour porpoise surface or acoustic behaviour without knowledge of their underwater behaviour and this is an area that requires further investigation.

Naval activities have been linked to the mass-strandings of beaked whales species and have been shown to impact other cetacean species (Baird et al. 2005; Barlow and Gisinier 2006; MMC 2007; Piantadosi and Thalman 2004; Tyack et al. 2005) and may also impact harbour porpoises (Parsons et al. 2000b). A reduction in harbour porpoise sightings was correlated with the onset of military exercises west of Scotland indicating porpoises may be affected by these exercises and displaced (Parsons et al. 2000a).

In general, the effects of these noise sources on the marine environment remain poorly understood but the consensus is that there is potential for significant impacts on marine species (MMC 2007). Increases in anthropogenic noise have been coupled with increased concern from the scientific community and in the public arena about the anthropogenic component of ocean noise and how it is affecting marine mammals and other marine fauna. This issue has been raised at a number of national and international policy meetings over the past 5 years (ASCOBANS 2006; ICES 2009; MMC 2007).

However, not all sources of sound are unintentional by-products of industrial processes – some sounds are directly introduced into the environment to warn animals of the presence of fishing nets and to scare predators away from aquaculture facilities (Jefferson and Curry 1996).

1.4.1 Aquaculture in Scotland

Over the last 30 years, the marine-aquaculture industry – the farming of marine and diadromous fish species and shellfish - has grown considerably, with production rates increasing 10-fold globally (FAO 2008). In Scotland, this expansion has led to aquaculture becoming one of the major economic activities on islands of Orkney and Shetland and across the west coast of Scotland and the Outer Hebrides (FRS 2007). The majority of farms produce Atlantic salmon (*Salmo salar*) but halibut (*Hippoglossus hippoglossus*), cod, haddock, whiting and Arctic charr (*Salvelinus alpinus*) have also been successfully farmed (FRS 2007). Mussels (*Mytilus edulis*), brown and rainbow trout (*Salmo trutta* and *Oncorhynchus mykiss* respectively)(in freshwater) are also farmed and are an important component of the industry. Farmed salmon production has increased over the past 20 years from approximately ~12,000 tonnes in 1987 to ~129,000 tonnes in 2007 (with a peak in 2003 of ~169,000 tonnes)(FRS 2007) - accounting for a farm gate value of produce of ~£324 million in 2008 (Scottish_Government 2009b).

Fish farms share the marine environment with a complement of fish-eating predators – some of which naturally predate on the species being reared in aquaculture. In addition, it is thought predatory and scavenging species are present at most fish farm sites (Quick et al. 2004). Many of these marine predators are attracted to and interact with aquaculture sites. Moreover, there is potential for aquaculture sites to attract wild fish species and their predators. Grey and harbour seals are considered to cause the biggest predation problem at Scottish sites – though otters and bird species have also been reported to be a problem at some sites. In 2001, a questionnaire survey of 376 marine salmon farms found - from 195 responses - that harbour seals were a problem at 70% of sites and grey seals at 59% of sites (bird species were reported as a problem

at 40% of sites)(Quick et al. 2004). A more recent survey in 2009 reported that seals were sighted at 90% of sites around Scotland and 68% of sites reported that they had (or used to have only) minor problems with seals. At 10 sites (12%) seals were reported to be a major problem (SARF in press).

Marine mammal interactions with fish farm sites can result in lower production for a number of reasons: as a consequence of direct mortality of fish, as a result of increased fish-stress from predation events, and predation events causing damage to nets leading to fish escaping from cages. These predation problems have prompted the development of anti-predator control methods to limit the impacts of interactions. 'Predator netting' has been used at sites to provide a physical barrier between wild animals and the cages. However, the additional netting can cause the entanglement of predator and non-predator animals, especially if poorly maintained (SARF in press). Most sites have adopted net-tensioning methods or have adapted the shape and stiffness of nets to limit the ability of seals to trap caged fish. The success of these methods has varied, often depending on how these nets are deployed and/or maintained (Ross 1988).

Removals of “problem” animals and population control have also been used to limit interactions (Quick et al. 2004), but actual attacks are rarely witnessed and it is often not possible to identify that the ‘correct’ animal has been removed. However, lethal removals can be problematic as they may significantly impact upon a population (especially if the number of animals removed is under-reported)(Ross 1988). In addition, 'rogue' individuals being removed can quickly be replaced by newly arriving animals (Ross 1988). Some form of predator control was in use at 97% of sites in 2001 (Quick et al. 2004) and at all sites surveyed at the time of this study (Calderan, pers. comm).

The other common method of reducing seal-interactions is the use of high source level underwater sounds to deter seals from sites (Jefferson and Curry 1996). Acoustic devices have also been used to reduce interactions between marine mammals and commercial fisheries. As with other anti-predator control methods, questions remain about the use of acoustic devices, principally over their efficacy and potential impacts on non-target species (Jacobs and Terhune 2002).

1.4.2 Use of acoustic devices in aquaculture

Commercial acoustic devices have been designed over the past 20 years in an effort to limit interactions between marine wildlife and aquaculture and/or fisheries. In general, devices used as a by-catch mitigation measure have been classed as 'acoustic deterrent devices' (ADDs). These devices are characterised by emitting relatively low source levels (<150 dB re 1 μ Pa @ 1

m) of sound typically between 10 kHz – 100 kHz (ACCOBAMS 2006). The devices used to limit seal-interactions at aquaculture sites are sometimes colloquially referred to 'seal scarers' and have also been described (to distinguish from the by-catch mitigating devices) as 'acoustic harassment devices' (AHDs) in the bulk of the literature (Jacobs and Terhune 2002; Shapiro et al. 2009). These aquaculture-mitigation devices generally emit sounds at source levels >185 dB re $1 \mu\text{Pa}$ @ 1 m between 5 – 30 kHz. There is contention in the literature over the use of the term 'harassment' as it emotive and has a particular behavioural context – moreover, precisely how the devices affect animals is unclear and there are no data to support the notion of 'harassment'. Therefore the use of this term is not used in this study. It has been suggested that all such acoustic devices be referred to as 'ADDs' (Gordon and Northridge 2002) as their principle function is that of a deterrent. However, to avoid confusion, a distinction should be drawn between two different types of acoustic devices. They are functionally different and will likely be perceived differently by animals encountering them. Therefore, when discussing 'seal scarers' here, they will be referred to as Commercial Aquaculture Acoustic Devices (CAADs) as first described in Lepper et al. (2004).

A range of CAADs exist and most of these devices operate under the same principle – producing intense sounds that are aimed at the best hearing sensitivity of the target species (the exception is the Terecos model, which uses a high degree of randomness in sounds produced to remove animals). The acoustic characteristics of devices commonly used in Scotland are summarised below (Table 1.1). The majority of studies investigating their effects on seals have focused on the Airmar model, though Ferranti Thompson models have also been investigated. The efficacy of devices in deterring seals from fish farm sites has been variable between studies. Trials by Yurk and Trites (2000) found that the Airmar CAAD yielded an immediate and significant decrease in seal predation at the study site in British Columbia, however they did not conduct follow-up studies. Jacobs & Terhune (2002) recorded no observed responses by seals exposed to an Airmar CAAD (SL range: 172 - 179 dB re $1 \mu\text{Pa}$ @ 1 m) and no change in behaviour was observed between periods of CAAD activity and inactivity. A study in Orkney investigating the efficacy of an Airmar CAAD on harbour seals found no difference in response from seals in the water between 'control' (CAAD off) and 'exposure' (CAAD on) sessions (Robertson 2004). Götz (2008) conducted trials using a lower frequency sound stimulus with a peak frequency at 0.95 kHz and source level of 180 dB re $1 \mu\text{Pa}$ at 1 m at a site with no aquaculture activity. They reported significantly reduced seal numbers within 250 m of the sound source when it was active compared with control periods.

Most CAADs are continuously active. However, Ace-Aquatec developed a predator trigger-system which helped reduced the duty cycle significantly (Ace-Aquatec 2002). Salmon “panic” movements detected when a seal was present activated the triggers. An internal company document reported on a series of trials of the device at fish farm sites in Scotland. Decreases in seal predation were reported at 3 of the 4 sites – with zero predation in two of these cases (Ace-Aquatec 2002). In the other trial, the device was found to have no effect. The species of seals observed in the study were not documented. Unfortunately, these experiments included no control trials or study design and lacked any statistical analysis.

The manufacturer’s specifications for devices are from calculations made under controlled conditions. Under field conditions the performance of devices has been shown to vary from the signal characteristics provided by manufacturers (Haller and Lemon 1994). Field studies using the Airmar dB Plus II indicate that it produces a consistent pulsed-sound centred at 10.3 kHz with equally spaced and well-defined harmonics > 20 kHz (Haller and Lemon 1994; Lepper et al. 2004; Yurk and Trites 2000). Pulses are 1.8 ms in length, with 40 ms intervals between pulses. Pulses are grouped into trains lasting for approximately 2.3 seconds followed by a gap of 2.1 seconds (Haller and Lemon 1994). The source levels of devices measured in these studies have varied: 152 dB (Taylor et al. 1997)(all values re 1 μ Pa at 1 m RMS unless stated), 179 dB pk-pk (Jacobs and Terhune 2002), 181 dB (not stated) (Johnston 2002), 192 dB (Lepper et al. 2004) and 194 dB (Haller and Lemon 1994; Yurk and Trites 2000). In the cases where low source levels were documented, it was most likely that the measurements were affected by attenuation due to fouling build-up on the transducers and/or nets and/or by damaged cabling or low battery voltage (Gordon and Northridge, 2002).

A further consideration in assessing the long-range effects of CAADs is the issue of how the sound propagates in the environment. Received levels of sound will generally be a function of source level, distance from the device and rate of propagation loss. However, the topography, salinity, temperature (where strong halo- and/or thermoclines exist), bottom sediment type, the depth of the source and the time-frequency sound characteristics may all affect the rate of propagation loss. In areas of complex topography, propagation will vary to a greater extent. Islands may provide barriers between source and receiver, though not completely exclude sounds from the shadowed regions (Morton and Symonds 2002). Furthermore, topographic features such as narrow channels and sounds may serve to aid the propagation of sound.

Table 1.1 - The characteristics of five CAADs. Max SL: maximum source level. Table adapted from Gordon and Northridge (2002) with additional data from Lepper et al. (2004).

Name of Device	Frequency (kHz)	Max SL (dB re 1 μ Pa @ 1m	Transmission Duration	Pulse Duration	Duty Cycle
Airmar dB Plus II	10 (tonal)	194 dB	2.25 seconds	1.4 – 2 ms	40-50%
Ferranti-Thomson Mk2	8-30 (broadband)	194 dB	20 seconds	20 ms	~3%
Ferranti-Thomson Mk2 4x	8-30 (broadband)	200 dB	20 seconds	20 ms	~3%
Mk2 with Ace Aquatec Trigger	8-30 (broadband)	194 dB	20 seconds	20 ms	Activity dependent
Terecos	2.5 - 100 variation	179 dB (146 dB at frequencies > 27 kHz)	15 seconds – 2 minutes	200 ms – 8 seconds	50/50

An Airmar CAAD was detected at a range of 16 km in a narrow channel (Calderan et al. 2007) and it has been suggested such a device could theoretically be detected at up to 20.2 km from the source, depending on ambient conditions (Jacobs & Terhune, 2002). Consequently, sound propagation will vary significantly on a site-by-site basis and the pattern of signal intensity with range may not be straightforward. Shapiro et al. (2009), investigating variability in Sound Exposure Levels (SEL) of a Lofitech CAAD (repeated 200 ms pulse @ 15.6 kHz, SL = 193 dB re 1 μ Pa at 1 m) with range, documented variability of up to 19 dB for a given range on a constant bearing from the source (Shapiro et al, 2009).

As has been discussed, there are questions over the efficacy of CAADs on their target species. A further issue is how these devices may affect non-target species (e.g. cetaceans, otters, diving birds and fish species). Species most likely affected by CAADs are those with acute hearing sensitivities at the frequencies produced by the devices and those species with important habitat in areas in which devices are installed. On the west coast of Scotland, the vast majority of marine aquaculture is found in near-shore regions and thus species with an inshore distribution are most likely to encounter fish farms and CAADs.

1.4.3 Relevant Legislation

All cetacean species in Europe are protected under Annex IV of the EC 'Habitats Directive' (Council Directive 92/43/EC), as “*animal [and plant] species of community interest in need of strict protection*”. Two sections of Article 12 are of particular relevance: 12(b) which prohibits “*deliberate*

disturbance of these species, particularly during the period of breeding, rearing, hibernation and migration” and 12(d) which prohibits “*deterioration or destruction of breeding sites or resting places*”. The UK is a signatory to the Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas (ASCOBANS) and Resolution 4 of the Conservation and Management Plan stipulates continued effort towards “*the prevention of [other] significant disturbance, especially of an acoustic nature*” be made (ASCOBANS 2006). The issue of the anthropogenic impacts of noise on marine species and the need for additional research has also been raised in the UK Biodiversity Action Plan (UKBAP) and cetacean species are further protected against disturbance under Schedule 5 of the Wildlife and Countryside Act (1981) and the Countryside and Rights of Way Act (2000). In Scotland, all cetacean species are given protection under the Conservation Regulations 1994 as European Protected Species (listed on Schedule 2 and 4 of the Habitats Regulations 1994). The most recent amendment to this is the Conservation (Natural Habitats, &c.) Amendment (No. 2) (Scotland) Regulations (2008). Any deliberate or reckless activity causing injury or disturbance as a consequence of an activity is considered an offense requires a license to be carried out legally. Under these regulations, disturbance includes “*harassing an animal or group of animals*” in any stage of life, in such a way as to “*impair it’s ability to survive, breed, reproduce, rear or otherwise care for it’s young*”. The licensing authority is the ‘Scottish Government Licensing Team’ (run between Scottish Government and Scottish Natural Heritage). The Marine (Scotland) Act (2010) permits the designation of ‘Nature Conservation marine protected areas’ to conserve marine flora and/or fauna and if such a MPA is established the “*disturbance of animals or plants of any description in the protected area*” is prohibited.

1.4.4 Potential Impacts of CAADs

1.4.4.1 Masking

Masking is the influence that one sound (the masker) has on the detection of another sound (the signal) and it reduces an animal’s ability to detect those signals. Sound is particularly important for marine animals and is often the main source of information on the environment. For marine mammals, sound is used in communication, orientation, finding prey and mates and avoiding predators, thus the loss of important biological information via masking could be significant. However, the masking sound only affects a signal if they contain similar frequencies as the signal and they come from the same direction. Directionality of hearing has been investigated in harbour porpoises (Dudok van Heel, 1962; Andersen, 1970 , as cited in Richardson et al. 1995), bottlenose dolphins (Renaud and Popper 1975) and harbour seals (Terhune 1974, 1991). These studies identified that all species have strong directional localisation capabilities. Bottlenose dolphins have a lowest Minimum Audible Angle (MAA) of 0.7° to 0.9° for broadband clicks centred at 64 kHz (Renaud and Popper, 1975). Harbour porpoises, tested with tonal sounds,

had MMAs of 3° at 2 kHz (Andersen, 1970, as cited in Richardson et al. 1995), 3.5° at 3.5 kHz and 6° at 6 kHz (Dudok van Heel, 1962, as cited in Richardson et al. 1995). Seals tested appeared to have less directional hearing than cetaceans: MMA: 1.5° – 4.5° (Terhune 1974). It is presumed that similar marine mammal species will have comparable capabilities to those species tested.

Effective masking will only occur if the signal and the masker either overlap in frequency – i.e. if the masker sits within a critical frequency band (CB) around the signal of interest (Urlick 1983). Thus, CAAD signals would only mask signals that were within the CB of the frequencies produced by the CAAD. At these frequencies, CBs are generally less than 10% of the centre frequency. Consequently, masking would only occur in very narrow frequency band around their output frequency. These factors indicate that masking by CAADs may not be a significant issue for cetaceans in general (Gordon and Northridge, 2002). Critical ratios (CR)(the lowest signal-to-noise ratio at which a subject can detect a signal in broadband background noise) were investigated in harbour porpoise (Kastelein et al. 2009). CR were investigated using tones at a range of frequencies (8 and 16 kHz were the closest measurements made to the 10 kHz centre frequency of an Airmar CAAD) and at 8 and 16 kHz, CR of 22 and 24 dB were recorded respectively. This indicates that harbour porpoises are able to detect tonal sounds well in broadband white noise at these frequencies (Kastelein et al. 2009). This provides further evidence that masking is unlikely to be caused by Airmar CAAD signals in harbour porpoise.

1.4.4.2 Stress

In human and terrestrial mammals, chronic exposure to noise can also cause stress. In the marine environment, repeated and prolonged exposures to underwater sound may be a significant source of stress to marine animals (Wright et al. 2007). However it is difficult to quantify stress in marine mammals and consequently few direct studies have been conducted. It is likely that marine animals would respond in a manner consistent with terrestrial species studied (Wright et al. 2007). In studies on terrestrial and marine mammals, both short-term and extended exposure to stressors caused shifts away from normal life-history strategies in favour of emergency behaviours. These include but are not limited to: increased physical activity, dispersal of groups, suspension of feeding/reproduction and abandonment of breeding grounds (Romero and Butler 2007). Such emergency behaviours are innate and adaptive in nature, but if performed in response to repeated or chronic exposures to stressors, they may be detrimental to an animal (Bejder et al. 2006; Wright et al. 2007). If animals do not tolerate the sounds and exposures to stimuli last over 2 or 3 weeks then a number of pathological effects can also develop, such as immune suppression and/or reproductive malfunction (Romero and Butler

2007). Studies have investigated the impacts of disturbance by small boats on cetacean species (Currey et al. 2009; Higham et al. 2008; Lusseau 2003, 2004, 2005; Lusseau and Bejder 2007; Williams et al. 2009; Williams et al. 2006). Declines in abundance were observed in Shark Bay, Australia, in response to a long-term increase in tourism boats (no change in abundance was observed at a control site with no tourism boats)(Bejder et al. 2006). Additionally, the behavioural budget of cetacean species has been altered in response to interactions with tourism boats. Increased respiration rates, and changes in short-term travel path, reduced foraging and swimming speed have all been linked to increased vessel presence (Dans et al. 2008; Lusseau and Bejder 2007; Williams et al. 2009). It is unclear whether the physical presence of vessels or the noise produced by them causes such responses. This suggests that short-term disturbances and the resulting avoidance or behavioural change can lead to more biologically significant consequences. Noise from small vessels could impact cetacean vocal communication by virtue of increased background noise conditions, which may also increase stress (Jensen et al. 2009; Nowacek et al. 2001; Parks et al. 2007; Parks et al. 2009). When considering the impacts of exposure to CAAD signals, it is important to note that the magnitude of effects will likely vary depending on the characteristics of the sound (e.g. frequency, length, source level and duty cycle) and the state of the animal (e.g. age, sex, prior exposure to sound, the behavioural state of the animal, the habitat being exposed in etc.)(Weilgart 2007). Increased heart-rate in captive bottlenose dolphins (Miksis et al. 2001) and stress hormones levels in captive beluga whales (Romano et al. 2004) have both been observed in response to noise stimuli. Increased respiration and surfacing rates during noise-stimuli exposures in studies investigating shifts in auditory capabilities have also been observed (Mooney et al. 2009a; Mooney et al. 2009b). Thomas et al. (1990) observed no change in stress hormone levels in captive belugas in response to oil platform drilling noise.

1.4.4.3 Effects on Auditory Systems

Marine mammals, and small cetaceans in particular, have the most acute underwater hearing at the frequencies at which CAADs operate, and are thus most vulnerable to their signals. The hearing threshold is the sound pressure level at which a sound becomes just audible to the animal. Hearing damage results in a loss of sensitivity and occurs first as a short-term shift in hearing threshold that is recovered from in a matter of hours or days (Temporary Threshold Shift - TTS). If the exposures are of high-intensity sound or moderate-intensity sound over a longer temporal period, the threshold shift can become more permanent (Permanent Threshold Shift – PTS). No studies have directly investigated the effect of CAAD signals on the auditory systems of marine mammals (Gordon & Northridge, 2002) and so it is necessary to make extrapolations from studies on captive marine mammal species exposed to other noise stimuli.

In studies on humans, levels causing TTS are often used to infer the levels of exposure that would cause PTS.

To date, work involving direct measurements of threshold shifts in marine mammals has been conducted on beluga, bottlenose dolphins and harbour porpoises, as well as a number of pinniped species. The studies thus far have used a range of transient and more prolonged sounds. In general, there are a number of factors that can affect the magnitude of the TS. The amplitude, frequency content, duration and duty cycle will all have an impact. Au et al. (1999a) subjected bottlenose dolphins to a 5-10 kHz fatiguing stimuli for a total of 30 minutes over a 60 minute period and observed no TTS with received levels of 171 dB but significant TTS (12-18 dB elevation in hearing threshold) at 179 dB re 1 μ Pa. Work by Schlundt et al. (2000) involved measuring the levels of loud tonal sounds required to cause a 6 dB elevation in masked hearing threshold (considered to be a significant elevation – Southall et al. (2007)) in beluga and bottlenose dolphins. They found that fatiguing tones made at 10 and 20 kHz with received levels of 192 dB re 1 μ Pa were sufficient to cause 'masked TTS' (mTTS). Masked TTS is where measurements are taken against a constant, simulated background noise (instead of in a quiet, controlled setting). The result of such experiments is are 'masked thresholds' as opposed to absolute thresholds (generated from controlled experimental setup). Observed shifts in masked thresholds are generally smaller than the absolute TTS that would be observed with the same fatiguing stimuli. These trials were conducted with highly trained animals and it is noteworthy that significant behavioural reactions were observed at these frequencies when exposed to RLs of 180 dB re 1 μ Pa. Later experiments on beluga determined further mTTS using fatiguing tones of 0.4 and 30 kHz. Source levels of 226 dB re 1 μ Pa p-p / 186 dB re 1 μ Pa²-s were sufficient to cause a 7 dB shift at 0.4 kHz and a 6 dB at 30 kHz (Finneran et al. 2002). No mTTS was observed in a bottlenose dolphin exposed to the same experiment. A different study on a bottlenose dolphin initiated a 10 dB masked threshold shift (mTS) in response to a 179 dB, 7.5 kHz fatiguing stimulus. Repeats of the experiment resulted in 2-18 dB mTS. The same fatiguing stimulus but presented at 165 and 171 dB were not sufficient to cause mTTS (Nachtigall et al. 2003). Finneran et al. (2005) determined that SELs of approximately 195 dB re 1 μ Pa²-s (meaning exposure of 195 dB re 1 μ Pa for up to 1 second) caused TTS in two bottlenose dolphins when exposed to tones at 3 kHz. In bottlenose dolphin, TTS was induced using a mid-frequency sonar (5.6 kHz tonal) fatiguing stimuli with a SEL of 214 dB re 1 μ Pa²-s (Mooney et al, 2009a).

Temporary threshold shifts have been induced in harbour porpoises in response to short, broadband pulses caused TTS in harbour porpoises at SPLs of 199.7 dB pk-pk re 1 μ Pa and

SELs as low as 164.3 dB re 1 $\mu\text{Pa}^2\text{-s}$ (measured at 4 kHz) and 145 dB re 1 $\mu\text{Pa}^2\text{-s}$ were sufficient to cause aversive behavioural reactions in the test animals (Lucke et al. 2009).

An equal energy model predicts that two noise exposures will induce similar threshold shifts if the exposures are equal in sound energy, irrespective of the temporal nature of the sound energy. Therefore, according to an equal energy rule, a doubling of exposure duration and a 3-dB increase in amplitude should induce similar threshold shifts. The effect of source level and duration of the fatiguing stimuli have been directly investigated in studies on pinnipeds (Kastak et al. 2005) and cetaceans (Mooney et al. 2009a). Kastak et al. (2005) found that doubling the exposure duration had a greater effect on threshold shift than a 15 dB increase in exposure amplitude. Similarly, a study on bottlenose dolphins found that TTS levels increased as a function of exposure duration (while sound pressure level was kept constant) and a strong positive relationship was found between length of exposure and the size of threshold shift (Mooney et al. 2009a). Therefore, using the equal energy rule may result in conservative estimates of the exposures necessary to cause TTS (Mooney et al. 2009a). Recovery times of animals from peak TS back to pre-exposure baseline hearing sensitivities varied among studies and individuals tested. In general, recovery times for the most studied species were between 20-45 minutes from the last exposure (Mooney et al. 2009a; Mooney et al. 2009b; Nachtigall et al. 2003), with recovery times less than 20 minutes being rare in studies (Finneran et al. 2005; Mooney et al. 2009b). Mooney et al. (2009a) estimated that recovery rates were logarithmic (approximately -1.8 dB/doubling of time) and that recovery times increased as a function of exposure duration. In the single study on harbour porpoises, it was estimated to take 55 hours for the test animal to recover from a 202.1 dB exposure (measurements were only taken to 29 hours post-exposure but the hearing sensitivity had not returned to baseline at that point – the 55 hour value comes from predicting over a log-fitted recovery curve)(Lucke et al. 2009).

However, it should be considered that these studies all used small sample sizes (i.e. low number of individuals tested) in a controlled, captive setting in investigating the practical potential for TTS/PTS and the patterns observed in captivity may be different in the marine environment and vary between individuals impacted.

1.4.4.3.1 Noise Exposure & Damage Risk Criteria

As noted previously, noise exposure criteria have been adapted and extrapolated for marine species – in some cases from human criteria. Taylor et al. (1997) calculated theoretical zones of influence for three CAADs applying a human Damage Risk Criteria (DRC) of 130 dB above the hearing threshold (for single exposures – though the authors give no explanation where this

weighted threshold came from). They predicted that at ranges of < 7 m PTS would be induced in harbour porpoises in response to the loudest CAAD measured, the Ferranti-Thomson Mk 4x model CAAD (8-30 kHz, SL: 200 dB re 1 μ Pa). This calculation was based on Anderson's (1970) audiogram for the harbour porpoise. More recent data (Kastelein et al. 2002), which showed porpoises to be more sensitive at that frequency, suggested a damage zone of approximately 30 m (calculated in Gordon and Northridge, 2002). Taylor et al. (1997) also used a device that is likely the Airmar CAAD model (listed as AHD2) as it had similar signal characteristics (duration: 1.8 ms, inter-pulse interval: 40 ms). Using this device, they calculated theoretical zones of 'severe disturbance' (> 130 dB re 1 μ Pa) and 'hearing damage or injury' (> 180 dB re 1 μ Pa) and suggested that 'severe disturbance' would occur within a radius of 17 m and that 'hearing damage or injury' would not occur based on that source level and their weighting system (the device would need to produce sound levels > 180 dB re 1 μ Pa). However the Airmar device used in that study had a source level of 152 dB, which is 42 dB lower than the maximum reported SL of Airmar dB II units. Consequently, Airmar devices performing at full source level would exceed the 'hearing damage' and 'disturbance' thresholds, within 20 m and ~ 1600 m of the source respectively (based on spherical spreading from a SL of 194 dB re 1 μ Pa).

Gordon and Northridge (2002) adapted Schlundt's et al. (2000) findings, of TTS induced in bottlenose dolphins, to estimate the ranges from an Airmar CAAD at which TTS would be induced in harbour porpoises. They calculated that a single exposure to an Airmar CAAD at 185 – 189 dB, which would be encountered at ranges less than 2-3 m from the device, would be necessary to cause TTS. They also calculated extrapolated TTS thresholds for common seals and determined that animals would need a single exposure to 204 dB from an Airmar device – which is above its source level – however repeated exposures to lower received levels could impact hearing thresholds.

Southall et al. (2007) developed noise exposure criteria for species groupings exposed to different categories of sound. They identified three categories: 'single pulsed sounds' (e.g. explosion, single airgun, single sonar ping), 'multiple pulsed sounds' (e.g. serial or sequential 'single pulsed sounds') and 'nonpulsed sounds' (e.g. vessel passes, drilling). In this overview, they categorised the sounds of ADDs (pingers) and CAADs as 'nonpulsed' sounds but acknowledged that many CAADs contain signals that are pulsed. Given that we are interested in the effects of a CAAD, which produces pulse trains and falls within the 'multiple pulse sounds' definition we will consider them using the criteria for 'multiple pulsed sounds' (it is highly unlikely that an animal would be exposed to a single pulse from a CAAD). Southall et al. (2007) proposed injury criteria with SELs of 198 dB re 1 μ Pa²-s for multiple pulse sounds. These levels would be encountered by

“high-frequency odontocetes” such as the harbour porpoise, (and thus PTS would be induced) at ranges less than 2 m from an Airmar device – however if an animal was exposed repeatedly, as is likely with CAADs, the zone within which this would occur would increase in size.

However, recent work suggests that harbour porpoises may be much more sensitive than their categorisation under the Southall et al. (2007) criteria. Masked TTS was initiated in response to a 164.3 dB re 1 $\mu\text{Pa}^2\text{-s}$, significantly lower than any other species tested and the ‘high-frequency odontocete - multiple pulse criteria’ (Lucke et al. 2009; Southall et al. 2007).

Based on Lucke et al.’s (2009) TTS study on harbour porpoises, Götz (2008) proposed that TTS onset would occur in harbour porpoises if they were exposed to 10-35 kHz signals at 145 dB re 1 $\mu\text{Pa}^2\text{-s}$. Furthermore, he estimated that a continuous exposure of 10 seconds from a SL of 194 dB re 1 μPa (SEL = 204 dB re 1 $\mu\text{Pa}^2\text{-s}$) would result in a TTS-onset zone out to 438 m from the source for the species (based on a stationary animal being exposed, spherical spreading and 5 dB / km absorption).

Schlundt et al. (2000) noted in their experiments that it was difficult to make highly trained animals maintain station during intense sound exposures, with behavioural reactions recorded in response to fatiguing stimuli of 178-193 dB re 1 μPa . With this in mind it seems likely that wild animals would remove themselves to avoid these extreme sound levels. However, it is important to consider that wild animals may be motivated to remain in and utilise a given area, such as an important feeding resource or passage between sites and thus be exposed to CAADs at close range for prolonged periods. The questions over the efficiency of these devices on seals could indicate that animals are motivated to stay close to sites. Harbour porpoises have been observed close to a number of fish farm sites off the west coast of Scotland, both when CAADs were active and inactive (discussed in further detail below)(SARF in press).

1.4.4.4 Disturbance & Habitat Exclusion

The behavioural responses of marine mammals to anthropogenic noise are unpredictable. However, a number of studies have investigated the effects of CAADs on the distribution of marine mammals. The effects of these devices on seals have already been discussed but a number of studies have documented habitat exclusion in cetacean species. Two studies into the effects of Airmar devices on the distribution of harbour porpoises have been conducted in Canada. Olesiuk et al. (2002) conducted an experiment in Broughton Archipelago, British Columbia and found the relative abundance of porpoises dropped significantly in periods when the CAAD was active. Sighting rates during active periods were between 1.9 and 3.8 % (depending on sector scanned) of those recorded during control periods and only 1% of the

predicted number of animals within 600 m of the active CAAD was observed. Furthermore, animals were completely excluded out to 200 m from the active CAAD and though the effect of the device appeared to diminish with distance, and significantly reduced relative abundances were recorded out to 3.5 km (8.1% of expected sightings were observed between 2.5 - 3.5 km from source) and the effects of the CAAD likely extended beyond the 3.5 km survey limit. The device remained on for three x three week periods (each following a three-week control period of inactivity) and no detectable change in tolerance was observed (Olesiuk et al. 2002). The effect on porpoise density of the CAAD being activated was almost immediate, with no animals being observed in scans following the device being switched on (animals had been observed on 26% of surveys on the days preceding activation). Sighting rates returned to normal during the four days of observation following the deactivation of the device. In a study in the Bay of Fundy, Johnston (2002) recorded significantly lower sighting rates when the CAAD was active than during control periods within 1.5 km of the device. During active periods the closest observed approach (COA) was 645 m from the device (mean = 991 m). The calculated received level of sound at the point of COA and mean COA were 125 dB re 1 μ Pa and 128 dB re 1 μ Pa respectively. The exposure sessions only last 2 hours and as a result it was not possible to investigate any changes in tolerance to the sounds. Morton & Symonds (2002) also recorded a dramatic effect on killer whale (*Orcinus orca*) sightings in a 15-year study in the Broughton Archipelago. Numbers remained stable throughout the study period in the Johnstone Strait (where there are no CAADs – thus acting as a control) but sightings dropped significantly after CAADs were installed at four sites throughout the Archipelago. Sighting rates returned to their pre-CAAD installation levels after the CAADs were removed from the fish farm sites in the Broughton Archipelago. Morton (2000) also reported a decline in Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) after CAADs were installed in the area, but provided no statistical support for this claim.

A study in Orkney in Scotland, investigating the effects of an Airmar device on harbour porpoises, observed a significant decrease in porpoise sightings in regions with CAADs (Robertson 2004). In control regions, animals were sighted on 39.5% of days and on only 10% of days in regions impacted by the CAAD. T-PODs were also used in this study and recorded significantly fewer detections of porpoises within the audible range of the CAAD than away at control sites ($\chi^2=18.62$, $df=1$, p -value<0.001). Moreover, Robertson (2004) observed an increase in number of porpoise-positive days within the CAAD impact zone after the CAAD was removed indicating animals returned quickly, though this was not investigated statistically. They recorded no obvious change in seal haulout numbers and behaviour at a nearby site with respect to CAAD use.

A study in the Sound of Mull and Loch Sunart conducted between August 2008 – May 2009 used T-PODs to investigate harbour porpoise presence around active CAADs. T-PODs were deployed out to 3,000 m from fish farm sites with active CAADs. The initial T-POD deployment (between 12th August and 31st August 2008) revealed low detection positive minutes (DPM) at all of the T-POD sites. Over the whole study period, they observed that the number of porpoise click positive minutes (DPM) was higher in periods during which CAADs were turned off than when they were active, suggesting animals were responding to CAAD noise levels (SARF in press). The greatest increase in DPM after the CAAD was removed was observed at the T-POD closest to the fish farm. Animals were sighted close to fish farm cages whilst CAADs were active however and DPM generally decreased with increasing distance from the fish farm, indicating that porpoises were not completely excluded from the vicinity (SARF in press).

1.4.5 CAAD use in Scotland

There are few official statistics on the number and models of acoustic devices in use at fish farms around Scotland. Surveys between 1990 and 1998 indicated that between 12-16% of fish farms around Scotland were using some form of acoustic device in response to seal predation (Ross 1988). Quick et al. (2004) reported that CAADs were installed at 52% (102 of 195) sites, marking a considerable increase between 1998 and 2001. The most recent survey of CAAD usage around Scotland indicated that devices are used at approximately half of surveyed sites (40 out of 81 sites interviewed) and that Airmar and Terecos brands are the most common models (SARF in press). The devices most commonly used on the west coast of Scotland are the Airmar and Terecos models, although some fish farms are still using Ace Aquatec and Ferranti Thompson models (Calderan pers. comm.; SARF in press). At 16 of the 40 sites that use CAADs, the devices are constantly active. At 12 sites, the devices are activated only once the farmed fish reach a certain size (SARF in press).

1.5 Identification of suitable areas as SACs

This study follows on from the work of Embling (2007) who conducted visual and acoustic line-transect surveys from 2003 to 2005 west of Scotland and used these data to build predictive models for harbour porpoises. The survey effort and detections collected between 2003 and 2005 by Embling were used in this thesis together with three additional years of data collected between 2006 – 2008. The modelling analysis methods used here are different to those used by Embling (2007; et al. 2010).

The overarching aim of this thesis is to assess the suitability of the west coast of Scotland as an area to be conserved for harbour porpoise. One method of protection is via the establishment of SACs for the species. Embling et al. (2010) proposed a number of potential sites for harbour porpoises for the west coast of Scotland based on the guidelines established by European Commission (EU, 2007; Habitats Committee, Hab. 01/05). The highest density areas identified by Embling et al. (2010) were the Sound of Sleat, Sound of Jura, parts of the Firth of Lorn and the inshore regions west of Mull.

One of the issues in the identification of regions suitable for designation as MPAs for a species is that they should be consistently used among years (and within the year, although seasonal variation is less likely to impact an area being designated as an SAC). Marubini et al. (2009) found up to four-fold variation in relative abundance among years (1993 – 1997) in the Minch indicating significant variability among years there, although the surveys were limited to late July and early August. Using more recently collected data Embling et al. (2010) did not find any significant variation among years studied in the southern region of the Inner Hebrides. This may be an indication that the northern region is more variable than the Inner Hebrides. One of the main aims in this thesis is to determine the effect of year in harbour porpoise habitat preference and distribution and whether there are consistently important regions for the species west of Scotland.

An additional consideration is that the west coast of Scotland is much larger than any of the SACs already established (the area covered in this study is $\sim 25,000 \text{ km}^2$) and likely too large to be considered as a single SAC. However, it may be possible to identify a pragmatic network of smaller SACs at different sites throughout the west of Scotland to capture any potential geographical spread and/or a range of important habitats. When identifying a suitable area to be protected, a trade-off must be made between maximising the area for protection and minimising the cost of managing an area (Moilanen et al. 2009). The majority of marine SACs in the UK occur in inshore regions and the size of these areas varies. Most of sites are between 10 km^2 and $1,000 \text{ km}^2$ in size (JNCC 2010b). The only SACs specifically for cetacean species in the UK are in the Moray Firth (Scotland) and Cardigan Bay (Wales) and are $1,513 \text{ km}^2$ and 958 km^2 in size respectively (JNCC 2010a). In this thesis, I also investigate habitat preference and the consistent importance of more ‘manageable’ regions across the west of Scotland.

Another conservation approach is by elimination or reduction of the impacts of man-made activities on a species. In such cases, it may be that designating an area as an SAC is not the best conservation approach. As discussed previously, the use of seal scarers in the marine

environment has a number of potential impacts of marine species, in particular harbour porpoises. Here I also investigate the extent to which these devices are used, their impacts of harbour porpoises and whether there is a need to control or mitigate CAAD use in aquaculture.

1.6 Thesis Structure

The same methods are used in the collection, processing and analysis of data in the modelling chapters of this thesis. Consequently, materials and methods are collectively presented in Chapter 2.

Chapters 3, 4 and 5 analyse visual and acoustic line-transect survey data collected from the Hebridean Whale and Dolphin Trust's research vessel *Silurian* to build predictive models of harbour porpoise habitat preference and distribution. In Chapter 3, models were constructed to investigate whether habitat preference and distribution patterns were consistent among years in the study. In Chapter 4, intra-annual variations were investigated to determine whether monthly or seasonal patterns of habitat use were present within the data. In Chapter 5, regional models were constructed after partitioning the datasets to investigate whether the spatial extent of models influenced model outputs.

Chapter 6 is a study of CAAD usage over the west of Scotland in 2007 and 2008 and investigates the sound fields of Airmar CAADs at specific sites. Additionally, the potential impacts of extensive CAAD use on harbour porpoises in the region are investigated. Methods used in this chapter are different to those outlined in Chapter 2 and so this chapter has its own methods section.

Chapter 7 (General Discussion) provides a synthesis of the results of this study and discusses some of the patterns observed under the scope of how harbour porpoises use the west of Scotland region and will focus on the discussion of potential SACs that could be designated there based on the results of this study.

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Chapter 2

Methods and Materials

2.1 Data collection

2.1.1 Survey methods

Visual and acoustic detections of harbour porpoises (*Phocoena phocoena*) were recorded during systematic line transect surveys carried out from the Hebridean Whale and Dolphin Trust's (HWDT) 18 m motor-sailor vessel *Silurian*. These surveys were conducted on the west coast of Scotland (55° 10' – 58° 40' N, 5° 0' – 8° 35' W; Figure 2.1b), between April and September (inclusive) during daylight hours. Visual surveys were carried out from 2003 to 2008 and towed acoustic surveys were conducted simultaneously during the 2004 to 2008 seasons. In the 2003 & 2004 seasons, surveys were focused on the waters around the islands of Mull, Islay and Jura (55° 10' – 57° 0' N, 5° 30' – 6° 50' W; core area shown in Figure 2.1a) and they gradually extended further north and west during 2005-2008. Every month at least one 10-day survey was designed and conducted to provide near even coverage of the core area investigated in 2003-2004. The constraints of the weather and finding safe anchorages at night were considered when designing and executing these surveys.

2.1.2 Visual Surveys

Visual surveys were carried out by teams of two trained observers, one situated on either side of the mast, standing on the front deck of the vessel, (2 m above water level). Each observer surveyed one side each from 0° (ahead of the vessel) to 90° (abeam of the vessel) with the naked eye and 7 x 50 binoculars (Marine Opticron and Plastimo). Observers were rotated every hour to avoid fatigue. Visual data were collected in sea conditions of Beaufort sea state ≤ 5 , but only data collected in sea state ≤ 3 were considered in this study. A survey speed of 6 knots was maintained during surveys; the majority of survey time was spent under motor. When sufficient wind was available surveys were carried out under sail, with the boat's engine off. These survey conditions were recorded during the survey. When cetaceans were sighted, the species was identified (if possible) and the time of first sighting, the estimated distance to the animal(s), the bearing to the animal(s) relative to the boat (determined from angle boards on deck) and the heading of the animal(s) relative to the boat were recorded. Group size and behaviour of the animal(s) were also recorded. These sighting data were relayed to a data-recorder, who manually

entered them into the data recording software *Logger 2000* (developed by the International Fund for Animal Welfare – IFAW) which ran continuously, logging GPS positional and NMEA feed data, and stored this in a Microsoft Access database in real-time (see §2.1.4 for further details).

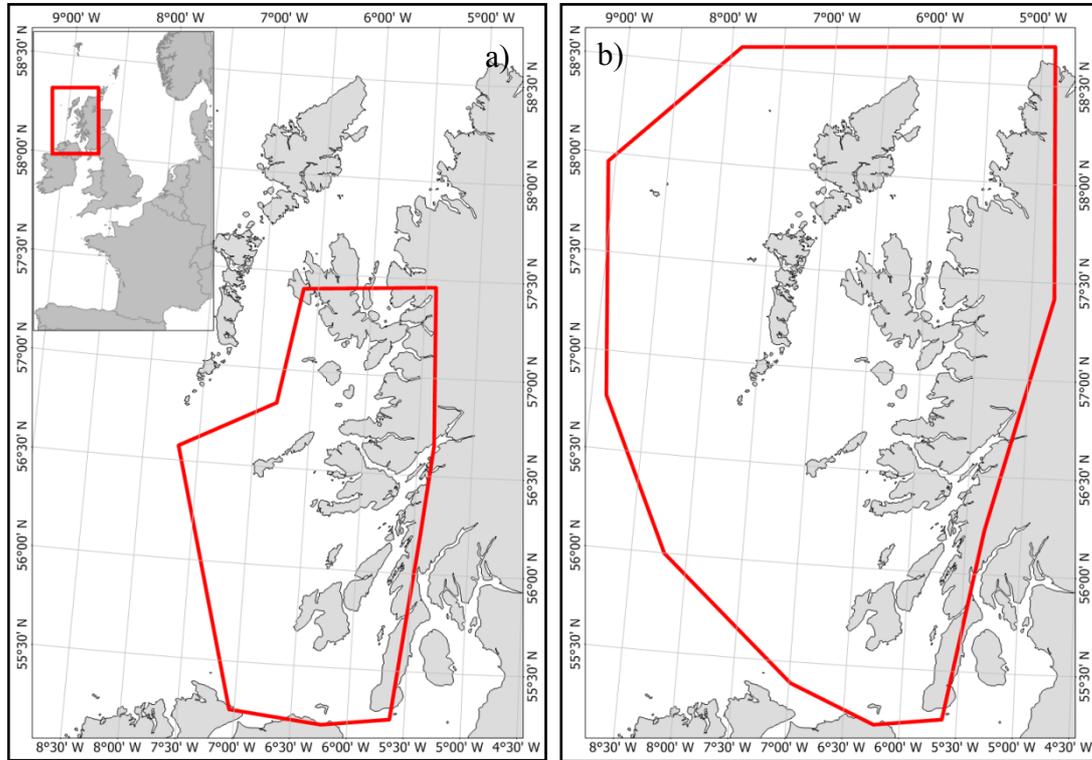


Figure 2.1a & b - Study boundaries for the (a) 2003-2004 and (b) 2005 - 2008 surveys. Location of study site is shown inset.

2.1.3 Acoustic Surveys

Passive acoustic monitoring (PAM) was conducted using a towed hydrophone array on surveys from 2004 to 2008. Acoustic surveys were carried out in all sea states, during daylight hours and in waters >10 m depth. Two different PAM systems were used during the study period (one from 2004-2005, which was then superseded by a new and improved system in 2006-2008). These systems used different hydrophone arrays and the signal processing and acoustic detection software also differed. Both types of hydrophone arrays comprised two high-frequency elements (HS150 elements - Sonar Research & Development Ltd) with highest sensitivity at 150 kHz and a near flat frequency response between 2 - 140 kHz. Each element was coupled to an adjacent pre-amplifier, providing 35 dB of gain. In the array used in 2004-2005, the hydrophone elements were separated by 3 m, whereas in 2006-2008, the elements were separated by 0.25 m. Both sets of elements were housed in a streamlined sensor section consisting of 10m of 35 mm diameter polyurethane tubes filled with ISOPAR-M oil. This was towed 100 m behind the boat attached by Kevlar-strengthened towing cable. A replacement hydrophone was used for some

surveys during the 2008 season. This hydrophone (from Seiche instruments) had the same HS150 elements, was solid potted and was used in the Small Cetaceans in the European Atlantic and North Sea project (SCANS-II 2008) and are thus considered equivalent. The replacement hydrophone array was longer than other arrays used in the study (200 m of cable; compared with 100 m for the other hydrophones) but it was towed 100 m behind the survey vessel as with the other hydrophone arrays used in the study.

2.1.3.1 Acoustic Set-up: 2004-2005

The signal from the hydrophone array was fed into a ‘porpoise detection box’ (Seiche Instruments) which split it in three different frequency bands; the ‘porpoise band’ (115 – 145 kHz) and two ‘control bands’ with centre frequencies at 50 and 71 kHz. In each frequency band, a signal envelope was traced using analogue circuitry and digitised (at 25 kHz) and displayed in the detection software; *Porpoise Detector* (Version 4.00.0001; (Gillespie and Chappell 2002). Clicks were automatically classified based on the relative amplitude of the signal in each of the three bands and also on the shape of the pulse, as either ‘Porpoise’, ‘Broadband’ or ‘Unknown’. The program also calculated a bearing to the source based on the difference in arrival time at each element (with no left/right discrimination). The bearing and relative amplitude of all detected sounds were displayed. (Figure 2.2).

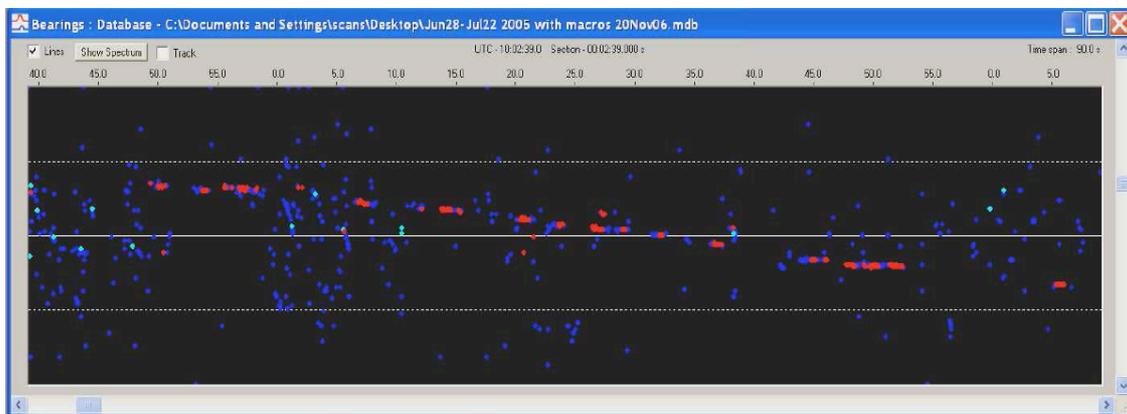


Figure 2.2 – Screen grab from Porpoise Detector showing a porpoise click train (red dots) amidst unidentified noise sources (blue dots) and high frequency sounds (light blue dots). Time is represented on the x-axis (window width \approx 90 seconds). The top of the screen represents ‘ahead’ of the hydrophone, the solid line represents ‘abeam’ of the hydrophone and the bottom represents sounds heard behind the hydrophone array (from Embling 2007).

2.1.3.2 Acoustic Set-up 2006-2008

The hydrophone array was connected to an amplifier with a high pass filter at 20 kHz (Seiche Instruments) onboard the survey vessel and signals from the hydrophone array were digitised, sampling at 500 kHz using a PCI-6250 data acquisition sound card (National Instruments Ltd)

installed in a desktop computer. During the surveys, the digitised signals were processed in real-time and analysed using *Rainbow Click* software (Version 4.04.0001, IFAW/Doug Gillespie). An advantage of this program is that it stores a sample of the full bandwidth waveform around each detected click allowing the raw waveform and spectrum to be examined in later analysis. It also samples the entire bandwidth of the improving detection accuracy. *Rainbow Click* distinguished the clicks of harbour porpoises from ambient noise using digital trigger algorithms (Gillespie et al. in prep.). Clicks are classified if they exceed a pre-set trigger threshold, which are set relative to a measure of background noise. For this analysis a click trigger threshold of 10 dB was used. The threshold level always provides a balance between processing a large number of clicks by using a lower trigger level and risking missing porpoise clicks entirely with a higher trigger level. Once a candidate click was detected, a bearing to the source was calculated (with a left/right ambiguity) by measuring the difference in time of arrival between one element and the other (Figure 2.3), the click was then classified (§2.2.2) and displayed in real time.

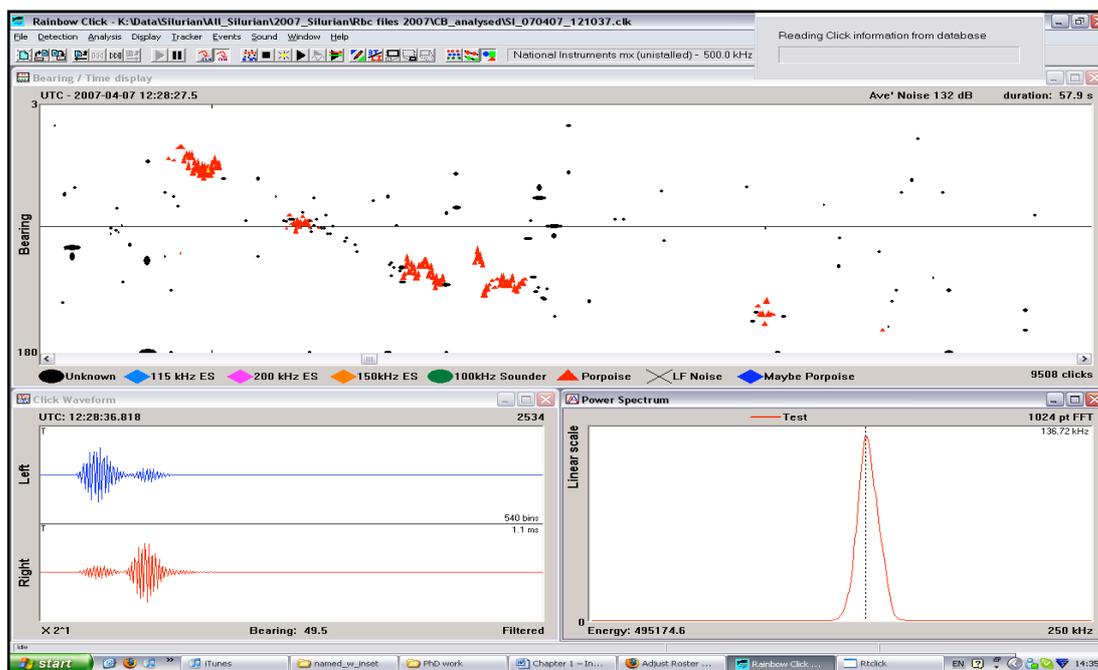


Figure 2.3 - Rainbow Click during a harbour porpoise ‘single-track’ detection. Porpoise clicks are shown by red triangles and unidentified clicks by black dots. Time is shown on the x-axis (window width = 58 secs) Bearing is on the y-axis; the top of the main window represents sounds heard ahead of the hydrophone and the bottom represents sounds heard behind the hydrophones. The waveform and power spectra of a single click are shown in the bottom left and bottom right, respectively.

2.1.4 Logger 2000

The data collection software *Logger 2000* ran continuously and was connected through a serial interface to the vessel’s NMEA feed. Positions (from GPS) were logged every 10 seconds along with the vessel speed, course, wind speed and direction. Whether the boat engine was on or off

was recorded by a manually by an observer every 30 minutes and whenever the status changed. Survey conditions were recorded every 15 minutes, or whenever they changed significantly during survey effort. Specifically, the sea state (Beaufort scale), swell, glare and general weather conditions were logged. During the 2008 field season, a temperature probe was deployed 1.5 m below the hull, off the stern of the vessel to record sea surface temperature every 2 minutes during searching effort (Table 2.1).

Survey effort status was also recorded in Logger. When visual observers were in place, the vessel's effort status was "On Effort". When a sighting occurred the vessel's speed was held constant until the data had been entered. Once this was completed, the survey vessel broke survey and deviated from the transect line to identify species and/or carry out photo-identification of dolphin species and minke whales (*Balaenoptera acutorostrata*). During such deviations from track-line, the vessel survey effort was changed to "With Whales". Once the sighting was over, the vessel returned to its survey lines and the visual observers resumed their positions and the survey effort status was changed to "On Effort". Detections (visual or acoustic) made during "With Whales" survey effort status were not included in the final analysis.

2.1.5 Sources of covariate data

Data to be used as model covariates were obtained from a range of external sources (Table 2.1). A number of studies have identified links between cetacean distribution and environmental and oceanographic covariates (like serving as proxies for prey distribution or other biologically significant phenomena)(Acevedo 1998; Baumgartner 1997; Cañadas et al. 2003; Davis et al. 1998; Fiedler and Reilly 1994; Gaskin 1984; Gowans and Whitehead 1995; Gregr and Trites 2001; Karczmarski et al. 2000; Loughlin et al. 1999; Marubini et al. 2009; Moore 2000; Mullin et al. 1994; Naud et al. 2003; Panigada et al. 2008; Rowe et al. 2003; Smith et al. 1986; Tynan et al. 2005; Wilson et al. 1997; Wimmer and Whitehead 2005). Previous studies have investigated whether cetaceans make diurnal shifts in behaviour, distribution or habitat preferences (Dietz and Heide-Jørgensen 1995). To assess whether harbour porpoise exhibit such shifts 'Time of Day' was included in the models - as continuous indexes between 0 and 1 to incorporate spatial and temporal variation in the data. 'Time of Day' was included in models as a ratio; calculated by dividing the time elapsed since sunrise by the time between sunrise and sunset for the survey day. The time of sunrise and sunset was determined from POLTIPS (Version 3.0, Proudman Oceanographic Laboratory) for Tobermory, the start and end point of the majority of surveys.

Cetacean distribution has been associated with state of tide, with animals appearing more

prevalent or more detectable during certain phases of tide (e.g. slack, flood, ebb). For harbour porpoises in particular, a range of studies of their distribution have identified site-specific patterns associated with tidal activity (Calderan 2003; Embling et al. 2010; Johnston et al. 2005; Pierpoint 2008; Skov and Thomsen 2008). Here, 'Position Relative to Tidal Range' and 'Position in Daily Tidal Cycle' were used to determine whether the same patterns were occurring west of Scotland. For tidal variables it was necessary to determine the nearest tidal port from which to source tidal data in POLTIPS. Distances to 15 sea-ports for which tidal predictions were available were calculated using a custom routine in Manifold (Version 8.00. 32-bit, Manifold® Systems). Maximum spring tidal range for the closest tidal port and tidal range for the tide cycle that the data point fell within were determined. Position Relative to Tidal Range provides an indication of variations in the lunar tidal cycle (i.e. the spring-neap tidal cycle). This was calculated by first determining the tidal range for the time and location for each data point and subtracting from it the minimum tidal height for the same location. This value was then divided by the maximum spring tidal range for the nearest tidal port for the current lunar cycle, to generate providing a value between 0 and 1. Values close to 0 represent times close to neap tides and values close to 1 were indicative of periods close to full spring tides. Position in the daily tidal cycle was calculated by dividing the time from the nearest low water to the data point by the time elapsed between successive low waters for that day. This ratio provided values between 0 and 1, where values 0.0 – 0.1 and 0.9 – 1.0 represented the low water slack tide; 0.1 – 0.3 represented the flood tide; 0.3 – 0.6 was the slack high water tide and 0.6 – 0.9 represented the ebb tide (from Embling 2007). Current speed data were obtained from the POLCOMS CS20 model – resolution: 1.8 km); which predicted the maximum current speed at the time and location of each data point. While this model provides excellent coverage of the west coast of Scotland, it does not cover the northern Sound of Jura, northeast region of the Firth of Lorn and the Sound of Mull. Tidal current models developed for these regions by Andrew Dale (at the Scottish Association of Marine Science - SAMS) were used. The Sound of Mull model had a resolution of 200 metres and the Firth of Lorn/Sound of Jura model at 100 m.

A number of studies have used 'Distance to nearest land' as a covariate. This may function as a proxy for other oceanographic factors, e.g. salinity, (Mann and Lazier 2006) or as a reflection of a species remaining close to land for shelter, or navigational cues – e.g. the harbour porpoise echolocation clicks do not travel > 300m so it may be difficult to resolve information from deeper, offshore regions (Able 1995; Alerstam 2006; Mouritsen 2001). Distance to nearest land for each data point was calculated using a script written by Clint Blight (SMRU) in Manifold. The minimum recorded distance to land was 10 m. Sediment data were obtained primarily from

United Kingdom Hydrographic Office (UKHO) and for regions not covered by these data, the Marine European Seabed Habitats (MESH) EUNIS model was used. These datasets were only available as categorical data (RSDB codes describing the different sediment types from the UKHO), so they were converted into percentages of gravel, sand and mud in the sediment using the Folk Classification (Folk 1980). Both depth and slope have been found to be important in explaining cetacean distribution in many regions (Acevedo 1998; Azzellino et al. 2008; Bailey and Thompson 2009; Baumgaertner and Mate 2005; Brager et al. 2003; De Segura et al. 2008; Forcada et al. 1996; Panigada et al. 2008; Wilson et al. 1997). Depth may be made important by prey species occurring certain depth ranges, focusing the distribution of predators. It has been suggested that slope may help drive productivity at fine scales by functioning as anchor points for eddies and currents (Mann and Lazier 2006). Bathymetry data (average seabed depth and average seabed slope), were sourced from EDINA as they provided the best coverage of the study region and the highest resolution available (EDINA averages depth and slope data over a 200 x 200 m grid). Average slope is the change in depth over the resolution of the grid. Slopes of over 20° exist on the west coast of Scotland, though these are extremes. The majority of slope measurements found there are between 0 - 6° (by comparison the slope of the continental shelf is typically around 3-6° and rarely exceeds 10° (Pinet 2009)).

Table 2.1 – Details of covariates used in models showing details of sources, units and temporal/spatial resolution of data used. Acronyms: UKHO – United Kingdom Hydrographic Office; MESH – Mapping European Seabed Habitats; NEODAAS - NERC Earth Observation Data Acquisition and Analysis Service; POL – Proudman Oceanographic Laboratory; SAMS – Scottish Association for Marine Science.

Covariate	Information	Resolution	Unit	Source
Date/Time	Recorded <i>in situ</i> from vessel GPS	every 10 seconds (≈ 30 m)	--	<i>In situ</i>
Boat Speed	Recorded <i>in situ</i> from vessel GPS	every 10 seconds (≈ 30 m)	Knots	<i>In situ</i>
Sea State	Recorded by Observers	every 30 minutes (≈ 5.2 km)	Beaufort Sea State	<i>In situ</i>
Engine Status	Recorded by Observers	--	On / Off	<i>In situ</i>
Time of Day	Ratio: Time from Sunrise/Time between sunrise and sunset for day	at every GPS location	--	POLTIPS
Position Relative to Tidal Range	Ratio: (Tidal Range at location on day – The minimum tidal height at location on day)/ Maximum Spring Tidal Range for location	at every GPS location	--	POLTIPS
Position in Daily Tidal Cycle	Ratio: Time since Low water for nearest tidal port / Time between successive low waters for nearest tidal port	at every GPS location	--	POLTIPS
Max. Spring Tidal Range	Maximum Spring Tidal Range for nearest tidal port	at every GPS location	m	POLTIPS
Distance from Land	Calculated in Manifold	at every GPS location	m	Manifold
Percentage Gravel	Calculated from RSDB codes	Variable	%	UKHO / MESH EUNIS
Percentage Sand	Calculated from RSDB codes	Variable	%	UKHO / MESH EUNIS
Percentage Mud	Calculated from RSDB codes	Variable	%	UKHO / MESH EUNIS
Depth	Depth of seabed	0.2 km	m	EDINA
Slope	Slope of seabed	0.2 km	°	EDINA
Current Speed	Maximum current speed	POL: 1.8 km / SAMS: 0.1 or 0.2 km	m / s	POLCOMS / SAMS
Chlorophyll	Average chlorophyll concentration for midpoint of each 2 km segment	2 km	mg m ⁻³	NEODAAS
Temperature	Average temperature for the midpoint of each 2 km segment	2 km	°C	NEODAAS / <i>in situ</i>
Noise: 100 – 150 kHz	Calculated from <i>in situ</i> recordings	every 2 minutes (≈ 600 m)	dB re 1 μ Pa	<i>In situ</i> recordings
Noise: 50 - 75 kHz	Calculated from <i>in situ</i> recordings	every 2 minutes (≈ 600 m)	dB re 1 μ Pa	<i>In situ</i> recordings

Chlorophyll-a concentration and sea surface temperature (SST) were sourced from Natural Environmental Research Council Earth Observation Data Acquisition and Analysis Service (NEODAAS) satellite data. Due to the presence of cloud cover over the study area, weekly (or if unavailable, fortnightly) composites of satellite-derived values were used. Even with the use of composites, it was only possible to obtain useable chlorophyll-a and SST data for approximately 60% of the total dataset. In 2008, sea temperature data were also collected *in situ* using an autonomous temperature probe (Vemco 8-bit Mini Data Logger) deployed off the stern of the survey vessel at an approximate depth of 1.5 metres.

To investigate the impact of noise on the detection of harbour porpoises, ambient noise measurements were made (sampling at 500 kHz) using the towed hydrophone array during the 2007 & 2008 seasons. To enable this, recordings were made every 2 minutes for between 2 and 5 seconds whilst the hydrophone was deployed. Sound levels were calculated (in dB re 1 μ Pa) averaged over two frequency bands: the ‘porpoise band’ between 100 – 150 kHz; the frequency range over which harbour porpoises vocalise and a ‘control band’; between 50 – 75 kHz. The ‘control band’ frequency range was chosen as it represents the measure used in *Rainbow Click* as a control, against which noise in the porpoise band is compared in determining porpoise detections. ‘DC Noise’ levels, a measure of background noise measured in *Porpoise Detector* were also included in some of the yearly models (2004 & 2005) to see if it impacted acoustic detection rates.

2.2 Data Processing

2.2.1 Acoustic Processing: 2004-2005

Data collected in 2004 & 2005 were analysed by Embling (2007). In brief, Embling’s methods comprised using *Porpoise Detector* software to automatically classify clicks as porpoises. An operator then manually checked each detection to eliminate any false positives. Porpoise click events were classified as a ‘porpoise click train’ if the clicks had a minimum amplitude of >105 dB re 1 μ Pa in the porpoise frequency band (115 – 145 kHz) and there was > 30 dB difference over the mean amplitude in both the control (50 and 71 kHz) bands. Encounters were identified and the porpoise clicks in each click train were marked and porpoise clicks were arranged into ‘groups’ with an estimated number of porpoises in each event. Each porpoise group was linked to a GPS position from *Logger 2000* using a pre-written macro (Gillespie, pers. comm).

2.2.2 Acoustic Processing: 2006-2008

The *Rainbow Click* software automatically classified clicks using four parameters measured from

each click: the peak frequency in the click spectrum, the energy ratio between the ‘porpoise band’ (100 – 160 kHz) and the ‘control band’ (40 – 90 kHz), the bandwidth of the main frequency peak and the duration of the click. Clicks were classified as porpoises if they met all of the following criteria: the click had a peak frequency between 100 and 160 kHz, if the energy ratio was >3 dB, the bandwidth of the frequency peak was < 20 kHz and the click was < 2 ms in duration (Gillespie et al. in prep.). Non-porpoise clicks were classified as ‘unknown’ (i.e. no identified source), echo-sounders (with centre frequencies of: 100, 115, 120, 150 or 200 kHz) or ‘low frequency noise’. Once clicks had been automatically classified, they were displayed visually with their bearing, waveform and power spectrum in the *Rainbow Click* program window (Figure 2.3). An operator manually checked the automatic detections, changed classification if necessary and identified acoustic ‘events’. Acoustic analysis was always completed without reference to visual data collected at the same time. Acoustic events were assessed using the same classifications as developed for the SCANS-II acoustic analysis as follows: click events were defined as a ‘Porpoise Click’ (one or two individual clicks only), ‘Single Track’ (a train of porpoise clicks with a clear and defined track from a single animal), ‘Multiple Track’ (trains of porpoise clicks with clear and defined tracks from one or more animals) or ‘Event’ (a series of porpoise clicks with no clear or defined track)(SCANS-II 2008). For each porpoise detection, the number of animals vocalising was estimated. Animals were considered to be in the same group (i.e. a ‘multiple track’ detection) if click trains overlapped in time or if they occurred within 92 seconds of one another (it takes 92 seconds to cover 300 m when travelling at 6 knots). This time-window was decided on as it is the length of time it takes for the survey vessel to move past a stationary porpoise, (at an average survey speed of 6 knots and a porpoise cruising speed of 1.25 knots (Read and Westgate 1997)). This allowance accounted for porpoises travelling in the same direction as the survey vessel (which would result in longer detections). Additionally, ~ 300 m is likely maximum detection range for the species (Gillespie et al. in prep.). A table was created in the MS Access database linking the GPS data collected in *Logger 2000* (Gillespie and Chappell, 2002), with the number of animals logged in each porpoise detection. Each detection was linked to a GPS fix for the start-time of the detection by a custom macro (Gillespie, pers. comm.).

2.2.3 Comparison of acoustic systems

In order to use both the acoustic datasets collected using the two different acoustic systems across the study period, it was important to compare the detection rates of the two systems. Therefore, the two detection systems were run concurrently on acoustic surveys carried out over 34 days (30th July - 25th August 2008 and 18th - 24th Sept 2008) with the hydrophone arrays

arranged to ensure that the elements were at the same distance behind the vessel. To remove any potential bias caused by the location of the hydrophones with respect to one another, or from issues of directionality in the elements, the side of the boat that each hydrophone array was deployed from was determined randomly for each survey day. Both systems were set-up and data were analysed as described in §2.2.1 and §2.2.2.

All *Rainbow Click* files were analysed in order to build acoustic models for 2008. A subset of all the raw *Porpoise Detector* collected from when the two systems were deployed concurrently was randomly selected. The subset of *Porpoise Detector* files were processed independently of the *Rainbow Click* dataset and the sightings data collected on *Silurian*. Porpoise detections were marked and the numbers of animals vocalising in each group was estimated. The time and location of each detection was then linked to GPS data collected by *Logger 2000*.

Detections made first on system A and detected within 92 seconds (≈ 300 m at 6 knots) of system B were considered to be the same detection event (and visa versa). To investigate whether there were significant differences in detection rates between the two systems, a Yate's corrected test for association (contingency table) was used (i.e. the null hypothesis = there is no association between the two systems).

Over the time period that the two systems were run concurrently a total of 81 acoustic detection were estimated on *Porpoise Detector* and 122 detections were estimated on *Rainbow Click*. Using *Porpoise Detector* 95% of all detection estimated a single animal, where as 82% of detection events in *Rainbow Click* were of a single animal with 7% being of 2 animals. 64% of all detections events were registered on both systems, with an mean difference in time of detection of 20 seconds (se = 17 seconds). Of the remainder, 27% of detections were only made on *Rainbow Click* and only 9% of detections were registered on *Porpoise Detector*. Though slightly more animals were estimated using the *Rainbow Click* system, no significant difference was observed between detections on the two systems ($\chi^2 = 22.28$, $p < 0.01$, $df = 1$, Yate's corrected) indicating that it is reasonable to compare the data from different acoustic systems.

2.3 Data Analysis

2.3.1 Pre-statistical analysis

All visual and acoustic survey effort tracklines were divided into 2 km segments for this analysis. This was equivalent to the coarsest resolution of the available oceanographic covariates in the models. Prior to segmenting, values for predictor variables were calculated for each GPS data

point of trackline. For sea state, engine status, boat speed and effort status this was done in MS Access. The other variables were dealt with in Manifold queries, macros and pre-written routines. Because porpoise sighting rates are significantly impacted by sea state (Palka 1996), survey effort was limited to data collected in Beaufort sea state ≤ 3 for the visual data models. For the acoustic survey effort, data collected in all sea states were included. The mean value of each variable was then determined over each segment. Values for sea state were rounded to the nearest half-sea state and engine status was rounded to the nearest value. Additionally, the total number of detections in each 2 km survey segment was calculated.

Collinearity between covariates, if unaccounted for, in models can cause inflated or underestimated standard errors and p -values and lead to poor model selection. To avoid this, collinearity between predictor variables was investigated prior to modelling using ‘generalised variance inflation factors’ (GVIF) (Cox and Snell 1989; Fox and Monette 1992) using the *vif* function in the car package in R. GVIFs were deemed more appropriate than VIFs because the degrees of freedom (df) for each covariate was >1 . Large VIF values indicate collinearity but there are no set rules for which values of GVIF indicate unacceptable collinearity, it is understood that if a covariate is well-predicted by another covariate (e.g. $R^2 = 0.9$) then the $GVIF = 1/(1-0.90) = 10$. Therefore, in this study a threshold of $GVIF \leq 10$ was used. In the case of the ‘percentage sediment’ data - which are not strictly orthogonal - $GVIF^{1/2Df}$ was used which adjusts for the dimensions of the confidence ellipsoid and was more appropriate here (Fox and Monette 1992)(§2.4.3).

2.3.2 Model Selection

In this analysis, the number of harbour porpoises detected per 2 km of survey effort was modelled with respect to survey and oceanographic covariates. Generalised Additive Models (GAMs) built within a Generalised Estimating Equations (GEEs) model construct were used to identify harbour porpoise habitat preferences. GAM is a method to analyse non-normal data responses using non-linear smooths of predictor variables and have the general form:

$$g(E(Y_i)) = \beta_0 + s_1(x_{1i}) + s_2(x_{2i}) + s_3(x_{3i}) + \dots$$

where $E(Y_i)$ is the expected value of the response variable (number of porpoises per 2 km of survey effort), $g(\cdot)$ is the function linking the response to the non-linear smooths s_j of the covariates x_k and β_0 is the intercept term. Because the response data in this study are counts data, a Poisson distribution was assumed (with log link function):

$$f(y; \lambda) = \frac{\lambda^y e^{-\lambda}}{y!}$$

where

y is the number of porpoises seen.

λ is the expected number of porpoises seen in a 2 km segment.

GAMs have been extremely useful in modelling marine mammal distributions and investigating habitat preferences (Bailey and Thompson 2009; Cañadas and Hammond 2008; Embling 2007; Marubini et al. 2009; Skov and Thomsen 2008). However, one of the assumptions of GAM methods is that the model errors are independent. This is unlikely to be the case with these datasets as observations were collected close together in space and time. Unless this is accounted for in the model covariates, this temporal and/or spatial autocorrelation pattern will be represented in the model errors. Falsely assuming independence within the dataset can result in incorrect model conclusions, over- or underestimation of model standard errors, resulting in p -values that are too small and covariates being retained in the final model. Panigada et al. (2008) suggested that a more appropriate method for modelling marine mammal distribution was to use GAM-based methods but utilise Generalised Estimating Equations models to generate the standard errors and p -values which are used to determine govern model selection (Liang and Zeger 1986). Similar methods to those used by Panigada et al. (2008) were adopted in this study.

GEEs are an extension of Generalised Linear Models (GLMs), facilitating regression analyses longitudinal data and non-normally distributed variables (Liang & Zeger 1986). GEEs can be used to account for temporal and spatial autocorrelation within a dataset by replacing the assumption of independence with a correlation structure. Data within the model are grouped into a series of ‘panels’, within which model errors are allowed to be correlated and between which data are assumed to be independent. It is important that appropriate ‘panels’ are chosen and that a suitable correlation structure is used, although Hardin & Hilbe (2002) suggest that GEEs are relatively robust to misspecification of these two elements. GEE models also allow for overdispersion within the data (via a dispersion scale parameter ϕ).

In this study, autocorrelation function plots were generated using the *acf* function in R to select suitable ‘panel’ size for each of the models. A simple *working* independence correlation model structure was also selected. This model structure provides identical coefficients to those of a standard GAM-based approach, but the standard errors will differ significantly under the GEE

structure, strongly influencing final model selection results, avoiding the inclusion of covariates. An alternative working correlation structure (e.g. AR(1)) could have been used here instead, but standard errors to this user-specified correlation structure were desired here (as seen in Panigada et al. 2008).

The overdispersion in these GEE models means that their fitting must be based on quasi-likelihoods, so stepwise model selection was based on the QIC statistic (Ballinger 2004). For all models, each covariate was permitted to be present in the model as a curve (with a *B*-spline (deBoor 1978) fitted with knots placed at the mean for each covariate), as a linear term or removed from the model. Factor variables were permitted to be included as either a factor, a linear term or omitted entirely. The full model was fitted using the *geeglm* function in the *geepack* package (Halekoh et al. 2006) and GEE-based *p*-values were used to determine if covariates should stay in the model. The function *anova.geeglm* in the *geepack* package performs stepwise selection using QIC but, as this will only add terms sequentially and the model selection results depended on the order that covariates were inputted, it was necessary to identify a suitable input ordering for the covariates. Reduced models were therefore created, each one of which having one covariate omitted. Each of these models was then compared to the relevant full model (containing all the covariates) using a simple *anova.glm* method, to determine if each covariate was important in explaining that dataset. The ‘important’ terms were then fitted in order of significance and investigated using the sequential *anova.geeglm* to determine the final ‘best’ model.

Visual and acoustic data were modelled separately to allow for differences in data collection methods to be incorporated in models. The statistical package R (64-bit Mac version 2.9.0, R Core Development Team, 2009) was used for all analyses in this thesis. The *splines* and *geepack* (Halekoh et al. 2006) packages in R were used to fit the models.

2.3.3 Model Evaluation – Goodness of Fit

The performance of the final models was evaluated using a cross-validation method. The method involved randomly partitioning the data into two equal sized datasets – the ‘training’ and ‘test’ subsets. The final model was fitted to the ‘training’ subset and used to predict over both subsets. Because the data are considered to be quasi-Poisson, and therefore have error variances proportional to expectations, the mean-square errors were scaled by the appropriate predicted values. This approach is similar in spirit to the R^2 and ‘deviance explained’ metrics and is a measure of goodness of fit of the model to the data.

The predictive performance (*F*) was calculated as:

$$F = \frac{\sum_{i_in_TEST} \frac{(PRED_i - OBS_i)^2}{PRED_i}}{\sum_{j_in_TRAIN} \frac{(PRED_j - OBS_j)^2}{PRED_j}}$$

Where:

OBS_i is the actual number of detections within cell i .

$PRED_i$ is the number of detections the final model, fitted to the ‘training’ subset, predicted for cell i .

TEST is the set of cells in the ‘test’ subset.

TRAIN is the set of cells in the ‘training’ subset.

This process was carried out 1000 times, and the mean and 95% confidence intervals of F were calculated. If the models were perfectly correct representations of the patterns that generated the data, each replicate would produce a value of F close to 1. The variability in F will depend on the size and structure of the dataset. Upper bounds of confidence intervals less than 1 are evidence that the model doesn’t fit as well and has failed to capture some part of the process underlying the data.

For visually assessing the relationship between the predictor variables and the response, the smoothed response curves and confidence intervals were calculated. For the spatial predictions, the final models were all predicted over a 4 x 4 km spatial grid, which was selected to be twice the size of the segment length – as recommended for visual comparison of models over different temporal and spatial scales (Hedley 2000).

2.4 Data

2.4.1 Model covariate data

A range of model variables was included in the analysis and summary statistics for these variables are shown for visual and acoustic surveys in Table 2.2 and 2.3, respectively. In the full and year-specific visual and acoustic models, a subsample of the survey data collected was not used in the analysis due to the lack of available oceanographic covariates for those regions in which surveys were conducted (e.g. northern Loch Linnhe, the inner Loch Sunart and inside some of the sea lochs in the study area). However, the vast majority of the study area was covered and a suite of covariates was consistently sampled throughout the study period. Harbour porpoise sighting rates are heavily impacted by sea states (Palka 1996) and so only survey effort conducted in sea states from 0 (optimal, calm conditions) to 3 (small waves, cresting)

were included in the visual analysis. Survey effort conducted in sea states of 0 to 6 was used in the acoustic analysis because there is no evidence to indicate that acoustic surveys are impacted by sea state.

Over the course of the study period, there was a general increase in the range of the variables surveyed as the geographic extent of the surveys increased (Table 2.2 and 2.2 show data for Chapter 3 and Appendices A.1 – A.6 show covariates data used in Chapter 4 and 5). As surveys spread from the initial core area in 2006 - 2008, deeper waters and more offshore regions were surveyed leading to increases in maximum depth and distance from land. The maxima for depth, slope, current speed and distance from land all varied among years, but the mean and standard deviations remained relatively constant indicating that these outliers did not markedly impact the centre or spread of the covariate dataset.

The west coast of Scotland consists of complex coastline and is a topographically variable environment (Figure 2.4 a-f). There is a marked variation in bottom topography between the north and south of the study region. The majority of the southern ‘core’ (2003 – 2004) study area is < 100 m in depth, but the bottom topography varies considerably with deep channels present in the northeast Firth of Lorn, Sound of Jura and south of Islay (Figure 2.4 a & b). In the northern part of the region, there is little water <50 m deep and there are a number of banks and islands rising sharply out of deeper water leading to regions with steep slopes. In coastal waters, in particular, depth is variable with a number of steeply sloped submarine canyons and banks. Further offshore, depth generally increases as a function of distance from land and slopes are shallower.

Tidal range also varies throughout the study region, most areas have ranges of >3 metres (Figure 2.4 c). The notable exception is the Sound of Jura in the south of the region where Spring Tidal Range (STR) drops to less than 2 metres – the result of two water masses (Irish Sea and Atlantic flow) being 180° out of phase and converging in the region (Simpson et al. 1979). Maximum tidal ranges were observed around the Isle of Skye: in the Little Minch and Minch. The dominant sediment type varies across the Inner Hebrides (Figure 2.4 d-f). In coastal regions, most sediment is composed of a high-percentage mud and sand, although gravel is most common off the west coast of Islay, southwest of Coll and Tiree and the north limits of the study region. Sand and some gravelly regions dominate sediment to the west of the Outer Hebrides. The resolution of sediment data varies across the study site. In some regions, (e.g. the Firth of Lorn, Little Minch and the Minch) high-resolution, fine scale data were available but in others, (e.g. Sound of Jura) only coarse-resolution data were available. This is due to the data

used to compile the sediment datasets being compiled from different surveys collecting at different resolutions.

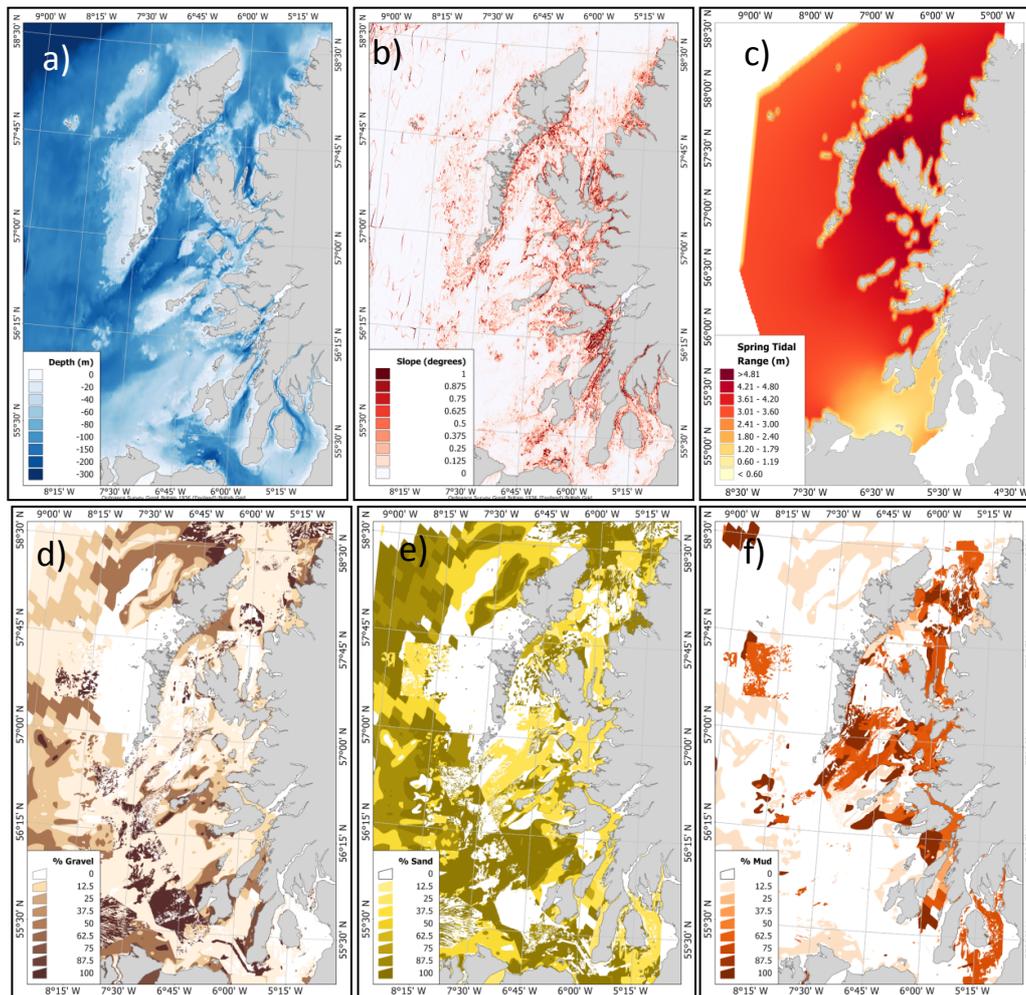


Figure 2.4 – Distribution of covariates used in models on the west coast of Scotland (units shown in parentheses) – from top left to bottom right: (a) Depth (m); (b) Slope ($^{\circ}$); (c) Maximum Spring Tidal Range (m); (d) Percentage Gravel; (e) Percentage Sand; (f) Percentage Mud.

Some studies have investigated the extent to which covariate ranges and means varied significantly within the temporal unit of interest (e.g. comparing among years)(Embling 2007; Heinrich 2006). While there is some variation in the ranges in this study, this is not investigated further here, as the precision of model parameters encompasses any differences in the covariates on which the models are built, and no bias should result.

Table 2.2 - Summary statistics for covariates retained in the best models for the six years of visual surveys from 2003 - 2008.

		2003	2004	2005	2006	2007	2008
Survey Effort (km)		3310.63	2732.21	3003.74	7042.84	7987.15	10384.49
No. Segments		1656	1367	1502	3522	3994	5193
Number of Segments with Sightings		83	77	115	167	270	302
Percentage of Segments with Sightings		5%	5.6%	7.7%	4.7%	6.7%	5.8%
Sea State	<i>Range</i>	0 - 3	0 - 3	0 - 3	0 - 3	0 - 3	0 - 3
(Beaufort Scale)	<i>Median (IQR)</i>	2 (1 - 2)	2 (1 - 2)	2 (2 - 2)	1.5 (1 - 2)	2 (1.5 - 2)	2 (1.5 - 3)
Boat Speed (knots)	<i>Range (knots)</i>	0.3 - 10.6	0.6 - 10.7	0.73 - 11.1	1.2 - 11.1	2.4 - 10.8	1.2 - 12.0
	<i>mean (standard deviation)</i>	6.3 (1.3)	6.4 (1.3)	6.5 (1.1)	6.0 (1.0)	6.3 (0.7)	5.9 (0.9)
Time from Sunrise	<i>Range</i>	0.04 - 0.95	0.10 - 0.92	0.11 - 0.95	0.001 - 0.94	0.06 - 0.94	0.09 - 0.95
	<i>Median (IQR)</i>	0.44 (0.29 - 0.61)	0.51 (0.35 - 0.66)	0.50 (0.35 - 0.63)	0.54 (0.40 - 0.67)	0.53 (0.39 - 0.65)	0.51 (0.37 - 0.65)
Position Relative to Tidal Range	<i>Range</i>	0.06 - 1.0	0.10 - 1.0	0.10 - 1.0	0.09 - 1.0	0.08 - 1.0	0.09 - 1.0
	<i>Median (IQR)</i>	0.47 (0.29 - 0.78)	0.50 (0.39 - 0.68)	0.48 (0.49 - 0.82)	0.54 (0.38 - 0.80)	0.50 (0.33 - 0.79)	0.50 (0.34 - 0.81)
Position in Daily Tidal Cycle	<i>Range</i>	0 - 1.0	0 - 1.0	0 - 1.0	0 - 1.0	0 - 1.0	0 - 1.0
	<i>Median (IQR)</i>	0.49 (0.29 - 0.82)	0.54 (0.36 - 0.74)	0.55 (0.33 - 0.65)	0.44 (0.30 - 0.65)	0.49 (0.32 - 0.65)	0.51 (0.34 - 0.69)
Spring Tidal Range (metres)	<i>Range</i>	0.92 - 5.08	0.99 - 5.16	0.91 - 5.60	0.77 - 5.77	0.85 - 5.49	0.96 - 5.02
	<i>mean (standard deviation)</i>	3.20 (1.24)	3.41 (1.09)	3.60 (1.35)	3.83 (1.13)	3.92 (1.04)	3.99 (0.97)
Depth (metres)	<i>Range</i>	10 - 197	10 - 203	10 - 200	10 - 232	10 - 278	10 - 283
	<i>mean (standard deviation)</i>	52.5 (32.5)	53.5 (32.6)	52.5 (34.8)	54.1 (36.4)	61.64 (36.5)	66.55 (40.0)
Slope (degrees)	<i>Range</i>	0 - 12.2	0 - 18.3	0 - 12.6	0 - 20.2	0 - 14.6	0 - 18.8
	<i>mean (standard deviation)</i>	1.43 (1.70)	1.71 (2.12)	1.62 (1.72)	1.94 (2.14)	1.80 (1.86)	1.93 (1.95)
Current Speed (m/s)	<i>Range</i>	0 - 2.0	0 - 1.34	0 - 1.70	0 - 2.79	0 - 1.96	0 - 2.16
	<i>mean (standard deviation)</i>	0.26 (0.23)	0.22 (0.18)	0.23 (0.19)	0.19 (0.18)	0.19 (0.16)	0.19 (0.16)
Distance from Land (km)	<i>Range</i>	<1 - 32.8	<1 - 30.4	<1 - 28.7	<1 - 68.6	<1 - 61.4	<1 - 68.6
	<i>mean (standard deviation)</i>	5.7 (6.2)	4.6 (5.3)	3.7 (4.2)	4.5 (8.7)	4.2 (5.0)	4.0 (5.0)
Percentage Gravel (%)	<i>Range</i>	0 - 100	0 - 100	0 - 100	0 - 100	0 - 100	0 - 100
	<i>Median (IQR)</i>	5 (5 - 55)	5 (5 - 33)	5 (5 - 55)	5 (2 - 18)	5 (2 - 18)	5 (2 - 18)
Percentage Sand (%)	<i>Range</i>	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95
	<i>Median (IQR)</i>	40 (20 - 90)	35 (14 - 84)	35 (20 - 70)	35 (20 - 84)	30 (20 - 84)	30 (14 - 40)
Percentage Mud (%)	<i>Range</i>	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95
	<i>Median (IQR)</i>	0 (0 - 62)	4 (0 - 62)	4 (0 - 65)	4 (0 - 65)	4 (0 - 65)	33 (0 - 65)

Table 2.3 - Summary statistics for model covariates retained in models from five years of acoustic surveys from 2004 - 2008.

		2003	2004	2005	2006	2007	2008
Survey Effort (km)		--	6154.80	2995.78	9148.89	13390.41	10962.86
No. Segments		--	3104	1498	4575	6696	5482
Number of Segments with Acoustic Detections		--	284	124	783	1296	880
Percentage of Segments with Acoustic Detections		--	9.1%	8.2%	17.1%	19.4%	16.1%
Sea State (Beaufort Scale)	<i>Range</i>	--	0 - 6	0 - 2	0 - 6	0 - 6	0 - 6
	<i>Median (IQR)</i>	--	3.0 (2-3.5)	2 (2 - 2)	2 (1.5 - 3.0)	2.5 (2 - 3.5)	2.0 (2 - 3)
Boat Speed (knots)	<i>Range (knots)</i>	--	0.9 - 11.8	0.7 - 11.1	1.3 - 11.1	2.8 - 10.5	1.2 - 11.0
	<i>mean (standard deviation)</i>	--	6.29 (1.32)	6.5 (1.06)	6.0 (0.98)	6.3 (0.72)	5.9 (0.84)
Time from Sunrise	<i>Range</i>	--	0.1 - 0.96	0.11 - 0.94	0.004 - 0.94	0.04 - 0.94	0.04 - 0.94
	<i>Median (IQR)</i>	--	0.51 (0.37 - 0.63)	0.49 (0.34 - 0.62)	0.54 (0.41 - 0.66)	0.51 (0.39 - 0.63)	0.52 (0.39 - 0.64)
Position Relative to Tidal Range	<i>Range</i>	--	0.05 - 1.0	0.11 - 1.0	0.11 - 1.0	0.04 - 1.0	0.08 - 1.0
	<i>Median (IQR)</i>	--	0.47 (0.33 - 0.78)	0.48 (0.29 - 0.78)	0.51 (0.28 - 0.76)	0.50 (0.31 - 0.73)	0.50 (0.32 - 0.76)
Position in Daily Tidal Cycle	<i>Range</i>	--	0 - 1.0	0 - 1.0	0 - 1.0	0 - 1.0	0 - 1.0
	<i>Median (IQR)</i>	--	0.56 (0.33 - 0.70)	0.49 (0.3 - 0.64)	0.46 (0.35 - 0.65)	0.50 (0.32 - 0.66)	0.49 (0.37 - 0.67)
Spring Tidal Range (metres)	<i>Range</i>	--	0.99 - 5.16	0.91 - 5.6	0.77 - 5.77	0.85 - 5.49	1.05 - 5.02
	<i>mean (standard deviation)</i>	--	3.31 (1.18)	3.6 (1.35)	3.93 (1.19)	3.95 (1.13)	3.99 (0.97)
Depth (metres)	<i>Range</i>	--	10 - 204	10 - 200	10 - 231	10 - 274	10 - 249
	<i>mean (standard deviation)</i>	--	57.2 (33.1)	52.5 (34.9)	56.65 (34.5)	64.1 (37.5)	68.1 (38.0)
Slope (degrees)	<i>Range</i>	--	0 - 17.2	0 - 12.6	0 - 20.1	0 - 22.9	0 - 16.3
	<i>mean (standard deviation)</i>	--	1.65 (1.96)	1.61 (1.73)	1.98 (2.13)	1.81 (1.94)	1.79 (1.82)
Current Speed (m/s)	<i>Range</i>	--	0 - 1.33	0 - 2.41	0.002 - 1.79	0 - 1.92	0 - 2.12
	<i>mean (standard deviation)</i>	--	0.23 (0.14)	0.24 (0.24)	0.20 (0.13)	0.19 (0.12 - 0.25)	0.20 (0.14)
Distance from Land (km)	<i>Range</i>	--	<1 - 31.4	<1 - 25.5	<1 - 59.5	<1 - 32.0	<1 - 57.8
	<i>mean (standard deviation)</i>	--	5.1 (5.4)	3.6 (4.0)	4.1 (6.4)	4.2 (4.8)	4.3 (4.6)
Percentage Gravel (%)	<i>Range</i>	--	0 - 100	0 - 100	0 - 100	0 - 100	0 - 100
	<i>Median (IQR)</i>	--	5 (5 - 33)	5 (5 - 55)	5 (5-18)	5 (5 - 18)	5 (5 - 18)
Percentage Sand (%)	<i>Range</i>	--	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95
	<i>Median (IQR)</i>	--	35 (20 - 84)	35 (20 - 70)	33 (20 - 84)	30 (20 - 84)	30 (0 - 70)
Percentage Mud (%)	<i>Range</i>	--	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95
	<i>Median (IQR)</i>	--	4 (0 - 62)	4 (0 - 65)	8 (0 - 65)	32 (0 - 65)	33 (0 - 65)

2.4.2 Survey Raw Data

2.4.2.1 Summary of Survey Characteristics – Chapter 3

In Chapter 3, the distribution and habitat preferences of harbour porpoises over 2003 – 2008 are investigated. A total of 38,710 segments were included in this analysis (visual: 17,354; acoustic: 21,356), corresponding to 34,461 km of visual survey effort from 2003-2008 (in Beaufort sea state ≤ 3) and 42,653 km of acoustic survey effort 2004-2008 (in all sea states). Both visual and acoustic survey effort varied among study years ranging from 2,732 – 10,385 km and 2,996 – 13,390 km respectively. In 2003 and 2004, survey effort was concentrated in a core area in the south of the study region. As project funding increased, survey effort increased and generally extended north and west in 2005 – 2008. Full details are shown below (Table 2.4 & Figure 2.5 a & b and Figure 2.6 a – k). On visual surveys 2003 – 2008, 2,381 harbour porpoises were detected visually in favourable sighting conditions (Beaufort sea states ≤ 3), (0.069 animals per km). Detection rates varied considerably between 0.047 – 0.126 animals per km among years. On acoustic surveys 2004-2008, in sea states ≤ 6 , 4,927 acoustic detections were made (0.116 detections per km). In general, porpoise detections were generally most common in regions close to shore (Figure 2.5 a & b 2.6 a – k).

Table 2.4 – Survey effort, detections and detection rates for visual and acoustic line transect surveys in favourable conditions (visual: sea states 0 - 3; acoustic: sea state 0 -6) from 2003-2008. Detections rates are in animals detected per kilometre (km).

Year	Visual			Acoustic		
	Survey Effort (km)	Sightings	Detection Rate	Survey Effort (km)	Detections	Detection Rate
2003	3310.6	220	0.066	N.A.	N.A.	N.A.
2004	2732.2	149	0.055	6154.8	517	0.084
2005	3003.7	379	0.126	2995.7	456	0.152
2006	7042.8	333	0.047	9148.8	1113	0.122
2007	7987.1	674	0.084	13390.4	1747	0.130
2008	10384.4	626	0.060	10962.8	1094	0.100
Total	34461.0	2381	0.069	42652.7	4927	0.116

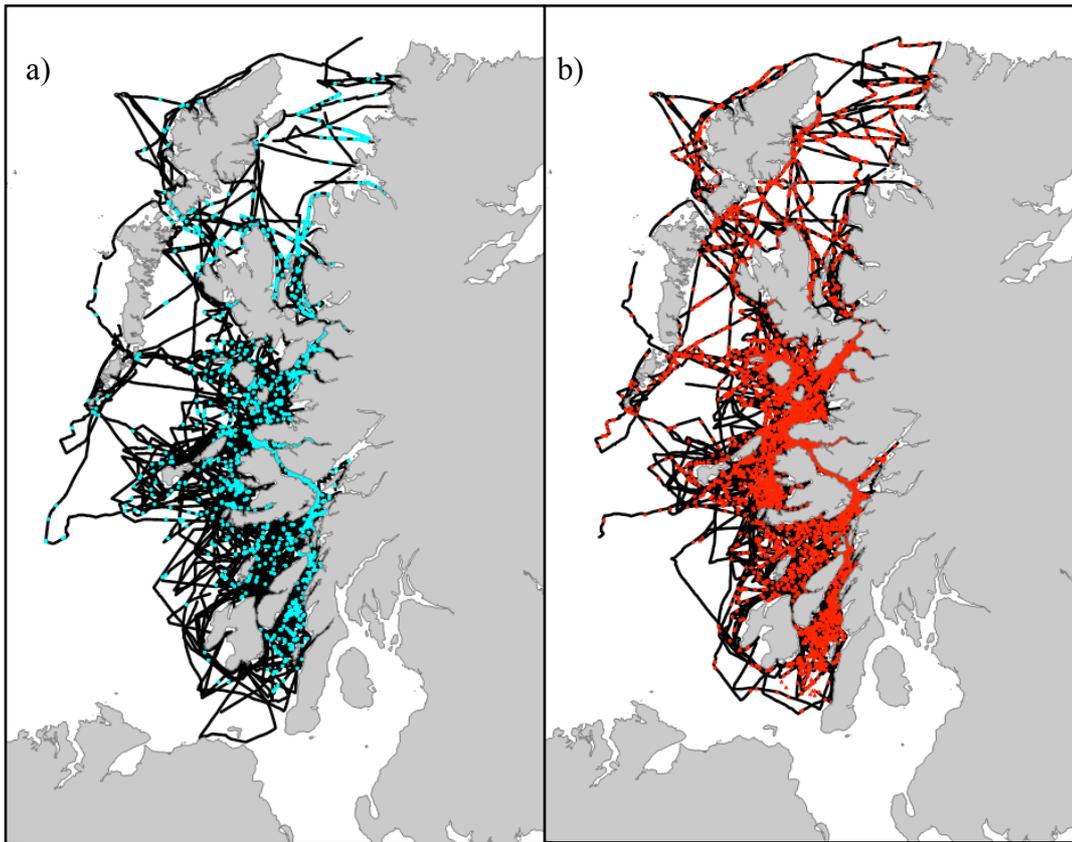


Figure 2.5 a & b - Survey effort tracklines and 2 km segments with detections from visual surveys (2003 – 2008) and acoustic surveys (2004 – 2008). Visual detections are shown in light blue and acoustic detections in red.

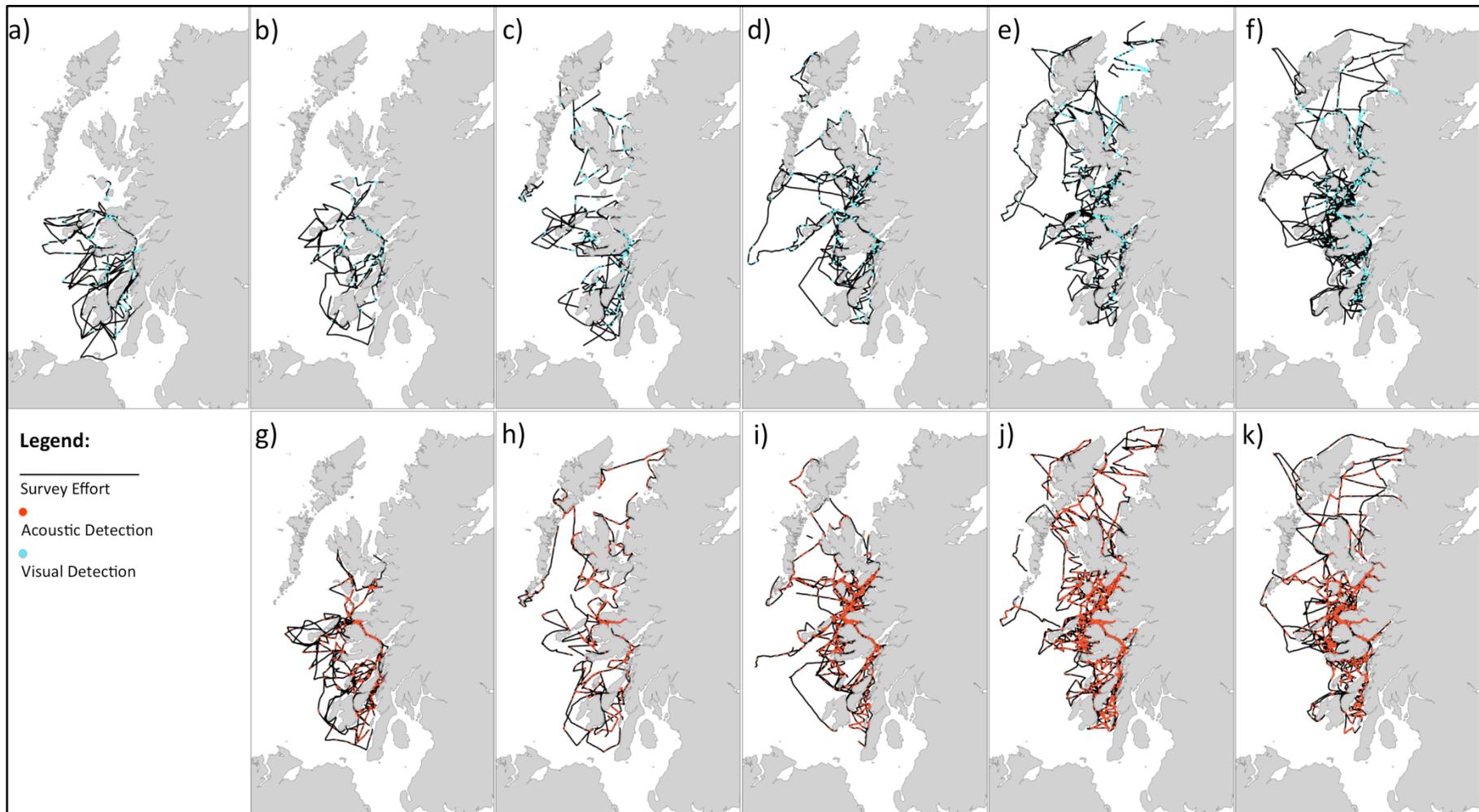


Figure 2.6 a - k - Survey effort track-lines and 2 km segments with detections for acoustic surveys in 2004 - 2008 (a - e) and sightings for visual surveys in 2003 - 2008 (f - k). Legend is shown in top left of figure.

2.4.2.2 *Summary of Survey Characteristics – Chapter 4*

In Chapter 4, intra-annual variations in harbour porpoise distribution and habitat preferences are investigated. Survey effort and detections data collected over six years were pooled and then temporally segregated into months, from April to September, and grouped into early and late ‘seasonal’ arrangements of April – June and July – September. Survey effort varied among months, from 3,167 km in April to 8,123 km in July for visual surveys and between 4,240 km in April and a high of 11,412 km in August for acoustic surveys (full details are shown in Table 2.5). This variation was mostly driven by survey conditions. In April, May and September, weather and sea conditions were generally poorer meaning there were fewer days available to survey. In June, July and August, survey and general weather conditions were better and days were longer allowing for more survey effort to be conducted. Also, as weather conditions became more stable in the summer months, it made more exposed and remote regions, such as the Outer Hebrides and Minch available to be surveyed (Figure 2.7 a – l). On visual surveys between April and September, detection rates varied with 0.027 – 0.117 animals per km being sighted in favourable conditions (Beaufort sea state ≤ 3) with the lowest detection rates in April and highest detection rates occurring in August. Similarly, on acoustic surveys between April and September, in sea states ≤ 6 , detection rates varied between 0.086 and 0.145 acoustic detections per km with a peak in August.

As part of this analysis, to investigate shifts in distribution and/or habitat preferences at a slightly more coarse temporal resolution, monthly data were also grouped into seasonal groupings of April – June and July – September. These monthly groupings are henceforth discussed as ‘S1’ and ‘S2’ respectively. Survey effort varied between these groupings with more effort being conducted in S2 (visual: 21,181 km; acoustic: 26,280 km) than in S1 (visual: 13,279 km; acoustic: 16,364 km) (Table 2.5). As discussed above, the spatial extent of the survey region expanded as the survey season went on. Consequently, some regions (e.g. the northern Outer Hebrides and The Minch) were not surveyed in S1 but were in S2 (Figure 2.7 and 2.8). Visual detection rates were three times higher in S2 than in S1, with considerably more porpoises detected later in the season with 0.032 animals sighted per km in S1 and 0.092 animals sighted per km in S2. Acoustic detection rates were different between S1 and S2 though not as big a difference was observed as in the visual data. In S1, 0.105 animals / km were detected while in S2, 0.122 animals per km were detected.

Table 2.5 - Survey effort, detections and detection rates for visual and acoustic line transect surveys in favourable conditions (visual: sea states 0 - 3; acoustic: sea state 0 - 6) from April-September and in 'S1': April - June and 'S2': July - September. Detections rates are in animals detected per kilometre (km).

Year	Visual			Acoustic		
	Survey Effort (km)	Sightings	Detection Rate	Survey Effort (km)	Detections	Detection Rate
April	3167.8	86	0.027	4240.1	363	0.086
May	4229.8	151	0.036	5135.1	580	0.113
June	5878.3	188	0.032	6889.4	754	0.109
July	8123.9	610	0.075	8438.1	815	0.097
August	8046.5	942	0.117	11412.9	1655	0.145
September	4994.5	402	0.080	6437.0	732	0.114
S1	13279.9	425	0.032	16364.8	1725	0.105
S2	21181.2	1956	0.092	26280.0	3195	0.122

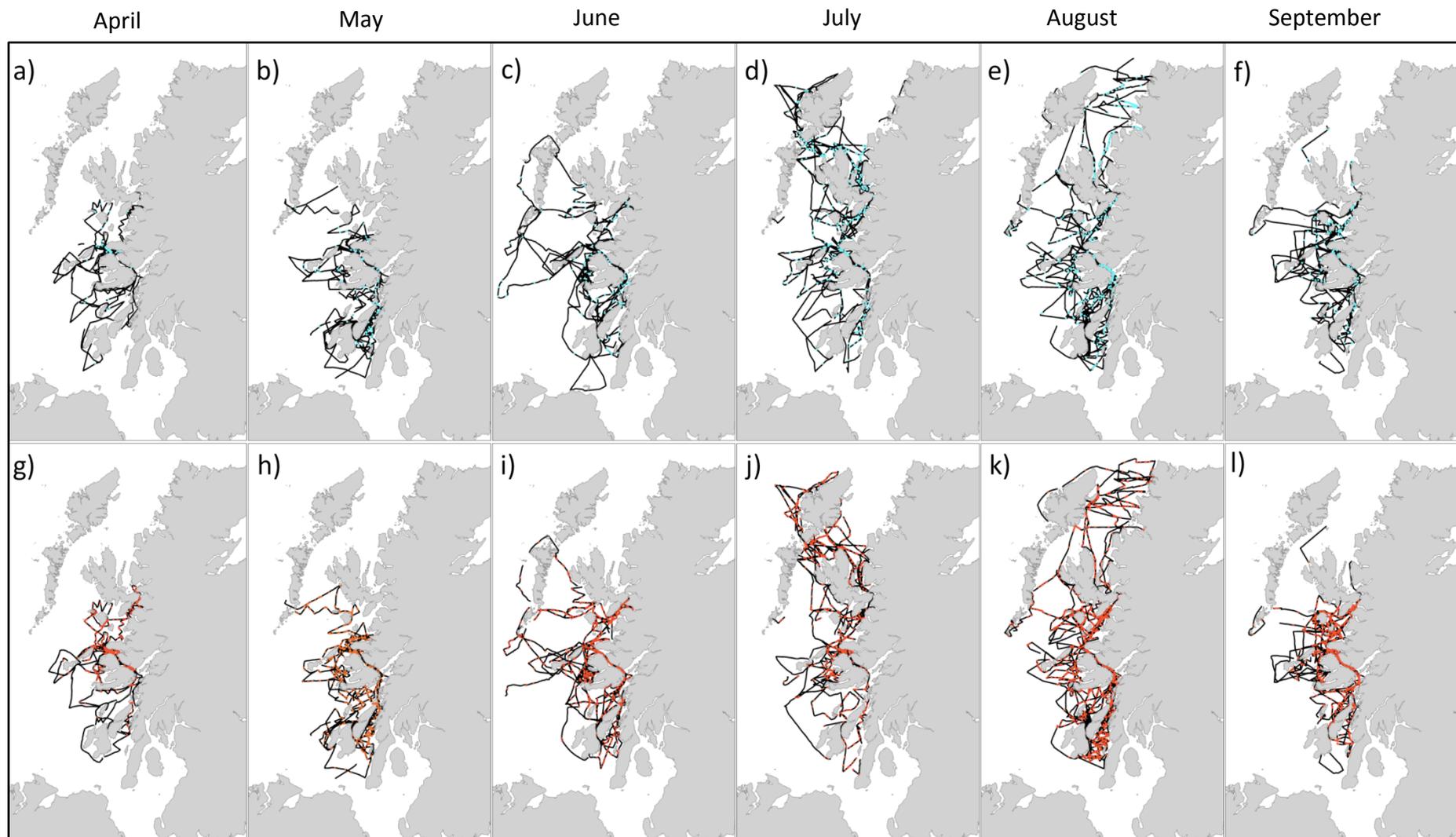


Figure 2.7 - Survey effort tracklines and 2 km segments with detections in April – September for visual (a – f) and acoustic (g – l) surveys. Visual detections are shown in blue, acoustic detections are shown in red.

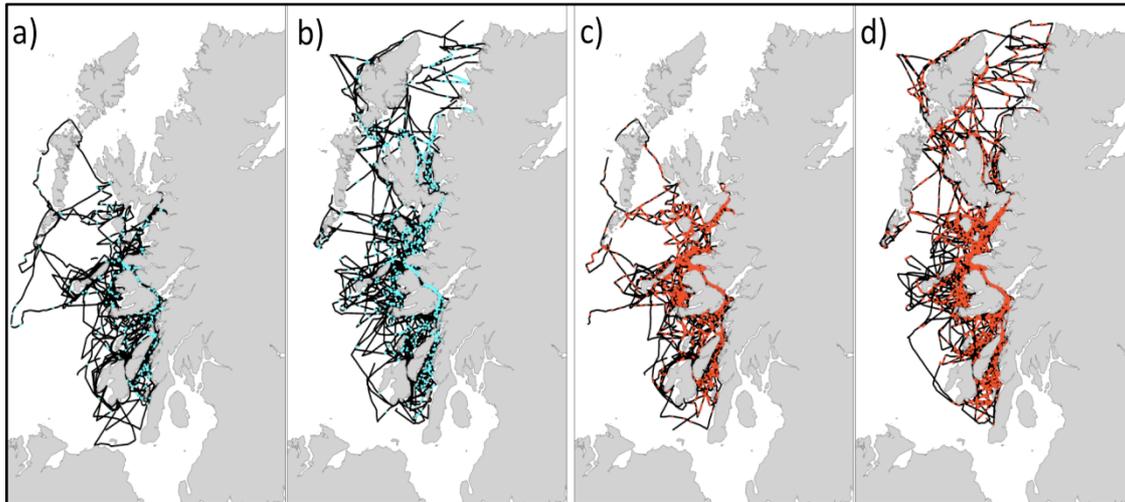


Figure 2.8 a – d - Survey effort tracklines and 2 km segments with detections in seasonal groupings: a) Visual: April – June (S1); b) July – September (S2); c) Acoustic: April – June (S1); d) July – September (S2). Segments with acoustic detections are shown in red and sightings are shown in light blue.

2.4.2.3 Summary of Survey Characteristics – Chapter 5

In Chapter 5, harbour porpoise habitat preferences were studied at finer spatial scales, to investigate whether there were spatially distinct patterns of habitat usage and whether model results changed when modelling smaller sub-regions rather than the entire study area all at once. To do this, the study region and the effort/detection data were broken down into a number of smaller sub-regions, which were each modelled separately. Eight sub-regions were selected based on the size of the areas and the distinct, static oceanographic features in the region (Figure 2.9). The survey effort varied considerably among sub-regions and not all sub-regions were visited every year or month of the survey seasons (Appendix A.5 & A.6). Due to low numbers of visual and acoustic detections in the Atlantic region and low numbers of sightings in the Sea of Hebrides, it was not possible to construct models using these datasets. Survey effort was lowest in the Atlantic region, west of the Outer Hebrides (visual: 1,386 km; acoustic: 1,436 km) and highest in the West of Mull sub-region (visual: 7,366 km; acoustic 9,007 km)(Table 2.6). Detection rates of harbour porpoises also varied considerably among sub-regions. Both visual and acoustic detection rates were lowest in the Atlantic sub-region with 0.019 and 0.058 animals per km respectively and almost all detections were made in the northern extent of that region (Figures 2.10 a – h and 2.11 a- h). Both visual and acoustic detection rates were generally high in the Minch, the Small Isles, the Sound of Mull and the Sound of Jura sub-regions (Table 2.6).

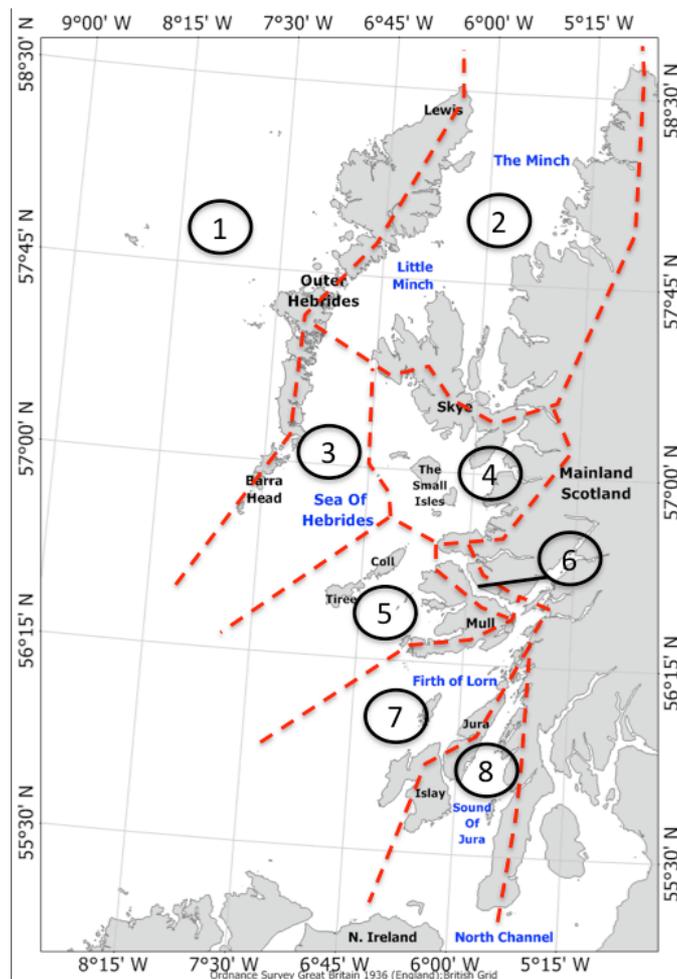


Figure 2.9 - shows the breakdown of the study area into eight sub-regions to be modelled separately. 1) Atlantic; 2) The Minch; 3) Sea of Hebrides; 4) The Small Isles; 5) West of Mull; 6) Sound of Mull; 7) Firth of Lorn; 8) Sound of Jura. The red dashed line shows the delineation lines separating sub-regions.

Table 2.6 - Survey effort, detections and detection rates for visual and acoustic line transect surveys in favourable conditions (visual: sea states 0 - 3; acoustic: sea state 0 - 6) made in each survey model region. Detections rates are in animals detected per kilometre (km).

Model Region	Visual			Acoustic		
	Survey Effort (km)	Sightings	Detection Rate	Survey Effort (km)	Detections	Detection Rate
The Minch	3963.7	572	0.144	5482.1	596	0.109
Sea of Hebrides	--	--	--	2460.7	197	0.080
Small Isles	6042.3	419	0.069	8020.6	1303	0.162
West of Mull	7366.7	326	0.044	9007.8	782	0.087
Sound of Mull	2616.3	319	0.122	3399.4	518	0.152
Firth of Lorn	6888.3	339	0.049	7726.6	732	0.095
Sound of Jura	3983.9	262	0.066	5093.0	715	0.140

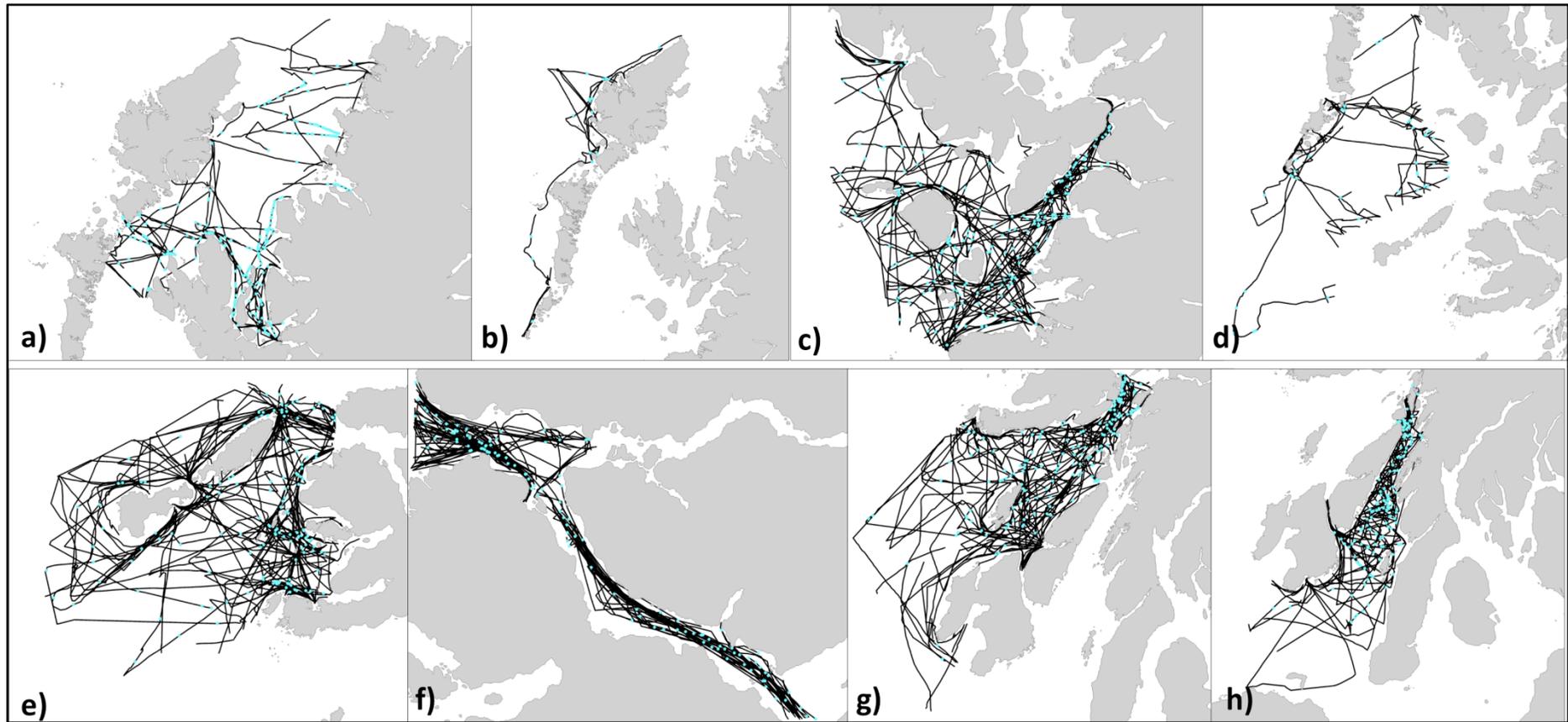


Figure 2.10 - Survey effort tracklines and 2 km segments with sightings for visual surveys made in each model region: a) The Minch; b) The Atlantic; c) The Small Isles; d) The Sea of Hebrides; e) West of Mull; f) The Sound of Mull; g) The Firth of Lorn; h) The Sound of Jura. Segments with sightings are shown in light blue.

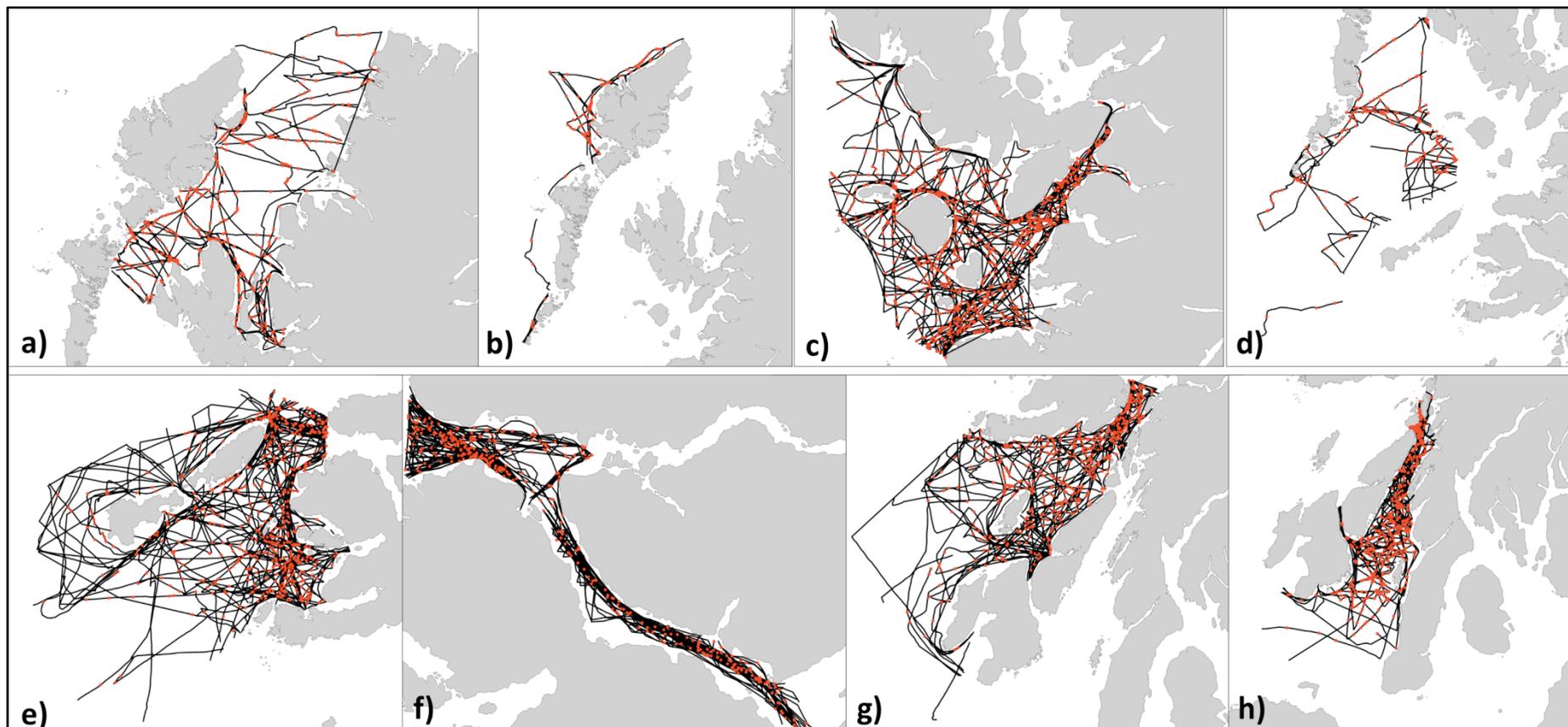


Figure 2.11 - Survey effort tracklines and 2 km segments with detection for acoustic surveys made in each model region: a) The Minch; b) The Atlantic; c) The Small Isles; d) The Sea of Hebrides; e) West of Mull; f) The Sound of Mull; g) The Firth of Lorn; h) The Sound of Jura. Segments with acoustic detections are shown in red.

2.4.3 Modelling Details

2.4.3.1 Assessing Multicollinearity

Multicollinearity between model covariates was investigated using ‘Generalised Variance Inflation Factors’ (GVIF) which measure the impact of collinearity on the standard errors of the model estimates. Multicollinearity was assessed in the full dataset (Table 2.7). GVIF and $\text{GVIF}^{(1/2df)}$ values indicated that none of the variables were sufficiently strongly predicted by one another to impact the model standard errors. It is noteworthy but unsurprising that percentage gravel, sand and mud in the sediment had large GVIF values because these are percentages (e.g. a data point with 60% sand can only have a maximum of 40% of other sediment types). $\text{GVIF}^{(1/2df)}$ is more appropriate for non-orthogonal data and these values were < 5 for the sediment covariates, indicating they do not impact the standard errors of model estimates.

Table 2.7 – GVIF score assessing collinearity in model covariate data. A threshold of 10 (equating to $R^2 = 0.9$) was used, below which collinearity was deemed acceptable.

Covariate	Acoustic	Visual	Collinearity Metric
Year	1.91	2.70	GVIF
Month	2.79	2.52	GVIF
Boat Speed	1.63	1.62	GVIF
Speed Variations	3.63	3.72	GVIF
Sea State	1.31	1.40	GVIF
Time Of Day	1.29	1.64	GVIF
Distance to Land	2.06	2.30	GVIF
Maximum Tidal Range	4.14	4.78	GVIF
Position Relative to Tidal Range	1.76	2.00	GVIF
Position in Daily Tidal Cycle	1.39	1.47	GVIF
Percentage Gravel	2.03	1.99	$\text{GVIF}^{(1/2*df)}$
Percentage Sand	2.42	2.40	$\text{GVIF}^{(1/2*df)}$
Percentage Mud	2.62	2.52	$\text{GVIF}^{(1/2*df)}$
Slope	1.81	2.03	GVIF
Depth	2.06	2.12	GVIF
Current Speed	2.00	1.76	GVIF
DC Noise 2004	2.49	2.32	GVIF
DC Noise 2005	3.65	3.89	GVIF
Porpoise Band 2007	4.76	4.30	GVIF
Porpoise Band 2008	4.95	4.38	GVIF
Control Band 2007	4.66	4.10	GVIF
Control Band 2008	2.96	3.01	GVIF

2.4.3.2 Determining GEE ‘panel’ size

When using a GEE model construct, it is necessary to specify ‘panels’ in the model data to help accommodate temporal and spatial autocorrelation. Residual autocorrelation was investigated using autocorrelation function (ACF) plots to determine a suitable ‘panel’ size for each of the models. For the full visual and acoustic models in Chapters 3 and 4 a panel size of 10 segments (equal to 20 km survey track-line) was determined to be suitable for dealing with the autocorrelation within the data. Therefore, errors within 20 km effort groupings were permitted to be correlated and errors between 20 km effort groups were assumed to be independent. In Chapter 5, a panel size of 5 segments (equal to 10 km survey effort) was deemed suitable. In assessing models from Chapters 3 additional models were constructed with larger panel sizes (20 segments; 40 km effort) than determined via ACF plots. In this analysis, we found that both sets of models, the larger panel sizes had no impact on model selection results. Consequently, we can be confident that the panel sizes used in the models were suitable.

2.4.3.3 Assessing the ‘relative importance’ of covariates

In the modelling process, it is possible for covariates to be retained at the end of the model selection – not because they are biologically important in explaining harbour porpoise distribution, but instead because they soak up some of the remaining variability and ‘improve’ the model. While the model selection process used here (outlined in §2.3.2) is considered robust to such an issue, it is still possible that the same covariate could be retained for this reason. Consequently the ‘relative importance’ of covariates in each of the final models was assessed using a marginal R^2 metric to rank the covariates in order of importance.

The marginal R^2 is a simple extension of the R^2 metric, introduced by Zheng (2000) to be used with GEE models. Marginal R^2 can be interpreted as “the amount of variance in the response that is explained by the fitted model” (Hardin and Hilbe 2002) and here was calculated as (from Ballinger 2004):

$$mR^2 = 1 - \frac{\sum_{t=1}^T \sum_{i=1}^n (Y_{it} - \hat{Y}_{it})^2}{\sum_{t=1}^T \sum_{i=1}^n (Y_{it} - \bar{Y}_{it})^2}$$

Where \bar{Y}_{it} is the marginal mean across all datapoints.

The marginal R^2 (henceforth mR^2) was calculated for the final models (the full model) and a reduced model was created to investigate the effect of each term - i.e. similar to the final model, but with one covariate removed (a series of reduced models). The difference in mR^2 between the each full and reduced model was calculated and converted to a percentage. Covariates were then ranked according to the size of the percentage reduction – i.e. the largest percentage reduction in mR^2 was ranked as first and the smallest reduction in mR^2 was ranked as last. The percentage reduction values for the mR^2 for each covariate and model are shown in Appendix A.7 - A.10. An index was created to assess whether covariates were consistently retained late in the model selection process – and thus potentially less indicative of biological patterns. To adjust for the differing number of covariates in each final model, the ranks were divided by the total number of covariates in the model, providing an index value for each covariate in each model. Values close to 0 were indicative of being selected late in the model selection process and values close to 1 were representative of being retained early on in the process. The results of the marginal R^2 are discussed in the context of all the models in Chapter 7 (§7.1.2.2).

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Chapter 3

Inter-annual variation in habitat preference and distribution of harbour porpoises west of Scotland

3.0 Abstract

The harbour porpoise (*Phocoena phocoena*) is the most common cetacean species off the west coast of Scotland. It is listed under Annex II of the EU Habitats Directive, indicating a requirement to specify areas to be Special Areas of Conservation (SACs) for the species. Identifying areas that are consistently important for highly mobile species such as the harbour porpoise is challenging. The goal of this analysis was to determine key regions and habitat preference for harbour porpoise off the west coast of Scotland, and to determine the extent to which these patterns of distribution were consistent among years. Designed line-transect visual and towed-array acoustic surveys were conducted between 2003 – 2008 and 2004 – 2008, respectively, from the Hebridean Whale and Dolphin Trust (HWDT) survey vessel *Silurian*. Generalised Estimating Equations (GEEs) were used to determine relationships between the relative density of harbour porpoises and temporally and spatially variable environmental and oceanographic covariates. Visual and acoustic datasets were modelled separately to account for the different survey biases in the data collection methods. The best models for the ‘full’ (all years together) datasets for both visual and acoustic datasets retained depth, slope, distance to land and spring tidal range. Year and month were also included in both models indicating that there are significant temporal variations in harbour porpoise habitat preference. Survey variables were also retained in the best models indicating that survey conditions impacted the detection of animals. Spatial predictions using the full models indicated a strongly coastal distribution for the species. To further investigate the impact of year on the models, individual models were built for each year independently. Results showed that a consistent suite of covariates was included – month, and depth and/or slope were most consistent, although distance to land and spring tidal range were also commonly selected. In general, the coastal distribution observed in the full models was present in the yearly models. The notable exception was in 2005, when porpoise distribution appears to have changed to a slightly more offshore distribution. Also the Sound of Jura appeared to become increasingly important as the study went on, with the highest predicted

densities being found there, especially in 2006 – 2008. This is investigated in greater details in later chapters. These results are considered for the purpose of identifying important areas that could be suitable for designation as SACs.

3.1 Introduction

Annex II of the European Union (EU) Habitats Directive lists species of European Community interest, which are afforded the designation of Special Areas of Conservation (SACs). An SAC is defined as a “*site of Community importance where necessary measures are applied to maintain, or restore, to a favourable conservation status, the habitats and/or populations of the species for which the site is designated*” (Council Directive 92/43/EEC).

The designation of protected areas is a widely applied method for conserving a species. However, for highly mobile species like the harbour porpoise, the identification of suitable areas for protection (using the above definition), the implementation of appropriate management strategies and the monitoring of the protected area are very challenging. In fact, this may be one factor contributing to the absence of currently designated areas for protected for this species (Pinn 2009).

A list of candidate SACs was reviewed in 1999 and all proposed sites were deemed insufficient as they failed in clearly identifying an area representing features essential to the species life and reproduction (as specified in Article 4.1)(Evans and Wang 2003; Pinn 2009). An *ad hoc* experts’ meeting in 2007 convened and recommended criteria with which identification of candidate areas would be made easier (EU 2007). They concluded that an area can be considered important for a species if there is:

- 1) Continuous or regular presence of the species (although subject to seasonal variations)
- 2) Good population density (in relation to neighbouring areas)
- 3) A high ratio of young to adults during certain periods of the year

The case for regions of the west coast of Scotland to be candidate SACs has been outlined using the above criteria by Embling et al. (2010). The majority of surveys in this region were conducted in spring, summer and autumn, but sightings of harbour porpoises have been made in every month of the year on the west coast of Scotland (Reid et al. 2003), indicating a year round presence (thus meeting criterion 1). The Inner Hebrides region has one of the highest densities of harbour porpoises in Europe (SCANS-II 2008)(meeting criterion 2) and aerial surveys as part of the SCANS-II program identified the area as having a high porpoise calf:

adult ratio (10% of all sightings made in good/moderate conditions included a calf)(SCANS-II, unpublished). Consequently, the west coast of Scotland would appear to be a strong candidate to investigate at a finer scale for a potential SAC.

The west coast of Scotland is an oceanographically diverse region. It is topographically complex with numerous fjordic sea lochs and deep (>200 m) steep-sided submarine canyons coupled with several islands, inlets and channels providing a wide range of environments and sea conditions (Ellett 1979; Ellett and Edwards 1983; Gillibrand et al. 2003; McKay et al. 1986). Some areas have extreme tidal ranges, generating high current speeds (Gillibrand et al. 2003; Inall et al. 2009). The region is one of the most biologically rich in British waters with a wide range of ecosystems supporting a wide range of top predators and 24 species of cetaceans have been reported here since 1980 (Shrimpton and Parsons 2000). Harbour porpoises are the most common cetacean species, but minke whales (*Balaenoptera acutorostrata*), short-beaked common dolphins (*Delphinus delphis*), white-beaked dolphins (*Lagenorhynchus albirostris*), bottlenose dolphins, (*Tursiops truncatus*), Risso's dolphins (*Grampus griseus*) and killer whales (*Orcinus orca*) are also commonly encountered in the region.

The main threat to harbour porpoise in European waters is by-catch in bottom-set gill nets and tanglenet fisheries (ICES 2009). While some tanglenet fishing occurs on the west coast of Scotland, there is little recorded by-catch (CEC 2002) due to very little gillnet fishing effort occurring there. However, there is also a substantial aquaculture industry in this region and fish farms are considered to be a potential source of significant anthropogenic pollution in the form of the noise disturbance caused by 'seal scarers', (hence forth referred to as CAADs - see §1.4.2). These are loud, underwater devices deployed to deter seals from attacking the fish that are in fish farm cages. However, they are audible to harbour porpoises and other cetacean species and have been shown to cause habitat exclusion in harbour porpoises during studies on both the west and east coasts of Canada (Johnston 2002; Olesiuk et al. 2002). These devices are extensively used on salmon farms on the west coast of Scotland (further details of the sound characteristics due to the devices can be found in §1.4.2) and the potential impacts on harbour porpoises are investigated in Chapter 6.

Other sources of anthropogenic noise in this region are shipping, recreational traffic and naval activities (MMC 2007) – there is some evidence for a correlation between a decrease in harbour porpoise sighting rates and the occurrence of naval activities suggesting these tri-annual activities may be displacing harbour porpoises (Parsons et al. 2000a; Parsons et al. 2000b), though this was not investigated statistically and it is unclear where porpoises were displaced to.

One activity potentially impacting harbour porpoises and other marine life in the future is an increase in the marine renewable energy (MRE) industry. The Scottish Government set a target of 40% of all energy to be generated from renewable sources by 2020 (Scottish_Government 2009). Renewable sources come in the form of wind, tidal, wave sources and there have already been a number of sites west of Scotland could be suitable for marine renewable installations (Scottish_Government 2009). There is potential for interactions between MRE installations and marine mammals (Carter 2007; NERC 2009). Therefore it is important to have an understanding of what areas are important for marine species in order to assess the potential impacts of MRE sites.

Identifying important areas for many species is a challenge. One effective, and increasingly popular, method is the use of spatial habitat models to identify key areas (Bailey and Thompson 2009; Cañadas et al. 2005; Embling et al. 2010; Hooker et al. 1999; Panigada et al. 2008). For practical reasons, protected areas usually have fixed spatial boundaries that are often linked to the important environmental features that explain the distribution of a species (as they are usually measurable proxies for prey distribution). In order to ensure effective conservation and management of a species, it is necessary not only to identify important habitat variables but also to determine how consistent these patterns are over time and space. In particular, the analysis of models built using data collected over several years provides a better understanding of inter-annual variations and trends in relative densities and consequently aids the identification of consistently important regions. The marine environment is complex and dynamic but SACs are small, static features. In order for SACs to be effective, it is essential to identify and designate regions that have consistently high-densities of a species.

The majority of cetacean distribution studies have used boat-based visual surveys as the primary data collection method (Acevedo 1998; Azzellino et al. 2008; Ballance and Pitman 1998; Barlow 1995; Evans and Hammond 2004; Ferguson et al. 2006; Forney and Barlow 1998; Hammond et al. 1995; SCANS-II 2008; Vidal et al. 1997). In the case of species which are small, undemonstrative and difficult to see, such as the harbour porpoise, visual surveys are heavily impacted by sea state, with sightings decreasing dramatically as sea states increase > 1 (Palka 1996). Passive acoustic monitoring (PAM) has been extensively used in surveys for vocally distinct species (i.e. species that can be readily distinguished from others on the basis of their vocalisations), such as the harbour porpoise (Barlow and Taylor 1998; Boisseau et al. 2007; Gillespie et al. 2005; Gordon et al. 2000; Hastie et al. 2003; Leaper et al. 2000; Whitehead 2000). PAM systems have been used to complement visual survey methods (Akamatsu et al.

2001; Barlow and Taylor 1998; Boisseau et al. 2007; CODA 2009; Oleson et al. 2007; SCANS-II 2008; Swartz et al. 2003) but visual and acoustic surveys are subject to very different survey biases and so such datasets need to be analysed separately.

To investigate harbour porpoise distribution and habitat preference, I used a six-year, visual and acoustic line-transect data set to: (i) identify key regions for harbour porpoises on the west coast of Scotland and (ii) investigate inter-annual variations in harbour porpoise distribution and whether that is explained by detectable changes in habitat preference. Both of these aims were be considered as part of a larger goal: to identify consistently important areas for harbour porpoise on the west coast of Scotland which could be designated for designation as marine SACs and to better inform potential future industrial developments in the region.

3.2 Materials and Methods

The methods used in the data collection, processing and modelling stages are described fully in §2.1, §2.2 and §2.3 respectively. Details of raw survey and detection data and how they were processed for this analysis are outlined in §2.4.

3.3 Results

3.3.1 Visual Full Model

To begin investigating whether there are consistent temporal patterns of usage by harbour porpoises on the west coast of Scotland, all years were modelled together in a single model. The best visual model structure and the relationship between predictor variables and the response are shown below (Table 3.1 and Fig 3.1). ‘Year’ and ‘Month’ were modeled as factor variables and both were retained in the best visual model. Sighting rates varied among years with the highest detection rates in 2005. Visual detections generally increased with month from April to August, but then decreased slightly in September. Of the survey variables, sea state and vessel speed were selected in the best model. Sighting rates were highest when surveying in Beaufort sea states of 0 – 1, above which they decreased precipitously. Visual detection rates decreased as vessel speed increased. Topographical covariates seabed depth, distance to land and slope were also retained in the best model. Porpoises were more likely to be seen in waters between 50 – 150 m

Table 3.1 - Model structure matrix showing the retained covariates in the best full (all year) visual and acoustic models. An 'X' is shown if a covariate was retained.

Data	Model	Time		Survey			Sediment			Tidal			Topographic			
		Year	Month	Sea State	Boat Speed	Time of Day	Percentage Gravel	Percentage Sand	Percentage Mud	Position Relative To Tidal Range	Position in Daily Tidal Cycle	Current Speed	Maximum Spring Tidal Range	Depth	Slope	Distance to Land
Visual	Full	X	X	X	X				X				X	X	X	X
Acoustic	Full	X	X		X								X	X	X	X

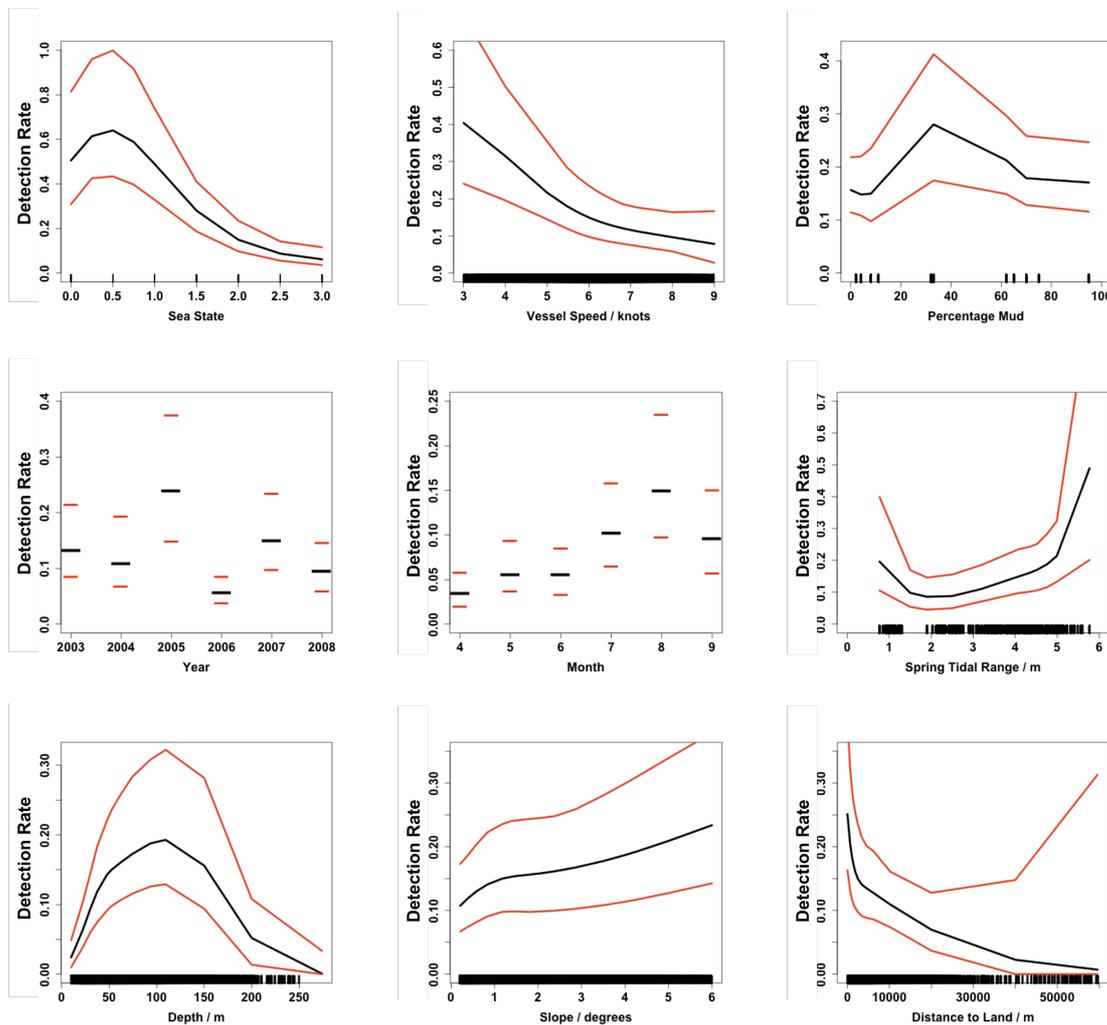


Figure 3.1 - Plots showing the relationships between the predictor variables and harbour porpoise sightings (offset by effort). Black lines show the relationship, with 95% confidence intervals shown by the red lines. Tick marks above the x-axis of each plot show the spread of the explanatory variable data, N.B. The scales on each y-axis vary between plots.

in depth with fewer sightings in water <50 m and >150 m. The sighting rate decreased as distance from land increased with the highest rate made within <1 – 20 km of land. Sighting rates increased with increasing slope and also varied depending on the spring tidal range (STR) encountered. Sighting rates were highest in regions of STR < 2 m and >4 m with highest detection rates in regions with STR of 5 m. Percentage of mud was also found to impact harbour porpoise sighting rates, with the highest rates occurring in \approx 20 - 60 % mud.

The performance of the full visual models was tested using the cross-validation method described in the Methods (§2.3.3), assessing predictive performance over 1,000 iterations, with the output being between 0 and 1. Values of F close to 1 indicate the model is performing well. The best visual model had an F value of 0.722 (95% confidence interval = 0.703 – 0.742) indicating it performed reasonably well but failed to capture all the underlying relationships in the raw data (Table 3.2).

Table 3.2 - Model evaluation (cross-validation) scores for the full model and yearly visual and acoustic models. The 95% confidence intervals for F scores are shown.

Dataset	Visual		Acoustic	
	Cross Validation Score	95 % C.I.	Cross Validation Score	95 % C.I.
Full	0.722	0.703 - 0.742	0.850	0.816 - 0.884
2003	0.167	0.110 - 0.224	N.A.	N.A.
2004	0.301	0.269 - 0.333	0.960	0.954 - 0.958
2005	0.999	0.999 - 0.999	0.980	0.978 - 0.981
2006	0.664	0.616 - 0.711	1.000	0.999 - 1.000
2007	0.508	0.476 - 0.540	1.000	0.999 - 1.000
2008	0.582	0.549 - 0.616	1.000	0.999 - 1.000

The full visual model predicted a strongly inshore distribution for harbour porpoises throughout the west coast of Scotland (Figure 3.2 a). The highest relative densities were predicted in the northern Sound of Jura, northeast Firth of Lorn, within the Sound of Mull, around the Treshnish Isles to the west of Mull and throughout the Small Isles (particularly in the Sound of Sleat). Additionally, there were high-predicted relative densities along the east coast of Outer Hebrides, throughout the Little Minch (between Skye and the Outer Hebrides) and within the more coastal reaches of the Minch. Low relative densities were predicted in the southwest part of the study region and to the west of the Outer Hebrides islands (particularly North and South Uist). There do appear to be some boundary issues in the predicted output, with some high-predicted relative densities apparent at the edge of the study region.

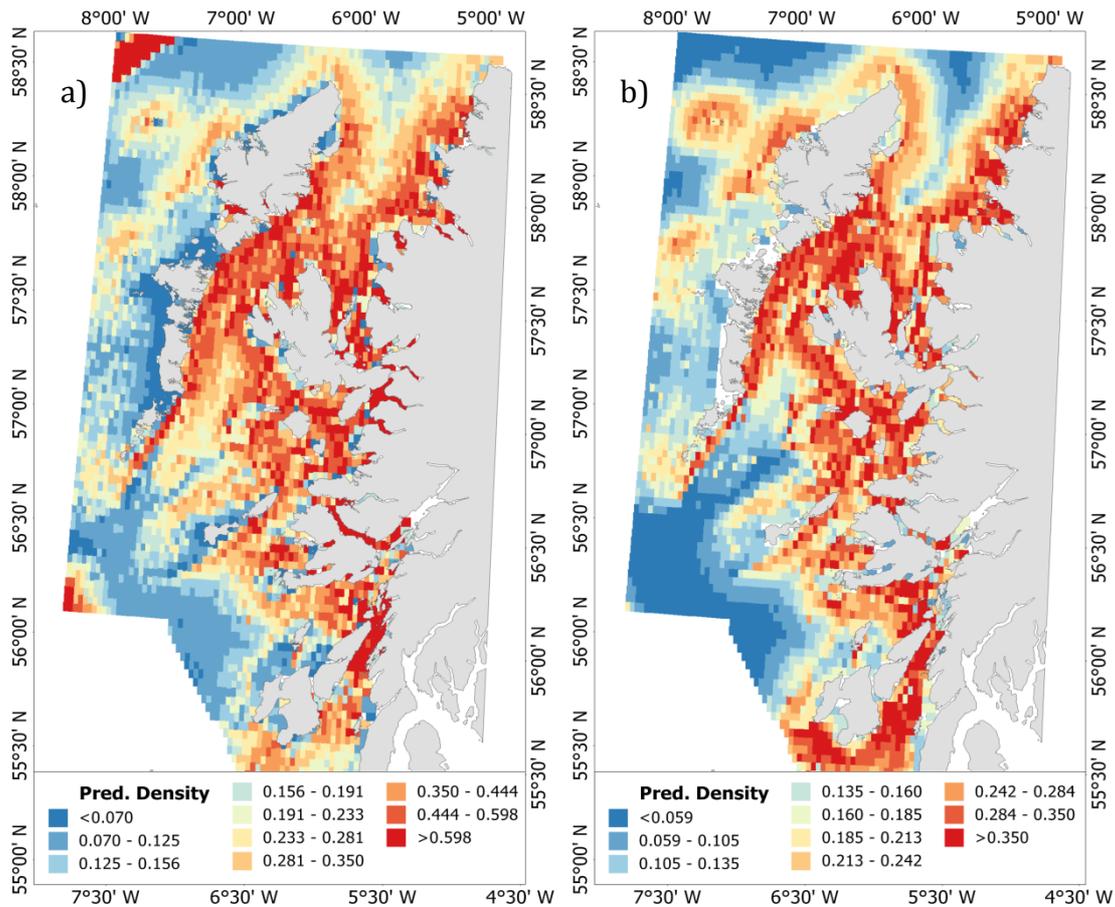


Figure 3.2 a & b – Predicted density surfaces for the (a) visual and (b) acoustic full models. For temporally varying covariates, fixed values were chosen to predict with the highest confidence (i.e. peak values where confidence intervals were narrowest) as follows: sea state = 1, vessel speed = 6.1 knots, year = 2007, month = August. Colour gradation in each map is based on eight quantile levels (the densities that correspond to the 12.5th, 25th, 37.5th, 50th, 62.5th, 75th, 82.5th percentiles) of the predicted harbour porpoise densities from each model (animals per km).

3.3.2 Acoustic Full Model

Acoustic detections of harbour porpoises varied among and within years, being highest in 2005 and in August (Figure 3.3). Of the survey variables (sea state, vessel speed, variations in boat speed, engine on/off – noise was only assessed in the inter-annual models due to data limitations - § 3.3.5), only vessel speed was found to impact acoustic detection of harbour porpoises. A general negative trend was observed. As vessel speed increased to 6 knots, acoustic detection rates decreased, beyond which detection rates appeared to be unaffected by boat speed. As observed in the visual full model, depth, slope, distance to land and STR were retained in the best model. Detection rates were highest in waters between 50 – 150 metres depth with fewer detections made in waters <50 m and >150 m depth. Detection rates increased with increasing slope and decreased as distance to land increased. A bimodal distribution of acoustic detection

rates was observed with respect to STR. The highest detection rates were in areas with STR of $\approx 1 - 2$ m and $\approx 4 - 6$ m.

The model evaluation revealed that the acoustic full model performed reasonably well ($F = 0.850$, 95% C.I. = $0.816 - 0.884$, based on 1,000 iterations), slightly better than the visual full model (Table 3.2).

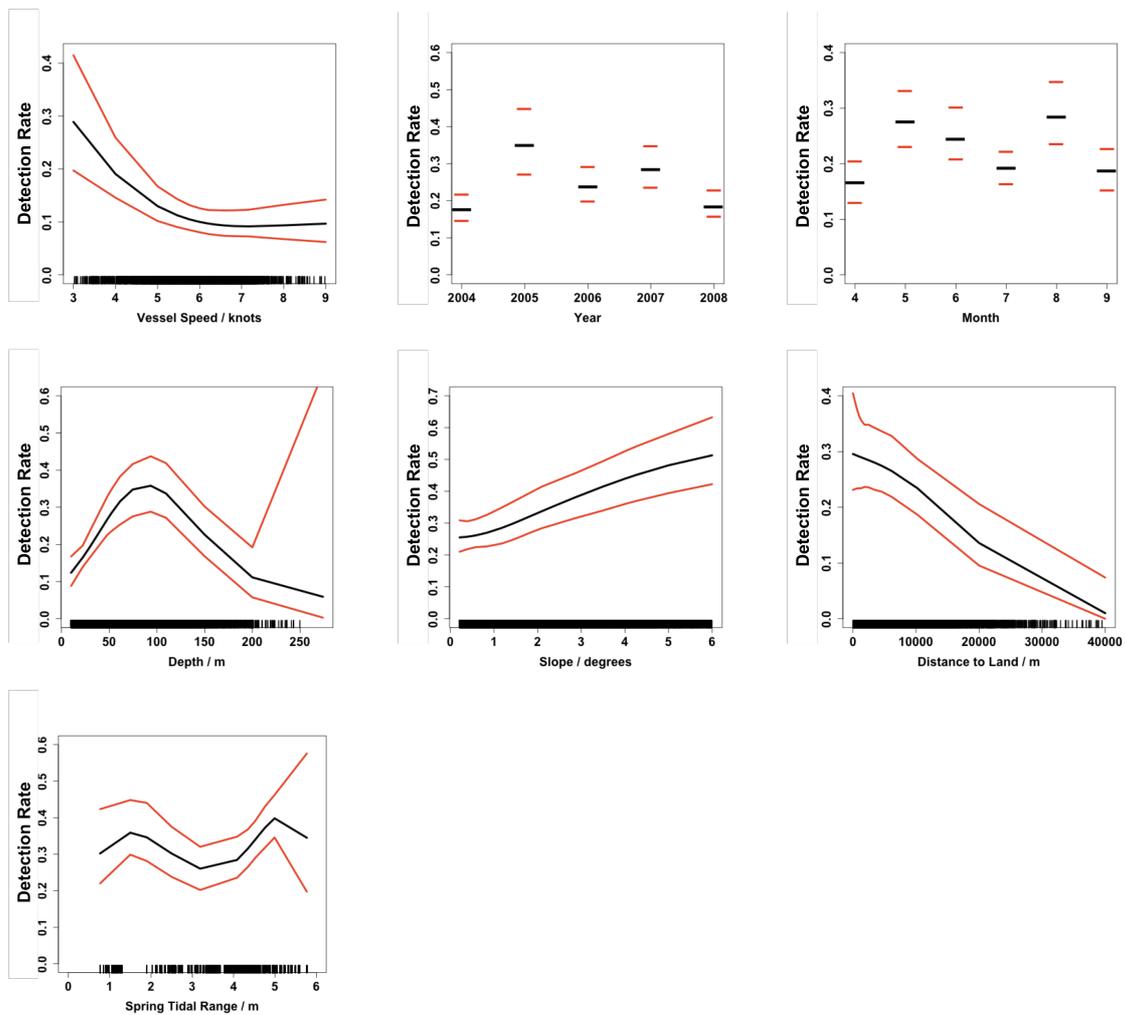


Figure 3.3 - Plots showing the relationship between the predictor variables and harbour porpoise acoustic detections (offset by effort). Black lines show the relationship, with 95% confidence intervals shown by the red lines. Tick marks above the x-axis show the spread of the explanatory variable data. N.B. The scale on the y-axis varies between plots.

The predictive map of harbour porpoise distribution based on the acoustic full model shows a strongly inshore distribution (Figure 3.2 b), very similar to the distribution predicted based on the visual full model. The main differences are the additional high-density areas predicted for the entire Sound of Jura and around the south of Islay (as opposed to only the northern Sound of Jura and patches around Islay as observed in the visual full model prediction). Low predicted

densities were observed in the northern Sound of Sleat, and around Colonsay and to the west of Islay.

3.3.5 Investigating Inter-annual Variations

Significant yearly variations were observed in both the full models. Here I investigate the ‘year effect’ by modelling each year individually to investigate whether (i) harbour porpoise distribution is consistent among years; (ii) there are inter-annual variations in habitat preference; and (iii) if it is possible to identify consistently important (or consistently poor) areas for harbour porpoises on the west coast of Scotland?

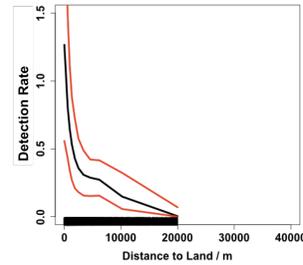
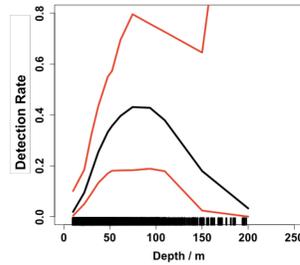
3.3.5.1 Inter-annual Variations (Visual)

Visual models were built for the six years for which there were survey data to investigate whether there are consistent patterns of habitat use and habitat preference for harbour porpoises in the study region. The model structures and selected relationships from the best models are shown below (Table 3.3 & Figure 3.4). Of the survey covariates included in the models, vessel speed was retained in four of the six years, with porpoise sighting rates decreasing with increasing speed. Sea state was the most commonly selected variable in the best models for each year – being retained in five of the six yearly models (it was not retained in 2003). As observed in the full models, harbour porpoise sighting rates declined significantly once sea states >1 .

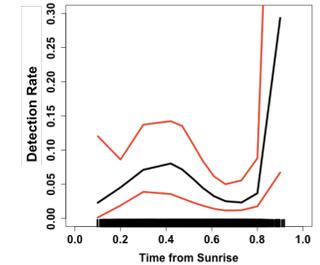
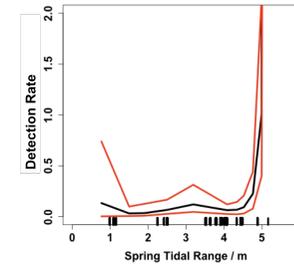
Table 3.3 - Model structure matrix showing the retained covariates in the best visual yearly models. An 'X' is shown if a covariate was retained.

Data	Model	Time		Survey				Sediment			Tidal		Topographic			
		Year	Month	Sea State	Boat Speed	Speed Variations	Time of Day	Percentage Gravel	Percentage Sand	Percentage Mud	Position Relative To Tidal Range	Position in Daily Tidal Cycle	Current Speed	Maximum Spring Tidal Range	Depth	Slope
Visual	Full	X	X	X	X					X			X	X	X	X
	2003		X		X									X		X
	2004			X			X						X		X	
	2005			X										X		
	2006		X	X	X							X				
	2007		X	X			X				X					X
	2008		X	X	X											X

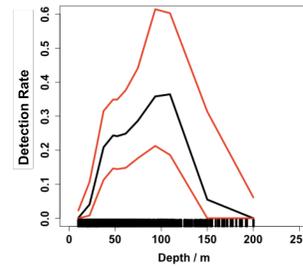
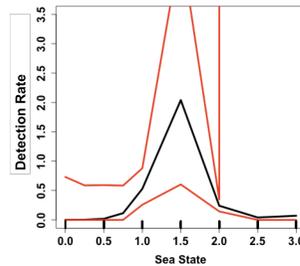
2003:
VisDet ~
as.factor(Month) +
s(BoatSpeed) +
s(DistanceToLand) +
s(Depth)



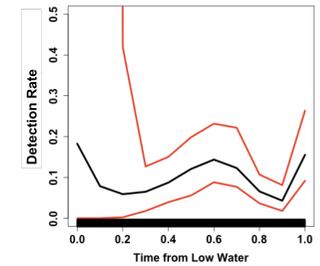
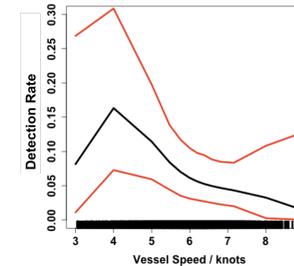
2004:
VisDet ~ *s*(SeaState)
+ *s*(Slope) +
s(SpringTidalRange) +
s(TimeOfDay)



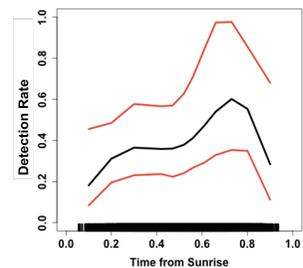
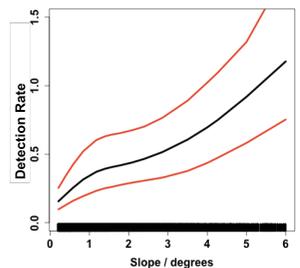
2005:
VisDet ~
s(SeaState) +
s(Depth)



2006:
VisDet ~
s(BoatSpeed) +
s(SeaState) +
as.factor(Month) +
s(DailyTidalCycle)



2007:
VisDet ~
s(SeaState) +
as.factor(Month) +
s(Slope) +
s(TimeOfDay) +
s(Rel.TidalRange)



2008:
VisDet ~
s(BoatSpeed) +
s(SeaState) +
as.factor(Month) +
s(Slope)

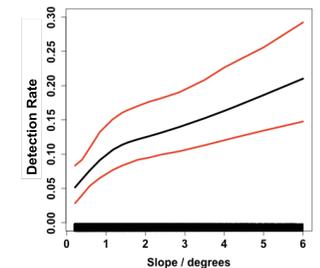
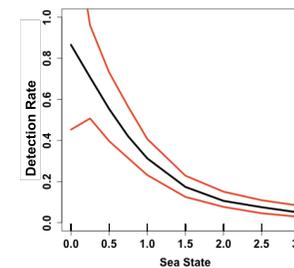


Figure 3.4 - Plots showing the model structures (*s* = fitted as a smoothed term, *as.factor* = fitted as a categorical term) and the relationship between the predictor variables and harbour porpoise sightings (offset by effort) for the best visual yearly models. Black lines show the relationship, with 95% confidence intervals shown by the red lines. Tick marks above the x-axis show the spread of the explanatory variable data. N.B The scale on the y-axis varies between plots.

Month was retained in four of the six best yearly models (2003, 2006, 2007, 2008) indicating that, within these years, there are significant daily variations in harbour porpoise sightings. In all of the models where month was retained, sighting rates generally increased from April to June, peaking in June and/or August, before dropping slightly in September. Other temporal variables were retained in best models but their inclusion and relationships were inconsistent among years. For example, 'Time of Day' was retained in 2004 and 2007, but in 2004, the highest sighting rates were observed in the late morning, decreasing in the afternoon before peaking once again more markedly just before sunset. In 2007, sighting rates generally increased as the survey day went on, peaking in the late afternoon, and then decreasing just before sunset.

Tidal variables: Spring Tidal Range (STR), Position Relative to Tidal Range and Position in the Daily Tidal Cycle were all retained in one model each. STR was retained in 2004, with the highest sighting rates occurring in regions of $STR > 4$. Position in the daily tidal cycle was retained in 2006 with most animals being observed in the low and high water slack periods and sighting rates decreasing during both the flood and ebb tides. Position Relative to Tidal Range was included in the best model for 2007.

Of the topographical covariates, depth and/or slope were retained in five of the six best models. Depth was retained in 2003 and 2005 and the same relationship as the full visual model was observed, with the highest sighting rates occurring in waters between 50 – 150 m depth. Similarly, the relationship between slope and porpoise sighting rates was the same as in the full models, with an almost linear increase in sighting rates with increasing slope. Slope was retained in 2004, 2007 and 2008. Distance to land was also included in visual models in 2003 only, with decreasing sighting rates as distance to land increased.

Measures of ambient and system noise levels were included as potential covariates in the yearly visual and acoustic models (data were only available in 2004, 2005, 2007 and 2008). 'DC Noise' levels, a measure of background noise measured in *Porpoise Detector* (2004 & 2005) and direct measurements of ambient and system noise (in the porpoise band (100 – 150 kHz) and a control band (50 – 75 kHz)(2007 & 2008) were included as potential covariates in the yearly models in 2007 and 2008. None of these covariates was retained in the final visual or acoustic models.

The yearly models were evaluated using the same cross-validation method used on the full models (Table 3.2). Scores indicated that most of the yearly visual models generally performed poorly in capturing all of the underlying processes in the data (F ranged from 0.167 in 2003 to

0.664 in 2006), with the exception of 2005 where the F value was 0.949 and the 95% confidence intervals include 1.0 indicating the 2005 visual model captured the underlying processes and performed well.

The predicted maps for each yearly visual model indicated some variation in the predicted distribution of harbour porpoises among years (Figure 3.5). As stated above, the visual yearly models did not capture all the processes driving porpoise distribution (2005 being an exception); this should be considered when interpreting the predictive plots. In 2004, 2007 and 2008 a similar distribution to the full visual model was observed – with a generally inshore distribution being predicted by the models. The Small Isles, west of Mull, Firth of Lorn and the Sound of Jura were all the highest predicted relative density areas. However, it is noteworthy that the predictive surfaces looked ‘patchier’ than those produced from the full models – i.e. cells with high-predicted relative density next to cells with lower predicted densities. In 2005 the predictive maps indicated that more offshore regions were important for harbour porpoises, in particular the Minch, Little Minch and northwest of the Outer Hebrides had the highest predicted relative densities. Despite this variation, high-predicted relative densities were still observed in some coastal regions, for example the western Small Isles (around Canna, Rum and Eigg) and the southern Sound of Jura. In 2006 the final model did not include any spatially-varying covariates resulting in equal predicted relative densities in each cell of the predicted surface (as governed by the chosen values of the temporally-varying covariates). Hence, the predicted relative density map is not included here.

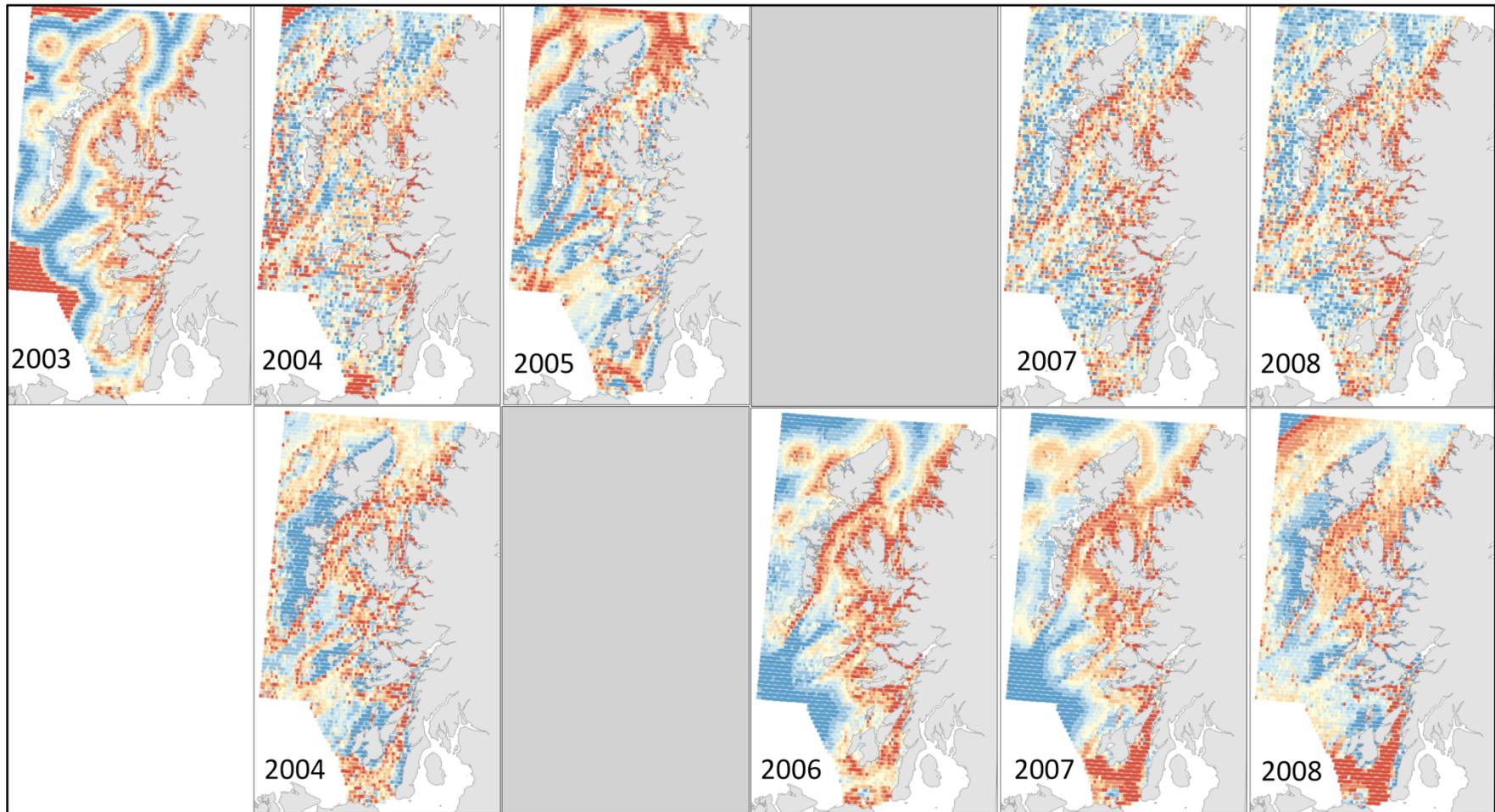


Figure 3.5 - Predicted surfaces for the best visual and acoustic yearly models. For temporally varying covariates, fixed values were chosen to predict with the highest confidence (i.e. peak values where confidence intervals were narrowest). Colour gradation in each map is based on eight quantile levels (the densities that correspond to the 12.5th, 25th, 37.5th, 50th, 62.5th, 75th, 82.5th percentiles) of the predicted harbour porpoise densities from each model (animals per km).

3.3.5.2 Inter-annual Variations (Acoustic)

As with the visual yearly models, acoustic models were constructed for years 2004 – 2008 to investigate inter-annual variations in acoustic data. The best model structures and selected covariate relationships are shown below (Table 3.4 & Figure 3.6). Vessel speed was retained in all the yearly acoustic models, with detection rates generally decreasing with increasing vessel speed. Sea state was retained in just two of the yearly models (2005 & 2006). In 2005, only sea states between 0 and 2 were surveyed acoustically and detection rates varied spasmodically across this range. In 2006, acoustic detection rates peaked between sea states 2 – 4. Measures of ambient and system noise levels were included as potential covariates in the yearly acoustic models (in 2004, 2005, 2007 and 2008). None of these covariates were retained in the final models.

Table 3.4 – Model structure matrix showing the retained covariates in the best acoustic yearly models. An ‘X’ is shown if a covariate was retained. See §2.1.4 for explanations of covariate terms.

Data	Model	Time		Survey			Sediment			Tidal				Topographic		
		Year	Month	Sea State	Boat Speed	Time of Day	Percentage Gravel	Percentage Sand	Percentage Mud	Position Relative To Tidal Range	Position in Daily Tidal Cycle	Current Speed	Maximum Spring Tidal Range	Depth	Slope	Distance to Land
Acoustic	Full	X	X		X							X	X	X	X	
	2003	
	2004		X		X									X	X	
	2005			X	X						X					
	2006		X	X	X									X	X	X
	2007		X		X							X	X	X	X	X
	2008		X		X						X	X	X	X		

Month was retained in four of the five yearly models (it was not included in 2005). In 2004, 2006 and 2007 a general increase in acoustic detection rates was observed from April to July, peaking in August and then decreasing slightly in September. This pattern is very similar to that observed in the visual models. However, in 2008 acoustic detection rates were very similar from April to June, then dropped in July and maintained this lower through August and September.

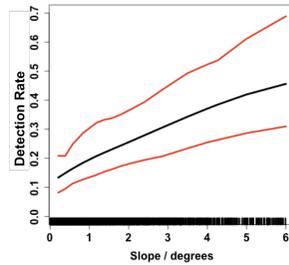
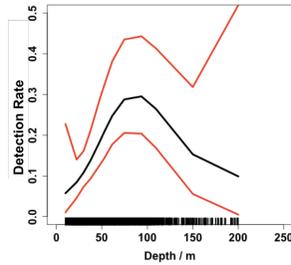
Of the tidal variables, spring tidal range was retained in 2007 and 2008. In both years, a bimodal distribution in acoustic detections was observed, similar to the full models, with highest detection rates occurring in regions with STR between 0 – 2 and between 4 – 6 m. Position

Relative to Tidal Range was included in 2005. Current speed was retained in acoustic models in 2005 and 2008 though different relationships were observed between years. In 2005, acoustic detection rates decreased almost linearly as current speed increased from 0 – 0.6 m per second and beyond this speed, no detections were made. Conversely in 2008, detection rates increased as current speed increased up to the maximum observed current speed of 1 ms⁻¹.

Topographical variables were, as with the visual models, consistently retained. Depth and slope were retained in the best models in 80% of the models (neither were selected in 2005) and peak detection rates were observed in 50 – 150 m depth, though there was some variation in the exact peak among years. As observed in the full models, increased detection rates were observed as slope increased. Distance to land was included in 2006 and 2007 with decreasing detection rates and distance from land increased.

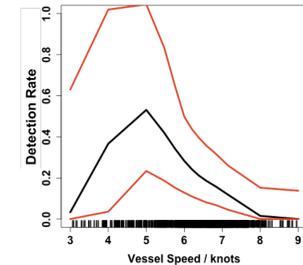
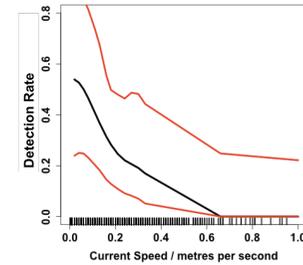
2004:

$AcDet \sim as.factor(Month) + s(BoatSpeed) + s(Slope) + s(Depth)$



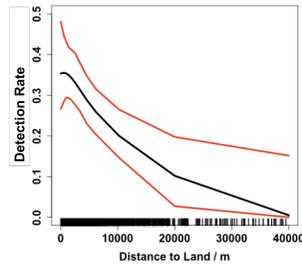
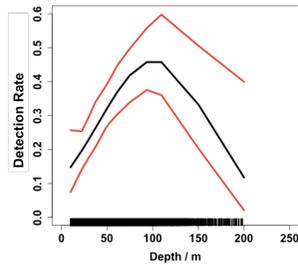
2005:

$AcDet \sim s(SeaState) + s(BoatSpeed) + s(CurrentSpeed)$



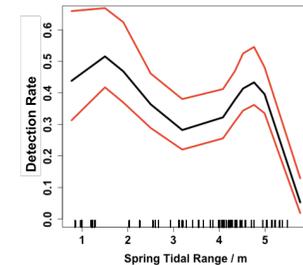
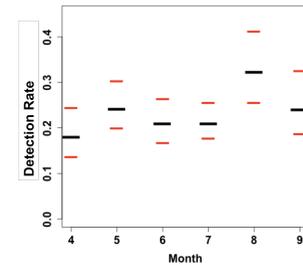
2006:

$AcDet \sim as.factor(Month) + s(BoatSpeed) + s(SeaState) + s(Slope) + s(DistanceToLand) + s(Depth)$



2007:

$AcDet \sim as.factor(Month) + s(BoatSpeed) + s(SpringTidalRange) + s(Slope) + s(Depth) + s(DistanceToLand)$



2008:

$AcDet \sim s(Slope) + s(BoatSpeed) + as.factor(Month) + s(Depth) + s(SpringTidalRange) + s(CurrentSpeed)$

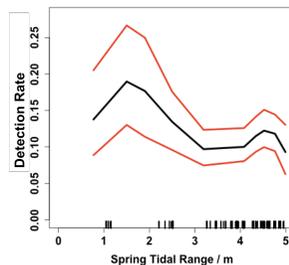
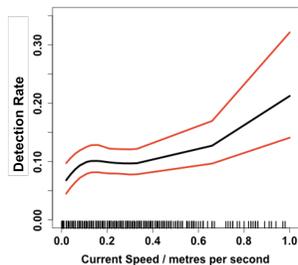


Figure 3.6 - Plots showing model structures (s = fitted as a smoothed term, $as.factor$ = fitted as a categorical term) and the relationship between the predictor variables and harbour porpoise detections (offset by effort) for the best acoustic yearly models. Black lines show the relationship, with 95% confidence intervals shown by the red lines. Tick marks above the x-axis show the spread of the explanatory variable data. N.B The scale on the y-axis varies between plots.

The yearly acoustic models were assessed with a cross-validation method (Table 3.2). Results of this evaluation indicate that all of the models based on acoustic detections performed well and were strong representations of the patterns that represent the data (i.e. all values were close to, or were equal to 1) in particular the 2006, 2007 and 2008 datasets, where the models captured the important underlying relationships in the data very well.

The predicted surfaces based on the acoustic models are similar among years and to the full acoustic model, with a strong inshore distribution identified for most years (2005 was the exception – see below). In 2004, 2006, 2007 and 2008, high densities were predicted for the coastal regions of the Minch, the deeper waters close to the western Outer Hebrides, around the Small Isles, the Firth of Lorn and Sound of Jura. In particular in 2006, 2007 and 2008 the Sound of Jura appeared to be an increasingly important area as it was the site of the very highest predicted relative densities, extending round to the southwest coast of Islay. The offshore regions in the southwest of the study region, the west of North and South Uist and the around to the southeast and southwest of Colonsay were consistently predicted to be low porpoise relative density areas. In 2005, no covariates that varied spatially were retained in the model meaning the predicted relative densities were equal in every cell (as with 2006 in the visual models). As with the full model predictive maps, the yearly based predicted surfaces were generally close to those observed in the raw acoustic detections data.

3.4 Discussion

Correlations between cetacean distributions and environmental and oceanographic data have been the focus of a number of studies. A range of analytical methods has been applied to study a wide range of species. This chapter presents results on the habitat preference and distribution of harbour porpoises, the most abundant cetacean species on the west coast of Scotland. Harbour porpoise densities were modelled using visual and acoustic detection data, using GAMs and GEEs to determine which environmental covariates explained variation in porpoise distribution. Predicted outputs were used to identify particularly important regions for the species in the study region.

3.4.1 Survey impacts on visual and acoustic models

The overall detection rates from the visual and acoustic surveys were significantly different throughout the study period. Acoustic detection rates were approximately twice that of visual

detection rates. Visual surveys for porpoises were heavily impacted by sea state, with detections decreasing significantly above Beaufort sea state 1. This effect of sea state found here is consistent with observations from a number of studies on porpoises (Embling 2007; SCANS-II 2008) and best described by Palka (1996). Both sightings and acoustic detections of porpoises were negatively impacted by the speed of the survey vessel. The negative impact of boat speed may be explained by the amount of time spent surveying in each survey segment. As explained in methods (§2.3.1), survey effort was organised into 2 km segments. When travelling at low speeds, there is more time in which to visually and acoustically search for animals and because harbour porpoises are highly mobile, there is longer for animals to move into detection range and be detected. As speed increases, this leads to less time being spent surveying in each segment, which explains the decrease in detection rates observed. Another potential explanation is that there may be a responsive movement of porpoises away from survey vessels influencing the detection rates for vessel-based surveys (Palka and Hammond 2001). If vessel noise increased with boat speed then a greater level of avoidance might occur due to the vessel being detected by animals further away. Variation in boat speed was not retained in any of the best models, which indicates that shifts in boat speed and/or engine revolutions were not impacting the detection of animals. Additionally, ambient and system noise levels were included in four of the six yearly models as potential covariates, but were not retained in any of the best models indicating that these were not significantly impacting detection rates. This finding is interesting because previous studies using PAM to study porpoises have found that noise levels were a factor impacting the detection of animals (Embling 2007; SCANS-II 2008). In future studies, treating the data as detections per unit of effort in time, rather than by effort in distance would alleviate this issue.

3.4.2 Habitat preference of harbour porpoises

While there were different detection rates and different survey covariates impacting the acoustic and visual full models, the covariates retained and their relationships with porpoise density in the best ‘all year’ visual and acoustic models were very similar. In both visual and acoustic models, porpoise density was best predicted by: year, month, average depth, average slope, distance from land and spring tidal range. Percentage mud in the sediment was only retained in the best visual model.

Both year and month were retained in the best visual and acoustic models. This indicates that over the extent of the study region there were significant temporal variations in harbour porpoise sighting and acoustic detection rates over both between study years and within the March – September

survey period. In both the models, no clear trend was observed and detection rates fluctuated among years. The highest detection rates were observed in 2005, followed by 2007. Embling (2007) observed that in 2005 there was a “significant change in the ecosystem” of the Inner Hebrides. Minke whales had been abundant in previous years and their sighting rates decreased significantly in 2005. Concurrently basking shark (*Cetorhinus maximus*) sightings increased significantly and a number of seabird species failed to fledge chicks (Stevick et al. 2007). This is discussed further in §3.4.3.

Seasonality in the models could be explained by either genuine changes in harbour porpoise density and/or distribution or by changes in detection probability (e.g. weather conditions, changes in group size, behavioural changes etc could all result in animals more or less available at the surface to be sighted or more or less vocal – impacting sightings/acoustic detection rates). Seasonal variation in harbour porpoise habitat preference and distribution in European waters are poorly understood and have only been investigated in a handful of recent studies (Evans et al. 2003; Gilles et al. 2009; Siebert et al. 2006; Verfuss et al. 2007; Weir et al. 2007). This study investigated porpoise distribution from April –September and found significant variation in porpoise detection rates among months during the study period. A general trend was observed with detection rates being lowest in April and May, and then increasing through the survey season, peaking in August, before dropping slightly in September. July and August have been the months in with peak detection rates in other studies (Gilles et al. 2009; Siebert et al. 2006; Verfuss et al. 2007). It has been suggested that in the NW Atlantic during the summer and autumn months, porpoises tended to aggregate in more coastal waters (Read 1999), although Northridge (1995) observed that animals were generally more dispersed across the Gulf of Maine in June than in April and May. Furthermore, they observed that animals were aggregated in the northern Gulf of Maine and the Bay of Fundy from July to September (Northridge 1995).

It is also noteworthy that in the present study porpoise group size generally increased in August and September. If animals are travelling more as a group then it is more likely that one animal in the group would be at the surface at any given time, increasing the chances that the group would be sighted (Buckland et al. 2001). This could explain some of the increase in sighting rates. Group size was not included as a covariate in this analysis.

It is not clear from the full models what is driving these inter-annual and intra-annual variations and what has been presented here is speculative. Inter-annual variations will be discussed in more detail here (§ 3.4.3) and intra-annual variations in porpoise distribution and habitat use are the subject of investigation in Chapter 4.

Harbour porpoise distribution was impacted by topographical variables, such as depth of seabed and angle of seabed slope in both the models built on visual and acoustic detection data. Porpoise density was at its peak in regions with between 50 and 150 metres water depth. A similar preference for these depths has been recorded in other studies around the west coast of Scotland (Embling et al. 2005; Goodwin and Speedie 2008; MacLeod et al. 2007; Marubini et al. 2009). Depth has also been important predictor in other studies further afield though the preferred depths have varied considerably. Porpoises have been found most commonly in both shallow waters (30 - 60 m:(Carretta et al. 2001; Shucksmith et al. 2009) and in deeper shelf water regions (>100 m:(Raum-Suryan and Harvey 1998; Watts and Gaskin 1985). Studies using static acoustic detectors (T-PODs/C-PODs, Chelonia Ltd, UK) have also documented porpoise acoustic activity in relatively shallow waters in the North Sea and around Denmark where the devices were deployed (~30 m) (Siebert et al. 2006; Todd et al. 2009). The increased harbour porpoise detections observed between 50 – 150 m in this study could be explained by the availability of prey species in these regions. The major prey items for porpoises on the west coast of Scotland are juvenile whiting, haddock/saithe/pollock, other gadoid species and to a lesser extent sepiolids and sandeels (Santos et al. 2004). These fish species tend to inhabit waters up to 200 metres depth (whiting: 40 – 200 m (Persohn et al. 2009), cod: 30 – 200 m (Santos et al. 2005), sandeels: 30 – 120 m (Wright et al. 2000) and the depth ranges they inhabit may be a major driving force governing the harbour porpoise habitat use patterns observed here. Porpoise have also been documented feeding on a number of demersal flatfish species (Herr et al. 2009; Santos and Pierce 2003). Studies of harbour porpoise dive behaviour have revealed animals routinely dive to depths of 73 – 99 m and are capable of diving to over 200 m (Otani et al. 2001; Otani et al. 1998; Westgate et al. 1995) indicating they are capable of feeding both demersally and pelagically in the preferred depth range observed here. However, diving deeper would likely incur a greater energetic cost and it is not clear whether demersal species would be of sufficiently higher value to make this diving behaviour cost efficient.

Seabed slope has been found to influence marine mammal distribution in a number of studies (Bailey and Thompson 2009; Hui 1985; Jaquet and Gendron 2002; Yen et al. 2004). Similarly, in

this study porpoise sighting and acoustic detection rates were most likely in regions with a highly sloped seabed (up to a maximum slope angle of 6°). Slope was also a significant predictor of porpoise acoustic detection rates in the Inner Hebrides, with increasing detections as slope increased (Embling, 2007). Burmeister's porpoise (*Phocoena spinipinnis*) distribution has also been linked to regions of high slope (Heinrich 2006). In contrast to that which was observed here, high-use porpoise regions have also been identified in areas with very shallow slopes ($<0.5^\circ$) – though these were generally deep (>125 m) waters with flat bottoms (Raum-Suryan and Harvey 1998). Upwelling is a common phenomenon in coastal regions of high slope as cold, nutrient rich water is forced to the surface, increasing productivity and enhancing prey densities, which consequently can attract top predators (Mann and Lazier 2006; Mooers et al. 1979; Sverdrup et al. 1942; Yen et al. 2004). Slope (along with seabed friction) also functions to drive productivity by influencing the movement of currents (Inall et al. 2009) and slope-driven upwelling is considered to be temporally and spatially-predictable, often centred around land features, such as headlands which can serve as anchor points for eddies, rips and upwelling (Mann and Lazier 2006; Yen et al. 2004; Zamon 2003).

Distance to land was retained in the visual and acoustic models and in both cases, density was found to decrease steadily as distance from land increased. The highest predicted relative densities were in regions $<1 - 20$ km from land indicating that animals are exhibiting a strongly inshore distribution. The west coast of Scotland is a diverse oceanographic environment with an uneven, fjordic coastline meaning the relationship between depth and distance from land is highly variable. Initially, it seems unlikely that there is any biological significance in a variable like 'distance to land' but it may have been retained in the model as a proxy for other unmeasured biologically significant variables. As discussed above, land-features, such as capes and headlands can provide the anchor-points for upwelling and fronts, meaning that regions of upwelling occurring closer to the shore (Mann and Lazier 2006; Yen et al. 2004). Additionally, salinity is thought to generally decrease as distance from land increases as the level of freshwater input is diminished further offshore (Gillibrand et al. 2003). Freshwater plume fronts (influxes of freshwater meeting seawater masses) are common in inshore regions and lead to increased mixing and so an increase in productivity and aggregation (Mann and Lazier 2006).

Spring tidal range (STR) was included in both the visual and acoustic models. In both cases, a bimodal distribution of detection rates with respect to STR was observed with peak detection rates at $0 - 2$ m and $4 - 6$ m. Between $2 - 4$ m significantly fewer animals were detected. STR of $0 - 2$ m

are only observed in the Sound of Jura and to the southwest of Islay in the south of the study region and STR values >4 m are only observed in the waters around the Isle of Skye, in the Minch and Small Isles. The low tidal range in the Sound of Jura and SW of Islay is a result of two tidal water masses - one from the Atlantic water and the other moving up the North Channel of the Irish Sea - converging at this point. These two tidal currents are 180° out of phase and this means the two tides cancel one another out. The result is little or no tidal range in these regions (Gillibrand et al. 2003, Simpson et al. 1979). This does not mean that there is no tidal current in this region, however. Because there is significant tidal range in the Firth of Lorn to the NW, water travels down the 'sea-height' gradient and there considerable tidal currents are generated at the points of transfer, especially where the effects of tide are strengthened by passing through narrow channels (in the Gulf of Corryvreckan, Sound of Luìng, Sound of Islay and in the Islay Front zone). Current speed (generated from tidal movements) was not selected in the final full models, which indicates that over the entire west coast current speed is less important, but it may be reflected in finer scale tidal processes (e.g. eddies, tidal rips) that are not clear at this resolution of these models. Porpoise distribution and habitat preference over smaller extents are investigated in Chapter 5 and this may provide explanations of the patterns observed here.

Percentage mud in the sediment was retained in the best all year model indicating that porpoises were more likely to be sighted in regions of $\approx 20 - 60\%$ mud. This could be explained by prey availability as other studies have investigated links between preference for sediment types and suitable habitats for prey species; minke whale presence in this area has been linked to sandeel (sand/gravel) and pre-spawning herring habitat (mainly gravel)(MacLeod et al. 2004) and grey seals were observed most commonly in regions of sand and gravel which were attributed to sandeel habitats (Aarts 2006). Embling (2007) observed that porpoise acoustic detections were highest on the west coast of Scotland in regions of high percentage mud. In this study, more porpoises were sighted in regions of moderate mud in the sediment. Whiting, which are thought to constitute the bulk of porpoise prey species in the region (and around the UK)(Roberts 2005; Santos et al. 2004), are known to prefer muddy sand sediments which could explain this pattern (Hislop 1984). Similarly, flatfish species have been documented in UK porpoise diet and are known to inhabit muddy sediment (Herr et al. 2009; Santos and Pierce 2003; Santos et al. 2005; Santos et al. 2004).

The regions of predicted high-relative density for porpoises appeared to be similar for both the visual and acoustic models. This was expected given the similarity in covariates retained and

relationships observed in the best models. High densities were predicted revealing a strongly coastal distribution, which appears similar to the observed distribution patterns in the raw data when compared visually. The highest predicted densities were in the coastal Minch regions on both the mainland and east coast of the Outer Hebrides, around the inshore waters of the Isle of Skye, the Small Isles, Firth of Lorn and Sound of Jura. The southwest region of the study area and the majority of the Atlantic coast of the Outer Hebrides had low observed and predicted densities. One possible explanation for the strong inshore distribution patterns observed is that animals are moving throughout the west coast. The species is considered to be highly mobile and has exhibited ranging behaviour in other distributional studies (Johnston et al. 2005; Read and Westgate 1997; Teilmann et al. 2008). Cetacean species are thought to use a range of cues to navigate through their environment, including using underwater topographic features (Pryor 1990), salinity and temperature gradients (Nachtigall and Hall 1984; Wartzok and Ketten 1999; Watkins and Wartzok 1985), currents (Lohmann et al. 2008), using odours, tastes and sounds (Hoelzel 2002; Wartzok and Ketten 1999). The observed habitat use pattern is discussed further in Chapter 7.

3.4.3 Inter-annual variations

For effective conservation using protected areas, it is important to investigate and understand the temporal variability in a species distribution. Additionally, the investigation of habitat preference over a range of temporal scales is important to help better understand the ecology of the species. To investigate the effect of year on harbour porpoise distribution and habitat preference, individual yearly models were built. Some relationships were similar to what was observed in the full models, but significant inter-annual variations in habitat preference were also observed.

Models were evaluated using a cross-validation method to assess how much of the underlying relationships in the data were captured by the models. Many of the visual models had low cross-validation scores indicating that they were not capturing all of the patterns generating the data. Only in 2005 did the model have an F score close to 1 (indicating much of the important processes were captured by the model). This should be considered when assessing the visual models. Model evaluation indicated that the acoustic yearly models performed well, capturing the underlying processes that generated the data.

3.4.3.1 Inter-annual variation in habitat preference

In this analysis, there were consistent predictor variables selected in the best models. Sea state (visual only), vessel speed, month and slope or depth were retained in most years and their relationships did not change dramatically among years. Sea state was included in all yearly visual models, except 2003, where it was excluded from the best model. In years 2004 – 2008, sightings declined significantly above Beaufort sea state > 1 as with the best full visual models. Additionally vessel speed was retained in the 2003, 2006, 2007 and 2008 visual models and all acoustic models. In these models, sightings decreased as vessel speed increased. Month was retained in four of the six visual yearly and four of five acoustic models. The same pattern as in the full models was observed in each year, with increasing sightings from April to July and peaks in August. Slope and/or depth were important in explaining porpoise distribution in five of the six years (visual) and four of five year (acoustic) and the same relationships were observed as in the full models – with increasing sightings with slope and peaks in sightings in areas with 50 – 150 m depth – indicating that these are temporally consistent patterns driving harbour porpoise distribution in this region.

Some additional covariates were retained in some of the yearly models, though no consistent relationships with the response were observed. For example, ‘time of day’ was retained in the 2004 and 2007 visual models, but the relationships varied among years. In 2004, peaks in sightings were in the late morning and at dusk. In 2007, sightings increased as the day went on, peaking in late afternoon, then decreasing at dusk. Cetacean species have been documented to exhibit diel changes in behaviour in response to horizontal and vertical prey migrations (Benoit-Bird and Au 2003). A number of fish species are known to have diurnal patterns of activity; for example, sandeels emerge from sandy refuges during daylight hours to feed (Wright et al. 2000). It is not clear if such migrations would make prey more or less susceptible to predation by harbour porpoises and how it would impact harbour porpoise surface behaviour and thus how easily animals would be detected during surveys. Another possibility is that the retention of ‘time of day’ was that it is representative of an observer effect, with fatigue influencing the sighting rates. The absence of such a pattern in the acoustic data – which is autonomous and so could not carry such a bias – may be indicative of this. However, this is subjective and requires further investigation.

Position in the daily tidal cycle was retained in the 2006 visual model. Significantly more porpoises were sighted during both the high and low water slack periods between the flood and ebb tides in 2006. Position in the daily tidal cycle has been shown to be an important factor in a number of

studies on harbour porpoises, and increased occurrence has been associated with all phases of tide: the slack (Embling et al. 2010), the ebb (Pierpoint 2008) and the flood tides (Calderan 2003; Johnston et al. 2005; Sekiguchi 1995). Bottlenose dolphins were observed resting at the surface significantly more during slack tides than other phases of tide (Mitcheson et al. 2008) but it is unknown if such behavioural patterns exist in harbour porpoises. Position relative to tidal range (a measure of position relative to the spring-neaps cycle - §2.1.5) was retained in the best visual model in 2007 as most sightings were made during tides shortly after neap tides with sightings decreasing as spring tides approached. It is not clear why porpoise sightings would be influenced by position in the spring or neap tides. Gaskin and Watson (1985) observed a pattern with higher sighting rates during neap tides in porpoise in the Bay of Fundy and suggested it may be a consequence of animals avoiding areas with extreme current velocities. The pattern observed in this study runs counter to what was observed in the region in 2004 - 2005 where more porpoises were sighted during spring tides (Embling 2007). This was attributed to prey being more concentrated during spring tides due to stronger currents (Embling et al. 2010). However, the literature suggests that such phenomena are spatially and temporally variable. It has been documented that fish behaviour differs greatly between spring and neap tides and that the tidal cycle can be greatly impacted by coastal geography (Arnold 1981). Demersal species (such as sandeels, sole, flounder etc) regulate their activity patterns during strong spring tides, to avoid being displaced by strong tidal currents (Gibson 1978). For example, plaice are known to bury deeply into sediment avoiding displacement during periods of strong tidal currents (Arnold 1969) and so conversely would be more available during less tidally active periods. If during spring tides, porpoise prey species are more difficult to find then animals may be more actively feeding during neap tides. However, it is not clear whether animals would be more or less detectable if more actively feeding. This pattern of neap tide selection is curious and requires further investigation. Sea states can also be impacted by tidal currents due to the disturbance and mixing associated with large volumes of water being forced over variable topography, which may impact visual detection rates.

The most noteworthy pattern observed in the yearly acoustic models was that current speed was retained in two yearly acoustic models, though it had not been selected in the full models. Current speed was retained in the 2005 and 2008 models, though the relationship between current speed and the response was different between these years. In 2005, porpoise detections decreased as current speeds increased and in 2008, a positive relationship was observed with more porpoises observed in regions with high currents. Current speeds have been important in a number of

cetacean habitat distribution studies (Calderan 2003; Mendes et al. 2002; Tynan et al. 2005), however most of these studies were focused on fine-scale regions of high tidal currents and only the Embling (2007) study investigates current speed preference over a larger survey area (and thus range of current speeds). On the west coast of Scotland, the areas of high currents are all associated with headlands and channels, where land masses serve to intensify the current speeds. In open water, the current speeds are generally lower (Mann and Lazier 2006). As in 2005, a preference was found for lower current speeds; this could be a proxy for a preference for more open water regions, further offshore as observed in the visual model prediction for 2005. The opposite was true in 2008 and this may be indicative of animals being more prevalent close to land, where the effects of tide are magnified.

3.4.3.2 Inter-annual predicted distribution

Model selection results were generally consistent with between years, with strong monthly patterns and topographical covariates being routinely selected. Sea state and vessel speed were the important survey variables retained in most models. The similarity in model selection results between visual and acoustic models is in spite of the model evaluation metric used in this study indicating that the visual models were not capturing the relationships in the data well. The exception here was 2005 where the model evaluation indicated the model was performing well in this respect. Despite the poor model evaluation scores in 2003-2004, 2006 - 2008, the predicted surfaces for each yearly model had some similar patterns of distribution. In 2003 a very strong coastal distribution was predicted, likely reflecting the inclusion of distance to land in the best 2003 model. In 2004, 2007 and 2008, a generally coastal distribution was predicted though there was a lot of variation between neighbouring cells. The predictions in 2003 & 2004 were generally similar to those made in an earlier study of the region (Embling 2007), though the 2005 prediction in this study was quite different.

In 2005, a very different distribution pattern was predicted (Figure 3.5). In most regions, harbour porpoise distribution was predicted to be slightly further offshore, in contrast to a strong coastal pattern predicted in other years. In particular, high-predicted densities were observed in the Little Minch, in the middle of the Minch and in the deeper waters west of the Outer Hebrides. Low predicted densities were observed for most of the inshore regions south of Skye, though the

exception to this was in southern Sound of Jura and south of Islay where the North Channel tidal current reaches the Inner Hebrides where there were high-predicted densities.

As noted earlier, a change in the ecosystem was documented in 2005 with a dramatic decrease in minke whale sightings and an increase in basking shark sightings (Stevick et al 2007). At the same time, a very significant drop in salinity (> 1 psu) was observed in the region (Inall, pers. comm.). This decrease in high salinity water began in January 2005 and continued over the next 22 months before salinity levels returned ‘normal’ levels in summer, 2007 (Inall, pers. comm.). The mechanisms behind this shift have not been investigated but could be attributed to reduced influence of Atlantic origin water in the Inner Hebridean islands (Inall et al. 2009). Frontal systems, i.e. changes in waters masses, like this one are known to determine the preferential use of areas by top predators (Bost et al. 2009). If, in this study, Atlantic origin water, carrying with it Atlantic plankton species, did not penetrate the waters of the Inner Hebrides in 2005, then food webs relying on such influxes could be impacted – either leading to a poor year for the top predators (Lindstrom et al. 2009; Stevick et al. 2008) or a shift in their distribution (Stevick et al. 2008). In most regions, harbour porpoise distribution predicted to be further offshore, especially in the deeper waters of the Minch and Atlantic coast of the Outer Hebrides and this may be a reflection of prey availability as a consequence of the different distribution of Atlantic-origin water. However this reduced salinity event lasted for 22 months and it is not clear why this pattern was not observed in 2006. It is possible that after the initial shift in salinity and/or Atlantic water distribution, porpoises and/or their prey adjusted their diet or behaviour. It is also possible that the increasing salinity during 2006 was indicative of sufficient Atlantic water entering the Inner Hebrides fuelling the food-webs. This is speculative and further investigation is necessary before any firm conclusions can be made. It was noteworthy that the relative densities in the Sound of Jura were still high in the southern Sound of Jura and south of Islay in 2005 (similar to the patterns observed in all other years). This may be because in this area nutrients are largely supplied via the Irish Sea Water through the North Channel and it is unaffected by Atlantic water influxes in normal years (Gillibrand et al. 2003; Simpson et al. 1979).

The prediction maps from the acoustic yearly models were reasonably consistent indicating a coastal distribution for harbour porpoises in 2004 and 2006 – 2008. Similar distributions were predicted for these models as observed in the full models, with a strong coastal pattern. Unfortunately it was not possible to generate useful predicted surface for 2005 (acoustic) to investigate whether the same

patterns in distribution in the 2005 visual models were observed in the acoustic data (see below). It was noteworthy that in 2006, 2007 and 2008 the predicted distribution surfaces revealed a consistent inshore pattern. In particular, the regions around Skye appeared to become slightly less important from 2006 onwards and an increase was observed in the importance of the Sound of Jura over the study period.

The absence of predicted surfaces in 2005 (acoustic) and 2006 (visual) here is misleading. These models retained only covariates that had to be specified in the prediction stage meaning the predicted density was the same for each cell. There were spatially varying relationships retained in the model, but they were dynamic covariates that were variable time *and* space (such as water temperature) meaning they could not be reflected in the predictions.

3.4.4 Identification of high-use regions

One fundamental goal of this thesis is to identify consistently important regions for harbour porpoises on the west coast of Scotland, while gaining a better understanding of the processes explaining their distribution and the scales at which they operate. The full models developed here indicate that both visual and acoustic survey methods captured some of the important predictors and predicted a strongly inshore distribution. An investigation of inter-annual variations indicated that a suite of core variables and their relationships with the response were consistent among years, though additional covariates were also retained and their inclusion varied among years. Nonetheless, spatial predictions indicated similar distributions for each of these years that in most cases were similar to those predicted under the full models. So while there are some variations in distribution among years, a generally consistent pattern of coastal usage was demonstrated.

The following chapters of this thesis further investigate these variations in *intra*-annual habitat use and distribution (Chapter 4) and the effect of local spatial covariates impacting the models at larger scales (e.g. current speed may be important in only one small region, but the relationship is sufficiently strong that is retained in the full model). To do this I built models for a series of regions on the west coast, rather than a single model encompassing the whole study region. This helped to determine which predictors are particularly important at smaller scales and to investigate porpoise density at a series of potential SAC sites (Chapter 5). In Chapter 7, the importance of sites is further considered and suitable SAC sites are put forward.

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Chapter 4

Intra-annual variation in harbour porpoise distribution and habitat preference west of Scotland

4.0 Abstract

The efficacy of a marine protected area in conserving a species is, in part, dependent on the design of the area. Currently, the majority of the boundaries of such areas for cetaceans are built around static oceanographic features, e.g. bathymetry, that can help define an important area for a species. However, a large number of cetacean species are known to make seasonal movements and this should be considered when assessing potential areas for the conservation of cetacean species. The aim of this analysis was to investigate whether there are identifiable shifts in habitat preferences and distribution of harbour porpoises off the west coast of Scotland and to determine at what temporal scales the patterns of distribution were consistent among years.

Designed line-transect visual and towed-array acoustic surveys were conducted between 2003 – 2008 and 2004 – 2008, respectively, from the Hebridean Whale and Dolphin Trust (HWDT) survey vessel *Silurian*. Survey effort and detection data were pooled for all years and then partitioned into ‘monthly’ (for April – September) and seasonal (S1: April – June; and S2: July – September groupings) to investigate intra-annual patterns. Modelling methods were similar to those used in Chapter 3; Generalised Estimating Equations models (GEEs) were used to investigate relationships between the relative density of harbour porpoises and biotic and abiotic covariates. Models built using the visual and acoustic datasets were treated separately to account for the different survey biases in the data collection methods. The best models for the monthly datasets for both visual and acoustic datasets showed variation in the covariates that were important in each month. However, depth and slope were consistently retained in acoustic models. These patterns indicate some variability in porpoise habitat usage (and/or detectability) between April and September. They may also be a reflection of the temporal scales used and that the survey effort was too coarse to capture very fine scale temporal variations in the data. Despite these variations in predicted habitat preferences, the predicted distributions for each of these models indicated a general inshore pattern for the species, though there were some variations between months, and it was difficult to determine any one region that was consistently

important over any other. In the seasonal analysis consistent patterns of habitat preferences and distribution were observed in both the S1 and S2 periods from both the visual and acoustic data, which suggest this may be a more appropriate temporal resolution at which to analyse these data. A number of inshore regions were important, similar to what was observed in the full models of Chapter 3. Finer scale variations in habitat preference are investigated in Chapter 5. These findings can be used to determine whether a temporal aspect should be considered in the boundaries of areas suitable for designation as SACs for harbour porpoises.

4.1 Introduction

The efficacy of marine protected areas (MPAs) as a management tool for conservation is dependent on appropriate design and management measures (Agardy 1994; Agardy 2000). In the designation of an MPA, boundaries will typically be placed using the static factors that help explain a species distribution, providing a biological rationale for the spatial limits of an MPA. However this may not be the best design, as species distribution may vary temporally depending on fluid environmental characteristics as well as the movements and abundance of prey species and the potential for breeding (during certain periods) (Wilson et al. 2004). Consequently, it is crucial to have an accurate knowledge of the target species' distribution and whether its habitat usage is subject to significant temporal variations (Agardy 1994; Cañadas et al. 2005; Hooker et al. 1999; Rayment et al. 2010) so that the spatial (and possibly temporal) boundaries of a protected area can evolve with improving knowledge, to ensure appropriate management for the species.

Many cetacean species have been found to exhibit seasonal changes in distribution and/or behaviour (Ballance et al. 2006; Baumgaertner and Mate 2005; Cañadas and Hammond 2008; Forney and Barlow 1998; MacLeod et al. 2004; Mattila and Clapham 1989; Moore et al. 2000; Neumann 2001; Northridge et al. 1997; Reilly 1990; Siebert et al. 2006; Tynan et al. 2005; Walker 1996; Weir et al. 2007). The best studied seasonal movements are the long, annual migrations that a number of baleen whales species make between profitable feeding grounds and appropriate breeding/calving grounds (Jones and Swartz 2002; Payne 1983; Whitehead and Moore 1982). Other species make intra-annual inshore/offshore movements, most likely to take advantage of meso- and macro-scale shifts in prey distribution (Cañadas and Hammond 2008; Neumann 2001) and similar intra-annual shifts have been observed in dolphin species around the UK (Northridge et al. 1995; Wilson et al. 1997).

Seasonal changes in distribution may also be accompanied by a shift in acoustic behaviour. For example, Jacobs et al. (1993) documented a change in bottlenose dolphin vocal behaviour between summer and autumn months, attributing a doubling in vocalisation rates to a shift from mostly socialising behaviour during the summer, to mainly foraging during the autumn. A similar pattern has been observed in bowhead whales with increased vocalisation rates and a wider vocal repertoire being employed during spring compared with during the winter periods (Tervo et al. 2009).

A number of studies have observed seasonal shifts in harbour porpoise distribution and/or occurrence (Gilles et al. 2009; Northridge 1995; Siebert et al. 2006; Teilmann et al. 2008; Verfuß et al. 2007). Northridge (1995) observed, from aerial survey data collected between 1978 and 1988 in the Gulf of Maine, that animals were generally more dispersed across the region in June than in April and May. Additionally, they observed that animals were aggregated in the northern of the area during July - September (Northridge 1995). Incidental sightings and strandings data collected over a decade in the German Baltic and North Seas revealed a 'strong seasonality' in harbour porpoise occurrence with the highest numbers in during July and August (Siebert et al. 2006). However, methods used in that study had some biases in the data collection, in that there was unequal sightings effort and differing lengths of time of submersion for the stranded carcasses. A study using porpoise echolocation data loggers (T-PODs) observed a significant increase in porpoise positive days in July – September when compared with activity in January – March, whilst observing that porpoises were present throughout the year in the region (Verfuß et al. 2007). Gilles et al. (2009) conducted aerial surveys in the German North Sea to further investigate annual habitat usage patterns. They observed that porpoises moved into 'distinct areas' in spring months, with peak encounter rates in May and June. This suggests that in this region animals become more evenly dispersed in the autumn months, with this dispersion starting in September (Gilles et al. 2009). Teilmann et al. (2008) used a combination of satellite tagging, aerial surveys and shipboard surveys to investigate high-density regions and found seasonal variability in the relative importance of particular regions in waters in Denmark.

Harbour porpoises have been observed around Scotland throughout the year, though there have been higher encounter rates recorded in summer months (Evans et al. 2003; Reid et al. 2003; Weir et al. 2007). Weir et al. (2007) investigated harbour porpoise distribution off the east coast of Scotland and observed that porpoises were present throughout the year. No animals were detected in January and February but detection rates generally increased from March, peaking in August and September, before decreasing in October (Weir et al. 2007).

While a number of studies have observed seasonal changes in distribution and/or occurrence, very few studies exist that have investigated seasonality in habitat preferences in harbour porpoises. A study in the Bay of Fundy included an intra-annual measure in the form of ‘lateness of season’ when investigating habitat preferences of harbour porpoises (Watts and Gaskin 1985). However, it was found that it was not significantly correlated with mean sighting frequency. A study in the eastern Pacific Ocean documented shifts in habitat preferences in harbour porpoises between the spring (May and June) and summer (July and August) (Tynan et al. 2005). Animals were more commonly associated with high-salinity upwelled water during the spring months, which occurred close to shore. In summer, animals were found further offshore, once again correlating strongly with the location of an upwelling which had shifted (Tynan et al. 2005). In an earlier analysis using some of the data used in this study and different analytical methods, porpoise habitat preferences and distribution were investigated on the west coast of Scotland (Embling 2007; Embling et al. 2010). Month was not retained in the best models, indicating that in that analysis it was not a significant factor impacting porpoise detection rates in those models. Other studies of harbour porpoises habitat preferences have data collected over a limited time period or have not included month as a covariate in the analysis (Bailey and Thompson 2009; MacLeod et al. 2007; Marubini et al. 2009).

In Chapter 3 I investigated the inter-annual variations in harbour porpoise habitat preferences and distribution on the west coast. I found when investigating the full models, that there was significant intra-annual variation in porpoise detection rates, as ‘month’ was retained in both the best visual and acoustic models (§3.3.1 and §3.3.2). In this study, I investigated intra-annual variations in harbour porpoise distribution and habitat preferences off the west coast of Scotland by building individual monthly and seasonal models (using a pooled six-year dataset). The key aims of this work were: (i) determine whether clear monthly or seasonal shifts in distribution and habitat preferences exist in this region and if so (ii) to determine if any intra-annual patterns need to be considered in a protection framework for harbour porpoises in this region. This work is ultimately aimed at improving knowledge of harbour porpoise distribution and habitat usage off the west coast of Scotland to inform future conservation and management efforts.

4.2 Materials and Methods

The methods used in data collection, processing and modelling are described in §2.1, §2.2 and §2.3 respectively. Raw survey and detection data and how they were processed for this analysis are outlined in §2.4.

4.3 Results

4.3.1 Monthly Models

4.3.1.1 Visual Models

Visual survey models were built for each of the six months over which surveys were conducted. The best models constructed for each month and selected covariate relationships are shown below (Table 4.1 and Figure 4.1). In general, the best models were quite different among months, with different covariates being retained in each monthly best model.

Of the survey variables included in the visual models, sea state was the most commonly selected, being retained in five of the six monthly models (not included in April). Harbour porpoises sighting rates were highest between Beaufort sea states 0 and 1 but decreased markedly once sea states increased > 1. Boat speed was included in three of the six monthly models; detection rates decreased as boat speed increased. Year was retained in two of the six best monthly visual models: in August and September. In both months, no clear pattern was observable, with detection rates fluctuating among years. The highest detection rates were observed in 2005 and 2007 in both these months.

Table 4.1– Covariates retained in the best monthly visual models for each month of the survey. An ‘X’ is marked if a covariate was retained. Details of covariates are in §2.1.4.

Data	Model	Time		Survey			Sediment			Tidal				Topographic		
		Year	Month	Sea State	Boat Speed	Time of Day	Percentage Gravel	Percentage Sand	Percentage Mud	Position Relative To Tidal Range	Position in Daily Tidal Cycle	Current Speed	Maximum Spring Tidal Range	Depth	Slope	Distance to Land
Visual	<i>April</i>											X	X		X	
	<i>May</i>			X	X					X		X			X	
	<i>June</i>			X												X
	<i>July</i>			X	X									X		
	<i>August</i>	X		X						X				X	X	
	<i>Sept.</i>	X		X	X		X						X	X		X

Tidal variables: Spring Tidal Range (STR) and ‘Position Relative to Tidal Range’

(Rel.TidalRange) (defined in §2.1.5) were both retained in two models. STR was retained in the April and September models. In April, the most animals were observed in regions with STR of > 4 m. In September, peak detection rates were observed in regions with STR <1.5 m and > 4 m. In both cases, significantly lower detection rates were observed in regions with STR >2 and

< 4 m. Current Speed was retained in April and May, with highest detection rates observed in current speeds of between 0 – 0.5 ms⁻¹ in April. In May, detection rates peaked in low current speeds (< 0.2 ms⁻¹) and slowly decreased as current speeds increased. Position relative to tidal range was retained in the best models for May and August. However, different patterns were observed among months, e.g. in May, peak detections were observed close to neap tides whilst in August, the highest detection rates were observed in the tidal phase between full neaps and full spring tides.

Of the topographical covariates, either depth or slope was retained in five of the six monthly visual models. Slope was retained in April, May and August and sighting rates increased almost linearly, as the degree of seabed slope increased. Depth was a significant predictor in July, August and September and in all months a parabolic relationship was observed; in July the highest detection rates were observed in waters between 100 – 200 m depth and in August & September a narrower peak was observed between 50 – 150 m. Distance to land was retained in June and September and in both months detection rates decreased as distance from shore increased. In June, sightings decreased slowly out to 20 km from land and then the relationship flattened out. However in September, detection rates decreased markedly out to 3 km from land, then decreased slowly out to 20 km, beyond which no detections were made.

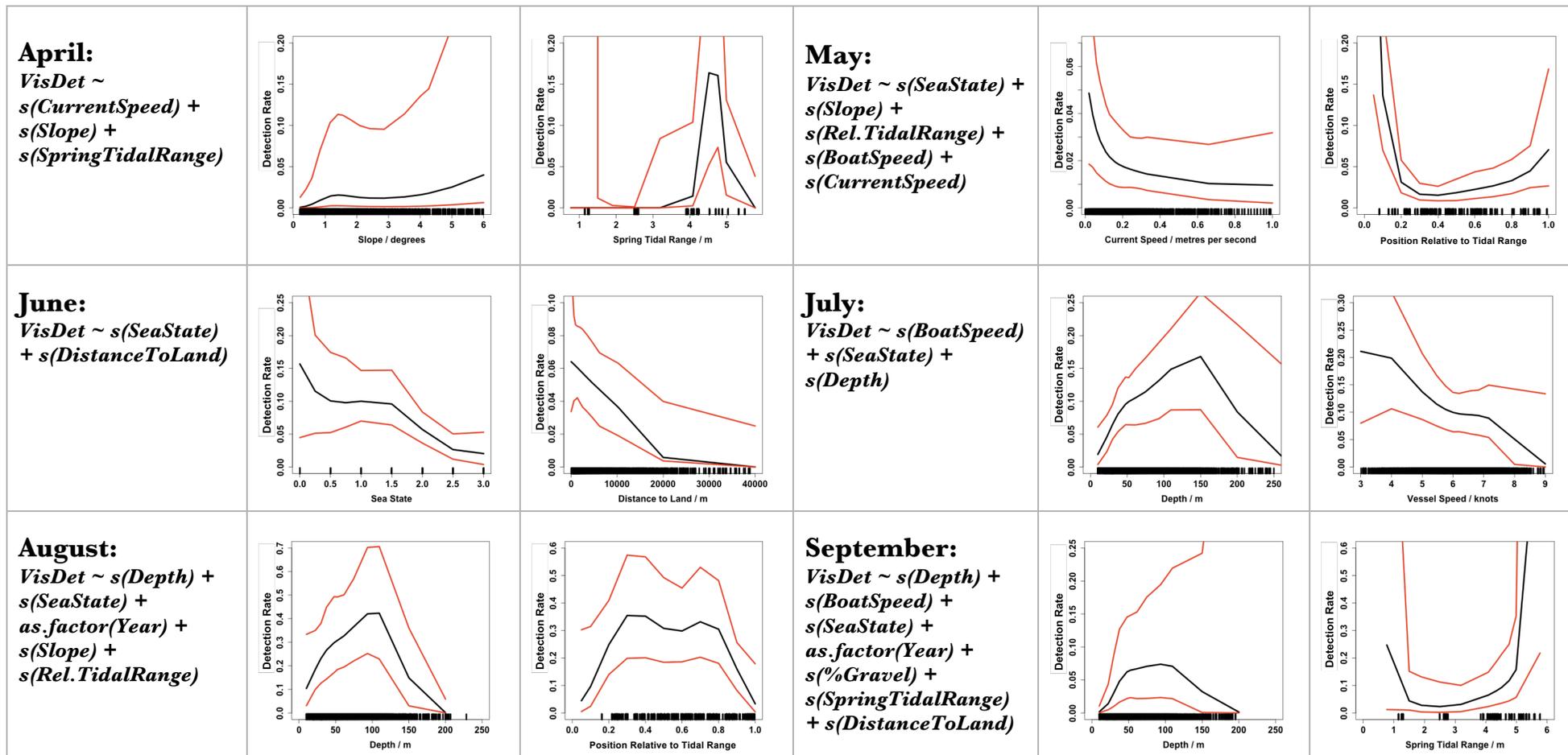


Figure 4.1–The model structure for each monthly visual model (s = fitted as a smoothed term, $as.factor$ = fitted as a categorical term) along with selected relationships (black lines) from each model. 95% confidence intervals are shown (red line).

The performance of the monthly models was evaluated using the cross-validation method, assessing predictive performance over 1,000 iterations (see §2.3.3 for full details). Values of F close to 1 indicate the models are capturing the underlying processes that generated the data (Table 4.2). Scores for the visual monthly models indicated there was variability in the performance of models. The models for April, May, June and September had F values ranging from 0.417 to 0.570 indicating they were not capturing all of the patterns that generated the data. In July and August, the F scores were higher (0.725 and 0.804 respectively) indicating that those models performed better, but in neither model did the 95% confidence intervals include 1.0, indicating that the models did not capture all of the underlying relationships in the data.

Table 4.2–Results of the model evaluation for the visual and acoustic monthly models. F scores and 95% confidence intervals are shown.

Model	Visual		Acoustic	
	Cross Validation Score (F)	95 % C.I.	Cross Validation Score (F)	95 % C.I.
April	0.570	0.363 - 0.782	1.157	1.140 - 1.174
May	0.417	0.382 - 0.451	1.000	1.000 - 1.000
June	0.530	0.503 - 0.556	1.000	1.000 - 1.001
July	0.725	0.690 - 0.762	1.000	1.000 - 1.001
August	0.804	0.643 - 0.964	1.000	1.000 - 1.000
September	0.462	0.374 - 0.550	1.040	1.036 - 1.044

Despite variations in the best model structures among months, some generally consistent inshore patterns observed in the predicted distributions for each of the visual monthly models (Figure 4.2 a - f). As stated above, the visual monthly models failed to capture all of the underlying processes best explaining porpoise distribution and this should be considered when interpreting the predicted surfaces. The distribution maps in April, May, August and September are relatively similar, with higher predicted relative densities being found in the inshore regions, and lower predicted relative densities in more open-water regions. In June, this pattern is more extreme, with predicted relative densities being much higher close to land. In July, a more ‘offshore’ distribution is predicted with highest predicted relative densities in the NW of the study region, in particular the Sea of Hebrides, The Minch and Little Minch. In this month, in the inshore regions of the SE of the study regions, the lowest predicted densities were found, though reasonably high-predicted densities were predicted for some regions of the southern Sound of Jura. Some of the predictive surfaces look quite ‘patchy’ – i.e. cells with high-predicted relative densities adjacent to cells with low predicted densities.

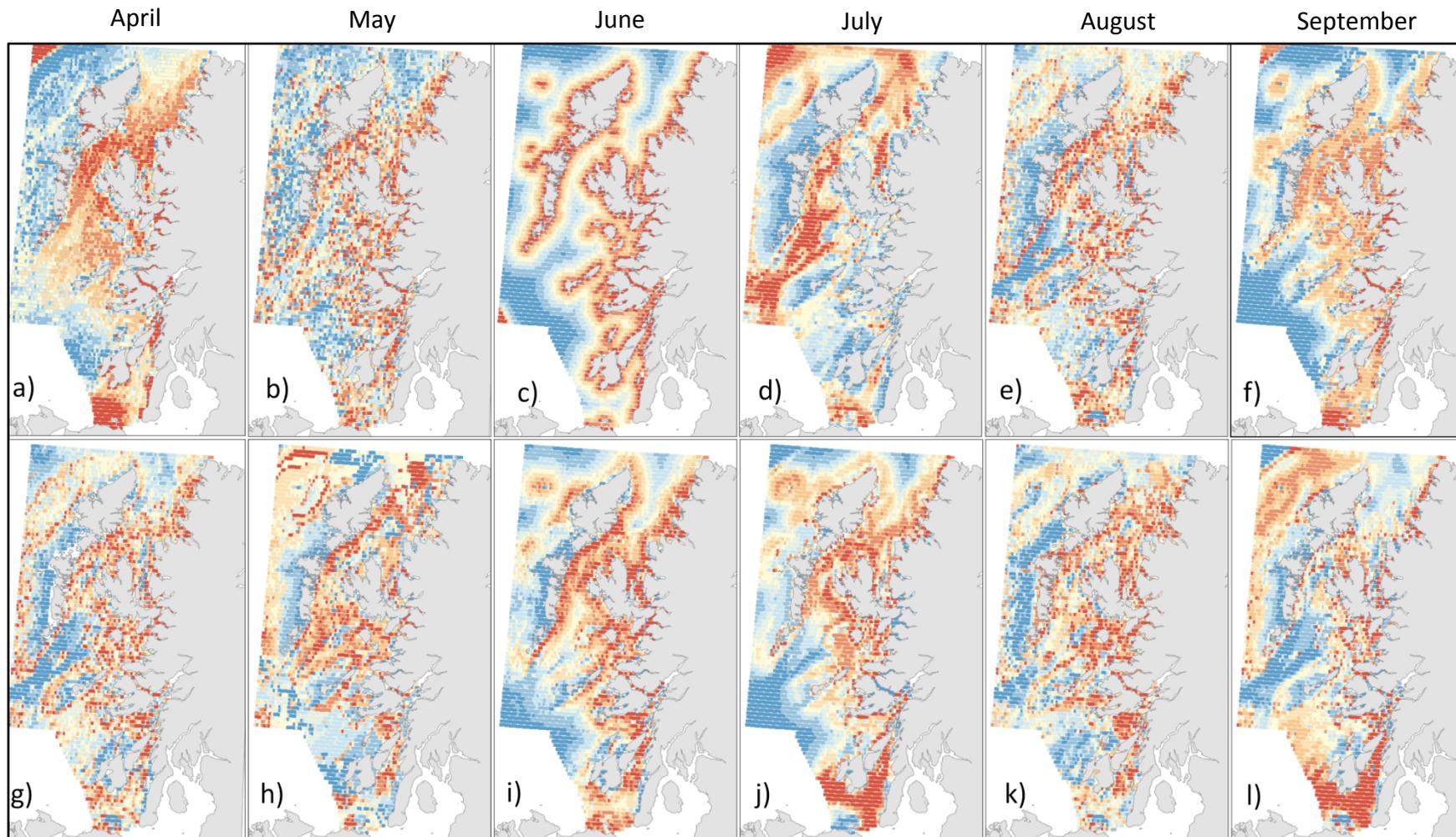


Figure 4.2 – Predicted distributions for the monthly visual (a-f) and acoustic (g – l) models. For temporally varying covariates, fixed values were chosen to predict with the highest confidence (i.e. peak values where confidence intervals were narrowest). Colour gradation in each map is based on eight quantile levels (the densities that correspond to the 12.5th, 25th, 37.5th, 50th, 62.5th, 75th, 82.5th percentiles) of the predicted harbour porpoise densities from each model (animals per km).

4.3.1.2 Acoustic Models

As with the visual monthly models, acoustic data were used to construct individual models for April – September to investigate intra-annual variations in distribution and habitat preference. The best models for each month are shown below (Table 4.3 & Figure 4.3). As observed with the visual monthly models, there was some variation in which covariates were important in explaining variation in harbour porpoise distribution.

Table 4.3–Model structures for the best acoustic monthly models for April – September. An ‘X’ signifies that a covariate was retained.

Data	Model	Time		Survey			Sediment			Tidal			Topographic			
		Year	Month	Sea State	Boat Speed	Time of Day	Percentage Gravel	Percentage Sand	Percentage Mud	Position Relative To Tidal Range	Position in Daily Tidal Cycle	Current Speed	Maximum Spring Tidal Range	Depth	Slope	Distance to Land
Acoustic	<i>April</i>	X										X		X	X	
	<i>May</i>				X		X	X	X					X	X	
	<i>June</i>				X					X		X		X	X	X
	<i>July</i>	X			X							X		X		X
	<i>August</i>	X			X				X					X	X	
	<i>Sept.</i>	X			X							X	X	X	X	

Boat speed was retained in five of the six monthly models (not a significant predictor in April), with detections decreasing as boat speed increased. Year was retained in four of the six monthly models and in these cases, acoustic detection rates varied a lot among years, with peak detection rates in 2005 in the July and August models and a peak in 2007 in the April and September models.

Spring tidal range was retained in the July and September models and in both months peak detection rates were observed where STR was between 0 – 2 m and 4 – 6 m. Position relative to tidal range was significant in July when peak detection rates were observed during neap tides, decreasing as the values increased up to 0.5 (representing the periods between neap and spring tides), then increasing slightly approaching periods of spring tides. Current speed was retained in the best models from the April and June datasets. In April, peak acoustic detection rates were observed at 0.3 ms⁻¹, beyond which rates decreased. In June, detection rates increased as current speeds increased towards 1 ms⁻¹.

Sediment covariates were retained in two of the six months (May & August): in May detection rates were highest when mud made up >70% of the sediment and when gravel and sand were approximately 10 – 30 % of the sediment. In August, percentage mud was retained; a general increase in detection rate was observed as % mud in the sediment increased.

The most consistently retained covariates were the ‘topographical variables’ water depth and seabed slope, which were retained in every monthly acoustic model. Slope was retained in five of the six monthly acoustic models (not in July) and depth was retained in all of the monthly models. Detection rates increased as slope increased. Areas with water depths between 50 – 150 m were most important, though in June a slightly wider peak depth range was observed between 80 – 180 m. The almost linear relationship between detection rates and slope remained relatively constant through the study period. Distance to land was retained in the June and July models, with detection rates decreasing as distance from land increased.

The monthly acoustic models were assessed with a cross-validation method (Table 4.2). Results indicated that all of the acoustic models captured the underlying patterns that generated the data (i.e. all values were close to or were equal to 1). In April and September, the *F* scores were >1 with values of 1.157 and 1.040 respectively.

Predicted surfaces were generated for each acoustic monthly model and, similar to the visual models, there was some variation in predicted distributions observed among months (Figure 4.2 g – l). In general, an inshore distribution was observed with high densities predicted for the coastal regions surrounding the Small Isles, The Firth of Lorn, the Sound of Jura and throughout the Minch. Low relative densities were predicted in the offshore regions in the southwest, e.g. the Sea of Hebrides. Particularly high relative densities were generated for the Sound of Jura and south of Islay from June to September. Also in September the region to the west of the Outer Hebrides had reasonably high relative densities. The predicted distribution using the acoustic model for May looks quite different to the other monthly model surfaces. However the model evaluation indicated that the model performed well in representing the patterns that were generated in the data.

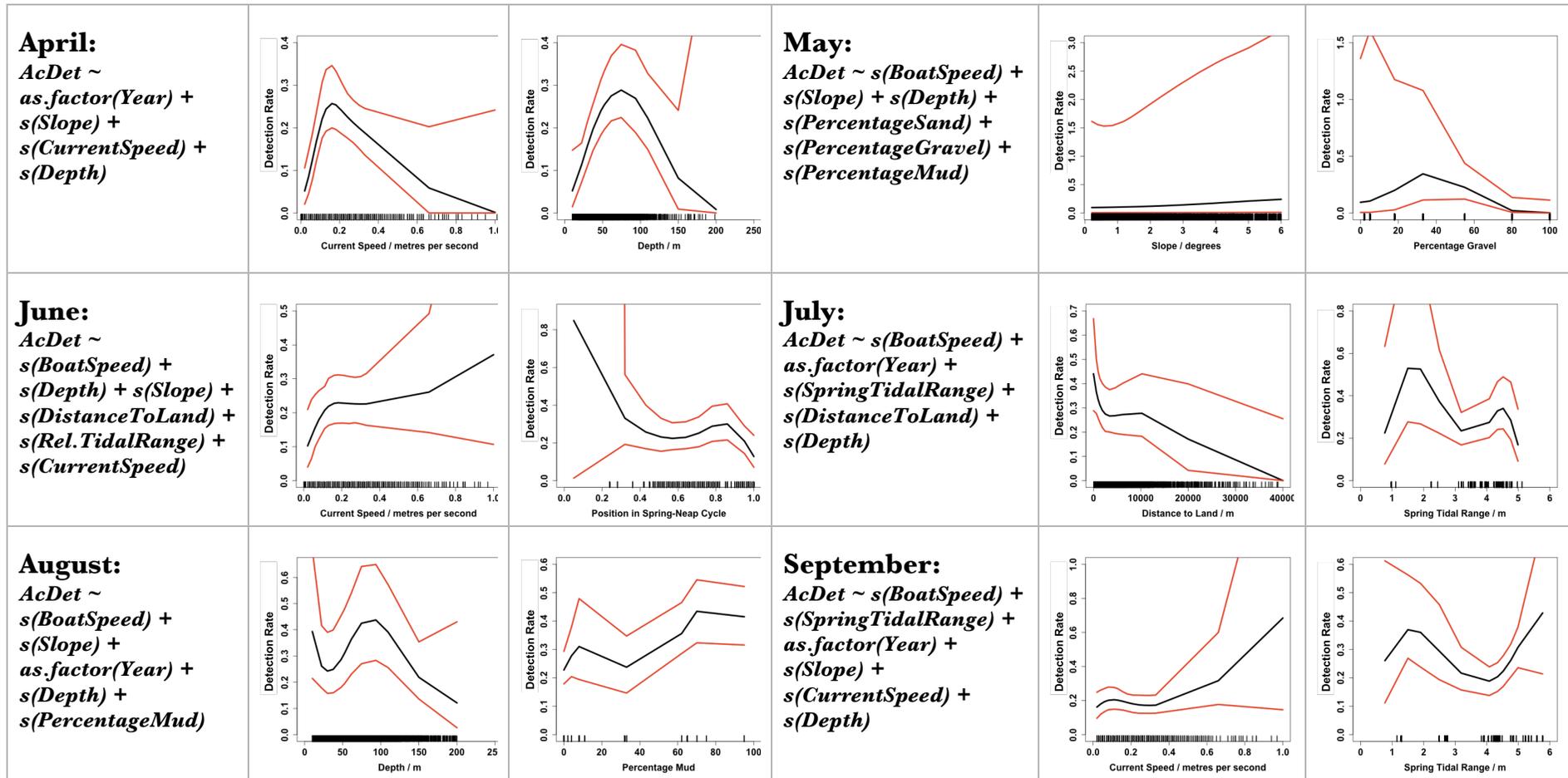


Figure 4.3 - The model structure for each monthly acoustic model (s = fitted as a smoothed term, $as.factor$ = fitted as a categorical term) along with selected relationships (black lines) from each model. 95% confidence intervals are shown (red line).

4.3.2 Seasonal models

To investigate intra-annual variations in porpoise distribution and habitat preferences at a coarser temporal scale, monthly data were grouped together into seasonal groupings. Models were constructed for April, May and June combined (S1) and July, August and September (S2) treating the visual and acoustic datasets separately. The best visual and acoustic models for each season and selected covariate relationships are shown below (Table 4.4 and Figure 4.4).

4.3.2.1 Visual Models

Survey variables sea state and boat speed were retained in both the S1 and S2 visual models. Porpoise sighting rates were highest during sea states between 0 and 1, beyond which they decreased markedly. Sighting rates also decreased almost linearly as boat speed increased. Position relative to tidal range was an retained in visual model, although the relationship was different between S1 and S2. In S1, peak detection rates were observed at values < 0.2 and > 0.8 . Conversely, during S2 detection rates were lowest during neap tide periods and slowly increased towards spring tides, before decreasing again during spring tide periods. Depth and slope were both retained in the S1 and S2 models. Porpoise sighting rates increased as slope increased in both models and parabolic relationships were observed between detection rates and depth. In S1, peak detection rates were observed between 60 – 110 m and in S2 a wider peak was observed, with the highest detection rates in areas of 50 – 150 m water depth. In the S1 visual model, distance to land was retained, with decreasing detection rates as distance from land increased. In the S2 model, percentage sand in the sediment was retained, with the two peaks observed – the highest detection rates were in regions with sediment with either between 0 and 40 % or >80 % sand.

Table 4.4–Best model structures for the S1 (April – June)& S2 (July – September) visual and acoustic models. An ‘X’ indicates that

Data	Model	Time		Survey			Sediment			Tidal				Topographic		
		Year	Month	Sea State	Boat Speed	Time of Day	Percentage Gravel	Percentage Sand	Percentage Mud	Position Relative To Tidal Range	Position in Daily Tidal Cycle	Current Speed	Maximum Spring Tidal Range	Depth	Slope	Distance to Land
Visual	Season 1			X	X					X				X	X	X
	Season 2			X	X			X		X				X	X	
Acoustic	Season 1	X	X		X		X					X		X	X	X
	Season 2	X	X		X							X		X	X	X

The performance of the S1 and S2 models was investigated using the same cross-validation method as used in sections §4.3.1.1 and §4.3.1.2. Model evaluation (F) scores of 0.535 and 0.731 (with neither set of confidence intervals including 1) indicated that the visual models were not capturing all of the underlying processes generating the data (Table 4.5).

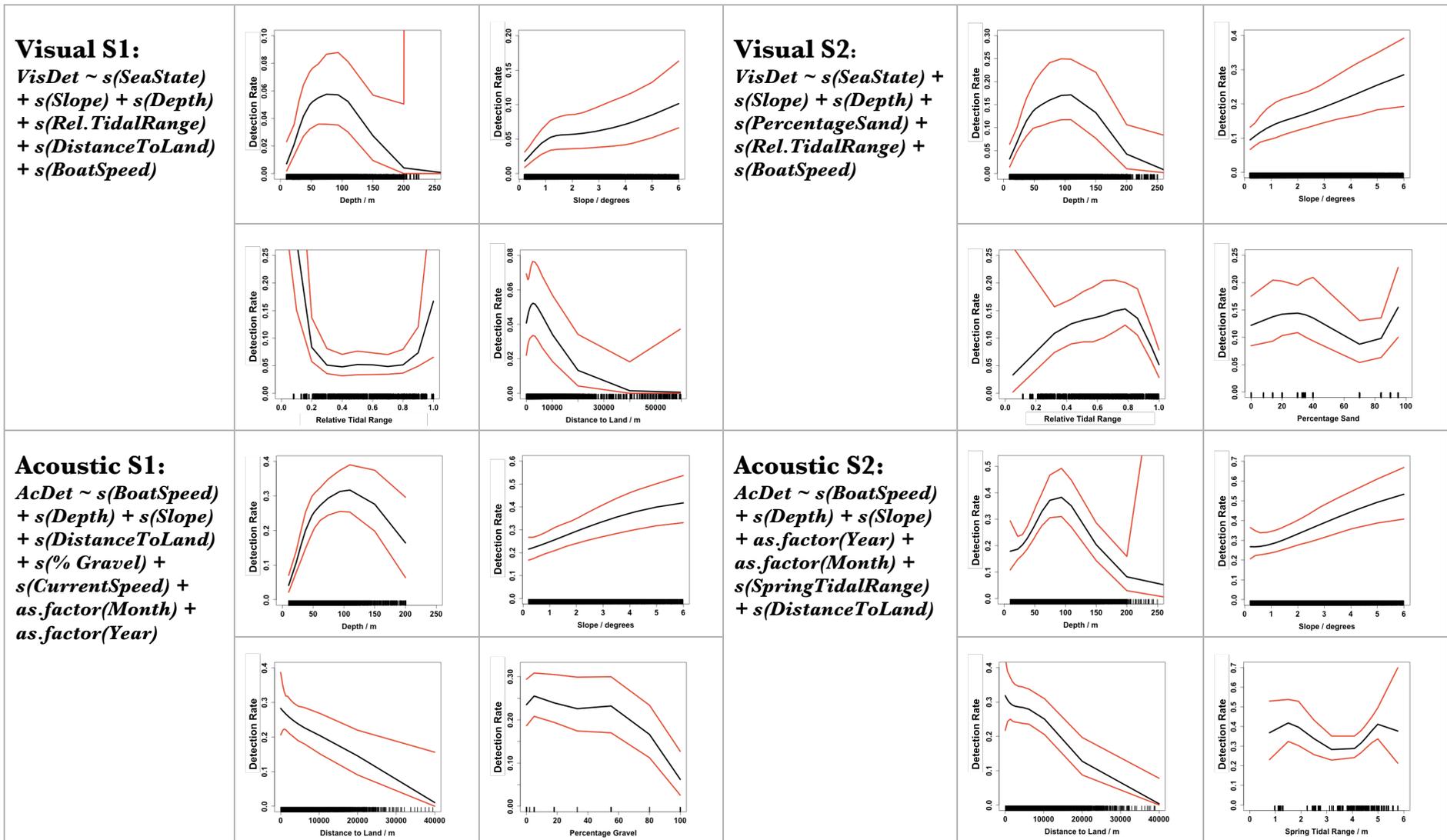


Figure 4.4 - The model structure for each of the best visual and acoustic S1 (April – June) and S2 (July – September) models (s = fitted as a smoothed term, $as.factor$ = fitted as a categorical term). Selected relationships are shown from the models (black lines). 95% confidence intervals for the relationships are shown (red line).

Table 4.5 – Model evaluation scores for the best S1 and S2 visual and acoustic models. 95% confidence intervals are also shown.

Model	Visual		Acoustic	
	Cross Validation Score (<i>F</i>)	95 % C.I.	Cross Validation Score (<i>F</i>)	95 % C.I.
S1	0.535	0.451 - 0.621	0.994	0.993 - 0.995
S2	0.731	0.704 - 0.758	1.000	1.000 - 1.000

The predicted surfaces for the S1 and S2 visual models look very similar (Figure 4.5 a & b), although the S2 distribution pattern has slightly higher densities away from the shore. A strong inshore pattern was observed in S1, and in both models the highest predicted relative densities occurred in the east coast of Outer Hebrides island chain, the Little Minch, the Small Isles, the Firth of Lorn and the Sound of Jura. There are some differences in predicted distributions between the S1 and S2 periods. Low relative densities were predicted for the waters west of Mull in S2, though this was an important area during S1. Also in S2, the deeper waters of the Minch become more important.

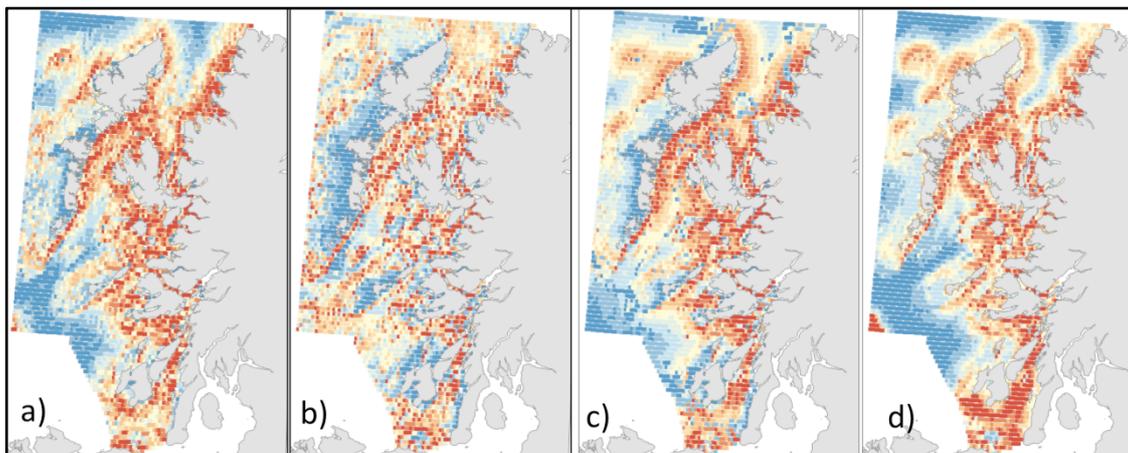


Figure 4.5–Prediction distribution for the (a) visual S1, (b) visual S2, (c) acoustic S1 and (d) acoustic S2. For temporally varying covariates, fixed values were chosen to predict with the highest confidence (i.e. peak values where confidence intervals were narrowest). Colour gradation in each map is based on eight quantile levels (the densities that correspond to the 12.5th, 25th, 37.5th, 50th, 62.5th, 75th, 82.5th percentiles) of the predicted harbour porpoise densities from each model (animals per km).

4.3.2.2 Acoustic Models

In the acoustic S1 and S2 models, the model structures were quite similar (Table 4.4). In both models, boat speed was retained, with acoustic detections rates decreasing as vessel speed increased. Both year and month were retained in the best models as factor variables indicating

significant variations both among years and within the S1 and S2 periods. In S1, detection rates generally increased from 2004 through to 2008 (though detection rates in 2005 were low) with the highest detection rates observed in 2007 and 2008. In S2, there was no clear trend in detection rates, though 2005 had the highest rates. Monthly peaks were observed in May (in S1) and August (in S2). Both depth and slope were retained in the best S1 and S2 models, with detection rates increasing almost linearly as the degree of slope increased. Peak detection rates were observed in waters between approximately 50 – 150 m depth in S1 and S2. Distance to land was found to impact porpoise acoustic detection rates, with rates decreasing almost linearly as distance from land increased. In the S1 model, current speed was retained, as detection rates increased with increasing current speeds. Percentage gravel in the sediment was retained in the S1 acoustic model. Detection rates were almost constant from 0 – 50%G but decreased once %G increased > 50%. In the S2 model, spring tidal range was retained with peak detection rates being observed in regions with STR of < 2 m and > 4 m.

Model evaluation of the acoustic S1 and S2 models revealed that both models were strong representations of the patterns that generated the data (with both *F* scores being very close to, or equal to 1)(Table 4.5).

The predictive maps generated from the acoustic data are visually similar to those produced using the visual models (Figure 4.5) and show little distribution change between the S1 and S2 periods. In both S1 and S2 acoustic plots, a strong inshore distribution was observed with high predicted densities for the coastal Minch, the Little Minch, around the Small Isles, west of Mull, the Firth of Lorn and Sound of Jura. Additionally, to the northwest of the Outer Hebrides, reasonably high relative densities were predicted. The low predicted relative densities were observed in the offshore regions in the southwest of the study area.

4.4 Discussion

Cetacean species distribution and habitat usage are known to vary temporally, both among years and within the year (Mate and Urban 2005; Mate et al. 1999; Neumann 2001; Northridge et al. 1997; Reilly and Fiedler 1994). Investigating inter-annual variations in harbour porpoise distribution was the focus of Chapter 3 and here intra-annual variations in habitat preferences and distribution were investigated. Harbour porpoise densities were studied using visual and acoustic datasets, which were split into monthly and seasonal groupings and modelled with GEEs to determine the static and fluid environmental characteristics that explained variation in porpoise distribution.

4.4.1 Model performance

All of the models constructed in this study were evaluated using a cross-validation method (§2.3.3) to determine how much of the underlying relationships in the data were captured by the models. In both the monthly and S1 and S2 models, the visual models generally performed less well than the acoustic models, which were good representations of the patterns in the data. All of the visual models had F scores with confidence intervals not including 1, indicating that they were failing to capture some of the underlying processes that generated the data. The acoustic models all appeared to perform well (all F scores were close to or equal to 1) indicating they were strong representations of the patterns that generated the data. This should be considered when assessing the results of the visual models.

4.4.2 Impact of survey variables on models

Survey covariates sea state and boat speed were important factors affecting the monthly and seasonal models. Sea state was retained in seven of the eight visual intra-annual models (not in the April model) and in all cases it heavily impacted visual surveys for harbour porpoises with sighting rates decreasing in sea states > 1 . The findings here are similar to what was observed in Chapter 3, but also are consistent with a number of boat-based surveys for harbour porpoises (Embling et al. 2010; SCANS-II 2008) and was best described by Palka (1996). In five of eight visual models and seven of eight acoustic models, the speed of the survey vessel impacted detection rates. In all models where boat speed was retained, detection rates decreased as vessel speed increased. As discussed in Chapter 3, the negative impact of boat speed may be explained by the amount of time spent surveying in each survey segment. As explained in methods (§2.3.1), survey effort was organised into 2 km segments. Low average speeds (e.g. 3 - 4 knots) lead to more time being spent surveying during each 2 km segment while higher average speeds (8 - 9 knots) result in less time being taken to survey over each 2 km segment. This may be particularly problematic in heavily tidal regions, where boat speed is influenced by tidal currents, leading to an increase or decrease in survey time depending on the direction of travel. Variation in boat speed was not retained in any of the best models indicating that changes in boat speed were not impacting the detection of harbour porpoises.

4.4.3 Monthly Variations

A large amount of variation was observed in the model outputs for the visual and acoustic monthly models. There were few consistent patterns in terms of the environmental covariates retained in the best visual models. In the acoustic monthly models, depth and slope were selected in almost all of the best models, and in each case a consistent relationship was observed:

detection rates were highest in highly sloped regions with water depths between ~ 50 and ~ 150 m in each case. A wider depth preference was observed in the visual model for July, with the peak detection rate being observed between $\sim 100 - 200$ m.

The variability observed in the covariates retained in the monthly models is discussed below but some generally consistent patterns were observed in the predicted distributions from those models, despite different covariates being important in explaining porpoise distribution in each month. In both the visual and acoustic models, there is a general inshore pattern observed, but the extent to which this is clear varies considerably among models. The predicted densities for the more temporally consistent seasonal models are discussed below (§4.4.5).

The distribution and habitat usage of a highly mobile species with complex ecology such as the harbour porpoise will be impacted by both extrinsic (i.e. biological and oceanographic) and ‘intrinsic’ (i.e. foraging ecology, reproductive strategy, social structure and inter-specific relationships) factors. In order to develop effective conservation measures, it is necessary to consider both of these sets of factors so that a better understanding of the species ecology can be attained. In the present study, it was not possible to determine or record many of the ‘intrinsic’ factors, which might have shed light on the patterns observed here. In previous chapters we have modelled at a more coarse temporal scale and it is likely that by including data collected throughout the year that a range of behaviour will have been encountered and be included in the data. However at the temporal resolution of this study, these monthly variations may be explained by shifts in behaviour, foraging ecology, social structure and inter-specific relationships.

When porpoises are detected the behaviour of the animals is often not clear. When an animal is detected during a survey it may be foraging, travelling between foraging spots or engaged in social interaction – all intrinsic factors that may impact habitat use. However, at the time of detection it was not possible to determine behavioural state, and thus, making inferences about habitat usage is complicated. However, there may also be other, finer-scale temporal changes in intrinsic factors that are not captured in the data analysed here.

Harbour porpoises breed in July and the bulk of neonate calves are observed in June and July suggesting a strongly seasonal reproductive period (Lockyer 1994). No clear change was observed in habitat preference or distribution for these periods, suggesting that if any shift in habitat usage exists in response to reproductive activity, it is not reflected in the data here.

Calves were occasionally sighted during visual survey effort, and when the presence of a calf was confirmed it was recorded in the sighting record. However, due to the inconspicuous nature of harbour porpoise it can be difficult to identify calves in sightings, unless sighting conditions are excellent. No information on the presence of calves can be determined during acoustic detection because little is known about porpoise acoustic communication and neonate acoustic behaviour.

A further factor that may have impacted the interpretation of results, is that some fine-scale (10 m – 1 km) oceanographic features may be too large (or too small) and temporally variable to be captured in the survey effort conducted in this study. The size and duration of the feature or process will impact whether it can be captured in this survey effort (e.g. potentially only passing through an area once may not be sufficient to capture its importance). For example, temporally varying features, such as submeso-scale (1 – 10 km) eddies and rips operate on temporal scales lasting between a day and many weeks and spatial scales of between 1 – 10 km (Wakefield et al. 2009) and the full effects of such features may not be captured entirely by the survey effort.

4.4.4 Seasonal models

In the monthly visual and acoustic models, there was considerable variation among the best models for each month. Consequently, the distribution and habitat preferences of harbour porpoises were assessed at a more coarse temporal scale to investigate whether more consistent patterns exist within the year. The results of this study indicated that, at this temporal scale, harbour porpoise distribution was relatively constant throughout the year. The best visual seasonal models and the best acoustic seasonal models were very similar, with a suite of covariates retained in each model, with some small variations in best model structures.

In the best S1 and S2 visual and acoustic models, sea state, boat speed, water depth, seabed slope and distance to land or position relative to tidal amplitude were all retained. The impact of sea state and boat speed has been discussed in §4.4.2.

Slope has been important in influencing cetacean distribution in a number of studies (Acevedo and Burkhart 1998; Heinrich 2006; Tynan et al. 2005), probably because it serves to increase productivity and/or prey availability by impacting the movements of currents (Inall et al. 2009), providing an anchor point for eddies, rips and jets which have the potential to enhance prey densities making them important foraging spots (Mooers et al. 1979; Wakefield et al. 2009; Zamon 2003). As in Chapter 3, regions with maximum water depths between 50 – 150 m were where the highest detection rates were observed. Depth has been important in a number of

studies of harbour porpoise distribution and habitat usage. The relationship with depth observed in this study has been recorded in a number of other studies in this region (Embling et al. 2005; Goodwin and Speedie 2008; MacLeod et al. 2007; Marubini et al. 2009)(it should be noted that the Embling et al. (2005) work used some of the data used in this study, but with different analytical methods). This consistently observed preference for regions with water depths between 50 and 150 m in a number of models suggests that this preference is particularly important and temporally robust. The relationship between porpoise density and depth could potentially be explained by the availability of prey species in such regions as a number of fish species are known to inhabit a similar range of water depths, e.g. whiting: 40 – 200 m (Persohn et al. 2009); cod: 30 – 200 m (Santos et al. 2005) and sandeels: 30 – 120 m (Wright et al. 2000).

When comparing the covariate relationships between the models built using the S1 and S2 datasets, the majority of relationships were the same in both models. The exception in the visual models was the position relative to tidal range, which was retained in both the S1 and S2 models, but the occurrence of peak detection rates varied between these periods. In April – June, peak sighting rates were observed during periods of low tidal amplitude, i.e. neap tidal periods, and a second peak during periods close to full spring tides. Conversely, in the July – September model, detection rates were low during neap tides, but increased when tidal ranges were moderate, peaking around spring tides. It is not clear why porpoise sightings would be influenced by proximity to spring or neap tides or why there are two distinct patterns observed between S1 and S2. Variation in detection rates with position in the spring-neaps cycle has been observed in other studies of harbour porpoises and there is no clear consensus in the literature of its functional significance. Embling et al. (2010), in an earlier analysis of some of the data used here, observed peak sighting rates during spring tides and attributed this to porpoise being more active during spring tides, perhaps due to vigorous surface foraging activity. Prey are likely to be more concentrated during spring tides than neap tides due to the currents generated by the greater volume of water shifting in the tidal cycle. Conversely, however, studies have observed peak sighting rates during neap tides in the Bay of Fundy, with the explanation being that animals may have been avoiding extreme current speeds (Embling et al. 2010; Gaskin and Watson 1985). However, this may also be explained by a probable increase in sea state when tidal velocities are high which will likely impact visual detection (Palka 1996). Another possible explanation is that the variation observed is a response to specific prey movements. A number of fish species have been documented to use ‘tidal-stream transport’ to move around (Weihs 1978). Furthermore, some prey species of harbour porpoise may become more available to be preyed upon depending on the state of tide (Arnold 1981; Gibson 1978). It is not clear whether porpoise

behaviour is different during the spring, neap or intermediate tidal phases or how the behaviour of animals will affect their detectability but these subjects need to be further investigated in order to understand the observed patterns. Additionally, it is noteworthy that this covariate was not retained in the acoustic models, which perhaps indicates, that whatever factors are impacting harbour porpoise distribution or detection in the visual data, are not significantly impacting porpoise acoustic behaviour. Foraging sounds (known as 'buzzes' (Johnson et al. 2008; Miller et al. 2004)) were not easily detected in the acoustic dataset, though an investigation of the distribution of buzz detections may yield different results focused on foraging-related habitat preferences.

In the S1 acoustic model, current speed and percentage gravel were significant factors while in S2, these covariates were replaced by spring tidal range. In the April – June model, acoustic detection rates were highest in regions with high ($> 0.5 \text{ ms}^{-1}$) current speeds. Strong currents are known to play an important role in coastal environments - driving tidal eddies and rips and impacting the distribution of piscivorous predators (Mann and Lazier 2006; Zamon 2003), and they were important in a number of cetacean habitat studies (Calderan 2003; Embling et al. 2010; Johnston et al. 2005; Pierpoint 2008). Tidal eddies and rips form when tidal currents flow past headlands, prominent land masses or steep-sided channels creating temporally and spatially predictable changes in plankton distribution which fish populations take advantage of and thus can attract top predators (Wolanski and Hamner 1988; Yen et al. 2004; Yen et al. 2005; Zamon 2003). The inclusion of STR in the best S2 model, is likely to indicate that particular spatial regions were important during S2, as the STR where peak detections rates were observed only exist in the waters around Skye and in the south extent of the study region.

There were some other differences in the best models in S1 and S2. For example, in April – June, distance to land was retained but in the S2 model this was replaced by percentage sand in the sediment. In S1, detection rates decreased steeply from $<1 \text{ km}$ out to 20 km from land, beyond which detection rates slowly decreased out to the maximum distance from land of $>60 \text{ km}$. This suggests a strongly inshore distribution during April - June. It is possible that in this instance, distance to land is a proxy for more biologically meaningful features for example, freshwater input generally decreases as distance from land increases meaning higher salinity water further from shore. Plume fronts (influxes of freshwater meeting seawater masses) are common in inshore regions and lead to increased mixing and so an increase in productivity and aggregation (Mann and Lazier 2006). Capes and headlands can serve as anchor points for fronts, providing potential for increased productivity in the photic zone occurring close to shore,

which could also explain the observed pattern (Wakefield et al. 2009; Yen et al. 2004). The composition of the sediment was retained in July - September visual models as percentage sand was retained in the model. Detection rates were highest in regions with either 0 – 40 % or > 80 % sand. Acoustic detection rates were impacted by sediment composition during S1; the highest rates in regions with between 0 – 50 % gravel in the sediment. A preference for regions with between 40 – 60 % mud (and so sand/gravel making up some proportion of the remaining 40 – 60 %) was observed in an earlier study by Embling (2007), which used some of the data included in this analysis. A number of studies have investigated links between fish species and habitat preferences and found links to certain sediment types. It may be that this peak in harbour porpoise acoustic detections in muddy regions is linked to prey availability. Harbour porpoise diet is poorly understood in west Scotland but they are considered to feed on a wide range of prey species around the UK (Herr et al. 2009; Santos and Pierce 2003; Santos et al. 2005; Santos et al. 2004). Generally, whiting is thought to constitute the bulk of porpoise prey on the west coast of Scotland (Santos et al. 2004) and is known to inhabit muddy sand regions (Santos et al. 2005). Similarly, porpoises have been documented to feed on a number of flatfish species which inhabit predominantly muddy sediment (Herr et al. 2009).

4.4.5 Predicted distributions from seasonal models

The seasonal models were much more consistent than the monthly models, both in model structure and the predicted distributions. The predicted distributions were very similar, though the visual models were slightly ‘patchier’ than the acoustic surfaces (i.e. with high predicted relative densities next to low predicted densities). As with the models in Chapter 3, a generally inshore pattern was observed in all seasonal models. The main aim of this thesis is to identify consistently important regions for harbour porpoises on the west coast of Scotland and, in terms of management and conservation, a ‘manageable’ area suitable for designation as a special area of conservation. However, from these maps it is difficult to determine any one region, because high predicted densities are observed all over the inshore regions of the west coast of Scotland and the Hebridean islands. Investigating habitat preferences and distribution at finer spatial scales by constructing ‘regional’ models is the subject of Chapter 5.

In this study, due to spatial variations in survey extent, densities were predicted for some regions in which I had little or no survey effort (e.g. The Minch and Outer Hebrides in S1). Caution must be exercised when extrapolating predictions in this way, because for any model to be used to predict for areas with no survey data, the variables must be spatially robust and the relationships must be similar (Araújo and Guisan 2006; Boyce et al. 2002). The results of the S1

and S2 predicted distribution surfaces and the variations in survey extent over these periods indicate that, at that these spatial scales, there are similar patterns of distribution between the regions surveyed in S1 (the Inner Hebrides) and S2 (the Inner Hebrides, plus the Minch and Outer Hebrides).

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Chapter 5

Regional variation in habitat preference and distribution of harbour porpoises west of Scotland

5.0 Abstract

A key issue in the designation of a Special Area of Conservation is determining an area that is both consistently important to a species but also of a size that can be realistically managed. Identifying areas that are consistently important for highly mobile species such as the harbour porpoise is challenging. Previous chapters have identified that the inshore regions west of Scotland are all high-density areas for the species. The goal of this analysis was to determine manageable and consistently important regions that could be suitable for designation as SACs. An additional question was whether habitat preferences for harbour porpoises varied among regions or whether they were homogenous across the entire study region. Designed line-transect visual and towed-array acoustic surveys were conducted between 2003 – 2008 and 2004 – 2008, respectively, from the Hebridean Whale and Dolphin Trust (HWDT) survey vessel *Silurian*. Data were partitioned into smaller regions and modelled individually using Generalised Estimating Equations (GEEs) and relationships between the relative density of harbour porpoises and a suite of oceanographic covariates were investigated. Visual and acoustic datasets were modelled separately to account for the different survey biases in the data collection methods. Depth and slope were retained in the majority of models, and their relationship with the response was consistent, indicating that there was consistency in the patterns of usage throughout the west of Scotland and that these features are important to the species in some function. The other covariates retained in the best models varied among regions indicating that there is still variation in the important features across the west coast region. The presence of year and month in the best models was used to assess consistency in the detection rates observed in each region and one or both of these temporal variables was retained in most regional models. The exceptions were the Small Isles and Sound of Jura models, which did not have year retained indicating detection rates were consistent among years in these regions. Predicted distributions indicated that of these two regions, the Sound of Jura and the Small Isles also had higher relative densities and so may be more appropriate sites suitable for designation as SACs for harbour porpoise.

5.1 Introduction

In the construction of predictive habitat models, sensible temporal and spatial scales need to be used in order to capture the important processes explaining a species distribution (Redfern et al. 2006; Scott et al. 2002). The outcome of modelling efforts will be impacted by the scales chosen (Wiens 1989). Furthermore, in the absence of prey abundance data, oceanographic variables are used as proxies to identify important processes, which themselves operate at different scales (Wakefield et al. 2009). In modelling, spatial scales can be considered in two ways: *extent* and *grain*. The *extent* is the overall geographic range being studied and *grain* refers to the size of units at which relationships are being examined (Wiens 1989). In distribution models, the relationships between species habitat usage and the underlying environmental processes are usually dependent on both the extent and grain chosen (Osborne and Suárez-Seoane 2002). The data collection methods used are subject to a trade-off between a high-intensity sampling, which can capture fine-scale patterns, and more broad-scale sampling to capture more coarse-scale patterns (Redfern et al. 2006). Sometimes patterns are consistent irrespective of the grain used in analysis (Redfern et al. 2008) and ultimately there is no 'correct' scale in modelling studies, as the appropriate scale will be goal-dependent (Scott et al. 2002).

One option in building predictive models to investigate a species distribution is to model the full extent of the survey area as a single region (Osborne and Suárez-Seoane 2002; Scott et al. 2002). However, it should be considered that by modelling a larger area, it is likely that heterogeneity in the model covariates will increase as the way that animals will utilise habitats may vary due to shifts in intrinsic factors (e.g. foraging and reproductive behaviour, social structure and inter-specific relationships)(Osborne and Suárez-Seoane 2002). Another consideration when selecting extent and grain is that the full range of an environmental relationship should be sampled using the chosen extent. If the full range is not sampled it can lead to incorrect interpretations of the relationships involved in explaining species distribution (Horne and Schneider 1995; Scott et al. 2002).

Variation in habitat usage can be investigated by partitioning the dataset before modelling. This can result in better models (Osborne and Suárez-Seoane 2002) and has been used successfully in cetacean species habitat modelling (Cañadas et al. 2005). I am not aware of any studies that have investigated such spatial variation with respect to harbour porpoises habitat preferences and distribution.

The overarching aim of this thesis is to identify important, high-use regions for harbour porpoise west of Scotland that could be suitable for designation as special areas of conservation (SACs).

The west coast of Scotland has one of the highest densities of harbour porpoise in the UK (SCANS-II 2008) and the extent surveyed in this study covers ~25,000 km². When considering an area to be protected, a trade-off must be made between maximising the area for protection and minimising the cost of managing a large area (Moilanen et al. 2009). The majority of marine SACs in the UK occur in inshore regions and with sizes ranging from <10 km² to >1,000 km² (JNCC 2010b). Some potential SACs (pSAC), candidate SACs (cSAC) and draft SACs (dSAC) also have been suggested, many of which cover large surface areas - the largest of these being located offshore (dSAC Hatton Bank: 15,694 km² and dSAC Dogger Bank: 15,057 km² (JNCC 2009; Pinn 2009) and the only established SACs for cetacean species, in the Moray Firth and Cardigan Bay are 1,513 km² and 958 km² respectively (JNCC 2010a). This may indicate that the inshore waters west of Scotland are too large to be managed as a single region but that a smaller important region may be identified and protected.

So far in this study, I have investigated temporal shifts in habitat preferences and distribution over the full extent of the survey region as a whole. Grain size has been held constant throughout this study, to try to capture processes at as fine a scale as possible (the minimum grain has been confined by the coarsest resolution of available covariate data).

The aim of this chapter is to investigate harbour porpoise habitat preferences and distribution using a finer spatial extent, by partitioning a five/six-year (acoustic/visual) dataset into a series of smaller regions and modelling each one separately. This will investigate whether porpoise habitat usage west of Scotland varies significantly among smaller regions, and how similar these results and the model's predicted distributions are to the full model's predicted distributions generated in Chapter 3. These results are considered with respect to identifying potential areas for protection as SACs.

5.2 Materials and Methods

The methods used to collect, process and model the visual and acoustic data used in these models are outlined in §2.1, §2.2 and §2.3 respectively. Details of how the survey effort and raw detections data were segregated and processed for this analysis are detailed in §2.4.2.3.

5.3 Results

In Chapters 3 and 4, a number of spatially explicit variables were retained in the best visual and acoustic models indicating a degree of spatial variation in preferences, e.g. certain current speeds and spring tidal ranges were only observed in specific regions. With this in mind, a series of regional models were built for eight regions on the west coast of Scotland. The model structures for each model (Table 5.1) and selected relationships between covariates and the response variable for each regional model are shown below (Figure 5.1 and 5.2). Model evaluation and predicted distributions for each model are described in §5.3.2 and §5.3.3 respectively.

Table 5.1 - Model structures for the best visual and acoustic models from each spatial region. An ‘X’ is marked to show whether or not each covariate was retained in the best models. N.B. there were insufficient visual detection data to make models for the Sea of Hebrides region.

Region	Dataset	Time		Survey			Sediment			Tidal				Topographic		
		Year	Month	Sea State	Boat Speed	Time of Day	Percentage Gravel	Percentage Sand	Percentage Mud	Position Relative To Tidal Range	Position in Daily Tidal Cycle	Current Speed	Maximum Spring Tidal Range	Depth	Slope	Distance to Land
The Minch	Visual		X	X								X		X		
	Acoustic	X			X								X			
Sea of Hebrides	Visual	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Acoustic	X			X			X				X				
Small Isles	Visual		X	X	X		X								X	
	Acoustic		X		X						X	X	X	X		
West of Mull	Visual	X		X								X				
	Acoustic		X	X	X							X	X	X	X	
Sound of Mull	Visual	X		X	X	X								X		
	Acoustic													X	X	
Firth of Lorn	Visual	X	X	X	X									X		
	Acoustic	X	X	X	X							X	X	X	X	
Sound of Jura	Visual			X				X					X			
	Acoustic		X		X			X			X		X			

5.3.1 Model Structures

5.3.1.1 The Minch

Survey covariates were retained in the best visual models for the Minch region (Figure 5.1). Sea state had a significant impact on sighting rates, as observed in many other models. Detection rates decreased as sea states increased above Beaufort 0. There were monthly variations in

detection rates. In the visual models, sighting rates were highest in September (though the 95% confidence intervals were much wider for this month than others). Sighting rates were found to increase as slope increased. Spring tidal range (STR) was retained in the Minch region visual models, with a very specific preference for regions with STR of $\sim 4.7 - 5.3$ m. Detection rates were markedly lower in regions with STR either side of this range.

Acoustic detection rates were impacted by boat speed, with the peak rates observed as speeds between 3 – 5 knots, above which detection rates decreased (Figure 5.2). Year was retained in the best acoustic model, though the region was only surveyed acoustically from 2006 – 2008, with peak detection rates being observed in 2007. Acoustic detection rates were at their peak in relatively shallow waters, around 50 m, but reasonably high detection rates were observed in waters up to 200 m in depth.

5.3.1.2 Sea of Hebrides

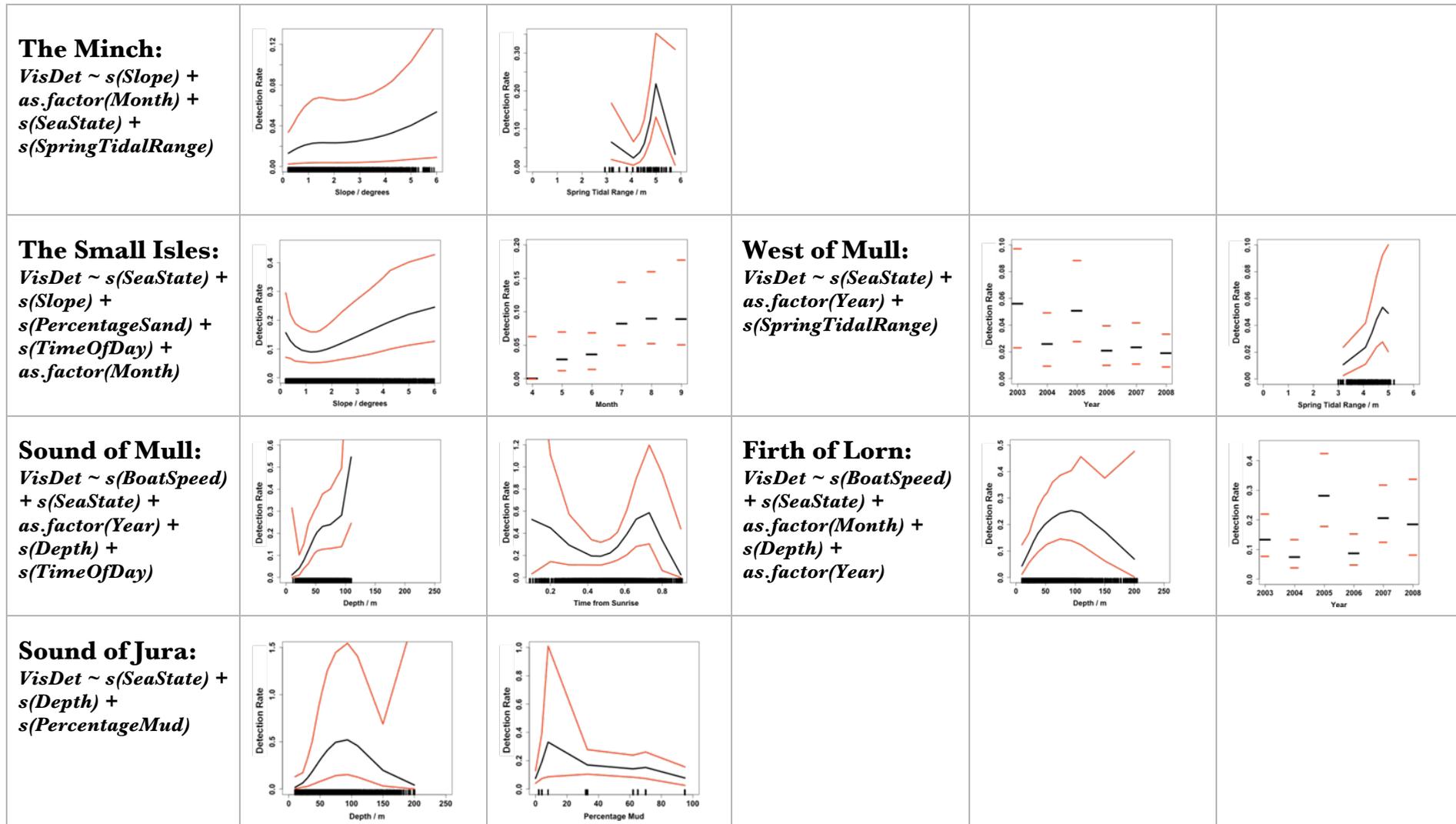
The best acoustic model retained boat speed, with detection rates decreasing from 3 – 6 knots, but then increasing slightly between 6 – 9 knots. Year was also retained with detection rates increasing from 2004 – 2007, before decreasing slightly again in 2008. Percentage sand was also retained in the best acoustic model, with the highest detection rates being observed in regions with from 0 – 40 % sand in the sediment. STR was also retained, with the highest detection rates observed in regions with ranges between 4 – 5.5 m.

The visual model built for the Sea of Hebrides region performed very poorly, likely due to a low number of sightings in the dataset and so was removed from the analysis.

5.3.1.3 The Small Isles

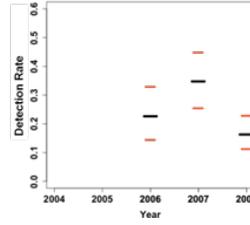
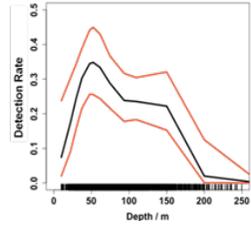
Sea state was kept in the best visual model as sighting rates decreased in sea states > 0.5 . Temporal variables, time of day and month were retained in the best visual models. The highest detection rates were observed early in the day, with lesser peaks observed around the middle of the day and again close to dusk. Sighting rates were lowest in April, increasing through to a peak in September. The composition of the bottom sediment was significant, with percentage sand being retained in the best model. Sighting rates were highest in regions with either between 0 – 40 % or > 80 % sand. Seabed slope was another important variable; detections were low in regions with little slope, but increased as the degree of slope increased beyond 1° .

Figure 5.1& 5.2 (next page) - Model structures and selected covariate relationships for each of the visual and acoustic regional models respectively. Covariate relationships with the response variables are shown by the black lines and 95% confidence intervals are shown in red. Axes vary between plots.



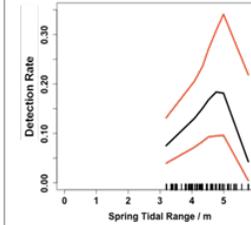
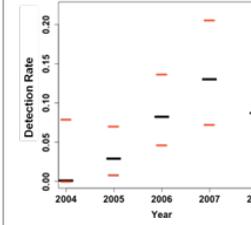
The Minch:

$AcDet \sim as.factor(Year) + s(BoatSpeed) + s(Depth)$



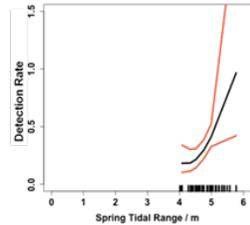
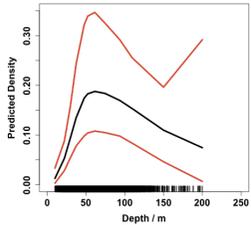
Sea of Hebrides:

$AcDet \sim s(BoatSpeed) + as.factor(Year) + s(SpringTidalRange) + s(PercentageSand)$



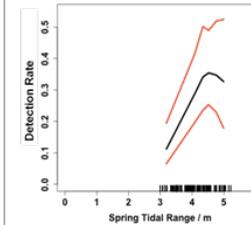
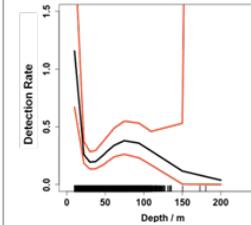
The Small Isles:

$AcDet \sim s(Slope) + s(BoatSpeed) + s(SpringTidalRange) + s(CurrentSpeed) + as.factor(Month) + s(Depth)$



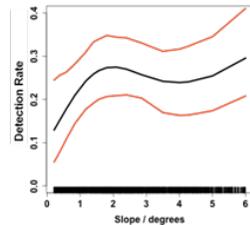
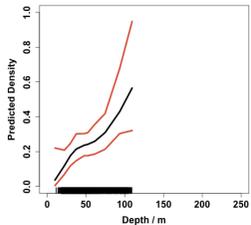
West of Mull:

$AcDet \sim s(SeaState) + s(BoatSpeed) + as.factor(Month) + s(SpringTidalRange) + s(DistanceToLand) + s(Depth) + s(Slope)$



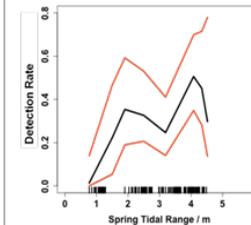
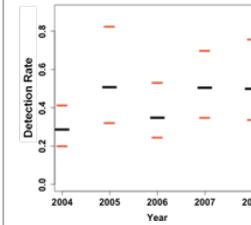
Sound of Mull:

$AcDet \sim s(Slope) + s(Depth)$



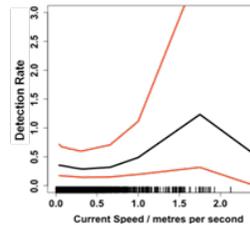
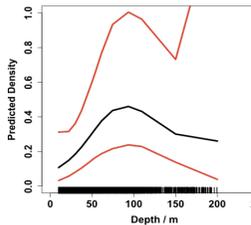
Firth of Lorn:

$AcDet \sim s(BoatSpeed) + s(SeaState) + as.factor(Month) + s(Depth) + s(Slope) + as.factor(Year) + s(DistanceToLand) + s(SpringTidalRange)$



Sound of Jura:

$AcDet \sim s(Depth) + s(BoatSpeed) + s(CurrentSpeed) + as.factor(Month) + s(PercentageMud)$



The best model from acoustic data was quite different in structure to the best visual model. Month was retained in both models but in the acoustic model the lowest detection rates were observed in April and September, with peak rates observed during June. Boat speed impacted acoustic detection rates, as they generally decreased as boat speed increased. Tidal variables, STR and current speed were retained in the best acoustic model, with detection rates increasing as STR increased (from 4 to 6 m – the minimum and maximum STR for the area). Detection rates also increased as current speeds increased from 0 to 0.3 ms⁻¹ and remained similar above 0.3 ms⁻¹ (up to 0.6 ms⁻¹, the maximum current speed observed in the region). Additionally, topographic variables, seabed slope and water depth were retained in the best model; detection rates increased as the slope of seabed increased. Detection rates were highest in regions with maximum water depths of between 40 and 120 metres, beyond which they decreased slowly.

5.3.1.4 West of Mull

Of the survey variables, sea state was retained in the visual models and detection rates decreased significantly in sea states > 0. Noteworthy yearly variations were observed, with particularly high detection rates in 2003 and 2005, and lower sighting rates in all other years. Of the oceanographic variables, only spring tidal range was retained in the visual model. STR varies between 3 and 5 m in the region and the highest detection rates were observed in regions with higher tidal ranges. Spring tidal range was also retained (along with a range of other covariates) in the best acoustic model and the same relationship was observed as in the visual model with peak detection rates in the areas with higher STR.

Boat speed and sea state were also retained in the acoustic model as detection rates decreased with increasing boat speed. The relationship with sea states was different to that observed in other models. Acoustic detection rates were lowest between sea states 0 and 1 and peak detection rates were observed between Beaufort 2 and 4. Significant monthly variations were observed, with May having the highest detection rates. Detection rates appeared stable through June, July and August but decreased in September. Distance to land was retained in the best acoustic model, increasing between < 1 km and 3 km from land, beyond which they decreased steadily. Slope and depth were also retained; detection rates increased almost linearly as the degree of slope increased. A noteworthy relationship was observed with depth. Acoustic detection rates decreased markedly between regions of 10 m (the peak detection rate observed) to 30 m, before increasing again to a second peak observed between 50 m and 140 m. There are few regions surveyed with water depths > 150 metres off the west coast of Mull.

5.3.1.5 Sound of Mull

Survey covariates, sea state and boat speed were retained in the best visual models for the region. Sighting rates decreased almost linearly as sea state increased and as boat speed increased from 3 to 8 knots, however between boat speeds of 8 and 9 knots a sharp increase in sighting rates was observed. Time of day was kept in the best visual model and the highest detection rates were observed early in the morning and in the late afternoon, though they decreased as dusk approached. Depth was also retained in the visual Sound of Mull model and sighting rates generally increased as water depth increased.

Only two covariates were retained in the acoustic model, depth and slope. The same relationship as in the visual model was observed with detection rates increasing with increasing depth (up to the maximum surveyed depth of 120 m). Acoustic detection rates increased swiftly with slope from 0 - 2°, above which they fluctuated slightly.

5.3.1.6 Firth of Lorn

The best visual and acoustic models were similar in this region, with yearly and monthly variations observed in both models and boat speed and depth both being retained. The highest sighting rates were observed during 2005 in the visual data. In the acoustic models, rates were similar in 2005, 2007 and 2008 but slightly lower in 2004 and 2006. Additionally the monthly patterns observed were different. In the visual model, detection rates were highest in June and August, while in the acoustic model rates increased from April, peaking in July, before decreasing again in August and September. In both models, the relationship with depth was the same, with the highest detection rates in water of between 50 – 140 m deep. Detection rates decreased with increasing boat speed.

The visual model retained sea state with peak detections observed between Beaufort 0 and 1, beyond which rates decreased. Sea state was not retained in the best acoustic model, though slope, distance to land and spring tidal range were also kept in. Detection rates increased with increasing slope up to 4°, above which rates were stable. Acoustic detection rates decreased as distance from land increased. A bimodal distribution was observed between STR and acoustic detection rates, with peak detections occurring in regions with tidal ranges of 2 m or 4 m.

5.3.1.7 Sound of Jura

Survey covariates were retained in the best visual and acoustic models for the Sound of Jura datasets. In the visual model, sea state impacted detection rates as they decreased with increasing Beaufort sea state. Acoustic detection rates decreased as boat speed increased.

There were some similarities observed in the other covariates retained in the best models. In both models, water depth and percentage mud in the sediment (% mud) were retained and while the depth relationships observed were similar (peak detection rates were observed in depths of 50 to 140 m), different patterns were seen between % mud in the visual and acoustic models. In the best visual model, detection rates were highest in regions with 0 – 15 % mud, beyond which they decreased steadily. Conversely in the acoustic model, a general increase in detection rates was observed as the percentage mud increased, up to ~ 80 % beyond which a slight decrease in rates was observed.

In the acoustic model, month was retained in the best model. Rates were similar from May through to August, but were lower in April and September. The Sound of Jura is linked to other regions by a series of narrow channels, in which high current speeds are generated. A preference for high current speeds was observed in the acoustic models; detection rates increased with current speed up to the maximum observed current speed in this region of 1.7 ms^{-1} .

5.3.2 Model Evaluation

Model evaluation was conducted using a cross-validation method (described in §2.3.3), where values of F close to, or equal to 1 are indicative of a model capturing most of the patterns that generated the data. The model evaluation of the visual models for many of the spatial regions indicate that they were not capturing all of the underlying relationships that generated the data, with the majority of the scores for $F < 0.55$ (Table 5.2). The exception was the Sound of Jura visual model, which performed better with an F value of 0.782. The acoustic models had consistently high scores, with all close to or equal to 1.0 (Table 5.2) indicating that acoustic models are providing a strong representation of the underlying processes that generated the data.

Table 5.2 - Cross-validation scores for the regional models (regions are listed from north to south) with 95% confidence intervals shown (Chapter 5). N.B. There were insufficient data for the visual Sea of Hebrides model.

Model	Visual		Acoustic	
	Cross Validation Score (<i>F</i>)	95 % C.I.	Cross Validation Score (<i>F</i>)	95 % C.I.
The Minch	0.517	0.486 - 0.548	1.002	1.002 - 1.002
The Small Isles	0.526	0.488 - 0.564	1.000	1.000 - 1.001
Sea of Hebrides	N.A.	N.A.	1.013	1.010 - 1.015
West of Mull	0.474	0.440 - 0.509	1.000	1.000 - 1.000
Sound of Mull	0.225	0.200 - 0.250	1.000	0.999 - 1.000
Firth of Lorn	0.361	0.291 - 0.431	1.000	1.000 - 1.000
Sound of Jura	0.782	0.735 - 0.829	1.000	1.000 - 1.000

5.3.3 Predicted Distributions

5.3.3.1 Visual & Acoustic Models

Predicted surfaces were generated for the six visual models and the seven acoustic models (Figure 5.3). Many of the predicted distributions were different between the models built on visual or acoustic survey data. In the Minch, a strongly inshore distribution was predicted by the best visual model, with highest densities very close to the mainland coastline. Moderate-to-high predicted relative densities were predicted for the southern portion of the Minch, including the Sound of Raasay and the Little Minch. A much more patchy distribution was predicted by the best acoustic model, with very specific regions being observed, e.g. around the Shiant Isles and north of Skye.

The predicted distributions for the Small Isles region were very different between models. The visual model predicted a patchy distribution with a number of very high-density areas close to lower density areas. Furthermore, it generally predicted higher relative densities for the western extent of the region, with more consistently moderate and some high densities being observed close around the islands. The acoustic model predicted that many of the regions close to the mainland would be important for harbour porpoises. In particular, the Sound of Sleat, Loch Nevis and Loch Hourn along with the waters immediately surrounding the Small Isles of Rum, Muck and Eigg were predicted to be important regions. Lower densities were predicted for many of the grid cells in the western extent.

The visual and acoustic models for the West of Mull region produced very different predicted densities. The visual model predicted the highest densities at the mouth of the Sound of Mull

and northeast of Coll, and densities dropped moving southwest through the region. The waters very close to the Isle of Mull coast were predicted to have very low densities. Conversely, these regions close to Mull were predicted to be the highest density regions in the acoustic models. The shallow waters around the Treshnish Isles were predicted to have the highest relative densities, as were the areas on north coast of Coll. Moderate relative densities were predicted for the region to the northeast of Coll.

The predicted surface for the acoustic Sea of Hebrides region predicted the highest densities for the northern extent of the region, close to the Little Minch. Generally, the predicted relative densities decreased moving south through the region, with some moderate predicted densities generated for the region west of Tiree.

The predicted surfaces generated from visual and acoustic models for the Sound of Mull, Firth of Lorn and Sound of Jura showed relatively similar distributions. In the Sound of Mull, high predicted densities were generated for certain cells in both models, indicating important regions in the northwest and southeast extents of the Sound. In the Firth of Lorn, the highest predicted relative densities were observed close to the mainland and south of Mull. However, to the western extent of the study region, moderate densities were predicted in the visual model, although these were the lowest density regions in the acoustic model. Similarly, the waters north and west of Islay were predicted as low densities in the visual models, but moderate-to-high densities in the acoustic models. The region to the south of Islay was predicted to be important in both models. Moderate-to-high relative densities were predicted throughout the deeper waters of the Sound of Jura in both models, with moderate relative density regions appearing to extend down into the North Channel and to the south of Islay.

Figure 5.3 (below) - Predicted distributions for the each of the visual and acoustic regional models. For temporally varying covariates, fixed values were chosen to predict with the highest confidence (i.e. peak values where confidence intervals were narrowest). Colour gradation in each map is based on eight quantile levels (the densities that correspond to the 12.5th, 25th, 37.5th, 50th, 62.5th, 75th, 82.5th percentiles) of the predicted harbour porpoise densities from each model (animals per km).

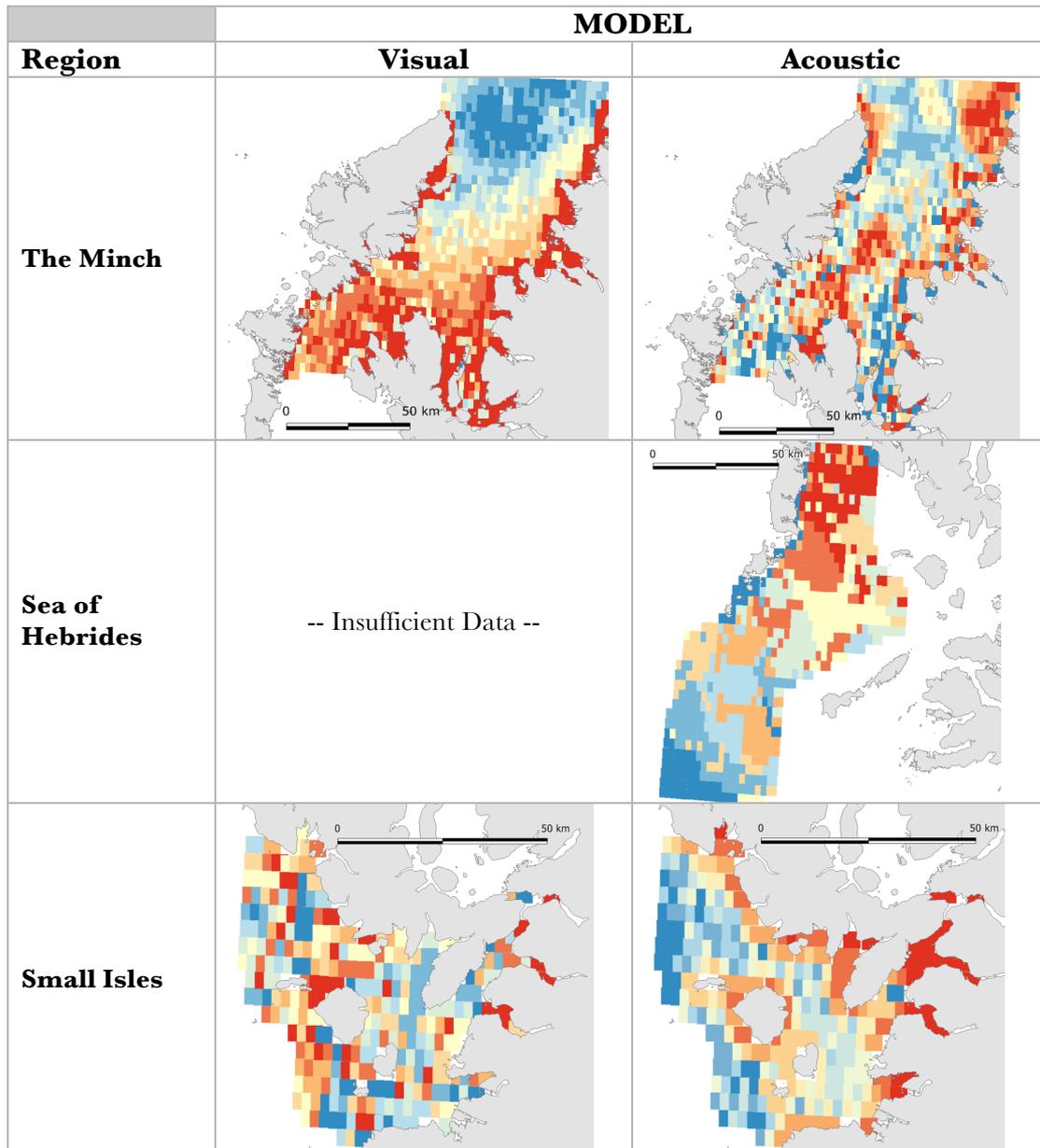
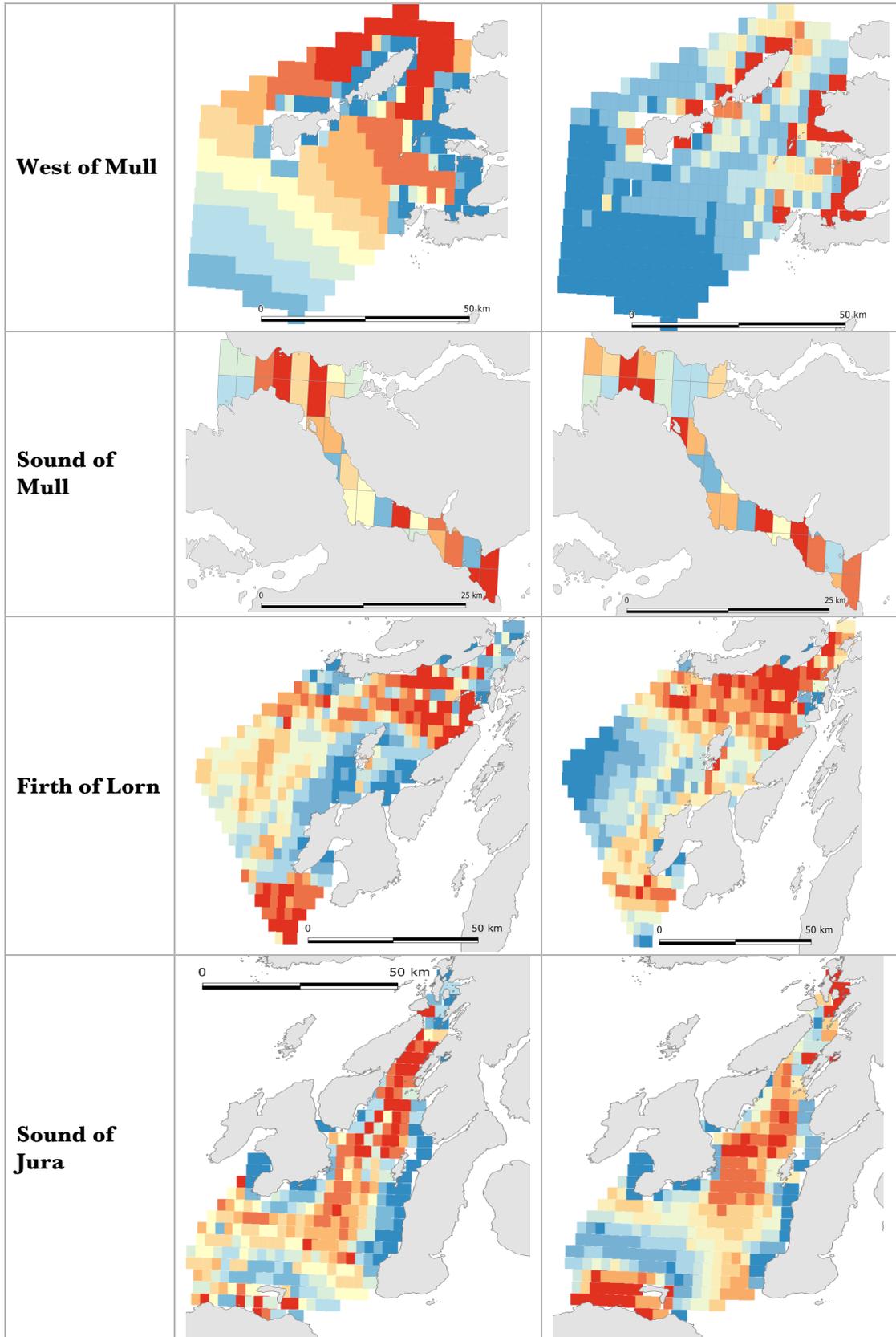


Figure 5.3 contd.



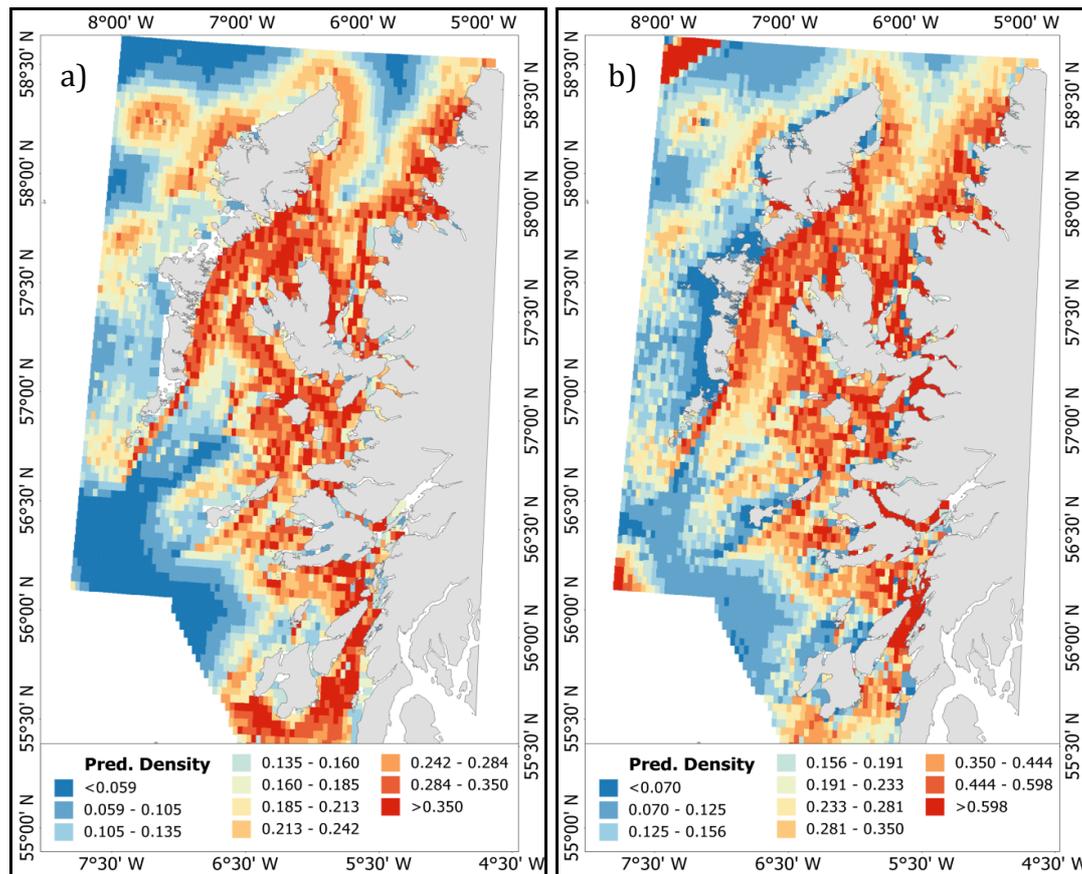


Figure 5.4 a & b - Predicted distributions for the full models from Chapter 3. Distribution surfaces are shown for the best (a) visual and (b) acoustic models. Colour gradation in each map is based on eight quantile levels (the densities that correspond to the 12.5th, 25th, 37.5th, 50th, 62.5th, 75th, 82.5th percentiles) of the predicted harbour porpoise densities from each model (animals per km).

5.3.3.2 Regional models vs ‘Full’ models

The predicted distributions for each of the regional models were compared by eye with the predictions for the same region from the full models (all years pooled together - §3.3.1 and §3.3.2) (Figure 5.4 a & b). Some similarities were observed between these predicted outputs. In both the visual and acoustic Firth of Lorn and Sound of Jura regional models, distributions were very similar to those generated for the region using the full models. High-predicted densities were generated for the northeast Firth of Lorn in all models, with lower predicted densities in the southwest of the region. In the Sound of Jura, moderate and high-predicted relative densities were generated for most parts of the region, as seen in the full model output. There were some lower predicted density regions predicted in the smaller-scale regional models for the region, e.g. in the eastern Sound of Jura, that were different to the predicted distributions from the full models. The acoustic model predicted distributions for the Sound of Mull and Sea of Hebrides also had similar patterns observed between the full and regional models. In the Sound of Mull,

in both cases, higher predicted densities were generated for the northwest and southeast entrances to the sound with patchiness in predicted relative densities in between. In the Sea of Hebrides, higher predicted densities were generated in both models for the northern part of the region, close to entrance to the Little Minch.

The distributions predicted from the regional models for the Minch, Small Isles, and West of Mull were all quite different to those observed from the full models. In the full model predicted distributions, high predicted relative densities were generated in inshore regions, with relative densities decreasing further from land. In the Minch acoustic model, predicted densities were very patchy, with high-density regions found around the Shiant Islands, north of Skye and very close to shore along the mainland coast. In the full model, high relative densities were predicted throughout the Small Isles and the region west of Mull out to Coll and Tiree.

5.4 Discussion

The aim of this analysis was to investigate whether harbour porpoise distribution and habitat preferences varied markedly across the west of Scotland. To investigate this, finer-scale regional models were built by partitioning the full datasets into smaller regions and constructing individual models for each area. The secondary focus of this analysis was to identify potentially suitable areas for designation as SACs for harbour porpoise.

5.4.1 Model evaluation

All of the regional models constructed in this analysis were evaluated using a cross-validation method (§2.3.3) to determine how well the models performed in capturing the underlying processes that generated the data. In all regions, the visual models did not perform as well as the acoustic models, which were good representations of the patterns in the data (i.e. all the F values were close to, or equal to 1). This should be considered when assessing the visual model results and predicted distributions.

In some of the acoustic models the F scores were larger than 1 (The Minch = 1.002 and The Sea of Hebrides = 1.013). The cross validation method used provides an estimate of model performance and so there will be some uncertainty associated with these estimates. One potential explanation for values > 1 is that if there is a rare, large detection event (i.e. a 2 km segment with a high number of sightings/acoustic detections) in a dataset and it is more commonly partitioned into the ‘test’ subset than the ‘training’ subset. If the opposite occurs (a large detection event being partitioned into the ‘training’ subset more often than the ‘test’ subset

resulting in scores shifted towards 1) then a lower F score may occur. This may be a factor in smaller datasets. The visual model evaluations will also be subject to this effect, but if the model evaluation scores are not ≥ 1 it is difficult to identify the models in which this has occurred. If model evaluation scores have wide confidence intervals, this may be further indication of a large detection event occurring in the dataset.

5.4.2 Spatial variation in model outputs

5.4.2.1 *Habitat preferences*

One important factor in the selection process in the designation of SACs is the continuous or regular presence of the species (subject to seasonal variation)(EU 2007). Thus, to investigate potential areas suitable for designation as SACs, determining that a region is consistently important over time is an important step. In the full models (Chapter 3 - §3.3.1 and §3.3.2) both year and month were retained in the best visual and acoustic models suggesting temporal variability over a large spatial extent. Consequently, year and month were used to investigate inter- and intra-annual variations in habitat preferences and distribution here at finer-spatial extents. Inter-annual variation was observed in The Minch (acoustic), Sea of Hebrides (acoustic), West of Mull (visual), Sound of Mull (visual), and in both the Firth of Lorn region models, indicating that there was significant variation in detection rates among years. Year was not retained in the best models for the Small Isles and Sound of Jura indicating that detection rates were consistent among years of the study in these regions.

Month was retained in both visual and acoustic models for the Small Isles and Firth of Lorn. Month was retained in selected models for The Minch (visual), West of Mull (acoustic) and Sound of Jura (acoustic). In the acoustic models, the lowest detection rates were observed in April and September and the patterns of usage varied between regions among May and August. Peak detection rates were observed in May and June in the Small Isles and West of Mull, June in the Firth of Lorn and August in the Sound of Jura. This may be indicative of a seasonal north to south change in distribution between regions although this needs to be investigated further.

It was interesting that, of the model variables, mostly spatially static covariates (e.g. depth, slope, distance to land) were retained in the best regional visual and acoustic models. The exceptions were current speed, which was retained in the acoustic models in the Small Isles and the Sound of Jura and Time of Day, which was retained in two visual models (Small Isles and Sound of Mull). Maximum Spring Tidal Range (STR) was kept in a number of models. In the Firth of Lorn, STR of between 0.8 and 4.5 m exists and peak detection rates were observed in the areas

with 2 and 4 m. In the Small Isles (acoustic) and West of Mull (both), the STR values occurring there were between 3 – 6 metres and higher detection rates were generally observed in areas with the larger tidal ranges. In the Sea of Hebrides and The Minch detection rates were highest in regions with ~ 5 m tidal range, though detection rates decreased in the regions with the highest tidal ranges.

The presence of spring tidal range and current speed in some of the best regional models may be linked. Currents play an important role in coastal ecosystems, particularly when combined with variable topography (Mann and Lazier 2006). In the Small Isles and the Sound of Jura detections were highest in the areas of high current. Where interactions between tidal water movements and land masses occur, eddies and rips are produced, serving to increase turbulence and productivity (Mann and Lazier 2006). Areas with large tidal ranges will result in a greater volume of water moving in the tidal cycle, which will increase the presence and strength of these aggregating features. Such spatially and temporally predictable features are known to impact the distribution of harbour porpoise prey species (Wolanski and Hamner 1988; Yen et al. 2004; Zamon 2003). The presence of islands (anchor points for eddies/rips) and channels (through which tidal water is forced thus increasing current speeds) throughout the Small Isles and the northern Sound of Jura (Ellett and Edwards 1983) may also explain why current speed was important in explaining porpoise distribution in these regions. Many studies have investigated harbour porpoise distribution and/or habitat preferences with respect to tidal features and observed site-specific relationships. The highest densities of harbour porpoises have been observed during flood tides (Calderan 2003; Johnston et al. 2005; Sekiguchi 1995), ebb tides (Isojunno 2006; Pierpoint 2008) and during the slack periods between flood and ebb (Embling et al. 2010 - using some of the same data from this study). Position relative to tidal cycle and position in the daily tidal cycle were not retained in any of the models in this analysis.

The absence of current speed in the best visual models for these regions, may be explained by the increased turbulence that is associated with strong currents (Mann and Lazier 2006) causing an increase in sea state, which would in turn impact the visual detection of animals (Palka 1996).

Time of Day was retained in two visual models, and different patterns were observed. Cetaceans have been observed to exhibit diel changes in behaviour in response to horizontal and vertical prey migrations (Benoit-Bird and Au 2003). Many species of fish have diurnal patterns of activity; for example, sandeels emerge from sediment refuges during daylight hours to feed (Wright et al. 2000). However, the effect of such prey movements on harbour porpoise surfacing

behaviour and so the impact on their detectability during surveys, is currently poorly understood.

Sediment preferences were observed in both visual and acoustic models in the Sound of Jura, with percentage mud being retained. In the Small Isles (visual) and Sea of Hebrides (acoustic), percentage sand was included. As discussed in previous chapters, studies have investigated relationships between sediment types and habitat preference for marine mammal prey species (Aarts 2006; MacLeod et al. 2004) and the retention of sediment variables here is likely representative of where harbour porpoise prey species are abundant.

The topographic covariates in the models, seabed depth and slope were retained in all but two of the regional models and in the majority of cases a consistent relationship was observed. The highest detection rates were observed in highly sloped regions with water depths between 50 – 150 metres. These patterns have been observed in many of the regional models in this analysis, indicating that these are spatially robust patterns. Slope has been important in a number of cetacean studies (Baumgartner 1997; Cañadas et al. 2002; Heinrich 2006; Panigada et al. 2008; Tynan et al. 2005). As has been discussed throughout this thesis, highly sloped regions may provide sites for increased productivity via upwelling and/or advection or by functioning as anchor points for eddies and rips (Hyrenbach et al. 2000; Mann and Lazier 2006; Mooers et al. 1979).

The depth range observed is supported by similar preferences found in a number of studies on harbour porpoises west of Scotland (Goodwin and Speedie 2008; MacLeod et al. 2007; Marubini et al. 2009). This depth range may be an indication of the habitat that harbour porpoise prey species favour. A number of fish species that constitute a portion of harbour porpoise diet around the UK inhabit these depth ranges (Crawford and Jorgensen 1990; Persohn et al. 2009; Santos et al. 2005; Santos et al. 1994; Wright et al. 2000). Variations in this depth range were observed in some of the regional models, in particular the Sound of Mull, in the Minch and West of Mull. In the Sound of Mull sighting and acoustic detection rates both increased with increasing depth up to the maximum surveyed depth in the region (~ 120 m). This indicates that harbour porpoises are favouring deeper waters in this region. In the Minch a slightly wider depth range was being utilised by harbour porpoises, as peak acoustic detection rates were observed around 50 m, beyond which reasonably high detection rates were observed out to regions with water depths of 200 m. Similarly in the West of Mull, peak detection rates were observed in waters around < 40 metres with a secondary peak observed between 60 – 100

m. It is not clear why there are these preferences for shallow water (particularly west of Mull). In a study in the German Baltic using, T-PODs deployed in relatively shallow water ($\sim 10 - 30$ m) registered high porpoise detections throughout the year (Verfuß et al. 2007). Given the heterogeneity in depth habitat, the high-frequency nature of porpoise echolocation clicks and that the detection distance of animals is < 300 m (Gillespie et al. in prep.), this consistent presence indicates that animals spend a reasonable amount of time in shallow waters in the German Baltic. However, how that relates to the preferences observed here is unclear. It may be that these shallower regions are being selected in the Minch and West of Mull in response to a shift in prey distribution or prey-switching. Currently, there are insufficient studies on variation in habitat use of harbour porpoise prey species in the literature and it is a subject that needs further investigation.

Because the partitioning of datasets in the study was based around the size of areas and distinct static oceanographic features, it may be that biologically significant relationships are not captured entirely within the boundaries of each area. For example, in the West of Mull and the Minch regions, further habitat partitioning could be more appropriate in order to identify the important relationships. It should also be considered that by partitioning the datasets, the models are built on fewer data and it may be that for some of these regions, there are insufficient data on which to build robust models. However, the acoustic models in particular appeared to perform well.

An interesting pattern observed in the acoustic regional models (which performed very well in capturing patterns in the data) was that the months of peak detection rates varied between regions. Peaks were observed in May (West of Mull), June (Small Isles), July (Firth of Lorn) and August (in the Sound of Jura)(month was not included in the best acoustic models for The Minch, Sea of Hebrides and the Sound of Mull). The observed could be an indication of a general southward shift between regions throughout the summer. However, it is not known whether this monthly pattern exists in every year or was driven by one or two years of high detection rates driving the predicted detection rates up. Unfortunately, it was not possible to build models for each year in each region to investigate this pattern further. This was because the sample sizes were quite small at such fine temporal and spatial scales.

There is no clear explanation for what would be driving such a monthly shift in distribution. Porpoise breed and give birth to calves in June and July (Lockyer 2003) and perhaps the peak detection rates in the Small Isles (June) and Firth of Lorn (July) indicate potential breeding areas.

It may also be that these shifts are explained by clear shifts in prey abundance and distribution. However, this is speculative and needs further investigation.

5.4.2.2 Predicted distributions

Some similarities were observed between the distributions predicted for each of the regional models when compared with the predictions from the full models (in Chapter 3). In particular the Firth of Lorn and Sound of Jura were the only two models that captured the same distribution patterns as the full model predictions. In both cases, moderate and high predicted relative densities were generated for inshore regions, in particular to the northeast of the Firth of Lorn and throughout the Sound of Jura. Despite some of the model covariates being different from those of the full models, the distributions produced by the models were similar.

The predicted distributions for the more northern spatial regions of the total survey extent were quite different to those predicted in the full models. This indicates that different factors are important between regions and vary depending on the extent used in the investigation. In one of the most consistent regions modelled, the Small Isles, the Sound of Sleat and nearby sea lochs were deemed the most important areas, with some high densities areas also predicted for the cells close to many of the islands in the region. Generally lower density areas were observed in the region, away from land. This differs from the full models, which predicted high densities throughout the Small Isles region. In the Sound of Mull, a patchy distribution was observed in places. Predicted densities were highest in the northwest of the region and from Fishnish down to the southeast limit of the region. In Chapter 6, the potential impacts of Commercial Aquaculture Acoustic Devices (CAADs §1.4.2) in the Sound of Mull on harbour porpoise is investigated and these patterns will be discussed further. Consistent patterns in regions and their suitability as SACs is discussed in detail in Chapter 7.

5.4.3 Identifying potential Special Areas of Conservation (SACs)

When trying to identify important areas for protection, it is important to consider the practical issues and find a balance between maximising the protection for a species provided by a SAC and minimising the cost of managing the area (Duck 2003; Moilanen et al. 2009). A number of studies have indicated the use of spatially distinct oceanographic features to provide the boundaries of protected areas (Agardy 1994; Hooker et al. 1999). In this study, depth and slope were consistently retained in the best models and the relationships observed have been robust between areas, indicating their significance in explaining harbour porpoise distribution across the west of Scotland. Additionally, very few dynamic features were deemed important in the

smaller regional models. It may be that using depth and slope features as loose boundaries, it is possible to identify suitable areas for designation of SACs.

This study follows on from work by Embling et al. (2010), which used the 2003 – 2005 data also used in this study, and identified a range of important regions for harbour porpoises across the Inner Hebrides that could be suitable for designation as SACs. These were the Sound of Sleat, the inshore waters west of Mull, the northeast Firth of Lorn and the Sound of Jura. This study used an additional three years of data and different analytical methods but the results indicate that similar regions have been important across all six-years. Parts of the Sound of Jura, Firth of Lorn, the inshore region west of Mull and parts of the Small Isles could be considered for designation as SACs. This study observed that similar predicted distribution patterns to those in 2003 – 2005 were observed through the 2006 – 2008 data. Some parts of the west coast of Scotland – e.g. the Sound of Mull and northeast Firth of Lorn - could not be modelled by Embling (2007; et al. (2010)) due to a lack of environmental data. These regions were included in this analysis (where suitable data became available) meaning a more detailed investigation of the important areas west of Scotland. The inclusion of those data confirms that these regions are also important for harbour porpoises and improves our knowledge harbour porpoise distribution and the consistently important regions.

In this study, the inclusion of year and month in the best models was used to determine whether the detection rates of harbour porpoises varied significantly within an area. Significant yearly variations were observed in most of the regions indicating that the importance of the region may fluctuate. In the Firth of Lorn, year was retained in the best models, though the detection rates still appeared reasonably consistent across years. However, some regions (the Small Isles and the Sound of Jura) did not include year in the best models, indicating consistent use across the six years of the study. All three of these regions are of similar size to the established Moray Firth SAC (Sound of Jura: 1331 km²; Firth of Lorn: 1212 km²; Small Isles: 2530 km²), which provides some indication that these are manageable sizes for cetacean SACs. Some of these regions could be considered as areas suitable for designation as an SAC. This is considered in detail in Chapter 7 with respect to SAC selection criteria.

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Chapter 6

Impacts of Commercial Aquaculture Acoustic Devices on harbour porpoises west of Scotland

6.0 Abstract

Cetacean species in the UK are protected under Annex IV of the EU Habitats Directive, which prohibits the deliberate disturbance of a species, and there is particular concern over the potential for acoustic disturbance from a range of noises produced from anthropogenic sources. The interaction between aquaculture and seals is a well-documented problem in many areas and powerful commercial aquaculture acoustic devices (CAADs) are often used to mitigate this. Questions remain over the efficacy of CAADs in deterring seals, and their impacts on non-target species, particularly cetaceans, is an issue of concern. The west coast of Scotland has one of the highest densities of harbour porpoises in Europe and also accommodates a large number of fish farms. Currently, the installation of CAADs to mitigate seal-aquaculture interactions is unlicensed. This opportunistic study mapped the sound fields of Airmar CAADs installed at operating fish farms to investigate the potential impacts of these devices on harbour porpoises. Recordings of Airmar CAADs were made routinely during visual and acoustic line-transect surveys for harbour porpoises (April - September: 2006 - 2008) using a calibrated towed hydrophone array. Sound level measurements were interpolated to calculate sound fields in a number of regions to reveal the areas being ensonified by CAADs. Propagation from the device was investigated and was found to generally follow expectations under a spherical spreading model, but marked variations in propagation were also observed as range to the device increased. Likely exposures to CAADs given the observed sound fields were calculated to explore the probability that established noise exposure criteria thresholds would be exceeded, leading to a risk of hearing damage. From this study, we suggest that there is potential for CAAD to induce temporary threshold shifts (TTS) in harbour porpoises. This is most likely to occur when animals are exposed to received levels over >150 re $1 \mu\text{Pa}$ (RMS); which can occur at ranges out to 750 m from the CAAD source. Studies in Canada have shown that porpoises are excluded from the vicinity of ADDs. In this study porpoise distribution was investigated in the Sound of Mull in relation to four fish farm sites in 2006 - 2008. In particular, I assessed the

effect of an additional CAAD being installed in 2008 at a site where acoustic devices had not previously been used. Analysis indicates that acoustic detection rates in 2008 were significantly lower than would have been expected based on data collected in previous years. The findings of this study suggest that there is potential for disturbance to harbour porpoises as a result of newly deployed CAADs and their use should be carefully managed in the future.

6.1 Introduction

Marine mammal species rely on the use of sound to communicate with other animals, for predator avoidance, mate selection and social interactions (Hafner et al. 1979; Janik 2009; Rendell and Whitehead 2004; Schulz et al. 2008). Additionally, most odontocete species produce echolocation clicks for orientation, navigation and to detect prey (Akamatsu et al. 1994; Au et al. 2004; Goodson and Sturtivant 1996; Hastie et al. 2006; Janik 2000; Madsen et al. 2005a; Madsen et al. 2005b). Coupled with this, they have a highly sophisticated sense of hearing with high sensitivity over a wide frequency range (Nedwell et al. 2004; Richardson et al. 1995; Southall et al. 2007), which some species utilise in prey detection (Burros and Myrberg 1987; Gannon et al. 2005). This reliance on the use of sound in their general ecology makes marine mammals particularly vulnerable to being affected by underwater noise.

Globally, a wide range of anthropogenic activities introduce sound into the marine environment on the west coast of Scotland. Some are incidental by-products of industrial processes – some are produced to warn animals of the presence of fishing gear or to scare predators away from aquaculture sites (Jefferson and Curry 1996). Underwater noise is generated by commercial shipping, oil and gas exploration, military activities, scientific research, fishing activities, recreational pursuits, marine renewable energy (MRE) installations and acoustic devices deployed on aquaculture sites (Carter 2007; Linley et al. 2009; Richardson et al. 1995; Shrimpton and Parsons 2000; SMRU_Ltd 2007). Relatively little is known about the impacts of such noise sources on marine fauna, but the consensus is that there is potential for impacts on marine species and a need for better understanding (ASCOBANS 2006; MMC 2007).

All cetacean species in the UK are protected under Annex IV of the EC 'Habitats Directive' (Council Directive 92/43/EC), as “*animal [and plant] species of community interest in need of strict protection*” with two sections of Article 12 being of particular relevance: 12(b) which prohibits “*deliberate disturbance of these species, particularly during the period of breeding, rearing, hibernation and migration*” and 12(d) which prohibits “*deterioration or destruction of breeding sites or resting places*”.

The UK is a signatory to the Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas (ASCOBANS) and Resolution 4 of the Conservation and Management Plan indicates that continued effort towards “*the prevention of [other] significant disturbance, especially of an acoustic nature*” must be made (ASCOBANS 2006). Furthermore, the potential impact of anthropogenic activities on marine species and the need for additional research have been raised in the UK Biodiversity Action Plan (UKBAP) and cetacean species are further protected against ‘*disturbance*’ under Schedule 5 of the Wildlife and Countryside Act (1981) and the Countryside and Rights of Way Act (2000). In Scotland, all cetacean species are given protection under the Conservation Regulations 1994 as European Protected Species (listed on Schedule 2 and 4 of the Habitats Regulations 1994). Any deliberate or reckless activity causing injury or disturbance as a consequence of an activity is considered an offense requires a license to be carried out legally. Under these regulations, disturbance includes “*harassing an animal or group of animals*” in any stage of life, in such a way as to “*impair it’s ability to survive, breed, reproduce, rear or otherwise care for it’s young*”. The licensing authority is the ‘Scottish Government Licensing Team’.

Aquaculture is one of the major economic activities on the west coast of Scotland with Atlantic salmon (*Salmo salar*) farming around the Scotland contributing ~£500 million to the UK Economy in 2008 (SSF 2009)(Figure 6.1). However, fish farms share the marine environment with a complement of fish-eating species and consequently, many species interact with aquaculture sites. Grey (*Halichoerus grypus*) and harbour (*Phoca vitulina*) seals are considered to cause the biggest problem at Scottish sites (Quick et al. 2004). Such interactions can lead to lower production in a number of ways: as a result of direct mortality to farmed species, from increased fish-stress and/or from damage to nets caused by predation attempts. A number of methods are utilised on fish farms to minimise interactions with seals including net tensioning, provision of additional ‘predator netting’ and lethal removal of individuals (Ross 1988).

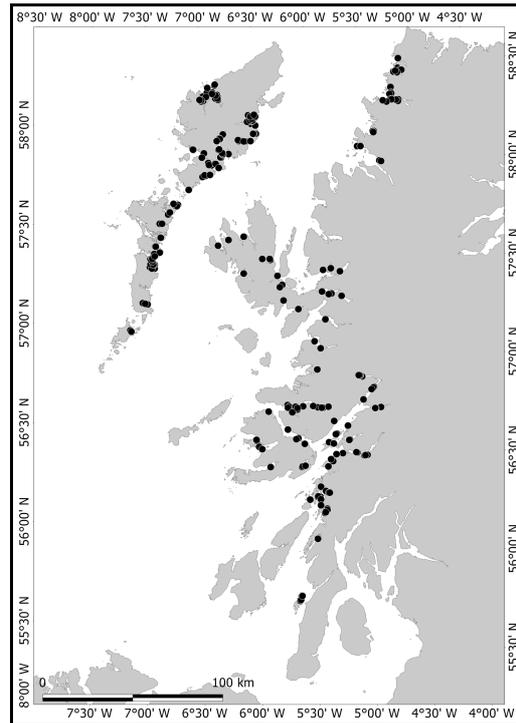


Figure 6.1 - The distribution of salmon aquaculture sites on the west coast of Scotland (black dots) (SMRU, unpublished data).

A commonly applied method for reducing seal-aquaculture interactions in Scotland is the use of high source-level underwater sounds, many of which are targeted at the range of best hearing sensitivity of seals, to deter them from sites (Jefferson and Curry 1996). These devices are most commonly referred to in the literature as Acoustic Harassment Devices (AHDs) or Acoustic Deterrent Devices (ADDs). However both names are misleading: ‘AHDs’ because there are no data to support the notion of ‘harassment’, and ‘ADDs’ because the term is more commonly used to describe a lower source level device used to mitigate by-catch (also known as ‘pingers’). Therefore to avoid confusion here, when discussing the aquaculture mitigation devices here they will be referred to as Commercial Aquaculture Acoustic Devices (CAADs) as first proposed in Lepper et al. (2004) and as a subdivision of Acoustic Mitigation Device (AMD_{CAAD}) by Balle et al. (2009).

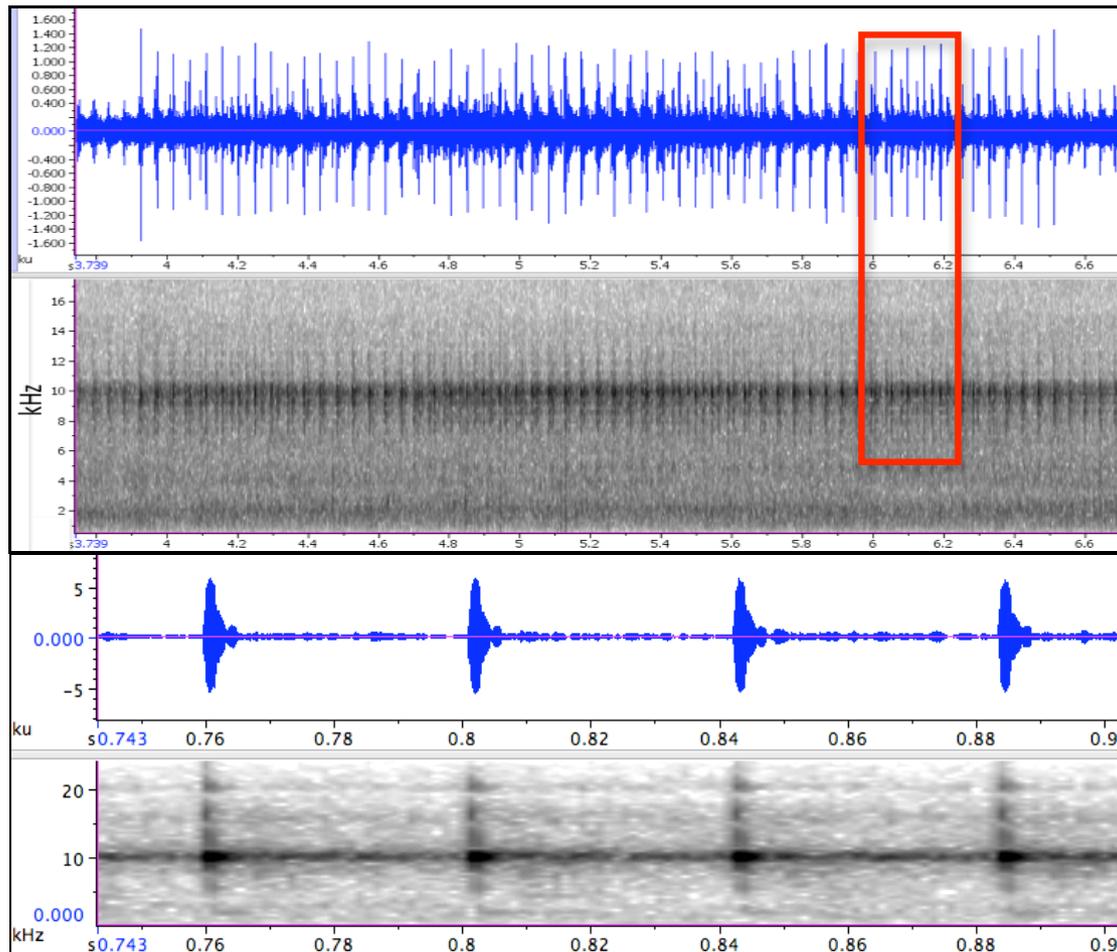


Figure 6.2 – (a) The waveform and spectrogram of an Airmar CAAD pulse train, the x- and y-axis are represented by amplitude and frequency (kHz) respectively (Hamming window, FFT = 512 samples). (b) A close-up of the signal from the red box in (a), showing the pulsed waveform and spectrogram for four Airmar pulses.

A range of CAADs is used to address the seal-interaction problems in Scotland. One of the most commonly used models is the ‘Airmar dB Plus II’ (Calderan, pers. comm.). A number of studies have investigated the acoustic properties of this model and its effect on marine mammals. The Airmar CAAD produces a consistent pulsed-sound centred at 10.3 kHz and equally defined harmonics have been reported at >20 kHz (Haller and Lemon 1995; Lepper et al. 2004)(Figure 6.2). Pulses are 1.8 ms in length and typically are produced in trains consisting of 57 – 58 tone bursts (Lepper et al. 2004) with an inter-pulse-interval of 40 ms. The trains last approximately 2.3 seconds and is repeated on a ~50% duty cycle resulting in an interval between trains of approximately 2.1 seconds (Haller and Lemon 1995; Lepper et al. 2004). Source levels reported for the Airmar CAAD have varied between studies: 152 dB (Taylor et al. 1997)(all values re 1 μ Pa at 1 m RMS unless stated), 179 dB pk-pk (Jacobs and Terhune 2002), 181 dB (not stated) (Johnston 2002), 192 dB (Lepper et al. 2004) and 194 dB (Haller and Lemon 1995; Yurk and Trites 2000). The lower source levels documented in some of these studies were likely the result

of the devices being affected by fouling build-up on the transducers, nets and/or damaged cables or low battery voltages (Gordon and Northridge 2002).

There are questions over the efficacy of CAADs in deterring seals from attacking fish farm sites, However, there is good evidence that such devices impact non-target species (discussed below). The species most at risk are those with acute hearing in the frequency range of the device and those most likely to encounter them. Given the inshore distribution of aquaculture sites around the Inner Hebrides, coastal species such as the harbour porpoise, are most likely to be impacted.

Noise can have behavioural and physiological impacts on cetaceans. Animals may exhibit an aversive response to sounds and potentially be excluded from important habitat. A number of studies have investigated if animals avoid areas where CAADs are installed and, if so, at what ranges.

Taylor et al. (1997) calculated three theoretical zones of influence for marine mammals exposed to a range of CAAD signals (including the Airmar dB Plus II): a 'zone of audibility', a 'zone of severe disturbance and discomfort' and a 'zone of hearing damage and injury'. The Airmar CAAD used in the study (which they assumed had a source level of only 152 dB re 1 μ Pa at 1 m (RMS) - much lower than observed in other studies) was estimated to be audible out to 12 km (under low ambient noise conditions). This device was also estimated to cause 'severe disturbance and discomfort' out to 17 metres from the device – at which distance they estimated that a received level of 130 dB would be encountered (Taylor et al. 1997). The Airmar device used in that study had a reported source level of 152 dB, which is 42 dB lower than the maximum reported SL of Airmar dB II Plus. If Airmar devices operate at the full reported source level, the threshold for 'hearing damage' and 'disturbance' thresholds, would be exceeded within 20 m and ~1600 m of the source respectively (based on spherical spreading).

Studies in Canada investigated the effects of the Airmar CAAD on harbour porpoises and observed that animals were significantly displaced by devices. Olesiuk et al. (2002) observed that porpoises were excluded completely out to 200 m from the devices and only 8.1% of the expected porpoise density was observed within 2.5 - 3.5 km of the active CAAD. It was also concluded that the effects of the CAAD likely extended beyond the largest observation distance (3.5 km) (Olesiuk et al. 2002). Another study, conducted in the Bay of Fundy, Canada found that porpoise density was significantly reduced in a region when an Airmar CAAD was active compared with when it was inactive (Johnston 2002). The closest observed approach (COA) of porpoises to the active device was 645 m (with a theoretical received level of 128 dB re 1 μ Pa)

which was significantly further away than when it was inactive (COA = 6 metres from the CAAD) (Johnston 2002). CAADs have also been shown to impact other cetacean species. Morton & Symonds (2002) observed a significant decrease in killer whale (*Orcinus orca*) sightings across a 15-year study in the Broughton Archipelago when CAADs were installed at four sites while numbers remained stable throughout the study period in the nearby Johnstone Strait (where there were no CAADs). Sighting rates returned to their pre-CAAD installation levels after the CAADs were removed from the fish farm sites. Morton (2000) also reported a decline in Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) after CAADs were installed in the area, but provided no statistical support.

Clearly, there is evidence that marine species, harbour porpoises in particular, can be displaced by the sounds produced by Airmar CAADs. However, in certain situations, animals may be motivated to remain in an area, for example if it represents an important foraging region. Under such circumstances, animals may be repeatedly exposed to sounds potentially leading to damage to the auditory system. Hearing damage is detected as a loss of sensitivity and occurs first as a short-term shift in hearing threshold, which is recovered from in a matter of hours or days (Temporary Threshold Shift - TTS). If the exposures are of high-intensity sound or moderate-intensity sound over a longer time period, the threshold shift can become permanent (Permanent Threshold Shift – PTS). It is unclear what the biological significance of threshold shifts are -such shifts occur commonly in humans and often go unnoticed (Gordon and Northridge 2002).

Sound Exposure Level (SEL) is a measure of energy that can be used to assess cumulative exposure. It is the dB level of the integral of the squared-instantaneous sound pressure normalised to a 1 second period (Southall et al. 2007). It is particularly useful as it enables comparison of sounds of different duration, and multiple exposures can also be calculated. No studies have directly investigated the effect of CAAD signals on the auditory systems of marine mammals although Gordon and Northridge (2002) make a number of extrapolations. Southall et al. (2007) reviewed the scientific literature on TTS in marine mammal after exposure to intense sound and proposed thresholds above exposures might result in TTS and then PTS. In the calculation of these thresholds, harbour porpoises were listed as ‘high-frequency cetaceans’ (based on their functional hearing capabilities - though no data on TTS was considered in this assessment since none was available) in which TTS would be elicited in response to SELs of 198 dB re 1 $\mu\text{Pa}^2\text{-s}$ (Southall et al. 2007). PTS thresholds are proposed to occur 15 dB above the SELs that cause TTS-onset (Southall et al. 2007). A recent study investigated masked threshold shifts in harbour porpoises in response to a seismic airgun stimulus and hearing sensitivity was

tested at 4 kHz (Lucke et al. 2009). In their study, TTS occurred in response to a SEL of 164.3 dB re 1 $\mu\text{Pa}^2\text{-s}$, suggesting harbour porpoises may be more sensitive to anthropogenic sound than proposed by Southall (Lucke et al. 2009; Southall et al. 2007).

A further consideration in assessing the potential impacts of CAADs is the issue of how the signal propagates in the environment. Received levels of sound will generally be a function of source level, range from the source and propagation loss (which is usually a function of range). Many factors, including, the bathymetry, salinity, temperature stratification, depth of the source and the receiver and the time-frequency sound characteristics may all affect how sound propagates at a site. Land masses will also impact propagation: islands may provide barriers between source and receiver, though not completely exclude sounds from the shadowed regions (Morton & Symonds, 2002) and narrow channels may serve to enhance the propagation of sound. Maximum detection ranges for an Airmar CAAD have been reported in two studies. Signals were detected > 16 km in the Sound of Mull (a narrow channel) on the west coast of Scotland in 2006 (Calderan et al. 2007) and it has been suggested such a device could theoretically be detected at up to 20.2 km, depending on ambient conditions (Jacobs and Terhune, 2002). Consequently, sound propagation will vary significantly on a site-by-site basis and the pattern of signal intensity with range may not be straightforward. Shapiro et al. (2009), investigating variability in SELs of a Lofitech CAAD (repeated 200 ms pulse @ 15.6 kHz, SL = 193 dB re 1 μPa at 1 m) with range, documented variability of up to 19 dB for a given range on a constant bearing from the source. It is unclear what effect this would have on cetaceans and whether it would negatively impact them because they have excellent directional hearing (Cranford et al. 2008; Mooney et al. 2008; Popov and Supin 1988; Popov and Supin 2009) and are likely commonly exposed to both loud biotic and abiotic sounds (Richardson et al. 1995).

To investigate the impact of CAADs on harbour porpoises on the west coast of Scotland 2D sound maps of Airmar CAAD signals in channels and sea lochs on the west coast of Scotland were calculated and the relationship between received levels and range for four of these CAAD sites was explored. Additionally, the potential for CAAD-induced hearing threshold shifts and disturbance was investigated at two sites. This work serves to provide a better understanding of the likely impact of the widespread use of CAADs over the west coast of Scotland and to better inform management measures for marine species in the region.

6.2 Materials & Methods

6.2.1 CAAD recordings

To investigate the received levels of CAAD devices, a series of recordings was made off the west coast of Scotland in 2007, 2008 and in 2009 (in Loch Sunart only) during dedicated visual and acoustic line transect surveys for harbour porpoises (that were conducted between 2003 – 2008, though only data collected between 2006 – 2008 were considered here because CAAD use was more stable during this period, that between 2003 and 2005 – see § 6.2.3.2). Two different, calibrated, hydrophone arrays were used in this study to determine CAAD received levels both containing two broadband elements (HS150 elements - Sonar Research & Development Ltd) with the highest sensitivity at 150 kHz and near flat response between 2 – 140 kHz. Elements were coupled with adjacent pre-amplifiers, providing 35 dB of gain. In 2007 – 2008, the first hydrophone fed into a Seiche amplifier and then into an m-Audio Quattro soundcard, through which the recordings were made at a sampling rate of 96 kHz. The same hydrophone was used in 2009 but the signals were fed into a National Instruments external soundcard (PCI-6250) and recordings were sampled at 500 kHz. The second hydrophone was used in 2009, connected to a Magrec amplifier and the signal was fed into an Edirol UA-20 soundcard, with which recordings were made, sampling at 96 kHz (Table 6.1).

Table 6.1 - Shows equipment variations across the study period and details of samples taken in this analysis.

Year	Hydrophone	Recording Unit	Sampling Rate	Number of RL Samples
2007	HS-150	m-Audio Quattro	96 kHz	200
2008	HS-150	m-Audio Quattro	96 kHz	1008
2009	HS-150 / AQ4	National Instruments / Edirol UA-20	500 kHz	575

6.2.1.1 CAAD Recording protocol

In 2007 during the regular line-transect surveys, acoustic monitoring sessions were performed to record and make note of identifiable ambient noise sources. When under motor, the survey vessel was slowed down every 15 minutes and an observer listened and recorded for a period of 1 minute and documented identifiable sounds heard (when sailing, the stations were performed every 15 minutes without slowing down as the engine was off under sail). Recordings were made using the calibrated towed hydrophone array wherever CAAD devices were heard. In 2008 during regular HWDT surveys, a more rigorous automated recording protocol was employed. When regions with known CAADs installed were approached, an automated routine was

initiated. This involved making a 15-second recording every minute until the CAAD device was no longer audible (recordings began before the region was entered, to determine where the CAAD became audible). In 2009, a dedicated survey was conducted in Loch Sunart and the same recording protocol was used. In some cases, long recordings were made as the survey vessel travelled through a region with a number active CAADs. These recordings were later sampled every minute and the received levels calculated for each sample.

The latitude and longitude position of each recording/sample was determined from the GPS data collected every 10 seconds by *Logger 2000*. The distance from each recording/sample to each fish farm was calculated for sites known to have the active CAADs using custom routines in Manifold (Version 8.00, 32-bit, Manifold® Systems). The vessel speed and sea state were also extracted for each recording/sample to investigate whether survey conditions were biasing the observed CAAD received levels.

6.2.2 CAAD signal processing

Airmar pulses are of constant frequency (centred at 10 kHz) and so all recordings were ‘band-pass’ filtered around the pulse centre frequency at 9 – 11 kHz. Sound level measurements (RMS) were made of the CAAD signal and of the ambient noise in each recording. To do this, recordings were binned by a FFT length of 512 for the recordings sampled at 96 kHz and 1024 for those made at 500 kHz. These bin lengths were chosen as they were just large enough to capture a single pulse from the Airmar CAAD, but not large enough that two overlapping CAAD signals (from two CAAD transducers) could be sampled at which. Had two CAAD signals been measured in a single bin, the resulting energy level measurement would have been inflated (and much higher than if a single pulse had been measured). This would result in an incorrect interpretation of the CAAD soundfield. Once recordings were binned, the energy in each bin was summed and 99th percentile (the CAAD signal) and 10th percentile (a measure of the ambient noise) signal levels were measured (Figure 6.3). To ensure that the 99th and 10th percentile were accurate measurements of the CAAD signal and ambient noise respectively, summed energy level measurements were cross-validated in Raven Pro (version 1.3 Cornell Lab of Ornithology). The measurements from Raven were found to correlate closely with those from the analysis described above meaning the 99th and 10th percentile measurements are accurate measures of the CAAD signal and ambient noise respectively.

Energy level measurements were converted into dB (RMS) values and corrected for gain used during the recordings. To avoid including samples that contained other broadband noise

sources around 10 kHz (e.g. ferries and shipping), only samples with a signal-to-noise ratio of >10 dB between the CAAD signal and the ambient noise were included in the final analysis.

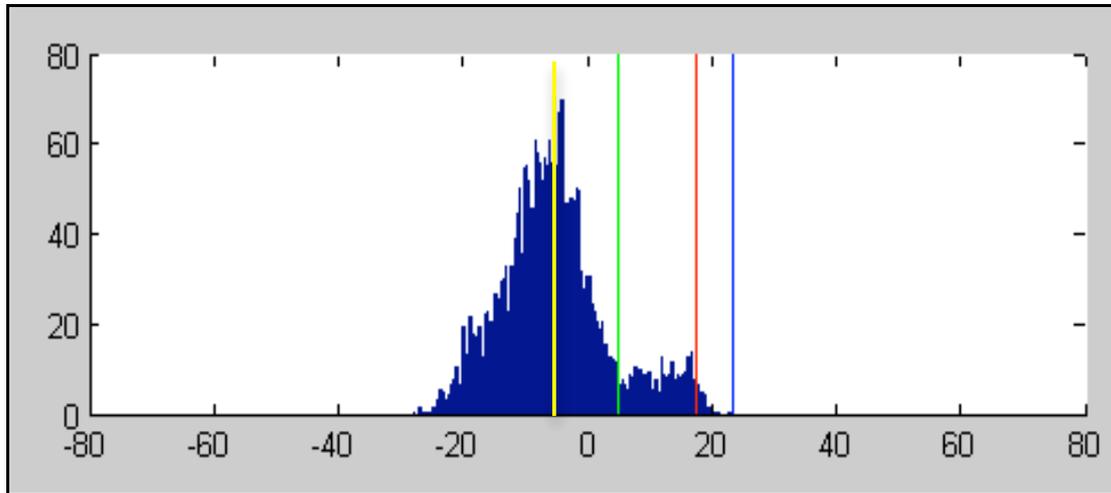


Figure 6.3 – A histogram of time-frequency bins from 1 recording showing the summed energy level in each bin of the recording sample (each sample is 5.3 msec in length and band-pass filtered between 9 – 11 kHz). The y-axis is the count and the x-axis represents the summed energy in each time-frequency bin. The red line represents the 99th percentile measurement (containing the CAAD signal) and the yellow shows 10th percentile measurement (a measure of the ambient noise). The green and blue lines represent the mean and maximum energy in each sample respectively.

Two-dimensional sound maps of received level (RL) were plotted from the analysed CAAD recordings. Received levels were interpolated spatially using a kriging method in Manifold. The maximum interpolation distance allowed was the maximum distance between adjacent samples to avoid large generalisations being made between a small number of sample points.

To investigate propagation loss of CAADs in different locations, RL was investigated as a function of range from the CAAD device in three regions: Loch Sunart, the Sound of Mull and Kerrera (Figure 6.4). CAADs were detected in other sites, but they have not been included in this part of the final analysis because of the small number of recordings at those sites.

In Loch Sunart and Kerrera, propagation loss was investigated to the maximum range that the CAAD was audible above the ambient noise. However, in the Sound of Mull, two fish farms with CAADs (Fiunary and Fishnish) are separated by approximately 7 km (Figure 6.5), and consequently at ranges > 5 km from each source, distant devices become audible, impacting the plots of RL vs range. So in this analysis, propagation losses were only investigated out to 5 km from both of these sites.

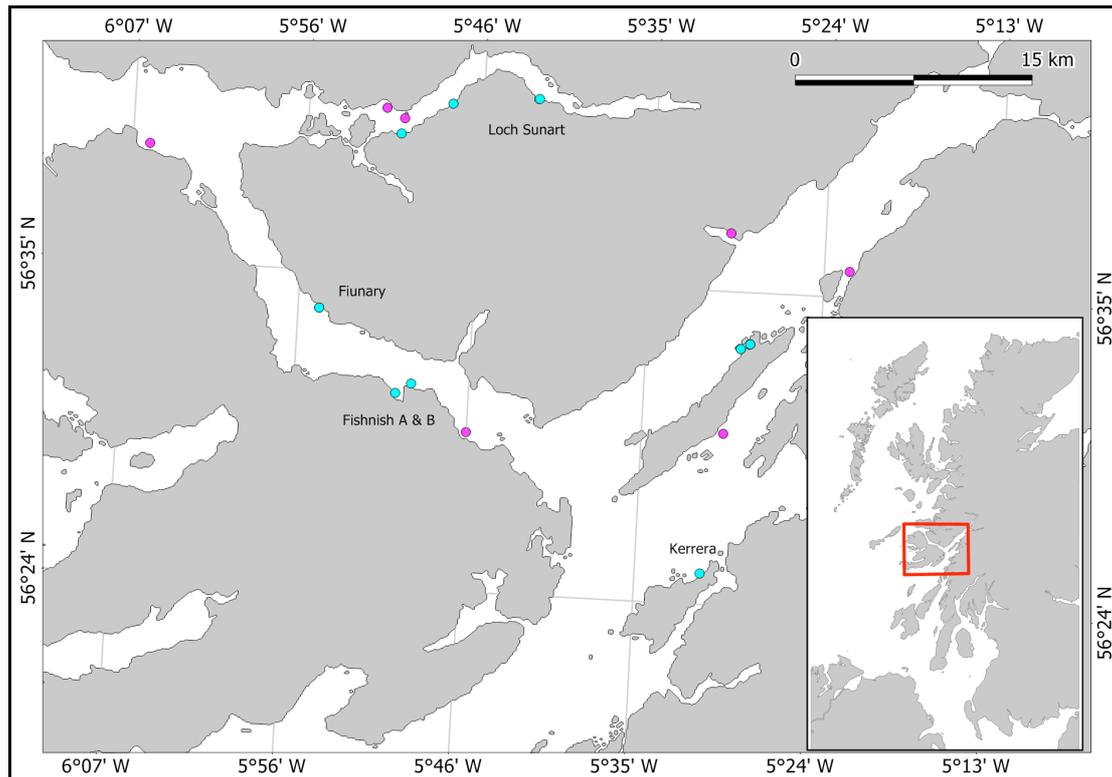


Figure 6.4 – Locations of the fish farms with active CAADs installed and included in this analysis. Sites with active CAADs are shown in blue; sites with inactive CAADs are shown in pink.

6.2.3 Investigating Potential Impacts of CAADs on porpoises

6.2.3.1 Investigating the potential for CAAD induced temporary threshold shifts

One aim of this opportunistic study was to investigate the possibility of exposure to CAAD signals causing TTS or PTS in harbour porpoises. The exposures (to CAAD signals) necessary to exceed published theoretical sound exposure level thresholds (Lucke et al. 2009; Southall et al. 2007) were calculated for the maximum CAAD received levels observed in each recording.

The time of exposure to CAAD signals at constant RL required to cause auditory threshold shifts was calculated from a SEL equation (from Kotecki 2008) :

$$SEL = RL + (10 * d) * \log_{10}(T)$$

re-arranged to:

$$T = \frac{10^{(SEL-RL)}}{(10 * d)}$$

Where T is time of exposure required to reach the SEL threshold in seconds, SEL is the SEL threshold of interest, RL is the received sound pressure level of the CAAD at a known position, d is the duty cycle of the CAAD signal (Wensveen, pers. comm.). The duty cycle for the Airmar device is $\sim 50\%$ and so in this analysis $d = 0.5$ was used in the calculations. One assumption being made here is that animals are not recovering from exposures between sequential pulse trains. Because Airmar devices emit pulse trains for ~ 2 seconds, followed by a ~ 2 second period of silence, it is possible that animals may recover slightly between pulses. However, in reality, because many Airmar transducers can be active at once, it is common that there will be overlap between pulse trains leading to almost constant exposure.

An equal energy model predicts that two noise exposures will induce similar threshold shifts if the exposures are equal in sound energy, irrespective of the temporal nature of the sound energy. Therefore, according to an equal energy model, a doubling of exposure duration and a 3-dB increase in amplitude should induce similar threshold shifts. The effect of source level and duration of the fatiguing stimuli have been directly investigated in studies on pinnipeds (Kastak et al. 2005) and cetaceans (Mooney et al. 2009) and shown that using the equal energy rule in calculations may result in conservative values for exposures causing TTS. Because this is an opportunistic study, I chose to use the equal energy rule in the models, because it is a simpler method of calculation and is still sufficient to give estimates of the exposures necessary to cause TTS.

There are two studies that have calculated SEL thresholds for TTS in harbour porpoises; 164.3 dB re 1 $\mu\text{Pa}^2\text{-s}$ and 198 dB re 1 $\mu\text{Pa}^2\text{-s}$, from Lucke et al. (2009) and Southall et al. (2007) respectively. PTS thresholds were derived from these TTS-onset exposure values plus an additional 15 dB above the TTS threshold as used in Southall et al. (2007). Consequently, PTS-onset thresholds of 179.3 dB re 1 $\mu\text{Pa}^2\text{-s}$ and 213 dB re 1 $\mu\text{Pa}^2\text{-s}$ were also used in this analysis (from Lucke et al. 2009 and Southall et al. 2007 respectively). These thresholds will henceforth be discussed as the Lucke and Southall TTS and PTS thresholds.

6.2.3.2 CAAD-induced disturbance

To investigate the impact of CAADs on harbour porpoise distribution, the relative densities of porpoises around four fish farm sites in the Sound of Mull were explored (Figure 6.5). Survey effort, harbour porpoise sightings and acoustic detections data were collected and analysed as described in Chapter 2 (§ 2.1).

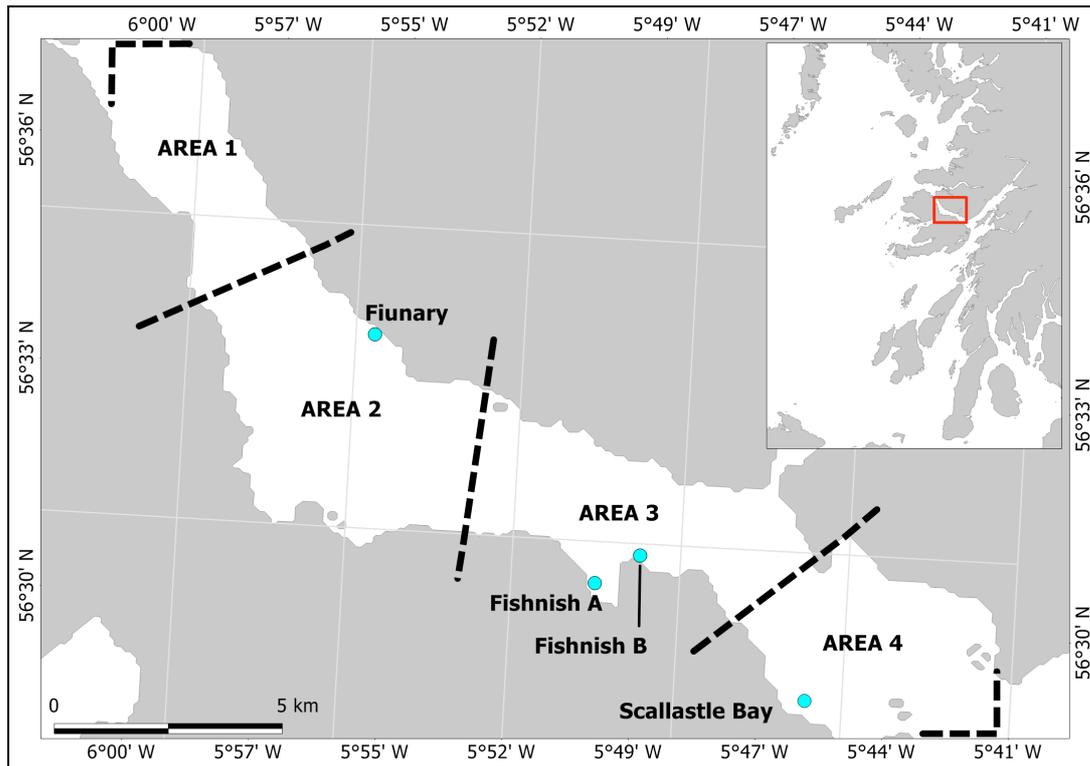


Figure 6.5 - Fish farms in the Sound of Mull and the ‘study areas’ in the analysis of porpoise density.

Two different CAAD models have been used at the Fishnish A and/or Fishnish B sites from 2001 onwards. The CAAD model was changed in 2004 and again in 2005 when the Airmar dB Plus II models were installed (but were not changed after this point). Consequently, in this analysis, survey data collected from 2006 – 2008 were used as this is the period in which CAAD use has been reasonably stable and surveys have been conducted). Airmar CAADs were present at the Fishnish A and/or B sites from 2006 – 2008 and a new Airmar dB Plus II was installed at the Fiunary site in early January 2008 and remained on during 2008 (all sites are owned and maintained by Scottish Sea Farms Ltd.). No CAADs were audible near Scallastle Bay during 2005 – 2008 (operated by Lighthouse Caledonia Ltd).

The study region was divided into four regions of approximately equal area, two of which comprised some of the fish farm sites of interest (Figure 6.5). Area 1 and Area 4 did not contain any CAAD devices throughout the study period and Area 2 did not have any CAADs installed during 2006 – 2007 but, as discussed above a new Airmar device was deployed there in 2008. Airmar CAADs were operating in Area 3 throughout the 2006 – 2008 study. Sea state has been shown to have a significant impact on visual surveys for harbour porpoises, with sighting rates decreasing strongly in sea states > 1 (Palka 1996). Preliminary analysis of porpoise survey data revealed that there were highly variable sighting rates in the region during 2006 – 2008 likely due to sea state (see results of Chapter 3 – 5). Acoustic detection rates were higher and less

affected by sea state. Therefore, only acoustic detection data and survey effort were considered in this analysis to maintain an adequate sample size.

Acoustic detection rates were calculated (porpoise detections per km of survey effort) for each of the regions in 2006 – 2007 (combined) and 2008. Because of the small sample sizes in this study, differences in detection rates between these two time periods were investigated statistically using the Fisher’s exact test to determine whether there was significant difference in porpoise detections between 2006 – 2007 (combined) and 2008 in the four study areas. The closest observed detection (COD) and closest approach of the vessel to the fish farm (CAV) were determined for each year at the Fiunary and Fishnish B to investigate finer-scale distribution.

In Chapter 5, regional models were for the Sound of Mull across the 2003 – 2008 study period. Here, the impact of CAADs on porpoise distribution is investigated in the Sound of Mull between 2006 - 2008. To determine whether CAADs were impacting porpoise distribution across this period (when different CAADs were active), an additional Sound of Mull acoustic model was constructed. In this model, acoustic detection and survey data collected between 2006 – 2008 were used and received level of CAADs (RL) was included as a covariate to determine if they are a significant predictor of harbour porpoises detection rates. Due to the small sample sizes in the Sound of Mull in each year, it was not possible to build individual models for each year among 2006 – 2008. Instead the data were pooled across 2006 - 2008 and a single acoustic model was constructed for the period. The methods used in data processing and modelling are described in detail in §2.3 and §2.4.2.3).

6.3 Results

6.3.1 Investigating Airmar CAAD usage

Acoustic monitoring surveys were conducted in 2007 and 2008 to identify the locations and extent of Airmar CAAD usage on the west coast of Scotland. The data presented here represent a total of 24,253 km of acoustic survey effort (2007: 13,390 km; 2008: 10,963 km)(Figure 6.6). During this time, notes and recordings were made wherever CAADs were heard. A core area was identified where a cluster of sites had continuously active Airmar devices installed (Figure 6.6 & 6.7). This region comprised Loch Sunart, the Sound of Mull, Loch Linnhe and the northern part of the Firth of Lorn. Additionally a single site at the mouth of Loch Na Keal had an Airmar device installed, as did two sites in Loch Nevis. Another model of CAAD (‘Terecos’) was documented in Loch Duich during the study and is used elsewhere on the west coast of Scotland (Calderan, pers. comm.).

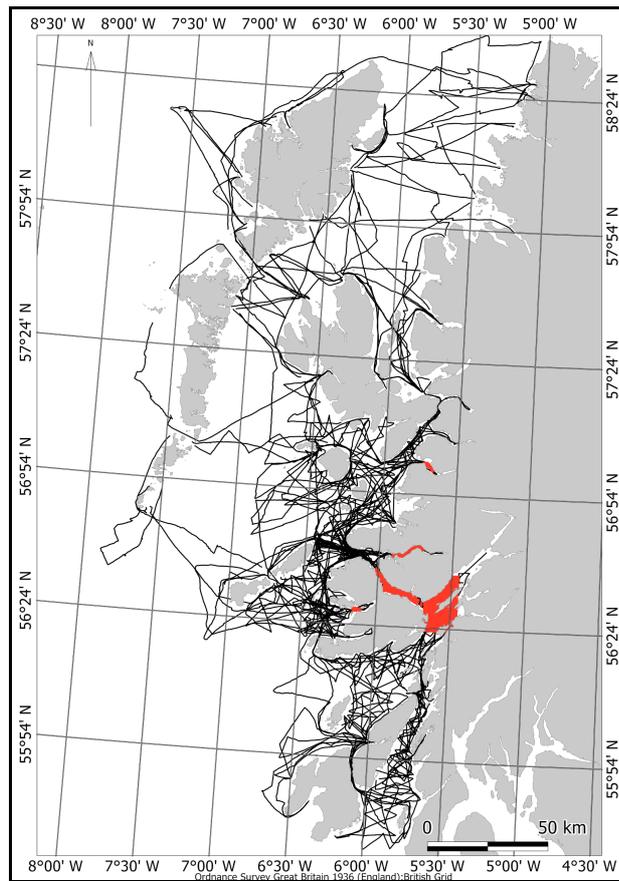


Figure 6.6 - Distribution of acoustic survey effort in 2007 & 2008 (black lines). Locations of CAADs recorded are shown in red.

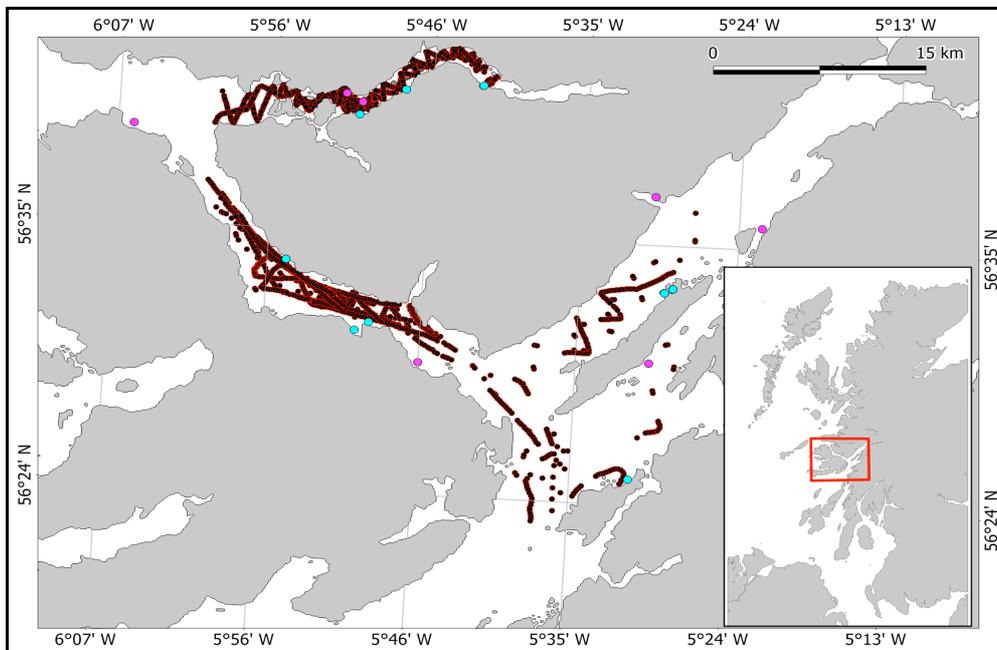


Figure 6.7 - The distribution of CAAD recordings in the core region made during 2007 - 2009 (black points). Active CAADs are shown in blue and fish farms without CAADs are shown in pink.

Interpolated sound fields were calculated for sites in Loch Sunart, the Sound of Mull, Loch Linnhe and near Kerrera. This revealed a core region (consisting of six sites with active Airmar CAADs, and an additional three in Loch Sunart), 275.2 km² in size, which was almost constantly ensonified by CAAD signals in 2008 (Figure 6.8). This zone extends from the entrance to Loch Spelve in the southeast to the entrance to Tobermory harbour in the northeast, resulting in almost all of the Sound of Mull being ensonified. Additionally much of the southern portion of Loch Linnhe and the majority of Loch Sunart appear to be constantly ensonified by Airmar CAADs.

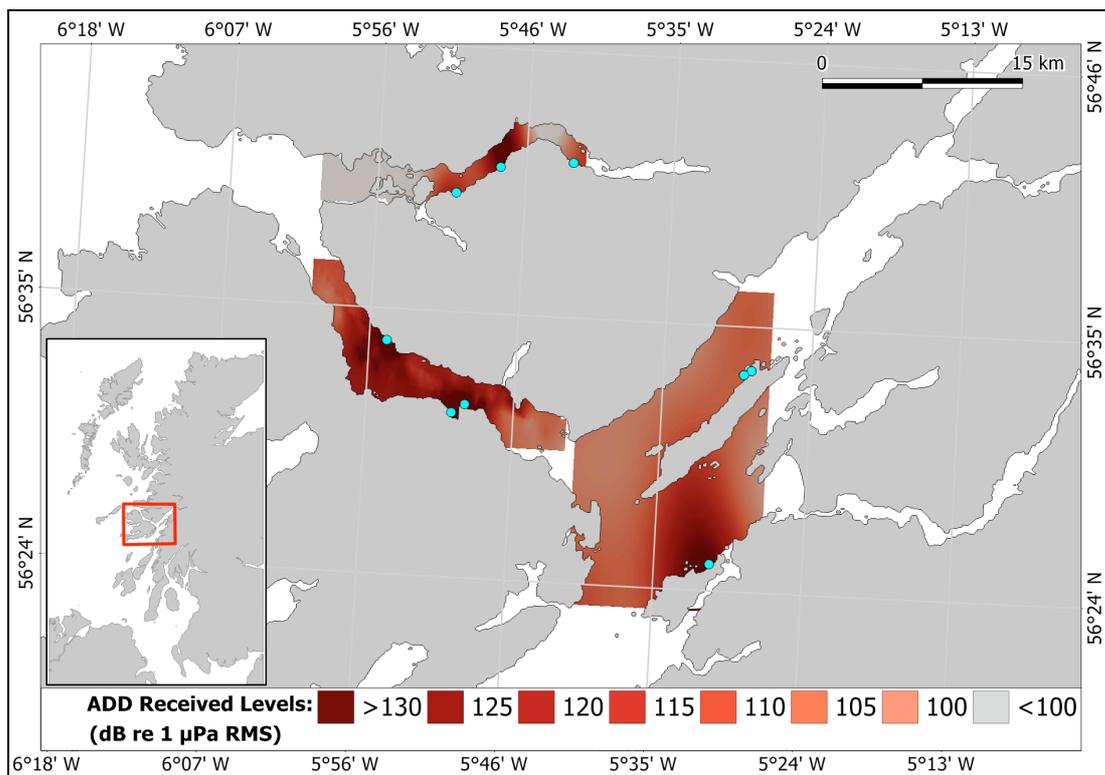


Figure 6.8 - Interpolated sound fields of the main cluster of CAADs observed on the west coast of Scotland. Light blue dots show the position of the CAAD sites. Received level legend and scale bar are shown. Airmar CAAD Source Level: 194 dB re 1 µPa (RMS).

6.3.2 Propagation loss of CAAD signals

To investigate whether this extensive CAAD use was impacting harbour porpoises in the area, the received levels (RL) of CAADs were examined with respect to range at the four sites. The Fishnish B site was not included in the final analysis as the survey vessel was not able to get within 2 km of the source (Figure 6.9).

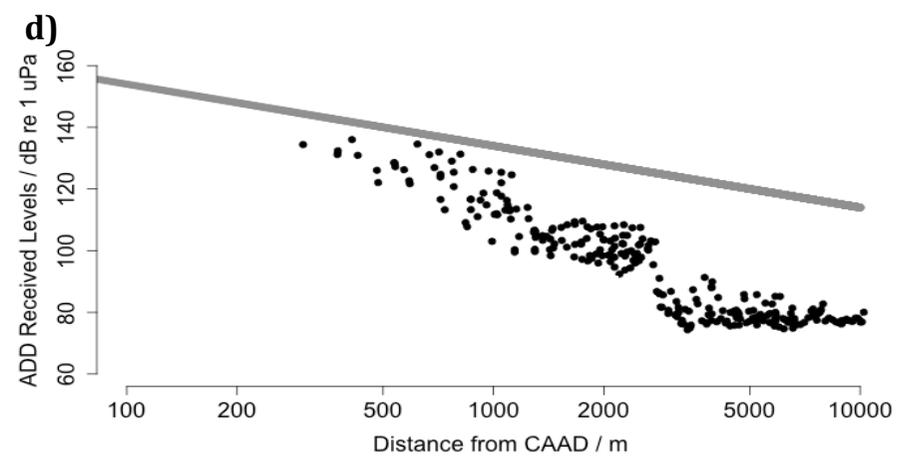
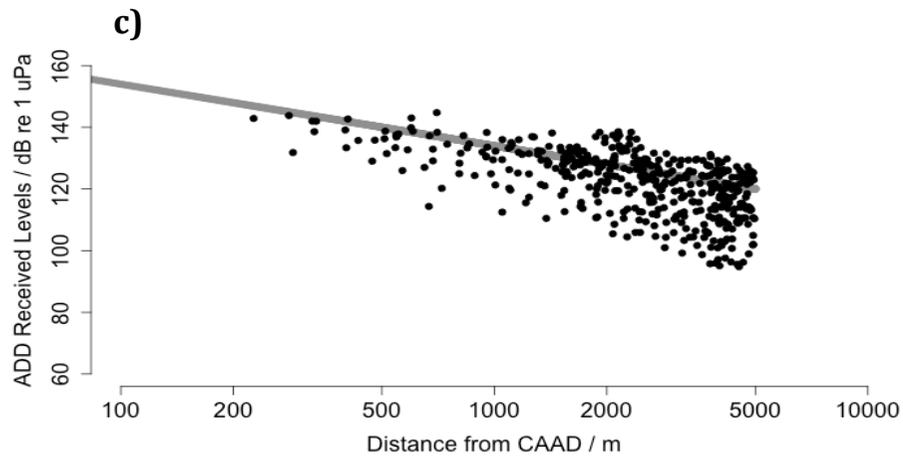
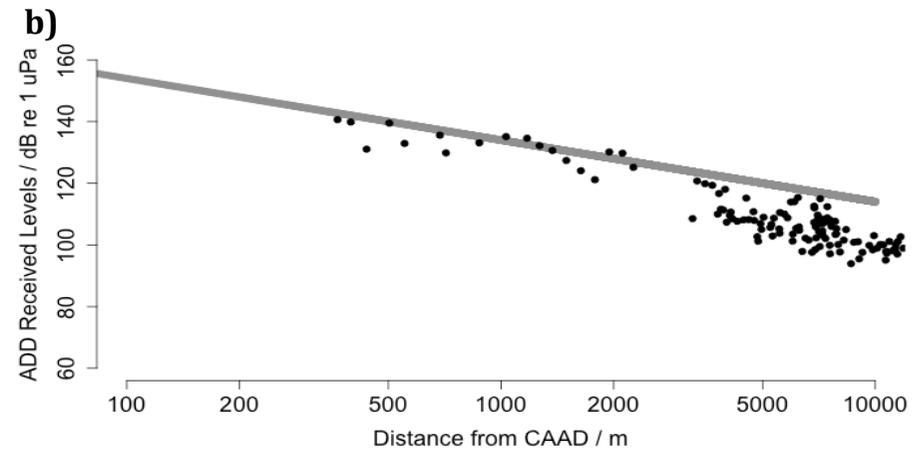
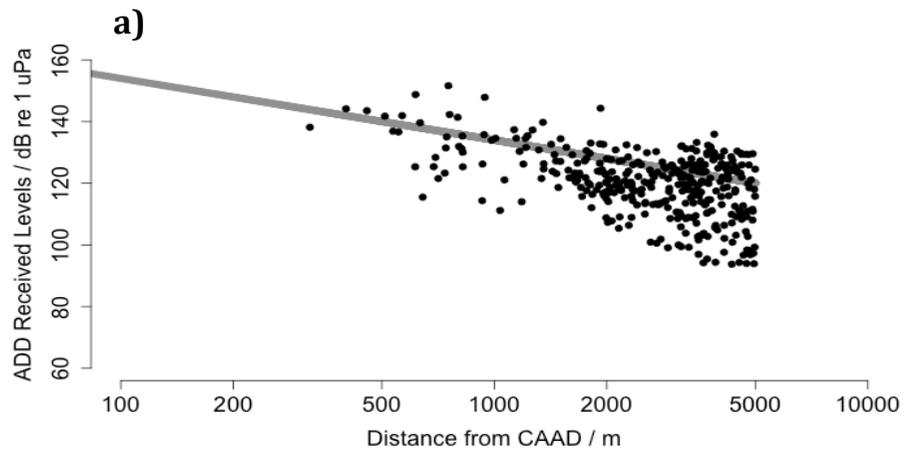


Figure 6.9 – The relationship between Received Level (RL) and distance from the active CAADs for four sites in the Inner Hebrides: (a) Fishnish B (in the Sound of Mull); (b) Kerrera; (c) Fiunary (in the Sound of Mull) and (d) Loch Sunart. The received levels of CAAD signals are represented by the black dots and the expected propagation loss under a spherical spreading model (from a source level of 194 dB re 1 μ Pa) is shown by the grey line.

An overall trend of decreasing RLs with increasing range from the source was observed at four sites (Figure 6.9 a – d). Propagation losses were generally as expected under a spherical spreading model (i.e. $20 * \log_{10}(R)$, where R is the range from the device) at 3 of the four sites, however RL were variable at constant ranges (on different bearings from the source) and in many cases the highest RLs were not observed in the recordings made closest to the source (Table 6.2). For example, at the Fiunary site, at a distance of 1000 m around the source CAAD, received levels of 124.4 – 138.3 dB re 1 μ Pa were observed. This variability was further highlighted in the Sound of Mull where received levels of approximately 144 dB re 1 μ Pa were observed at 282 m, 401 m, 701 m and 1924 m from the nearest source CAADs. In Loch Sunart, propagation losses occurred much more quickly than at the other sites (Figure 6.9 d). Variations in RL at constant ranges (but different bearings) were also observed here, e.g. RL of between 99.1 – 122 dB at 1000 m from a CAAD source. These were similar to those observed in the Sound of Mull and Kerrera.

Table 6.2 - shows the closest approach made by the survey vessel to each fish farm and highest received levels (RL) observed in that approach. The range from the source at which the highest RL was observed (and the RL itself) are shown.

	CAAD Location			
	Kerrera	Fishnish B	Fiunary	Loch Sunart
Closest Approach to Device	366 m	401 m	226 m	302 m
Received Level	140.6 dB	143.9 dB	142.9 dB	116.4 dB
Range at which loudest RL observed	366 m	753 m	701 m	355 m
Received Level	140.6 dB	151.6 dB	144.8 dB	136.0 dB

The relationship between sea state, vessel speed and received levels of CAADs was investigated to ensure that variations observed in RL were not impacted by these factors. No relationship was found between CAAD received levels and these survey conditions indicating they were not impacting the measured received levels here (Figure 6.10).

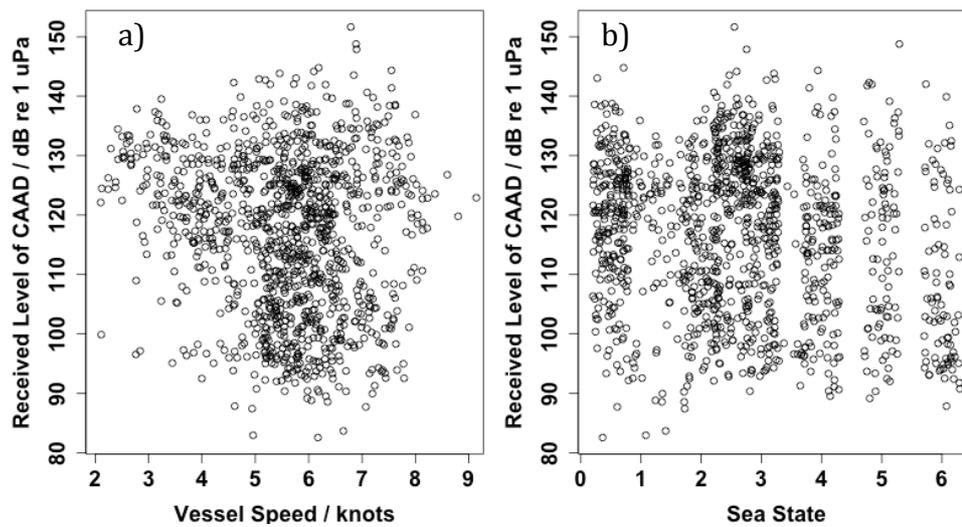


Figure 6.10 – The relationship between received level and (a) vessel speed and (b) sea state investigated in the study. N.B. The points in plot (b) have been jittered for clarity.

6.3.3 Investigating the impact of CAADs on harbour porpoise

6.3.3.1 Potential for impacts on hearing

The potential impacts of these devices on harbour porpoises was investigated with respect to temporary and permanent threshold shifts around at 10 kHz (TTS and PTS) as a consequence of exposure to Airmar CAAD signals from two sites in the Sound of Mull (the Fishnish B and Fiunary sites). The received level of Airmar CAADs at known ranges to the source were used to calculate the exposures necessary to exceed the Lucke and Southall TTS and PTS thresholds, (Figure 6.11).

This analysis revealed that relatively short exposures to CAAD signals could be sufficient to cause TTS in harbour porpoises. The highest received level recorded in this study was observed 753 m from the source and at this position and RL an exposure of 24.6 minutes would have been sufficient to exceed the Lucke TTS threshold. An exposure of 2 years and 2 months would be needed to exceed the Southall TTS threshold. A porpoise would need to be exposed for approximately three month at such a RL in order for a PTS to occur based on the Lucke PTS threshold (PTS would not occur within the lifespan of an animal based on the Southall PTS threshold). The next highest observed received levels of 148.8 dB and 147.9 dB were encountered 615 and 942 metres from the nearest CAADs respectively. At these received levels, animals would need to be exposed for between 2.1 – 3.5 hours for TTS to be caused (animals would need to be exposed for > 1 year at this RL to exceed the Lucke PTS threshold). As noted previously, received levels of approximately 144 dB were encountered at 282 and 1924 m from

the source, indicating large variations in RL with range. At such received levels exposures of approximately 21 hours would be needed before the Lucke TTS threshold would be exceeded.

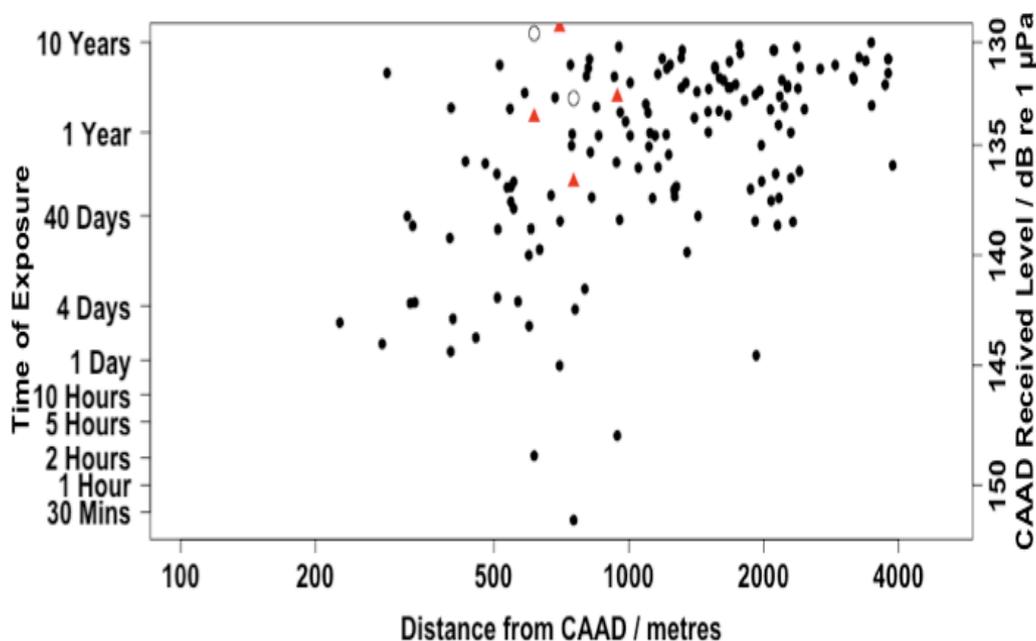


Figure 6.11 – The potential for TTS and PTS in response to CAAD signals. The exposures necessary (on the left y-axis) at a given received level (on the right y-axis) and the distance from the device at which these received levels were encountered (x-axis). Selected exposures required to exceed the Lucke TTS (black circles), Southall TTS (white circles) and Lucke PTS (red triangles) are shown.

6.3.3.2 Impact of CAADs on harbour porpoise distribution

The impact of CAADs on harbour porpoise distribution was investigated in relation to four fish farm sites in the Sound of Mull. In 2006 & 2007, Airmar devices were deployed at Fishnish A & B (see Figure 6.5) while no CAADs were active at Fiunary or Scallastle Bay. In January 2008, a new Airmar device was installed at the Fiunary site (with no devices at Scallastle Bay).

Acoustic surveys were conducted from 2006 – 2008 in the Sound of Mull resulting in a total of 801 km of survey effort. Survey effort and acoustic detections of porpoises were divided into the four study areas described earlier and detection rates were calculated for each area (Table 6.3). In the Sound of Mull in general, detection rates were lower in 2008 than observed in 2006 – 2007, with 0.10 animals per km in 2008 compared with 0.19 animals per km in 2006 and 2007 combined, although this difference was not statistically significant (Figure 6.12).

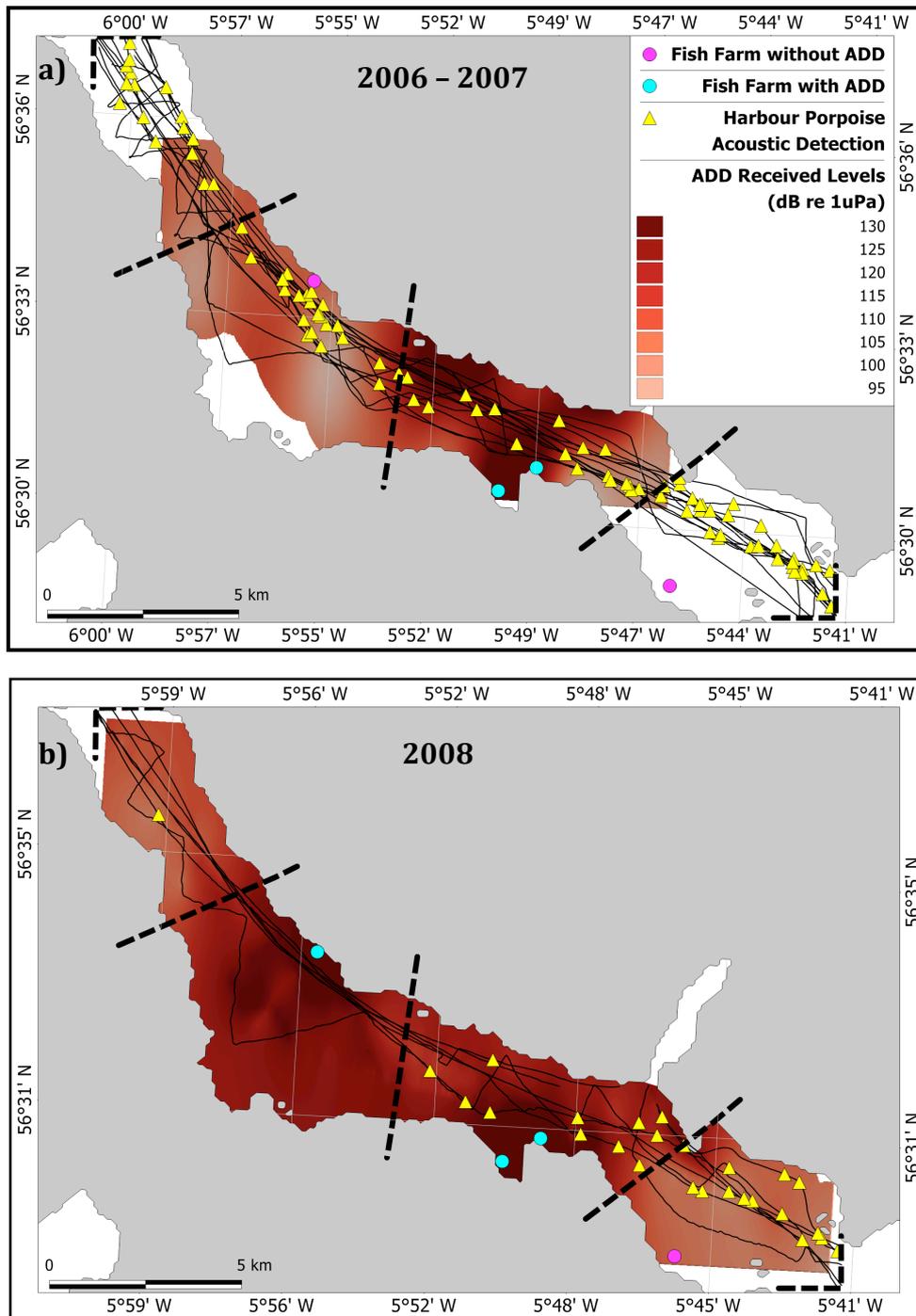


Figure 6.12 (a) - Distribution of acoustic survey effort (black lines) and acoustic detections of harbour porpoise in 2006-2007 (yellow triangles). Locations of two CAADs active over that period and interpolated sound fields are also shown. (b) – Distribution of acoustic survey effort and detections of harbour porpoises in 2008. An additional CAAD was active and the new interpolated sound field for these three CAADs are shown. The boundaries outlining the analysis areas and legend are shown. N.B There was fewer recordings made in 2006-2007 compared with 2008 leading to a spatially-limited extrapolation in the southeast region in 2006-2007. There were no recordings for this region and so no calculations were made. It is probable that the patterns observed in the southeast in 2008 are what would have been observed in 2006/2007.

Detection rates were highest in Area 4 in all years of the study and a slight decrease was observed there in 2008, though this was not significant. In 2008 a decrease was observed in detection rates in Area 2 (containing the Fiunary site with the installed CAAD) with zero detections, significantly fewer than expected based on detection rates in 2006 – 2007 and the effort conducted in 2008 ($p < 0.05$, $\chi^2 = 4.82$, $df = 1$). A single acoustic detection was made in Area 1 in 2008, resulting in a detection rate of 0.02 animals per km, which was lower than in previous years, though this difference was not significant. In Area 3, which contains two established CAADs, detection rates did not vary significantly between study periods.

Table 6.3 – Breakdown of effort (in km), detections and detection rates (acoustic detections per km) for the study areas and years of the study. The observed and expected numbers of detections are shown (the expected values are based on the amount of effort conducted in an area in 2008 and the detection rates for that area from 2006 and 2007 combined).

Year	Statistic	Area 1	Area 2	Area 3	Area 4	Total
2006	Effort (km)	27.6	46.2	73.6	52.8	200.2
	Detections	5	7	6	15	33
	Det. Rate	0.18	0.15	0.08	0.28	0.16
2007	Effort (km)	85.6	104.7	100.2	63.5	354.0
	Detections	11	15	17	21	64
	Det. Rate	0.13	0.14	0.17	0.33	0.18
2006 & 2007 (combined)	Effort (km)	113.2	151.0	174.1	115.5	553.8
	Detections	26	22	23	36	107
	Det. Rate	0.14	0.14	0.13	0.31	0.19
2008	Effort (km)	50.7	59.2	77.8	67.2	254.9
	Observed Detections	1	0	11	14	26
	Expected Detections	5	6	11	18	40
	Det. Rate	0.02	0	0.14	0.21	0.10

Table 6.4 – Details of the closest observed detections (COD) to the Fiunary and Fishnish B sites, along with the received levels (RL) observed there and the closest pass to the fish farm/CAAD made by the survey vessel in each year. * - at Fiunary in 2006 and 2007 there was no CAAD so RL are from Fishnish B. † - in 2008 the COD to Fiunary was actually closer to the Fishnish B site so RL may be from that site, or a combination of the two sound fields.

Year	Fiunary			Fishnish B		
	Closest Detection	RL at COD	Closest Approach by Vessel	Closest Detection	RL at COD	Closest Approach by Vessel
2006	319 m	104.8 dB*	192 m	849 m	133.4 dB	284 m
2007	415 m	104.4 dB*	401 m	815 m	114.4 dB	260 m
2008	4327 m	115.4 dB†	324 m	1049 m	130.8 dB	282 m

The closest observed detection (COD) to Fishnish B and Fiunary was also calculated (Table 6.4). Similar patterns were observed between 2006 & 2007 at both Fiunary and Fishnish B. The COD to Fiunary in 2006 and 2007 was 319 m and 415 m respectively at which point the RL were 104.8 dB and 104.4 dB (note that these RL are from Fishnish A/B approximately 7 km away). In 2008, no acoustic detections were made within 4,327 m of the Fiunary site, despite the fact that a large amount of effort was conducted close to the site (Figure 6.10) – at this point the RL was 115.4 dB (but this detection was made closer to Fishnish than Fiunary). At Fishnish B, the closest detections were made at 849 m and 815 m from the CAAD in 2006 and 2007, respectively (RL of 133.4 dB and 114.4 dB, respectively). In 2008 a slight increase in COD was observed with no detections being made closer than 1,049 m from the farm site although the RL at this point was lower than COD received level observed in 2006.

To investigate whether or not any impact of CAAD received level on harbour porpoise distribution could be detected using predictive modelling, an acoustic model was built for 2006 – 2008 including RL as a covariate. It was not possible to build predictive models for each year due to the small sample sizes within each yearly dataset. Received level was not retained in the best acoustic models. The results of the 2006 - 2008 acoustic model was very similar to that of the 2004 – 2008 model constructed in Chapter 5, as only depth and slope were retained in the best model and the same relationships with the response were observed. Detection rates increased with increasing depth (up to the maximum sampled depth of 121 m) and slope.

6.4 Discussion

It should be noted, that while even coverage was achieved over the west coast coastal waters, the focus of these surveys was investigating harbour porpoise distribution and so a number of sea lochs and inlets (particularly in the Outer Hebrides) were not surveyed acoustically. Consequently, the results presented here do not represent the full extent of CAAD usage on the west coast of Scotland (Calderan pers. comm.). However, a number of sites using Airmar CAADs were identified and the transmission of signals were investigated there.

6.4.1 Investigating CAAD usage on west Scotland

In this study, acoustic surveys from 2007 – 2008 highlighted a region of Airmar CAAD usage within the west coast study area, extending through the Sound of Mull, Loch Linnhe and northeastern Firth of Lorn. Additionally, devices were present in Loch Sunart, Loch Nevis and the mouth of Loch Na Keal. The area over which CAADs were recorded above the ambient noise in 2008 was 275.2 km². This represents <1% of the total region surveyed in 2008. A

number of sea lochs across the region were not sampled so there are likely more devices than documented in this study. But this study still represents a good indication of CAAD use across the more open regions of the west of Scotland.

Studies of porpoise movements and habitat usage using satellite telemetry in Canada and Denmark revealed that porpoises are a highly mobile species. In the Bay of Fundy, Canada harbour porpoises spent time in focal regions of between 122 – 415 km² while also occasionally ranging over much larger areas (4,728 – 22,103 km²) (Johnston et al. 2005) and animals have been estimated to range over ~50,000 km² (Read and Westgate 1997) though it's not clear how this range was calculated. Satellite telemetry studies of harbour porpoises in Denmark have revealed similar patterns, as animals have utilised larger focal ranges of ~400 – 1600 km² and made transits of > 1000 km (Teilmann et al. 2004; Teilmann et al. 2008). The area surveyed in this study covers 25,109 km² and chapters 3, 4 and 5 have focused on identifying important areas for harbour porpoises and found that the Small Isles, Firth of Lorn and Sound of Jura have the highest detection rates across the west of Scotland. If animals exhibit similar ranging behaviour to that observed in Canada and Denmark, it may be important for animals to use channels and sounds (like the Sound of Mull) to transit between important focal regions and consequently be exposed to CAAD signals.

6.4.2 Variations in propagation of CAAD signals

CAAD signals were found generally to decrease as distance from the source increased. At three of the four CAAD sites investigated, the transmission loss was close to that expected under a spherical spreading model. However, in Loch Sunart, received levels decreased more quickly with range than was observed at the other three sites.

It is noteworthy that pronounced variability in received levels was observed at constant ranges (on different bearings) from the device of up to 13.9 dB in the Sound of Mull. Similar variations in RL were observed in experiments using a Lofitech CAAD (Shapiro et al. 2009). Some of the variations in received sound levels observed here may be explained by a phenomenon called 'Lloyd's mirror' in which sound paths can be constructive (when the direct and surface or bottom reflected sound paths of the CAAD signal are in phase) or destructive (when they are 180° out of phase) and so generate interference between the direct transmission path and the surface and bottom reflected paths of sound. Such effects could cause high RL to be encountered at large ranges from CAAD sources (due to constructive sound paths), or low RL close to CAADs (because of destructive paths). The transmission of sound in shallow water is

highly variable and is strongly influenced by the acoustic properties of the environment (Richardson et al. 1995; Urick 1983). The bathymetry, bottom sediment and current speeds of the area may impact transmission losses. The bathymetry in the Inner Hebrides is extremely variable with a number of deep (>100 m), steeply sloped submarine canyons. This will also impact how sound propagates in the environment. The aspect of the slope face will affect reflection of sound and so sound levels can be elevated or reduced depending on the bathymetry encountered (Richardson et al. 1995; Urick 1983). Additionally, variations in temperature and salinity with depth impact the speed of sound within the water column, affecting propagation and resulting in either reduced or enhanced sound transmission (Richardson et al. 1995). Given the coastal nature of aquaculture sites and the dynamic nature of the environment in the Inner Hebrides, there is likely to be significant freshwater input near to fish farm sites that will impact salinity and temperature variations in the water column.

A possible explanation for the different propagation loss patterns observed between sites is that the CAADs may not have been operating at the full output of the device. A number of studies using CAADs have noted that the output specifications from the device manufacturer do not always correspond with field measurements of source level (Lepper et al. 2004). Jacobs & Terhune (2002) made measurements of the Airmar CAAD devices they used and found their maximum source levels were 178 and 179 dB (16- 17 dB lower than the manufacturer's specification of 194 dB). Additionally, fouling build-up on transducers or surrounding net structures, damaged cabling and/or low battery levels could all impact SL (Gordon and Northridge 2002). The source levels of the particular devices operating at the site are not known but different characteristics of individual transducers could explain the variability in the received levels recorded. Additionally, underwater structures built around a fish farm site may impact sound propagation by shielding the CAAD signals.

6.4.3 Potential impacts of CAADs on porpoise hearing

I investigated the exposures to Airmar CAADs necessary to cause threshold shifts in porpoise hearing and found that there was potential for TTS to be caused by relatively short periods of exposure. In addition, calculations were made using the equal energy rule, which can result in conservative values in the exposures necessary to exceed TTS/PTS thresholds (Kastak et al. 2005; Mooney et al. 2009). Therefore the values presented here are likely slight underestimations of the exposures necessary to exceed thresholds. It should be noted that TTS itself might have no biological significance. Such shifts occur commonly in humans and often go unnoticed (Gordon and Northridge 2002).

The highest received level of Airmar CAADs recorded was 151.6 dB re 1 μ Pa and was observed at 751 metres from the source. At this received level an exposure of 24.6 minutes at this received level would be sufficient to cause TTS (based on Lucke's TTS threshold). We have seen that the propagation of CAAD signals is variable and it is unclear how temporally stable these observed propagation patterns are. Thus whether these RL would have been present 753 m from the device for sufficient time to cause TTS is unknown. It should be considered that in the Lucke et al. (2009) study, TTS was observed at 4 kHz in response to a broadband stimulus. The exposures to Airmar CAADs would be centred at 10 kHz, at which frequency harbour porpoise hearing is 5 - 13 dB more sensitive (Andersen 1970; Kastelein et al. 2002; Nedwell et al. 2004) and so the SELs required to cause TTS may be lower. This study calculated that exposures of over 2 years would be necessary for the Southall TTS threshold to be exceeded. The potential for more permanent threshold shifts PTS was also investigated using the Lucke and Southall thresholds. PTS could be caused if an animal was continually exposed at 151.6 dB for 95 days. The Southall PTS threshold would not be exceeded within the lifespan of a porpoise at this received level.

6.4.4 Potential for CAAD-induced displacement

The results of this study indicate that in certain circumstances, CAADs can impact harbour porpoise distribution on the west coast of Scotland. Airmar devices were active at the 2 sites studied in the Sound of Mull in 2006 and 2007 and reasonably consistent porpoise densities were observed close to the CAADs in both these years. Similarly, at the nearby Fiunary fish farm site, consistent porpoise densities were observed during this period. However, in 2008, after the installation of additional Airmar CAAD transducers at the Fiunary site, acoustic detection rates decreased over the region as a whole and no acoustic detections were made within 4.3 km of the Fiunary site. This closest observed detection (COD) was much lower than recorded in 2006 – 2007 when no CAAD was installed (COD: 319 and 415 m, respectively). At the Fishnish B site the CODs were similar across the survey period, though they were > 800 m in all years (much greater than 2006 and 2007 at Fiunary), which may be an indication of animals avoiding the higher sound levels found closer to the CAAD source. It is unclear if animals are resident in the Sound of Mull or using it as a thoroughfare. If animals are resident close to Fishnish B, they will be repeatedly exposed the noise generated by a ferry that runs throughout the year, docking next to the fish farm many times a day. This may be an additional factor explaining why animals are found further from Fishnish B. The extent to which small displacements (< 1000 m) impact animals at a population level remains poorly understood.

Displacement by Airmar seal scarers has been also been observed in other studies on harbour porpoises. (Johnston 2002; Johnston and Woodley 1998; Olesiuk et al. 2002). This study compliments previous studies in which both significant short-term (Johnston 2002) and longer-term (Olesiuk et al. 2002) decreases in porpoise density were observed in response to Airmar CAADs being activated. Olesiuk et al. (2002) did not observe any animals within 200 m of an active CAAD and only observed 1% of the expected number within 600 m of the device. They also observed that porpoise density was 92% lower than expected between 2.5 and 3.5 km from the device. Furthermore, they hypothesised that the effect of the CAAD extended beyond the 3.5 km study limit. In a study in the Bay of Fundy, no porpoises surfaced within 645 m of an active Airmar CAAD (estimated RL of 128 dB re 1 μ Pa) and on mean exclusion ranges extended out to 991 m from the device (estimated RL of 125 dB re 1 μ Pa). These values are similar to those observed at Fishnish B in this study where animals were found at approximately 800 m and RL of 130.8 – 133.4 dB re 1 μ Pa). The closest observed approach of porpoises to the inactive device was 6 m (Johnston 2002). A study in Orkney observed that fewer porpoises were detected acoustically when an CAAD was active than inactive (Robertson 2004)

It is noteworthy that the exclusion pattern observed at Fiunary in 2008 comes from data collected in April to September 2008. The CAAD was installed at the fish farm site in late December 2007. This indicates that if the observed decrease in detection rates was caused by the additional CAAD being installed, then their effects have persisted over at least 4 months (from the time of deployment to the first survey) and potentially up to 9 months post-deployment (the time of the last survey in this study). Between August 2008 and May 2009, T-PODs were deployed around the Fiunary fish farm site (200 – 3,000 m away) and the initial deployment (12th August – 31st August 2008) revealed low detection positive minutes at all of the T-POD sites which is consistent with the acoustic detection rates observed here (SARF in press). During later deployments T-PODs close to the Fiunary site logged a lot of DPM and porpoises were sighted close to the fish farm cages indicating animals were not completely excluded from the vicinity. Over the whole study period, they observed that DPM was higher in period when CAADs were inactive than when they were active which indicates animals may be responding to CAAD noise levels (SARF in press).

This analysis was based on a substantial amount of survey effort and there is good support for the hypothesis that a new CAAD caused changes in harbour porpoises densities in the Sound of Mull. However, this study represents a single trial and there may have been other unrecorded factors causing a shift in harbour porpoise distribution that coincided with the deployment of

the new Airmar CAAD at Fiunary. Displacement was observed close to the Fiunary site, but unchanged densities were observed around the Fishnish A and B sites. It may be that these areas around Fishnish represent higher quality habitat and consequently animals are motivated to remain there in spite of disturbance or other effects on individuals. Alternatively, if animals are resident, it may be an indication of tolerance to Airmar CAAD signals by certain individuals. Results of a predictive model constructed for the Sound of Mull were similar to those observed in Chapter 5 (modelled over 2004 – 2008) indicating that there were consistent patterns of habitat usage and that received level of CAAD was not significantly impacting porpoise distribution. This suggests that if CAAD are displacing porpoises, the pattern is not strong enough to show up in the model relationships at the scale investigated (which is much larger than those from Olesiuk et al. (2002) and Johnston (2002)).

Harbour porpoise may not be the only ‘non-target’ species impacted by CAADs on the west coast of Scotland. Observations of killer whales indicated a significant reduction in the use of feeding areas over a large (>100 km²) area in the Broughton Archipelago (Morton and Symonds 2002). Another study reported a decline in Pacific white-sided dolphin presence in the same area (Morton 2000). Killer whales are sighted on the west coast of Scotland along with a number of other dolphin species (Reid et al. 2003) though it is not known how these and other species are affected by CAADs in this area.

6.4.5 Mitigating the use of CAADs

Currently it is necessary to procure a license from the ‘Scottish Government Licensing Team’ (which is run between Scottish Government and Scottish Natural Heritage) in order to carry out an activity which could (deliberately or recklessly) disturb a European protected species. As discussed previously, disturbance of species protected under Annex IV of the EU Habitats Directive (92/43/EC) is prohibited and Resolution 4 of the ASCOBANS Conservation and Management Plan aims for “*the prevention of [other] significant disturbance, especially of an acoustic nature*” (ASCOBANS 2006). In Scotland, all cetacean species are protected as European Protected Species under the Conservation Regulations 1994 (listed on Schedule 2 and 4 of the Habitats Regulations 1994). As such any deliberate or reckless activity causing injury or disturbance as a consequence of an activity is considered an offense requires a license to be carried out legally. Disturbance includes “*harassing an animal or group of animals*” in any stage of life, in such a way as to “*impair it’s ability to survive, breed, reproduce, rear or otherwise care for it’s young*”. Scottish Natural Heritage (SNH) has advised the Scottish Government that in the case that protected species are disturbed by CAADs, users will need a license in order to continue using

the devices to mitigate seal-aquaculture interactions. Here I have presented data exhibiting the extent of Airmar CAAD use throughout a potentially important site for harbour porpoises (the Sound of Mull and surrounding area). This study provides further evidence that there is significant potential for CAADs to cause disturbance and therefore that this is an issue of concern for the protection of harbour porpoises on the west coast of Scotland and should be considered in future management decisions.

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Chapter 7

General Discussion

7.0 Synthesis

The harbour porpoise is listed on Annex II of the EU Habitats Directive (EU Habitats Directive 92/43/EEC 1992), and consequently there is a requirement to identify sites suitable for designation as Special Areas of Conservation (SACs) for it. One increasingly common method of identifying important habitats for a species is the use of predictive modelling. This method has been used to ascertain areas suitable for designation as marine protected areas (MPAs) for a range of cetacean species (Cañadas et al. 2005; Embling et al. 2010; Hooker et al. 1999; Notarbartolo-di-Sciara 2008; Panigada et al. 2008; Rayment et al. 2010), and to improve the conservation goals of already established sites (Bailey and Thompson 2009; Moulins et al. 2008). MPAs have fixed geographical boundaries, usually aligned with the environmental features important to a species, or their prey (Agardy 1994; Cañadas et al. 2005; Hooker et al. 1999). Hyrenbach et al (2000) categorised habitat features with respect to MPAs according to their dynamism and predictability: (i) static bathymetric (e.g. submarine canyons, reefs, banks and seamounts), (ii) persistent hydrographic (e.g. currents and frontal systems) and (iii) ephemeral hydrographic (e.g. upwelling regions, cold core rings and gyres). Traditionally marine protected area designs are particularly effective in static habitats but sometimes unrealistic, as many important environmental features are neither fixed nor predictable.

The overarching aim of this thesis was to investigate the consistency in habitat use and distribution patterns for harbour porpoise west of Scotland, with a view to identifying key areas within the region, which have potential to be designated as SACs for the species. This study followed on from the work of Embling (2007), who built predictive models for harbour porpoises using data collected between 2003 and 2005 in the region, and identified areas suitable for designation as SACs (Embling et al. 2010). Embling et al. (2010) found that mostly dynamic features, such as maximum tidal current in a region, position in the lunar (spring-neap tidal) cycle and spring tidal range, were important in explaining harbour porpoise distribution. Additionally, Embling et al (2010) found that, based on these models, the highest use regions for harbour porpoises were in the Sound of Sleat, Sound of Jura, parts of the Firth of Lorn and inshore regions west of Mull.

Pinn (2009), in a discussion of the suitability of sites as SACs for harbour porpoise around the UK, stated that given the high level of mobility of the species on a seasonal and annual scale, any investigation using local data should cover a period of at least five years. Here we investigated the temporal and spatial consistency in harbour porpoise habitat preferences west of Scotland using acoustic and visual line-transect survey data collected over five and six years respectively. The main foci were to determine the variability in inter-annual and intra-annual habitat usage and identify consistently important regions for harbour porpoise in the region.

7.1 Habitat Preferences and Distribution

7.1.1 Survey methodology

Both visual and acoustic line-transect data were used to construct models in this study. Overall detection rates were different between the two datasets. In general, visual sightings of cetaceans are likely to be impacted by survey factors (sea conditions, platform height, observer experience) and species factors (group size, surfacing pattern of species, behaviour of individuals encountered)(Barlow et al. 2001; Palka 1996; Palka and Hammond 2001). Sea state was retained in the majority of the models constructed using sighting data (Table 7.1) and sighting rates were reduced in sea states >1 . Increased sea state can either be caused by the wind acting on the water's surface, generating waves, or by hydrological processes occurring the water column causing turbulence at the surface. For example, sea states are generally higher in regions of high tidal current due to the disturbance and mixing associated with large volumes of water being forced over variable topography. Acoustic detections of cetaceans are also subject to variations due to vocalisation rates, changes in sound propagation conditions, ambient and survey vessel noise, and the acoustic behaviour of the individuals (DeRuiter et al. 2009; DeRuiter et al. 2010; Gordon et al. 2000). Previous studies have found ambient and vessel noise levels to be factors in reducing acoustic detections for cetacean species (Embling 2007; Gordon et al. 2000; Hastie et al. 2005; SCANS-II 2008). The results from this study do not support these prior observations. Noise levels were included as potential covariates in the yearly models for 2004, 2005, 2007 and 2008 (noise level measurements were not available in all years). However, none was retained in any of the best yearly visual or acoustic models. This indicates that in regions with higher ambient noise levels, harbour porpoise distribution was not significantly impacted, and that detection rates in the surveys were also not impacted by noise. This is not to say that noise levels do not impact detection rates at all; it is that the other oceanographic covariates retained in the models were more important in explaining harbour porpoise habitat preferences and distribution than noise levels. Many of the visual and acoustic models had vessel

speed retained (Table 7.1), with detection rates decreasing as vessel speed increased. As discussed in Chapter 3, this is likely a function of the time spent surveying in each 2 km segment varying depending on the vessel speed during the segment. At higher boat speeds, it will take less time to travel 2 km than at lower speeds. A further possibility is that animals are making a responsive movement to the survey vessel prior to being available for detection (Palka and Hammond 2001). Both of these issues should be considered in future analyses. None of the models retained 'Variation in boat speed' over each 2 km segment, which gives us confidence that detection rates were not impacted by changes in engine revolutions during surveys.

The models built using acoustic detection data consistently performed better than the models constructed using visual data, when evaluated using a cross-validation method. The majority of the acoustic models had F scores close to, or equal to 1 indicating the models had performed well in capturing the underlying processes that generated the acoustic data. None of the visual models F scores had confidence intervals encompassing 1 indicating that they were not capturing all of the patterns in the data. It is not clear why the acoustic models consistently performed better than that visual models and this warrants further investigation.

7.1.2 Consistency in habitat use

Throughout this study, we have observed consistent patterns in the covariates retained in the best models across a range of temporal and spatial scales: the full and inter-annual models (Chapter 3), seasonal models (Chapter 4) and regional models (Chapter 5). Depth and/or slope were retained in 87% of the temporal models (Chapter 3 and 4), in six of the seven regions modelled individually, and in 79% of all regional models (Table 7.1 and 7.2). In all models where these variables were retained, consistent relationships with the response were observed. Peak visual and acoustic detection rates were observed in regions with between ~ 50 and 150 m water depth with a highly sloped seabed (Figure 7.1 & 7.2). Distance to land was the next most commonly retained covariate in the best models, being kept in 40% of all models. The same relationship was observed in those models with detection rates decreasing almost linearly with increasing distance from land. These relationships are consistent with those of other studies of harbour porpoises in this region (Embling et al. 2005; MacLeod et al. 2007; Marubini et al. 2009), and in other areas in the northwest Atlantic (Read and Westgate 1997) and northeast Pacific (Raum-Suryan and Harvey 1998), although they are different to the results of Embling (2007) and Embling et al. (2010) – this is discussed in §7.1.2.1.

A number of studies have drawn links between harbour porpoise distribution and spatially dynamic, tidal features (Calderan 2003; Embling et al. 2010; Johnston et al. 2005; Pierpoint

2008; Skov and Thomsen 2008; Weir and O'Brien 2000). The patterns observed in this study run counter to those findings; tidal covariates were only retained in a small percentage of the best visual and acoustic models in Chapter 3 & 4. The main exceptions were that spring tidal range (STR) and current speed were kept in 34% and 27% of models respectively. STR was a reflection of the maximum spring tidal range observed in the region (which varied only spatially) and not the tidal range for the day of detections (which itself was incorporated in 'Position relative to tidal range' which was retained in some of the seasonal models, perhaps indicating within-month variations).

Year and month were also retained in a number of models indicating that there were temporal variations in the data. However the repeated retention and consistent relationships between depth and slope and how they affect harbour porpoise distribution is an indication of consistent habitat use patterns.

Table 7.1 - Model structures for the best visual and acoustic models from all of the full and temporal datasets. An 'X' is marked to show whether or not each covariate was retained in the best models. N.B. there were no acoustic data on which to construct models in 2003.

Model	Data	Temporal		Survey			Sediment			Tidal				Topographic		
		Year	Month	Sea State	Boat Speed	Time of Day	Percentage Gravel	Percentage Sand	Percentage Mud	Position Relative To Tidal Range	Position in Daily Tidal Cycle	Current Speed	Maximum Spring Tidal Range	Depth	Slope	Distance to Land
Full	Visual	X	X	X	X				X				X	X	X	X
	Acoustic	X	X		X								X	X	X	X
Yearly models (Chapter 3)																
2003	Visual		X		X									X		X
	Acoustic		-	-	-	-	-	-	-	-	-	-	-	-	-	-
2004	Visual			X		X						X		X		
	Acoustic		X		X								X	X		
2005	Visual			X									X			
	Acoustic			X	X						X					
2006	Visual		X	X	X						X					
	Acoustic		X	X	X								X	X	X	
2007	Visual		X	X		X				X				X	X	
	Acoustic		X		X							X	X	X	X	
2008	Visual		X	X	X									X	X	
	Acoustic		X		X						X	X	X	X		
Monthly & seasonal models (Chapter 4)																
April	Visual											X	X		X	
	Acoustic	X										X		X	X	
May	Visual			X	X					X		X		X		
	Acoustic				X		X	X	X					X	X	
June	Visual			X												X
	Acoustic				X					X		X		X	X	X
July	Visual			X	X									X		
	Acoustic	X			X							X	X	X		X
August	Visual	X		X						X				X	X	
	Acoustic	X			X				X					X	X	
Sept.	Visual	X		X	X		X					X	X	X		X
	Acoustic	X			X							X	X	X	X	
Season 1	Visual			X	X					X				X	X	X
	Acoustic	X	X	X	X		X				X			X	X	X
Season 2	Visual				X			X		X				X	X	
	Acoustic	X	X		X							X	X	X	X	X

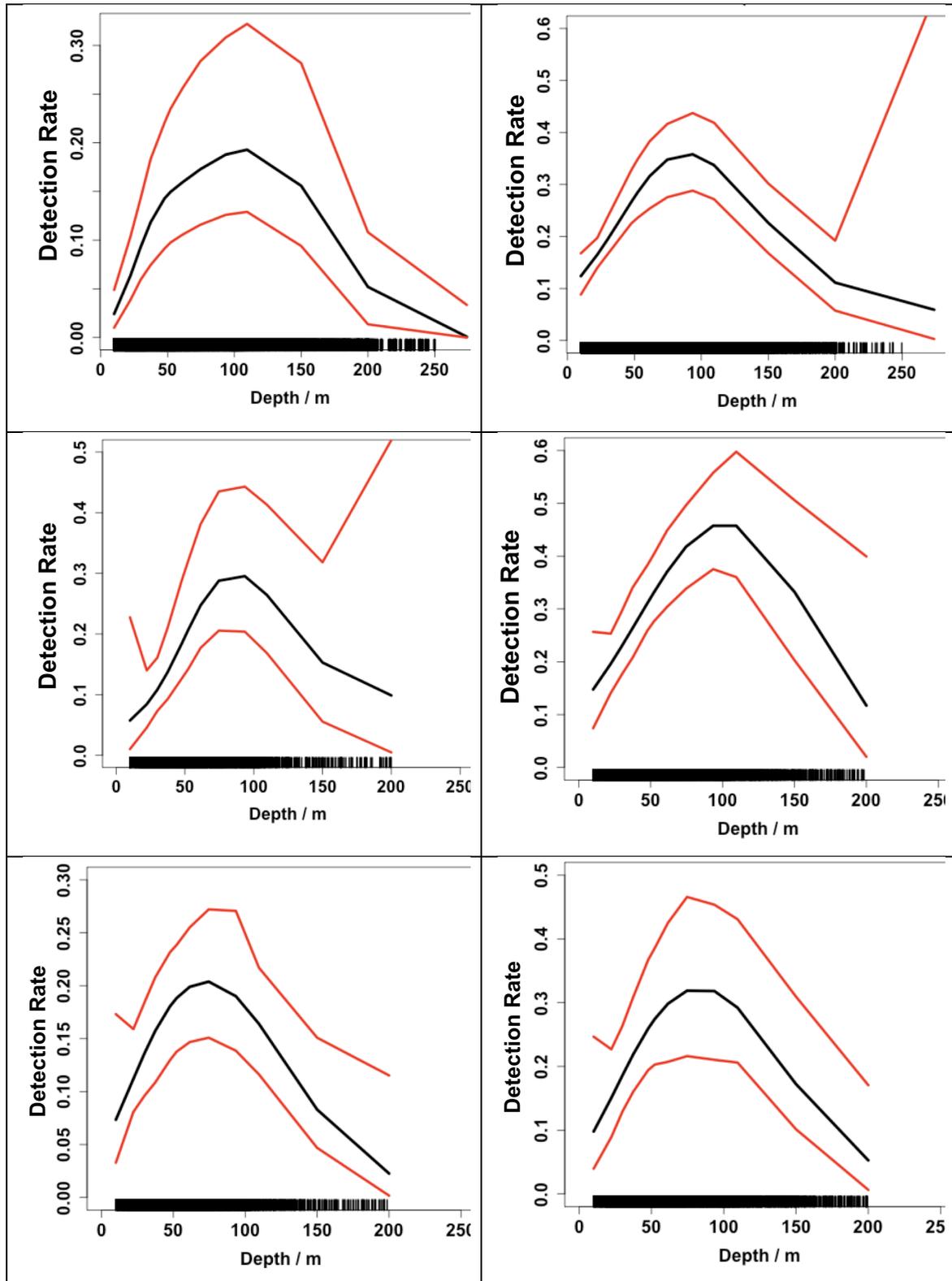


Figure 7.1 - Selected relationships for depth from the final models constructed in this study. The black lines show covariate relationships with the response variable and 95% confidence intervals are shown in red. Note that y-axes vary between plots

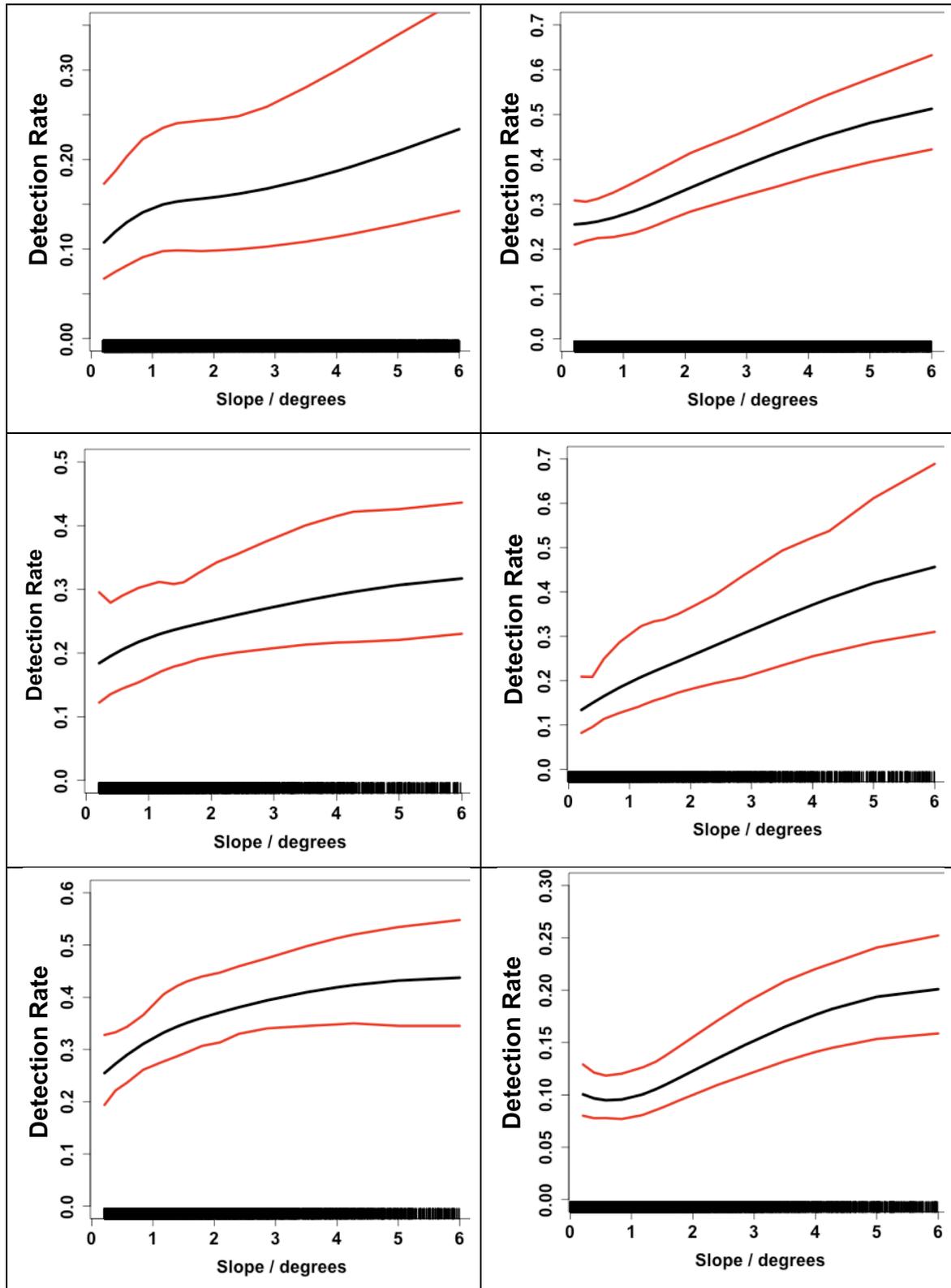


Figure 7.2 - Selected relationships for slope from the final models constructed in this study. The black lines show covariate relationships with the response variable and 95% confidence intervals are shown in red. Note that y-axes vary between plots

7.1.2.1 Goodness of Fit: Visual vs Acoustic models

A consistent pattern observed across almost all the models built in Chapters 3, 4 and 5 was that acoustic models performed better than the visual models when their goodness-of-fit was evaluated using a cross-validation method. It is not clear why this pattern was repeatedly observed.

One potential explanation is that detection rates were always higher in the acoustic datasets than in the sightings datasets. Therefore the sightings datasets contained a larger number of segments with zero porpoise detections. During the partitioning of the dataset into a test and training subset, as part of the model evaluation, the patchy distribution of sightings throughout the dataset could mean that the test and training datasets were less likely to be balanced (when they are balanced the model fits equally well to either random half of the full dataset), which could lead to low cross-validation scores. The acoustic dataset had a higher percentage of segments with detections in them (16%) than the visual dataset (6%), and thus the acoustic dataset may have been less impacted by issues in the partitioning of data during the model evaluation stage.

Despite the variations in the goodness-of-fit, many of the visual models still had similar model structures and distribution patterns to those from the acoustic models. However, in future analyses, it would be prudent to investigate this issue further, and potentially use a GEE that copes better with heavily zero-inflated data, like the visual dataset here.

7.1.2.2 Assessing the importance of covariates

Towards the end of model selection processes, covariates can be retained because they help account for some of the remaining variability in the models, but not because they represent a meaningful relationship. To ensure this wasn't occurring in the models presented here (which would invalidate some of the conclusions discussed throughout chapters 3, 4 and 5 and §7.1.2), the relative importance of covariates was investigated using marginal R^2 (methods described in §2.4.3.3). Results are shown in Appendices A.7 – A.10. As discussed above, depth and slope were retained in a large percentage of models and they ranked high in importance among the environmental covariates in both the visual and acoustic models (mean ranks shown in A.8 and A.10). Distance to land and STR scored slightly lower in the acoustic models than in the visual models. It was noteworthy that in the acoustic models, % gravel scored very low and that in the visual models % sand and % mud in the sediment scored low indicating they were explaining the least of all the covariates retained in the final models. Additionally in the visual models

‘Time of Day’ scored very low, indicating it contributed relatively little to the models. Sea state explained a low amount of variance in the acoustic models overall, despite its inclusion in four models. Overall the important patterns - indicating the importance of slope and depth in explaining harbour porpoise distribution and boat speed and sea state impacting the detection of animals - observed in this thesis are validated by their mean rank and marginal R^2 values presented here.

7.1.2.3 Modelling differences

As discussed previously, this study follows on from the work of Embling (2007), who observed that tidal processes were important in models constructed from data collected in 2003 - 2005. This is different to the general habitat preferences observed from the models produced in this study (using the 2003 – 2005 and new data collected between 2006 – 2008). There is a range of possible explanations for this. Firstly, the main modelling methods used here were different to those used by Embling (2007), and the method by which spatial and temporal autocorrelation in the raw data was dealt with also differed between these studies. The use in this study of Generalised Estimating Equations (GEEs) instead of a Generalised Additive Model (GAM) (as used in Embling, 2007) may be sufficient to explain some of the differences in outcomes, as model selection tends to be more robust within a GEE framework than in a GAM (e.g. in Panigada et al. (2008)). This is because unless the model covariates within the GAM capture the autocorrelation in full, it will be represented in the model errors, thus influencing model selection and potentially leading to the inclusion of covariates that are not important.

Models were also constructed differently in this study. Embling (2007) fitted survey variables (sea state, vessel speed, engine status, noise levels) first as they were considered likely to impact detection of animals. A disadvantage of this method is that it involves the forcing of variables to be included first, meaning that some of the data are used up before any of the environment covariates can be added. This can result in some other covariates being included in models when they should not. Here, no *a priori* consideration was made of the order of fitting covariates. Instead we built full models and compared them with reduced models (the full model minus the covariate being investigated).

Additionally, not all of the covariates were the same in both studies, which will likely impact model selection results. For example, ‘maximum tidal current speed’ for each segment was used in models by Embling (2007) whereas in this study, tidal current speed at the time and location

of each segment was used (thus variation in current speed at each location was taken into account).

This study provides further evidence that the use of GEEs in cetacean habitat modelling can result in consistent modelling patterns and potential for improvement over the model selection for GAMS.

7.1.2.4 Consistency in regional models

In Chapter 5, models were constructed at finer spatial extents than in Chapter 3 & 4, to investigate whether the same relationships observed across the west of Scotland held when each region was considered separately. Additionally, this was done to identify regions in which there were low temporal variations in harbour porpoise usage (both between years and within the year). These areas could be considered to be consistently important across the study period.

As with the models from the full spatial extent of the surveys, depth and/or slope were retained in six of the seven regions modelled individually (Table 7.2), and the same relationships with detection rates were observed. Two regions were observed to be consistent among years, the Sound of Jura and the Small Isles. In both of these regions, current speeds were retained in the best models. In the Firth of Lorn model some small (but significant) inter-annual variations were also observed. The suitability of these three regions as potential SACs is considered below (§7.3).

7.1.3 Explaining predicted distributions

7.1.3.1 Full spatial extent models

The predicted surfaces from the majority of the models built over the full geographical extent (Chapter 3 and 4) revealed a consistent inshore distribution, with the highest predicted densities being generated close to land and low predicted relative densities in more open water regions. We know from full model evaluations that the observed patterns are likely to be a good representation of how porpoise use the region. Also, in spite of differences in the retained model covariates between the Embling (2007) study and this study (using the same data), we find very similar distribution patterns.

From this analysis it is unclear how individual harbour porpoises utilise the waters west of Scotland: that is, whether they are utilising small focal ranges in specific regions, or ranging throughout the west of Scotland (or a combination of the two). Whether the west coast of Scotland is one population using the entire region as its home range (with smaller focal regions)

or several small populations only using small regions is a question that needs to be answered in order to ensure that effective conservation and management goals can be set.

Table 7.2 - Model structures for the best visual and acoustic models from each spatial region. An 'X' is marked to show whether or not each covariate was retained in the best models. N.B. there were insufficient visual detection data to make models for the Sea of Hebrides region.

Model	Data	Temp.		Survey			Sediment			Tidal				Topographic		
		Year	Month	Sea State	Boat Speed	Time of Day	Percentage Gravel	Percentage Sand	Percentage Mud	Position Relative To Tidal Range	Position in Daily Tidal Cycle	Current Speed	Maximum Spring Tidal Range	Depth	Slope	Distance to Land
Regional models (Chapter 5)																
The Minch	<i>Visual</i>		X	X								X		X		
	<i>Acoustic</i>	X			X								X			
Sea of Hebrides	<i>Visual</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Acoustic</i>	X			X			X				X				
Small Isles	<i>Visual</i>		X	X		X		X						X		
	<i>Acoustic</i>		X								X	X	X	X		
West of Mull	<i>Visual</i>	X		X								X				
	<i>Acoustic</i>		X	X	X							X	X	X	X	
Sound of Mull	<i>Visual</i>	X		X	X	X								X		
	<i>Acoustic</i>													X	X	
Firth of Lorn	<i>Visual</i>	X	X	X	X									X		
	<i>Acoustic</i>	X	X	X	X							X	X	X	X	
Sound of Jura	<i>Visual</i>			X				X						X		
	<i>Acoustic</i>		X		X			X			X		X			

Studies investigating harbour porpoise movements and habitat use in the northwest Atlantic and around Denmark have indicated that porpoise are highly mobile and utilise meso- and macro-scale home ranges. A recent study in the Bay of Fundy, Canada, indicated that porpoises occupy focal regions for periods of days to months, while also occasionally utilising greater, expanded ranges (Johnston et al. 2005). These focal ranges were between 122 and 415 km² and the total ranges that animals utilised in the two months of the study were between 4728 and 22,103 km² (Johnston et al. 2005). An earlier satellite telemetry study of harbour porpoise movements observed daily movements in the Bay of Fundy of between ~14 and 59 km. The authors estimated that animals were utilising a range of ~50,000 km² (Read and Westgate 1997). Recent studies from Denmark indicated some similarities to the work in Canada. Focal regions were

slightly larger than observed in the Bay of Fundy with animals ranging between 400 km² and 1,600 km² (Teilmann et al. 2004; Teilmann et al. 2008). One animal was also observed to travel north over 1,000 km from Danish waters to Shetland (Teilmann et al. 2004; Teilmann et al. 2008), indicating animals do make macro-scale movements. It is unclear whether harbour porpoises exhibit such movement behaviour off the west coast of Scotland, as observed in Canada and Denmark. The area covered by the highest (>80th percentile) densities of harbour porpoises and a visual representation of the focal ranges in the discussed satellite telemetry studies are shown below (Figure 7.2).

Cetaceans have a number of potential navigational cues available to them including land marks and bottom topography, salinity and temperature gradients, currents, odours, tastes and sounds (Hoelzel 2002). Currently, the cues important to harbour porpoises in guiding their movements are poorly understood. Read and Westgate (1997) observed satellite-tagged porpoises making large-scale transits along the 92 m isobath suggesting they may have been using bottom contours to navigate. In the same study, 55% of all satellite positions were in regions with water depths between 92 and 183 m (33% of the positions were in waters <92 m). This depth range may be indicative of bottom features that can be used for navigation, but also of habitats providing proximity to prey resources inhabiting those depth ranges. It is well understood that harbour porpoises need to remain close to prey resources and consume prey regularly in order to meet the demands of their daily activities (Koopman 1998). Additionally pregnant females are income breeders and will increase energy intake in response to the demands of pregnancy and lactation (Read 2001). As we have discussed here and throughout Chapters 3, 4 and 5, the habitat preference of porpoises west of Scotland is for highly sloped regions in waters between 50 – 150 m depth. These patterns can be explained by the enhanced productivity and suitable prey species that likely inhabit such regions (Hastie et al. 2004; Persohn et al. 2009; Wright et al. 2000; Zamon 2003). The west of Scotland is characterised by a complex topographic environment with a convoluted coastline, and the relationship between water depth and distance from land varies considerably across the region. Consequently, throughout the inshore regions, steeply sloped submarine canyons and channels exist close to land. This means that animals could remain close to shore while navigating but still close to important prey resources.

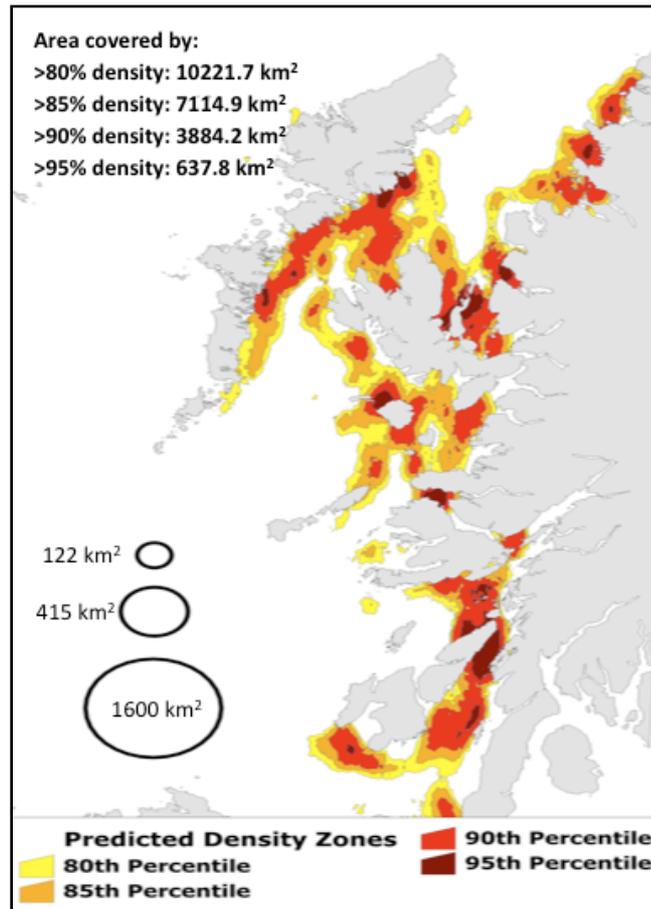


Figure 7.2 – Map showing the highest density regions for harbour porpoise based on the full acoustic model. The density surface was created by kriging and the regions with density over the 80th, 85th, 90th and 95th percentiles are shown along with the area they cover. Also shown (black rings) are the minimum and maximum focal ranges taken from Johnston et al. (2005) and Teilmann et al. (2004).

Porpoises may also use echolocation to identify underwater land features aiding navigation. Because harbour porpoise clicks are very high frequency, they attenuate quickly in water (Urlick 1983). Based on the transmission loss of such high-frequency signals, maximum two-way detection ranges (i.e. the distance over which animals can produce clicks and detect the return-echo) are likely to be <300m (DeRuiter et al. 2010). This means that porpoises should be able to resolve underwater topographic-features at ranges of < 300 m and potentially navigate with respect to prominent land features (Pryor 1990), though there is limited direct evidence for this. However, porpoises may not necessarily have to use active sonar to navigate as animals may also detect passive cues, such as noise produced from breaking waves or tidally induced turbulence. Such sounds are generally low in frequency and so will be audible over considerable ranges (Richardson et al. 1995; Urlick 1983) and thus may provide better navigational cues for animals. Other marine organisms, e.g. crustaceans are known to orientate themselves with respect to

coastlines based on the sound of wave action (Jeffs et al. 2005). It is not known whether harbour porpoises have the auditory capacity at low frequencies to resolve this information and use it for navigation.

The influx of freshwater from the mainland, and to a lesser extent, from the islands of the Hebrides may also provide a navigational cue and potential foraging sites. A strong positive east-to-west salinity gradient exists off the west coast of Scotland (Gillibrand et al. 2003). Odontocete species have the capability to determine salinity differences in water and thus could navigate according to changes in salinity (Nachtigall and Hall 1984; Wartzok and Ketten 1999; Watkins and Wartzok 1985). Additionally, freshwater plume fronts are often sites of high productivity and it may be that animals forage around such features (Mann and Lazier 2006). Harbour porpoises have been observed to forage on the mixing side of a front in the Irish Sea (Weir and O'Brien 2000) and bottlenose dolphins and sperm whales have been found to orientate and forage along density fronts (Mendes et al. 2002). As we observed in Chapter 3, a different distribution pattern was observed in 2005 compared with the other years of the study, attributed to a change in the influx of Atlantic water and a drop in salinity in the Inner Hebrides (Inall et al. 2009). Porpoise distribution appeared to mirror this shift in water movements with higher detection rates in the northern extent of the region, in deeper water and decreased rates in the Argyll Islands. This may be a further indication that animals are responding to salinity differences, or at least the change in prey distribution that these differences induce.

The highest relative densities were predicted close to land in the majority of models, with low densities predicted for open water regions. Porpoises may avoid the more open regions of the west of Scotland, which are typically deeper water and may not be suitable foraging grounds. However, the Little Minch (between the Isle of Skye and the Outer Hebrides) may provide an important region for porpoises functioning as a narrow passageway between the Inner and Outer Hebrides habitats.

7.1.3.2 Regional model distribution patterns

As discussed in Chapter 5, in the southern extent of the west coast of Scotland, similar distribution patterns were observed to those from the full spatial extent models (from Chapter 3 & 4). As discussed earlier, neither year nor month were retained in the best models for the Small Isles indicating that habitat use patterns were consistent across the study. However the model relationships and distribution patterns were different from the full-spatial extent models and differed between the visual and acoustic models. It is unclear why this occurred and

consequently, it is difficult to draw strong conclusions as to whether this region represents a consistently important region for porpoises. The one region with consistent patterns in both the model relationships and predicted distributions was the Sound of Jura and surrounding areas in the southern Inner Hebrides. These regions are discussed as suggested SACs in §7.3.2.

7.2 Impact of CAADs on harbour porpoises

The results from Chapter 6 are consistent with previous studies investigating the potential for CAAD-induced disturbance from Airmar devices. What is needed now is an investigation of the ramifications of potential CAAD-induced disturbance and how it may impact harbour porpoises. Additionally, consideration is needed as to how such disturbance fits in with the statutory requirements of Annex IV of the EU Habitats Directive, primarily Article 12(b) which prohibits “*deliberate disturbance of these species, particularly during the period of breeding, rearing, hibernation and migration*” and 12(d) which prohibits “*deterioration or destruction of breeding sites or resting places*”.

There are additional questions about how CAADs in the Sound of Mull might impact porpoises. Firstly, how patterns of distribution change over longer-periods with respect to devices. Do animals become tolerant of CAAD signals? One possibility is that animals are initially impacted in the short-term ($\sim <1$ year), but over time begin to tolerate CAAD noise. This would explain the patterns observed around established CAADs at fish farms. However, if CAAD usage changes considerably among years, it may result in animals never fully tolerating the sounds due to the changing soundscape in the marine environment. If animals do tolerate CAAD sounds, this has the potential to impact hearing thresholds, especially if exposures are prolonged. The functional significance of hearing thresholds being impacts in harbour porpoises remains unclear. There is likely an evolutionary significance in their high hearing sensitivity at mid-frequencies (1 - 30 kHz) considering they echolocate at much higher frequencies (100 – 150 kHz). It may be their mid-frequency hearing helps in detecting and avoiding predators and/or other marine threats.

Cetacean species have been impacted in the short term by repeated disturbance from tourism boats leading to longer-term avoidance patterns and shifts in behavioural budgets, with potential for longer-term consequences (Bejder et al. 1999; Lusseau 2003, 2004, 2006; Lusseau and Bejder 2007; Williams et al. 2006). It is not clear from those studies whether it is increased noise levels from boat traffic or the presence of boats themselves that cause the biggest problems. Also, there is potential for increased stress to be caused by repeated exposure to sounds, which may impact viability and fitness at both individual and population levels (Lusseau and Bejder 2007;

Wright et al. 2007). Both of these issues could be impacting harbour porpoise populations west of Scotland, although boat traffic, and in particular tourist boat traffic in the area is relatively low.

If increased noise levels do cause these short-term and longer-term shifts in behaviour, there could be potential for barrier effects to be caused by extensive CAAD use, and other noise sources, removing/excluding animals from important habitat. Depending on how animals use the west of Scotland, this may further exclude animals from important habitat and may impact the effectiveness of protected regions. This is a subject that needs further investigation.

7.3 Identifying important areas as SACs

One of the most common approaches to conservation of the marine environment is the establishment of marine protected areas (MPAs)(Agardy 1994; Agardy 2000; Cañadas et al. 2003; Faucher and Weilgart 1992; Hooker et al. 1999; Hoyt 2005; Hyrenbach et al. 2000; Notarbartolo-di-Sciara 2008; Notarbartolo-Di-Sciara et al. 2008). However, questions remain over how useful they are (Boersma and Parrish 1999; Hoyt 2005; Kelleher and Kenchington 1992) and it is important to consider whether the establishment of an MPA is the most appropriate solution to whatever problem is facing the cetacean species of interest (Cañadas et al. 2005; Notarbartolo-di-Sciara 2008). There are several important conservation and/or mitigation measures that can be implemented without designating special localities as protected areas. For example, measures to reduce by-catch of cetaceans in fishing gear can be implemented without need for an MPA (Evans 2008). However, despite some concerns over their efficiency in achieving conservation goals, they are considered an important conservation tool by many international regulatory bodies (e.g. The OSPAR Convention 1992; The EU Habitats Directive 1992; ACCOBAMS 1996; ASCOBANS 2006; EU 2007).

The designation of a region as an MPA represents one step in the process of conserving cetacean species. It is necessary that clear conservation goals are defined at the outset and that there is an appropriate management plan in place to facilitate the meeting of the goals. Additionally monitoring protocols must be established to determine whether or not the pre-determined conservation goals are being met.

One of the main disadvantages of a single MPA for cetacean species, is that many species have too large a range to be encompassed by a single protected region. A solution to this is to create a network of smaller MPAs. One advantage of this is that a network of site can cover more of the

natural range of a species than a single site (Notarbartolo-di-Sciara 2008). This is particularly important with highly mobile species such as the harbour porpoise.

In the UK, SACs are designed around areas where pre-existing boundaries exist (e.g. in relation to a fixed feature or geographical configuration)(Pinn 2009). Here we have identified consistent patterns in harbour porpoise habitat use over the west of Scotland with depth and/or slope being retained in most of the models in this study – though in some models other dynamic covariates were also retained. Static bathymetric features could provide suitable fixed boundaries around which SACs could be designed and are an indication of regional stability and consistency. A further consideration in selecting regions suitable for designation as SACs is the practicality of managing a region. The high-density regions for porpoises west of Scotland cover ~10,000 km² (Figure 7.2) - too large to be managed as a single SAC. Additionally, it is unclear what the best conservation goals should be for the harbour porpoise in this region. During the establishment of the Moray Firth SAC for bottlenose dolphins, one significant obstacle to be cleared was the identification of a clear threat to the species (Wilson 2008). Without such a clear goal for management, and many agencies and stakeholders involved, it became difficult to identify a clear best practice in how to maximise success of the SAC (Wilson 2008). In identifying suitable regions for harbour porpoise SACs west of Scotland, there are two options. Firstly, it is well known that there are high densities of animals found here across the region and so one important conservation goal could be to maintain the abundance in the region. However, with many communities and economies in the region invested in the marine environment it may, as observed during the Moray Firth SAC efforts, be difficult to achieve a consensus on the best practise to maintain abundance. Additionally, it is important to determine how animals are using this region: whether the porpoises there are isolated into small sub-populations with little ranging among regions across the west of Scotland, or if they are a single sub-population, ranging over a large area. Another conservation goal can be to minimise the threat of an activity impacting a species. Here we have observed that there is potential for CAADs to impact harbour porpoise distribution similar to that observed in studies from Canada (Johnston 2002; Olesiuk et al. 2002). Furthermore, there have been movements towards the installation of marine renewable energy facilities west of Scotland and their impacts are poorly understood. Porpoises have been shown to be displaced from regions with pile driving (a key step in the installation of marine wind, tide or turbines) and more generally there is concern over the many potential impacts of these facilities on the marine environment: e.g. interaction with operational turbines (Carter 2007; SNH 2009) and ecosystem impacts (e.g. predator distribution

being impacted due to the prey distribution shifts away from sites caused by shifts in currents, sediment preferences etc)(NERC 2009; SNH 2009)

One potential conservation aim is to determine the full extent of impacts on the species of this and other activities, and, if necessary identify mitigation strategies, to minimise such impacts. As discussed above, it may not be necessary to designate a region as an SAC in order to achieve the goal of minimising the impacts of CAADs.

7.3.1 Fulfilling SAC selection criteria

Pinn (2009) outlined detailed criteria from Annex III of the Habitats Directive and more recent EU guidance for consideration of sites for designation as SACs. They included assessing the size and density of the population of harbour porpoises in relation to porpoise populations throughout the UK's waters. Aerial surveys conducted during the SCANS surveys estimated the harbour porpoise population to be 12,100 (CV = 0.43) animals on the west coast of Scotland. The SCANS II survey in July 2005 estimated the total European population to be 386,000 (CV = 0.20) so the west coast represents around <1% of the total European population (west population estimate: 12,100, CV = 0.34)(SCANS-II 2008). SCANS-II data indicated that the west of Scotland has one of the highest densities of any region in northwest Europe (SCANS-II 2008). The present study was conducted over six months and found animals were present in high relative densities throughout the study period. Furthermore, other studies have recorded porpoises being present in all months of the year off the west coast of Scotland (Evans 1980; Evans et al. 2003; Reid et al. 2003).

Two other considerations are the degree of isolation of a harbour porpoise population with respect to the natural range and the importance of the region with respect to neighbouring areas. While harbour porpoises appear to range over reasonable distances, thus making it difficult to consider them isolated, their ranging behaviour west of Scotland is unknown and should be investigated further. Pinn (2009) suggests that there are two recognised sub-populations in UK waters, an Irish and Celtic Sea group and a North Sea group. In her review, she considered the west coast of Scotland group to be part of the North Sea group due to the low number of sightings between Northern Ireland and west of Scotland in the SCANS II project (SCANS-II 2008). A small scale survey was conducted between the west of Scotland and Wales in 2002 – 2004 (Goodwin and Speedie 2008). They identified that harbour porpoises abundance was significantly higher west of Scotland than any of the regions surveyed to the south. In the SCANS II project, low-predicted densities were also generated for the region to the

west of Orkney which would perhaps indicate that the west of Scotland group could be considered more isolated than previously thought and potentially a separate sub-population. That said, it has also been stated that there are insufficient data to define boundaries between any (sub-) populations in and around the North Sea (ASCOBANS 2008). Results of a genetics study of harbour porpoises around the UK indicated that there were likely two subpopulations; one “Irish/West Britain” group and the North Sea grouping (Walton 1997). Though in that study the author observed that there were no breaks in distribution of the 24 haplotypes found – suggesting there is some historic movement (and resultant gene flow) between regions around the UK. However, they also suggest evidence for some sub-structure in the population between the Celtic & Irish Seas and the North Sea (Walton 1997). Other genetic studies from around northwest Europe indicate historical segregation over larger geographic distances (Andersen et al. 2001; Rosel 1997; Tolley and Rosel 2006) but only a few studies have looked at such fine spatial and temporal scales as we are investigating here (Wiemann et al. 2010). Pinn (2009) also proposed that for the purposes of assessing the potential importance of regions for harbour porpoises, the context should be of biologically meaningful populations and not the national population as adopted in previous efforts to report on the conservation status of species in the UK under the Habitats Directive.

7.3.2 Possible harbour porpoise SACs

Even though the whole west of Scotland meets some of the designation criteria, in practice it may be too large to be considered practical as an SAC in its entirety. Therefore one option is to identify one or a network of smaller, consistently important region(s) for harbour porpoises. The models built in Chapter 5 identified that the Small Isles and Sound of Jura regions (and potentially the Firth of Lorn) as consistently important regions as they had high densities and year was not retained in the final models indicating low inter-annual variability in detection rates. The Minch region was surveyed in three years of the total study period and some variability was observed in detection rates among years. However, the predicted density surface indicates that small sub-regions within the Minch are high-use areas (marked by dashed lines and named 1, 2 and 3 in Figure 7.3) and that modelling the Minch region as a single region may not have been the best approach. In the future, these need to be considered individually to determine their suitability as SACs.

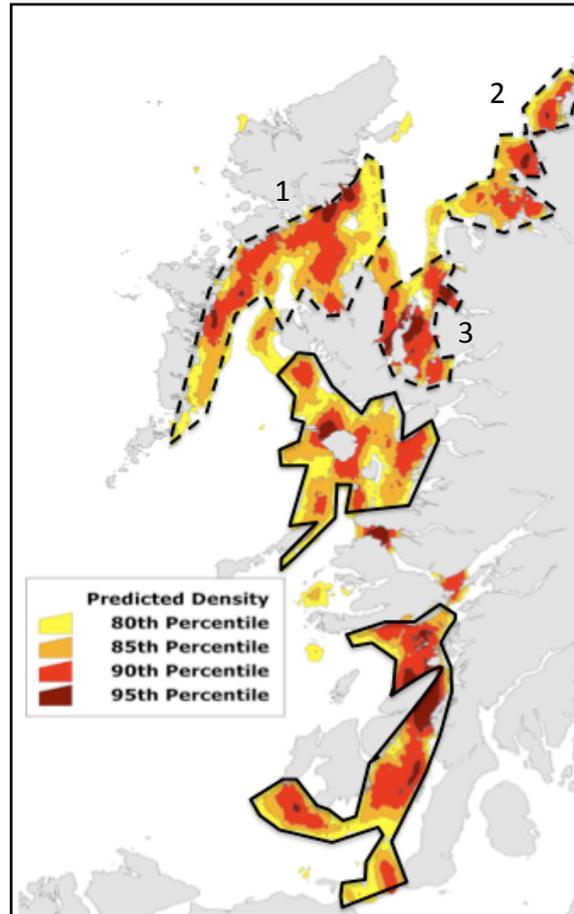


Figure 7.3 – Potential regions for protection based on the consistently highest densities regions for harbour porpoises. The coloured regions show predicted densities above the 80th percentile (as in Figure 7.2). The solid black line show boundaries of potential areas and the dashed black line show regions could be suitable but were modelled together in the Minch model, but individually they could be considered for protection (1. The Little Minch, 2. The northern Wester-Ross and 3. The Inner Sound/Sound of Raasay regions).

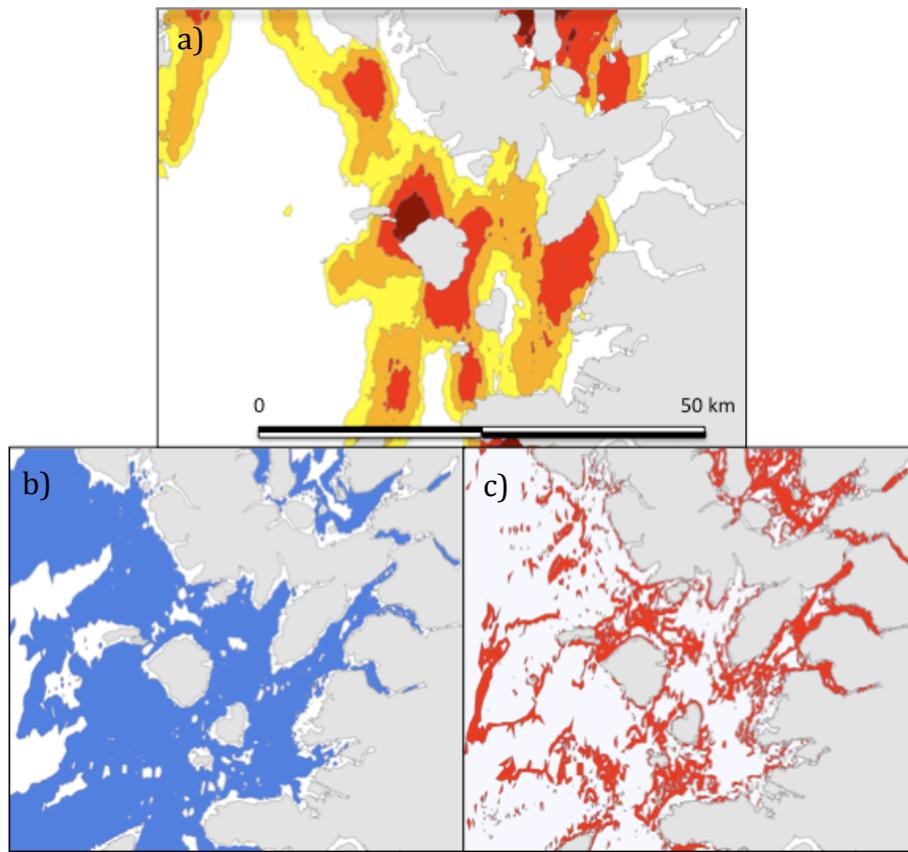
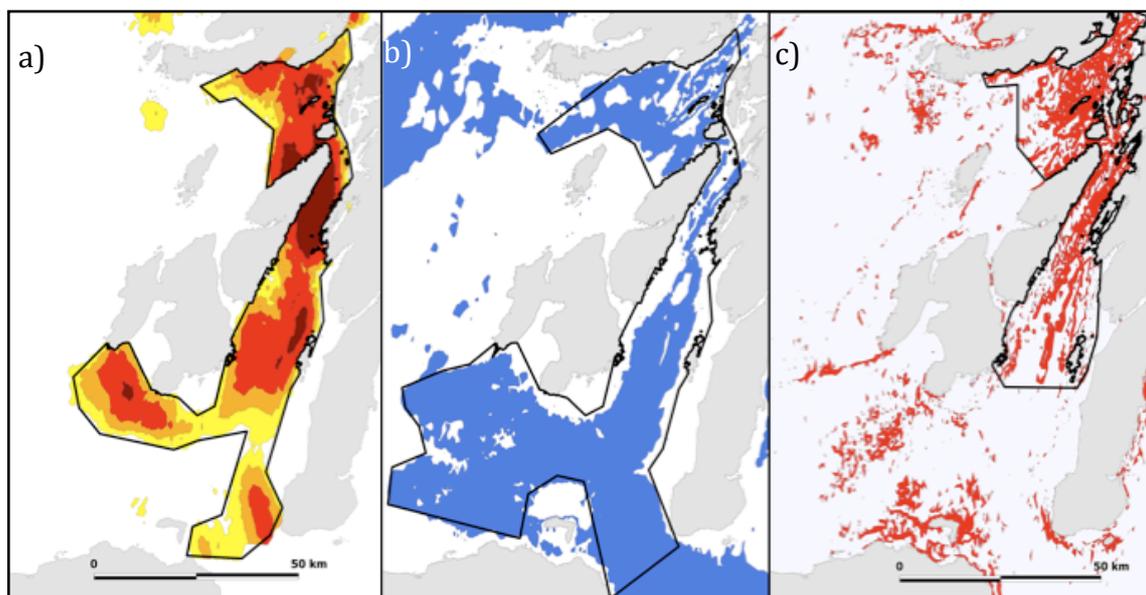


Figure 7.4 & 7.5 - Suggested SACs regions (the Small Isles - 7.4, above; Firth of Lorn/Sound of Jura - 7.5, below) based on the consistently highest densities regions for harbour porpoises. In both figures, (a) shows predicted densities above the 80th percentile (b) the distribution of water depths between 50 -150 m and (c) the distribution of regions > 2° slope. In Figure 7.5 the black lines show the borders of the SAC based on each feature (a - density, b - depth, c - slope).



This suggested Small Isles and Firth of Lorn/Sound of Jura SAC regions (Figure 7.4 and 7.5 respectively) have some of the highest densities of harbour porpoise on the west of Scotland. In the Small Isles site it is not clear what oceanographic features could be used as boundaries for the suggested SAC – as current speed and monthly spring tidal range were retained in the model for the region – indicating dynamic oceanographic features are important there (Figure 7.4 a - c). At the Sound of Jura site (Figure 7.5 a), static bathymetric boundaries could be used and drawn with respect to a combination of depth (Figure 7.5 b) and slope (Figure 7.5 c).

The Small Isles region and Firth of Lorn/Sound of Jura suggested SAC regions cover 2530 km² and 2514 km² respectively (based on the predicted model surface in Figure 7.5 a), which is larger than the SACs that exist for bottlenose dolphins in the Moray Firth (1513.4 km²) and Cardigan Bay (958.6 km²), which provide a reasonable model for a manageable size of area.

Here I have identified a number of potentially suitable sites for SACs for harbour porpoises. A strong case can be made for the southern Inner Hebrides (the Firth of Lorn and Sound of Jura) as it was the most consistent region over the study period. In 2005, we observed that the distribution of porpoises in the northwest of the study region might be impacted by the flux of Atlantic water from the southwest (Inall et al. 2009). It is unclear how commonly shifts in Atlantic water influx occur but such patterns should be considered (as porpoises may shift their distribution to take advantage of the spatial shift in prey distribution). Because the Sound of Jura and northeast Firth of Lorn are fed almost exclusively by water from the Irish Sea, these areas are unlikely to be impacted by changes in the flux of Atlantic water.

Based on these findings, the Sound of Jura/Firth of Lorn region discussed appears to be the most suitable for designation as an SAC on the west coast of Scotland. The Small Isles region also appears to be a strong candidate site, though there are still some questions about the patterns of distribution in the area and it is not immediately clear where boundaries would be drawn but it is clear that it is a high use area for harbour porpoise. Depending on the conservation goals of a protected area west of Scotland, a case could be made for the Sound of Mull to be included in protected areas in order to control the use of CAADs in regions important for harbour porpoises. Finally, the regions in the Minch need to be investigated further to determine whether some of the smaller sub-regions outlined could be appropriate sites for an SAC.

7.4 Future research

7.4.1 *Habitat Use*

The results of predicted distributions from the full models and those from the regional extent models, have posed further questions about how animals may be using the west coast of Scotland. As discussed previously, the use of telemetry has been successful in elucidating harbour porpoise movement patterns in the northwest Atlantic and in Denmark and the North Sea. Given the distribution patterns observed in this study, a key step would be to use telemetry techniques to investigate harbour porpoise movements west of Scotland. Such studies could investigate the extent to which porpoises are ranging throughout the region, whether they utilise sounds and channels to transit between important focal regions, or whether animals tend to be more isolated in smaller sub-populations.

This study has identified that there are intra-annual patterns (Chapter 4) in harbour porpoise habitat preferences within the period studied (April to September). Little is known about harbour porpoise presence, distribution and habitat preferences throughout the year outside of these months, though animals have been sighted in every month (Reid et al. 2003). Further year-round surveys would be required to determine whether habitat preferences and distribution are consistent throughout the year and assess the importance of the site throughout the year. Visual surveys would likely be difficult given the generally poor sea conditions during winter months in this region. This study has shown that acoustic detection rates were largely unaffected by sea state and consequently using acoustic surveys may be an appropriate method. Additionally aerial methods have been used to study harbour porpoises throughout the year and are likely suitable (Gilles et al. 2009; Northridge 1995).

While some generally consistent patterns were observed with depth and slope being retained in the best models, there were also some variations observed in the covariates retained in best models in the inter-annual (Chapter 3) and intra-annual (Chapter 4) models. Some of the variation may be explained by the grain at which the models were constructed, which may have failed to capture some of the additional environmental processes shaping prey distributions. Modelling at a finer grain would capture some of the finer scale tidal processes that may be important, while a coarser scale may fully capture some of the meso-scale environmental features. Similarly, in the regional models (Chapter 5), some small spatial variations in depth patterns were observed, particularly in the Minch and to the west of Mull. It is not clear what caused these patterns, but there may be intrinsic factors impacting harbour porpoise distribution.

As discussed above, data collected across three years was used to model the Minch region as a single region. Once more data become available, the consistency of distribution patterns across the whole Minch area and smaller sub-regions (marked in Figure 7.3) could be investigated separately to determine whether the Sound of Raasay, Little Minch and northern Wester-Ross regions could be considered as SACs for harbour porpoise.

This study used Generalised Estimating Equations models (GEEs) to investigate harbour porpoise habitat usage and the consistency in model results is encouraging. Using different modelling methods to investigate patterns in datasets can provide different results (Bravington et al. 2002; Evans and Wang 2003). While an independent review found that the methods used by Bravington et al. (2002) were robust (Pinn 2009), as statistical modelling techniques evolve, it may be useful to revisit existing datasets (e.g. SCANS, CODA, the Joint Cetacean Database), to help derive as much information as possible from these large survey datasets. The GEE method of dealing with temporal and spatial autocorrelation in datasets, thus potentially improving model selection results, may be useful in maximising the value of expensive, pre-existing survey datasets like the ones discussed.

7.4.2 Impact of CAADs on harbour porpoises

This study observed that newly installed CAADs impacted harbour porpoise distribution. However, this study represents one treatment (based around the Fiunary site which installed the new device) and there may have been other factors impacting porpoise behaviour and distribution that were not controlled for. Furthermore, porpoises may behave differently at different sites west of Scotland. It should be considered that this analysis was a small section of a much larger study. Further studies are required to better explain the variations in CAAD received levels via controlled measurements of the CAAD sound field and the environment at the time of measurements. Additionally, more detailed survey effort around sites with controlled CAAD usage may provide better information on the extent of potential impacts on harbour porpoises. As discussed above, telemetry studies may provide an interesting insight into how porpoises move around the west coast, in particular with respect to heavy-CAAD-use regions.

This study opportunistically investigated the potential for exposure to CAAD signals to impact animals hearing. This was done by calculating estimated lengths of exposures required at the CAAD received levels data point in the study using an equal energy rule (§6.2.3.1). This may lead to conservative values of the exposures required to exceed established TTS criteria.

Additionally, a number of other factors could not be controlled for in this analysis (e.g. the pre-exposure hearing sensitivity of animals exposed to the CAAD signal). Further work should include controlled experiments in captivity to determine the full extent of the impacts of CAAD signals on harbour porpoise hearing

About half the fish farm sites that use CAADs west of Scotland use Airmar CAADs, and their impacts were investigated in this study. However, the other half of sites uses Terecos or other CAADs, which have very different acoustic characteristics to the Airmar device. Currently, nothing is known about the impacts of those devices on seals or cetacean species, and so further investigation is required. A similar study investigating patterns around Terecos sites would therefore also be prudent.

Another potential impact of repeated exposure to CAADs is that animals may alter their behaviour, which may have short-term and potentially longer-term impacts on individuals and populations. Consequently, an investigation of behavioural budgets, respiration rates and the potential for stress around sites with active CAADs and no prior CAAD use would be useful. Furthermore, it is important to gain a better understanding of how intrinsic factors, such as behavioural state, age and gender may impact how animals respond to CAAD sounds. As discussed, little is known about the movements of porpoises west of Scotland and whether the animals there are part of a single population. If this is the case, there is potential for exclusion and/or barrier effects (with respect to real or perceived barriers) to be caused by the presence of CAADs in important transit routes or foraging sites.

7.5 References

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Appendices

Table A.1 - Summary statistics for covariates retained in models for the six months of visual surveys between 2003 - 2008.

		APRIL	MAY	JUNE	JULY	AUGUST	SEPTEMBER
Survey Effort		3167.80	4229.80	5878.30	8123.90	8046.40	4994.50
No. Segments		1584	2115	2939	4062	4024	2499
Number of Segments with Sightings		42	84	115	289	352	132
Percentage of Segments with Sightings		2.6%	4.0%	3.9%	7.1%	8.7%	5.3%
Year	<i>Range</i>	2003 - 2004, 2007- 2008	2003 - 2008	2003 - 2008	2003 - 2008	2003 - 2008	2003, 2005 - 2008
Sea State (Beaufort Scale)	<i>Range</i>	0 - 3	0 - 3	0 - 3	0 - 3	0 - 3	0 - 3
	<i>Median (IQR)</i>	2 (1.5 - 2)	2 (1.5 - 2.5)	2 (1 - 2)	2 (1.5 - 2)	2 (1 - 2)	2 (1.5 - 2)
Boat Speed (knots)	<i>Range (knots)</i>	0.56 - 10.78	1.19 - 10.98	1.22 - 10.14	0.73 - 11.05	1.15 - 11.1	0.28 - 11.95
	<i>mean (st.dev)</i>	6.50 (5.98 - 6.96)	6.28 (1.06)	5.98 (1.02)	6.10 (0.98)	6.16 (0.96)	6.08 (0.97)
Time from Day	<i>Range</i>	0.10 - 0.87	0.10 - 0.95	0.10 - 0.92	0.11 - 0.95	0.09 - 0.96	0.04 - 0.97
	<i>Median (IQR)</i>	6.47 (0.96)	0.51 (0.39 - 0.63)	0.52 (0.39 - 0.64)	0.54 (0.40 - 0.65)	0.51 (0.36 - 0.67)	0.48 (0.31 - 0.65)
Position Relative To Tidal Range	<i>Range</i>	0.06 - 0.99	0.10 - 1.00	0.09 - 1.00	0.10 - 1.00	0.10 - 1.00	0.07 - 1.00
	<i>Median (IQR)</i>	0.49 (0.34 - 0.63)	0.50 (0.30 - 0.71)	0.51 (0.31 - 0.68)	0.5 (0.52 - 0.89)	0.53 (0.35 - 0.64)	0.67 (0.50 - 0.76)
Position in Daily Tidal Cycle	<i>Range</i>	0 - 1.0	0 - 1.0	0 - 1.0	0 - 1.0	0 - 1.0	0 - 1.0
	<i>Median (IQR)</i>	0.49 (0.29 - 0.82)	0.51 (0.31 - 0.66)	0.53 (0.30 - 0.68)	0.44 (0.30 - 0.65)	0.49 (0.32 - 0.65)	0.51 (0.34 - 0.69)
Spring Tidal Range (m)	<i>Range</i>	1.15 - 5.49	0.91 - 4.95	0.77 - 4.61	0.92 - 5.12	1.10 - 5.56	1.15 - 5.77
	<i>mean (st.dev)</i>	4.16 (0.91)	3.22 (1.27)	3.24 (0.94)	3.81 (0.89)	4.06 (1.19)	4.19 (1.09)
Depth (metres)	<i>Range</i>	10 - 198	10 - 204	10 - 224	10 - 283	10 - 229	10 - 196
	<i>mean (st.dev)</i>	52.4 (28.8)	58.7 (36.1)	57.3 (39.2)	63.7 (40.6)	60.2 (36.9)	57.6 (34.6)
Slope (degrees)	<i>Range</i>	0 - 16.3	0 - 12.62	0 - 20.21	0 - 18.8	0 - 16.6	0 - 1.94
	<i>mean (st.dev)</i>	1.92 (2.10)	1.79 (1.85)	1.72 (2.08)	1.87 (1.88)	1.73 (1.96)	0.18(0.12 - 0.23)
Current Speed (m/s)	<i>Range</i>	0 - 1.96	0 - 2.16	0 - 1.45	0 - 2.0	0 - 2.79	0 - 1.94
	<i>mean (st.dev)</i>	0.20 (0.17)	0.24 (0.24)	0.20 (0.16)	0.19 (0.16)	0.19 (0.19)	0.20 (0.15)
Distance from Land (km)	<i>Range</i>	<1 - 32.4	<1 - 68.6	0 - 68.6	<1 - 34.2	<1 - 65.3	<1 - 21.8
	<i>mean (st.dev)</i>	3.6 (4.3)	4.0 (4.8)	5.6 (9.5)	4.0 (4.7)	4.5 (5.7)	3.6 (3.9)
Percentage Gravel (%)	<i>Range</i>	0 - 100	0 - 100	0 - 100	0 - 100	0 - 100	0 - 100
	<i>Median (IQR)</i>	5 (5 - 18)	5 (5 - 33)	5 (2 - 18)	5 (2 - 18)	5 (5 - 18)	5 (5 - 18)
Percentage Sand (%)	<i>Range</i>	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95
	<i>Median (IQR)</i>	35 (30 - 84)	33 (14 - 40)	30 (0 - 84)	33 (20 - 84)	35 (20 - 84)	30 (20 - 40)
Percentage Mud (%)	<i>Range</i>	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95
	<i>Median (IQR)</i>	4 (0 - 65)	32 (0 - 65)	4 (0 - 65)	4 (0 - 65)	4 (0 - 65)	62 (0 - 65)

Table A.2 - Summary statistics for model covariates retained in the six monthly models from acoustic surveys collect between 2004 - 2008.

		APRIL	MAY	JUNE	JULY	AUGUST	SEPTEMBER
Survey Effort		4240.10	5135.10	6889.40	8438.10	11412.90	6437.00
No. Segments		2125	2574	3449	4225	5712	3220
Number of Segments with Acoustic Detections		293	422	586	525	963	566
Percentage of Segments with Acoustic Detections		13.80%	16.3%	17.0%	12.4%	17.6%	12.4%
Year	<i>Range</i>	2004, 2007, 2008	2004 - 2008	2004 - 2008	2004 - 2008	2004 - 2008	2005 - 2008
Sea State (Beaufort Scale)	<i>Range</i>	0 - 6	0 - 6	0 - 6	0 - 6	0 - 6	0 - 6
	<i>Median (IQR)</i>	2.5 (2 - 3.5)	2 (2 - 3)	2 (1.5 - 3.5)	2 (2 - 3)	2 (2 - 3)	2 (2 - 3.5)
Boat Speed (knots)	<i>Range (knots)</i>	1.77 - 11.86	3.05 - 9.00	0.96 - 10.51	0.72 - 11.05	1.08 - 11.05	1.79 - 9.18
	<i>mean (st.dev)</i>	6.36 (0.99)	6.26 (0.93)	5.97 (1.03)	6.05 (0.94)	6.22 (0.90)	6.01 (0.83)
Time from Day	<i>Range</i>	0.13 - 0.96	0.15 - 0.88	0.04 - 0.96	0.16 - 0.94	0.04 - 0.96	0.04 - 0.94
	<i>Median (IQR)</i>	0.5 (0.39 - 0.61)	0.52 (0.39 - 0.63)	0.51 (0.39 - 0.62)	0.53 (0.42 - 0.65)	0.53 (0.38 - 0.66)	0.50 (0.35 - 0.64)
Position Relative To Tidal Range	<i>Range</i>	0.08 - 1.00	0.10 - 1.00	0.10 - 1.00	0.16 - 1.00	0.05 - 1.00	0.11 - 0.99
	<i>Median (IQR)</i>	0.51 (0.37 - 0.76)	0.49 (0.37 - 0.72)	0.48 (0.37 - 0.62)	0.50 (0.33 - 0.85)	0.51 (0.33 - 0.70)	0.49 (0.35 - 0.76)
Position in Daily Tidal Cycle	<i>Range</i>	0 - 1.0	0 - 1.0	0 - 1.0	0 - 1.0	0 - 1.0	0 - 1.0
	<i>Median (IQR)</i>	0.49 (0.34 - 0.81)	0.44 (0.30 - 0.65)	0.49 (0.29 - 0.82)	0.49 (0.31 - 0.66)	0.51 (0.34 - 0.69)	0.50 (0.36 - 0.68)
Spring Tidal Range (m)	<i>Range</i>	1.15 - 5.49	0.91 - 4.95	0.77 - 4.61	0.96 - 5.12	1.10 - 5.56	1.15 - 5.77
	<i>mean (st.dev)</i>	4.14 (1.02)	3.35 (1.20)	3.27 (1.00)	3.85 (0.85)	4.03 (1.26)	4.3 (1.11)
Depth (metres)	<i>Range</i>	10 - 198	10 - 204	10 - 222	10 - 274	10 - 223	10 - 201
	<i>mean (st.dev)</i>	54.6 (30.2)	59.4 (35.2)	60.4 (36.3)	66.8 (40.5)	64.0 (37.7)	59.1 (33.1)
Slope (degrees)	<i>Range</i>	0 - 14.6	0 - 9.9	0 - 19.7	0 - 22.9	0 - 18.2	0 - 16.3
	<i>mean (st.dev)</i>	2.04 (2.11)	1.70 (1.76)	1.76 (1.98)	1.79 (1.89)	1.74 (1.92)	1.88 (1.88)
Current Speed (m/s)	<i>Range</i>	0 - 1.92	0 - 1.84	0 - 1.52	0 - 0.95	0 - 2.41	0 - 1.77
	<i>mean (st.dev)</i>	0.22 (0.15)	0.22 (0.17)	1.77 (0.12)	0.19 (0.10)	0.20 (0.17)	0.20 (0.12)
Distance from Land (km)	<i>Range</i>	<1 - 31.4	<1 - 45.7	<1 - 59.6	<1 - 45.7	<1 - 57.8	<1 - 32.0
	<i>mean (st.dev)</i>	3.5 (4.3)	4.0 (3.8)	4.9 (6.5)	4.4 (5.5)	4.5 (5.4)	3.5 (3.7)
Percentage Gravel (%)	<i>Range</i>	0 - 100	0 - 100	0 - 100	0 - 100	0 - 100	0 - 100
	<i>Median (IQR)</i>	5 (5 - 18)	5 (5 - 33)	5 (5 - 18)	5 (2 - 18)	5 (5 - 18)	5 (5 - 18)
Percentage Sand (%)	<i>Range</i>	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95
	<i>Median (IQR)</i>	35 (30 - 84)	33 (14 - 70)	30 (0 - 70)	34 (20 - 84)	33 (20 - 84)	30 (20 - 70)
Percentage Mud (%)	<i>Range</i>	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95
	<i>Median (IQR)</i>	32 (0 - 65)	8 (0 - 65)	4 (0 - 65)	4 (0 - 65)	8 (0 - 65)	62 (0 - 65)

Table A.3 – Summary statistics for model covariates retained in the seasonal models from visual surveys collect between 2003 - 2008.

		APRIL/MAY/JUNE	JULY/AUG/SEPT
Survey Effort		13279.9	21181.2
No. Segments		6640	10594
Number of Segments with Sightings		241	774
Percentage of Segments with Sightings		3.6%	7.3%
Year	<i>Range</i>	2003 - 2008	2003 - 2008
Sea State (Beaufort Scale)	<i>Range</i>	0 - 3	0 - 3
	<i>Median (IQR)</i>	2 (1.5 - 2.5)	2 (1 - 2)
Boat Speed (knots)	<i>Range (knots)</i>	0.56 - 10.98	0.28 - 11.95
	<i>mean (st.dev)</i>	6.19 (1.04)	6.12 (0.97)
Time from Sunrise	<i>Range</i>	0.10 - 0.90	0.04 - 0.91
	<i>Median (IQR)</i>	0.51 (0.38 - 0.63)	0.51 (0.37 - 0.66)
Position Relative To Tidal Range	<i>Range</i>	0.05 - 1.00	0.11 - 1.00
	<i>Median (IQR)</i>	0.51 (0.35 - 0.67)	0.50 (0.37 - 0.74)
Position in Daily Tidal Cycle	<i>Range</i>	0 - 1.0	0 - 1.0
	<i>Median (IQR)</i>	0.52 (0.35 - 0.69)	0.50 (0.33 - 0.65)
Spring Tidal Range (metres)	<i>Range</i>	0.77 - 5.49	0.92 - 5.77
	<i>mean (st.dev)</i>	3.67 (1.12)	4.29 (1.07)
Depth (metres)	<i>Range</i>	10 - 224	10 - 283
	<i>mean (st.dev)</i>	56.6 (36.0)	51.3 (37.9)
Slope (degrees)	<i>Range</i>	0 - 20.2	0 - 18.8
	<i>mean (st.dev)</i>	1.79 (2.01)	1.82 (1.91)
Current Speed (m/s)	<i>Range</i>	0 - 2.16	0 - 2.79
	<i>mean (st.dev)</i>	0.21 (0.19)	0.19 (0.17)
Distance from Land (km)	<i>Range</i>	<1 - 68.6	<1 - 68.5
	<i>mean (st.dev)</i>	4.7 (7.3)	4.1 (5.1)
Percentage Gravel (%)	<i>Range</i>	0 - 100	0 - 100
	<i>Median (IQR)</i>	5 (5 - 18)	5 (2 - 18)
Percentage Sand (%)	<i>Range</i>	0 - 95	0 - 95
	<i>Median (IQR)</i>	33 (14 - 84)	33 (20 - 84)
Percentage Mud (%)	<i>Range</i>	0 - 95	0 - 95
	<i>Median (IQR)</i>	4 (0 - 65)	4 (0 - 65)

Table A.4 – Summary statistics for model covariates retained in the seasonal models from acoustic surveys collect between 2004 - 2008.

		APRIL/MAY/JUNE	JULY/AUG/SEPT
Survey Effort		16364.8	26280.0
No. Segments		8198	13153
Number of Segments with Acoustic Detections		1313	2053
Percentage of Segments with Acoustic Detections		16.0%	15.6%
Year	<i>Range</i>	2004 - 2008	2004 - 2008
Sea State (Beaufort Scale)	<i>Range</i>	0 - 6	0 - 6
	<i>Median (IQR)</i>	2 (2 - 3)	2 (2 - 3)
Boat Speed (knots)	<i>Range (knots)</i>	0.96 - 11.86	0.72 - 11.05
	<i>mean (st.dev)</i>	6.2 (1.02)	6.1 (0.90)
Time from Sunrise	<i>Range</i>	0.09 - 0.96	0.04 - 0.95
	<i>Median (IQR)</i>	0.50 (0.39 - 0.62)	0.51 (0.39 - 0.65)
Position Relative To Tidal Range	<i>Range</i>	0.08 - 1.00	0.05 - 1.00
	<i>Median (IQR)</i>	0.52 (0.47 - 0.78)	0.65 (0.47 - 0.83)
Position in Daily Tidal Cycle	<i>Range</i>	0 - 1.0	0 - 1.0
	<i>Median (IQR)</i>	0.49 (0.32 - 0.65)	0.49 (0.32 - 0.65)
Spring Tidal Range (metres)	<i>Range</i>	0.77 - 5.49	0.96 - 5.77
	<i>mean (st.dev)</i>	3.52 (1.14)	4.04 (1.12)
Depth (metres)	<i>Range</i>	10 - 221	10 - 274
	<i>mean (st.dev)</i>	58.5 (34.5)	63.7 (37.7)
Slope (degrees)	<i>Range</i>	0 - 20.2	0 - 22.9
	<i>mean (st.dev)</i>	1.83 (2.00)	1.79 (1.91)
Current Speed (m/s)	<i>Range</i>	0 - 2.12	0 - 2.41
	<i>mean (st.dev)</i>	0.22 (1.53)	0.20 (0.14)
Distance from Land (km)	<i>Range</i>	<1 - 59.6	<1 - 57.8
	<i>mean (st.dev)</i>	4.3 (5.3)	4.3 (5.1)
Percentage Gravel (%)	<i>Range</i>	0 - 100	0 - 100
	<i>Median (IQR)</i>	5 (5 - 18)	5 (5 - 18)
Percentage Sand (%)	<i>Range</i>	0 - 95	0 - 95
	<i>Median (IQR)</i>	33 (14 - 84)	33 (20 - 84)
Percentage Mud (%)	<i>Range</i>	0 - 95	0 - 95
	<i>Median (IQR)</i>	8 (0 - 65)	4 (0 - 65)

Table A.3 - Summary statistics for covariates retained in some of the regional models using visual survey data.

		THE MINCH	SMALL ISLES	SEA OF HEB.	W. OF MULL	SOUND OF MULL	FIRTH OF LORN	SOUND OF JURA
Survey Effort		3963.8	6042.3	2485.9	7366.8	2616.3	6888.3	3983.9
No. Segments		1982	3021	1243	3684	1311	3444	1992
Number of Segments with Sightings		228	190	38	139	112	162	130
Percentage of Segments with Sightings		11.5%	6.3%	3.0%	3.7%	8.5%	4.7%	6.5%
Year	<i>Range</i>	2005 - 2008	2003 - 2008	2003 - 2008	2003 - 2008	2003 - 2008	2003 - 2008	2003 - 2008
Sea State (Beaufort Scale)	<i>Range</i>	0 - 3	0 - 3	0 - 3	0 - 3	0 - 3	0 - 3	0 - 3
	<i>Median (IQR)</i>	2 (1.5 - 2.5)	2 (1.5 - 2.5)	2 (1.5 - 2.5)	2 (1.5 - 2.5)	2 (1.5 - 2.5)	2 (1.5 - 2.5)	2 (1.5 - 2.5)
Boat Speed (knots)	<i>Range (knots)</i>	2.59 - 11.05	1.15 - 10.28	1.22 - 8.37	0.73 - 9.90	0.27 - 8.65	0.56 - 10.98	1.72 - 11.95
	<i>mean (st. dev)</i>	6.1 (0.8)	6.0 (0.86)	6.3 (0.88)	6.2 (0.94)	6.1 (1.04)	6.22 (1.04)	6.25 (1.39)
Time from Sunrise	<i>Range</i>	0.09 - 0.93	0.06 - 0.96	0.16 - 0.90	0.09 - 0.95	0.08 - 0.91	0.09 - 0.94	0.08 - 0.92
	<i>Median (IQR)</i>	0.53 (0.39 - 0.66)	0.52 (0.37 - 0.67)	0.53 (0.43 - 0.64)	0.50 (0.36 - 0.68)	0.52 (0.41 - 0.61)	0.49 (0.35 - 0.63)	0.48 (0.34 - 0.62)
Position Relative To Tidal Range	<i>Range</i>	0.10 - 0.99	0.11 - 1.00	0.06 - 1.00	0.09 - 1.00	0.10 - 1.00	0.08 - 1.00	0.05 - 1.00
	<i>Median (IQR)</i>	0.50 (0.24 - 0.75)	0.53 (0.32 - 0.78)	0.50 (0.30 - 0.79)	0.51 (0.24 - 0.79)	0.48 (0.26 - 0.75)	0.50 (0.32 - 0.75)	0.47 (0.30 - 0.75)
Position in Daily Tidal Cycle	<i>Range</i>	0 - 1.0	0 - 1.0	0 - 1.0	0 - 1.0	0 - 1.0	0 - 1.0	0 - 1.0
	<i>Median (IQR)</i>	0.49 (0.29 - 0.82)	0.51 (0.34 - 0.69)	0.49 (0.32 - 0.65)	0.44 (0.30 - 0.65)	0.45 (0.31 - 0.68)	0.51 (0.42 - 0.72)	0.51 (0.34 - 0.66)
Spring Tidal Range (metres)	<i>Range</i>	2.93 - 5.60	3.65 - 5.77	2.90 - 5.77	2.99 - 5.22	2.98 - 4.93	0.77 - 4.57	0.77 - 2.72
	<i>mean (st. dev)</i>	4.61 (0.51)	4.76 (0.40)	3.93 (0.73)	3.90 (0.48)	4.15 (0.43)	3.60 (0.76)	1.38 (0.58)
Depth (metres)	<i>Range</i>	10 - 283	10 - 195	10 - 224	10 - 142	11 - 128	10 - 205	10 - 201
	<i>mean (st. dev)</i>	89.3 (43.9)	62.6 (30.2)	84.9 (50.4)	45.0 (24.6)	53.3 (21.7)	51.3 (34.4)	59.1 (38.7)
Slope (degrees)	<i>Range</i>	0 - 18.8	0 - 13.2	0 - 9.4	0 - 20.2	0.1 - 11.02	0 - 18.34	0 - 12.2
	<i>mean (st. dev)</i>	1.93 (1.99)	2.14 (1.78)	1.12 (1.19)	1.28 (1.51)	3.27 (2.17)	1.81 (2.36)	1.99 (1.82)
Current Speed (m/s)	<i>Range</i>	0.02 - 1.06	0 - 0.45	0 - 0.46	0 - 0.58)	0 - 0.97	0 - 2.09	0 - 2.79
	<i>mean (st. dev)</i>	0.16 (0.11)	0.14 (0.06)	0.17 (0.07)	0.20 (0.07)	0.21 (0.11)	0.19 (0.18)	0.37 (0.38)
Distance from Land (km)	<i>Range</i>	<1 - 64.1	<1 - 68.6	<1 - 68.6	<1 - 68.4	<1 - 32.4	<1 - 64.1	<1 - 65.3
	<i>mean (st. dev)</i>	5.4 (6.1)	3.1 (3.6)	12.4 (12.8)	3.9 (4.5)	1.5 (2.8)	4.4 (5.1)	3.3 (3.8)
Percentage Gravel (%)	<i>Range</i>	0 - 100	0 - 100	0 - 100	0 - 100	0 - 100	0 - 100	0 - 100
	<i>Median (IQR)</i>	5 (2 - 5)	5 (5 - 5)	5 (0 - 18)	18 (5 - 55)	2 (2 - 5)	5 (5 - 18)	33 (5 - 55)
Percentage Sand (%)	<i>Range</i>	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95
	<i>Median (IQR)</i>	30 (20 - 90)	30 (0 - 30)	30 (0 - 40)	40 (20 - 84)	35 (30 - 84)	40 (20 - 95)	30 (20 - 40)
Percentage Mud (%)	<i>Range</i>	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95
	<i>Median (IQR)</i>	4 (0 - 65)	65 (2 - 70)	4 (0 - 70)	4 (0 - 65)	62 (8 - 65)	4 (0 - 62)	32 (0 - 62)

Table A.4 - Summary statistics for covariates retained in some of the regional models using visual survey data.

		THE MINCH	SMALL ISLES	SEA OF HEB.	W. OF MULL	SOUND OF MULL	FIRTH OF LORN	SOUND OF JURA
Survey Effort		5482.0	8020.6	2460.7	9007.4	3399.3	7726.7	5093.9
No. Segments		2741	4012	1231	4511	1704	3872	2553
No. of Segments with Acoustic Detections		390	877	162	557	358	492	452
% of Segments with Acoustic Detections		14.2%	21.9%	13.1%	12.3%	21.0%	12.7%	17.7%
Year	<i>Range</i>	2005 - 2008	2003 - 2008	2003 - 2008	2003 - 2008	2003 - 2008	2003 - 2008	2003 - 2008
Sea State (Beaufort Scale)	<i>Range</i>	0 - 6	0 - 6	0 - 5	0 - 6	0 - 6	0 - 6	0 - 6
	<i>Median (IQR)</i>	2 (2 - 3)	2 (2 - 3)	2 (1.5 - 3)	2 (2 - 3)	2 (2 - 3)	2 (2 - 3)	2 (2 - 3)
Boat Speed (knots)	<i>Range (knots)</i>	2.79 - 11.05	1.09 - 10.99	1.37 - 8.12	0.73 - 8.99	1.41 - 8.77	1.20 - 10.97	0.97 - 11.8
	<i>mean (st. dev)</i>	6.17 (0.76)	6.00 (0.87)	6.14 (0.82)	6.12 (0.92)	6.09 (0.90)	6.18 (1.02)	6.31 (1.32)
Time of Day	<i>Range</i>	0.10 - 0.94	0.06 - 0.93	0.16 - 0.82	0.10 - 0.88	0.12 - 0.93	0.10 - 0.95	0.05 - 0.90
	<i>Median (IQR)</i>	0.52 (0.40 - 0.66)	0.52 (0.39 - 0.66)	0.52 (0.42 - 0.61)	0.52 (0.39 - 0.65)	0.54 (0.46 - 0.62)	0.50 (0.36 - 0.64)	0.51 (0.40 - 0.61)
Position Relative To Tidal Range	<i>Range</i>	0.09 - 0.99	0.12 - 1.00	0.12 - 1.00	0.07 - 1.00	0.11 - 1.00	0.05 - 1.00	0.07 - 0.99
	<i>Median (IQR)</i>	0.52 (0.34 - 0.84)	0.53 (0.28 - 0.81)	0.50 (0.34 - 0.82)	0.54 (0.31 - 0.80)	0.48 (0.35 - 0.76)	0.49 (0.30 - 0.76)	0.48 (0.29 - 0.76)
Position in Daily Tidal Cycle	<i>Range</i>	0 - 1.0	0 - 1.0	0 - 1.0	0 - 1.0	0 - 1.0	0 - 1.0	0 - 1.0
	<i>Median (IQR)</i>	0.47 (0.24 - 0.78)	0.49 (0.29 - 0.67)	0.54 (0.38 - 0.70)	0.48 (0.30 - 0.63)	0.44 (0.30 - 0.65)	0.49 (0.32 - 0.65)	0.53 (0.34 - 0.70)
Spring Tidal Range (metres)	<i>Range</i>	2.93 - 5.60	3.65 - 5.77	2.90 - 5.77	2.99 - 5.22	2.98 - 4.93	0.77 - 4.57	0.77 - 2.77
	<i>mean (st. dev)</i>	4.6 (0.52)	4.8 (0.41)	4.1 (0.68)	4.0 (0.48)	4.26 (0.43)	3.5 (0.82)	1.41 (0.58)
Depth (metres)	<i>Range</i>	10 - 274	10 - 200	10 - 222	10 - 180	12 - 122	10 - 205	10 - 200
	<i>mean (st. dev)</i>	90.6 (41.9)	63.5 (29.7)	88.5 (46.8)	48.3 (24.2)	53.9 (22.5)	52.7 (35.1)	62.2 (39.7)
Slope (degrees)	<i>Range</i>	0 - 22.9	0 - 13.4	0 - 9.89	0 - 20.2	0.09 - 11.32	0 - 18.16	0 - 13.30
	<i>mean (st. dev)</i>	1.78 (1.98)	2.09 (1.75)	1.18 (1.31)	1.30 (1.54)	3.28 (2.19)	1.78 (2.33)	2.0 (1.82)
Current Speed (m/s)	<i>Range</i>	0 - 0.85	0 - 0.72	0.02 - 0.52	0.03 - 0.79	0 - 1.00	0 - 2.20	0 - 2.42
	<i>mean (st. dev)</i>	0.18 (0.09)	0.18 (0.08)	0.20 (0.08)	0.23 (0.09)	0.23 (0.10)	0.19 (0.17)	0.30 (0.28)
Distance from Land (km)	<i>Range</i>	<1 - 50.7	<1 - 57.8	<1 - 59.6	<1 - 45.7	<1 - 33.8	<1 - 37.4	<1 - 29.0
	<i>mean (st. dev)</i>	5.9 (6.3)	3.1 (2.9)	10.7 (9.2)	4.1 (4.5)	1.4 (2.3)	4.3 (4.5)	3.3 (3.4)
Percentage Gravel (%)	<i>Range</i>	0 - 100	0 - 100	0 - 100	0 - 100	0 - 100	0 - 100	0 - 100
	<i>Median (IQR)</i>	5 (2 - 18)	5 (5 - 5)	5 (0 - 18)	18 (5 - 55)	2 (2 - 5)	5 (5 - 18)	33 (5 - 55)
Percentage Sand (%)	<i>Range</i>	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95
	<i>Median (IQR)</i>	30 (20 - 90)	30 (0 - 30)	30 (0 - 40)	40 (30 - 84)	35 (30 - 84)	40 (20 - 95)	30 (20 - 35)
Percentage Mud (%)	<i>Range</i>	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95	0 - 95
	<i>Median (IQR)</i>	4 (0 - 65)	65 (4 - 70)	4 (0 - 70)	4 (0 - 65)	62 (0 - 62)	4 (0 - 62)	30 (0 - 65)

Table A.7 – Percentage reduction in marginal R² caused by the removal of each covariate from the acoustic full models from Chapters 3, 4 and 5.

Model	Year	Month	Boat Speed	Sea State	Time Of Day	Distance to Land	Spring Tidal Range	Pos. in Lunar Tidal Cycle	Pos. in Daily Tidal Cycle	% Gravel	% Sand	% Mud	Slope	Depth	Current Speed	Chapter
Full	4.9	14.5	42.3			4.4	7.8						14.7	10.4		
2004		33.2	63.0										28.9	0.4		
2005			37.9	9.6				49.2							42.0	3
2006		13.8	35.9	4.3		7.7							1.8	17.8		
2007		16.2	3.7			11.1	11.2						11.9	30.9		
2008		18.2	21.9				3.1						1.9	14.0	8.5	
April	36.1												22.1	17.0	14.7	
May			29.0							1.6	20.8	12.7	3.9	9.8	15.3	
June			21.5			11.2	6.7						1.4	22.9	22.4	
July	56.1		39.4	2.3		5.0	1.0	5.8						11.2		4
August	20.5		45.5									22.1	22.2	1.0		
Sept.	21.1		15.5				7.8						12.4	15.7	8.8	
S1	2.1	33.3	24.8	1.9		2.8				2.4			2.2	16.3	9.8	
S2	19.8	16.2	40.7			2.4	7.1						15.5	7.1		
Minch	64.8		62.9											17.4		
SoH	25.8		45.8				16.1				19.6					
S.I.		13.9	62.7				0.5						35.5	6.5	3.1	
WoM		24.1	13.4	4.4		4.2							5.6	34.8		5
SoM													52.3	58.8		
FoL	9.5	14.3	35.1	16.7		10.4	9.9						3.5	23.4		
SoJ		24.6	14.3				22.9					11.8		22.7	11.3	

Table A.8 – The relative importance of each covariate based on the marginal R² values generated from reduced models (the removal of each covariate from the full model) for the acoustic full models from Chapters 3, 4 and 5. Values close to 0 indicate that the covariates were retained late in the model. Mean rank is also shown at the base of the table. This provides a measure of where each covariate ranked across all the models.

Model	Year	Month	Boat Speed	Sea State	Time Of Day	Distance to Land	Spring Tidal Range	Pos. Lunar Tidal Cycle	Pos. Daily Tidal Cycle	% Gravel	% Sand	% Mud	Slope	Depth	Current Speed	Chapter
Full	0.143	0.571	0.857			0.000	0.286						0.714	0.429		
2004		0.750	0.500										0.250	0.000		
2005			0.250	0.000				0.750							0.500	3
2006		0.500	0.833	0.167		0.333							0.000	0.667		
2007		0.667	0.000			0.167	0.333						0.500	0.833		
2008		0.667	0.833				0.167						0.000	0.500	0.333	
April	0.750												0.500	0.250	0.000	
May			0.857							0.000	0.714	0.429	0.143	0.286	0.571	
June			0.500			0.333		0.167					0.000	0.833	0.667	
July	0.857		0.714	0.143		0.286	0.000	0.429						0.571		4
August	0.200		0.800									0.400	0.600	0.000		
Sept.	0.833		0.500				0.000						0.333	0.500	0.167	
S1	0.111	0.889	0.778	0.000		0.444				0.333			0.222	0.667	0.556	
S2	0.714	0.571	0.857			0.000	0.286						0.429	0.286		
Minch	0.667		0.333											0.000		
SoH	0.500		0.750				0.000				0.250					
S.I.		0.500	0.833				0.000						0.667	0.333		
WoM		0.667	0.500	0.167		0.000							0.333	0.833		5
SoM													1.000	1.000		
FoL	0.125	0.625	0.875	0.500		0.375	0.250						0.250	0.750		
SoJ		0.833	0.333				0.667					0.167		0.667	0.000	
Mean	0.490	0.658	0.627	0.163	N.A.	0.215	0.199	0.448	N.A.	0.167	0.482	0.332	0.371	0.495	0.349	

Table A.9 – Percentage reduction in marginal R² caused by the removal of each covariate from the visual full models from Chapters 3, 4 and 5.

Model	Year	Month	Boat Speed	Sea State	Time Of Day	Distance to Land	Spring Tidal Range	Position in Lunar Tidal Cycle	Position in Daily Tidal Cycle	Percentage Gravel	Percentage Sand	Percentage Mud	Slope	Depth	Current Speed	Chapter
FULL	29.9	20.3	12.8	44.3		8.0	6.6					0.6	5.7	17.7		
2003		33.1	31.9			46.3								22.4		
2004				20.9	5.5		84.3						12.7			
2005				69.6										46.0		3
2006		34.5	36.8	14.8					34.7							
2007		59.0	17.3	48.1	11.5				13.4				33.5			
2008		11.6	14.7	62.9									14.7			
April			10.4	5.5		50.6	29.5						21.0			
May			1.2	40.8				59.6					5.8		14.8	
June				63.0		45.7										
July			17.7	51.0										33.8		
August	20.8			45.2				6.4	24.1				36.8	10.3		4
Sept.	48.2		14.3			16.4	3.6		10.6							
S1			13.9	57.0				31.5					27.2	16.0		
S2			10.8	61.6				7.8		6.0			18.5	14.8		
Minch	1.6	30.9		24.9			29.5						26.0			
S.I.		26.0		55.4	18.5					14.5			21.3			
WoM	1.0			70.0			22.2									
SoM	35.3		22.5	25.8	5.6									14.8		5
FoL	32.4	45.6	16.9	23.9										6.3		
SoJ				36.5								16.8		51.4		

Table A.10 – The relative importance of each covariate based on the marginal R² values generated from reduced models (the removal of each covariate from the full model) for the visual full models from Chapters 3, 4 and 5. Values close to 0 indicate that the covariates were retained late in the model. Mean rank is also shown at the base of the table. This provides a measure of where each covariate ranked across all the models.

Model	Year	Month	Boat Speed	Sea State	Time Of Day	Distance to Land	Spring Tidal Range	Pos. Lunar Tidal Cycle	Pos. Daily Tidal Cycle	% Gravel	% Sand	% Mud	Slope	Depth	Current Speed	Chapter
Full	0.778	0.667	0.444	0.889		0.333	0.222					0.000	0.111	0.556		
2004		0.500	0.250			0.750								0.000		
2005				0.500	0.000		0.750						0.250			3
2006				1.000										1.000		
2007		0.250	0.750	0.000					0.500							
2008		0.833	0.333	0.667	0.000				0.167				0.500			
April		0.250	0.500	0.750									0.500			
May			0.000	0.200		0.800	0.600						0.400			
June			0.000	0.600				0.800					0.200		0.400	
July				1.000		1.000										4
August			0.000	0.667										0.333		
Sept.	0.333			0.833				0.000	0.500				0.667	0.167		
S1	0.800		0.400			0.400	0.000		0.200							
S2			0.200	0.800					0.600				0.400	0.000		
Minch			0.333	0.833				0.167			0.000		0.667	0.500		
SoH	0.000	0.800		0.200			0.600						0.400			
S.I.		0.600		0.800	0.200						0.000		0.400			
WoM	0.000			0.667			0.333									5
SoM	0.800		0.400	0.600	0.000									0.200		
FoL	0.600	0.800	0.200	0.400										0.000		
SoJ				0.333								0.000		0.667		
Mean	0.473	0.588	0.293	0.618	0.050	0.657	0.418	0.392	0.342	N.A.	0.000	0.000	0.409	0.342	0.400	

