

**HABITAT PREFERENCES OF SYMPATRIC COASTAL CETACEANS
AT CONTRASTING SPATIAL AND TEMPORAL SCALES: HABITAT
PARTITIONING OF BOTTLENOSE DOLPHINS (*TURSIOPS
TRUNCATUS*), HARBOUR PORPOISES (*PHOCOENA PHOCOENA*),
AND MINKE WHALES (*BALAENOPTERA ACUTOROSTRATA*) IN
THE OUTER SOUTHERN MORAY FIRTH, NORTH-EAST SCOTLAND**

Thomas S Bean

2012

“A project submitted in partial fulfilment of the requirements for the
Bachelors Degree in Animal Conservation and Biodiversity for the
University of Greenwich”.



the
UNIVERSITY
of
GREENWICH



ACADEMIC SESSION: 2011-2012 PROJECT DECLARATION

"This project report is the result of the independent work of Thomas Stephen Bean. All other work reported in the text has been attributed to the original authors and is fully referenced in the text, and listed in the Reference section".



This project was conducted
In association with the
Cetacean Research & Rescue Unit

Student Name: Thomas Stephen Bean

Student Signature:

Date:

ACKNOWLEDGEMENTS

This project was only possible with the help and support of the following people.

Special thanks go to Kevin Robinson for introducing me to the cetaceans of the Moray Firth in 2010 and then welcoming me back to the CRRU research team as a volunteer and friend in 2011. I am so grateful for the support, feedback and knowledge you shared which kept me on track.

Many thanks go to my project supervisor, Pam Worrall for all the help and advice, and for suggesting opportunities to expand my horizons.

Additional thanks must be expressed to Ben Forbes who gave extensive commitment to helping me apply GIS to this project. It wouldn't have been possible without your input.

I would also like to thank Kerry Williamson for her patient support with statistics and Colin Macleod who gave prompt and clear replies by email in regards to the use of GIS and cetaceans.

Extended thanks go to the numerous committed staff and volunteers at CRRU who have helped towards data collection.

Thanks go to my parents for their continual support throughout this project and in everything I do, and my sister for keeping my sense of humour when I was struggling to see the end.

ABSTRACT

Studies which compare the spatio-temporal distributions of sympatric balaenopterid, delphinid and phocoenid species to indicate habitat partitioning are rare to date. However, the influence of the surrounding marine environment upon cetacean distributions is well known. Underwater areas with fixed physiography and predictable oceanography are preferred by prey species, which ultimately influence cetacean distribution. In the outer southern Moray Firth, bottlenose dolphins (*Tursiops truncatus*), minke whales (*Balaenoptera acutorostrata*) and harbour porpoises (*Phocoena phocoena*) are found in overlapping coastal areas during the summer months, May to October. A study was carried out to investigate if significant difference was observed between the distribution of any two species over the habitat characteristics measured and during different months. The study used geographical information systems to determine the values of environmental variables at every sighting of each species. Results showed the most significant spatial difference was between bottlenose dolphins and harbour porpoises, in order to minimise competition for an overlap in diet. Spatial partitioning between bottlenose dolphins and harbour porpoises, as well as bottlenose dolphins and minke whales occurred over all the environmental scales investigated, but was most significant by water depth and distance to nearest shore. Bottlenose dolphins preferred shallower inshore waters to forage for mid-trophic fish, while minke whales and harbour porpoises were largely distributed in similar areas due to the abundance of lesser sandeel (*Ammodytes marinus*) prey. However, harbour porpoises showed more adaptability in their diet and habitat utilisation than minke whales. These findings support the presence of fine-scale resource and habitat partitioning as a strategy for sympatric cetaceans to co-exist. However, it also opens questions about the dietary niches filled by especially bottlenose dolphins at times of limited resources leading to direct competition with both harbour porpoises and minke whales. Subsequently, fishing activities should be monitored to minimise disturbance of this cetacean community during the summer months.

CONTENTS

1.0.	Introduction	1
2.0.	Literature Review	3
2.1.	Cetaceans.....	4
2.1.1.	Overview	4
2.1.2.	Baleen whales	4
2.1.3.	Toothed whales	6
2.1.4.	Habitat preferences in the marine environment.....	7
2.1.5.	Conservation threats	8
2.2.	Cetaceans in Scottish waters.....	9
2.3.	The Moray Firth Study Site	12
2.3.1.	Location.....	12
2.3.2.	Description	13
2.3.3.	Biodiversity	13
2.3.4.	CRRU	15
2.4.	The Study Species.....	15
2.4.1.	The Minke Whale.....	15
2.4.2.	The Harbour Porpoise	17
2.4.3.	The Bottlenose Dolphin	18
2.5.	Sympatry of cetaceans.....	21
2.5.1.	Co-existence strategies	21
2.5.2.	Competitive Interactions.....	22
2.5.3.	Mixed-species associations.....	23
2.5.4.	Habitat partitioning application	23
2.6.	Aims and objectives	24
2.7.	Hypotheses	25
3.0.	Methods	26
3.1.	Survey methods	27
3.2.	Geographical Information Systems (GIS).....	29
3.3.	Statistical analysis.....	30
4.0.	Results	31
4.1.	Spatial habitat preferences	32
4.2.	Evidence of spatial partitioning	39

4.3.	Spatio-temporal habitat preferences	42
4.4.	Evidence of spatio-temporal partitioning	48
5.0.	Discussion	51
5.1.	Interpretation of results	52
5.2.	Limitations	57
6.0.	Conclusion	58
7.0.	Future Work.....	60
8.0.	Referencing	62
9.0.	Appendices	80

FIGURES

Figure 2.1. Showing the feeding apparatus of a mysticete whale with the plates of baleen hanging from the roof of the mouth which are used to filter out prey from the seawater (From Reeves <i>et al.</i> , 2002).....	6
Figure 2.2. Critical habitat for whales, dolphins and porpoise within the UK coastline (From Clark <i>et al.</i> , 2010)	10
Figure 2.3. Map of the Moray Firth in northeast Scotland indicating the inner firth Special Area of Conservation (SAC) and the position of the study area along the 80km southern coastline between Lossiemouth and Fraserburgh. The arrows indicate the direction of the Dooley current flow (From Robinson <i>et al.</i> , 2009).	12
Figure 2.4. The three main coastal cetacean species examined in the present investigation: the bottlenose dolphin (left), minke whale (middle) and the harbour porpoise (right). (Photo credits: Kevin Robinson, CRRU)	14
Figure 2.5. Diagram of a minke whale (From Shirihai and Jarrett, 2006).....	16
Figure 2.6. Harbour porpoise distribution (From IUCN Red List of Threatened Species; 2011)	17
Figure 2.7. Diagram of a harbour porpoise (From Shirihai and Jarrett, 2006).....	18
Figure 2.8. Diagram of common bottlenose dolphin (From Shirihai and Jarrett, 2006)	20
Figure 2.9. Map of Scotland with crucial areas for bottlenose dolphins numbered (Area 1: Inner Moray Firth, Area 2: Southern Outer Moray Firth, Area 3: Grampian/Fife Coast, Area 4: Sound of Barra, Area 5: South of Skye and Area 6: Skye and North) (From Cheney <i>et al.</i> , 2012).....	20
Figure 3.1. The CRRU rigid-hulled-inflatable boats (RHIBs) with different observational frames attached (Photo credit: Kevin Robinson, CRRU)	27
Figure 3.2. A map of the study area and survey routes used during systematic boat surveys. There are 3 outer transect (routes 2 to 4), separated by 1.5km, plus an inner coastal transect (route 1) (From Robinson <i>et al.</i> , 2007).	28
Figure 3.3. The sediment grain size order classification (SBS Folk from British Geological Survey)	30
Figure 4.1. GIS map showing the distribution of minke whales (top), harbour porpoises (middle) and bottlenose dolphin (bottom) along the outer southern Moray Firth coastline as recorded by the CRRU research team between May and October 2001 to 2008 inclusive.	33

Figure 4.2. GIS map of the outer southern Moray Firth region showing water depth within the study area. Each study species' encounter frequencies are shown for each depth interval in the histogram plots below.	35
Figure 4.3. GIS map of the outer southern Moray Firth region showing seabed slope within the study area. Each study species' encounter frequencies are shown for each seabed slope interval in the histogram plots below.	36
Figure 4.4. GIS map of the outer southern Moray Firth region showing seabed sediments within the study area. Each study species' encounter frequencies are shown for each seabed sediment class in the histogram plots below.	37
Figure 4.5. Graphs to show the frequency of sightings in each distance to nearest shore interval per species	38
Figure 4.6. Box plot to indicate the most preferred distances to nearest shore of each species and the range used throughout the summer months May to October	40
Figure 4.7. Box plot to indicate the preferred depths of each species and the range used throughout the summer months May to October	41
Figure 4.8. Stack histograms showing the number of encounters per kilometre of survey effort in each depth interval by months June to September for minke whales (top), harbour porpoises (middle) and bottlenose dolphins (bottom).	44
Figure 4.9. Stack histograms showing the number of encounters per kilometre of survey effort in each seabed slope interval by months June to September for minke whales (top), harbour porpoises (middle) and bottlenose dolphins (bottom).	45
Figure 4.10. Stack histograms showing the number of encounters per kilometre of survey effort in each seabed sediment class by months June to September for minke whales (top), harbour porpoises (middle) and bottlenose dolphins (bottom).	46
Figure 4.11. Stack histograms showing the number of encounters per kilometre of survey effort in each seabed sediment class by months June to September for minke whales (top), harbour porpoises (middle) and bottlenose dolphins (bottom).	47

TABLES

Table 1.1. Table of cetacean species recorded in Scottish waters (adapted from Reid <i>et al.</i> , 2003)	9
Table 4.1. Results of chi-square tests (<i>P</i> values) used to determine significant difference between study species and different distance to nearest shore intervals.	40
Table 4.2. Results of chi-square tests (<i>P</i> values) used to determine significant difference between study species and different depth intervals	41
Table 4.3. Tables to show the mean and standard deviation of environmental variables by month, and encounters over sandy gravel as a percentage for minke whales (top), harbour porpoises (middle) and bottlenose dolphins (bottom).....	43
Table 4.4. Results of chi-square tests (<i>P</i> values) used to determine significant difference between study species and (a) depth (b) seabed slope (c) seabed sediment (d) distance to nearest shore, over months June to September.	49

APPENDICES

Appendix 9.1. CD containing raw encounter data used in this study, followed by an example of some raw data.	82
Appendix 9.2. GIS maps showing the monthly distribution of minke whales, harbour porpoises and bottlenose dolphin along the outer southern Moray Firth coastline as recorded by the CRRU research team between 2001 to 2008 inclusive. The frequency of encounter is noted in the bottom right corner of each map.....	84
Appendix 9.3. Areas identified for highest encounters of minke whales and harbour porpoise (top) and bottlenose dolphins (bottom)	87
Appendix 9.4. Depth calculations are displayed including the minimum, maximum, mean and standard deviation for each species	87
Appendix 9.5. Seabed slope calculations are displayed including the minimum, maximum, mean and standard deviation for each species	88
Appendix 9.6. Distance to nearest shore calculations are displayed including the minimum, maximum, mean and standard deviation for each species	88
Appendix 9.7. Results of chi-square tests (<i>P</i> values) used to determine significant difference between study species and different seabed sediment classes	89
Appendix 9.8. Results of chi-square tests (<i>P</i> values) used to determine significant difference between study species and different seabed slope intervals.....	89
Appendix 9.9. Box plot to indicate the preferred seabed slopes of each species and the range used throughout the summer months May to October	90
Appendix 9.10. The number of monthly encounters of each species, the survey effort per month and the derived no of encounters per kilometre per month for each species	90

1.0. Introduction

1.0. Introduction

Cetaceans living in the same habitat may partition the available resources by filling niches over spatial and temporal scales in order to avoid competition (Bearzi, 2005b). In north-east Scotland common bottlenose dolphins (*Tursiops truncatus*), harbour porpoises (*Phocoena phocoena*) and minke whales (*Balaenoptera acutorostrata*) co-occur in the coastal regions of outer southern Moray Firth (Robinson *et al.*, 2007). Encounter data for these three study species was collected by the Cetacean Research and Rescue Unit (CRRU) during dedicated survey between 2001 and 2008. Subsequent analysis will compare the encounters of each species against environmental parameters including water depth, seabed slope, seabed sediment and distance to nearest shore. Temporal association between encounters and the fixed environmental scales over the months of June to September will also be investigated. Further analysis will investigate significant differences in the preferences of each species to determine if any two species are partitioning the habitat spatially or temporally resulting in fine-scale segregation. With this being the case, the reasons and implications for conservation of this cetacean community, will be discussed.

2.0. Literature Review

2.0. Literature Review

2.1. Cetaceans

2.1.1. Overview

Whales, dolphins and porpoise belong to the order Cetacea. Cetaceans are highly mobile marine mammals which breathe air, regulate their body temperature and produce few young at a time, which are reliant on parental care for survival. Cetaceans offset their high metabolic rate as mammals- and their large body size results through the opportunity of a buoyant environment by adaptations allowing them to locate and consume an abundance of prey over a variety of trophic levels in nutrient rich areas (Tyack, 2001).

There are 86 distinctly recognised species of cetaceans (IWC, 2009). Subspecies, however, occur over different geographical locations, such as contrasting hemispheres, and taxonomy is regularly in discussion with advances in technology changing our knowledge on genetic relatedness (Tyack, 2001; Bannister, 2001; Bannister, 2009; Wells, 2009; Hooker, 2009).

Cetaceans are split into two suborders. The first are the mysticeti or baleen whales, comprising 14 recognised species, which have baleen plates instead of teeth to filter zooplankton and fish prey from the sea water. The other is the odontoceti or toothed whales, comprising 72 species, including dolphins and porpoises, which typically chase individual prey such as squid or fish (Tyack, 2001; Bannister, 2009).

2.1.2. Baleen whales

Baleen whales are made up of 4 families including right whales (Balaenidae, balaenids), pygmy right whales (Neobalaenidae, neobalaenids), gray whales (Eshrichtiidae, eschrichtiids) and roqual whales (Balaenopteridae, balaenopterids) (Bannister, 2009). They generally have a large size which has been driven by their life cycle of an annual migration between feeding and breeding grounds (Tyack, 2001; Bannister, 2009). The blue whale for example, is the largest known animal on Earth. Baleen whales are found in a variety of habitats from the open ocean to coastal ecosystems and from the poles to the tropics (Bannister, 2009). They feed intensively in the seasonal productivity of the summer months, usually in polar

regions, in order to build up fat reserves, before travelling to breeding and calving grounds, at lower latitudes- in the winter months (Tyack, 2001; Bannister, 2009; Bowen *et al.*, 2002). It is unknown for sure, how baleen whales navigate on migration, but suggestions for orientation include visual, acoustic, chemical and geomagnetic cues. Large size is favoured for engulfing as many prey items as possible to sustain animals through the non-feeding winter months and for swimming more efficiently over thousands of kilometres in migration (Tyack, 2001).

Pregnant and lactating females must increase their daily intake of food to 65% of their body weight to survive, which could explain why female baleen whales have adapted to be larger than males in order to successfully raise offspring (Bannister, 2009). Calving grounds are usually in calm, protected tropical waters with minimal predation risk (Tyack, 2001). The birthing interval is usually 2 to 3 years (Bannister, 2009).

Baleen whales produce low frequency sounds which travel vast distances underwater, most likely for communication (Tyack, 2001; Bannister, 2001; Bannister, 2009). All species are fairly social, and are especially concentrated at feeding grounds (Bannister, 2001). Baleen whales differ from odontocetes by having a paired blowhole, symmetrical skull and lack of ribs articulating with the sternum (Bannister, 2009).

All species are highly specialised filter feeders which gather prey by swimming open mouthed and gulping water with highly concentrated prey densities. Inside a baleen whales mouth, attached to the gum of the upper jaw, lie the baleen plates- a fringe of fine hairs (Fig. 2.1), made of keratin, the material making up mammalian hair and human fingernails. The water is able to pass through, while the prey is filtered out and collected to be transferred to the gullet and stomach for digestion (Bannister, 2009).

Targeted prey is variable between different species of foraging whales according to their speed. For example, fast swimming balaenopterids consume large amounts of quick moving prey- such as schooling fish- over a short time. While slow swimming balaenids gather slower moving prey- such as zooplankton- over a longer period. Furthermore prey may vary by location. For example, balaenopterids in the southern hemisphere are reliant on krill, while in the northern hemisphere they are more catholic foragers (Bannister, 2009). Balaenopterids are also typically larger in

the southern Hemisphere than the northern Hemisphere because of the more limited duration of seasonal feeding opportunities (Bowen *et al.*, 2002; Bannister, 2009).



Figure 2.1. Showing the feeding apparatus of a mysticete whale with the plates of baleen hanging from the roof of the mouth which are used to filter out prey from the seawater (From Reeves *et al.*, 2002)

2.1.3. Toothed whales

Odontocetes or toothed whales are made up 7 families including sperm whales (Physeteriidae), dwarf and pygmy sperm whales (Kogiidae), beaked whales (Ziphiidae), oceanic dolphins (Delphinidae), river dolphins (Platanistidae), porpoises (Phocoenidae) and narwhals and belugas (Monodontidae) (Tyack, 2001).

Limited information is known about the sperm whale and beaked whales- because they live far from shore and dive in the deepest parts of the sea in search of squid prey, infrequently surfacing for air. In beaked whales, many species are also quite similar looking and therefore hard to identify at sea (Hooker, 2009). However, the generally smaller but diverse dolphin and porpoise families are much better studied as they are often found in more accessible inshore waters. Dolphins and porpoise species all generally share a similar streamlined body shape to move through water. A single blowhole, pectoral flippers and numerous same structured teeth are present. In most species, males and females are similar in size and appearance. Although in male killer whales dorsal fin height is larger than females. Counter-shading of a darker dorsum and lighter ventrum is usually present to camouflage themselves while hunting prey and avoiding predators (Wells, 2009).

Odontocetes do not have as pronounced an annual feeding cycle as baleen whales. Most dolphins and larger toothed whales have a prolonged period of dependency of parental care. Large toothed whales generally have a prolonged maturation and don't live as long as baleen whales (Tyack, 2001).

2.1.4. Habitat preferences in the marine environment

Various studies have compared physical attributes of the marine environment with the distribution of cetaceans, including, sea bed slopes associated with submarine canyons and shelf edges or locally along the coastline (Gowans and Whitehead, 1995; Hooker *et al.*, 1998; Canadas *et al.*, 2002; Azzellino *et al.*, 2008; Weir *et al.*, in press), changing bathymetry between inshore and pelagic waters (Gowans and Whitehead, 1995; Hooker *et al.*, 1998; Ingram and Rogan, 2002; Canadas *et al.*, 2002; Yen *et al.*, 2004; Bearzi, 2005a; Kiszka *et al.*, 2007; Certain *et al.*, 2008; Marubini *et al.*, 2009; Gross *et al.*, 2009; Weir *et al.*, in press), and sediment types of the sea bed substrate (Macleod *et al.*, 2004). However, oceanographic variables, resulting from the physical environment, such as up or down-welling currents, further concentrate zooplankton as they swim against the flow of oxygenated, nutrient- rich, warmer water (Genin, 2004). Furthermore, strong tidal systems may produce eddy currents which are known to attract marine mammals to forage (Bearzi, 2005a; Ingram *et al.*, 2007; Certain *et al.*, 2008). Environmental changes, such as sea surface temperature (Gowans and Whitehead, 1995; Hooker *et al.*, 1998; Tetley *et al.*, 2008; Weir *et al.*, in press) or climate has a driving influence on habitat use and preference (Azzellino *et al.*, 2008), over temporal scales such as time of day (Bearzi, 2005b), month (Gowans and Whitehead, 1995) or season (Hooker *et al.*, 1998). Subsequently, both physical and oceanographic features of the marine environment are highly influential for the distribution of target prey which is the driving force for the spatio-temporal occurrence of all cetacean species (Bearzi, 2005a; Zerbini *et al.*, 2006).

Cetaceans may be disturbed from preferred habitat by detrimental human activities causing degradation of their immediate habitat (Moscrop, 1993). Accordingly, a good understanding of habitat preferences is vital to conservation efforts of highly mobile cetacean species, particularly those species living in more

susceptible coastal environments where degradation of the coastline more widely occurs.

2.1.5. Conservation threats

Many populations of marine mammals are under threat from humans (Tyack, 2001; Wilson, 2008). Commercial whaling, for example, for meat, fat and oil is an on-going issue (Gales *et al.* 2005; Clapham *et al.*, 2006). Marine mammals are further killed as by-catch in fishing gear (Read *et al.*, 2006; Davies *et al.*, 2009) and overfishing can result in habitat change with disastrous consequences for these animals. Collisions with vessels at sea are also a threat with large ships significant for some species (Laist *et al.*, 2001; Van Waerebeek *et al.*, 2007; Carrillo and Ritter., 2010), and high speed catamarans (Ritter, 2009) and smaller recreational vessels such as speedboats and jet-skis in other instances (Dolman *et al.*, 2006). Furthermore, toxic bio-accumulation of polychlorinated biphenyls (PCB's), organochlorines, and heavy metals from water contamination may result impaired reproduction, immune-suppression or subsequent poisoning (Tanabe *et al.*, 1994; Minh *et al.*, 2000; Watanabe *et al.*, 2000; Jepson *et al.*, 2005). Noise pollution is a significant effect and sources include military sonar, seismic exploration activities and shipping traffic (Nowacek *et al.*, 2007; Parsons *et al.*, 2008; Parsons *et al.*, 2009). Coastal populations are increasingly affected by whale-whaling vessels which may be disruptive to natural behaviours and foraging ability (Bejder *et al.*, 2006; Williams *et al.*, 2006).

Military activities have been thought to limit the distribution of cetaceans (Parsons *et al.*, 2000) and are thought to coincide with mass stranding events of deep diving odontocetes such as beaked whales and pilot whales (Jepson *et al.*, 2003; Dolman *et al.*, 2010). Climate change is also a growing concern for cetacean communities (Macleod *et al.*, 2005; Learmonth *et al.*, 2006; Simmonds and Elliott, 2009; Macleod, 2009).

2.2. Cetaceans in Scottish waters

The coastline surrounding the UK supports a high diversity of cetaceans (Weir *et al.*, 2001; Reid *et al.*, 2003; Clark *et al.*, 2010). Critical coastal areas include the Hebrides, north-east Scotland, south-west England and coastal Wales (Fig. 2.2) (Clark *et al.*, 2010). Scottish waters are particularly important for UK cetaceans with 24 species being recorded in these waters to date (Table 1.1).

Table 1.1. Table of cetacean species recorded in Scottish waters (adapted from Reid *et al.*, 2003)

Common Name	Scientific name
Northern right whale	<i>Eubalaena glacialis</i>
Blue whale	<i>Balaenoptera musculus</i>
Killer whale	<i>Orcinus orca</i>
Long- finned pilot whale	<i>Globicephala melas</i>
Risso's dolphin	<i>Grampus griseus</i>
Atlantic white- sided dolphin	<i>Lagenorhynchus acutus</i>
White- beaked dolphin	<i>Lagenorhynchus albirostris</i>
Striped dolphin	<i>Stenella coeruleoalba</i>
Short-beaked common dolphin	<i>Delphinus delphis</i>
Northern bottlenose whale	<i>Hyperoodon ampullatus</i>
Sowerby's beaked whale	<i>Mesoplodon bidens</i>
Sperm whale	<i>Physter macrocephalus</i>
Pygmy sperm whale	<i>Kogia breviceps</i>
Humpback whale	<i>Megaptera novaengliae</i>
Fin whale	<i>Balaenoptera physalus</i>
Sei whale	<i>Balaenoptera borealis</i>
Minke whale	<i>Balaenoptera acutorostrata</i>
Common bottlenose dolphin	<i>Tursiops truncatus</i>
Harbour porpoise	<i>Phocoena phocoena</i>
Beluga whale	<i>Delphinapterus leucas</i>
Narwhal	<i>Monodon monoceros</i>
Cuvier's beaked whale	<i>Ziphius cavirostris</i>
False killer whale	<i>Pseudorca crassidens</i>

All cetaceans in Scotland are protected under the Wildlife and Countryside Act (1981), the Nature Conservation (Scotland) Act (2004), the ASCOBANS agreement and the EC Habitats Directive (The Scottish Government, 2011a). However of the recorded cetacean in UK waters, many are infrequent visitors to coastal waters and limited information is available on their wider distribution (Clark *et al.*, 2010). It is considered that there are six frequent visiting and appropriately studied species of cetaceans which would benefit from Marine Protected Areas (MPA's) defined by critical habitats in the UK, with Scotland being particularly significant in this respect (Fig. 2.2) (Clark *et al.*, 2010). The UK Marine and Coastal Access Act 2009 and the Marine (Scotland) Act 2010 have a responsibility to create well managed MPAs to deliver wildlife conservation priorities (Clark *et al.*, 2010). The following is a discussion of those six key species.

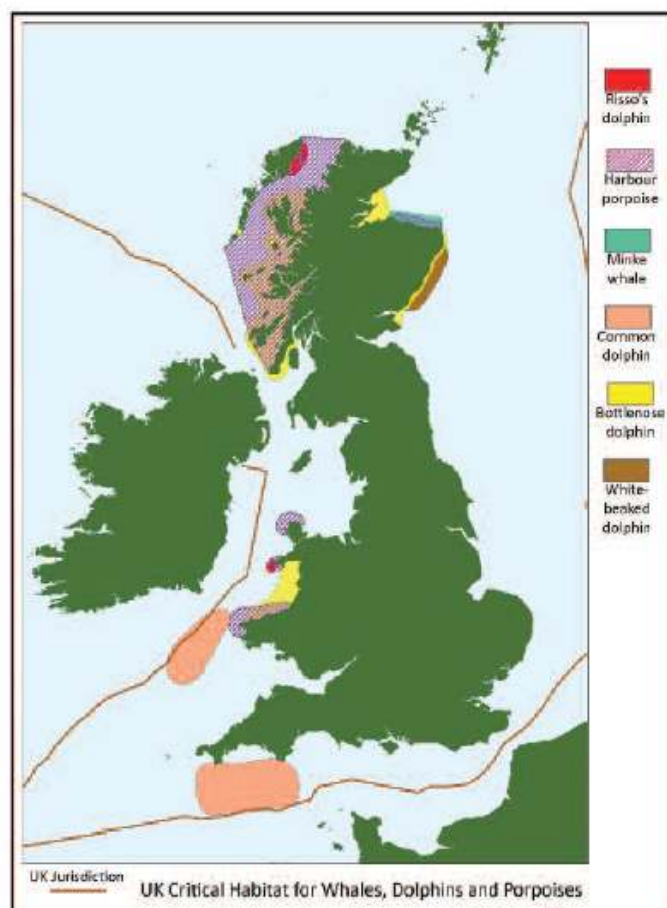


Figure 2.2. Critical habitat for whales, dolphins and porpoise within the UK coastline (From Clark *et al.*, 2010)

Minke whales (*Balaenoptera acutorostrata*), white-beaked dolphins (*Lagenorhynchus albirostris*) and harbour porpoise (*Phocoena phocoena*) are all highly observed in the north-western North Sea and the Aberdeenshire coast is believed to be a critical habitat for white-beaked dolphins in particular (Northridge *et al.*, 1995; Weir *et al.*, 2007; Clark *et al.*, 2010). According to SCANS (Small Cetacean Abundance in the North Sea) surveys in 1994 and SCANS-II surveys in 2005, the harbour porpoise is the most abundant cetacean throughout the whole North Sea, with a population estimate of over 335,000 animals (Hammond *et al.*, 2002; EU LIFE, 2006). It is also clear that the Hebrides on the west coast of Scotland also provides critical habitat for this species (Clark *et al.*, 2010). Critical habitat for minke whales and harbour porpoise is also the south coast of the outer Moray Firth (Robinson *et al.*, 2007; Robinson *et al.*, 2009; Clark *et al.*, 2010). Furthermore, a resident bottlenose dolphin (*Tursiops truncatus*) population exists in the coastal waters from the inner Moray Firth to St. Andrews Bay (Cheney *et al.*, 2012). Further critical habitat for this species has been identified in the Inner Hebrides and the Sound of Barra on the west coast of Scotland (Grellier and Wilson, 2003; Clark *et al.*, 2010). Evidence from photo-identification data of individual animals, has revealed that bottlenose dolphins may make long-distance movements between the Moray Firth, on the east coast, the inner Hebrides, on the west coast, of Scotland and even as far as the Republic of Ireland (Robinson *et al.*, in press). The other resident population of bottlenose dolphins in the UK is found in Cardigan Bay, Wales (Simon *et al.*, 2010; Clark *et al.*, 2010).

Short-beaked common dolphins (*Delphinus delphis*) have been observed in the north-western North Sea since 2006 (Robinson *et al.*, 2011). Another critical habitat for this species is the Celtic Sea in south west England (Clark *et al.*, 2010). There have been suggestions that increasing sea temperatures, above 14°C, have resulted in the range expansion of common dolphins (Robinson *et al.*, 2011) leading to potential inter-specific competition with white-beaked dolphins (*Lagenorhynchus albirostris*) in northern UK waters (Macleod *et al.*, 2008; Weir *et al.*, 2009).

Critical habitat for Risso's dolphins (*Grampus griseus*) has been established on the north-east Isle of Lewis in the outer Hebrides (Atkinson and Gill, 1996; Atkinson *et al.*, 1998) and off the coast of Wales- around Bardsey Island (De Boer, 2009).

2.3. The Moray Firth Study Site

2.3.1. Location

The Moray Firth is a large coastal embayment in north-east Scotland, geographically separated into a definable inner, estuarine region and outer coastal basin (Fig. 2.3) (Eleftheriou *et al.*, 2004). The inner region is located to the west of a line drawn from Helmsdale in the north to Lossiemouth in the south, while the outer region is defined as the area to the east of this line, stretching outwards to Duncansby Head in the north and Fraserburgh in the south (Harding- Hill, 1993).

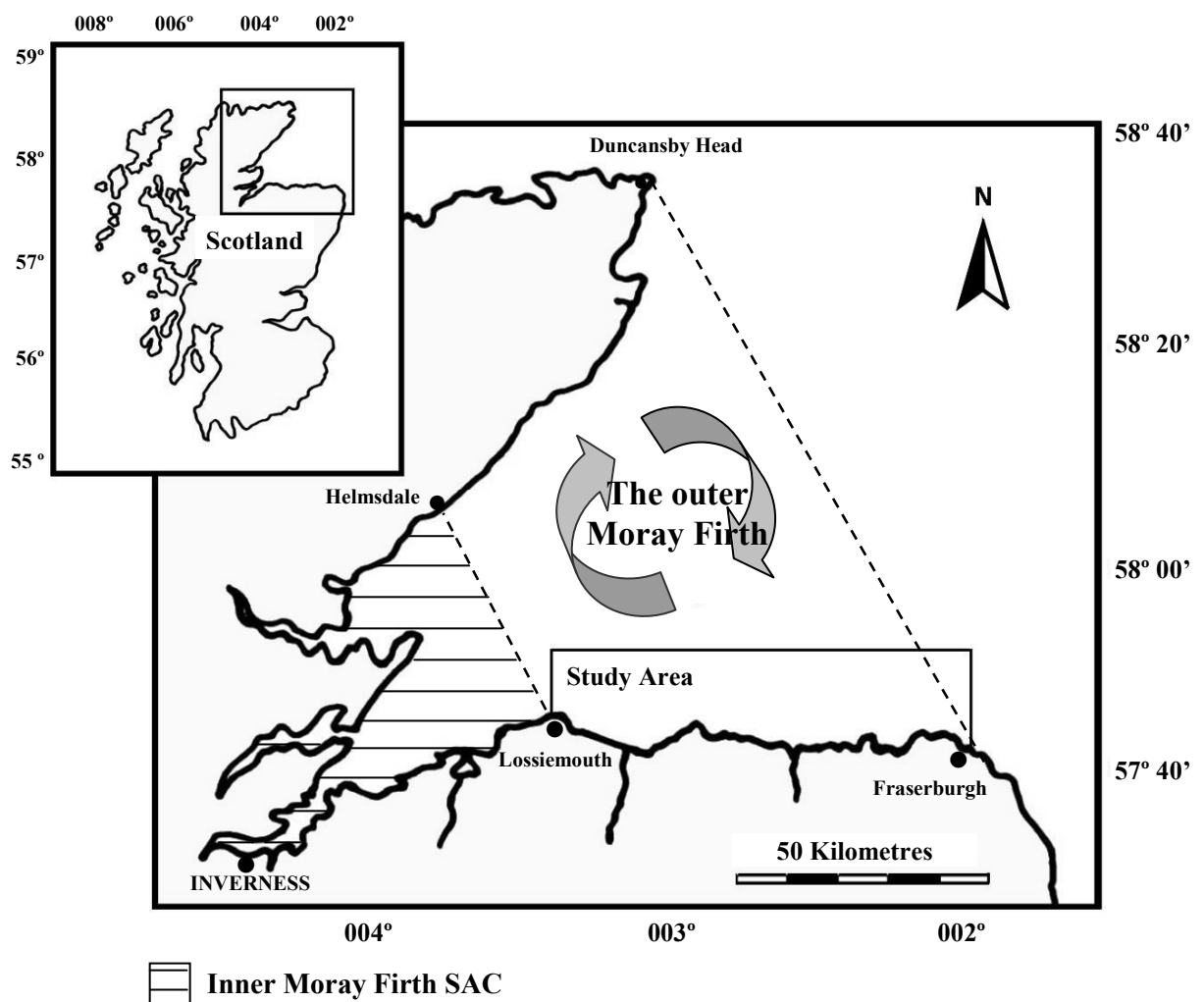


Figure 2.3. Map of the Moray Firth in northeast Scotland indicating the inner firth Special Area of Conservation (SAC) and the position of the study area along the 80km southern coastline between Lossiemouth and Fraserburgh. The arrows indicate the direction of the Dooley current flow (From Robinson *et al.*, 2009).

2.3.2. Description

Covering approximately 5,230km², the Moray Firth is a vast marine 'open system' (Wilson, 1995) and makes an integral part of the North Sea sharing water circulation and climate patterns alike (Eleftheriou *et al.*, 2004). It is recognised as an area of outstanding biological importance (Wright *et al.*, 1998) with the inner firth being recognised as a Special Area of Conservation (SAC) since 2005 (The Scottish Government, 2011b).

The deeper areas of the firth contain sandy or muddy sediments, while the shallower areas are predominantly sandy gravel sediments (Eleftheriou *et al.*, 2004). The southern trench in the outer firth, an enclosed basin between Banff and Fraserburgh at 7km from the shoreline, is unique in the area for its underwater topography, reaching depths of over 220m (Eleftheriou *et al.*, 2004; Clark, 2005). The inner firth has a slowly sloping seabed to a maximum depth of 50 metres while the outer firth resembles more the open sea (Harding-Hill, 1998).

The Moray Firth is a heterogeneous ecosystem with the Dooley current bringing colder waters from the north which circulate in a clockwise direction with warmer waters from the twelve major rivers flowing into the firth (Fig. 2.3) (Eleftheriou *et al.*, 2004; Robinson *et al.*, 2007). The current is strong and removes lighter sediments leaving a mixture of sand and gravel as dominant seabed substrates (Eleftheriou *et al.*, 2004). The warm fresh water brought into the embayment reduces the salinity and creates mixed nutrient-rich horizontal front in the summer months (Reid *et al.*, 2003; Holmes *et al.*, 2004; Tetley *et al.*, 2008). Additionally, steeply sloped seabed topography creates up-wellings of increased local productivity (Yen *et al.*, 2004).

2.3.3. Biodiversity

The nutrient rich waters of the Moray Firth support an abundance of fish species which are ecologically important for this area (Clark, 2005). Species of fish found in Scottish waters include herring (*Clupea harengus*), sprat (*Sprattus sprattus*), mackerel (*Scomber scomber*), lesser sandeels (*Ammodytes marinus*), cod (*Gadus morhua*), whiting (*Merlangus merlangius*), haddock (*Melanogrammus aeglefinus*) and Atlantic salmon (*Salmo salar*) (Harding-Hill, 1993; Greenstreet *et al.*, 1998; Lusseau

et al., 2004). The distribution of these fish species is determined by a combination of environmental, oceanographic and physiographic variables (Robinson *et al.*, 2009). In turn, these fish species support an abundance of seabirds and marine mammals which determine their distribution within the Moray Firth (Clark, 2005; Robinson *et al.*, 2009). The most abundant cetacean species in the Moray Firth and also the main study species of the CRRU, are the bottlenose dolphin (*Tursiops truncatus*), minke whale (*Balaenoptera acutorostrata*) and harbour porpoise (*Phocoena phocoena*) (Fig. 2.4) (Robinson *et al.*, 2007).



Figure 2.4. The three main coastal cetacean species examined in the present investigation: the bottlenose dolphin (left), minke whale (middle) and the harbour porpoise (right). (Photo credits: Kevin Robinson, CRRU)

There has been documented evidence of at least 14 additional species of cetaceans in the inshore waters of the outer southern Moray Firth, especially in summer months, which are generally considered pelagic species such as; killer whale (*Orcinus orca*), pilot whale (*Globicephala melas*), Risso's dolphin (*Grampus griseus*), Atlantic white- sided dolphin (*Lagenorhynchus acutus*), white- beaked dolphin (*Lagenorhynchus albirostris*), striped dolphin (*Stenella coeruleoalba*), common dolphin, (*Delphinus delphis*), northern- bottlenose whale (*Hyperoodon ampullatus*), Sowerby's beaked whale (*Mesoplodon bidens*), sperm whale (*Physeter macrocephalus*), humpback whale (*Megaptera novaengliae*), fin whale (*Balaenoptera physalus*), sei whale (*Balaenoptera borealis*) (Robinson *et al.*, 2007) and Cuvier's beaked whale (*Ziphius cavirostris*) (Robinson and Macleod, 2009).

A high biodiversity of seabirds including gannets (*Morus bassanus*), kittiwakes (*Rissa tridactyla*), gulls (*Larus spp.*), guillemots (*Uria aalge*), razorbills (*Alca torda*), shearwaters (*Puffinus spp.*, *Fulmeus glacialis*) and terns (*Sterna spp.*) further rely on

the summer abundance of fish for breeding success and survival, and may play important roles in helping to produce schooling fish bait balls for foraging cetaceans (Robinson and Tetley, 2007). Furthermore, grey (*Halichoerus grypus*) and common seals (*Phoca vitulina*) are commonly sighted in the Moray Firth and may cause conflict with salmon fisheries (Butler *et al.*, 2008).

2.3.4. CRRU

Established in 1997, the Cetacean Research and Rescue Unit (CRRU) is a non-profit research organisation based in Banff, north-east Scotland, dedicated to the welfare, conservation and protection of whales, dolphins and porpoises (cetaceans) through scientific investigation, environmental educations, and the provision of a 24 hour veterinary service for sick, injured and stranded individuals. Boasting an extensive publication list and broad educational outreach programme, the organisation currently provides internships for international students and plays host for the present investigation, providing long-term field data from 2001 to 2008 for the subsequent analysis.

2.4. The Study Species

2.4.1. The Minke Whale

At 7 to 10 meters in length, the common minke whale, *Balaenoptera acutorostrata*, is the smallest of the baleen whales in the Balaenopteridae or roqual family and the most abundant baleen whale species in European waters (Reid *et al.*, 2003; Bannister, 2009; Robinson *et al.*, 2009). The species has a unique feature of a white band on its flipper which is useful in identification (Reid *et al.*, 2003) and a dark-grey black dorsum and white ventrum, along with a sharply pointed snout and curved dorsal fin two approximately thirds along its back (Perrin and Brownell, 2009) (Fig. 2.5).

Minke whales are usually seen individually or in small groups but have been known to concentrate in groups of up to 15 at feeding grounds (Reid *et al.*, 2003; Bannister, 2009). Little is known about the migratory patterns of these whales, but they apparently show preference for inshore, coastal waters (Bannister, 2009;

Robinson *et al.*, 2009). The SCANS-II surveys in 2005, give an estimate of 10,500 minke whales in the North Sea (EU LIFE, 2006) indicating that the minke whales studied in the outer Moray Firth are likely to be part of a larger population (Tetley *et al.*, 2008; Robinson *et al.*, 2009). Minke whales reach sexual maturity at 6 to 7 years old, with age class and sex influencing segregation during migration (Perrin and Brownell, 2009). In the coastal areas of the outer southern Moray Firth, up to 60% of the minke whales sighted are juveniles, which may indicate spatial segregation by age class in these coastal waters (Tetley, 2004; Robinson *et al.*, 2009). It is thought that the calving interval of females is 2 to 3 years, with pregnancy lasting approximately 10 months (Bannister, 2009).

Minke whales employ a variety of feeding methods as fast swimming baleen whales (Bannister, 2009), including side and lunge feeding prey entrapment methods, and are often found associated with seabirds in north-east Scotland (Reid *et al.*, 2003; Robinson and Tetley, 2007; Anderwald *et al.*, 2011). The lower jaw is extendable to nearly 90 degrees to maximise foraging advantage (Bannister, 2009). Minke whales are highly catholic predators with high adaptability in their diet, including schooling and benthic fish as well as copepods, allowing them to seek out a range of high prey concentrations depending on availability (Reid *et al.*, 2003; Macleod *et al.*, 2004; Perrin and Brownell, 2009). Minke whale habitat use is known to be strongly correlated with maximum prey abundance at feeding sites (Macleod *et al.*, 2004; Tetley *et al.*, 2008; Robinson *et al.*, 2009).



Figure 2.5. Diagram of a minke whale (From Shirihai and Jarrett, 2006)

2.4.2. The Harbour Porpoise

Reaching a maximum of 1.8 metres, the harbour porpoise, *Phocoena phocoena*, is the smallest and most abundant species of cetacean in European shelf waters (Hammond *et al.*, 2002; Reid *et al.*, 2003). Globally the species is found throughout temperate waters of the Northern Hemisphere with preference for coastal areas within 10km of shore (Fig. 2.6) (Walker and Cresswell, 2008). The status of the species throughout its entire range is least concern, but subpopulations are under more immediate threat (IUCN Red List, 2008). The North Sea population is under threat from high levels of by-catch in fisheries (Clark *et al.*, 2010). In the outer Moray Firth, this species is the most commonly sighted cetacean, making up 60% of all encounters (Robinson *et al.*, 2007; Eisfield *et al.*, 2009).



Figure 2.6. Harbour porpoise distribution (From IUCN Red List of Threatened Species; 2011).

Porpoises usually socialise in small groups of up to three animals. However, larger groups may be found in prime feeding grounds (Reid *et al.*, 2003). It is well known that abundance and distribution of harbour porpoises is closely related to the availability of their target prey (Clark *et al.*, 2006; EU LIFE, 2006). Harbour porpoises have spade-shaped teeth (Bjørge and Tolley, 2009; Wells, 2009) and target small schooling surface fish such as sprat, with high lipid nutritional value at certain times of the year (Reid *et al.*, 2003). However, they may forage for demersal fish species, squid and crustaceans when these resources are not available. They may be

observed feeding independently or co-operatively in groups to herd fish together and towards the surface (Bjørge and Tolley, 2009).

Harbour porpoise are easy to identify by their small size, blunt snout, triangular dorsal fin (Fig. 2.7) and forward rolling behaviour when surfacing. Harbour porpoise make very little obstruction on the surface of the water, making them difficult to spot in all but the calmest conditions (Bjørge and Tolley, 2009). Harbour porpoise have a higher blubber percentage compared to total body mass compared to other cetaceans, which is an adaptation for insulation of their relatively small body in cold waters. This is especially the case in calves which have 37% of their body mass as blubber (Bjørge and Tolley, 2009). In the North Sea, calves and juvenile porpoise are typically recorded between June and September, when 35% of harbour porpoise groups have immature animals (Weir *et al.*, 2007; Robinson *et al.*, 2007). Calves grow and mature rapidly with shorter dependency on paternal care (Tyack, 2001; Wells, 2009).



Figure 2.7. Diagram of a harbour porpoise (From Shirihaï and Jarrett, 2006).

2.4.3. The Bottlenose Dolphin

Bottlenose dolphins (*Tursiops truncatus*) are social delphinids, usually living in small, resident groups of up to 50 individuals within 1km of shore in coastal areas (Bearzi, 2005b; Wilson, 2008). Larger groups, however, are known to occur usually in pelagic waters (Reid *et al.*, 2003). Bottlenose live in a fission-fusion society, with associations between individuals changing daily depending on age and sex class, as well as activity type (Reid *et al.*, 2003; Bearzi, 2005b; Wilson, 2008). However, long lasting associations also occur in more stable groups, of a mixture of females, males and

calves (Wilson, 2008). Bottlenose calves are commonly sighted with their mothers until 3 to 4 years of age when the next calf is born (Tyack, 2001). Reasons for co-operation in this species may include baby-sitting, for defence from interspecific predators and intraspecific infanticide, and hunting advantage (Patterson *et al.*, 1998; Wilson, 2008). Bottlenose dolphins show complex sociality and long-term memory of individual recognition (Wilson, 2008).

Bottlenose dolphins are opportunistic, feeders which have a highly adaptable diet to exploit the most abundant prey species (Bearzi, 2005b). Diet ranges from benthic and pelagic fish of both independent and schooling status, including cod (*Gadus morhua*), salmon (*Salmo salar*) and whiting (*Merlangius merlangus*) as well as cephalopods (Santos *et al.*, 2001; Bearzi, 2005b, Clark *et al.*, 2010). Individual co-operative hunting is known to occur, with the latter resulting in fish trapped against the water surface or shoreline (Liret *et al.*, 1994, Wilson *et al.*, 1997). Bottlenose dolphins in coastal areas show preference to river estuaries, sandbanks, uneven bottom slopes and strong tidal systems (Wilson, 2008).

Bottlenose dolphins use a range of short echolocation clicks for navigation and foraging, but may be used socially for communication. The gestation period is 12 months and birthing occurs between May and November in the UK, with calving intervals of 2 to 5 years (Wilson, 2008).

Bottlenose dolphins in the north-east Atlantic are 4 metres in length and are particularly robust, perhaps the biggest in the world, at the northern most extreme of their range (Wilson, 2008). They are light grey in colour on the dorsum fading to white on the ventrum (Fig. 2.8) (Reid *et al.*, 2003) and have short beaks lined with conical shaped teeth (Bjørge and Tolley, 2009; Wells, 2009).

Pointy teeth are designed for grasping individual prey items rather than for chewing (Tyack, 2001; Wells, 2009). The dorsal fin is central on the dorsum and sickle shaped, with markings along the trailing edge being used by researchers to identify one individual from another (Reid *et al.*, 2003). Estimates of bottlenose dolphins from the SCANS-II surveys, estimate 12,645 individuals in European Atlantic shelf waters (EU LIFE, 2006).



Figure 2.8. Diagram of common bottlenose dolphin (From Shirihi and Jarrett, 2006).

The resident bottlenose dolphin population of the Moray Firth is estimated, from collaborative studies using photo identification, to be around 195 animals (Cheney *et al.*, 2012), although these animals are known to be highly mobile over wider spatial areas as far away as the west coast of Scotland and the Republic of Ireland (Robinson *et al.*, in press). There are a variety of important areas in Scotland to bottlenose dolphins (Fig. 2.9) which are protected under the European Habitats Directive (Clark *et al.*, 2010).



Figure 2.9. Map of Scotland with crucial areas for bottlenose dolphins numbered (Area 1: Inner Moray Firth, Area 2: Southern Outer Moray Firth, Area 3: Grampian/Fife Coast, Area 4: Sound of Barra, Area 5: South of Skye and Area 6: Skye and North) (From Cheney *et al.*, 2012).

2.5. Sympatry of cetaceans

Direct sympatry is defined as the co-occurrence of two or more species in the same immediate habitat or wider geographic area (Bearzi, 2005b). Since, distributions of top predators are expected to be resource-limited (Hairston *et al.*, 1960), ecological separation by either diet, time or habitat use are strategies used by cetaceans in order to co-exist (Bearzi, 2005a; Bearzi, 2005b; Gross *et al.*, 2009; Kiszka, 2011b; Weir *et al.*, in press). Studies of sympatry in cetaceans are limited, but most examples are seen within the family *Delphinidae*. Sympatry may result in fine-scale resource and habitat partitioning or aggression between species as a result of interference competition (Bearzi, 2005b; Weir *et al.*, in press). Segregation may be spatial—by physiography (e.g. bathymetry, distance to shore, sediment type) and/or oceanography (environmental including climatic changes such as sea surface temperature or by sea currents, fronts and up-wellings)—or temporal e.g. time of day, month or season (see section 2.1.4) (Bearzi, 2003; Yen *et al.*, 2004; Kiszka *et al.*, 2011b; Weir *et al.*, in press).

2.5.1. Co-existence strategies

When in direct sympatry and when resources are limited, cetaceans may partition the available resources to reduce direct competition (Roughgarden, 1976). Dietary divergence and habitat partitioning are such strategies (Bearzi, 2003; Oveido, 2007) – and strategies may include targeting different prey species found at other spatial or temporal scales including different prey sizes, different feeding times, and different travel routes, thus leading to clear habitat partitioning (Bearzi, 2005b; Spitz *et al.*, 2006). For example, common bottlenose dolphins and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Chinese waters were found to target different prey by water depth and distance from shore, showing clear partitioning between inshore and offshore waters respectively (Wang *et al.*, 2000). In other cases, such as sympatry between short-beaked common dolphins and long-beaked common dolphins in California, however, partitioning may be less clear, since, just slight differences in diet may have allowed both species, in directly sympatric habitat of offshore waters, to reduce competition for resources just enough for co-occurrence (Bearzi, 2003). A difference of foraging strategy, between surface and bottom prey—of common

dolphins and bottlenose dolphins respectively; may be just enough to allow competing species to partition resources depending on depth in the water column (Ferretti *et al.*, 1998).

Furthermore, direct sympatry of short-beaked common dolphins, Atlantic white-sided dolphins (*Lagenorhynchus acutus*), and long-finned pilot whales (*Globicephala melas*) was investigated in a submarine canyon in the Scotian Shelf showing correlation of species distribution to the canyon, as well as slightly different spatial and temporal use of the same habitat (Gowans and Whitehead, 1995). Highly sloped areas of sea bed have predictable oceanography of currents and upwellings which create local productivity and concentrated prey abundances (Bailey and Thompson, 2010). Distributions of minke whales and fin whales in Canada are influenced by fine scale oceanographic features facilitating foraging as well as depth and slope (Ingram *et al.*, 2007). Variation of the same prey species at different times of the day or season may lead to temporal habitat partitioning (Bearzi, 2005b; Kiszka *et al.*, 2011b).

The diverse physiology of cetaceans as a taxonomic order (see sections 2.1.1 and 2.1.2) allows them as individual species to have an advantage in exploiting niche resources depending on fine scale changes in the physical marine habitat. For example, depending on the depth of the water at contrasting distances from shore, as seen between bottlenose dolphins and common dolphins in California (Bearzi, 2003), the predators' ability to trap the prey item against the sea surface and shore may be affected (Reid *et al.*, 2003). In the Bay of Biscay, bathymetry clearly affects the distribution and habitat partitioning of toothed cetaceans (Kiszka, 2007; Certain *et al.*, 2008).

The sediment of the seabed may indicate which type of prey is found there from habitat preferences information. Sighted cetaceans over known sediment types give good indications of target prey, which can later be used to analyse resource partitioning of predator species (Macleod *et al.*, 2004; Robinson *et al.*, 2009).

2.5.2. Competitive Interactions

If resources change and prey preferences begin to overlap, direct competition between species will occur (Bearzi, 2005b). In this case, one species may become more dominant over another, and this most commonly involves agonistic behaviour

from larger delphinids towards smaller, sympatric species which may ultimately result in avoidance behaviour (Ross and Wilson, 1996; Thompson *et al.*, 2004, Coscarella and Crespo, 2010).

Violent interactions between bottlenose dolphins and harbour porpoise around the UK, including the Moray Firth (Ross and Wilson, 1996) and Cardigan Bay (Simon *et al.*, 2010), are well recognised and thought to result from direct competition for food resources (Spitz *et al.*, 2006; Simon *et al.*, 2010; Robinson and Macleod in prep). This behaviour is also reported in California, and further hypothesis for its occurrence include, practice for intraspecific infanticide, maintaining fighting skills for male interactions, play-orientated behaviour, or as a result sexual frustration (Cotter *et al.*, 2012). Whatever the case, avoidance may result in fine scale resource partitioning where the two species co-occur (Thompson *et al.*, 2004).

2.5.3. Mixed-species associations

When food is abundant, some dolphin species have been known to form temporary mixed-species groups and target the same prey (Selzer and Payne, 1988; Gowans and Whitehead, 1995). Advantages of such cooperation include increased foraging opportunities, protection from predators and perhaps even social benefit (Querouil *et al.*, 2008). Spinner dolphins (*Stenella longirostris*) associate with spotted dolphins (*Stenella attenuata*) for protection from predators (Kiszka *et al.*, 2011a). Short-beaked common dolphins in minority numbers of the Mediterranean were found to rely on striped dolphins for foraging (Frantzis and Herzing, 2002). There are also a few documented associations between odontocetes and mysticetes; between Risso's dolphins and gray whales (*Eschrichtius robustus*) for example (Shelden *et al.*, 1995). In other cases, directly sympatric species may never associate in mixed schools (Bearzi, 2003; Bearzi, 2005c).

2.5.4. Habitat partitioning application

In view of the reasons for segregation of resources in sympatric cetacean communities, studies of habitat partitioning may help to predict and understand the ecological factors driving spatio-temporal of cetacean distributions. Since physical characteristics of the marine environment are fixed, habitat preferences of individual species' habitat can quickly be obtained and compared with other species. These

scales can ultimately be used to better understand the ecological and conservation requirements of these marine mammals, to help identify potential key sites of habitat use for cetaceans and their prey. This can then be used to predict past and present distribution patterns relating to underlying environmental variables to provide insights into species interactions (Robinson *et al.* 2009). Furthermore, spatial scales may be used in environmental modelling as a useful conservation tool for identifying and protecting key cetacean habitats (Canadas *et al.*, 2005; Hastie *et al.*, 2005; Kaschner *et al.*, 2006).

2.6. Aims and objectives

The main aim of this project is to investigate how the spatial and temporal preferences of minke whales (*Balaenoptera acutorostrata*), bottlenose dolphins (*Tursiops truncatus*) and harbour porpoise (*Phocoena phocoena*) in the southern outer Moray Firth allows direct sympatry by resource and habitat partitioning in coastal communities.

The current study will integrate environmental variables with cetacean sightings to determine individual species' habitat distributions using geographical information systems (GIS). The study will investigate the fine scale spatial— bathymetry (depth and slope), sediment type and distance to shore, and temporal— month, partitioning between co-occurring species. This will allow prediction of species distribution to aid conservationists and policy makers with regards to future habitat management and formation of useful Marine Protected Areas for conservation of coastal cetaceans in Scotland.

2.7. Hypotheses

Hypothesis 1

When sympatric coastal cetacean species co-occur in the same habitat, they tend to partition the available resources, over spatial and temporal scales, to reduce competition resulting in interspecific segregation.

Null hypothesis 1

When sympatric coastal cetacean species co-occur in the same habitat, they do not tend to partition the available resources, over spatial and temporal scales, to reduce competition resulting in interspecific segregation.

3.0. Methods

3.0. Methods

3.1. Survey methods

The data used in the current study was collated by the Cetacean Research & Rescue Unit (CRRU) during annual dedicated boat surveys in the outer southern Moray Firth between May and October, 2001 to 2008 inclusive. Rigid-hulled-inflatable boats (RHIBs) (Fig. 3.1) were used to follow four standardised routes positioned parallel to the shore between the coastal ports of Lossiemouth and Fraserburgh (Fig. 3.2), as described in the methodology section in Robinson *et al.*, 2007. The available dataset represents a total of 1,258 encounters of the three main study species; 168 bottlenose dolphin encounters, 729 harbour porpoise-and 361 minke whale encounters.



Figure 3.1. The CRRU rigid-hulled-inflatable boats (RHIBs) with different observational frames attached (Photo credit: Kevin Robinson, CRRU).

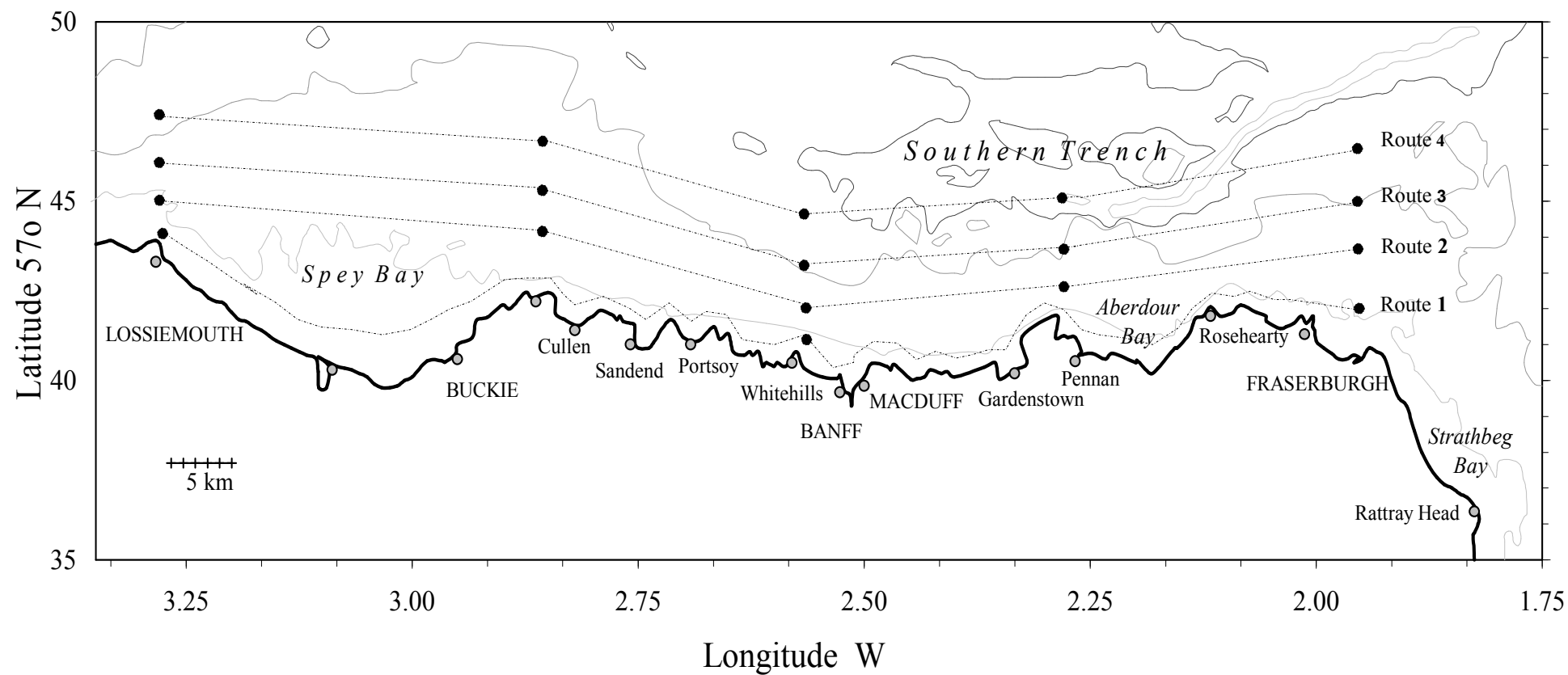


Figure 3.2. A map of the study area and survey routes used during systematic boat surveys. There are 3 outer transect (routes 2 to 4), separated by 1.5km, plus an inner coastal transect (route 1) (From Robinson *et al.*, 2007).

3.2. Geographical Information Systems (GIS)

The respective position of each sighting was plotted using a Geographical Information System (ArcGIS version 10). The data frame was set up using a projected coordinate system (British National Grid) which was adapted to centre on the study area. All layers subsequently added were projected using the same coordinate system

Depth data of the study area was obtained in an 'ASC-II file' from GEBCO (General Bathymetry Chart of the Oceans) and projected into raw depth points in ArcMap 10. These points were then interpolated into a raster surface made of (0.5km by 0.5km) 0.25km² blocks, using the IDW function. The depth raster was then converted to points and joined using the spatial join function with the sightings data to give each sighting an independent depth value.

A slope raster was projected, from the change in depth over known distances, from the depth raster using a slope function available in ArcMap 10. The slope raster was interpolated into 0.25km² blocks, using the IDW function. The slope raster was then converted to points and joined using the spatial join function with the latest sightings data so that each sighting now contained a depth and slope value.

Sediment types for the study area were obtained from the British Geological Survey 'Sea bed sediment (SBS) folk' database, under academic license. Sediment categories were presented in shape files for use in ArcMap 10. The sightings were joined to the closest shape file using the spatial join function to give each sighting a sediment type in addition to depth and slope already assigned. The sediments were ordered by grain size using the following classification (see Fig. 3.3).

A shape file of the UK coastline was downloaded from Edina Digimap. The 'Near' function was used to find the distance (in metres) from each sighting to the coastline shape file.

1. M = Mud
2. sM= Sandy Mud
3. (g)M= Slightly Gravelly Mud
4. (g)sM= Slightly Gravelly Sandy Mud
5. gM= Gravelly Mud
6. S= Sand
7. mS= Muddy Sand
8. (g)S= Slightly Gravelly Sand
9. (g)mS= Slightly Gravelly Muddy Sand
10. gmS= Gravelly Muddy Sand
11. gS= Gravelly Sand
12. G= Gravel
13. mG= Muddy Gravel
14. msG= Muddy Sandy Gravel
15. sG= Sandy Gravel
16. Rock

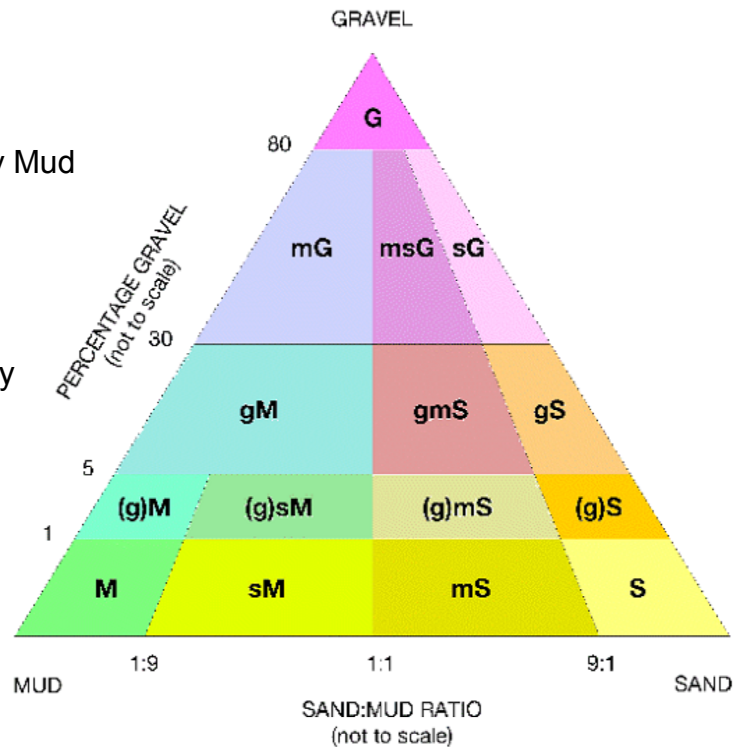


Figure 3.3. The sediment grain size order classification (SBS Folk from British Geological Survey)

3.3. Statistical analysis

Water depth intervals were divided by 10 metre intervals from 0 to 160 metres followed by one interval for depths over 160 metres. Seabed slope intervals were every 0.5 degree from 0 to 5 degrees. Sediments were classes into 16 types comprising of a mixture of mud, sandy, gravel. Distance to nearest shore was split into 500 metre intervals from 0 to 10,000 metres and one interval of over 10,000 metres.

The mean results are given as the mean $\pm$ the standard deviation. Chi-square tests were used to test significant difference between each interspecific distribution of encounters of each environmental variable; spatially (whole data set) and temporally (data of months June to September).

4.0. Results

4.0. Results

The three study species were encountered throughout the study months, May to October, and evidently overlap in their spatial ranges across the study area at this time. The distribution of sightings of bottlenose dolphins, harbour porpoises and minke whales within the study area are displayed using ArcMap 10 (Fig. 4.1). Between 2001 and 2008, harbour porpoises were most commonly encountered, 729 times, followed by minke whale encounters on 361 occasions, and finally bottlenose dolphins, 168 times. For a full list of the data used in this study see Appendix 9.1. Bottlenose dolphins showed a more consistent inshore distribution to the coastline than both minke whales and harbour porpoises. Minke whale and harbour porpoise encounters tend to be clustered in two key inshore areas in the east and centre of the study area (see Appendix 9.3) with particular inshore absence in the west of the study area.

4.1. Spatial habitat preferences

Fixed physical attributes of the study area at encounters were grouped by interval or class and subsequently investigated and compared between species. The environmental variables investigated included water depth, seabed slope, seabed sediment and distance to nearest shore.

Bottlenose dolphins showed preference for much shallower water depths of 11 ± 6 metres, never ranging past 32 metre water depths, than harbour porpoises (mean depth 31 ± 21 metres) and minke whales (mean depth 33 ± 24 metres) (see Appendix 9.4) which highly overlap in water depth preference over a similar range (Fig 4.2).

The three study species had a highly overlapping range by seabed slope (see Appendix 9.9). However, bottlenose dolphins showed a more balanced preference to a range of seabed slopes than minke whales and bottlenose dolphins which were both encountered much more frequently over flatter seabed (Fig. 4.3). Evidently, the mean seabed slopes of bottlenose dolphin encounters (1.37 ± 0.83 degrees) was higher than both harbour porpoises (0.80 ± 0.62 degrees) and minke whales ($0.85 \pm$

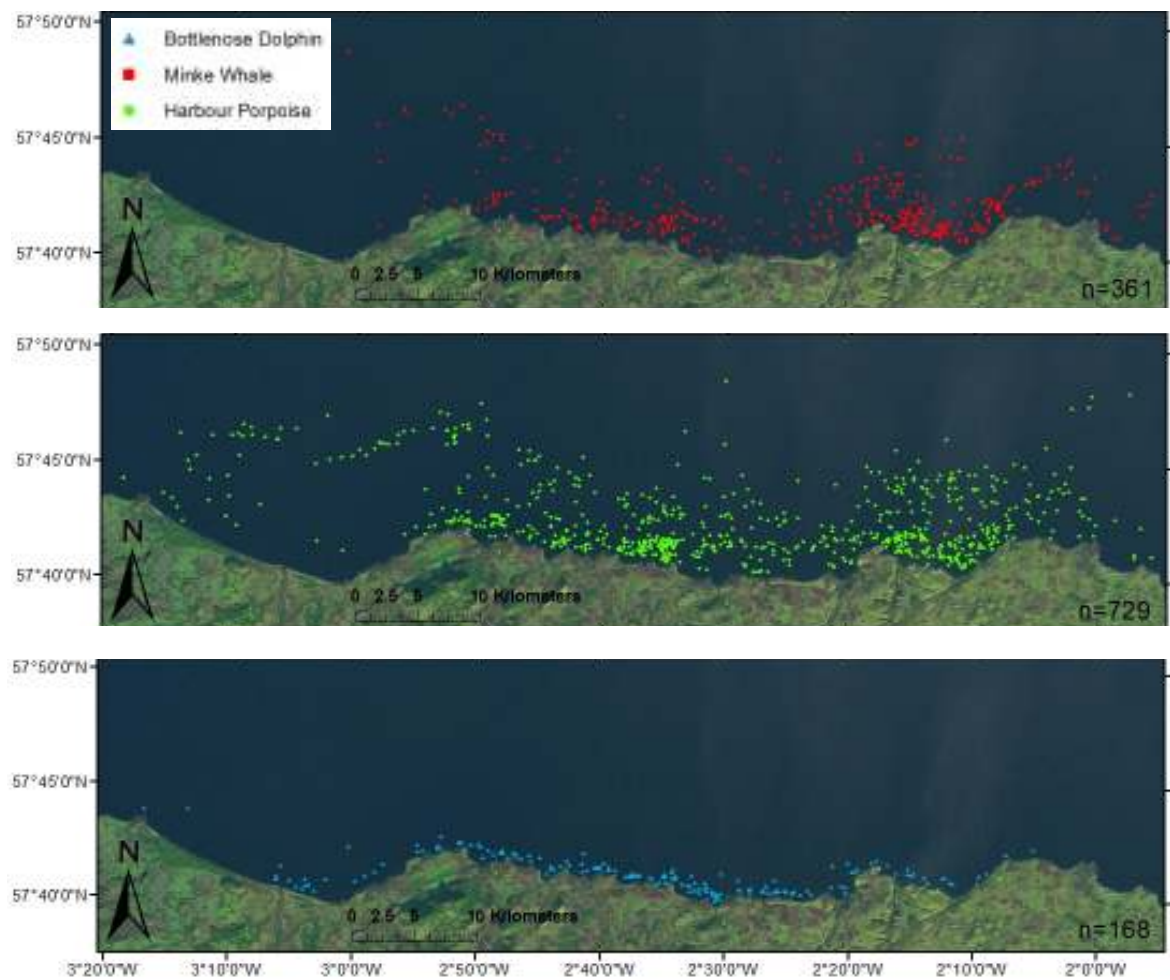


Figure 4.1. GIS map showing the distribution of minke whales (top), harbour porpoises (middle) and bottlenose dolphin (bottom) along the outer southern Moray Firth coastline as recorded by the CRRU research team between May and October 2001 to 2008 inclusive.

0.63 degrees) (see Appendix 9.5) which tend to have the highest overlap in distribution by seabed slope.

Sandy gravel was the most frequent seabed sediment in relation to the distribution of all three study species. However, sandy gravel is highly dominating in the study area (Fig 4.4). Bottlenose dolphins were sighted across five seabed sediment types, while harbour porpoise and minke whales were sighted across nine seabed sediment types, sharing eight of them. The seabed sediments where no sightings were made are not widespread throughout the study area. In cases where sightings were over 'rock', this is assumed to be associated with rocky shorelines, possibly accessible at high tides.

Bottlenose dolphins showed a clear preference to inshore areas of mean distances to nearest shore of 590 ± 448 metres, with a range between <1 metre and 3.5 kilometres (see Appendix 9.6). Meanwhile minke whales were found at mean distances to nearest shore of 2283 ± 1941 metres over a range between 101 metres and 14.2 kilometres. Harbour porpoises were found further from shore, at means of 2818 ± 2481 metres, over a similar range to minke whales between 82 metres and 15.2 kilometres. Minke whales and harbour porpoises appear to be frequent at further distances to nearest shore than bottlenose dolphins (Fig 4.5).

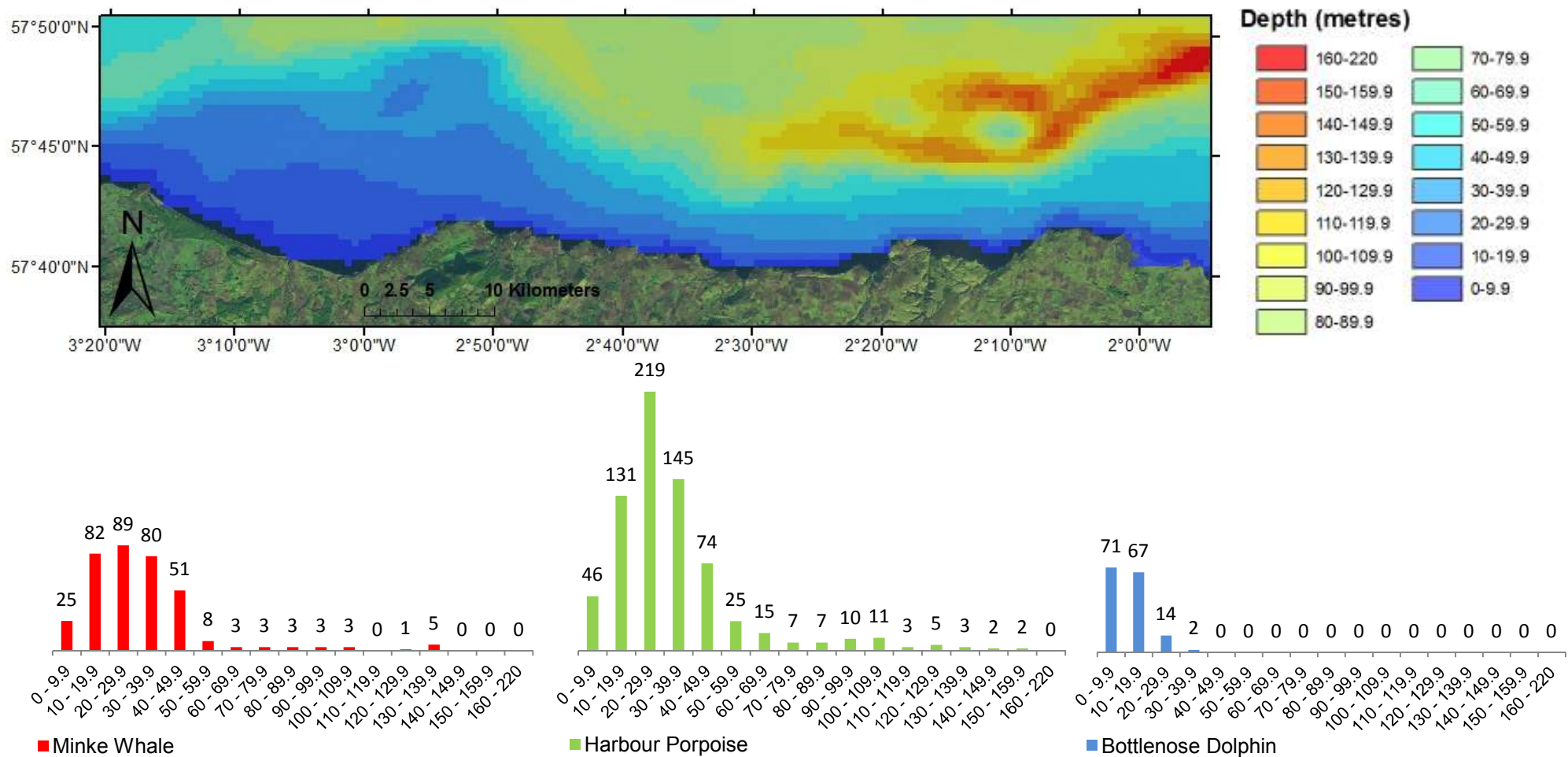


Figure 4.2. GIS map of the outer southern Moray Firth region showing water depth within the study area. Each study species' encounter frequencies are shown for each depth interval in the histogram plots below.

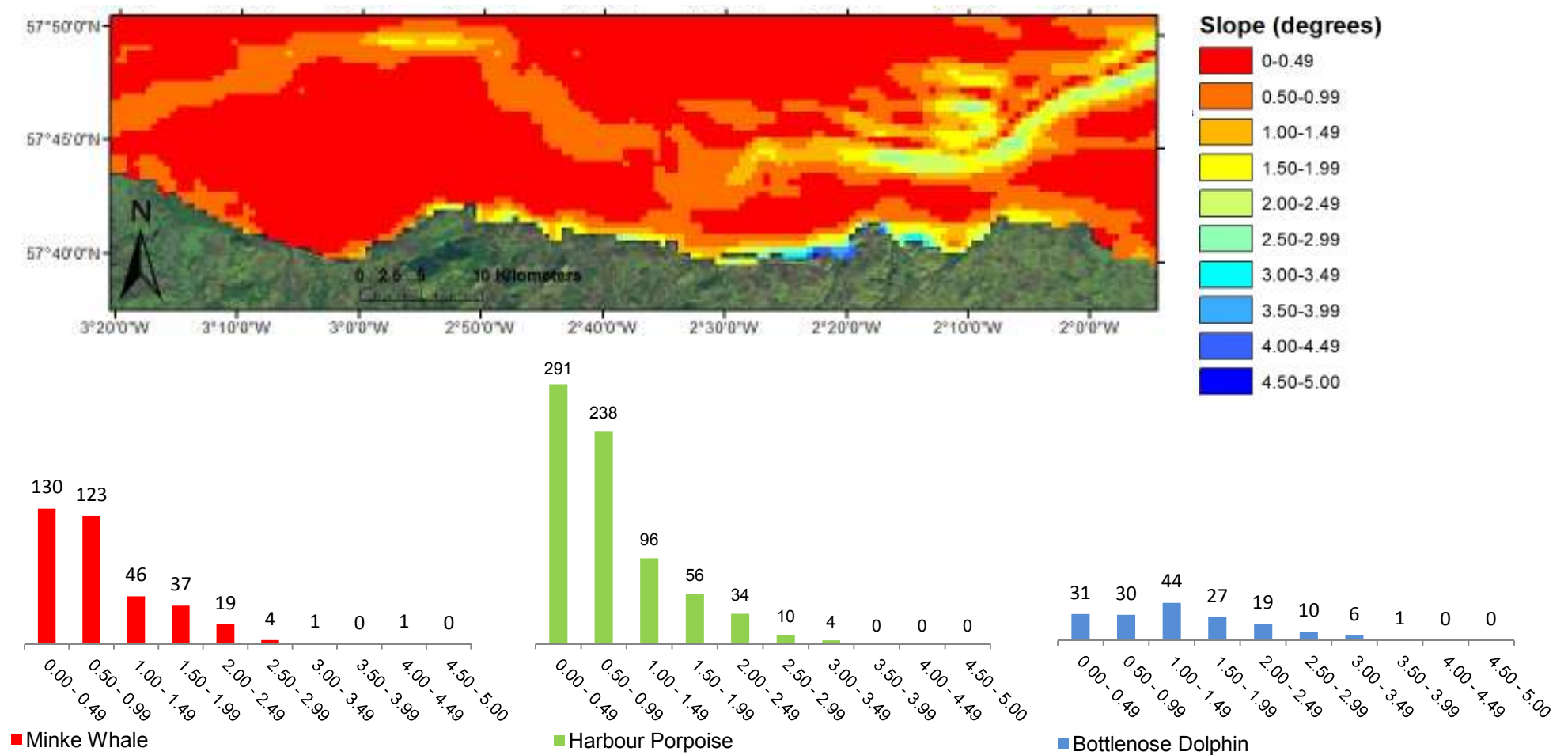


Figure 4.3. GIS map of the outer southern Moray Firth region showing seabed slope within the study area. Each study species' encounter frequencies are shown for each seabed slope interval in the histogram plots below.

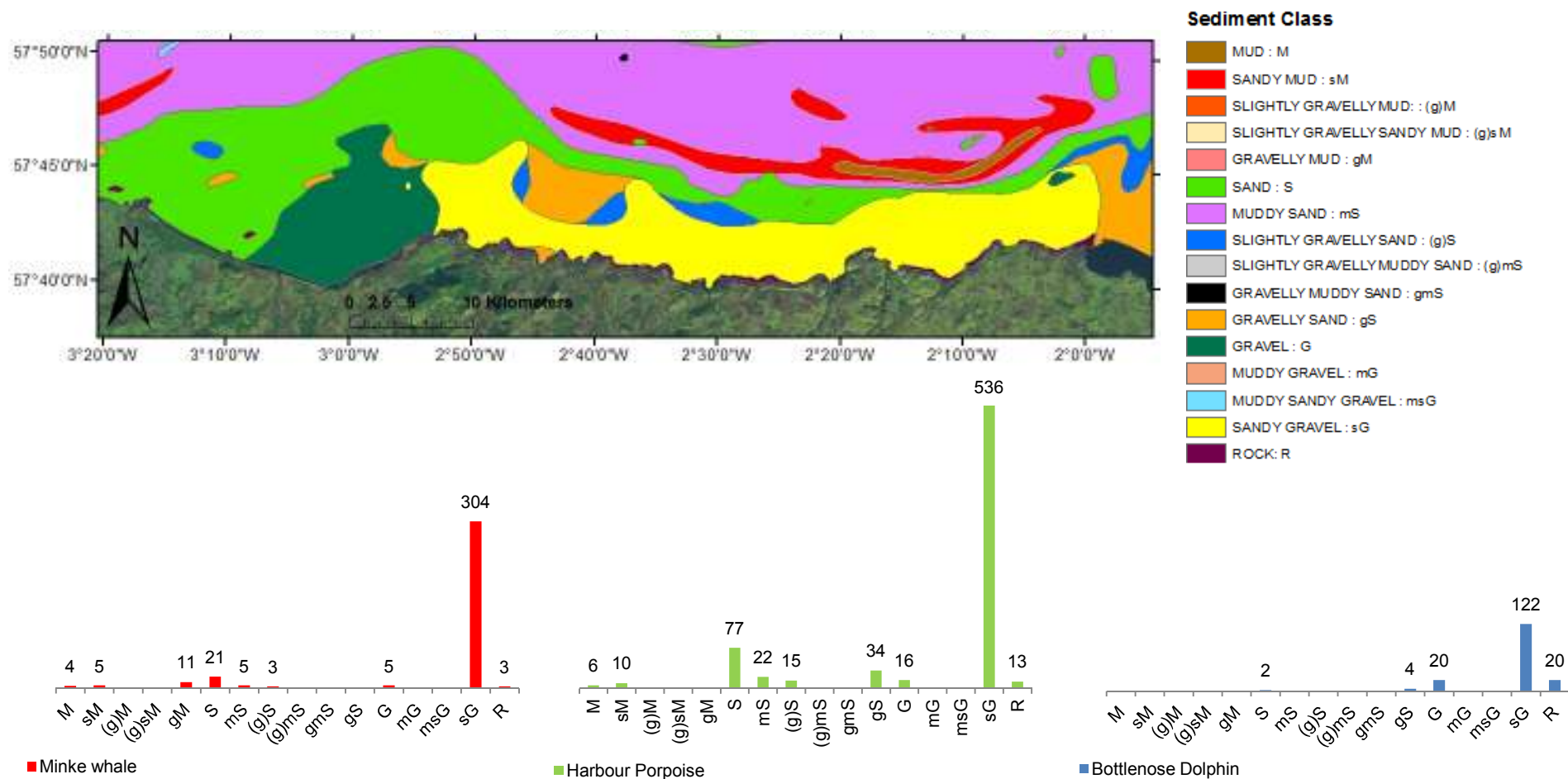


Figure 4.4. GIS map of the outer southern Moray Firth region showing seabed sediments within the study area. Each study species' encounter frequencies are shown for each seabed sediment class in the histogram plots below.

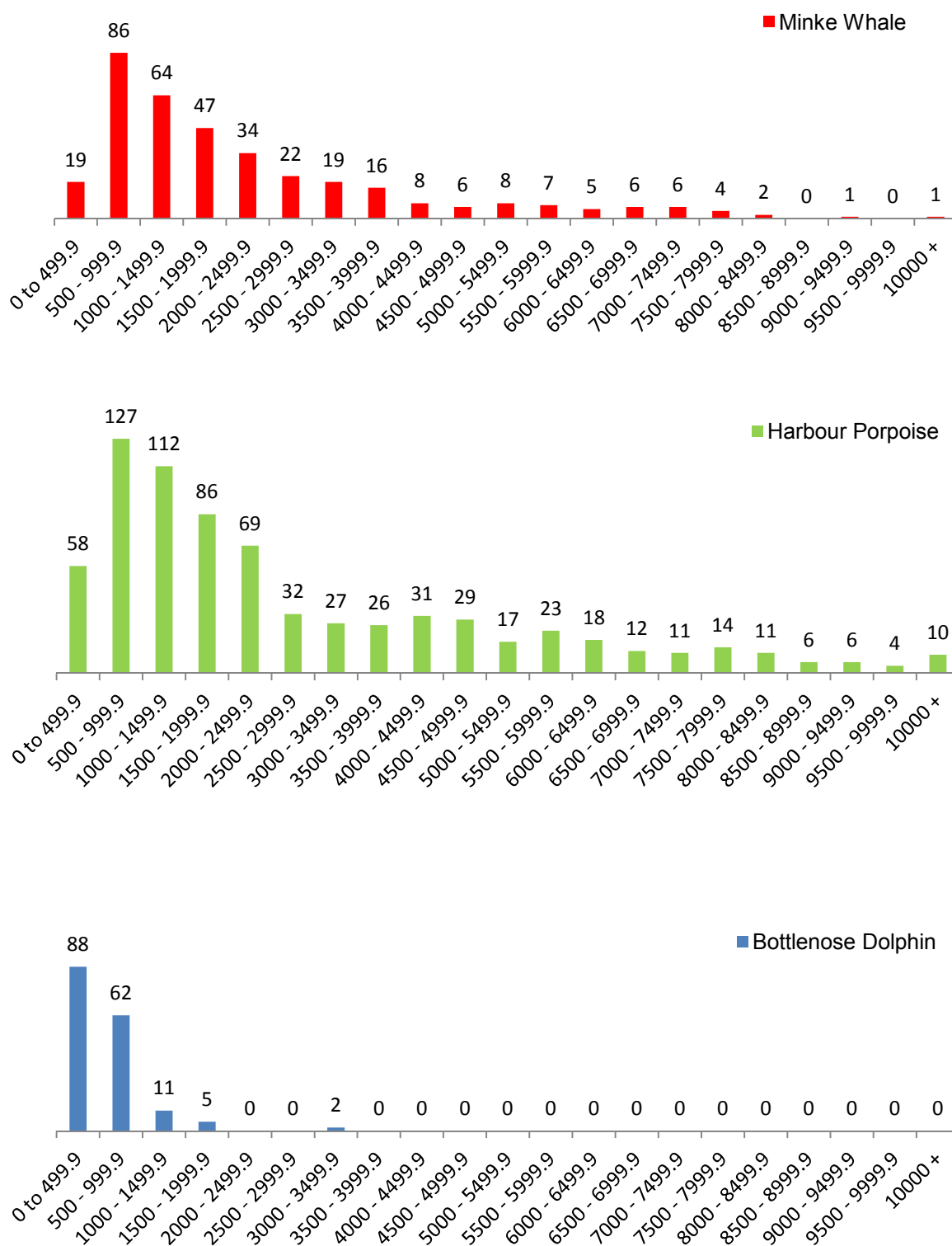


Figure 4.5. Graphs to show the frequency of sightings in each distance to nearest shore interval per species.

4.2. Evidence of spatial partitioning

Statistical analysis investigated the presence or absence of sympatric habitat partitioning between each inter-specific relationship.

Bottlenose dolphins and harbour porpoise were first to be statistically analysed for differences in habitat preferences. Evidently, partitioning occurs over all the spatial scales analysed. However, spatial partitioning was most significant by distance to nearest shore ($P = 1.1\text{e-}48$) (Fig 4.6) and water depth ($P = 2.7\text{e-}44$) (Table 4.2) between these species. Since increasing distances to nearest shore is expected to be linked to increasing water depth, it seems spatial partitioning between these species does occur, with bottlenose dolphins dominating shallow inshore areas and harbour porpoises in deeper, offshore areas. This inshore preference appears to result in association with steep rocky and gravelly shorelines.

Similar trends for differences in bottlenose dolphin and minke whale spatial distribution were found, but less significantly than between bottlenose and harbour porpoises. Distance to nearest shore ($P = 1.7\text{e-}37$) (Table 4.1) and water depth ($P = 2.4\text{e-}36$) (Fig 4.7) were most influential, with seabed slope (see Appendix 9.8) and seabed sediment less so. This suggests, since bottlenose dolphins remain inshore with the same environmental characteristics, that minke whales move further inshore than harbour porpoises.

Minke whales and harbour porpoise only spatially partition the habitat significantly by seabed sediment ($P = 7.9\text{e-}09$) (see Appendix 9.7) and distance to nearest shore ($P = 0.03$). As already discussed, minke whales appear to move further inshore than harbour porpoises during the study months. Accordingly, these two species occur in similar water depths with predominantly flat seabed slopes, but over more varied seabed sediment types. Minke whales would appear to have higher association with sandy gravel than harbour porpoises.

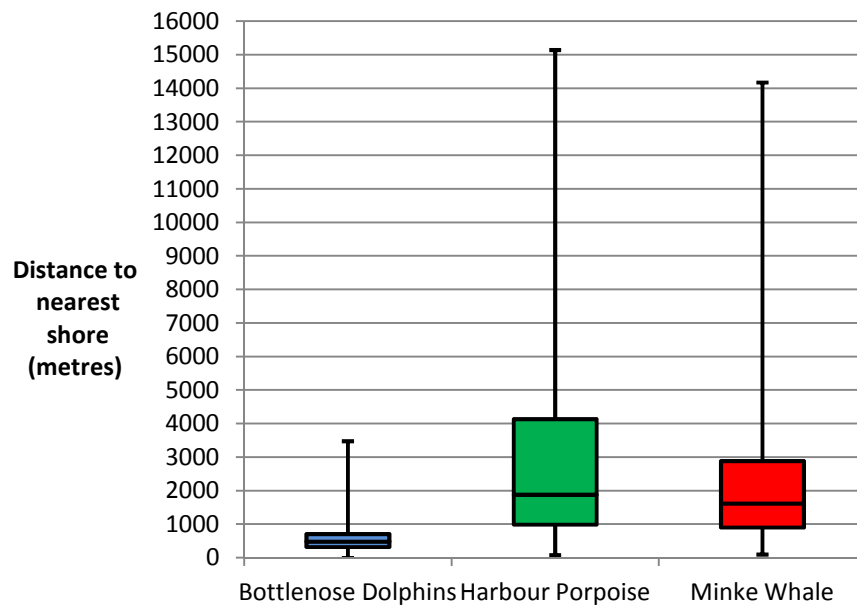


Figure 4.6. Box plot to indicate the most preferred distances to nearest shore of each species and the range used throughout the summer months May to October.

Table 4.1. Results of chi-square tests (P values) used to determine significant difference between study species and different distance to nearest shore intervals.

Difference by distance to nearest shore	Bottlenose Dolphin	Harbour Porpoise
Minke Whale	1.7e-37**	0.03*
Bottlenose Dolphin	#N/A	1.1e-48**

* indicates a significant difference ($P = <0.05$)

** indicates a very significant difference ($P = <0.01$)

Table 4.2. Results of chi-square tests (P values) used to determine significant difference between study species and different depth intervals.

Difference by depth	Bottlenose Dolphin	Harbour Porpoise
Minke Whale	2.4e-36**	0.09
Bottlenose Dolphin	#N/A	2.7e-44**

* indicates a significant difference ($P = <0.05$)

** indicates a very significant difference ($P = <0.01$)

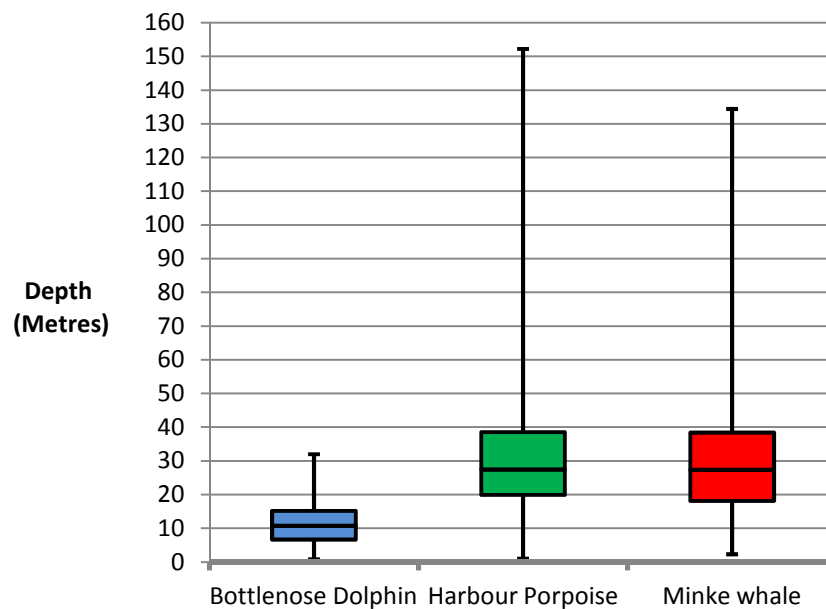


Figure 4.7. Box plot to indicate the preferred depths of each species and the range used throughout the summer months May to October.

4.3. Spatio-temporal habitat preferences

Monthly changes in habitat preference were analysed for significant difference between species in relation to the variables; water depth, seabed slope, seabed sediment and distance to nearest shore, to determine occurrence of temporal sympatric habitat partitioning. For distribution maps of each species by month see Appendix 9.2.

The number of encounters of each species per month (between June and September) was divided by monthly survey effort to give each species a number of encounters per kilometre of survey effort by month (see Appendix 9.10). The months of May and October were excluded from this part of the analysis, as there was too little survey effort in these months, resulting in lower encounter rates. Encounter rates were highly variable between months June to September for each environmental variable investigated (Fig. 4.8 to 4.11).

Each variable was investigated to find a mean and standard deviation by month, with the percentage of encounters over sandy gravel also calculated (see Table 4.3). The habitat preferences of bottlenose dolphins month by month for bottlenose dolphins remained fairly constant. However, a slight movement into shallower, more inshore areas with steeper sea beds is seen from July to September. Minke whales on the other hand show robust inshore movements, from 4000 to 2000 metres from shore, into shallower areas of sandy gravel seabed sediments, from June to July respectively, remaining here up to September. Harbour porpoises move inshore to shallower areas more gradually with less association to sandy gravel seabed sediments than minke whales, from June to September.

Table 4.3. Tables to show the mean and standard deviation of environmental variables by month, and encounters over sandy gravel as a percentage for minke whales (top), harbour porpoises (middle) and bottlenose dolphins (bottom).

Minke Whales	Depth (metres)	Slope (degrees)	Distance to nearest shore (metres)	Encounters over Sandy Gravel
June	52.5± 32.0	0.61± 0.52	3966± 2566	51.4%
July	30.9± 15.6	0.82± 0.57	2063± 1466	91.0%
August	24.6± 16.8	1.00± 0.78	2280± 2237	83.0%
September	28.2± 17.5	0.79± 0.56	1940± 1488	96.6%

Harbour Porpoise	Depth (metres)	Slope (degrees)	Distance to nearest shore (metres)	Encounters over Sandy Gravel
June	39.6± 27.6	0.75± 0.61	3638± 2940	58.8%
July	35.3± 23.6	0.83± 0.67	3001± 2559	71.3%
August	33.4± 26.4	0.83± 0.61	2760± 2524	78.6%
September	28.0± 16.0	0.71± 0.54	2410± 1986	80.9%

Bottlenose Dolphins	Depth (metres)	Slope (degrees)	Distance to nearest shore (metres)	Encounters over Sandy Gravel
June	11.6± 7.5	1.25± 0.83	582± 549	64.7%
July	12.4± 6.9	1.29± 0.97	669± 505	68.6%
August	12.1± 6.4	1.44± 0.70	578± 277	88.9%
September	10.6± 6.3	1.66± 0.89	559± 505	90.3%

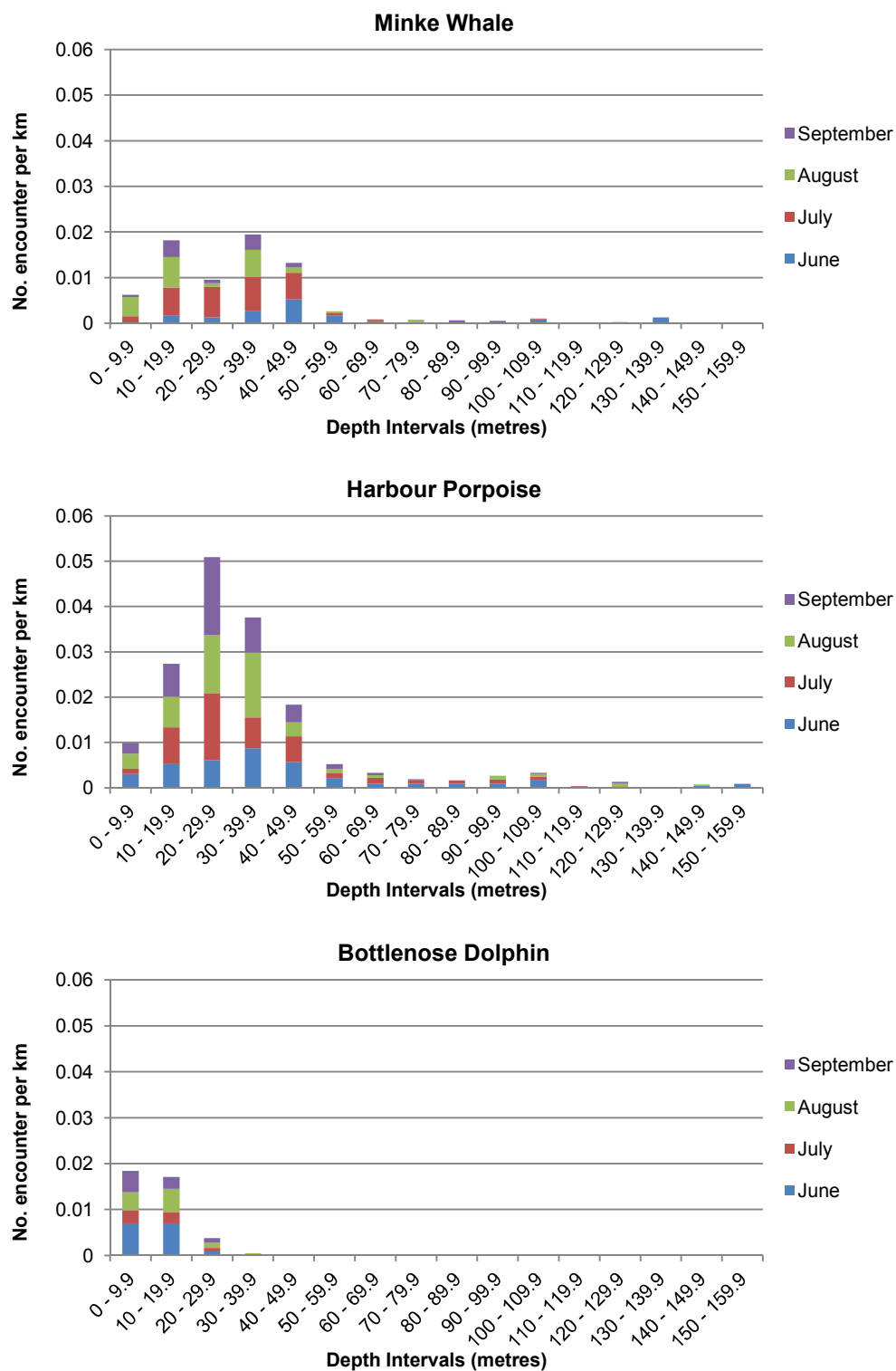


Figure 4.8. Stack histograms showing the number of encounters per kilometre of survey effort in each depth interval by months June to September for minke whales (top), harbour porpoises (middle) and bottlenose dolphins (bottom).

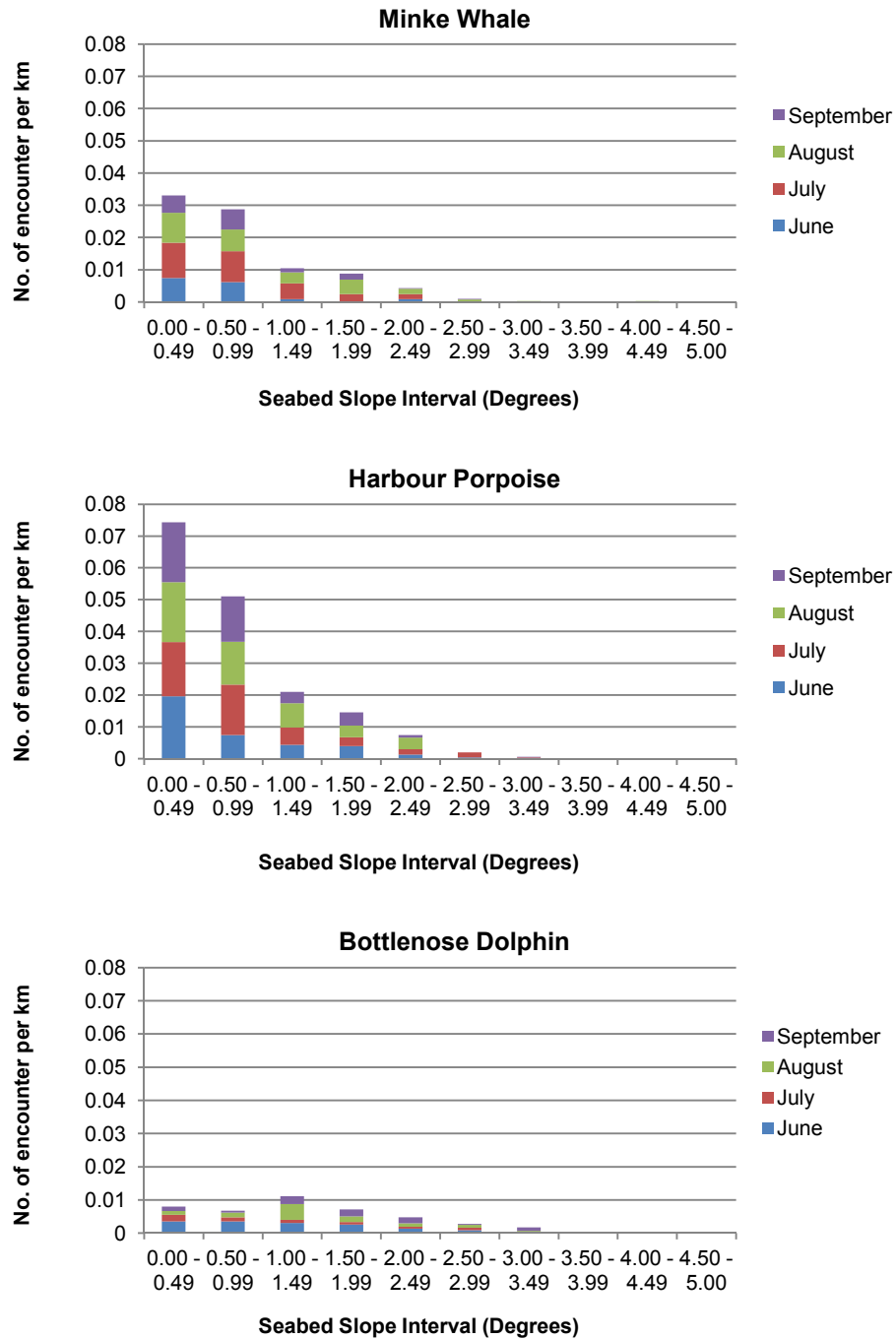


Figure 4.9. Stack histograms showing the number of encounters per kilometre of survey effort in each seabed slope interval by months June to September for minke whales (top), harbour porpoises (middle) and bottlenose dolphins (bottom).

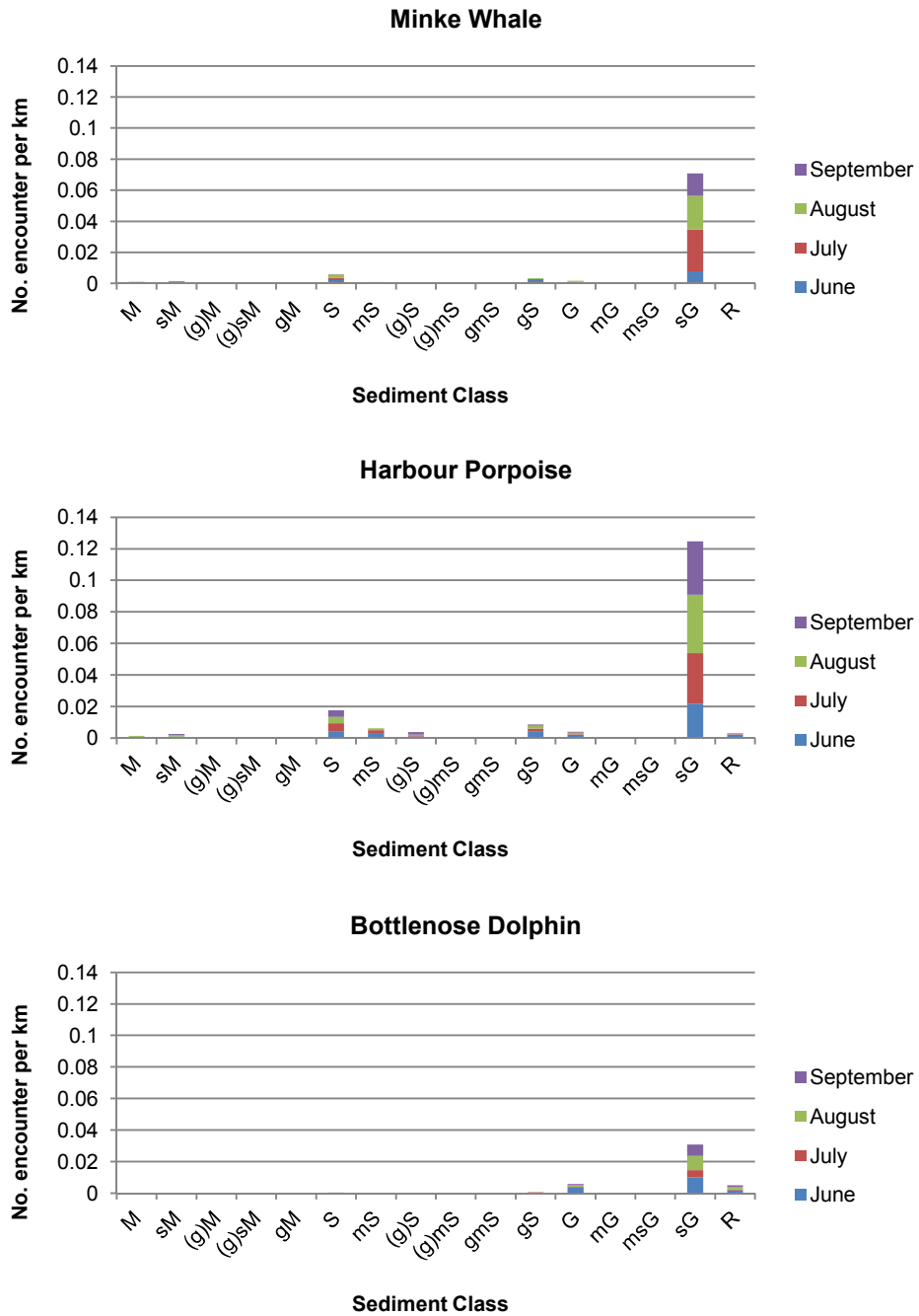


Figure 4.10. Stack histograms showing the number of encounters per kilometre of survey effort in each seabed sediment class by months June to September for minke whales (top), harbour porpoises (middle) and bottlenose dolphins (bottom).

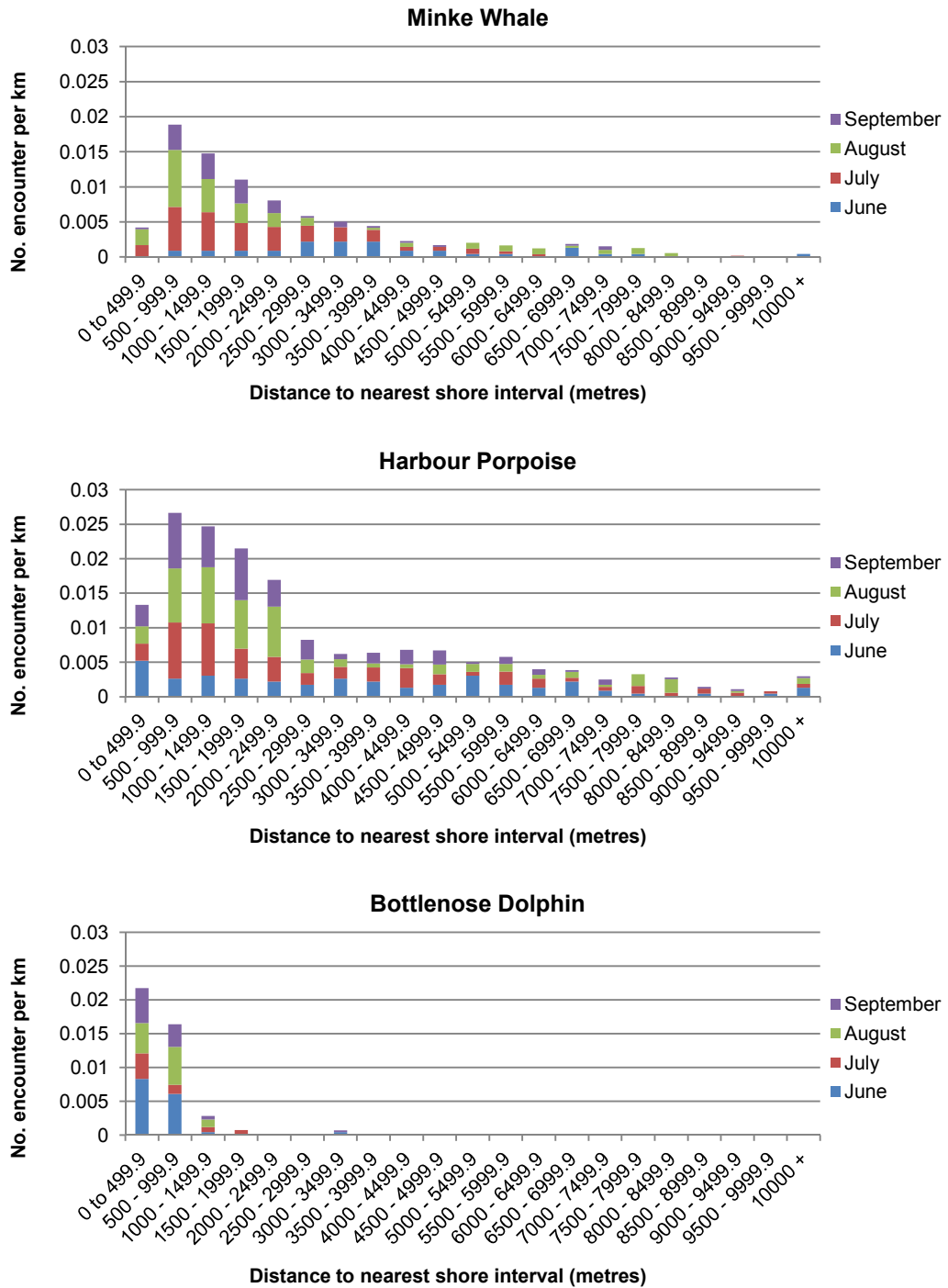


Figure 4.11. Stack histograms showing the number of encounters per kilometre of survey effort in each distance to nearest shore interval by months June to September for minke whales (top), harbour porpoises (middle) and bottlenose dolphins (bottom).

4.4. Evidence of spatio-temporal partitioning

Bottlenose dolphins and harbour porpoises, as well as bottlenose dolphins and minke whales have significant differences by all spatial scales investigated over all months from June to September (Table 4.4). Minke whales and harbour porpoises, temporally partition spatially by depth between July and September, and seabed sediment and seabed slope in July.

The most significant spatio-temporal partitioning between bottlenose dolphins and harbour porpoises was by depth in July ($P = 3.2e-13$), seabed slope in September ($P = 2.3e-11$), seabed sediment in August ($P = 4.6e-04$) and by distance to nearest shore in July ($P = 5.0e-10$). The most significant spatial difference between the two was by depth. This interspecific relationship was the most significantly different compared to the others by water depth, seabed slope and distance to nearest shore. Differences in seabed slope gradually became more significant between these species from June to September.

Bottlenose dolphins and minke whales most significantly partition by depth in July ($P = 6.2e-09$), seabed slope in September ($P = 5.1e-06$), seabed sediment in July ($P = 8.0e-07$) and by distance to nearest shore in July ($P = 5.4e-09$). The most significant spatial differences between these species is by depth and distance to nearest shore. However, it should be noted that the most significant difference in seabed sediment between any two species occurs between bottlenose dolphins and minke whales. Seabed slope preferences become more significantly different from June to September.

Harbour porpoises and minke whales most significantly partition by water depth in August ($P = 6.9e-05$), and only significantly partition by seabed sediment in ($P = 7.3e-03$) and distance to nearest shore ($P = 0.03$) in the month of July. Spatial difference by water depth was most significant between these species. In the remaining months, spatial partitioning does not significantly occur and the distribution of the two species is similar over multiple spatial variables. At other times, partitioning occurs by multiple spatial variables, such as July, including water depth, seabed sediment and distance to nearest shore. It should be noted that these species never have temporal significantly different preferences over seabed slopes.

Table 4.4. Results of chi-square tests (P values) used to determine significant difference between study species and (a) depth (b) seabed slope (c) seabed sediment (d) distance to nearest shore, over months June to September.

a)

Depth association by month between species	June	July	August	September
Bottlenose Dolphin & Harbour Porpoise	3.2e-07**	3.2e-13**	2.3e-08**	5.5e-11**
Minke Whale & Bottlenose Dolphin	2.2e-08**	6.2e-09**	0.01*	9.4e-06**
Minke Whale & Harbour Porpoise	0.07	0.04*	6.9e-05**	6.4e-04**

b)

Seabed slope association by month between species	June	July	August	September
Bottlenose Dolphin & Harbour Porpoise	0.04*	0.02*	2.6e-07**	2.3e-11**
Minke Whale & Bottlenose Dolphin	9.8e-03**	2.7e-03**	1.3e-03**	5.1e-06**
Minke Whale & Harbour Porpoise	0.10	0.34	0.07	0.58

c)

Seabed sediment association by month between species	June	July	August	September
Bottlenose Dolphin & Harbour Porpoise	7.9e-04**	5.1e-04**	4.6e-04**	3.3e-03**
Minke Whale & Bottlenose Dolphin	7.3e-04**	8.0e-07**	2.9e-03**	0.02*
Minke Whale & Harbour Porpoise	0.11	7.3e-03**	0.45	0.09

d)

Distance to nearest shore association by month between species	June	July	August	September
Bottlenose Dolphin & Harbour Porpoise	1.0e-05**	5.0e-10**	1.3e-08**	7.8e-08**
Minke Whale & Bottlenose Dolphin	8.2e-07**	5.4e-09**	7.1e-04**	3.1e-07**
Minke Whale & Harbour Porpoise	0.57	0.03*	0.24	0.47

* indicates a significant difference ($P = <0.05$)

** indicates a very significant difference ($P = <0.01$)

Both harbour porpoises and minke whales were most significantly different from bottlenose dolphins by water depth and distance to nearest shore in the month of July. It should however be noted that the number of minke whales and harbour porpoises, used to calculate significant difference, peaks in July, without amendment for survey effort. Additionally, minke whales and harbour porpoises begin to have significant differences by water depth from July onwards and by distance to nearest shore and seabed sediment in July only. This trend suggests that there is a fine-scale change in habitat preferences in this cetacean community from June to July.

5.0. Discussion

5.0 Discussion

5.1. Interpretation of results

The evidence of spatio-temporal segregation found within this sympatric cetacean community indicates partitioning of the available resources to reduce competition. Since target prey is a driving influence on cetacean distribution, each of the study species is likely to fill a dietary niche, over fine-scale differences in time and habitat preference, as a strategy to co-exist (Bearzi, 2005b).

The summer diet of bottlenose dolphins on the east coast of Scotland includes cod (*Gadus morhua*), saithe (*Pollachius virens*) salmon (*Salmo salar*), haddock (*Melanogrammus aeglefinus*) (Santos *et al.*, 2001) and mackerel (Robinson, personal communication). Bottlenose dolphins are highly adaptable in their diet (Bearzi, 2005b) and may evidently target the most abundant prey species at any time.

In the Moray Firth, the inshore distribution of bottlenose dolphins is thought to be highly influenced by the presence of migratory salmon in river mouths over the summer months (Robinson *et al.*, 2007). The River Spey and Deveron are known to be important spawning sites for Atlantic salmon (*Salmo salar*) in the outer southern Moray Firth (Harding-Hill, 1993) with sightings of bottlenose dolphin showing high site fidelity in these areas over the summer months (Armstrong, 2010) (see Appendix 9.3). Each of these areas is also dominated by seabed sediments of highest encounter rates of bottlenose in the present study. The mouth of the Spey is predominantly gravel, and the Deveron predominantly sandy gravel with the rest of the coastline associated to steep rocky shorelines accessible over high tides. It is these three sediments types which dominate bottlenose dolphin encounters, accounting for partitioning by seabed sediment from bottlenose and other study species, and supporting salmon as an important target prey species.

Despite salmon only accounting for 5.8% of the diet by weight of bottlenose dolphins (Santos *et al.*, 2001), evidence of salmon in stomach samples is difficult to determine as it is digested very quickly by marine mammals, leading to its importance as a prey item being undervalued (Boyle *et al.*, 1990).

In the River Spey, the number of salmon around the river mouth is thought to gradually decrease over the summer months up to September, as the number of fish reported to be caught by fisherman on the river gradually increases as fish move

along it into the spawning grounds in time for autumn (Butler *et al.*, 2006). Since salmon accessibility to bottlenose dolphins gradually decreases over the summer months, it is more likely that bottlenose dolphins may switch to a more abundant prey item later rather than earlier in the season.

Furthermore, cod is known to be an important prey item to bottlenose dolphins, making up 30% by weight (Santos *et al.*, 2001). Cod are a widespread ground fish which are found in both inshore and offshore waters (Gotceitas and Brown, 1992). They are demersal predators of sandeels, so are likely to be abundant in areas of sandeel habitat (Adlerstein and Welleman, 2000). In the summer months, migratory mackerel (*Scombur scombrus*) are additionally known to exploit sandeels (Robinson and Tetley, 2007) with bottlenose dolphins observed to target mackerel at some times (Robinson, personal communication). Additionally saithe (*Pollachius virens*), are fast swimming schooling pelagic predators which exploit similar prey to mackerel (Videler and Hess, 1984) and may also be abundant in the summer months, forming possible target prey items for bottlenose dolphins in the Moray Firth. Stomach samples indicate that saithe makes up 24% by weight of bottlenose diet in Scottish waters (Santos *et al.*, 2001). There is possible energetic advantages of foraging for mid-trophic fish species in shallow water, close to the shore (Bearzi, 2005b), which may add to explain the bottlenose dolphin distribution in this area.

The principal summer prey item for harbour porpoises and minke whales in Scotland is lesser sandeel (*Ammodytes marinus*) (Santos *et al.*, 2004; Pierce *et al.*, 2004).

This inshore movement by minke whales as intensive summer feeding baleen whales is thought to coincide with a peak in biomass of 0-group sandeels over spawning grounds in the Moray Firth during the summer months (Baumgartner, 2008). Furthermore, stomach samples of North Sea minke whales during June and July found that 87% of the diet by weight was made up of 0-group sandeels exclusively (Olsen and Holst, 2001). Sandeel spawning occurs in December and January in preferred settlement habitats of coarse sand and fine gravel sediments, for burrowing away from predators (Reay, 1970; Wright and Begg, 1997), and at depths of 20 to 70 metres (Wright *et al.*, 2000). Larvae hatch from February to May and after 1 to 3 months from hatching (May to August) (Wright and Bailey, 1996) larvae are fully developed and are up to 6cm in length classing them as 0-group

juveniles. Now with full fin development, juvenile sandeels are at their most mobile in the water column, concentrating at the surface during the day and moving to the seabed for settlement in sediments at night and protection from predators (Wright and Bailey, 1996; Jensen *et al.*, 2003). It is this concentration of juvenile sandeels at the surface during the summer months that attracts seabirds, predatory fish and marine mammals alike. With the outer southern Moray Firth coastline dominated by ideal spawning habitat for sandeels, there is a high recruitment of juvenile fishes supporting an extensively rich and bio-diverse ecosystem. Minke whales are consequently associated with sandy gravel seabed sediments in shallow depths e.g. preferred sandeel habitat.

On the west coast of Scotland, minke whales have been associated with sandeel habitat during the spring (Macleod *et al.*, 2004; Anderwald, 2012). At this time, adult sandeels are abundant in the water column during the day (Macleod *et al.*, 2004). As summer begins, adult sandeel abundance in the water column steeply declines during July and August (Pedersen *et al.*, 1999). It is at this time, that juveniles will be most prevalent at the water surface. The apparent shift of targeted prey by minke whales to sprat (*Sprattus sprattus*) (Anderwald, 2012) and herring (*Clupea harengus*) habitat (Macleod *et al.*, 2004) in this area during the summer months would therefore suggest poor sandeel recruitment (Baumgartner, 2008). This could be linked to insufficient spawning sites or overfishing.

Additional and perhaps not targeted prey items of minke whales include migratory mackerel which may be accidentally caught during feeding lunges towards sandeels (Olsen and Holst, 2001; Pierce *et al.*, 2004). This is possible because mackerel (*Scomber scombrus*) as predatory fish are thought to assist minke whales into corralling juvenile sandeels into dense surface bait balls. Subsequently, this would make sandeel prey more accessible to seabirds resulting in bird rafts (Robinson and Tetley, 2007). Additionally, auks are the only seabird which may independently concentrate fish, with minke whales possibly benefitting from association with these birds (Anderwald *et al.*, 2011). Minke whales therefore stand to gain foraging advantage by moving between bird rafts (Robinson and Tetley, 2007; Anderwald *et al.*, 2011).

Harbour porpoises have been observed foraging in the same immediate area as minke whales in the Moray Firth (Robinson, personal communication). Porpoises

may gain foraging advantage by feeding alongside minke whales, as they corral sandeels into dense bait balls and predictably indicate the presence of prey, making them more accessible to solitary individuals. This may occur in similar conditions to striped dolphins gaining foraging advantage from short-beaked common dolphins in the Mediterranean Sea (Frantzis and Herzing, 2002).

Although the high density of surface sandeels is preferred, harbour porpoises have a more adaptable diet to benthic and pelagic fish, including cod, mackerel, saithe, haddock (*Melanogrammus aeglefinus*), pollock (*Pollachius pollachius*) and others (Santos *et al.*, 2004), overlapping in diet with bottlenose dolphins (Santos *et al.*, 2001).

The difference in prey items explains some of the spatio-temporal distribution of the cetaceans found here. Since bottlenose dolphins forage for salmonids, found in river mouths, and benthic fish most efficiently caught in shallow inshore waters, their spatial partitioning from harbour porpoises and minke whales by especially water depth and distance to nearest shore is not surprising.

Minke whales are highly dependent on juvenile sandeel abundance in the water column, over the summer months in this area (Robinson *et al.*, 2009). Sea surface temperature is additionally important to local productivity influencing density of sandeel prey (Tetley *et al.*, 2008). The rapid movement of minke whales into shallow, inshore waters associated with steep sandy gravel seabed in July is thought to be associated to predictable high sandeel prey density from this time onwards.

Harbour porpoises follow minke whales into sandeel habitat to benefit from exploiting common prey in similar spatial areas. However, the same target prey species may be of different sizes and accessed at different times of the day and in different depths of the water column to reduce competition. Slight difference in foraging strategy was recognised to promote niche partitioning in sympatric cetaceans in the eastern tropical Atlantic in waters between Gabon and Angola (Weir *et al.*, in press). This is supported by harbour porpoises having fine-scale spatio-temporal differences in especially, July when inshore movement is more gradual than by minke whales, and by water depth from July to September. Simultaneously, porpoise seem to stay clear of bottlenose dolphins which have a highly overlapping diet in the summer months.

If and when certain prey resources become more limited to cetacean predators, they may adapt to different target species and change spatial distribution, coming into direct competition with other species. Competition may lead to aggression directed interaction from the dominant species (Bearzi, 2005b).

Over evolutionary time, this may have led to tendencies of avoidance behaviour between species. In particular, numerous account of violent interactions of bottlenose dolphins towards harbour porpoises (Ross and Wilson, 1996; Patterson *et al.*, 1998), as a result of dietary competition, may have led to avoidance and spatio-temporal partitioning by porpoises (Thompson *et al.*, 2004; Spitz *et al.*, 2006, Robinson and Macleod, in prep). Furthermore, KPR and colleagues from the CRRU witnessed an aggressive assault on a young adult minke whale by three bottlenose dolphins once in July 2008. The whale was driven out to sea by dolphins over approximately 800 metres by physical attacks on the tail stock of the whale, forcing the animal right out of the water as it attempted to flee (KP Robinson, pers. comm). This evidence enforces competition as a driving ecological process to spatio-temporal partitioning in this cetacean community.

The more frequently observed aggression by bottlenose dolphins towards harbour porpoises than minke whales is expected, because they have a higher overlap in diet of mid-trophic fish species. Evidently, bottlenose dolphins dominate, shallow inshore waters giving a foraging advantage, over harbour porpoises, by the ease of prey entrapment (Reid *et al.*, 2003). Harbour porpoises, using deeper water, further from shore subsequently exploit sandeel prey when available and supplement their diet with mid-trophic fish which are harder to catch at these depths, but may be abundant due to the presence of sandeel as a common prey source. Similar partitioning by water depth and distance to shore was observed between bottlenose dolphins and common dolphins in California (Bearzi, 2003).

Further considerations for the importance of these inshore waters to bottlenose dolphins and harbour porposies as calving, breeding and nursery grounds may support summer distribution (Robinson *et al.*, 2007). Bottlenose encounters included calves 80% of the time (Culloch and Robinson, 2008), while an increase in lactating harbour porpoises with calves to the area may be to support high energy demands (Robinson *et al.*, 2007).

5.2. Limitations

The frequency of encounters of the study species in different intervals of the environmental variables investigated is survey effort related. Encounters of species in areas regularly surveyed would therefore be biased. The statistical analysis compared frequency of each species in each interval or class without being adjusted for survey effort within.

Further limitations existed in the use of GIS in regards to data used to predict water depth and seabed slope. The bathymetry data obtained and used for this study was not suitable for predicting the water depth at encounters which were very close to shore. This is because the depth values do not account for tidal cycle which changes the depths in coastal areas. Furthermore, the resolution of the depth data may not have been fine scale enough to distinguish land from sea at encounters recorded nearest to the shore. Also, the GPS device used in the field may have had interference with steep cliffs during encounters close to the shore causing the exact location to change unpredictably. For any one of these reasons, 43 from 1258 encounters were not included in the depth analysis.

Additionally, seabed slopes for the study area were expected to be higher and more varied than observed. Some of the steeper slopes in the study area may have been too fine- scale for ArcMap 10 to detect with the data obtained. These slopes may have been overlooked for a number of reasons. Firstly, averaging of all the depths found in one 0.25km² block would flatten slopes, making them undetectable. Also, steep slopes may occur over very short distance e.g. less than 500 metre resolution, so were not detectable. Finally the difference in depth between blocks may give a false impression of real topography of the seabed, as interpolation of slopes from water depth data is prediction.

6.0. Conclusion

6.0. Conclusion

This study has shown that the fine-scale spatio-temporal habitat partitioning occurs between sympatric harbour porpoises, minke whales and bottlenose dolphins in the outer southern Moray Firth. These differences in the fixed environmental variables investigated, including water depth, seabed slope, seabed sediment and distance to nearest shore, against species' encounters were detected by the use of GIS.

The significance of partitioning between each species distribution was highly variable, resulting from niche dietary divergence. Bottlenose dolphin distribution differed most significantly from minke whales and harbour porpoises by water depth and distance to nearest shore. Bottlenose dolphins inhabit shallow coastal waters, less than 1 kilometre from shore, in the search for salmon and benthic fish prey. Bottlenose dolphins are the dominant competitor in the area, showing aggression to both harbour porpoise and minke whales when there is competition for food. Minke whales move inshore rapidly in the month of July for summer feeding on their principal prey of sandeel. Harbour porpoises are highly overlapping in the spatial distribution to minke whales, but have the highest overlap in diet with bottlenose dolphins. Porpoise move inshore during the summer months more gradually preferring a wider range of depths, further from the shore than minke whales in order to target sandeels and a range of mid-trophic fish species, while avoiding aggressive bottlenose dolphins.

Understanding the interactions between these cetacean species, and the wider environment and ecosystem, is important for conservation and management efforts to ultimately protect them. This study presents a baseline to inform the formation of a marine protected area, sustainable fishery activities, and future investigations by the CRRU into the spatio-temporal distribution of these sympatric cetacean species.

7.0. Future Work

7.0. Future Work

Areas for future work could include comparing spatio-temporal distribution between each study year or by the time of day of encounters. The study period could be updated to account for encounters between the years of 2001 and 2011. Other species recorded in the survey, such as short-beaked common dolphins, could be included in analysis.

To ensure water depths are accurate, the manual depths recorded at each sighting should be used. Finer-scale resolution depth data should try to be obtained for creating GIS rasters. The survey effort should also be balanced across the survey area and when comparing distribution for statistical analysis, encounter rate for each interval should be adjusted for survey effort. Correlation should also be tested between environmental variables for each species distribution.

Samples of prey species and sizes targeted at different times of the year could be investigated with spatio-temporal distribution of the study species. Furthermore, information on historic and current fisheries in the area should be obtained to determine densities of other key prey items which make up the diet of bottlenose dolphins and harbour porpoises in the area. Collaboration between organisations should seek to investigate similarities and differences of spatio-temporal preferences of the same species in different areas of the UK and further afield to increase knowledge and understanding of the ecology of sympatric cetacean communities.

8.0. Referencing

8.0. References

- Adlerstein, S. A., & Welleman, H. C., 2000. Diel variation of stomach contents of North Sea cod (*Gadus morhua*) during a 24-h fishing survey: an analysis using generalized additive models. *Canadian Journal of Fisheries and Aquatic Sciences*, 52(12), pp2363-2367.
- Anderwald, P., Evans, P. G., Dyer, R., Dale, A., Wright, P. J., & Hoelzel, A. R., 2012. Spatial scale and environmental determinants in minke whale habitat use and foraging. *Marine Ecology Progress Series*, 450, pp259-274.
- Anderwald, P., Evans, P. G., Gyax, L., & Hoelzel, A. R., 2011. Role of feeding strategies in seabird-minke whale associations. *Marine Ecology Progress Series*, 424, pp219-227.
- Armstrong, J., 2010. The long-term distribution, habitat use and site fidelity of bottlenose dolphins frequenting the outer southern Moray Firth coastline: a spatio-temporal analysis with implications for existing population management. MRes thesis. University of York.
- Atkinson, T., & Gill, A., 1996. *Risso's dolphins (Grampus griseus) in the coastal waters of the Eze peninsula, Isle of Lewis, Scotland*. WDCCS.
- Atkinson, T., Gill, A., & Evans, P. G., 1998. A photo-identification study of Risso's dolphins in the Outer Hebrides, Northwest Scotland. *European Research on Cetaceans*, 12: 102.
- Azzellino, A., Gaspari, S., Airoidi, S., & Nani, B., 2008. Habitat use and preferences of cetaceans along the continental slope and the adjacent pelagic waters in the western Ligurian Sea. *Deep Sea Research*, 55(1), pp296-323.
- Bailey, H., & Thompson, P., 2010. Effect of oceanographic features on fine-scale foraging movement of bottlenose dolphins. *Marine Ecology Progress Series*, 418(1), pp223-233.

- Bannister, J. L., 2001. Baleen Whales. In J. H. Steele, S. A. Thorpe, & K. K. Turekian, *Marine Biology* (pp. 391-402). London: Elsevier.
- Bannister, J. L., 2009. Baleen Whales (Mysticetes). In W. F. Perrin, B. Wursig, & J. G. Thewissen, *Encyclopedia of Marine Mammals, Second Edition* (pp. 80-89). London: Elsevier.
- Baumgartner, N., 2008. Distribution, diving behaviour and identification of the North Atlantic minke whale in northeast Scotland. MPhil thesis. University of Aberdeen.
- Bearzi, G., Politi, E., Agazzio, S., Bruno, S., Costa, M., & Bonizzoni, S., 2005c. Occurrence and present status of coastal dolphins (*Delphinus delphi* and *Tursiops truncatus*) in the eastern Ionian Sea. *Aquatic conservation: Marine and Freshwater Ecosystems*, 15(3), 243-257.
- Bearzi, M., 2003. Behavioural ecology of the marine mammals of Santa Monica Bay, California. PhD dissertation, University of California, Los Angeles.
- Bearzi, M., 2005a. Habitat partitioning by three species of dolphins in the Santa Monica Bay, California. *Southern California Academy of Sciences Bulletin* 1043(3), pp113-124.
- Bearzi, M., 2005b. Dolphin sympatric ecology. *Marine Biology Research*, 1, pp165-175.
- Bejder, L., Samuels, A., Whitehead, H., Gales, N., Mann, J., Conner, R., Heithaus, M., Watson-Capps, J., Flaherty, C., Krutzen, M., 2006. Decline in Relative Abundance of Bottlenose Dolphins Exposed to Long-Term Disturbance. *Conservation Biology*, 20(6), pp1791-1798.
- Bjørge, A., & Tolley, K. A., 2009. Harbour Porpoise, *Phocoena phocoena*. In W. F. Perrin, B. Wursig, & J. G. Thewissen, *Encyclopedia of Marine Mammals, Second Edition* (pp. 530-533). London: Elsevier.

- Bowen, W. D., Read, A. J., & Estes, J. A., 2002. Feeding Ecology. In A. R. Hoelzel, *Marine Mammal Biology* (pp. 217-246). Oxford: Blackwell Publishing.
- Boyle, P. R., Pierce, G. J., & Diack, J. S., 1990. Sources of evidence for salmon in diets of seals. *Fisheries Research*, 10, pp137-150.
- British Geological Survey, 2012. Seabed Sediment Folk data under licence.
- Butler, J. R., Middlemas, S. J., Graham, I. M., Thompson, P. M., & Armstrong, J. D., 2006. Modelling the impacts of removing seal predation from Atlantic salmon, *Salmo salar*, rivers in Scotland: a tool for targeting conflict resolution. *Fisheries Management and Ecology*, 13, pp285-291.
- Butler, J. R., Middlemas, S. J., McKelvey, S. A., McMyn, I., Leyshon, B., Walker, I., Thompson, P. M., Boyd, I. L., Duck, C., Armstrong, J. D., Graham, I. M., Baxter, J.M., 2008. The Moray Firth Seal Management Plan: an adaptive framework for balancing the conservation of seals, salmon, fisheries and wildlife tourism in the UK. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 18(6), pp1025-1038.
- Canadas, A., Sagarminaga, R., & Garcia-Tiscar, S., 2002. Cetacean distribution related with depth and slope in the Mediterranean waters off southern Spain. *Deep-Sea Research*, 49(1), pp2053-2073.
- Canadas, A., Sagarminaga, R., De Stephanis, R., Urquiola, E., & Hammond, P. S., 2005. Habitat preference modelling as a conservation tool: proposals for marine protected areas for cetacean in southern Spanish waters. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 15: pp495-521.
- Carrillo, M., & Ritter, F., 2010. Increasing numbers of ship strikes in the Canary Islands: proposals for immediate action to reduce risk of vessel-whale collisions. *Journal of Cetacean Research and Management*, 11(2), pp131-138.
- Certain, G., Ridoux, V., van Canneyt, O., & Bretagnolle, V., 2008. Delphinid spatial distribution and abundance estimates over the shelf of the Bay of Biscay. *ICES Journal of Marine Science*, 65, pp656-666.

- Cheney, B., Thompson, P. M., Ingram, S., Hammond, P. S., Stevick, P. T., Durban, J. W., Culloch, R. M., Elwen, S. H., Mandleberg, L., Janik, V. M., Quick, N. J., Islas-Villanueva, V., Robinson, K. P., Costa, M., Eisfield, S. M., Walters, A., Phillips, C., Weir, C. R., Evans, P.G., Anderwald, P., Reid, R. J., Reid, J. B., Wilson, B., 2012. Integrating multiple data sources to assess the distribution and abundance of bottlenose dolphins *Tursiops truncatus* in Scottish waters. *Mammal Review*, 42.
- Clapham, P. J., Childerhouse, S., Gales, N. J., Rojas-Braco, L., Tillman, M. F., & Brownell, R. L., 2007. The whaling issue: Conservation, confusion, and casuistry. *Marine Policy*, 31, pp314-319.
- Clark, J., Dolman, S. J., & Hoyt, E., 2010. *Towards Marine Protected Areas for Cetaceans in Scotland, England and Wales: A scientific review identifying critical habitat with key recommendations*. WDCS.
- Clark, N. M., 2005. The spatial and temporal distribution of the harbour porpoise (*Phocoena phocoena* L.) in the southern outer Moray Firth. MSc thesis, University of Wales, Bangor.
- Clark, N., Tetley, M. J., Culloch, R. M., Mitchelson-Jacob, E. G., & Robinson, K. P., 2006. Harbour porpoise (*Phocoena phocoena*) have declined in the southern outer Moray Firth, NE Scotland - a spatial and temporal view. *European Research on Cetaceans*, 20.
- Coscarella, M. A., & Crespo, E. A., 2010. Feeding aggregations and aggressive interaction between bottlenose (*Tursiops truncatus*) and Commerson's dolphins (*Cephalorhynchus commersonii*) in Patagonia, Argentina. *Journal of Ethology*, 28(1), pp183-187.
- Cotter, M. P., Maldini, D., & Jefferson, T. A., 2012. "Porpicide" in California: Killing of harbor porpoises (*Phocoena phocoena*) by coastal bottlenose dolphins (*Tursiops truncatus*). *Marine Mammal Science*, 28(1), pp1-15.

- Culloch, R. M., & Robinson, K. P., 2008. Bottlenose dolphins using coastal regions adjacent to a Special Area of Conservation (SAC) in north-east Scotland. *Journal of the Marine Biological Association of the United Kingdom*, 88(6), pp1237-1243.
- Davies, R. W., Cripps, S. J., Nickson, A., & Porter, G., 2009. Defining and estimating global marine fisheries bycatch. *Marine Policy*, 33(1), pp661-672.
- De Boer, M. N., 2010. Spring distribution and density of minke whale *Balaenoptera acutorostrata* and other marine mammals in the Central North Sea. *Marine Ecology Progress Series*, 408, pp265-274.
- Dolman, S. J., Pinn, E., Reid, R. J., Barley, J. P., Deaville, R., Jepson, P. D., Pinn, E., Stevick, P.T., Calderan, S., Robinson, K.P., Doyle, T.K., Browning, R.L., Simmonds, M.P., 2010. A note on the unprecedented strandings of 56 deep-diving whales along the UK and Irish coast. *Marine Biodiversity Records*, 3(16).
- Dolman, S., Williams-Grey, V., Asmutis-Silvia, R., & Isaac, S., 2006. *Vessel Collisions and Cetaceans: What happens when they don't miss the boat*. WDCS: Available at: <http://www.wdcs.org/submissions_bin/shipstrikes.pdf>.
- Edina Digimap, 2012. UK coastline and OS map downloaded.
- Eisfield, S., Keith, S., Pope, A., Still, D., Dolman, S., & Simmonds, M., 2009. *Outer Moray Firth Cetacean Research 2008*. WDCS.
- Eleftheriou, A., Basford, D., & Moore, D. C., 2004. *Synthesis of information on the benthos of area SEA5*. Report for the Department of Trade and Industry, SEA5: Available at: <http://www.offshore-sea.org.uk/consultations/SEA_5/SEA5_TR_Benthos_Elef.pdf>.
- EULife., 2006. *SCANS-II*, Available at: <<http://biology.st-andrews.ac.uk/scans2/inner-finalReport.html>> [Accessed March 15, 2012]

- Ferretti, S., Bearzi, G., & Politi, E., 1998. Comparing behavior of inshore bottlenose and common dolphins in the eastern Ionian Sea through focal group surfacing pattern analysis. Abstract,. *The World Marine Mammal Science Conference*. Monaco, France.
- Frantzis, A., & Herzing, D. L., 2002. Mixed-species associations of striped dolphins (*Stenella coeruleoalba*), short-beaked common dolphins (*Delphinus delphis*), and Risso's dolphins (*Grampus griseus*) in the Gulf of Corinth (Greece, Mediterranean Sea). *Aquatic Mammals*, 28(2), pp188-197.
- Gales, N. J., Kasuya, T., Clapham, P. J., & Brownell, R. L., 2005. Japan's whaling plan under scrutiny. *Nature*, 435, pp883-884.
- GEBCO, 2012. Bathymetry data downloaded from website.
- Genin, A., 2004. Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. *Journal of Marine Systems*, 50, pp3-20.
- Gotceitas, V., & Brown, J. A., 1993. Substrate selection by juvenile Atlantic cod (*Gadus morhua*): effects of predation risk. *Oecologia*, 93, pp31-37.
- Gowans, S., & Whitehead, H., 1995. Distribution and habitat partitioning by small odontocetes in the Gully, a submarine canyon on the Scotian Shelf. *Canadian Journal of Zoology*, 73(1), 1599-1608.
- Greenstreet, S. P., McMillan, J. A., & Armstrong, E., 1998. Seasonal variations in the importance of pelagic fish in the diet of piscivorous fish in the Moray Firth, NE Scotland: a response to variation in prey abundance? *ICES Journal of Marine Science*, 55, pp121-133.
- Grellier, K., & Wilson, B., 2003. Bottlenose dolphins using the Sound of Barra, Scotland. *Aquatic Mammals*, 29(3), pp378-382.

- Gross, A., Kiszka, J., Van Canneyt, O., Richard, P., & Ridoux, V., 2009. A preliminary study of habitat and resource partitioning among co-occurring tropical dolphins around Mayotte, southwest Indian Ocean. *Estuarine, Coastal and Shelf Science*, 84(1), pp367-374.
- Hairston, N. G., Smith, F. E., & Slobodkin, L. B., 1960. Community structure, population control, and competition. *The American Naturalist*, 94, 421-425.
- Hammond, P. S., Berggren, P., Benke, H., Borchers, D. L., Collet, A., Heide-Jorgensen, M. P., Heimlich, S., Hiby, A. R., Leopold, M. F., Oiens, N., 2002. Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent waters. *Journal of Applied Ecology*, 39, pp361-376.
- Harding-Hill, R., 1993. The Moray Firth Review. Scottish Natural Heritage, Northwest Region, Scotland, UK.
- Hastie, G. D., Swift, R. J., Slesser, G., Thompson, P. M., & Turrell, W. R., 2005. Environmental models for predicting oceanic dolphin habitat in the Northeast Atlantic. *ICES Journal of Marine Science*, 62, pp760-770.
- Holmes, R., Bulat, J., Henni, P., Holt, J., James, C., Kenyon, N., Leslie, A., Long, D., Musson, R., Pearson, S., Stewart, H., 2004. DTI Statagic Environmental Assessment Areas 5 (SEA5): Seabed and superficial geology and processes. British Geological Survey Report CR/04/064N. National Environment Research Council. Nottingham, UK.
- Hooker, S. K., 2009. Sperm Whales and Beaked Whales. In J. H. Steele, S. A. Thorpe, & K. K. Turekian, *Marine Biology* (pp. 403-410). London: Elsevier.
- Hooker, S. K., Whitehead, H., & Gowans, S., 1998. Marine protected area design and the spatial and temporal distribution of cetaceans in a submarine canyon. *Conservation Biology*, 13(3), pp592-602.
- Ingram, S. N., & Rogan, E., 2002. Identifying critical areas and habitat preferences of bottlenose dolphins *Tursiops truncatus*. *Marine Ecology Progress Series*, 244, pp247-255.

- Ingram, S. N., Walshe, L., Johnston, D., & Rogen, E., 2007. Habitat partitioning and the influence of benthic topography and oceanography on the distribution of fin and minke whales in the Bay of Fundy, Canada. *Journal of the Marine Biological Association of the United Kingdom*, 87, pp149-156.
- IUCN Red List., 2008. *Phocoena phocoena*. Available at:
<<http://www.iucnredlist.org/apps/redlist/details/17027/0>> [Accessed 20 April 2012]
- IUCN Red List., 2011. *Species Range*. Available at:
<<http://maps.iucnredlist.org/map.html?id=17027>> [Accessed 20 April 2012]
- IWC., 2009. *Classification of the order of Cetacea*. Available at:
<<http://www.iwcoffice.org/conservation/cetacea.htm>> [Accessed 19 April 2012]
- Jensen, H., Wright, P. J., & Munk, P., 2003. Vertical distribution of pre-settled sandeel (*Ammodytes marinus*) in the North Sea in relation to size and environmental variables. *ICES Journal of Marine Science*, 60, pp1342-1351.
- Jepson, P. D., Arbelo, M., Deaville, R., Patterson, I. A., Castro, P., Baker, J. R., Degollada, E., Ross, H. M., Harraez, P., Pocknell, A. M., Rodriguez, F., Howie, F. E., Espinosa, A., Reid, R. J., Jaber, J. R., Martin, V., Cunningham, A. A., Fernandez, A., 2003. Gas-bubble lesions in stranded cetaceans. *Nature*, 425, pp575-576.
- Jepson, P. D., Bennett, P. M., Deaville, R., Allchin, C. R., Baker, J. R., & Law, R. J., 2005. Relationships between polychlorinated biphenyls and health status in harbor porpoises (*Phocoena phocoena*) stranded in the United Kingdom. *Environmental Toxicology and Chemistry*, 24(1), pp238-248.
- Kaschner, K., Watson, R., Trites, A. W., & Pauly, D., 2006. Mapping worldwide distributions of marine mammal species using a relative environmental suitability (RES) model. *Marine Ecology Progress Series*, 316: pp285-310.

- Kiszka, J., Macleod, K., Van Canneyt, O., Walker, D., & Ridoux, V., 2007. Distribution, encounter rates, and habitat characteristics of toothed cetaceans in the Bay of Biscay and adjacent waters from platform-of-opportunity data. *ICES Journal of Marine Sciences*, 64(1), pp1033-1043.
- Kiszka, J., Perrin, W. F., Pusineri, C., & Ridoux, V., 2011a. What drives island-associated tropical dolphin to form mixed-species associations in the southwest Indian Ocean? *Journal of Mammalogy*, 92(5), pp1105-1111.
- Kiszka, J., Simon-Bouhet, B., Martinez, L., Pusineri, C., Richard, P., & Ridoux, V., 2011b. Ecological niche segregation within a community of sympatric dolphins around a tropical island. *Marine Ecology Progress Series*, 433(1), pp273-288.
- Laist, D. W., Knowlton, A. R., Mead, J. G., Collet, A. S., & Podesta, M., 2001. Collisions between ships and whales. *Marine Mammal Science*, 17(1), pp35-75.
- Learmonth, J. A., Macleod, C. D., Santos, M. B., Pierce, G. J., Crick, H. Q., & Robinson, R. A., 2006. Potential effects of climate change on marine mammals. *Oceanography and Marine Biology*, 44, pp431-464.
- Liret, C., Allali, P., Creton, P., Guinet, C., & Ridoux, V., 1994. Foraging activity pattern of bottlenose dolphins around Ile de Sein, France and its relationship with environmental parameters. *European Research on Cetaceans*, 8, pp. 188-191.
- Lusseau, D., Wilson, B., Hammond, P. S., Grellier, K., Durban, J. W., Parsons, K. M., Barton, T. R., Thompson, P.M., 2006. Quantifying the influence of sociality on population structure in bottlenose dolphins. *Journal of Animal Ecology*, 75, pp14-24.
- Macleod, C. D., 2009. Global climate change, range changes and potential implications for the conservation of marine cetaceans: a review and synthesis. *Endangered Species Research*, 7, pp125-136.

- Macleod, C. D., Bannon, S. M., Pierce, G. J., Schweder, C., Learmonth, J. A., Herman, J. S., Reid, R. J., 2005. Climate change and the cetacean community of north-west Scotland. *Biological Conservation*, 124(1), pp477-483.
- Macleod, C. D., Weir, C. R., Santos, M. B., & Dunn, T. E., 2008. Temperature-based summer habitat partitioning between white-beaked and common dolphins around the United Kingdom and Republic of Ireland. *Journal of the Marine Biological Association of the United Kingdom*, 88(6), pp1193-1198.
- Macleod, K., Fairbairns, R., Gill, A., Fairbairns, B., Gordon, J., Blair-Myers, C., Parson, E.C., 2004. Seasonal distribution of minke whales *Balaenoptera acutorostrata* in relation to physiography and prey off the Isle of Mull, Scotland. *Marine Ecology Progress Series*, 277(1), pp263-274.
- Marubini, F., Gimona, A., Evans, P. G., Wright, P. J., & Pierce, G. J., 2009. Habitat preferences and interannual variability in occurrence of the harbour porpoise *Phocoena phocoena* off northwest Scotland. *Marine Ecology Progress Series*, 381(1), pp297-310.
- Minh, T. B., Nakata, H., Watanabe, M., Tanabe, S., Miyazaki, N., Jefferson, T. A., Prudente, M., Subramanian, A., 2000. Isomer-specific accumulation and toxic assessment of polychlorinated biphenyls, including coplanar congeners, in cetaceans from the North Pacific and Asian coastal waters. *Archives of environmental contamination and toxicology*, 39(3), pp398-410.
- Moscrop, A., 1993. An assessment of threats to marine cetaceans resulting from the degradation of their habitats. MSc thesis, University of Greenwich.
- Northridge, S. P., Tasker, M. L., Webb, A., & Williams, J. M., 1995. Distribution and relative abundance of harbour porpoises (*Phocoena phocoena* L.), white-beaked dolphins (*Lagenorhynchus albirostris* Gray), and minke whales (*Balaenoptera acutorostrata* L.) around the British Isles. *ICES Journal of Marine Science*, 52(1), pp55-66.
- Nowacek, D. P., Thorne, L. H., Johnston, D. W., & Tyack, P. L., 2007. Responses of cetaceans to anthropogenic noise. *Mammal Review*, 37(2), pp81-115.

- Olsen, E., & Holst, J. C., 2001. A note on common minke whale (*Balaenoptera acutorostrata*) diets in the Norwegian Sea and the North Sea. *Journal of Cetacean Research and Management*, 3(2), pp179-183.
- Oviedo, L., 2007. Dolphin sympatric ecology in a tropical fjord: habitat partitioning by bathymetry and topography as a strategy to coexist. *Journal of the Biological Association of the United Kingdom*, 87, pp1327-1335.
- Parsons, E. C., Birks, I., Evans, P. G., Gordon, J. C., Shrimpton, J. H., & Pooley, S., 2000. The possible impacts of military activities on cetaceans in west Scotland. *European Research on Cetaceans*.
- Parsons, E. C., Dolman, S. J., Jasny, M., Rose, N. A., Simmonds, M. P., & Wright, A. J., 2009. A critique of the UK's JNCC seismic survey guidelines for minimising acoustic disturbance to marine mammals: Best practise? *Marine Pollution Bulletin*, 58(5), pp643-651.
- Parsons, E. C., Dolman, S. J., Wright, A. J., Rose, N. A., & Burns, W. C., 2008. Navy sonar and cetaceans: Just how much does the gun need to smoke before we act? *Marine Pollution Bulletin*, 56(7), pp1248-1257.
- Patterson, I. A., Reid, R. J., Wilson, B., Grellier, K., Ross, H. M., & Thompson, P. M., 1998. Evidence for infanticide in bottlenose dolphins: an explanation for violent interactions with harbour porpoises? *Proceedings of the Royal Society*, 265, pp1167-1170.
- Pedersen, S. A., Lewy, P., & Wright, P., 1999. Assessments of the lesser sandeel (*Ammodytes marinus*) in the North Sea based on revised stock divisions. *Fisheries Research*, 41(3), pp221-241.
- Perrin, W. F., & Brownell, R. L., 2009. Minke Whales. In W. F. Perrin, B. Wursig, & J. G. Thewissen, *Encyclopedia of Marine Mammals, Second Edition* (pp. 733-735). London: Elsevier.

- Pierce, G. J., Santos, M. B., Reid, R. J., Patterson, I. A., & Ross, H. M., 2004. Diet of minke whales *Balaenoptera acutorostrata* in Scottish (UK) waters with notes on strandings of this species in Scotland 1992-2002. *Journal of the Marine Biological Association of the United Kingdom*, 84, pp1241-1244.
- Querouil, S., Silva, M. A., Cascao, I., Magalhaes, S., Seabra, M. I., Machete, M. A., Santos, R. S., 2008. Why do dolphins form mixed-species associations in the Azores? *Ethology*, 114(1), pp1183-1194.
- Read, A. J., Drinker, P., & Northridge, S., 2006. Bycatch of marine mammals in U.S. and global fisheries. *Conservation Biology*, 20(1), pp163-169.
- Reay, P. J., 1970. Synopsis of biological data on North Atlantic sandeels of the genus *Ammodytes*. FAO Fisheries Synopsis, No.82.
- Reeves, R. R., Stewart, B. S., Clapham, P. J., & Powell, J. A., 2002. *Sea Mammals of the World*. London: A & C Publishers.
- Reid, J. B., Evans, P. G., & Northridge, S. P., 2003. *Atlas of cetacean distribution in the north-west European waters*. JNCC.
- Ritter, F., 2009. Collisions of sailing vessels with cetacean worldwide: First insights into a seemingly growing problem. *IWC Scientific Committee*.
- Robinson, K. P., & Macleod, C. D., 2009. First stranding record of a Cuvier's beaked whale (*Ziphius cavirostris*) in the Moray Firth in northeast Scotland. *Marine Biodiversity Records*, 2(57).
- Robinson, K. P., & Macleod, C. D., in prep. A comparison of intra-guild 'predation' in small toothed whales and terrestrial carnivores: can it help to explain fatal porpoise-dolphin interactions?
- Robinson, K. P., & Tetley, M. J., 2007. Behavioural observations of foraging minke whales (*Balaenoptera acutorostrata*) in the outer Moray Firth, north-east Scotland. *Journal of the Marine Biological Association of the UK*, 87(1), pp85-86.

- Robinson, K. P., Baumgartner, N., Eisfield, S. M., Clark, N. M., Culloch, R. M., Haskins, G. N., Zapponi, L., Whaley, A.R., Weare, J.S., Tetley, M.J., 2007. The summer distribution and occurrence of cetaceans in the coastal waters of the outer southern Moray Firth in northeast Scotland (UK). *Lutra*, 50(1), pp19-30.
- Robinson, K. P., Eisfield, S. M., Costa, M., & Simmonds, M. P., 2011. Short-beaked common dolphin (*Delphinus delphis*) occurrence in the Moray Firth, north-east Scotland. *Marine Biodiversity Records*, 3(55).
- Robinson, K. P., O'Brien, J. M., Berrow, S. D., Cheney, B., Costa, M., Eisfield, S. M., Haberlin, D., Mandleberg, L., O'Donovan, M., Oudejans, M.G., Ryan, C., Stevick, P. T., Thompson, P. M., Whooley, P., in press. Discrete or not so discrete: Long distance movements by coastal bottlenose dolphins in the UK and Ireland. *Journal of Cetacean Research and Management*, 12(3).
- Robinson, K. P., Tetley, M. J., & Mitchelson-Jacob, E. G., 2009. The distribution and habitat preference of coastally occurring minke whales (*Balaenoptera acutorostrata*) in the outer southern Moray Firth, northeast Scotland. *Journal of Coastal Conservation*, 13(1), pp39-48.
- Ross, H. M., & Wilson, B., 1996. Violent interactions between bottlenose dolphins and harbour porpoises. *Proceedings of the Royal Society*, 263: pp283-286.
- Roughgarden, J., 1976. Resource partitioning among competing species: a coevolutionary approach. *Theoretical Population Biology*, 9, pp388-424.
- Santos, M. B., Pierce, G. J., Learmonth, J. A., Reid, R. J., Ross, H. M., Patterson, I. A., Reid, D.G., Beare, D., 2004. Variability in the diet of harbour porpoises (*Phocoena phocoena*) in Scottish waters 1992-2003. *Marine Mammal Science*, 20(1), pp1-27.

- Santos, M. B., Pierce, G. J., Reid, R. J., Patterson, I. A., Ross, H. M., & Mente, E., 2001. Stomach contents of bottlenose dolphins (*Tursiops truncatus*) in Scottish waters. *Journal of the Marine Biological Association of the United Kingdom*, 81, pp873-878.
- Selzer, L. A., & Payne, P. M., 1988. The distribution of white-sided (*Lagenorhynchus acutus*) and common dolphins (*Delphinus delphis*) vs. environmental features of the continental shelf of the northeastern United States. *Marine Mammal Science*, 4(2), pp141-153.
- Shelden, K. E., Baldrige, A., & Withrow, D. E., 1995. Observations of Risso's dolphins, *Grampus griseus*, with gray whales, *Eschrichtius robustus*. *Marine Mammal Science*, 11(2), pp231-240.
- Shirihai, H., & Jarrett, B., 2006. *Whales, dolphins and other marine mammals of the world*. London: Princeton University Press.
- Simmonds, M. P., & Elliott, W. J., 2009. Climate change and cetaceans: concerns and recent developments. *Journal of the Marine Biological Association of the United Kingdom*, 89(1), pp203-210.
- Simon, M., Nuuttila, H., Reyes-Zamudio, M. M., Ugarte, F., Verfuß, U., & Evans, P. G., 2010. Passive acoustic monitoring of bottlenose dolphin and harbour porpoise, in Cardigan Bay, Wales, with implications for habitat use and partitioning. *Journal of the Marine Biological Association of the United Kingdom*, 90(8), pp1539-1545.
- Spitz, J., Rousseau, Y., & Ridoux, V., 2006. Diet overlap between harbour porpoise and bottlenose dolphin: An argument in favour of interference competition for food? *Estuarine, Coastal and Shelf Science*, 70(1-2), pp259-270.
- Tanabe, S., Iwata, H., & Tatsukawa, R., 1994. Global contamination by persistent organochlorines and their ecotoxicological impact on marine mammals. *Science of The Total Environment*, 154(2-3), pp163-177.

- Tetley, M. J., 2004. The distribution and habitat preference of the North Atlantic minke whale (*Balaenoptera acutorostrata acutorostrata*) in the southern outer Moray Firth, NE Scotland. MSc thesis. University of Wales, Bangor.
- Tetley, M. J., Mitchelson-Jacob, E. G., & Robinson, K. P., 2008. The summer distribution of coastal minke whales (*Balaenoptera acutorostrata*) in the southern Moray Firth, northeast Scotland, in relation to co-occurring mesoscale oceanographic features. *Remote Sensing of Environment*, 112(8), pp3449-3454.
- The Scottish Government., 2011a. *Legislation of Marine Mammals*. Available at: <<http://www.scotland.gov.uk/Topics/marine/marine-environment/species/19887/20813>> [Accessed 18 April 2012]
- The Scottish Government., 2011b. *Marine Mammals*. Available at: <<http://www.scotland.gov.uk/Topics/marine/marine-environment/species/19887>> [Accessed 18 April 2012]
- Thompson, P., White, S., & Dickson, E., 2004. Co-variation in the probabilities of sighting harbour porpoise and bottlenose dolphins. *Marine Mammal Science*, 20(2), pp322-328.
- Tyack, P. L., 2001. Marine Mammal Overview. In J. H. Steele, S. A. Thorpe, & K. K. Turekian, *Marine Biology* (pp. 381-390). London: Elsevier.
- USGS Earth Explorer. Landsat 7 ETM+ SLC. Satellite photo taken on 11.12.01.
- Van Waerebeek, K., Baker, A. N., Felix, F., Gedamke, J., Iniguez, M., Sanino, G. P., Secchi, E., Sutaria, D., van Helden, A., Wang, Y., 2007. Vessel collisions with small cetaceans worldwide and with large whales in the Southern Hemisphere, an initial assessment. *Latin American Journal of Aquatic Mammals*, 6(1).
- Videler, J. J., & Hess, F., 1984. Fast continuous swimming of two pelagic predators, saith (*Pollachius virens*) and mackerel (*Scomber scombrus*): A kinematic analysis. *The Journal of Experimental Biology*, 109, pp209-228.

- Walker, D., & Cresswell, G., 2008. *Whales and dolphins of the European atlantic: The Bay of Biscay, English Channel, Celtic Sea and coastal SW Ireland*. Hampshire: Wild Guides Ltd.
- Wang, J. Y., Chou, L. S., & White, B. N., 2000. Osteological differences between two sympatric forms of bottlenose dolphins (genus *Tursiops*) in Chinese waters. *Journal of Zoology*, 252, pp147-162.
- Watanabe, M., Kannan, K., Takahashi, A., Loganathan, B. G., Odell, D. K., Tanabe, S., Giesy, J. P., 2000. Polychlorinated biphenyls, organochlorine pesticides, tris(4-chlorophenyl)methane, and tris(4-chlorophenyl)methanol in livers of small cetaceans stranded along Florida coastal waters, USA. *Environmental Toxicology and Chemistry*, 19(6), pp1566-1574.
- Weir, C. R., Macleod, C. D., & Calderan, S. V., 2009. Fine-scale habitat selection by white-beaked and common dolphins in the Minch (Scotland, UK): evidence for interspecific competition or coexistence? *Journal of Marine Biological Association of the United Kingdom*, 89(5), pp951-960.
- Weir, C. R., Macleod, C. D., & Pierce, G. J., in press. Habitat preferences and evidence for niche partitioning amongst cetaceans in the waters between Gabon and Angola, eastern tropical Atlantic. *Journal of the Marine Biological Association of the United Kingdom*.
- Weir, C. R., Pollock, C., Cronin, C., & Taylor, S., 2001. Cetaceans of the Atlantic Frontier, north and west of Scotland. *Continental Shelf Research*, 21(1), pp1047-1071.
- Weir, C. R., Stockin, K. A., & Pierce, G. J., 2007. Spatial and temporal trends in the distribution of harbour porpoises, white-beaked dolphins and minke whales off Aberdeenshire (UK), north-western North Sea. *Journal of the Marine Biological Association of the United Kingdom*, 87(1), pp327-338.
- Wells, R. S., 2009. Dolphins and Porpoises. In J. H. Steele, S. A. Thorpe, & K. K. Turekian, *Marine Biology* (pp411-423). London: Elsevier.

- Williams, R., Lusseau, D., & Hammond, P. S., 2006. Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). *Biological Conservation*, 133(3), pp301-311.
- Wilson, B., 1995. The ecology of bottlenose dolphins in the Moray Firth, Scotland: A population at the northern extreme of the species range. PhD thesis. University of Aberdeen.
- Wilson, B., 2008. Bottlenose dolphin. In S. Harris, & D. W. Yalden, *Mammals of the British Isles: Handbook, 4th Edition* (pp. 709-715). Corby: The Mammal Society.
- Wilson, B., Thompson, P. M., & Hammond, P. S., 1997. Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. *Journal of Applied Ecology*, 34, pp1365-1374.
- Wright, P. J., & Bailey, M. C., 1996. Timing of hatching in *Ammodytes marinus* from Shetland waters and its significance to early growth and survivorship. *Marine Biology*, 126, pp143-152.
- Wright, P. J., & Begg, G. S., 1997. A spatial comparison of common guillemots and sandeels in Scottish waters. *ICES Journal of Marine Science*, 54, 578-592.
- Wright, P. J., Jensen, H., & Tuck, I., 2000. The influence of sediment type on the distribution of the lesser sandeel, *Ammodytes marinus*. *Journal of Sea Research*, 44, pp243-256.
- Wright, R., Ray, S., Green, D. R., & Wood, M., 1998. Development of a GIS of the Moray Firth (Scotland, UK) and its application in environmental management (site selection for an 'artificial reef'). *The Science of the Total Environment*, 223, pp65-76.
- Yen, P. P., Sydeman, W. J., & Hyrenback, K. D., 2004. Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: implications for trophic transfer and conservation. *Journal of Marine Systems*, 50(1), pp 79-99.

Zerbini, A. N., Waite, J. M., Laake, J. L., & Wade, P. R., 2006. Abundance, trends and distribution of baleen whales off Western Alaska and the central Aleutian Islands. *Deep Sea Research*, 53, pp1772-1790.

9.0. Appendices

9.0. Appendices

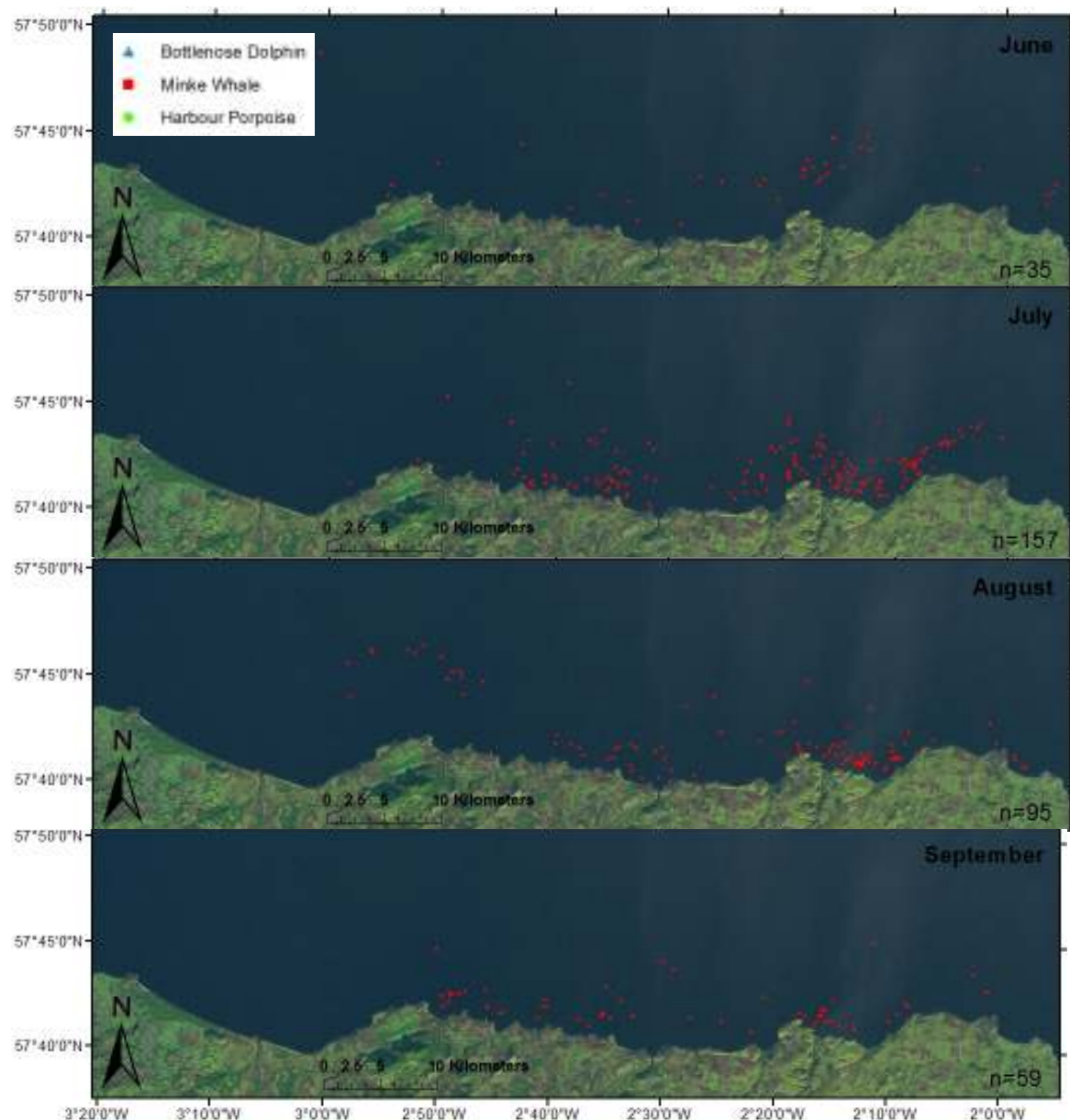
Appendix 9.1. CD containing raw encounter data used in this study, followed by an example of some raw data.

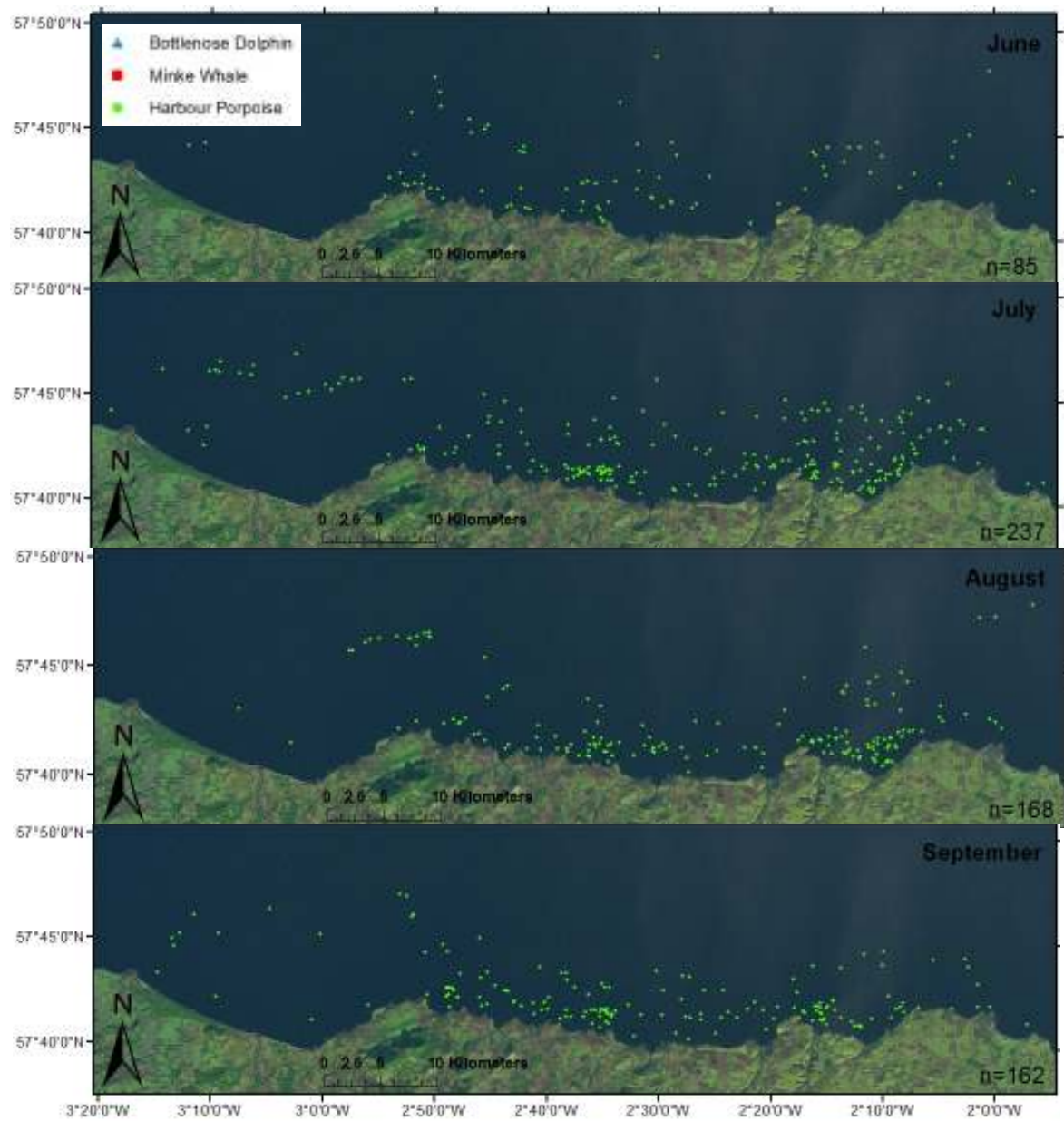


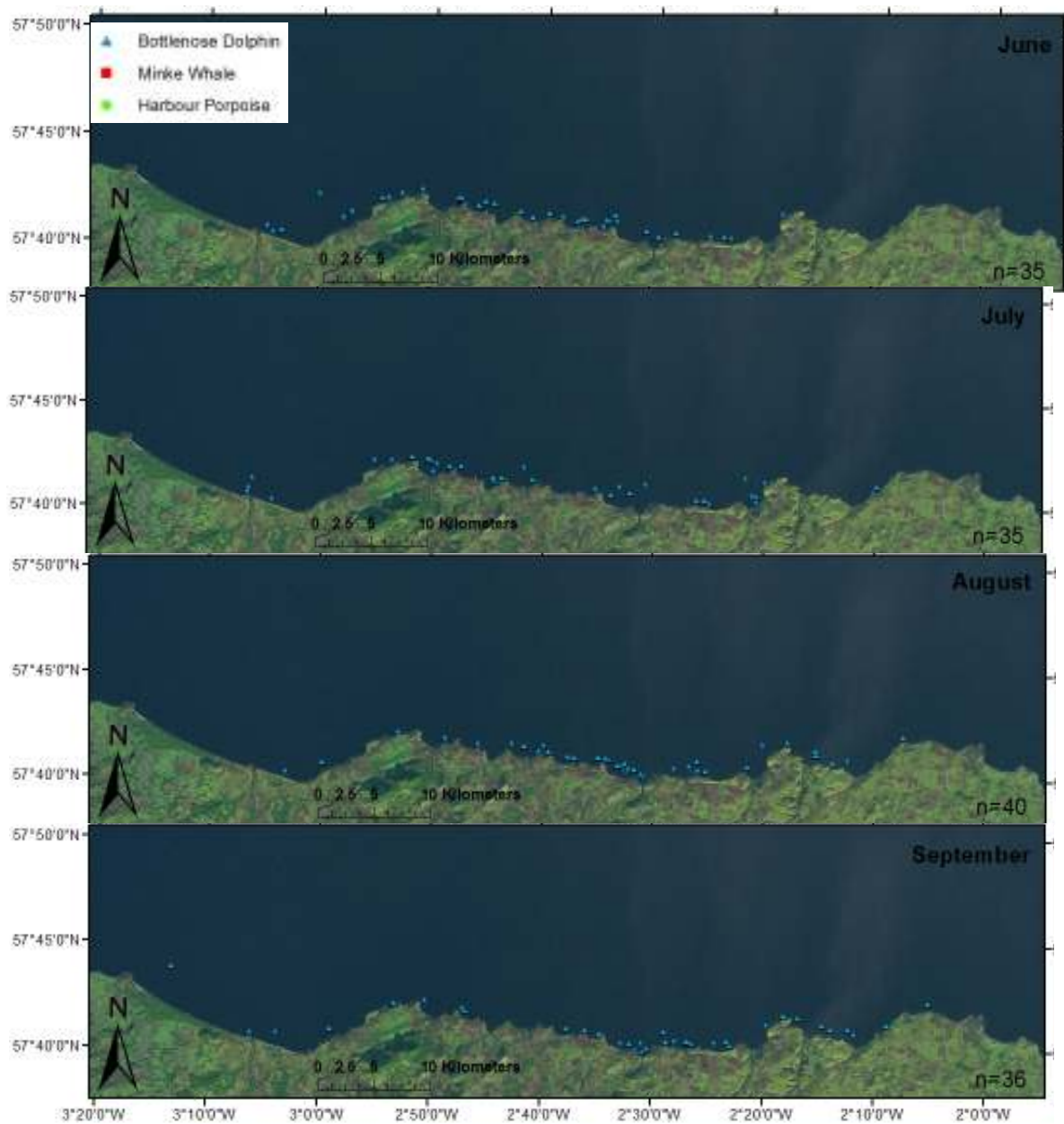
**This Box
Should
Contain A
Data CD Rom**

Date	Time	TimeZone	Lat	Long	SeaState	Species	Total Group
21/05/2001	16:38:00	GMT	57.6750000000	-2.5250000000	0	BND	11
25/05/2001	18:40:00	GMT	57.6745000000	-2.4670000000	1	BND	1
06/06/2001	17:40:00	GMT	57.6973166667	-2.7730000000	1	BND	17
10/06/2001	18:30:00	GMT	57.7053500000	-3.0070000000	1	BND	8
11/06/2001	16:35:00	GMT	57.7025000000	-2.3370000000	0	MW	1
12/06/2001	17:56:00	GMT	57.6754000000	-3.0770000000	3	BND	6
23/06/2001	8:15:00	GMT	57.6869166667	-2.6140000000	2	BND	21
28/06/2001	17:40:00	GMT	57.7166666667	-2.8500000000	3	HP	2
02/07/2001	17:15:00	GMT	57.7064166667	-2.9140000000	2	BND	16
04/07/2001	18:25:00	GMT	57.7064500000	-2.7396500000	0	HP	1
04/07/2001	18:40:00	GMT	57.7070500000	-2.7395000000	0	HP	6
10/07/2001	10:37:00	GMT	57.6796166667	-2.5570000000	3	BND	18
14/07/2001	17:20:00	GMT	57.6902333333	-2.3250000000	2	BND	13
14/07/2001	12:22:00	GMT	57.6835166667	-2.4570833333	2	HP	1
16/07/2001	14:46:00	GMT	57.7090000000	-2.8501666667	3	HP	1
17/07/2001	1:55:00	GMT	57.6896000000	-2.7300000000	3	BND	17
23/07/2001	17:05:00	GMT	57.6868500000	-2.1580000000	2	BND	17
23/07/2001	13:57:00	GMT	57.6887000000	-2.5736000000	2	MW	1
23/07/2001	18:50:00	GMT	57.7441500000	-2.3234833333	2	MW	1
24/07/2001	19:20:00	GMT	57.7389666667	-2.3228333333	3	MW	1
24/07/2001	19:25:00	GMT	57.7701333333	-2.6478333333	3	MW	1
25/07/2001	16:12:00	GMT	57.7191666667	-2.5878333333	3	HP	1
25/07/2001	18:16:00	GMT	57.7203833333	-2.2372166667	3	HP	1
25/07/2001	18:23:00	GMT	57.7180833333	-2.2824666667	3	HP	1
25/07/2001	18:25:00	GMT	57.7168500000	-2.2944666667	3	HP	1
25/07/2001	19:46:00	GMT	57.7166666667	-2.5771000000	3	MW	1
25/07/2001	20:00:00	GMT	57.7325000000	-2.5958333333	3	MW	1

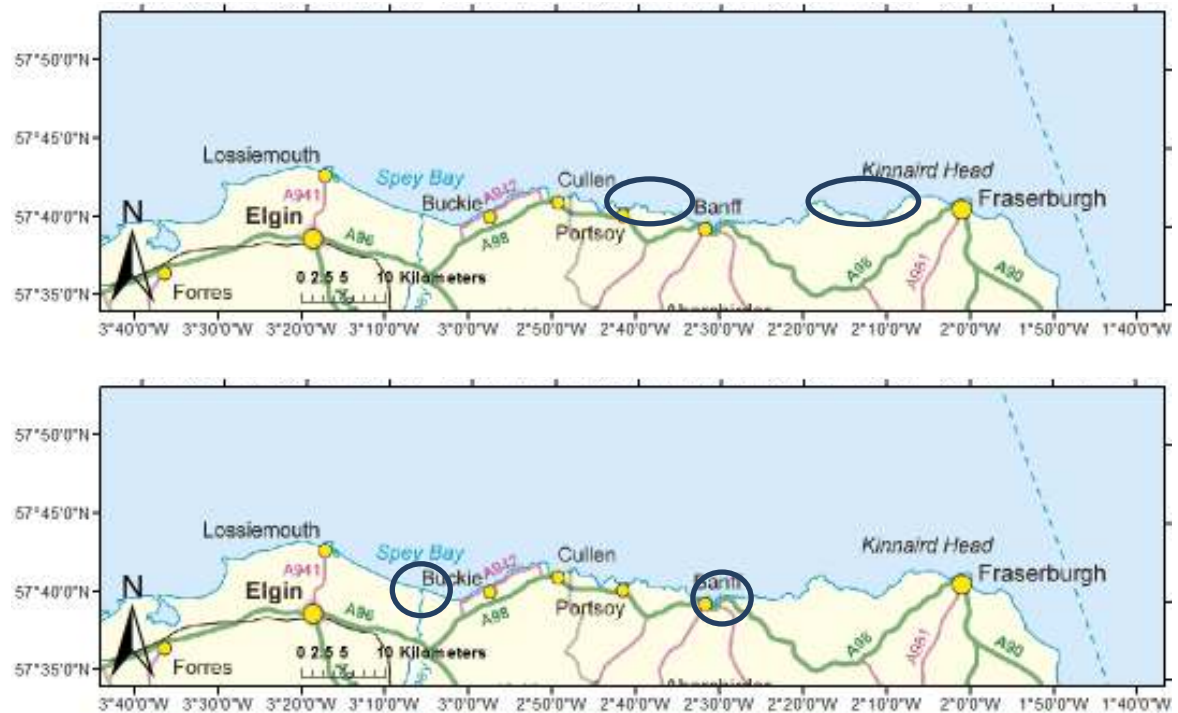
Appendix 9.2. GIS maps showing the monthly distribution of minke whales, harbour porpoises and bottlenose dolphin along the outer southern Moray Firth coastline as recorded by the CRRU research team between 2001 to 2008 inclusive. The frequency of encounter is noted in the bottom right corner of each map.







Appendix 9.3. Areas identified for highest encounters of minke whales and harbour porpoise (top) and bottlenose dolphins (bottom).



Appendix 9.4. Depth calculations are displayed including the minimum, maximum, mean and standard deviation for each species.

	Study Species		
Water depth (metres)	Bottlenose Dolphin	Harbour Porpoise	Minke Whale
Minimum	0.81	1.04	2.28
1 st Quartile	6.69	19.91	18.12
Median	10.77	27.72	27.36
3 rd Quartile	15.18	38.53	38.40
Maximum	31.97	152.21	134.40
Range	31.16	151.20	132.10
Mean	11.36	33.04	31.15
Standard Deviation	6.27	23.87	21.31
95% Confidence Interval	0.95	1.73	2.20
Total No. of Sightings	154	705	356

Appendix 9.5. Seabed slope calculations are displayed including the minimum, maximum, mean and standard deviation for each species.

	Study Species		
Slope (degrees)	Bottlenose Dolphin	Harbour Porpoise	Minke Whale
Minimum	0.09	0.01	0.02
1st Quartile	0.80	0.38	0.40
Median	1.19	0.58	0.65
3rd Quartile	1.93	1.02	1.13
Maximum	3.99	3.23	4.08
Range	3.90	3.22	4.06
Mean	1.37	0.80	0.85
Standard Deviation	0.83	0.62	0.63
95% Confidence Interval	0.12	0.04	0.07
Total Sightings	168	729	361

Appendix 9.6. Distance to nearest shore calculations are displayed including the minimum, maximum, mean and standard deviation for each species.

	Study Species		
Distance to Nearest Shore (metres)	Bottlenose Dolphin	Harbour Porpoise	Minke Whale
Minimum	0.81	82.29	101.24
1st Quartile	328.84	996.15	907.80
Median	490.34	1887.57	1627.23
3rd Quartile	715.28	4139.40	2891.83
Maximum	3481.55	15150.16	14182.58
Range	3480.74	15067.87	14081.34
Mean	591.22	2818.57	2283.40
Standard Deviation	447.91	2480.96	1940.95
95% Confidence Interval	67.73	180.10	200.22
Total Sightings	168	729	361

Appendix 9.7. Results of chi-square tests (*P* values) used to determine significant difference between study species and different seabed sediment classes.

Difference by seabed sediment	Bottlenose Dolphin	Harbour Porpoise
Minke Whale	3.5e-15**	7.9e-09**
Bottlenose Dolphin	#N/A	1.3e-17**

* indicates a significant difference (<0.05)

** indicates a very significant difference shore (<0.01)

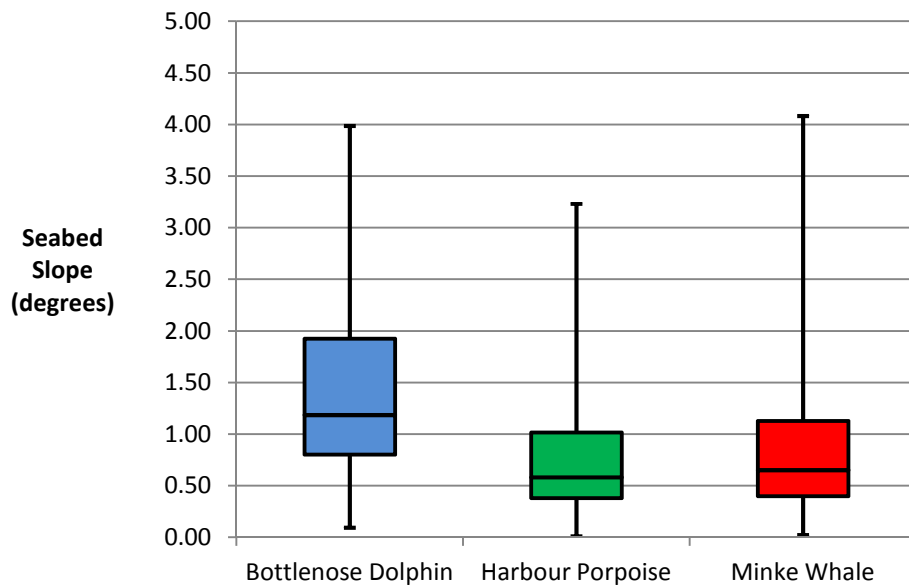
Appendix 9.8. Results of chi-square tests (*P* values) used to determine significant difference between study species and different seabed slope intervals.

Difference by seabed slope	Bottlenose Dolphin	Harbour Porpoise
Minke Whale	1.6e-11**	0.77
Bottlenose Dolphin	#N/A	2.5e-17**

* indicates a significant difference (<0.05)

** indicates a very significant difference shore (<0.01)

Appendix 9.9. Box plot to indicate the preferred seabed slopes of each species and the range used throughout the summer months May to October.



Appendix 9.10. The number of monthly encounters of each species, the survey effort per month and the derived no of encounters per kilometre per month for each species.

Survey month		June	July	August	September
Total no. of encounters	Bottlenose Dolphin	35	35	40	36
	Harbour Porpoise	85	237	168	162
	Minke Whale	35	157	95	59
Survey effort in km		2293.75	5282.55	3567.40	3860.20
Derived no. of per km	Bottlenose Dolphin	0.015	0.007	0.011	0.009
	Harbour Porpoise	0.037	0.045	0.047	0.042
	Minke Whale	0.015	0.03	0.027	0.015