PRIFYSGOL BANGOR UNIVERSITY

Fatal Interactions between Bottlenose Dolphins (*Tursiops truncatus*) and Harbour Porpoises (*Phocoena phocoena*) in Welsh Waters

Dissertation submitted in partial fulfilment of the requirements for BSc in Applied Marine Biology.

By

Rebecca Boys

500241603

Bangor University, Wales

In association with:

Sea Watch Foundation and CSIP

Acknowledgements

My primary thanks go to Peter Evans, founder of the Sea Watch Foundation, for all his encouragement and criticism as well as for directing me towards useful papers. I am truly grateful for all the feedback and for his generosity of time and knowledge.

Secondly, to Dr Line Cordes at Bangor University, for all her help with R, and for her kindness and time when I was feeling frustrated with statistics.

I would also like to thank CSIP, and in particular Rob Deaville, for answering my numerous questions and for all his encouragement and advice on strandings.

Additional thanks go to my supervisor at Bangor University, Dr John Turner, for his advice and encouragement.

Thanks also go to Charlie Lindenbaum, NRW, for his initial support and advice for MapInfo and to Dr Tom Stringell, NRW, for his constructive criticism and encouragement along the way.

Finally, I would like to thank my dad, for helping me with proof reading and for the many phone calls of advice as well for his encouragement throughout my entire degree.

Abstract

Competition between sympatric species is a well-known phenomenon throughout the animal kingdom (Ross and Wilson, 1996; Baird *et al.*, 1998) and can be direct or indirect. Competition over a shared resource often leads to aggressive interactions, which can be fatal to the inferior species (Polis *et al.*, 1989). Bottlenose dolphins were found to be the main agonists in many aggressive interactions between odontocetes. Bottlenose dolphins (*Tursiops truncatus*) and harbour porpoises (*Phocoena phocoena*) are two of the most commonly recorded cetaceans in UK waters. Aggressive interactions between these species were first recorded in the early 1990s (Ross and Wilson, 1996) and since have been reported with increasing frequency worldwide (Patterson *et al*., 1998; Kaplan, 2009; Cotter *et al*., 2011). Using strandings' data for Wales from 1991 to 2013, a total of 142 porpoises stranded-attacked by bottlenose dolphins were examined. Sightings data were used to examine geographical overlap and fish stock data were used to examine changes in fish abundance within ICES rectangle VIIa. Literature was reviewed to examine dietary overlap. These variables were put into a binomial GLMM using R, to examine which variables had an effect on the occurrence of a stranding due to attack by bottlenose dolphins. The study suggests that the cetaceans do compete for resources, and that dietary and geographical overlap significantly ($p<0.05$) affects the occurrence of stranded-attacked porpoises. Object-oriented play and testosterone levels, suggested in the literature were reviewed and examined for their occurrence, where possible, in Welsh waters. In Wales, high co-occurrence and interference feeding appear to explain many of the attacks, but other factors such as object-oriented play and testosterone levels are likely to further influence the seasonality and extent of these attacks.

Contents

1. Introduction 1
1.1 Study species 3
1.1.1 The Harbour Porpoise 3
1.1.2 The Bottlenose dolphin 4
1.2 Bottlenose dolphin attacks 5
1.2.1 Causes 7
1.2.2 Aberrant behaviour 7
1.2.3 Inter-species territoriality 8
1.2.4 Prey competition or feeding interference 8
1.2.5 Object-oriented play 8
1.2.6 Elevated testosterone levels 9
1.2.7 Skewed operational sex ratio or sexual frustration 9
1.3 Attacks in Wales 9
2. Methods 11
2.1 Study area 11
2.2 Data collection 12
2.3 Methods of data analysis 15
2.3.1 Strandings data 15
2.3.2 Inter-species territoriality 15
2.3.3 Prey competition or interference feeding 17
2.3.4 R analysis 17
2.3.5 Object oriented play 20
2.3.6 Skewed operational sex ratio or sexual frustration & elevated testosterone levels 20
3. Results and Analysis 21
3.1 Strandings data 21
3.2 Inter-species territoriality 24
3.3 Prey competition or feeding interference 34
3.4 Generalised Linear Mixed Modelling 46
3.5 Object-oriented play 47
3.6 Skewed operational sex ratio or sexual frustration & Elevated testosterone levels 48
4. Discussion 52
4.1 Territoriality 52
4.2 Prey competition 53
4.3 Object-oriented play 56
4.4 Sex ratio and elevated testosterone 57
4.5 Other cases of attacks 58
4.6 Attacks on porpoises by grey seals 60

5. Conclusions 61
5.1 Limitations 62
6. References 63
7. Appendix 1 71
8. Appendix 2 121

Figures and Tables

Figure 1. Harbour porpoise 3
Figure 2. Bottlenose dolphin 4
Figure 3. Map of UK with Cardigan Bay and the Welsh coast as an inset 11
Figure 4. Map of Harbour porpoise (a) and Bottlenose dolphin (b) distribution- Interpolated long term mean sightings from vessel counts per 10km, 1990-2009. (Baines and Evans, 2012) 13
Figure 5. ICES areas around the UK coastline. Scottish Sea Fisheries Statistics, 2009 14
Figure 6. The total amount of effort (km) carried out on vessel surveys, April-October, 2001-2014 (Cardigan Bay data) 16
Figure 7. Correlations between explanatory variables input in GLMM 19
Figure 8. Number of stranded harbour porpoises attacked by bottlenose dolphins in Wales, 1991-2013 21
Figure 9. Total number (post-mortem and expert) of stranded-attacked harbour porpoises in England and Wales, 1991-2013 22
Figure 10. Total percentage of harbour porpoise deaths along the Welsh coast due to each factor between 1990 and 2013 22
Figure 11. Body weight to length ratio of necropsied stranded-attacked harbour porpoises in Welsh waters, 1991-2013 (y=1.2492x+84.897, R^2=0.8549) 23
Figure 12. Body weight to length ratio of necropsied stranded-attacked harbour porpoises with decomposition state in Welsh waters, 1991-2013 (2a=Freshly dead, 2b=Slight decomposition, 3=Moderate decomposition, 4=Advanced decomposition) 23
Figure 13. Harbour porpoise-Long term quarterly mean sighting rates from vessel surveys, 1990-2009 (Baines and Evans, 2012) 24
Figure 14. Bottlenose dolphins-Long term quarterly mean sighting rates from vessel surveys, 1990-2009 (Baines and Evans, 2012) 25
Figure 15. Distribution of co-occurrence per km (corrected for effort) of the species and stranded-attacked harbour porpoises between April-July (a) and August-October (b), 2001-2014 26
Figure 16. Relationship between the co-occurrence density of the cetaceans and the number of stranded-attacked porpoises, 2002-2013 27
Figure 17. Relationship between the co-occurrence density of the species and the number of stranded-attacked porpoises by quarter, (1st=January-March, 2nd=April-June, 3rd=July-September, 4th=October-December) 28

Figure 18. Co-occurrence of cetaceans between each quarter (a)January-March, b)April-June, c)July-September, d)October-December) and distribution of stranded-attacked porpoise 30
Figure 19. Map of Cardigan Bay SAC with the location of T-PODS used to collect presence data of both harbour porpoises and bottlenose dolphins (Simon *et al.*, 2010) 31
Figure 20. Acoustic detection of harbour porpoises and bottlenose dolphins- average number of detection positive minutes per hour, 2005-2006. Values are means ±1 S.E. (Baulch, 2012)....... 33
Figure 21. Average number of detection positive minutes per hour of bottlenose dolphins and harbour porpoises during the tidal cycle. Values represent means ±1 S.E. (Baulch, 2012) 33
Figure 22. Average live weight (tonnes) of important fish prey species of both harbour porpoise and bottlenose dolphins, caught in ICES divisions VIIa, f and g, 1993-2014 36
Figure 23. Average live weight (tonnes) of important fish prey species of both harbour porpoise and bottlenose dolphin, caught in ICES divisions VIIa, f and g, for all months 37
Figure 24. Comparison of the total catch (weight) of haddock landed in Wales and the number of stranded-attacked harbour porpoise for each month 37
Figure 25. Number of harbour porpoises stranded due to starvation compared to those stranded-attacked, averaged per month, 1990-2013 38
Figure 26. Number of harbour porpoises stranded due to starvation compared to those stranded-attacked averaged per year, 1990-2013 38
Figure 27. Relationship between the abundance of sandeels in the Irish Sea (VIIa) and the number of porpoises stranded dead due to starvation, 1993-2013... 39
Figure 28. Relationship between the number of stranded-attacked harbour porpoises and the abundance of sandeels caught in beam trawl surveys, 2001-2014 39
Figure 29. Relationship between the number of bottlenose dolphin and harbour porpoise sightings and abundance (total number) of sandeels caught in beam trawl surveys, 2001-2014 . 40
Figure 30. Relationship between the total abundance of sandeels and the amount of co-occurrence between bottlenose dolphins and harbour porpoises, 2002-2014............................... 41
Figure 31. Relationship between the abundance of sprat and the number of stranded-attacked harbour porpoises, 2001-2013 41
Figure 32. Relationship between total abundance of sprat and the total co-occurrence density between cetacean species, 2002-2013.. 42
Figure 33. Relationship between the total abundance of sprat and the number of harbour porpoises stranded dead due to starvation, 2001-2013 42
Figure 34. Relationship between the number of stranded-attacked harbour porpoises and the abundance of poor-cod in beam trawl surveys, 2001-2014 43

Figure 35. Relationship between the abundance of poor-cod and the number of porpoises recovered dead due to starvation, 2001-2014 43
Figure 36. Relationship between the total abundance of poor-cod and the amount of co-occurrence between bottlenose dolphins and harbour porpoises, 2002-2014.......... 44
Figure 37. Relationship between the number of stranded-attacked harbour porpoises and the abundance of whiting in beam trawl surveys, 2001-2014 45
Figure 38. Relationship between the number of stranded-attacked porpoises and the live caught weight of whiting per month into Wales.......... 45
Figure 39. Length class distribution (cm) of (a) harbour porpoises and (b) bottlenose dolphins, stranded in the Moray Firth, Scotland, 1992-1997. Traumatic injuries= black, other causes of death= white (Patterson *et al*., 1998) 47
Figure 40. Length class distribution of stranded harbour porpoises attacked by bottlenose dolphins in Wales, 1991-2013 48
Figure 41. Total number of stranded-attacked harbour porpoises in Wales by month, averaged over 1991-2013 (y=0.5x+6, R^2=0.1004).......... 49
Figure 42. Total number of stranded harbour porpoises attacked by bottlenose dolphins by quarter (season) (1st=January-March, 2nd=April-June, 3rd=July-September, 4th=October-December).......... 49
Figure 43. Age/sex classes of necropsied stranded-attacked harbour porpoises, 1991-2013....... 50
Figure 44. Relationship by month between the extent of co-occurrence of bottlenose dolphins and harbour porpoises and the number of stranded-attacked porpoises 51
Figure 45. Seabed sediment types in the Irish Sea, preferred sandeel sediment is in yellow (sand) and gravelly sand (orange-brown), (Robinson *et al*., 2011). 55
Figure 46. Harbour porpoises stranded-attacked by bottlenose dolphins around the UK, 1991-2010 (Deaville and Jepson, 2011).......... 59

Table 1. Aggressive behaviour between sympatric species of odontocetes 2
Table 2. Types of behaviour displayed by bottlenose dolphins when harassing harbour porpoises (Cotter *et al*., 2011).......... 6
Table 3. Inter-tooth distances of cetaceans occurring in the North Sea and coastal waters of South West England (Ross and Wilson, 1996; Barnett *et al*., 2009).......... 7
Table 4. Variables input to GLMM, with an explanation of each variable 18
Table 5. Total number of detection positive minutes and percentage of simultaneous detections of both species within one minute (Simon *et al*., 2010) 32

Table 6. Variety of species fed on by harbour porpoises and bottlenose dolphins, with the average percentage of occurrence of each species per stomach (number of prey) and the average percentage of stomachs that had each species (frequency of occurrence). Shared prey species highlighted in bold (Browne, 1999; Santos *et al.*, 2004; Spitz *et al.*, 2006)................................35

Table 7. All models run using a GLMM with their AIC rating and weight 46

Table 8. Model 7-The best linear mixed-effects model fit by maximum likelihood, showing the relationship of each variable on the occurrence of a stranding due to bottlenose dolphin attack, April-October, 2001-2014...47

1. Introduction

For sympatric species, competition and other interactions are likely. Sympatric species can usually coexist by partitioning resources both spatially and temporally. However, if the resource becomes diminished, competition will ensue (Bearzi, 2005). This competition may be direct or indirect. Direct competition includes the interaction and interference of two species over a common resource (Spitz *et al.*, 2006), while the species do not need direct interaction to cause indirect competition, as the use of the resource by one species will detrimentally affect the other. Competition usually begins indirectly and as the resource becomes depleted direct competition begins. These interactions may escalate in areas where a resource becomes scarce, often leading to an increase in aggressive interactions. Aggression can be defined as a behaviour that causes 'repellent or harmful stimuli or physical injury to another organism' (Olivier and Young, 2002). This may lead to a superior species displacing a competitor, thus benefitting from a decrease in rivalry and can lead to fatal interactions (Polis *et al.*, 1989). Aggression within the animal kingdom can be split into two categories: offensive and defensive. Offensive aggression is where an animal intentionally harms another, such as inter-male aggression and territoriality. Defensive aggression is the infliction of harm due to a particular stimulus, such as maternal and fear-induced aggression (Vitiello and Stoff, 1997). These types of aggression can be classified as non-predatory aggression, whereas predatory aggression is predominantly determined by appetite (Olivier and Young, 2002).

Aggression is a widespread phenomenon throughout the animal kingdom and there are numerous documented non-predatory aggressive interactions between species of sympatric odontocetes (Ross and Wilson, 1996; Baird *et al.*, 1998; Thompson *et al.*, 2004; Wedekin *et al.*, 2004; Barnett *et al.*, 2009; Cotter *et al.*, 2011; De Stephanis *et al.*, 2014; see also Table 1). Bottlenose dolphins (*Tursiops truncatus*; Montagu, 1821) are involved in the majority of these aggressive non-predatory interactions within the Odontoceti, inflicting direct lethal aggression towards other species within this suborder (Cotter *et al*, 2011).

Table 1. Aggressive behaviour between sympatric species of odontocetes

Aggressors	**Victims**	**Location**	**References**
T. truncatus	*T. truncatus* (calves)	United States of America Scotland	Dunn *et al.*, 2002 Kaplan *et al.*, 2009 Patterson *et al.*, 1998 Robinson, 2014
T. truncatus	*P. phocoena*	Moray Firth, Scotland	Ross and Wilson, 1996
T. truncatus	*S. attenuata*	Bahamas	Herzing and Johnson, 1997
T. truncatus	*S. frontalis*	Bahamas	Herzing and Johnson, 1997
T. truncatus	*S. longirostris*	Hawaii	Baird *et al.*, 2001
T. truncatus	*S. guianensis*	Baía Norte, Brazil	Wedekin *et al.*, 2004
T. truncatus	*D. delphis*	Azores	Clua and Grosvalet, 2001
T. truncatus	*S. coeruleoalba*	Galicia, Spain	Alonso *et al.*, 2000
T. truncatus	*G. melas* *D. delphis* *S. coeruleoalba* *G. griseus*	South West England	Barnett *et al.*, 2009
L. obliquidens	*P. phocoena*	San Juan Island, Washington	Patterson *et al.*, 1998
S. frontalis	*T. truncatus*	Great Bahama Bank, Bahamas	Baird, 1998
S. longirostris	*S. attenuata*	Hawaii	Herzing *et al.*, 2003
G. griseus	*D. delphis*	Gulf of Corinth, Greece	Frantzis and Herzing, 2002
G. griseus	*S. coeruleoalba*	Gulf of Corinth, Greece	Psarakos *et al.*, 2003
G. griseus	*G. melas*	Santa Catalina Island, California	Shane, 1995
L. acutus	*P. phocoena*	Gulf of St. Lawrence	Larrat *et al.*, 2012
L. albirostris	*P. phocoena*	Belgium and the Netherlands	Haelters and Everaarts, 2011
G. melas	*T. truncatus* *Delphinus delphis*		Barnett *et al*., 2009

Harbour porpoises (*Phocoena phocoena*; Linnaeus, 1758) killed by bottlenose dolphin attacks are commonly recorded in the United States (Cotter *et al.*, 2011) and have also been noted in Northeast Scotland (Ross and Wilson, 1996; Patterson *et al.*, 1998; Robinson, 2014), North and West Wales (Pesante *et al*, 2008a, b; Feingold and Evans, 2014; Norrman *et al.*, 2015). Only a few such attacks have been directly observed (Ross and Wilson, 1996; Pesante *et al.*, 2008b; Robinson, 2014; Norrman *et al.*, 2015), and most evidence of interaction has been collected through the post-mortem of stranded harbour porpoises. Thus, data on factors influencing these attacks is sparse. It is likely that the number of aggressive interactions between these species is currently underestimated by the strandings' data.

1.1 Study species

Harbour porpoises and bottlenose dolphins are the two most abundant cetacean species in the coastal waters of the British Isles (Evans *et al.,* 2003) and are sympatric species in their coastal range (Reid *et al.*, 2003; Bearzi, 2005).

1.1.1 The Harbour Porpoise

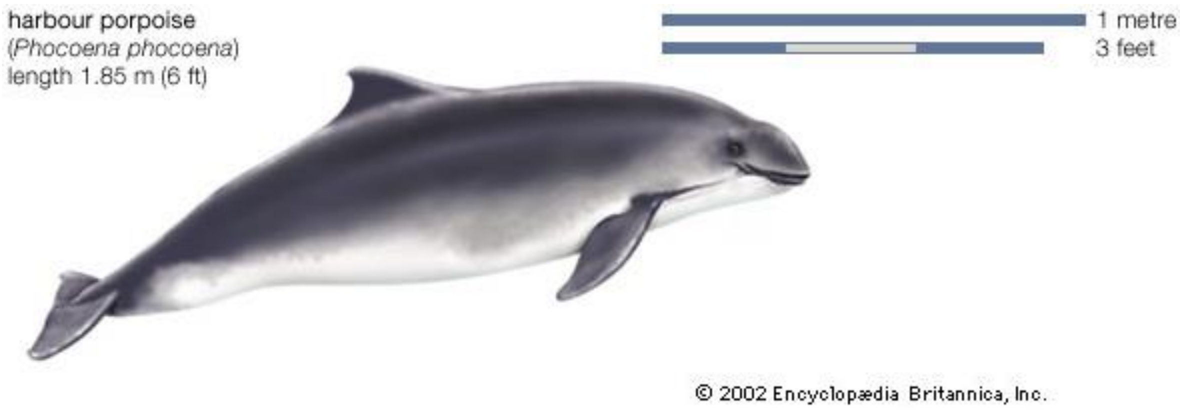


Figure 1. Harbour porpoise

The harbour porpoise (Figure 1) is the smallest and most abundant cetacean found in European waters, reaching a maximum of 1.8 metres. It inhabits the continental shelf in temperate waters of the Northern Hemisphere (Hammond *et al.*, 2002; Reid *et al.*, 2003; Hammond *et al.*, 2014). Although the species is circumpolar, animals from the Pacific, Atlantic and Black Sea are all reproductively isolated (Bjørge and Tolley, 2004). They are of least concern throughout their whole range; however, some small subpopulations are listed on the IUCN Red List (2014) as they are under more immediate threat, such as the Baltic Sea population, which is estimated to have just 447 (95% CI 90-997) mature animals (SAMBAH, 2014).

Harbour porpoises usually live in groups of 2-3 animals but larger aggregations may be found close to optimal feeding grounds (Evans *et al.*, 2003; Reid *et al.*, 2003). They have a relatively short life span of up to 15 years. They are largely piscivorous and their distribution tends to be related to their prey (Clark *et al.*, 2006). In European waters they tend to feed on herring (*Clupea harengus*), sprat (*Sprattus sprattus*) mackerel (*Scomber scombrus*), gobies (*Gobius* sp.), sandeel (*Ammodytes*) and gadoid fish such as whiting (*Merlangius merlangus*) (Evans and Hintner, 2010). However, their actual diet is dependent on prey availability and areas with high fishing pressures and depleted stocks may cause them to feed upon less optimal species.

Harbour porpoises have a small, rotund body and a thick blubber layer. They are often identified by their small, triangular dorsal fin and lack of a distinct beak. They can be difficult to spot as they show little of themselves on the surface of the water (Bjørge and Tolley, 2009). Around 15,200 harbour porpoises live in the Irish Sea (Evans, 2012). In Wales, the greatest numbers tend to be seen between July and October (Baines and Evans, 2012). During this time they may be seen in high density aggregations on prime feeding grounds, such as Point Lynas, North Wales, and Strumble Head and Ramsey Sound in Southwest Wales (Baines and Evans, 2012; CCW, 2013). These are often high energy sites or areas of upwelling.

1.1.2 The Bottlenose dolphin

Figure 2. Bottlenose dolphin

Bottlenose dolphins (Figure 2) are found in tropical and temperate coastal, shelf and oceanic waters worldwide (Reynolds *et al.*, 2000). In the temperate North-east Atlantic, they are particularly large and robust, inhabiting areas at the northern extreme of their global range, and growing up to 4 metres in length (Wilson, 2008). They are highly social delphinids, usually living in small groups of 5-15 individuals, but sometimes up to 50-100 animals, with sub groups forming a fission-fusion society (Evans *et al.*, 2003; Reid *et al.*, 2003; Wilson, 2008). Large aggregations tend to be seen in pelagic waters and on prime feeding grounds (Reid *et al.*, 2003).

Bottlenose dolphins are largely piscivorous. However, they are opportunistic feeders and feed upon the most abundant prey species (Bearzi, 2005). Their main prey species include: cod (*Gadus morhua*), whiting (*Merlangius merlangus*), salmon (*Salmo salar*), a variety of demersal and benthic species as well as cephalopods (Santos *et al.*, 2001; Bearzi, 2005; Evans and Hintner 2010). They are also very adaptable in their foraging tactics, with cooperative hunting seen worldwide. Bottlenose dolphins have a preference for estuaries and sandbanks in coastal areas, where there is often a strong tidal current (Wilson, 2008).

Bottlenose dolphins have a central dorsal fin, which is sickle-shaped, and a short beak with conical teeth (Wells and Scott, 2002). They are often seen bow riding and undertaking acrobatic displays. They are a species of least concern on the IUCN Red List (2013a). Around Wales there is a population of between 200 and 300 individuals, which mainly inhabit Cardigan Bay (Baines and Evans, 2012; Feingold and Evans, 2014). Between 2001 and 2008, the population in Cardigan Bay remained stable or slightly increased in size (Pesante *et al.*, 2008), but since then may be declining (Feingold and Evans, 2014; Norrman *et al.*, 2015).

1.2 Bottlenose dolphin attacks

Although few attacks upon porpoises have been directly observed, there appears to be a common pattern in how they are carried out. There is usually more than one individual dolphin involved and a range of aggressive behaviours are exhibited (Ross and Wilson, 1996; Cotter *et al.*, 2011; Table 2).

Table 2. Types of behaviour displayed by bottlenose dolphins when harassing harbour porpoises (Cotter *et al*., 2011)

Behaviour	Description
Sandwiching	Squeezing the harbour porpoise between the flanks of two bottlenose dolphins, forcing it to be lifted out of the water. This may cause fractured ribs and bilateral hematomas.
Drowning	Repeatedly pushing the porpoise's head underwater by dropping the dolphin's body onto it. Also, lifting the fluke of the porpoise with the rostrum of the dolphin, keeping the porpoise's head underwater. Causes tiring, disorientation and inability to breathe.
Tossing	Quick and violent throwing of the porpoise, either partially or completely out of the water, hitting it with the rostrum or fluke. Porpoise may somersault out of the water as it is often hit violently on both sides.
Ramming	The dolphin's rostrum and sides of the body are used repeatedly to hit the porpoise at high speed. Often by multiple animals.

Dolphins typically harass porpoises until they are exhausted and unable to flee (Jepson and Baker, 1998). The injuries sustained from these interactions are often fatal, and most are subcutaneous (Jepson and Baker, 1998) such as broken bones, bruising, blubber tearing and haemorrhaging, although external injuries such as tooth rake marks may also be observed. It is from these tooth rake marks, that bottlenose dolphins have been identified as the culprit, using the interdental distance (Table 3).

Table 3. Inter-tooth distances of cetaceans occurring in the North Sea and coastal waters of South West England (Ross and Wilson, 1996; Barnett *et al.*, 2009)

Species	Mean inter-tooth distance (mm)	95% confidence interval
Harbour porpoise (*Phocoena phocoena*)	3.61	3.36-3.87
Common dolphin (*Delphinus delphis*)	4.71	4.46-4.95
Striped dolphin (*Stenella coeruleoalba*)	5.34	No data
White- beaked dolphin (*Lagenorhynchus albirostris*)	6.87	6.26-7.48
Bottlenose dolphin (*Tursiops truncatus*)	11.60	10.97-12.32
Risso's dolphin (*Grampus griseus*)	16.48	15.28-17.67
Killer whale (*Orcinus orca*)	31.88	28.64-35.1
Pilot whale (*Globicephala melas*)	No data	No data

1.2.1 Causes

Throughout the literature authors have suggested reasons for the aggressive interactions towards harbour porpoises by bottlenose dolphins. A number of theories have been proposed, these include: aberrant behaviour (Ross and Wilson, 1996), inter-species territoriality (Cotter *et al.*, 2011), prey competition or feeding interference (Spitz *et al*, 2006; Cotter *et al.*, 2011), object-oriented play (Ross and Wilson, 1996; Patterson *et al.*, 1998), elevated testosterone levels or sexual frustration (Rose *et al*, 1991; Ross and Wilson, 1996) and a skewed operational sex ratio (Le Boeuf and Campagna, 1994). Each of these potential causes are discussed below:

1.2.2 Aberrant behaviour

Aberrant behaviour is a type of behaviour that is outside the usual repertoire of the species. Therefore, aberrant behaviour has been dismissed as the explanation for current attacks (Cotter *et al.*, 2011). This is due to the fact that this non-predatory aggressive behaviour by bottlenose dolphins has been directed towards many other cetacean species, besides harbour porpoises, in many locations. Not only have non-predatory attacks towards other species occurred, but the tactics and sequence in which they tend to be carried out are all similar (Ross and Wilson 1996; Jepson and Baker, 1998; Dunn *et al.*, 2002; Wedekin *et al.*, 2004; Cotter *et al.*, 2011).

1.2.3 Inter-species territoriality

Evidence has been found that attacks occur at times when harbour porpoise densities are greatest (Sekiguchi, 1995). Cotter *et al.* (2011) found that the seasonality and extent of the interactions mirrored the distribution and movement patterns of the harbour porpoises along the Californian coast. These facts may indicate that bottlenose dolphins direct territorial aggression towards harbour porpoises, due to geographic overlap, although they are not known to defend areas. However, due to the small body size and group size of harbour porpoises, it is unlikely that they present much of a threat except for prey competition resulting from dietary overlap (Spitz *et al.*, 2006; Cotter *et al.*, 2011). However, other studies have shown that there are no aggressive interactions between bottlenose dolphins and species which are in direct competition, such as the California sea lion (*Zalophus californianus*) (Cotter *et al.*, 2011).

1.2.4 Prey competition or feeding interference

Spitz *et al.* (2006) considered that interactions were likely to occur because of interference competition for food due to geographic and dietary overlap. However, although their ranges do partly overlap, the bottlenose dolphin also inhabits areas beyond the shelf edge and feeds on a wider variety of prey species (Spitz *et al.*, 2006; Cotter *et al.*, 2011) than harbour porpoises, although fish do dominate the diets of both species. Spitz *et al.* (2006) found that bottlenose dolphins tend to feed on larger specimens of prey species than do harbour porpoises. Therefore, there is partial dietary overlap. In sympatric species, one might expect some niche partitioning if some prey resources are shared. However, if resources are patchily distributed, this may lead to interspecific interactions (Spitz *et al.*, 2006).

1.2.5 Object-oriented play

Object-oriented play includes practice-fighting and infanticide, which is known to be practised by bottlenose dolphins (Patterson *et al.*, 1998; Kaplan, 2009; Robinson, 2014). Similar behaviours to those used in attacks on porpoises have been seen in direct observations of infanticide in bottlenose dolphins (Kaplan *et al.*, 2009; Robinson, 2014). Infanticide is practised by males to increase their reproductive success. Female bottlenose dolphins calve every two to eight years (average of three). However, after losing a calf, a female may become sexually receptive again after 7-11 days (Connor *et al.*, 1996). However, in times of high male harassment, females are able to go into a 'sham-estrous' to avoid being exploited by males (Connor *et al.*, 1996). Some strandings' studies have highlighted the fact that a large proportion of harbour porpoises killed by bottlenose dolphins are of a similar length to bottlenose dolphin calves (Ross and Wilson, 1996; Jepson and Baker, 1998; Patterson *et al.*, 1998). In California, Cotter *et al.* (2011) found that 92% of bottlenose dolphins involved in aggressive interactions were confirmed males, consistent with the theory that these may be practice for infanticide and that males are more aggressive. However, a female may also kill another female's calf to reduce competition, thereby increasing her offspring's survival fitness (Wolff, 1997).

In some areas, male competition is particularly high and, as a result, male sexual aggression is common (Connor *et al.*, 1996). Males will fight one another to gain access to females. However, direct fighting between large males for practice has a potential cost and so it is possible that harbour porpoises are used to practice their fighting skills without suffering the costs of fighting a conspecific (Cotter *et al.*, 2011).

1.2.6 Elevated testosterone levels

High levels of testosterone are known to be linked to heightened aggression in vertebrates, including humans (Archer, 1988). It is therefore possible that high levels of testosterone during the breeding season trigger an increase in aggressive behaviour, which is directed towards harbour porpoises (Higgins and Tedman, 1990; Rose *et al.*, 1991). In California, the period in which harbour porpoises and bottlenose dolphins co-occur most coincides with the peak in the breeding season (Cotter *et al.*, 2011). However, in the United Kingdom, given the variation in patterns in different regions, there is little seasonality in harbour porpoise strandings due to attacks and the two species co-occur year round (CSIP, 2013), although seasonal trends in stranded-attacked porpoises do occur in Wales (Evans and Hintner, 2010).

1.2.7 Skewed operational sex ratio or sexual frustration

A skewed ratio of males to females may lead to increased aggression due to the low number of sexually available females to males (Le Boeuf and Campagna, 1994). During times of low female numbers, there may be an increase in sexual frustration from inexperienced or low ranking males that are unable to attain females (Le Boeuf and Campagna, 1994).

1.3 Attacks in Wales

Attacks on harbour porpoises in British waters were first reported by Ross and Wilson (1996) in the early 1990s and since then these often fatal interactions, have been increasing in frequency (Penrose, 2006). Due to the regular occurrence of the attacks, the cause for them must be recurrent. These attacks are now a major source of mortality of harbour porpoises in Wales, which are becoming more notable than bycatch (Evans and Hintner, 2010; Deaville, 2014) (Figure 11). The fact that both species are protected under Annex II and Annex IV of the EU Habitats Directive and are spatially protected by Special Areas of Conservation (SAC) in parts of their range, and strictly protected against killing, injury and disturbance throughout their European range (European Protected Species), further complicates their conservation. Consequently, it is important that reasons for these attacks in Wales are established so that the cetaceans can be better managed.

The aim of this study was to examine the factors that are likely to influence the occurrence of this behaviour around the Welsh coast and to collate all of the current strandings data to observe any change in attack frequency, as well as temporal and spatial variation in their occurrence. An investigation into the reasons for the non-predatory, often fatal interactions between bottlenose dolphins and harbour porpoises was carried out using records of strandings from the Welsh coast from the Cetacean Strandings Invesitgation Programme (CSIP) database between 1990 and 2013, and sightings data from the Sea Watch Foundation boat surveys between 1990 and 2014. Fish stock data from ICES rectangles were used to investigate changes in fish abundance and catch, which may relate to fish stock abundance in Wales. This study hypothesised that when co-occurrence of the species is high, there would be more attacks. Overlap in dietary species and changes in prey abundance were hypothesised to be important causal factors of the aggressive interactions in Welsh waters, although there are likely to be a number of reasons for the attacks. The literature and primary data were assessed and conclusions were then drawn.

2. Methods

2.1 Study area

The Welsh coastline is approximately 2740 km long (Darkes, 2008). Lining the eastern edge of the Irish Sea, it is on the European Continental shelf. An important feature of the study area is Cardigan Bay (Figure 3), the largest bay in the British Isles, with an area of approximately 5500 km^2 (CCW, 2009). It has a gentle sloping shelf and reaches a depth of approximately 50 metres, with weak currents and a moderate tidal range (Baines *et al.*, 2000).

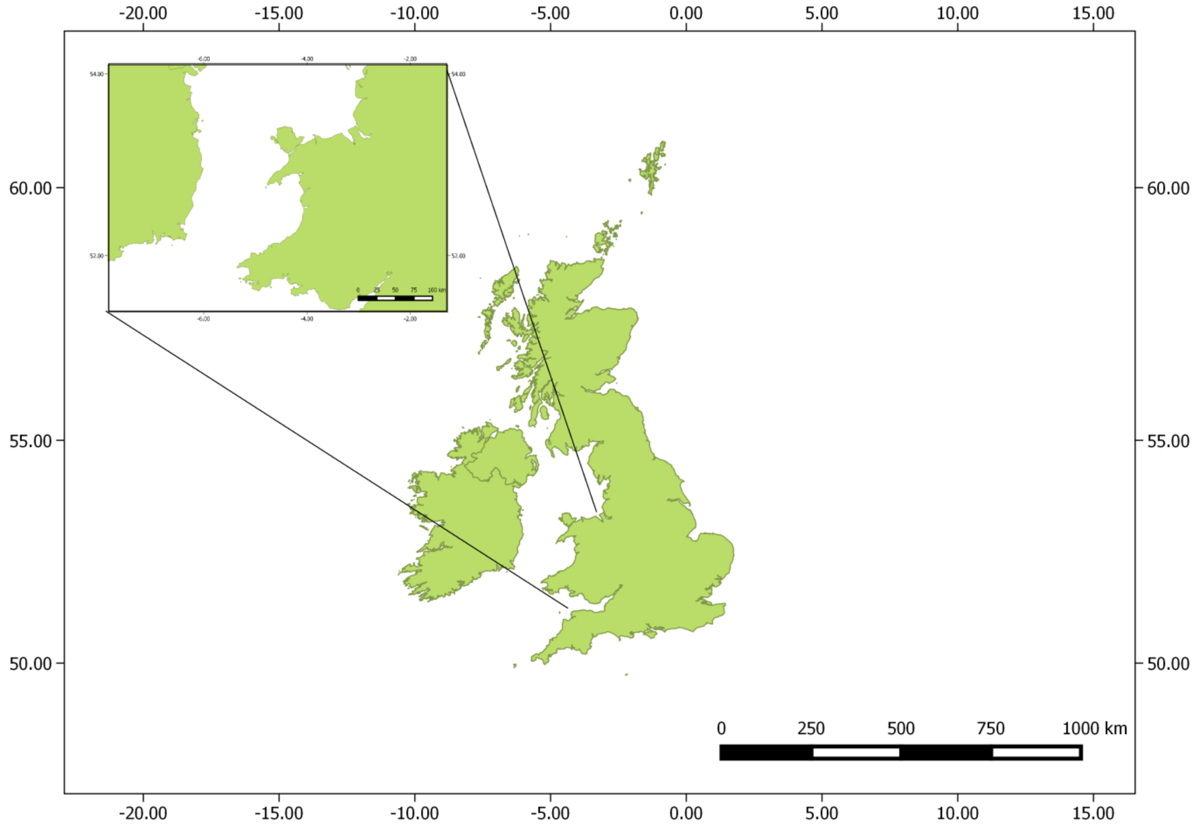


Figure 3. Map of UK with Cardigan Bay and the Welsh coast as an inset

Cardigan Bay has two Special Areas of Conservation (SAC) established under the European Habitats and Species Directive (Council Directive/92/43ECC); one in the South, named Cardigan Bay SAC, covering 95,860.36 hectares, and one in the North called Pen Llyn ar'Sarnau SAC. Bottlenose dolphins are features of both SACs, but Cardigan Bay was primarily designated for this species, which uses the area mainly in summer, for feeding and reproduction (Feingold and Evans, 2014). Harbour porpoises are found throughout Cardigan Bay but do not yet have designated SACs, although they are currently listed as present in both (Natural Resources Wales, 2015).

2.2 Data collection

From the literature, it was found that the non-predatory aggressive behaviour between bottlenose dolphins and harbour porpoises cannot be explained by aberrant behaviour as it is observed in so many locations worldwide. Therefore, aberrant behaviour was not considered further as a factor in this study.

Geographic distributions of the two species within the study area were compiled from the Atlas of Marine Mammals of Wales (AMMW) (Figure 4) (Baines and Evans, 2012), with more recent sightings data supplied by the Sea Watch Foundation. These data were used to investigate the idea of geographic overlap which, if significant, could implicate aggressive territorial behaviour.

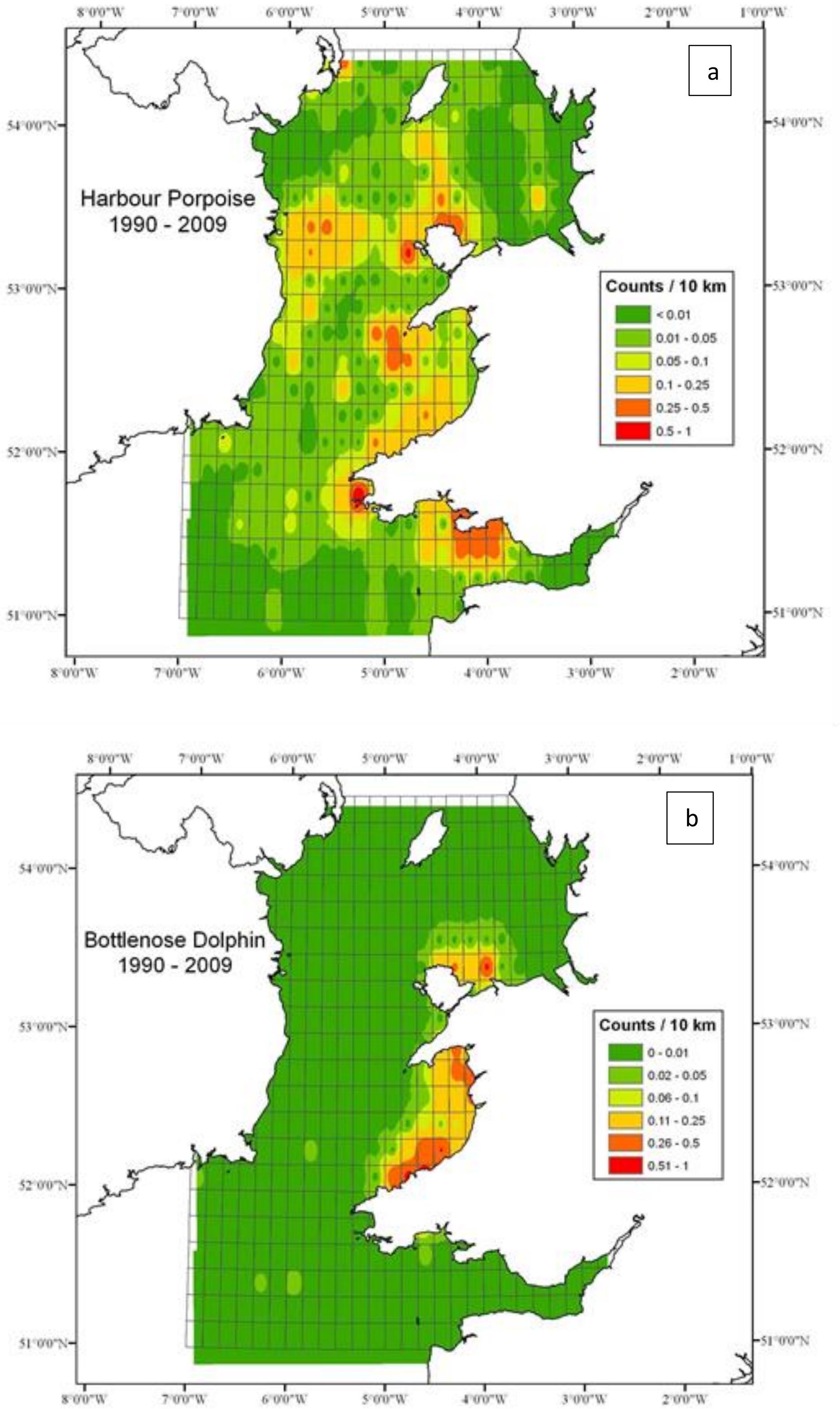


Figure 4. Map of Harbour porpoise (a) and Bottlenose dolphin (b) distribution- Interpolated long term mean sightings from vessel counts per 10km, 1990-2009. (Baines and Evans, 2012)

Past studies which investigated the stomach contents of both species in areas of their abundance, such as Moray Firth, Scotland, and the French and Spanish Bay of Biscay coasts, were used to review dietary overlap, which if significant could cause aggressive behaviour due to prey competition. A study of harbour porpoise diet in the Irish Sea (Browne, 1999) was also reviewed to establish the importance of particular prey species in the study area. Fisheries data from ICES (www.ices.dk) were analysed to review any changes in fish species abundances in area VIIa (Figure 5) that may indicate changes in prey and thus influence prey competition.

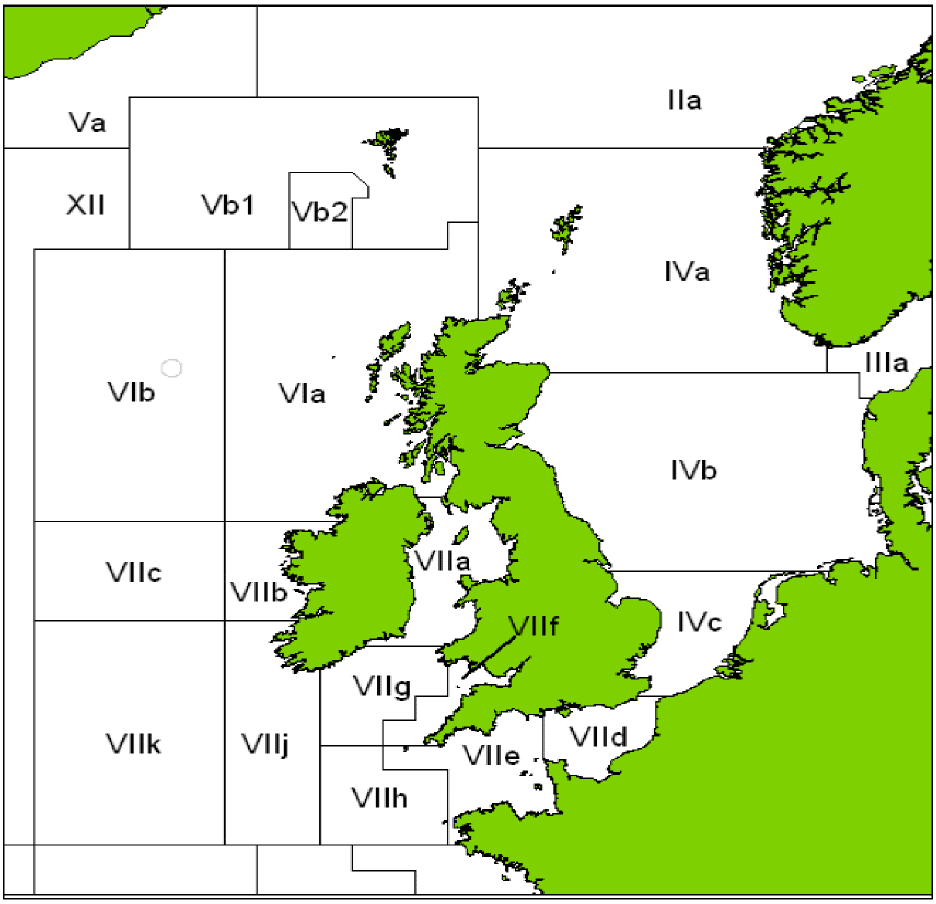


Figure 5. ICES areas around the UK coastline. Scottish Sea Fisheries Statistics, 2009

Strandings data were collected under the aegis of the Cetacean Strandings Investigation Programme (CSIP), which is jointly funded by DEFRA and the Devolved Administrations in Scotland and Wales. Using the strandings data of harbour porpoises attacked by bottlenose dolphins around the Welsh coast, an investigation into demographic factors that may show selection of porpoises was carried out. These included, gender, age or maturity, total length and weight.

Causes of harbour porpoise deaths in Wales were compared, including bottlenose dolphin attack, bycatch and disease. Areas of harbour porpoise strandings due to bottlenose dolphin attacks were plotted over time, to explore variation in the geographical extent of the attacks.

Object-oriented play could not be fully analysed for Wales as there have been no identified strandings of bottlenose dolphins, either calves or adults, which had been attacked by conspecifics. However, primary literature was reviewed for object-oriented play and data from Scotland on calves were compared with Wales, to determine whether infanticide or practice-fighting could be considered as factors for attacks on harbour porpoises in Wales.

Due to the difficulties in surveying marine mammals, the operational sex ratio of the population could not be determined, as this can only be accurately determined by examining the genital slits of all individuals. Constraints in the ability to give an estimated time of death mean that increased testosterone levels during the breeding season could not be fully investigated as a cause of aggression. However, monthly trends were investigated to give an approximation of seasonality in the attacks.

2.3 Methods of data analysis

2.3.1 Strandings data

The number of harbour porpoise strandings and reasons for death were examined using data from CSIP. These data were also used to determine any demographic factors that might increase the likelihood of a harbour porpoise being attacked by bottlenose dolphins. The sex and condition (weight:length) of attacked porpoises were investigated using ANOVA in SPSS (V.22). Decomposition states (freshly dead, slight decomposition, moderate decomposition and advanced decomposition) were taken into account.

2.3.2 Inter-species territoriality

All data were first cleaned and validated to remove any errors (missing values, incorrect coordinates and duplicates). The study area was split into a grid for analysis, using the grid tool in MapInfo (V.11); cells were plotted as a Universal Transverse Mercator 30N and then projected as WGS84. Data for Cardigan Bay were entered into this 961 cell grid, with cells of 0.033333’x 0.033333’, enabling the probability of interaction to be determined by investigating the density of each species within a cell in a certain month and year. Data were assigned a grid cell based on latitude and longitude (Datum WGS84); sightings and strandings data were then plotted. The original grid (10’x10’ cells) from the AMMW (Baines and Evans, 2012) was used to further the data analysis. All sightings’ data were summed together by cell, year and month, having been corrected for effort (kilometres travelled by the vessel). However, Cardigan Bay data was not corrected for sea state and observer bias. Data were then split by months, quarters and years to investigate spatial and temporal trends over differing time periods. Cardigan Bay data were limited to the years 2001-2014 and the months of April-October, as these periods had consistent effort (Figure 6). Data from AMMW included all months and the years 1990-2010. The latter were used to investigate monthly trends in strandings, and co-occurrence within the wider Irish Sea, and to give an overview of distribution and abundance of the cetaceans. Cardigan Bay data were compiled and all variables (strandings, co-occurrence, sightings, and fish abundance) were analysed, to investigate temporal and spatial patterns of attacks within Cardigan Bay.

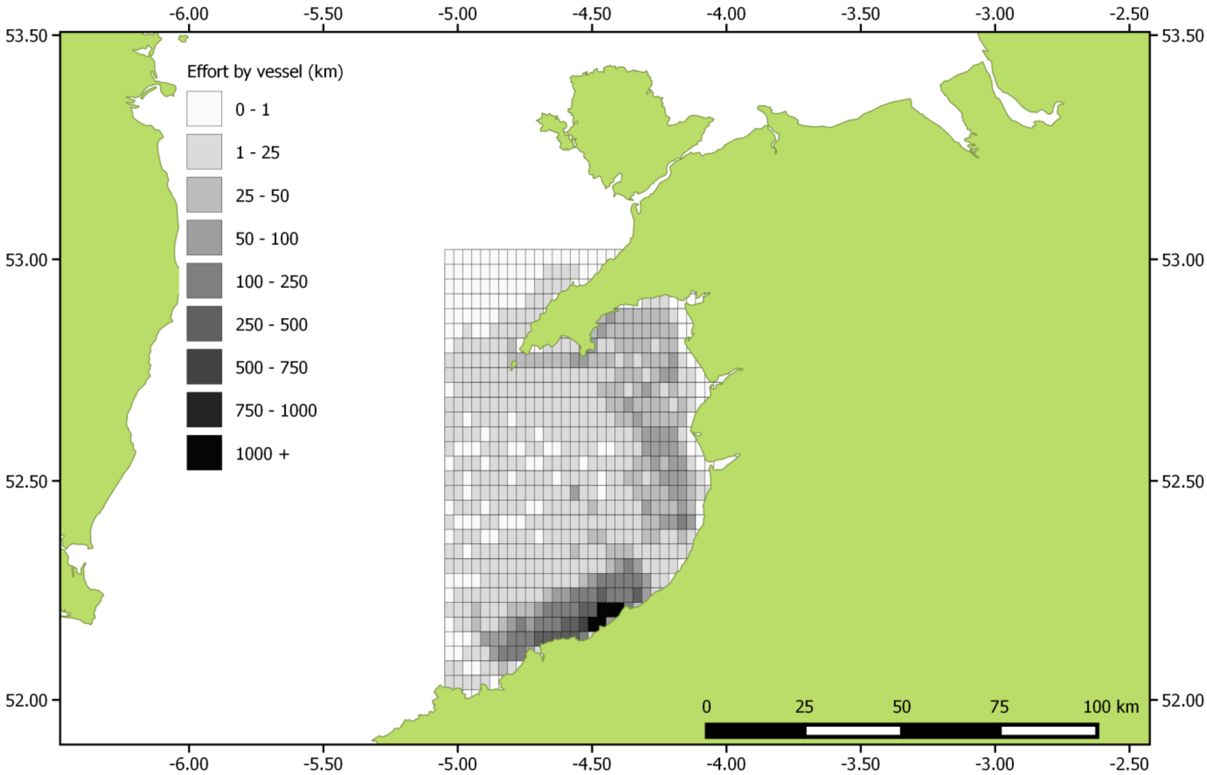


Figure 6. The total amount of effort (km) carried out on vessel surveys, April-October, 2001-2014 (Cardigan Bay data)

MapInfo and QGIS were used to plot sightings' data of harbour porpoises and bottlenose dolphins and to establish any seasonal and temporal changes in their distribution and abundance. These data were also used to plot maps of co-occurrence of the species, in which both species had to occur in the same cell within the same month and year to be considered as co-occurring. Sightings' data were plotted as the density of each species per cell, per month and per year, calculated as the total number of individuals in a sighting divided by effort, whilst co-occurrence densities were calculated by summing the density of each species within a cell, per month and per year.

2.3.3 Prey competition or interference feeding

Literature was reviewed for stomach contents analysis of each cetacean. Data were collated for ICES rectangle VIIa (Figure 5), from ICES, to investigate any significant change in the abundance and landings of particular fish species (sandeels, poor-cod, haddock, whiting, flounder, saithe, sole and sprat), that are considered important in the diet of both cetaceans. Relative fish abundance was calculated as the number of individuals per haul. These were added together to give total abundance per year. Landings data used live caught weight of each species, which were added together by year and month, to investigate temporal trends. Landings data should be viewed with caution as it is economically biased. Fish species abundance were plotted and correlated with stranded-attacked porpoise numbers, using Spearman's rank and Pearson's correlation, on SPSS (V.22). Data on porpoise deaths due to starvation from CSIP were also examined to further support changes in abundance of important prey species. These were investigated with correlations. All data conformed to normality, linearity, and were homoscedastic.

2.3.4 R analysis

A binomial Generalised Linear Mixed Model (GLMM) was used to account for the repeated sampling in the same cell within the same months and years. The model investigated the relationship between the occurrence of stranded-attacked porpoises and species co-occurrence, year, month, dolphin group size and fish species abundance. Cells were named as 'coastal' or 'offshore'. Co-occurrence, group size of both cetaceans and ratio of dolphins to porpoises were calculated for each coastal cell and 3x3 cells surrounding it. Cardigan Bay data were used and were summarised by year, month and cell. In total, 9083 observations of 15 variables (Table 4) were input to R (V.3.1.2) (R Core Team, 2013) and were used to form different models that could be tested for best fit. Firstly, correlations between explanatory variables were tested to observe any linearity (Figure 7). If there was a correlation, these variables were not used together in a model, as factors would be confounding and would affect the final output. A total of 13 models were run in R for this analysis and the linear mixed effect models were fitted by maximum likelihood. The best model used was based on the lowest AIC (Akaike's Information Criteria), which measures the relative complexity and fit of a model by giving it a number and weight.

Table 4. Variables input to GLMM, with an explanation of each variable

Explanatory Variable	**Description**
Stranding- Response variable	Whether a stranding of an attacked porpoise occurred (either 1 or 0)
Year	Year (ordinal)
Month	Month as a factor
Cell	The cell number (numbered 1-961)
Cell type	Coastal or offshore: coastal had to be bordered by land. Only coastal cells used in analysis.
Overlap	Number of cells with co-occurrence: these cells were 3x3 cells, (giving a total of 9 cells) that were 3 West and 3 South of the coastal cell in question
Ratio	Number of bottlenose dolphins per porpoise within a cell, month and year
Bottlenose dolphin group	Number of individuals in the encounter
Harbour porpoise group	The number of individuals in the encounter
Sandeels	Total abundance of sandeels (total number of individual fish) within ICES VIIa
Haddock	Total abundance of haddock (total number of individual fish) within ICES VIIa
Whiting	Total abundance of whiting (total number of individual fish) within ICES VIIa
Poor-cod	Total abundance of poor-cod (total number of individual fish) within ICES VIIa
Total fish	Total abundance of fish species (sum of all species abundance) within ICES VIIa
Effort	The amount of kilometres travelled by the vessel per cell, month and year.

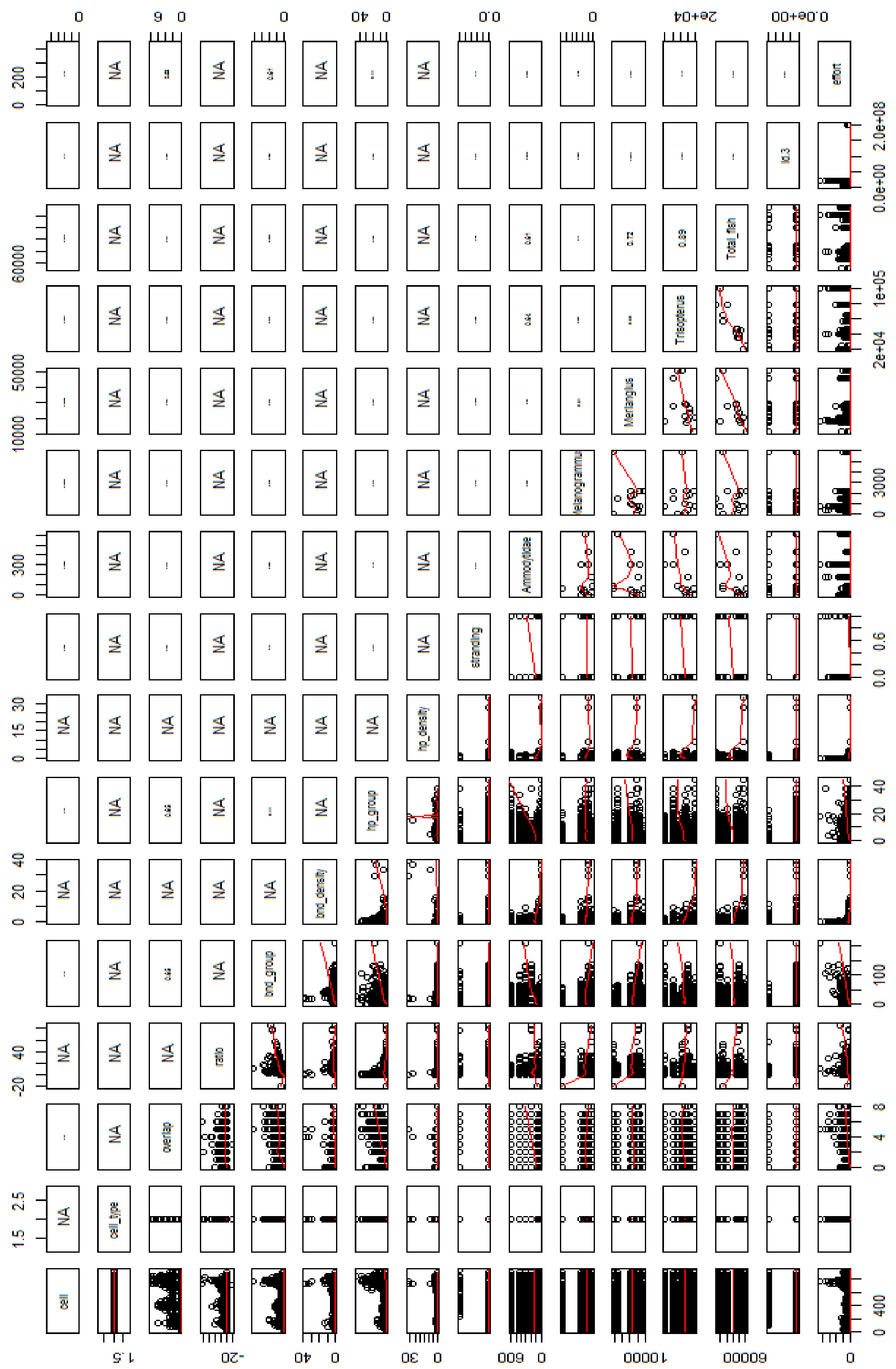


Figure 7. Correlations between explanatory variables input in GLMM

2.3.5 Object oriented play

Literature was also reviewed to determine whether there were any cases of bottlenose dolphin infanticides or fighting between adult males in the UK. Injuries sustained from these attacks were compared with those found on attacked harbour porpoises. The body lengths of the dolphins attacked were also compared with that of attacked harbour porpoises. Similarities in these, may point towards infanticide or practice-fighting as a cause for attacks on porpoises.

2.3.6 Skewed operational sex ratio or sexual frustration & elevated testosterone levels

Stranding data, included- date, location, time and cause of death. These were used to plot maps in QGIS of patterns in strandings due to bottlenose dolphin attacks. Spatial variations of attacks may indicate changes in movement patterns of the cetaceans. Although, the area of stranding is not necessarily indicative of the area of attack, as tides and currents may move an animal a long way before it strands. Seasonality of attacks was also reviewed using strandings' data, which may indicate increased aggression of bottlenose dolphins during particular months.

3. Results and Analysis

3.1 Strandings data

The number of stranded-attacked porpoises in Wales showed a non-significant increase between 1991 and 2013 (p=0.85) (Figure 8). However, data split into time periods (1991-2004 and 2004-2013) found the increase and subsequent decrease in strandings to be significant (Regression: 1991-2004 R^2=0.7978, p=0.004 and 2004-2013 R^2=0.7091, p=0.002). In 2004, the greatest number of attacks (n=28) occurred, whilst no attacks (n=0) occurred in 1992-1994 and 1997. However, 20.4% of stranded-attacked harbour porpoises were not sent for post-mortem due to limited funding yet were determined as attacked by bottlenose dolphins by an expert in the field.

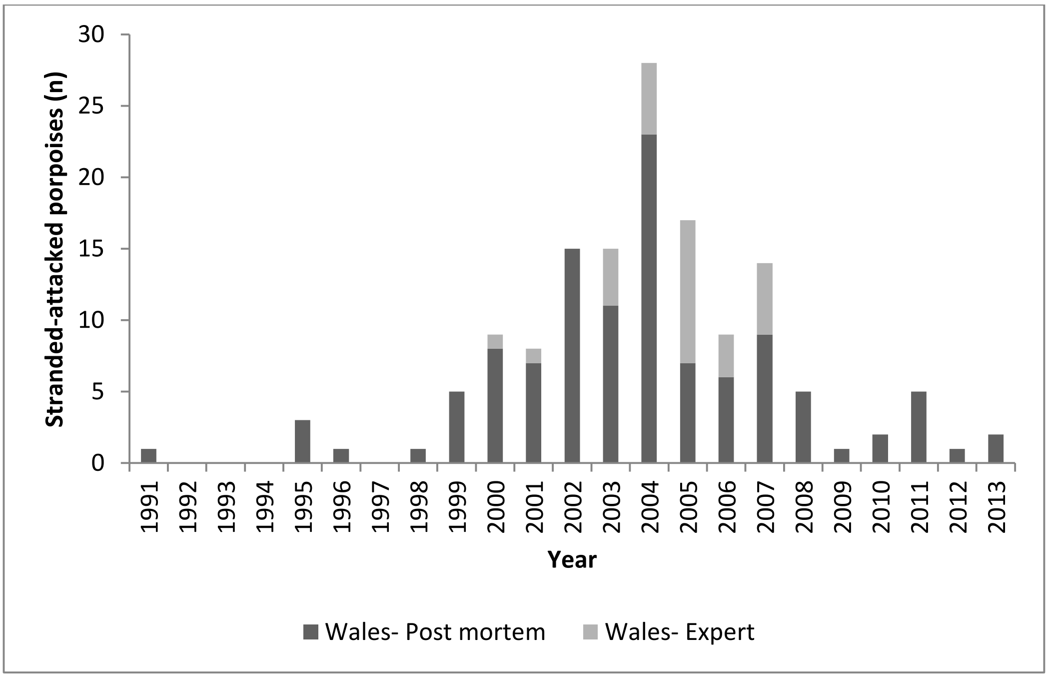


Figure 8. Number of stranded harbour porpoises attacked by bottlenose dolphins in Wales, 1991-2013

The number of stranded-attacked harbour porpoises varies significantly (T-test p=0.002) between England and Wales (Figure 9). Harbour porpoise strandings due to bottlenose dolphin attacks in Wales are a significant cause of death, accounting for over 20% (Figure 10) whereas in England, the attacks are the causal factor in only a small percentage of harbour porpoise deaths, bycatch being the most important at 17% (Deaville and Jepson, 2011).

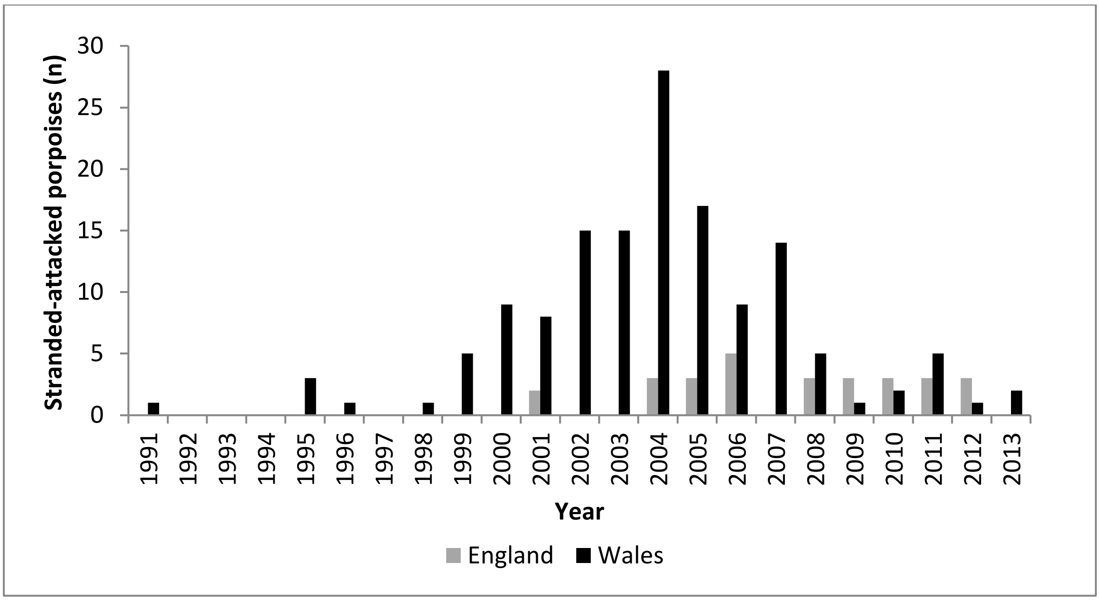


Figure 9. Total number (post-mortem and expert) of stranded-attacked harbour porpoises in England and Wales, 1991-2013

Causes of death for all harbour porpoises stranded along the Welsh coast highlights the large number (22%) of stranded porpoises due to physical trauma from bottlenose dolphins (Figure 11). This is most obvious in 2004 (Figure 8).

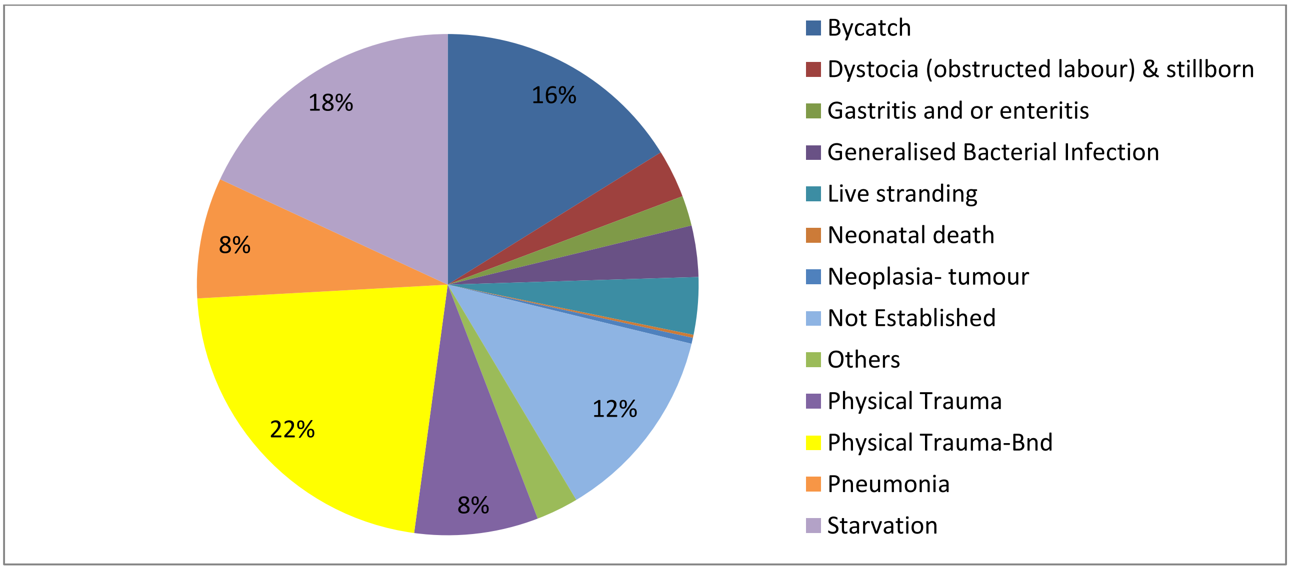


Figure 10. Total percentage of harbour porpoise deaths along the Welsh coast due to each factor between 1990 and 2013

Nutritional condition (weight:length) of necropsied harbour porpoises (Figure 11) was positively correlated (r=0.925,p=0.000). These data were then separated out to include variability due to decomposition (Figure 12). There was no significant difference in the ratio of body length:weight, between porpoises stranded-attacked and those stranded for other reasons (One-way ANOVA:$F_{99,6}$=3.253,P=0.068), suggesting that attacked porpoises attacked are not under- or over-sized and so bottlenose dolphins are unlikely to attack porpoises of a certain body condition.

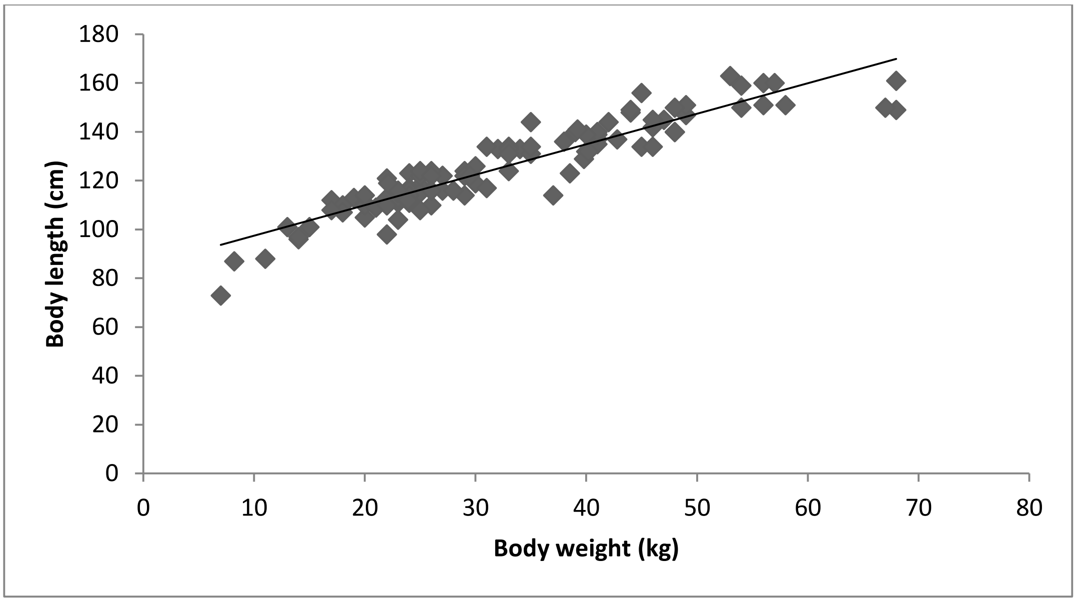


Figure 11. Body weight to length ratio of necropsied stranded-attacked harbour porpoises in Welsh waters, 1991-2013 (y=1.2492x+84.897, R^2=0.8549)

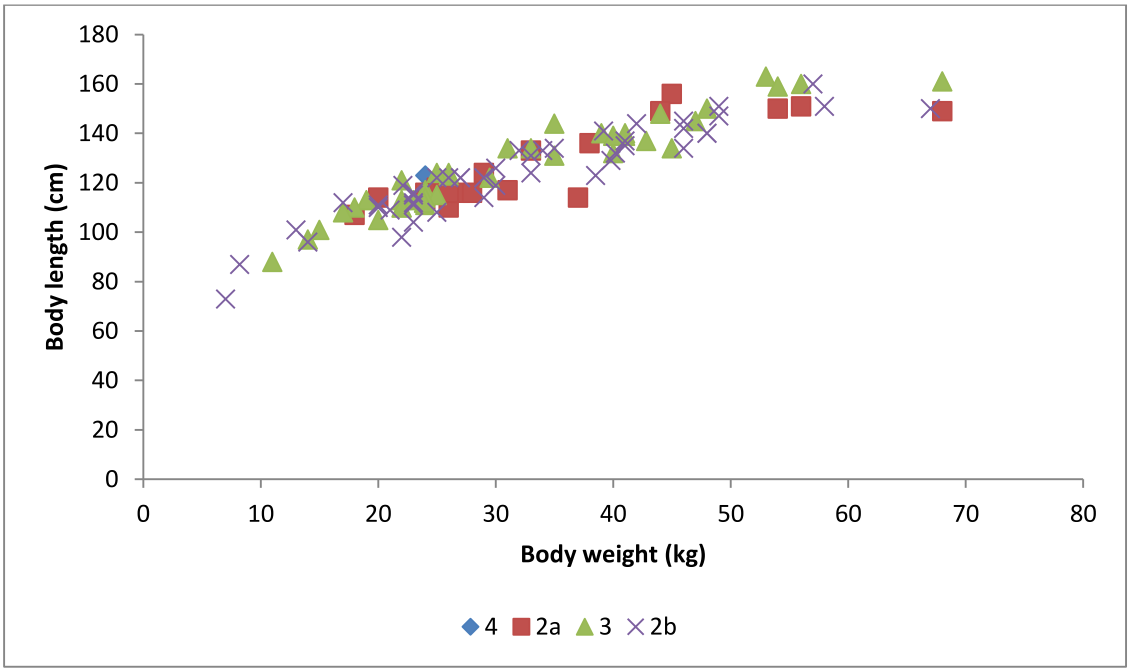


Figure 12. Body weight to length ratio of necropsied stranded-attacked harbour porpoises with decomposition state in Welsh waters, 1991-2013 (2a=Freshly dead, 2b=Slight decomposition, 3=Moderate decomposition, 4=Advanced decomposition)

3.2 Inter-species territoriality

Sightings of bottlenose dolphins and harbour porpoises peaked from April-September (Figures 13, 14). Bottlenose dolphins were sighted less than harbour porpoises from January-March, and October-December, although bottlenose dolphin densities within a cell tended to be higher than that of harbour porpoises.

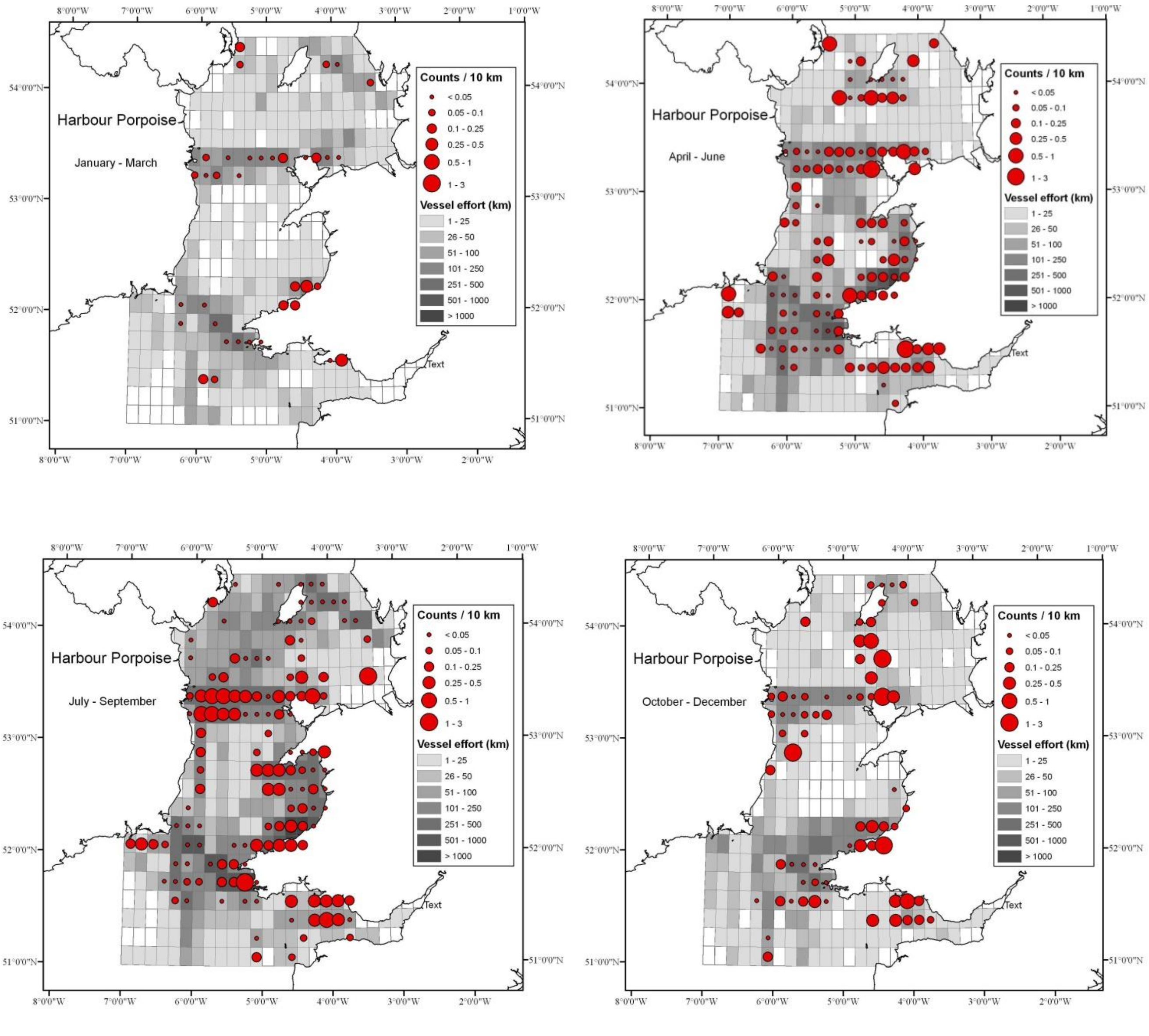


Figure 13. Harbour porpoise - Long term quarterly mean sighting rates from vessel surveys, 1990-2009 (Baines and Evans, 2012)

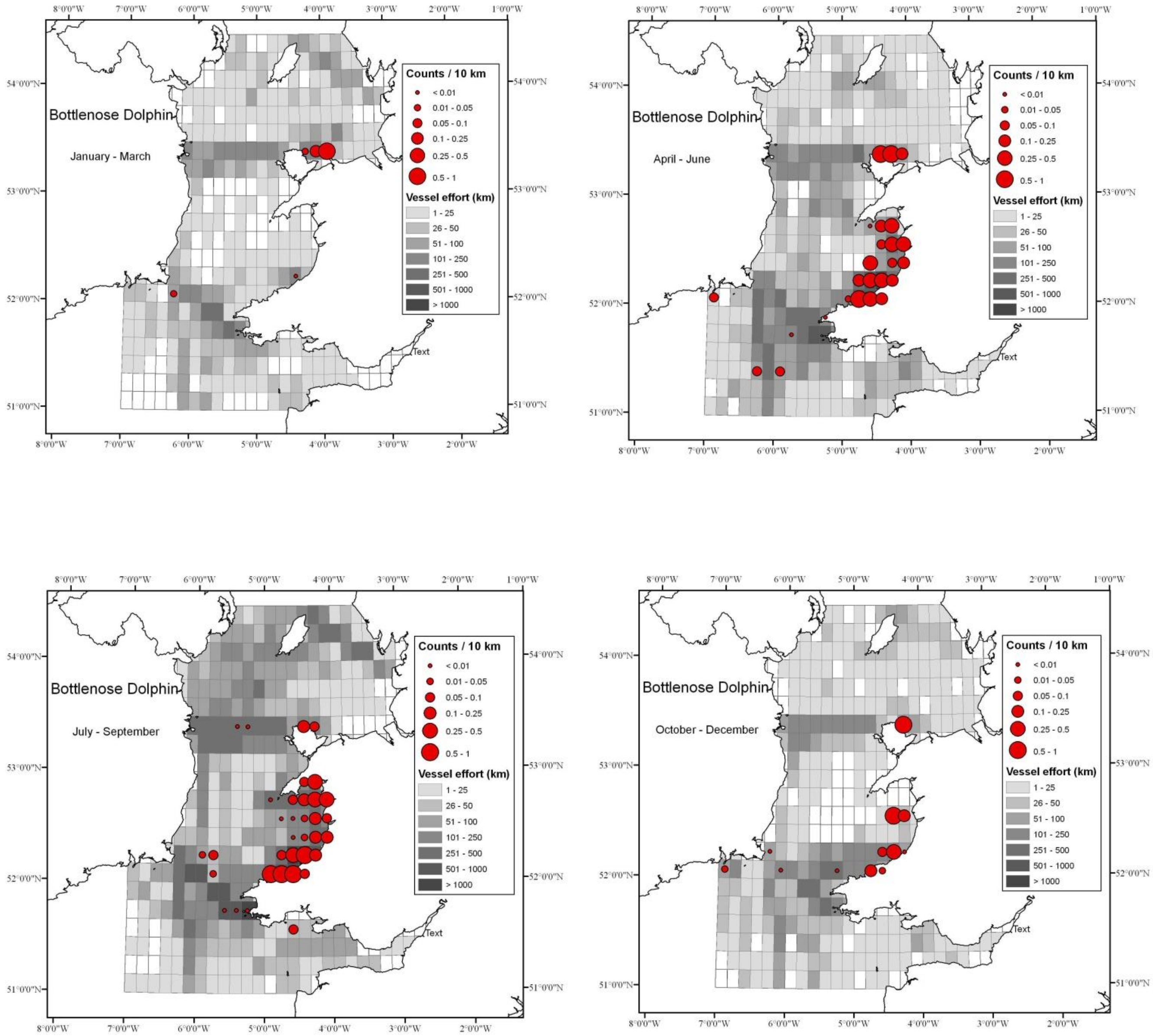


Figure 14. Bottlenose dolphins - Long term quarterly mean sighting rates from vessel surveys, 1990-2009 (Baines and Evans, 2012)

Co-occurrence existed throughout Cardigan Bay between April and October (Figure 15). Overall, strandings occurred throughout the study area in all months, with little change in temporal distribution (Figure 15).

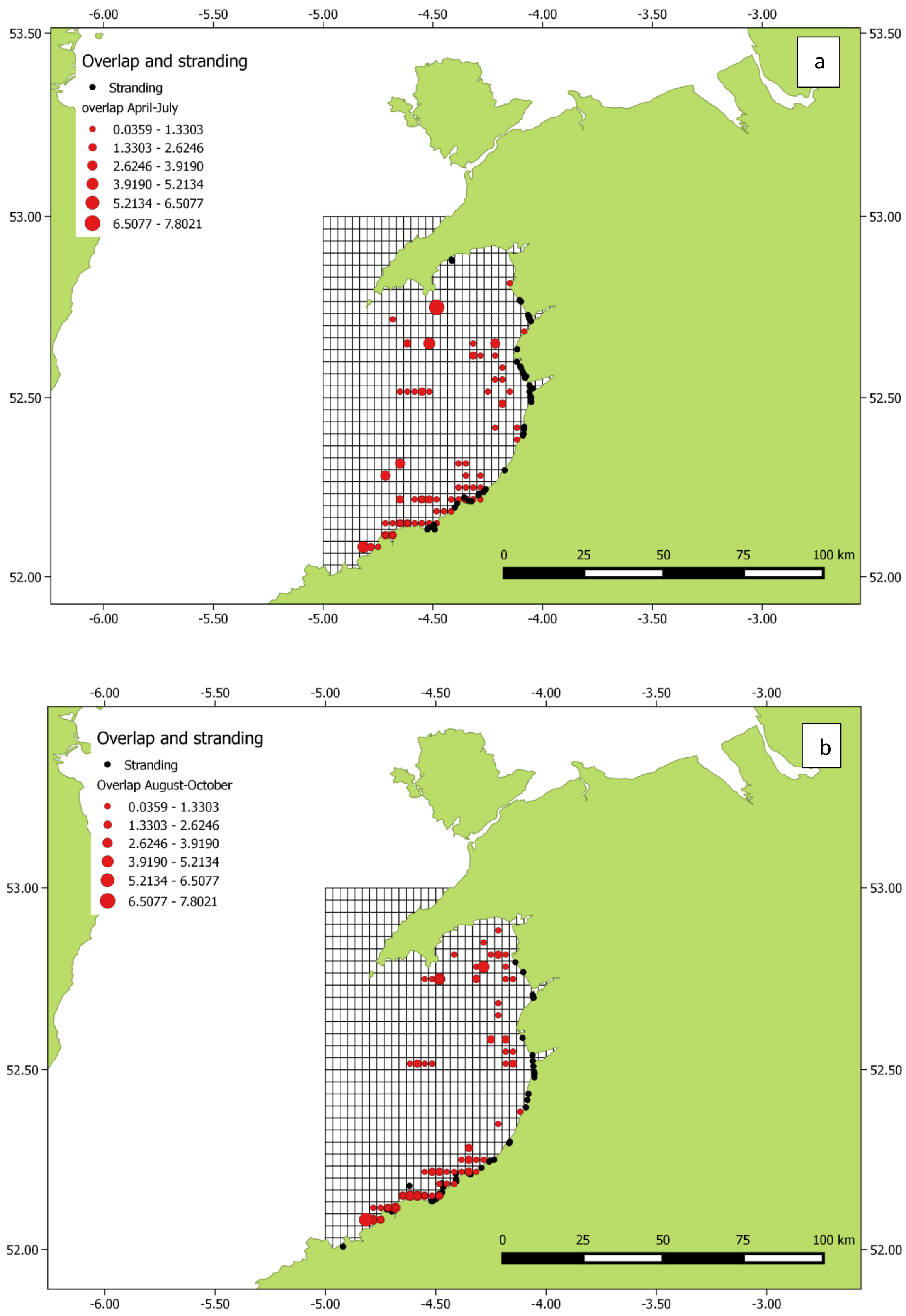


Figure 15. Distribution of co-occurrence per km (corrected for effort) of the species and stranded-attacked harbour porpoises between (a) April-July and (b) August-October, 2001-2014

When co-occurrence of the cetaceans is highest, the number of stranded-attacked porpoises tends to be highest along the Welsh coast (Pearson's correlation, p=0.049), such as in 2004 when co-occurrence density was 36 and the number of stranded-attacked porpoises reached a peak of 28 (Figure 16). However, in 2006, co-occurrence between the species was high but strandings were lower than expected.

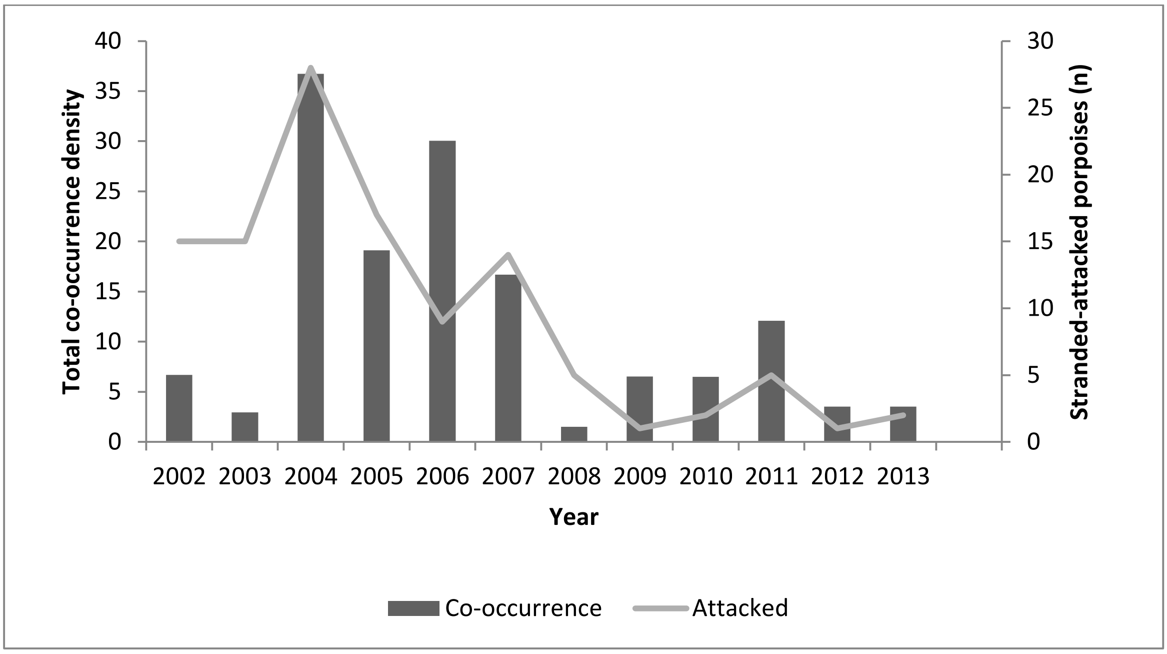


Figure 16. Relationship between the co-occurrence density of the cetaceans and the number of stranded-attacked porpoises, 2002-2013

The number of stranded-attacked harbour porpoises shows a similar trend as the co-occurrence density of the cetaceans (R^2=0.6505, p=0.193) with peaks of strandings occurring in the 2nd and 3rd quarters, during the time of peak co-occurrence (Figure 17).

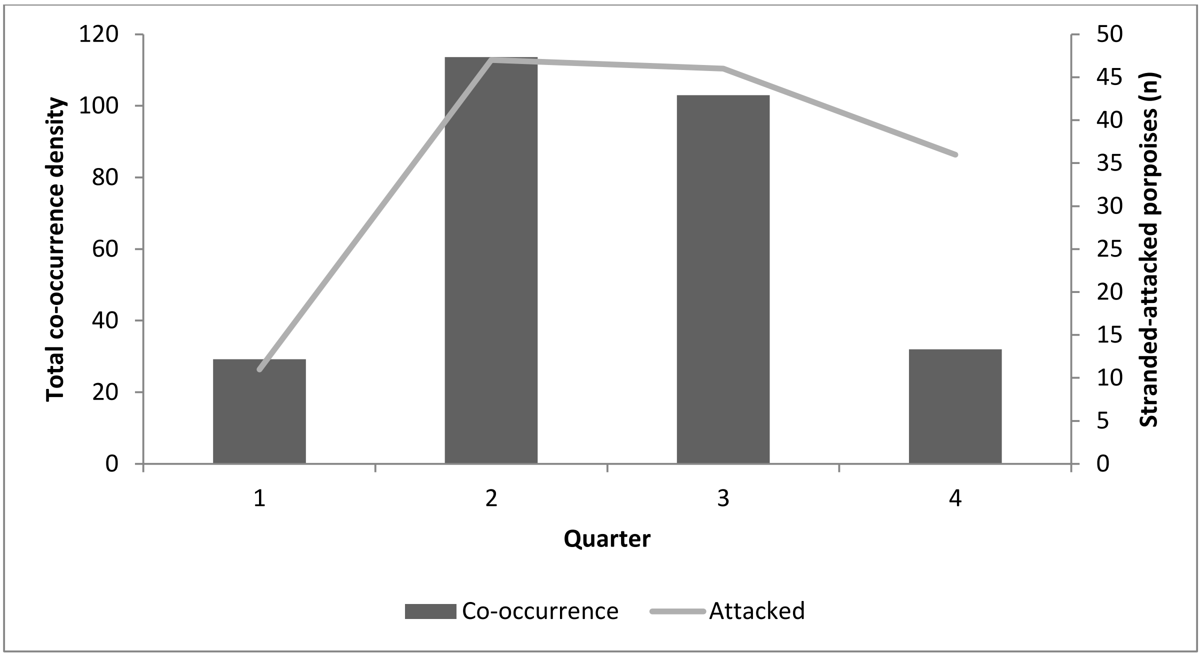
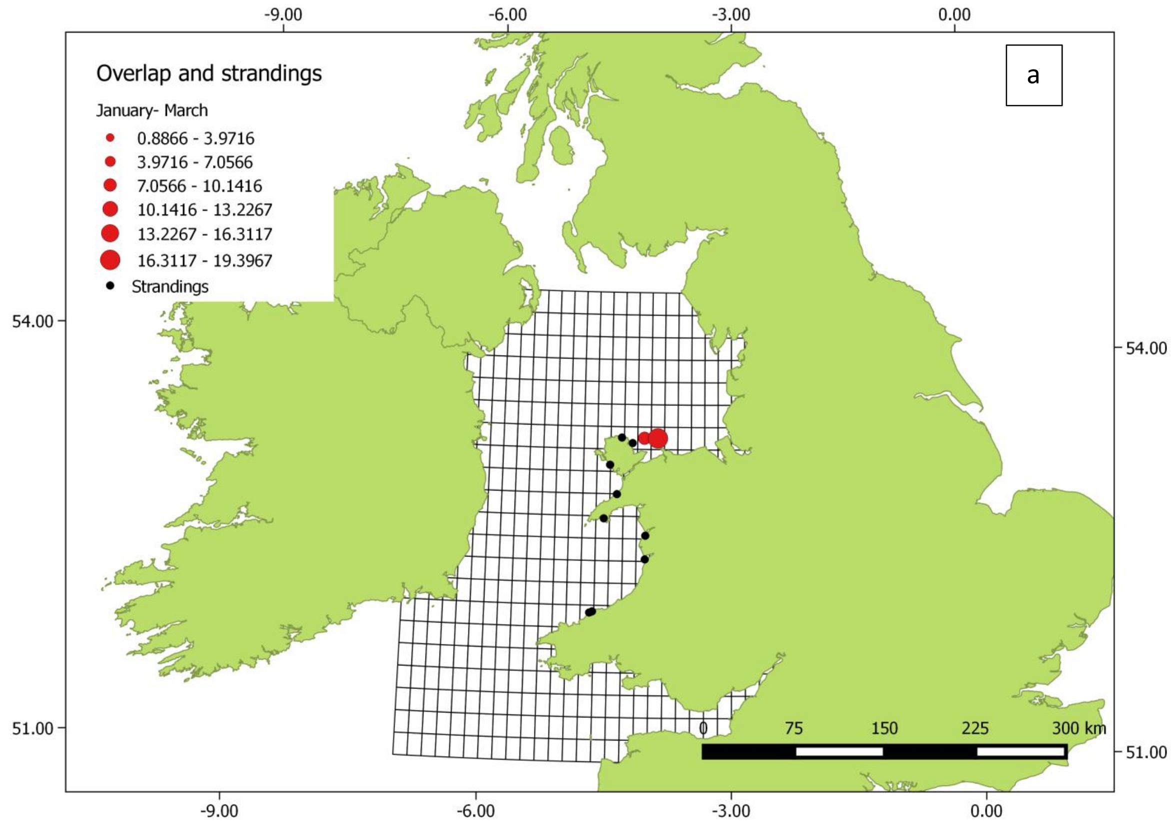
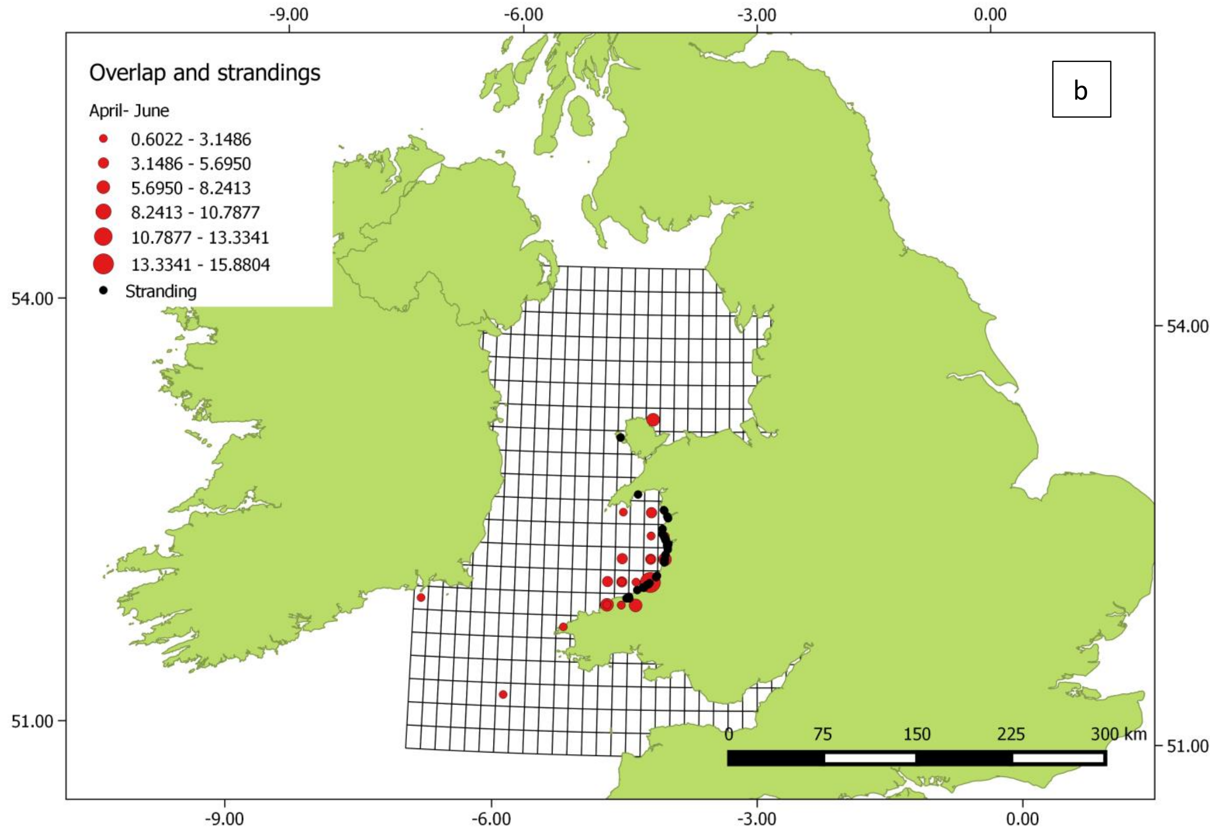


Figure 17. Relationship between the co-occurrence density of the species and the number of stranded-attacked porpoises by quarter, (1st=January-March, 2nd=April-June, 3rd=July-September, 4th=October-December)

Seasonal distribution maps were plotted using data from Baines and Evans (2012), showing that co-occurrence changed through the year, with low co-occurrence in North Wales from January-March (Figure 18a) and high co-occurrence from April-September throughout Cardigan Bay (Figure 18b-c). Occurrence of stranded-attacked porpoises follows a similar pattern. However, attacked porpoises also strand in southern Cardigan Bay during January-March (Figure 18a) when co-occurrence was found only in North Wales.


Overlap and strandings
January- March
0.8866 - 3.9716
3.9716 - 7.0566
7.0566 - 10.1416
10.1416 - 13.2267
13.2267 - 16.3117
16.3117 - 19.3967
Strandings
a
0 75 150 225 300 km


Overlap and strandings
April- June
0.6022 - 3.1486
3.1486 - 5.6950
5.6950 - 8.2413
8.2413 - 10.7877
10.7877 - 13.3341
13.3341 - 15.8804
Stranding
b
0 75 150 225 300 km

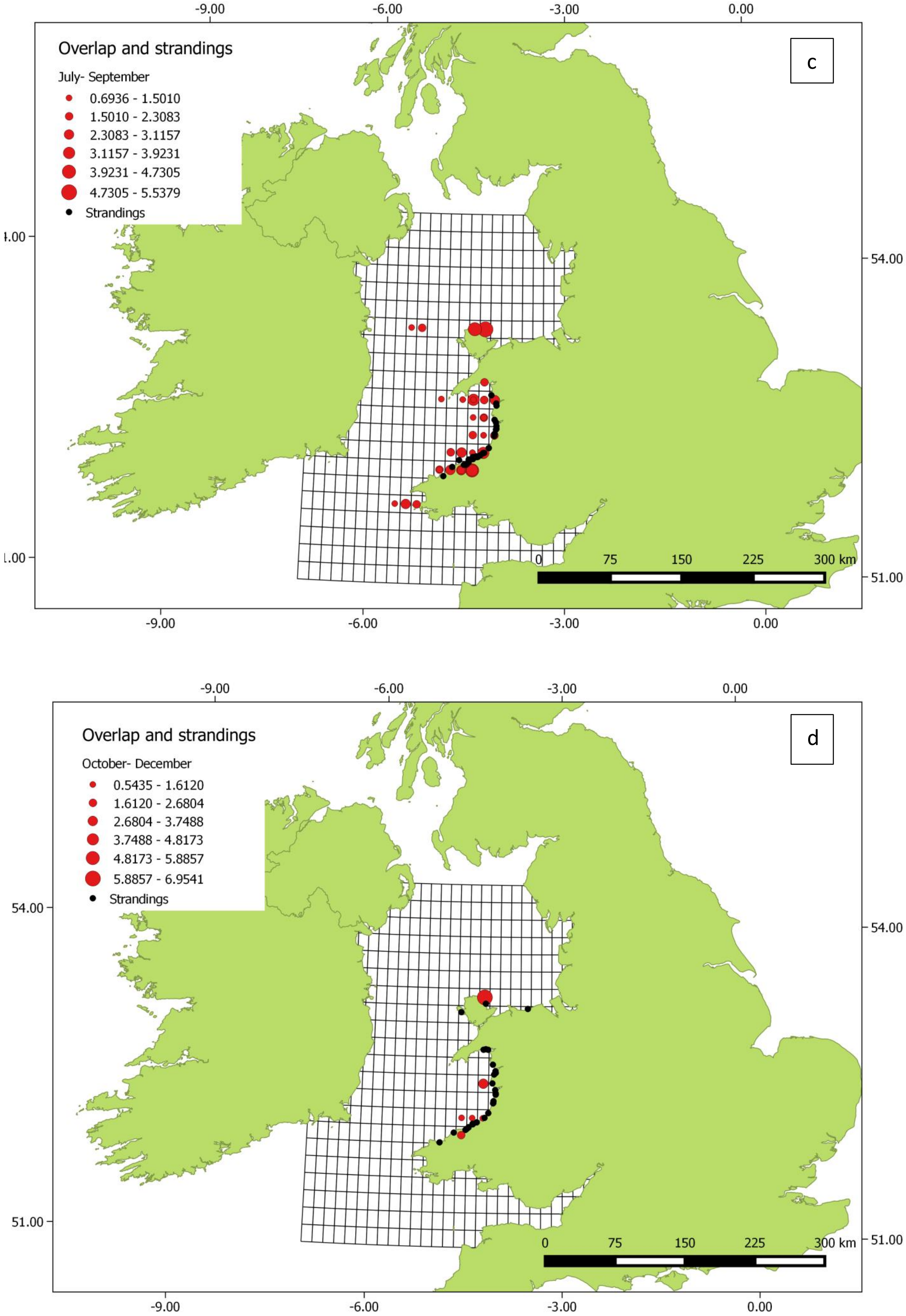


Figure 18. Co-occurrence of cetaceans between each quarter (a) January-March, b) April-June, c) July-September, d) October-December) and distribution of stranded-attacked porpoise

Using T-POD data from Simon *et al*. (2010), harbour porpoises were detected throughout 2005 and 2006, but showed a seasonal occurrence pattern which contrasted with that of bottlenose dolphin at the majority of sites (6 out of 8) (Figure 19, 20). The number of simultaneous detection positive minutes (DPM) of both species at the same T-POD was low (<8.5DPM), suggesting that the cetaceans avoid each other, or at least one species discontinues echolocation during the others' presence (Table 5).

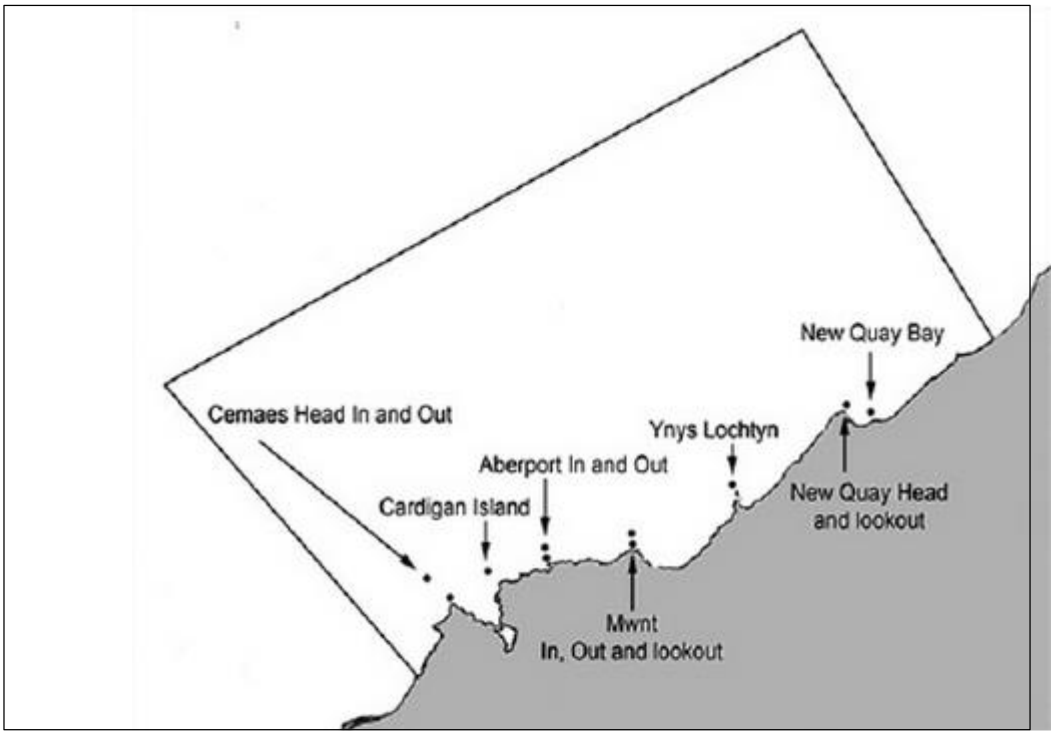


Figure 19. Map of Cardigan Bay SAC with the location of T-PODS used to collect presence data of both harbour porpoises and bottlenose dolphins (Simon *et al*., 2010)

Table 5. Total number of detection positive minutes and percentage of simultaneous detections of both species within one minute (Simon *et al*., 2010)

Location	Total detection positive minutes (DPM)	Detection positive minutes (DPM) for both species (%)
New Quay Bay	8410	0.6
New Quay Head	14747	0.8
Ynys Lochtyn	9214	0.6
Aberporth In	12110	0.7
Aberporth Out	21890	1.1
Mwnt In	9694	1.5
Mwnt Out	6932	0.1
Cardigan Island	8880	0.5
Cemaes Head In	6319	8.4
Cemaes Head Out	6121	0.0

Harbour porpoise detection peaked during months when bottlenose dolphin detection, and therefore abundance, was lowest. In general, there is seasonal temporal partitioning, with bottlenose dolphins most abundant in the SAC during summer and harbour porpoises most abundant in winter (Simon *et al*., 2010; Baulch, 2012; Figure 20). Harbour porpoises were detected significantly more during the ebb phase whilst bottlenose dolphins were detected during the flood. Dolphin activity peaked 1-2 hours before high water and at low water, whilst porpoises peaked 3 hours before high water and 2-3 hours after high water (Baulch, 2012; Figure 21). This pattern of abundance was consistent across the T-POD sites.

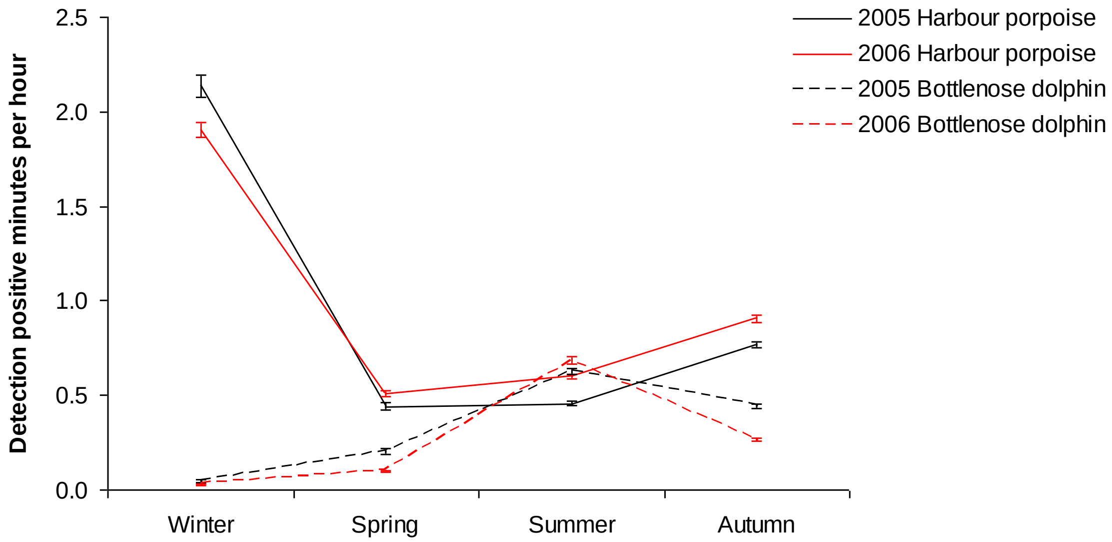


Figure 20. Acoustic detection of harbour porpoises and bottlenose dolphins - average number of detection positive minutes per hour, 2005-2006. Values are means ±1 S.E. (Baulch, 2012)

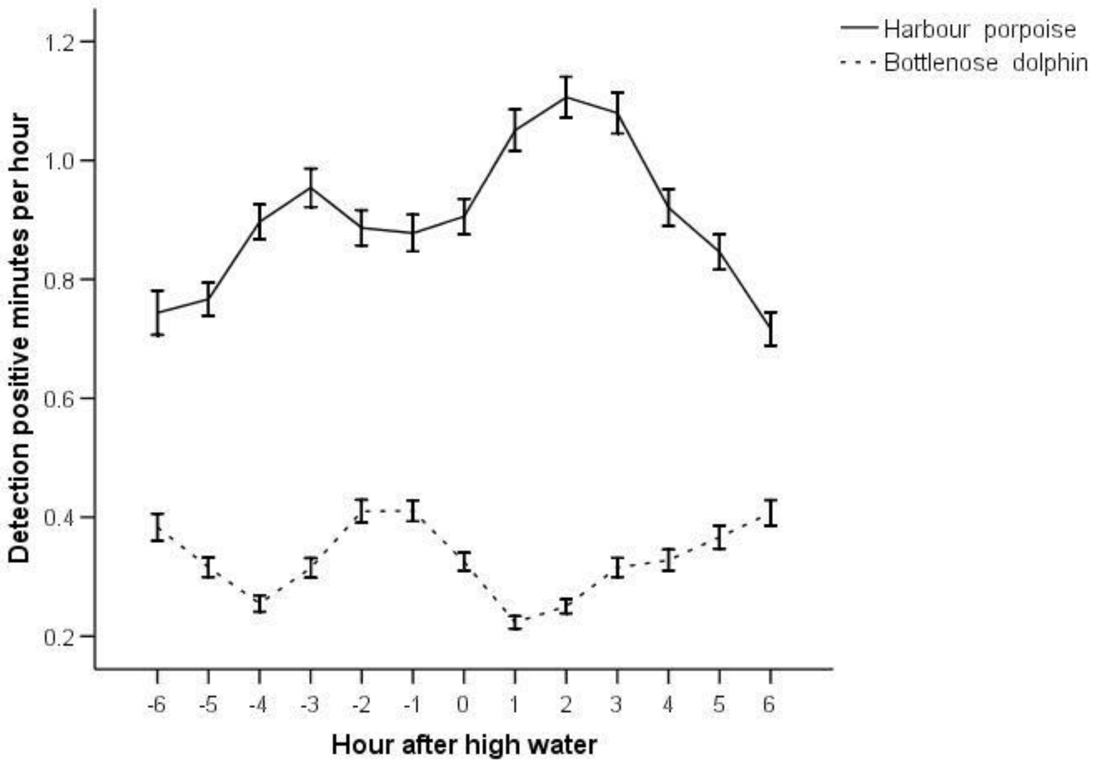


Figure 21. Average number of detection positive minutes per hour of bottlenose dolphins and harbour porpoises during the tidal cycle. Values represent means ±1 S.E. (Baulch, 2012)

3.3 Prey competition or feeding interference

Diets of each cetacean species were examined in the literature (Table 6). Shared prey species vary in importance for the two cetaceans, for example, sandeels tend to be more important in harbour porpoise diet, whereas hake (*Merluccius merluccius*) is more important for bottlenose dolphins (Table 6). All dietary data were collected from stranded or bycaught animals, which may have fed upon unusual prey species, therefore dietary data must always be viewed with caution. Often these stranded cetaceans may have also been moved by currents and the diet may therefore not reflect that of the local area (MacLeod *et al.*, 2007).

Table 6. Variety of species fed on by harbour porpoises and bottlenose dolphins, with the average percentage of occurrence of each species per stomach (number of prey) and the average percentage of stomachs containing each species (frequency of occurrence). Shared prey species highlighted in bold (Browne, 1999; Santos *et al.*, 2004; Spitz *et al.*, 2006)

	Harbour porpoise		**Bottlenose dolphin**	
Species	Average number of prey %	Average frequency of occurrence %	Average number of prey %	Average frequency of occurrence %
Argentine	0.00	0.00	0.20	4.80
Atlantic horse mackerel	**5.20**	**26.90**	**15.60**	**57.10**
Black seabream	0.00	0.00	2.40	23.80
Blue whiting	**18.50**	**38.50**	**13.00**	**33.30**
Cod	0.20	2.70	0.00	0.00
Common shrimp	0.00	0.00	1.50	4.80
Common squid	**0.43**	**11.75**	**1.10**	**9.50**
Curled octopus	0.20	4.35	0.00	0.00
Cuttlefish	0.00	0.00	0.10	4.80
European anchovy	**0.50**	**15.40**	**2.40**	**14.30**
European squid	**0.20**	**11.50**	**2.50**	**38.10**
Gobies	**11.16**	**16.05**	**0.30**	**9.50**
Haddock	**4.41**	**8.92**	**3.00**	**4.10**
Hake	**2.30**	**12.27**	**20.20**	**52.40**
Herring	19.80	61.17	0.00	0.00
Mackerel	**0.08**	**2.95**	**0.90**	**9.50**
Meagre	0.00	0.00	0.10	4.80
Nordic krill	12.70	11.50	0.00	0.00
Pearlsides	0.20	3.80	0.00	0.00
Pink glass shrimp	0.00	0.00	0.20	4.80
Pollock	10.37	11.90	0.00	0.00
Poor-cod	13.50	47.83	0.00	0.00
Red bandfish	0.00	0.00	0.20	4.80
Sand smelt	0.00	0.00	0.10	4.80
Sandeels	**67.61**	**48.90**	**2.60**	**9.50**
Sardines	**2.30**	**30.80**	**4.80**	**23.80**
Scad	0.01	1.10	0.00	0.00
Seabass	0.00	0.00	4.20	9.50
Seabream	0.00	0.00	0.30	4.80
Silvery pout	**0.20**	**7.70**	**0.10**	**4.80**
Sprat	**0.73**	**1.80**	**10.60**	**4.80**
Trisopterus sp.	33.12	47.90	0.00	0.00
Whiting	**16.46**	**39.56**	**0.30**	**9.50**

From ICES data (MMO, *pers. comm.*), overall landings into Wales of the study fish species, Whiting, Sandeels, Sprat, Cod, Saithe (*Pollachius* sp.), Haddock (*Melanogrammus aeglefinus*), Sole (*Solea solea*) and Flounder (*Paralichthys* sp.), have decreased from 1993-2014 in Welsh waters (Figure 22).

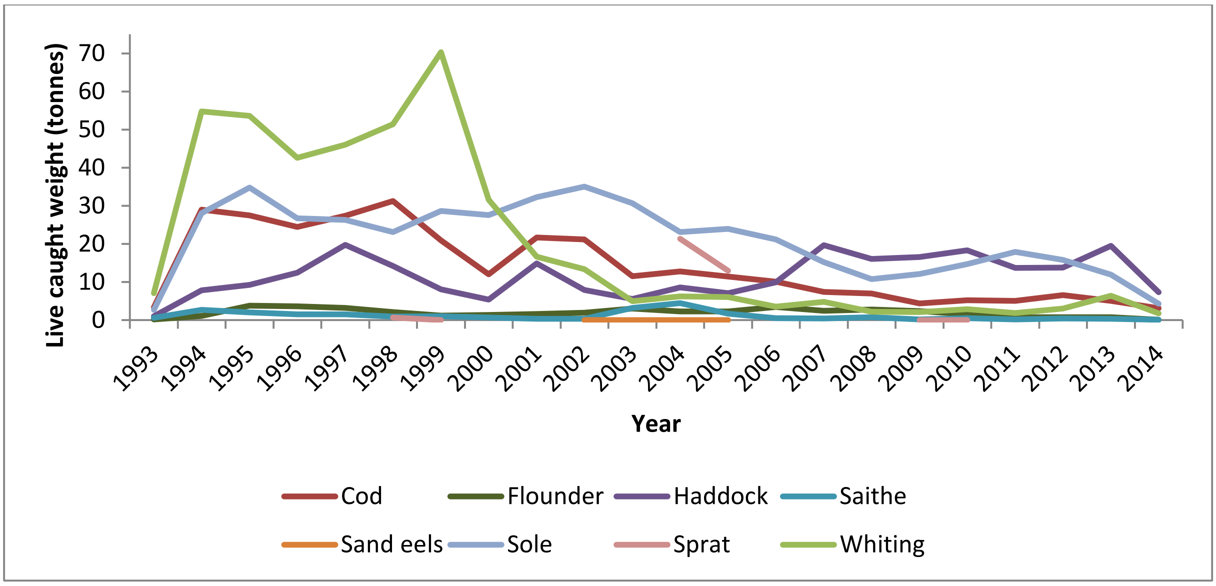


Figure 22. Average live weight (tonnes) of important fish prey species of both harbour porpoise and bottlenose dolphins, caught in ICES divisions VIIa, f and g, 1993-2014

Landings of fish species into Wales for per month (Figure 23) show a strong peak in the quantity of haddock landed in July and August (Figure 23, 24). This peak occurs during the summer when there is a low number of stranded-attacked porpoises (Figure 24, 41). The relationship between haddock landings and attacks on porpoises was not significant (Pearson's correlation, p=0.920).

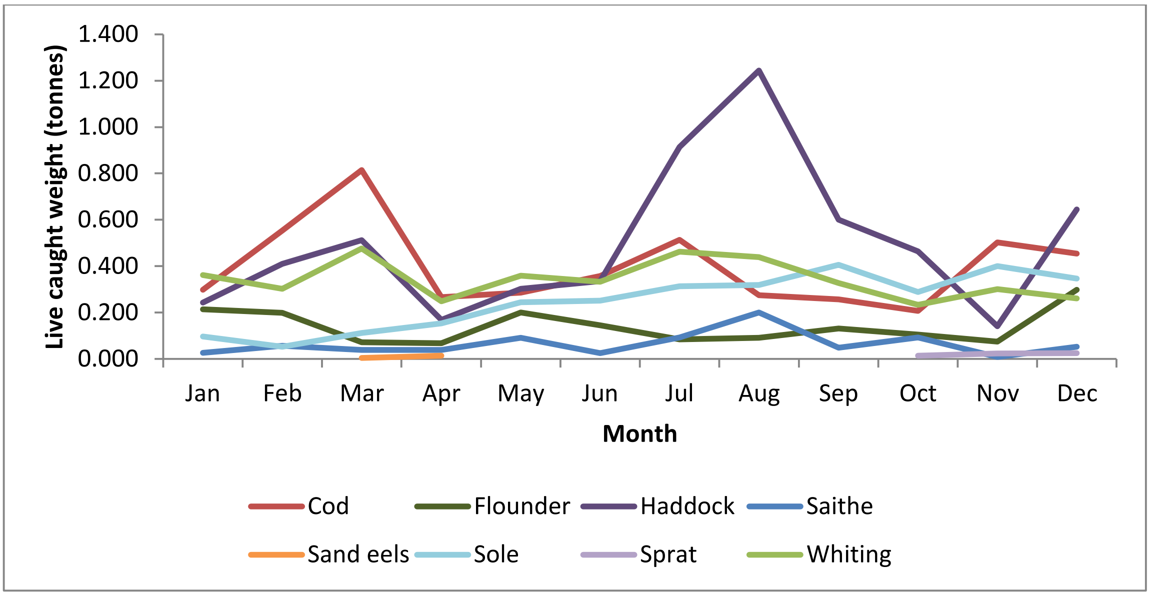


Figure 23. Average live weight (tonnes) of important fish prey species of both harbour porpoise and bottlenose dolphin, caught in ICES divisions VIIa, f and g, for all months

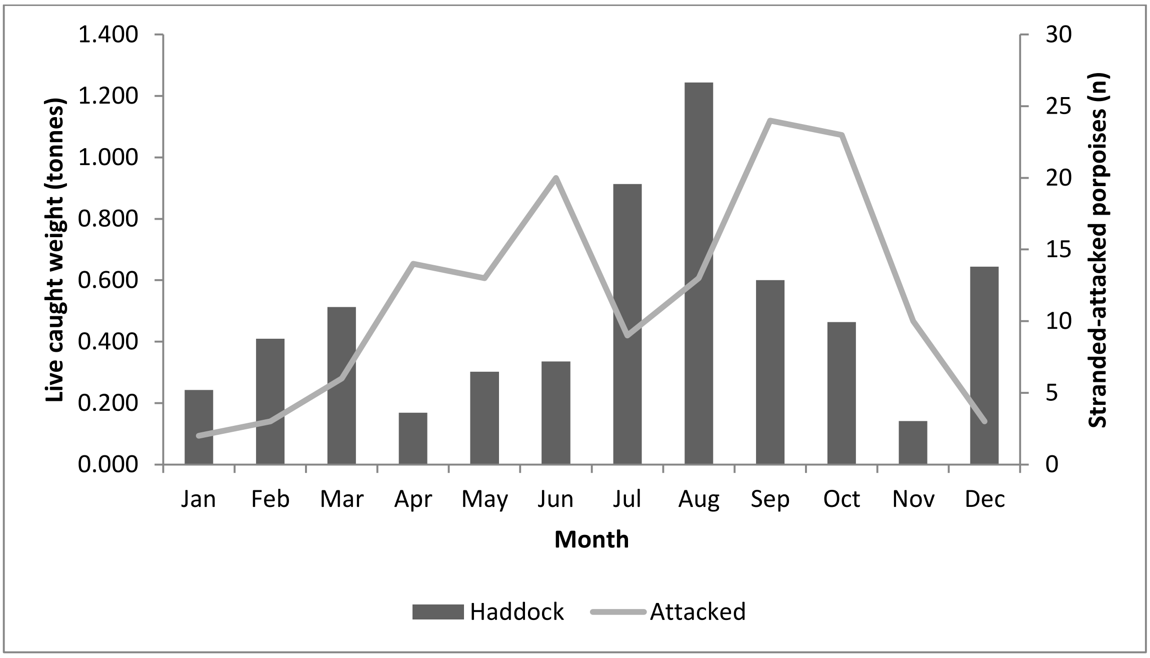


Figure 24. Comparison of the total catch (weight) of haddock landed in Wales and the number of stranded-attacked harbour porpoises for each month

Starvation of harbour porpoises has increased over recent years (Figure 26). The number of harbour porpoises that strand attacked by bottlenose dolphins tend to decrease during times when starvation has increased. Though the relationship is not significant, it can be seen on both a monthly (Pearson's correlation, p=0.267) and annual basis (Spearman's Rank, p=0.106) (Figure 25, 26).

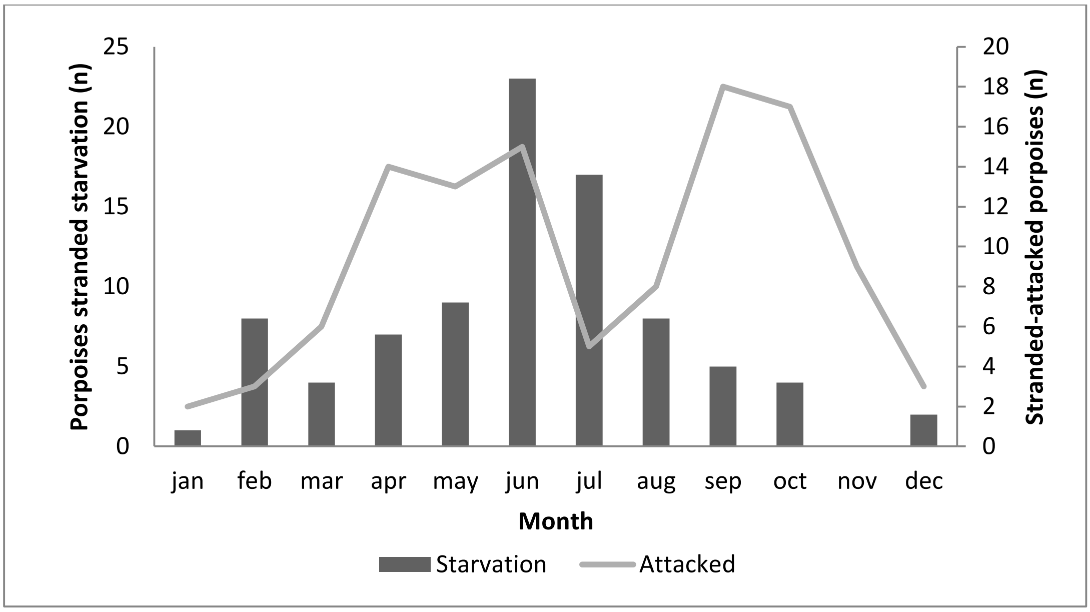


Figure 25. Number of harbour porpoises stranded due to starvation compared to those stranded-attacked, averaged per month, 1990-2013

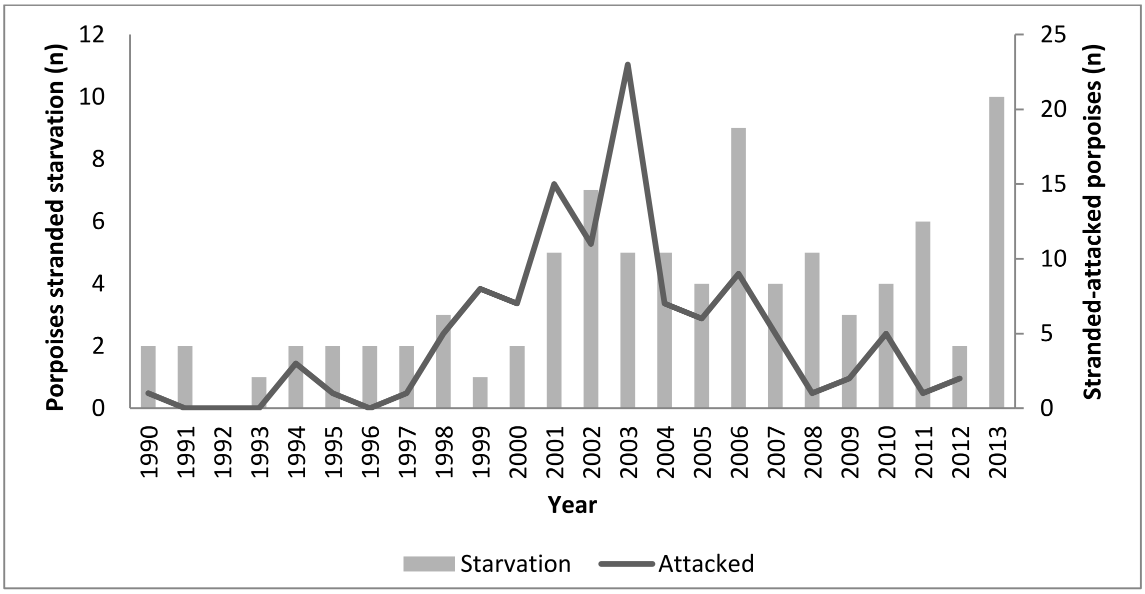


Figure 26. Number of harbour porpoises stranded due to starvation compared to those stranded-attacked, averaged per year, 1990-2013

Over time there has been a decrease in the abundance of sandeels and a general increase in the number of porpoises stranded due to starvation (Figure 27). This relationship was non-significant (Spearman's rank, p=0.394).

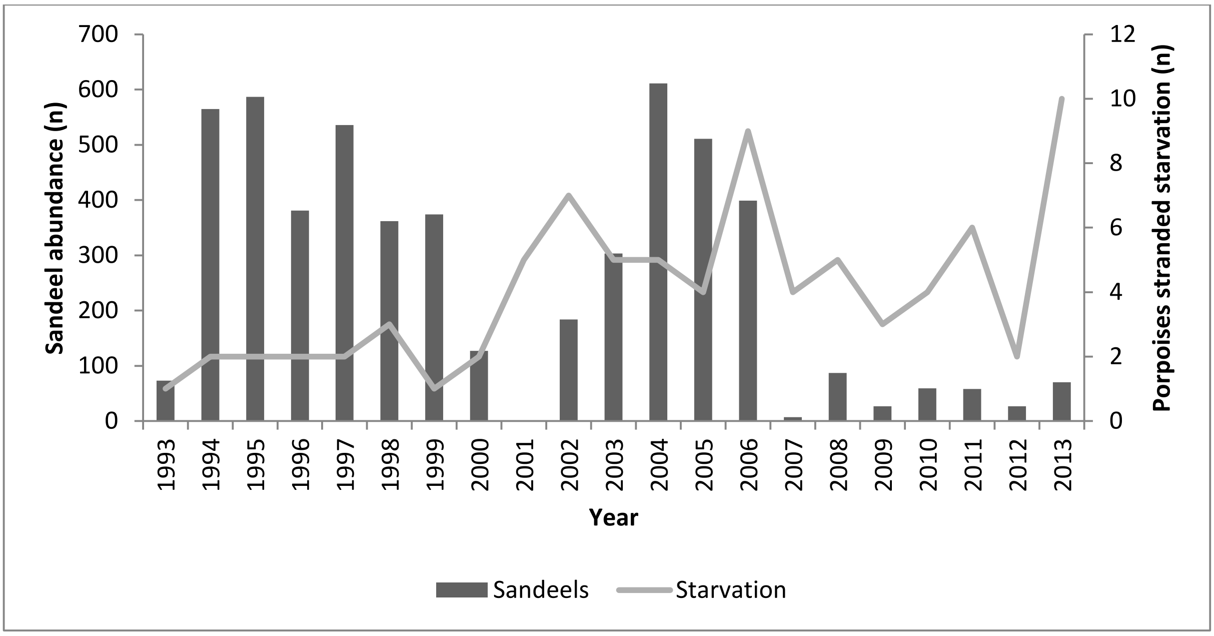


Figure 27. Relationship between the abundance of sandeels in the Irish Sea (VIIa) and the number of porpoises stranded dead due to starvation, 1993-2013

The number of attacked harbour porpoises since 2001 is correlated significantly to sandeel abundance (Pearson's correlation, p=0.002) (Figure 28).

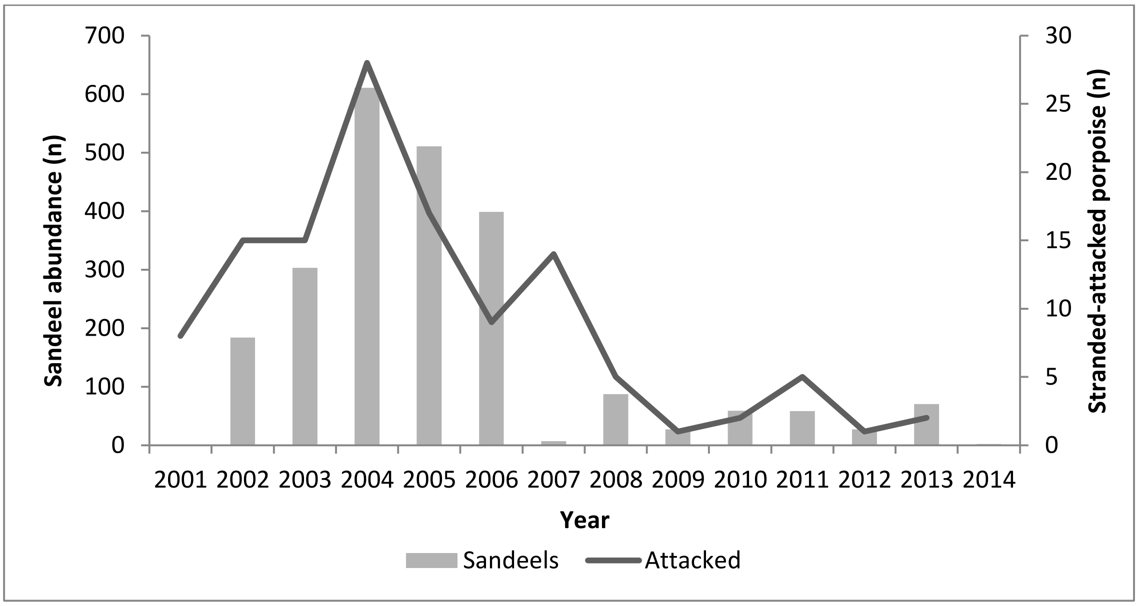


Figure 28. Relationship between the number of stranded-attacked harbour porpoises and the abundance of sandeels caught in beam trawl surveys, 2001-2014

There was a significant correlation between sightings of bottlenose dolphins and sand eels (Spearman's rank, p=0.042) and of harbour porpoises with sandeel abundance (Spearman's ranl, p=0.04) (Figure 29). Since 2005, sandeel numbers have declined along with the sightings of harbour porpoises.

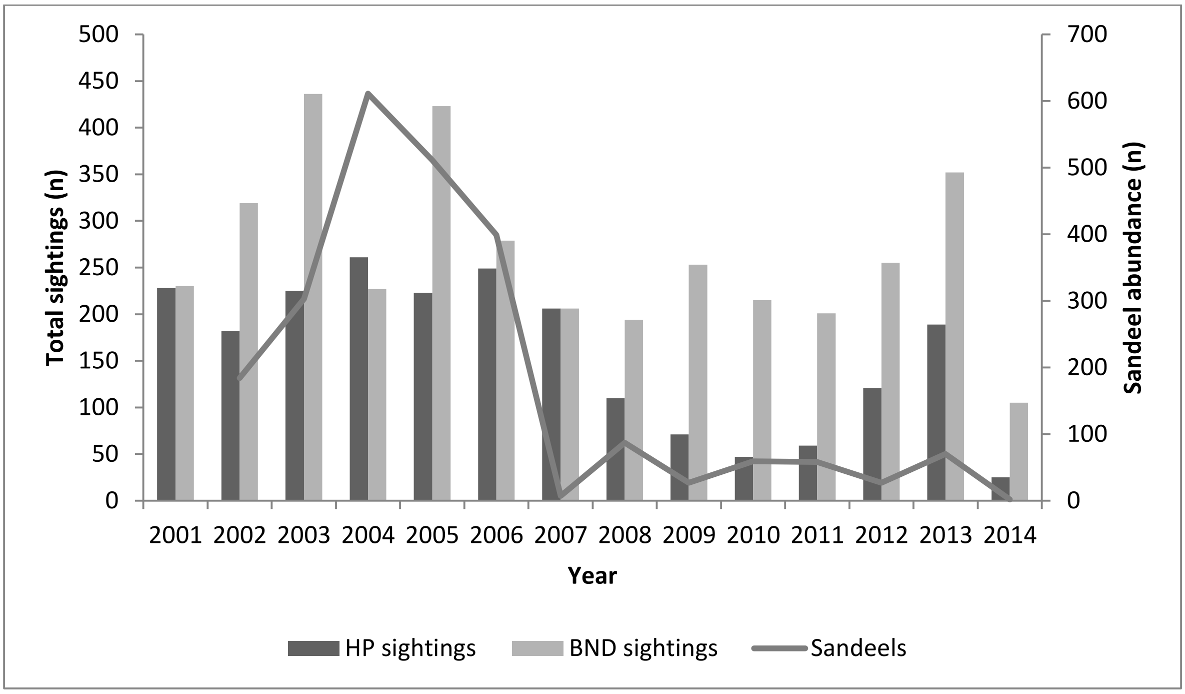


Figure 29. Relationship between the number of bottlenose dolphin and harbour porpoise sightings and abundance (total number) of sandeels caught in beam trawl surveys, 2001-2014

As sandeel numbers have decreased, the co-occurrence density has also decreased (Pearson's correlation, p=0.015) (Figure 30). In 2004, the co-occurrence density between the species and the abundance of sandeels was highest. This was also the year with the largest proportion of stranded-attacked harbour porpoises (Figure 28).

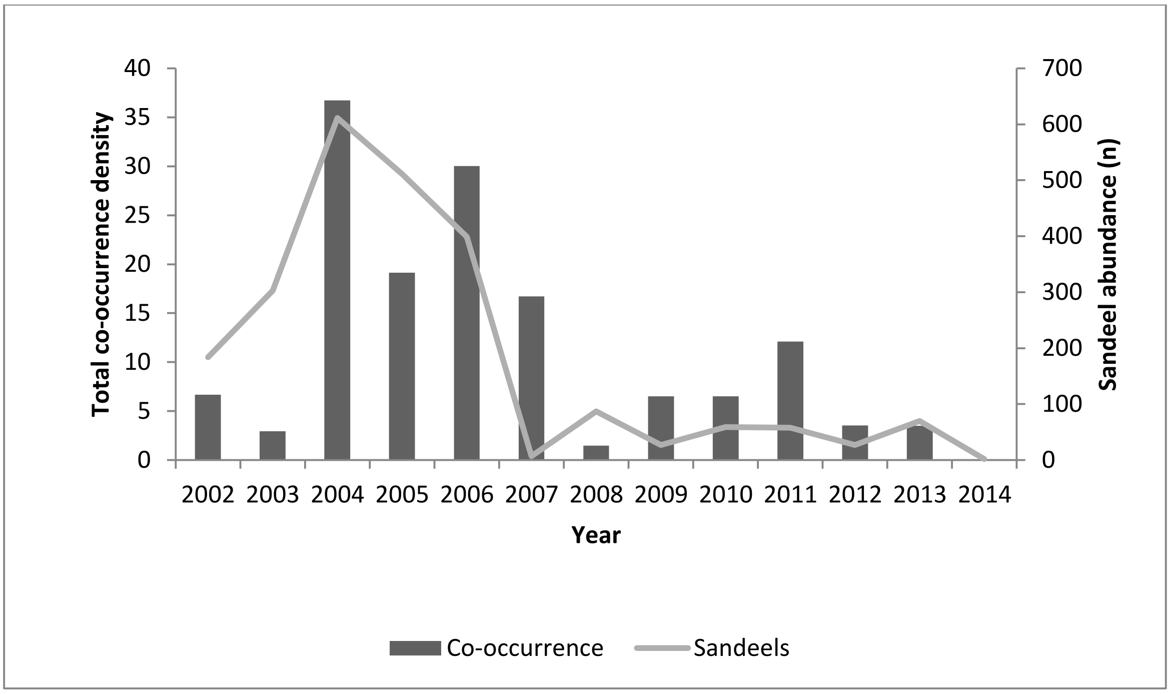


Figure 30. Relationship between the total abundance of sandeels and the amount of co-occurrence between bottlenose dolphins and harbour porpoises, 2002-2014

There appears to be little relationship between the number of attacks on harbour porpoises and the abundance of sprat, although the peak for both of these occurred in 2004 (Spearman's Rank, p=0.643) (Figure 31).

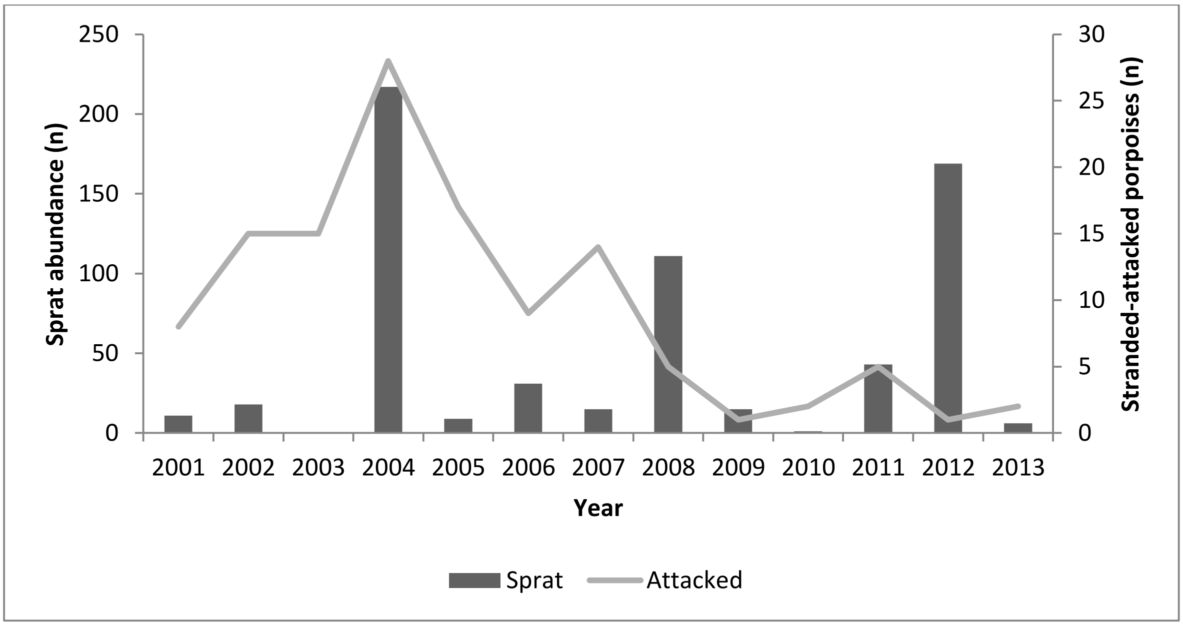


Figure 31. Relationship between the abundance of sprat and the number of stranded-attacked harbour porpoises, 2001-2013

Sprat abundance varies over time, peaking in 2004 along with a peak in co-occurrence density (Spearman's Rank p=0.601) (Figure 32).

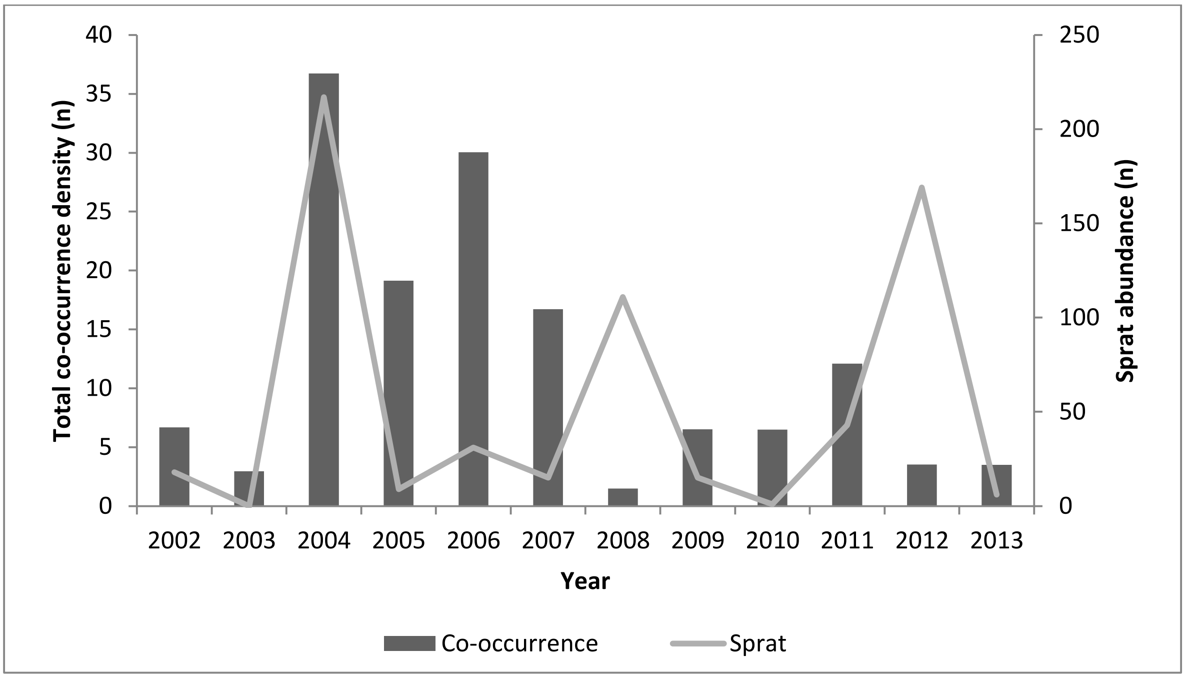


Figure 32. Relationship between total abundance of sprat and the total co-occurrence density between cetacean species, 2002-2013

In general, there is a trend of increased harbour porpoise starvation of during years of low sprat abundance (Spearman's Rank, p=0.965) (Figure 33).

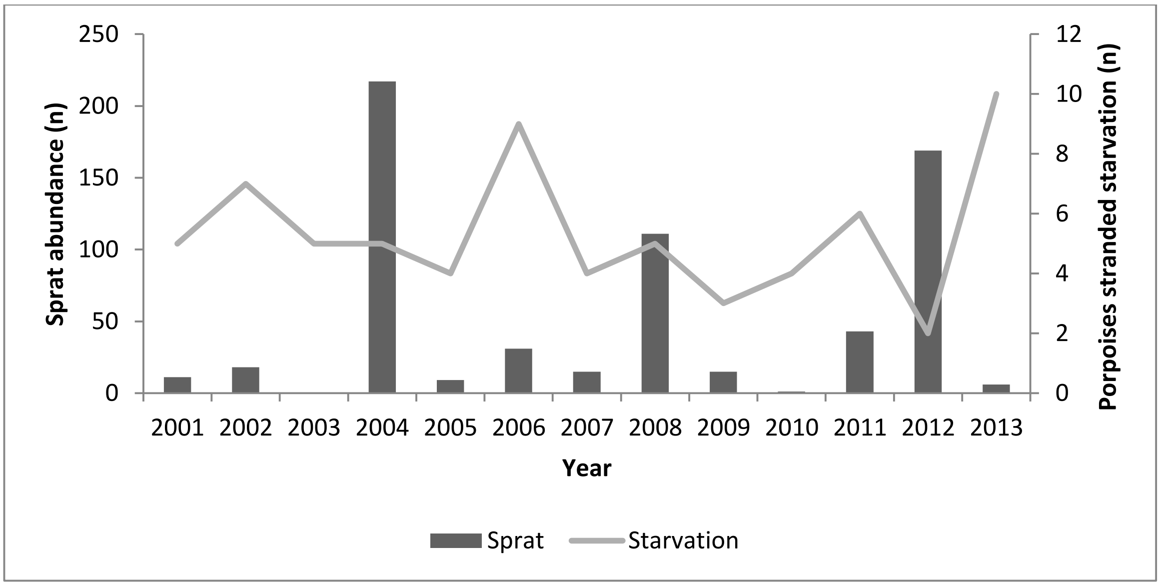


Figure 33. Relationship between the total abundance of sprat and the number of harbour porpoises stranded dead due to starvation, 2001-2013

There has been a general decrease in poor-cod abundance over time along with a decrease in attacked porpoise strandings (Figure 34), but numbers of harbour porpoises stranded due to starvation in Wales have increased (Figure 35). Peaks in abundance have not occurred at the same times as changes in porpoise strandings (Pearson's correlation, p=0.061) (Figure 34). The relationship between starvation and poor-cod was not significant (Spearman's rank, p=0.668).

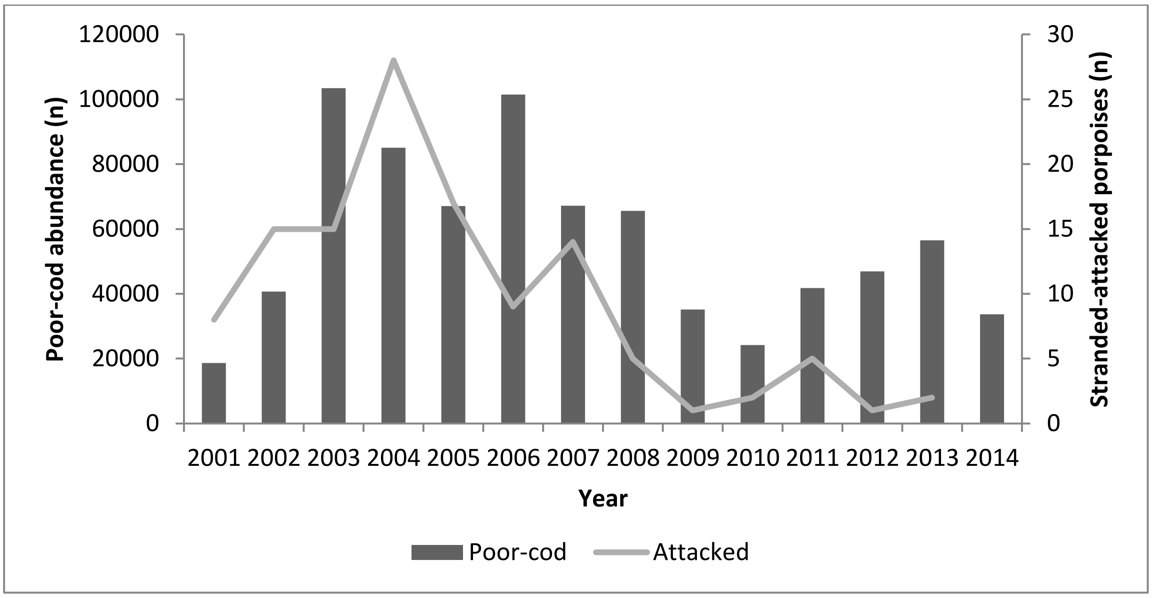


Figure 34. Relationship between the number of stranded-attacked harbour porpoises and the abundance of poor-cod in beam trawl surveys, 2001-2014

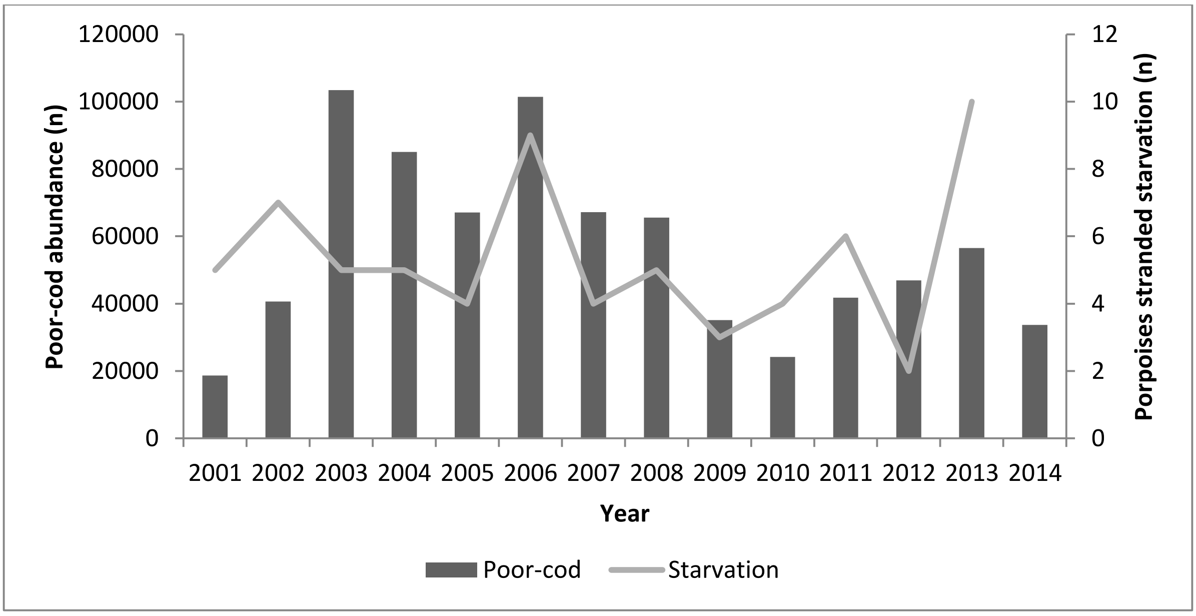


Figure 35. Relationship between the abundance of poor-cod and the number of porpoises recovered dead due to starvation, 2001-2014

The amount of co-occurrence between bottlenose dolphins and harbour porpoises follows a similar pattern to that of poor-cod abundance, decreasing over time, but is not significant (Spearman's rank, p=0.209) (Figure 36).

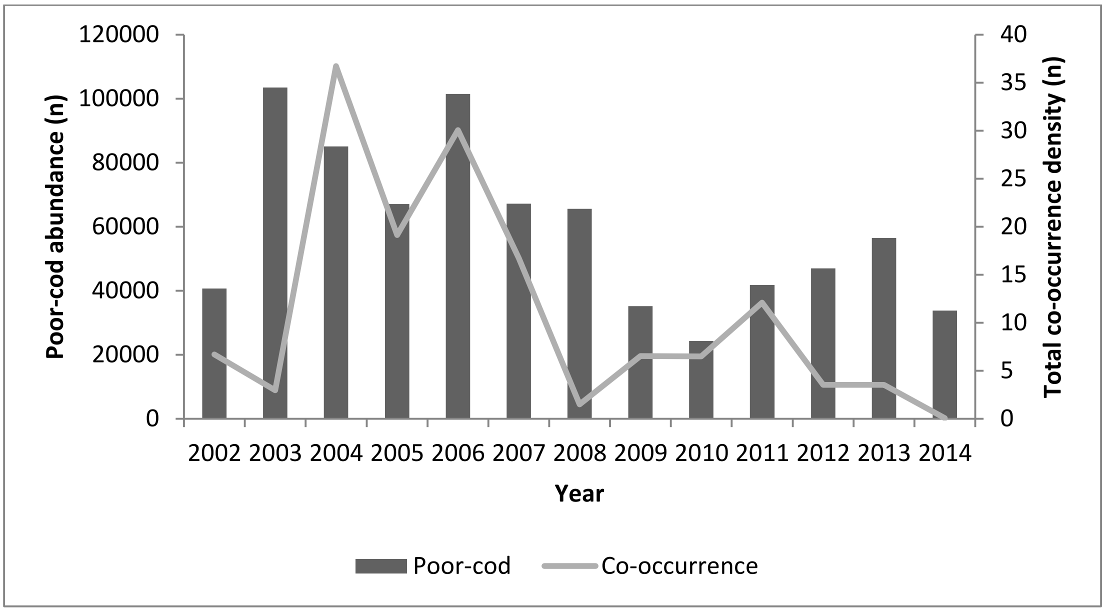


Figure 36. Relationship between the total abundance of poor-cod and the amount of co-occurrence between bottlenose dolphins and harbour porpoises, 2002-2014

The abundance of whiting appears to vary but not in a consistent manner, with little relationship to the number of stranded-attacked harbour porpoises (Pearson's correlation, p=0.950). However, in recent years, there has been a decline in attacked porpoises during years of high whiting abundance (Figure 37).

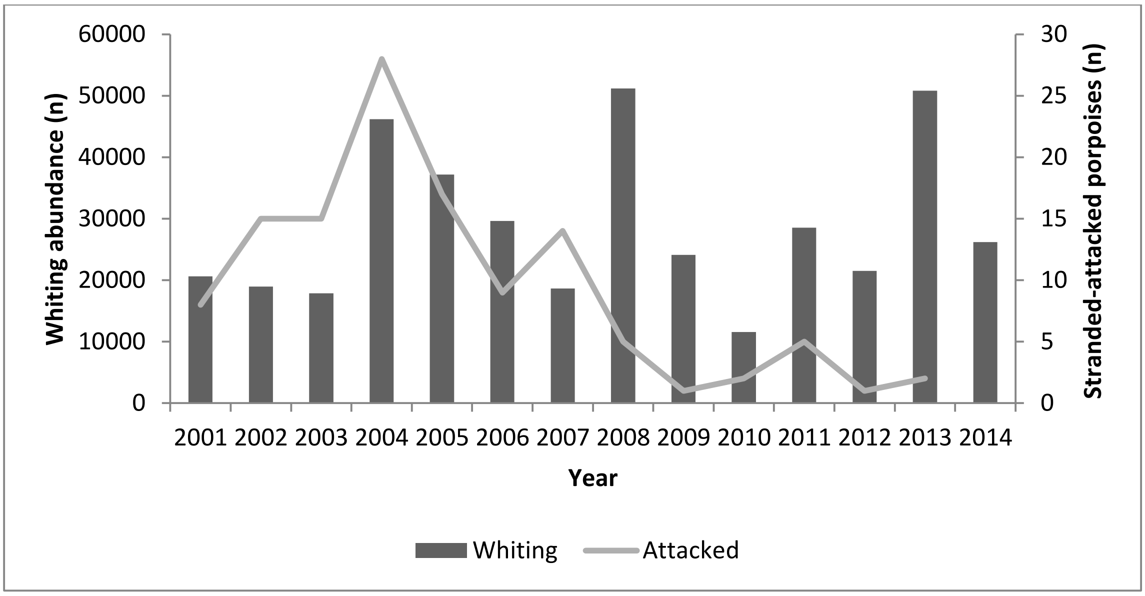


Figure 37. Relationship between the number of stranded-attacked harbour porpoises and the abundance of whiting in beam trawl surveys, 2001-2014

Live caught weight of whiting is highest in March, July and August when strandings of attacked harbour porpoises is lowest (Pearson's correlation, p=0.439) (Figure 38).

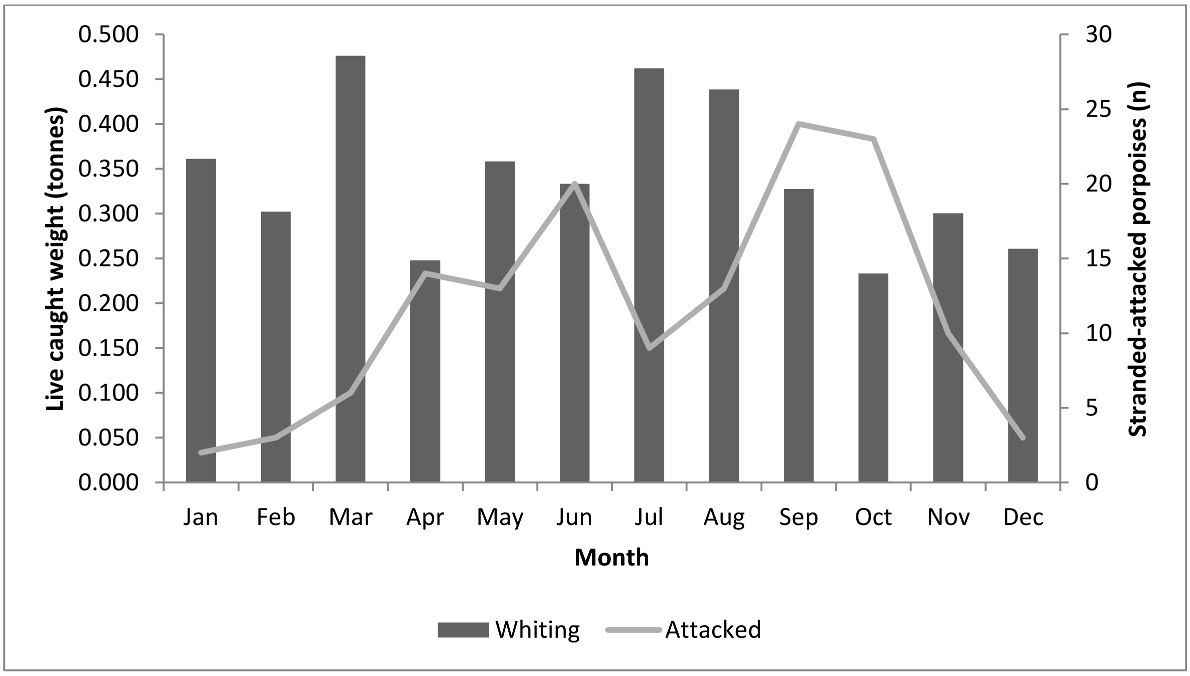


Figure 38. Relationship between the number of stranded-attacked porpoises and the live caught weight of whiting per month into Wales

3.4 Generalised Linear Mixed Modelling

The relationships between variables potentially explaining the occurrence of a stranding were analysed using a binomial generalised linear mixed model (Table 7). The AIC numbers were compared and the model with lowest AIC, which had the best fit, was chosen. This model also carried a high weight of 0.83, further supporting its good fit. The best model was model 7 (Table 8). Co-occurrence of harbour porpoises and bottlenose dolphins had a significant positive relationship with the occurrence of a stranding (p=0.05). Year and bottlenose dolphin group size did not have a significant effect on stranding. Sandeel abundance had a significant positive effect on the occurrence of strandings caused by bottlenose dolphins (p=0.0024) (Table 8); which meant when sandeels were abundant, more strandings occurred. This relationship can also be seen in Figure 28 where, from 2001-2014, the occurrence of strandings caused by bottlenose dolphins closely followed changes in the abundance of sandeels.

Table 7. All models run using a GLMM with their AIC rating and weight

Model		**AICc**	**AICc Wt**
7	stranding ~ overlap + year + bnd_group + Ammodytidae	0.00	0.83
1	stranding ~ overlap + year + bnd_group + Total_fish	5.40	0.06
10	stranding ~ overlap + year + bnd_group + Trisopterus	6.14	0.04
9	stranding ~ overlap + year + bnd_group + Merlangius	6.40	0.03
3	stranding ~ overlap + fmonth + year + bnd_group +Ammodytidae	7.58	0.02
8	stranding ~ overlap + year + bnd_group + Melanogrammus	8.80	0.01
13	stranding ~ overlap + fmonth + year + bnd_group + Ammodytidae + overlap*Ammodytidae	9.37	0.01
12	stranding ~ overlap + fmonth + year + bnd_group + Total_fish + overlap*Total_fish	9.62	0.01
2	stranding ~ overlap + fmonth + year + bnd_group + Total_fish	12.95	0.00
11	stranding ~ overlap + fmonth + year + bnd_group + Merlangius + overlap*Merlangius	13.09	0.00
6	stranding ~ overlap + fmonth + year + bnd_group + Trisopterus	13.69	0.00
5	stranding ~ overlap + fmonth + year + bnd_group + Merlangius	13.96	0.00
4	stranding ~ overlap + fmonth + year+ bnd_group + Melanogrammus	16.37	0.00

Table 8. Model 7-The best linear mixed-effects model fit by maximum likelihood, showing the relationship of each variable on the occurrence of a stranding due to bottlenose dolphin attack, April-October, 2001-2014

Explanatory variable	**Value (slope)**	**P- value**	**Standard error**
Overlap or co-occurrence	0.0012734	0.0555	0.00066492
Year	-0.0000765	0.5757	0.00013669
Bottlenose dolphin group	-0.0001103	0.1139	0.00006973
Sandeels	0.0000093	0.0024	0.00000304

3.5 Object-oriented play

Data analysis of stranded harbour porpoises and bottlenose dolphins in the Moray Firth, Scotland, between 1992 and 1997, revealed similarities in body length of individuals of both species that had been attacked by bottlenose dolphins (Figure 39).

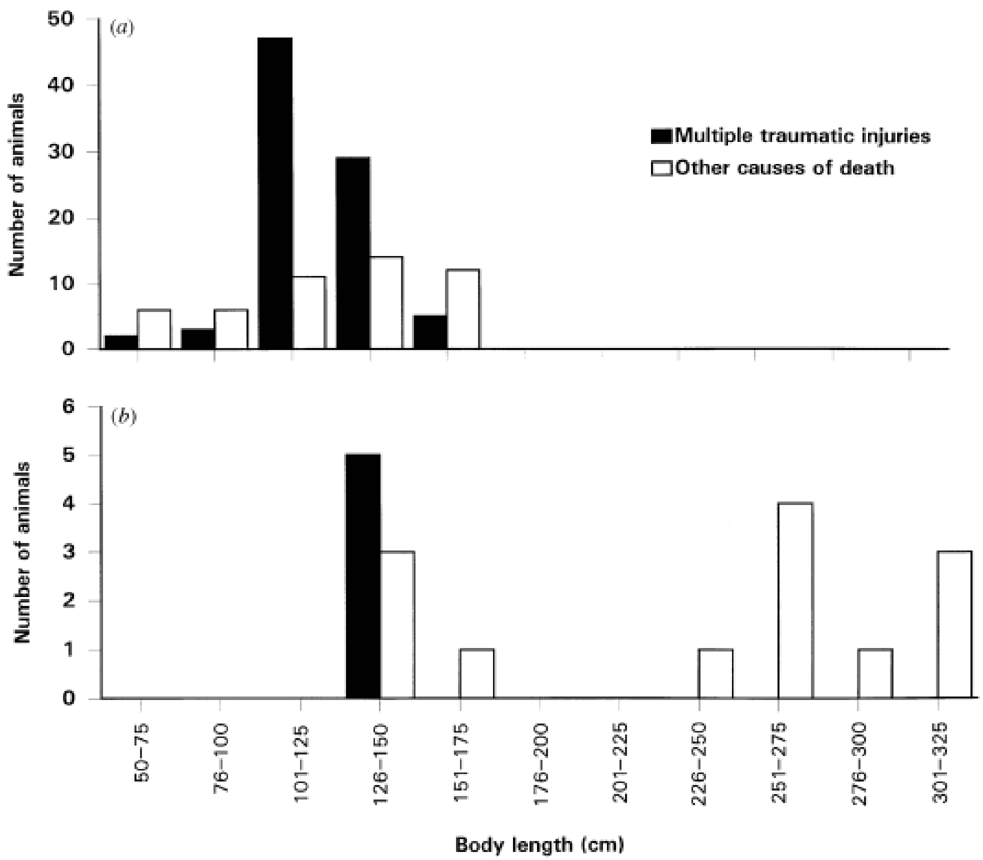


Figure 39. Length class distribution (cm) of (a) harbour porpoises and (b) bottlenose dolphins, stranded in the Moray Firth, Scotland, 1992-1997. Traumatic injuries = black, other causes of death = white (Patterson *et al*., 1998)

The most commonly attacked porpoises in Wales were 111-120cm in length, followed by those measuring 131-140cm (Figure 40). These represent sub-adult or juvenile animals and newly mature animals respectively, since porpoises are thought to mature around 130cm and have an average adult size of 160cm in UK waters (Lockyer, 1995).

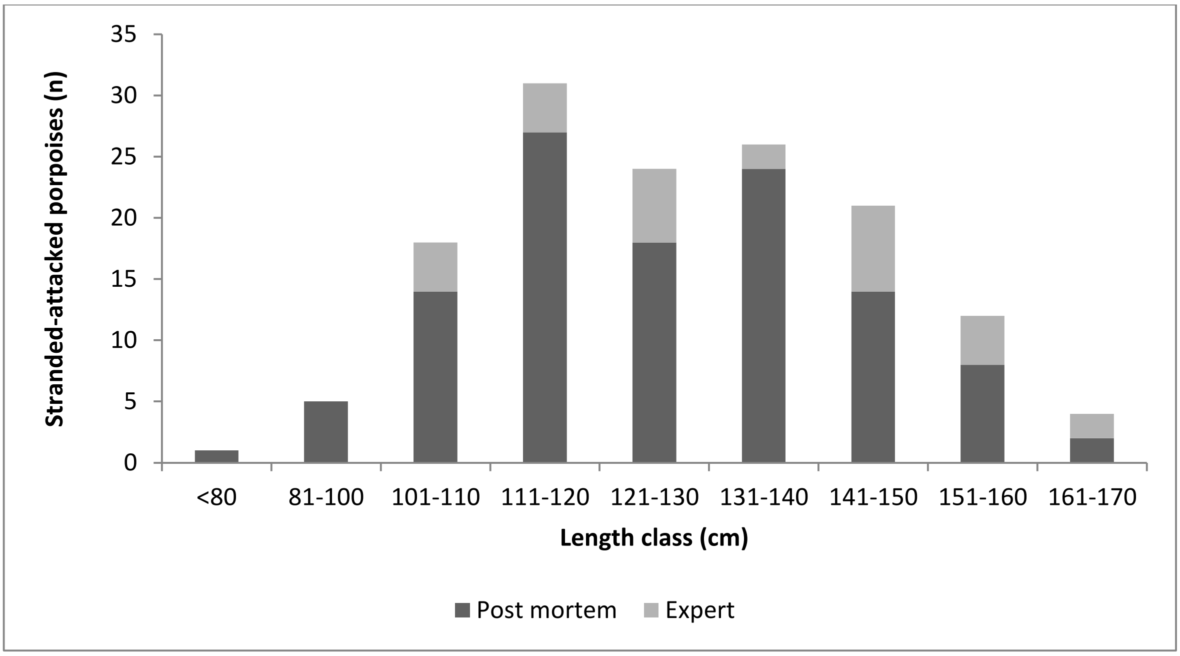


Figure 40. Length class distribution of stranded harbour porpoises attacked by bottlenose dolphins in Wales, 1991-2013

3.6 Skewed operational sex ratio or sexual frustration and elevated testosterone levels

Porpoise attacks peaked in the 2nd quarter (April-June), closely followed by the 3rd quarter (July-September) and were lowest in the 1st quarter (January-March) (Figure 42). The highest number of stranded-attacked porpoises occurred in September (n=24) including those determined in the field by an expert, though only 18 were identified through direct post-mortem examination. The lowest number of attacks occurred in January (n=2) (Figure 41).

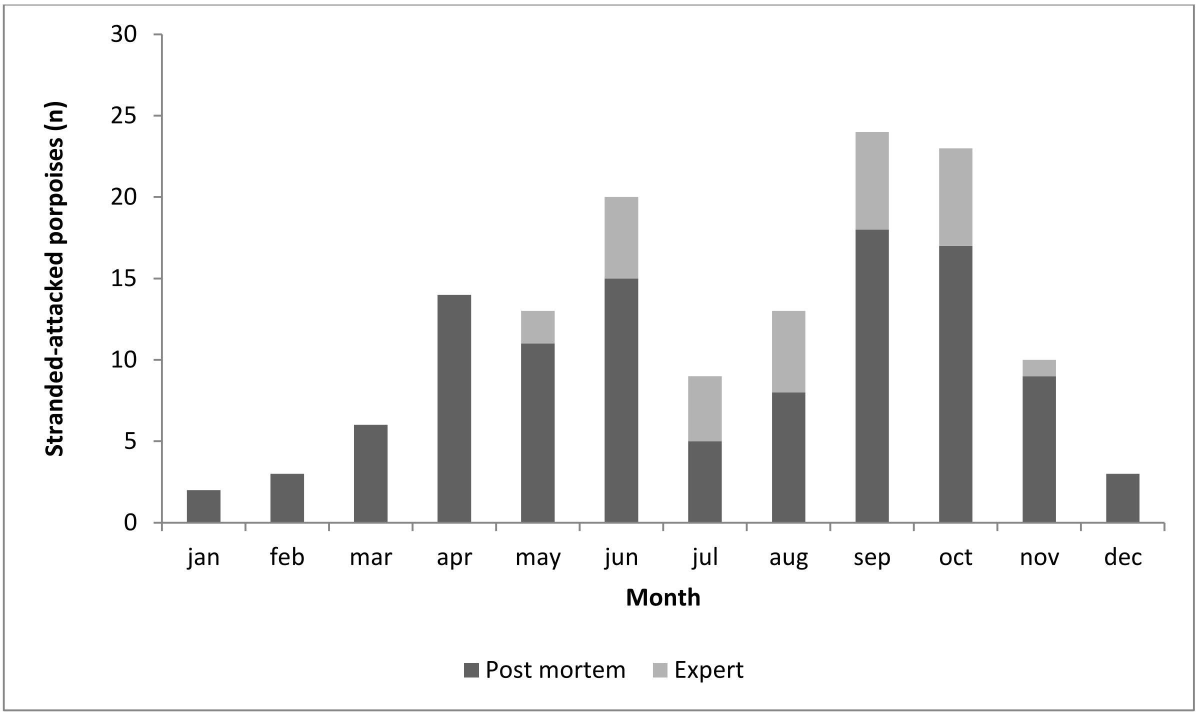


Figure 41. Total number of stranded-attacked harbour porpoises in Wales by month, averaged over 1991-2013 ($y=0.5x+6$, $R^2=0.1004$)

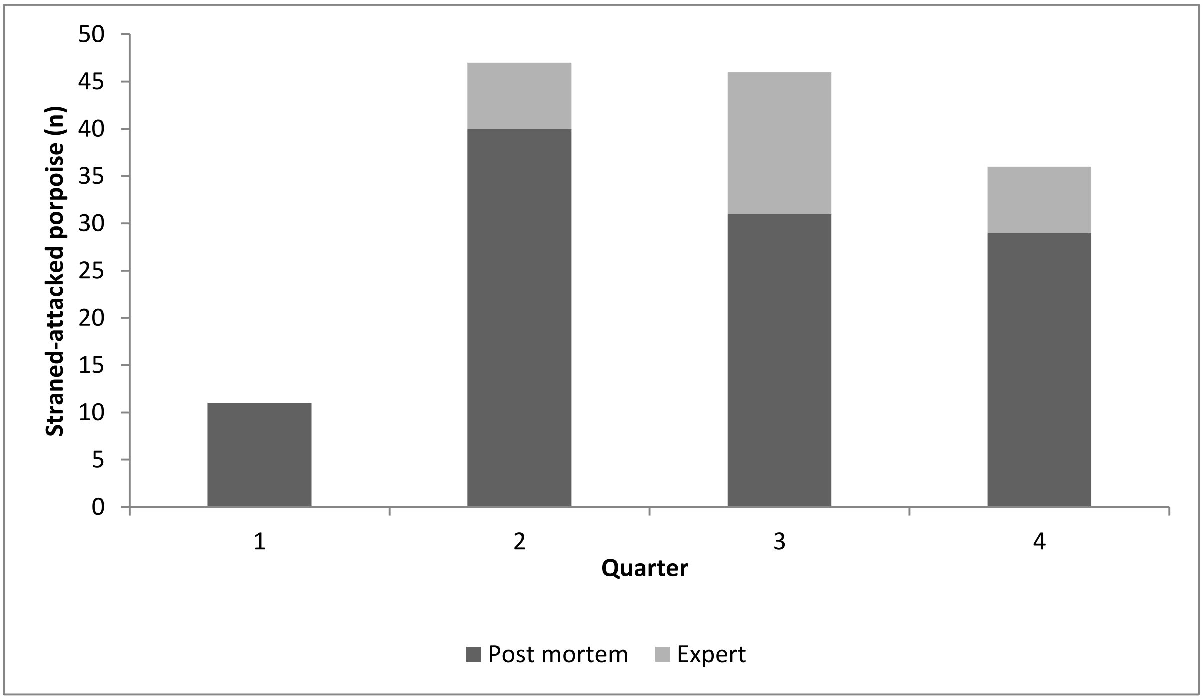


Figure 42. Total number of stranded harbour porpoises attacked by bottlenose dolphins by quarter (season) (1st=January-March, 2nd=April-June, 3rd=July-September, 4th=October-December)

A larger proportion of the harbour porpoises stranded-attacked by bottlenose dolphins were males (n=65) compared with 48 females, this difference was not significant (T-test, p=0.715) (Figure 43). All harbour porpoises were sexed during necropsy and were classified by their life stage. Three porpoises were neonates (male n=2, female n=1) and six were sub-adults (male n=4, female n=2). Juveniles comprised 58.4% of the stranded individuals (male n=36 and female n=30), whilst 32.7% were adults (male n=22 and female n=15) (Figure 43).

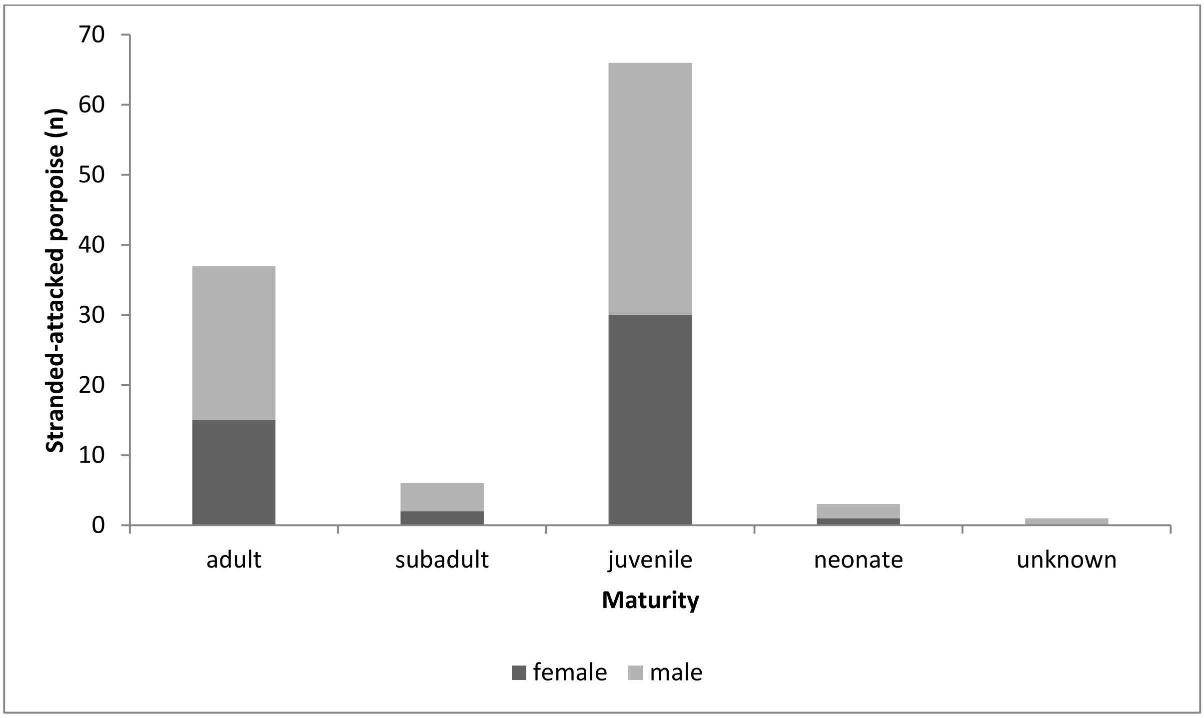


Figure 43. Age/sex classes of necropsied stranded-attacked harbour porpoises, 1991-2013

Monthly sightings data for Cardigan Bay show an increase in co-occurrence in summer months and a decrease in co-occurrence during winter. There is a similar pattern amongst stranded-attacked porpoises, although the peak in strandings occurs in September as co-occurrence begins to decrease. There is a low number of strandings in July when co-occurrence is quite high (Figure 44).

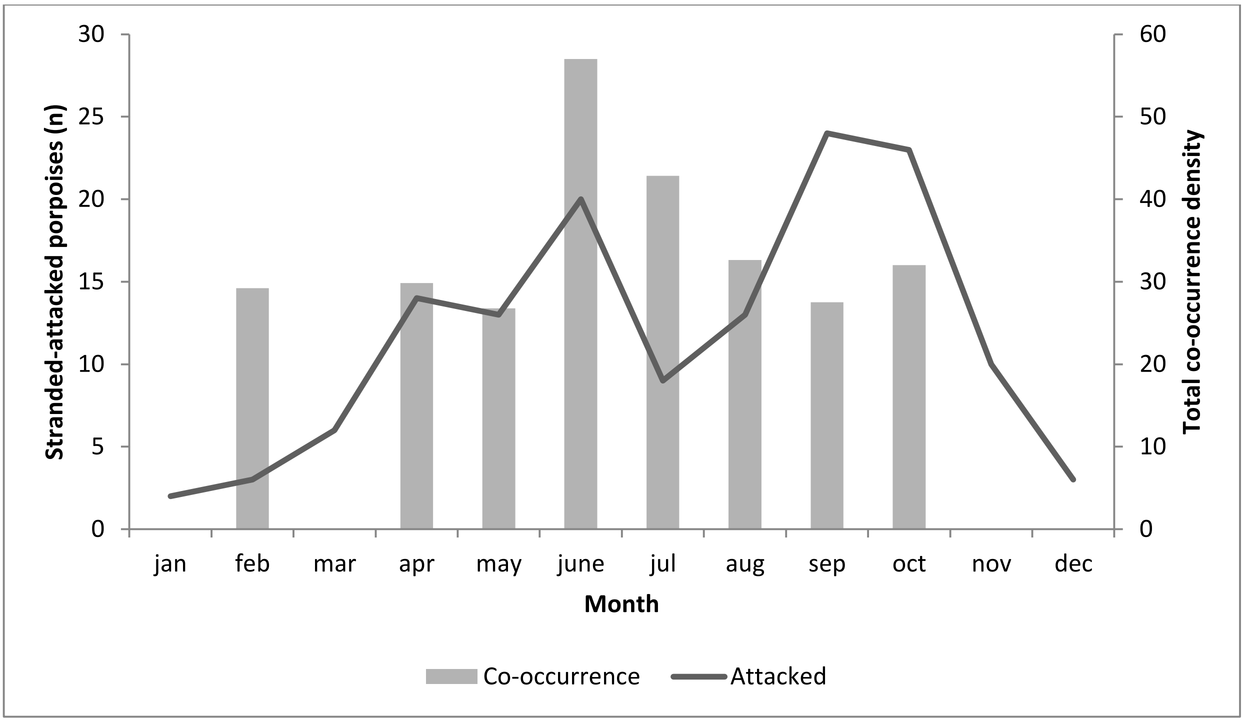


Figure 44. Relationship by month between the extent of co-occurrence of bottlenose dolphins and harbour porpoises and the number of stranded-attacked porpoises

4. Discussion

4.1 Territoriality

In the UK, harbour porpoises appear to avoid bottlenose dolphins in most areas where both species exist, particularly in the Moray Firth and Cardigan Bay, where their abundance is inversely related (Evans *et al.*, 2015). These are also areas where resident bottlenose dolphin populations exist year round and regularly attack harbour porpoises, which also inhabit the area. This suggests that in these areas where some co-occurrence does occur, the resources must be important enough for harbour porpoises to risk potential attacks by remaining in the area. This may be due to a particular prey preferring habitats where bottlenose dolphins reside, leading to competition for habitat resources.

In general, harbour porpoises are more widely distributed than bottlenose dolphins. This can be seen in Figure 4. Bottlenose dolphin sightings tend to be close to the coast whereas harbour porpoises are found across the continental shelf (Reid *et al.*, 2003). Acoustic studies within Cardigan Bay SAC (Simon *et al.*, 2010; Baulch, 2012) found that harbour porpoises showed a marked preference for offshore sites (if only 500 metres from inshore sites), whilst bottlenose dolphins favoured inshore sites. Detection rates of bottlenose dolphins and harbour porpoises varied seasonally, with bottlenose dolphin peak detections in the summer, corresponding with their calving season (Evans *et al.*, 2003); whereas, harbour porpoise detections peaked in the winter (Pesante *et al.*, 2008; Simon *et al.*, 2010). Occurrence of both species is affected by the relative abundance of their preferred prey. Although they share considerable dietary overlap, porpoise density is likely to increase in the winter due to whiting peaks in the North-East Irish Sea and in the past due to herring abundance (Borjesson *et al.*, 2003), which are now a recovering stock. They may also avoid the relatively high numbers of bottlenose dolphins which migrate into Cardigan Bay during the summer, at least partly to calve. This partitioning may be the result of reduced competition or to avoid aggressive interspecific interactions.

The pattern of harbour porpoise abundance in relation to the tidal cycle in Cardigan Bay SAC was the opposite to that of bottlenose dolphins. Bottlenose dolphins were most abundant at the flood tide, during low water and two hours before high water. In comparison, harbour porpoises were most abundant during the ebb tide, at three hours before and two to three hours after high water. This may be in part due to aggregations of prey that use the tidal currents for active and passive transport (Gibson, 2003).

This study found that the number of attacks was highest during periods of greatest co-occurrence on an annual scale. However, on a monthly scale, high co-occurrence in sightings occurred during July and August when the number of stranded-attacked porpoises was low, possibly due to calm weather washing ashore fewer stranded animals. However, more reliable acoustic data shows greatest co-occurrence in April and September (Simon *et al*., 2010). There was a sharp increase in strandings in September, linked to the high acoustic co-occurrence and possibly from attacks that may have occurred in August. It is possible that although co-occurrence is high during these months, there are adequate resources for both species and so strandings are reduced. Strandings continue to occur in areas where it appears there is no co-occurrence at a particular time (Figure 18), suggesting that the species remain within the area but in lower abundance and so are missed by surveys, which are also reduced in effort.

Within Cardigan Bay, both cetacean species show a similar trend, with high densities in southern Cardigan Bay from 2001 to 2004, followed by an increase in dispersal within the bay, possibly relating to a change in prey distribution. During the winter, there is a northward movement of bottlenose dolphins. Whilst in the summer months they remain largely within southern Cardigan Bay, likely due to the use of the area for mating and calving. The strandings of attacked harbour porpoises appear to follow little pattern, occurring along the Welsh coast throughout the year, so there may be more co-occurrence between the cetaceans than is being seen through surveys, which are very summer biased.

It appears that harbour porpoises and bottlenose dolphins have evolved habitat partitioning through diurnal, seasonal and tidal patterns of behaviour. This is likely to have occurred due to spatial and prey overlap, leading to a need for reduced resource competition as well as avoidance behaviour exhibited by porpoises. However, the increase in bottlenose dolphin attacks over the past 15 years may be a consequence of increased competition for resources, due to changes in fish stock abundance through overfishing (Pinnegar *et al.*, 2002), augmented by climate change and habitat degradation.

4.2 Prey competition

Asymmetry between competitors is more likely to cause aggressive interactions (Maynard Smith, 1982), which could be a factor in the case of bottlenose dolphins and harbour porpoises feeding on the same prey. Regrettably, there are no published studies to date on stomach contents analysis of these species from Welsh waters. Identifying a relationship between diet and attacks is therefore difficult. However, in Northern Anglesey an observed attack on a porpoise revealed the stomach to be dominated by whiting (Evans, *pers. comm.*). Detailed dietary analysis studies of these species in British waters and in the Bay of Biscay have found a number of fish species common to the diets of both species, although there was variability in the size of fish taken and the percentage of the diet which an individual fish species comprised. In marine ecosystems, resources tend to be patchily distributed both spatially and temporally. Therefore, dietary overlap in just one prey species could lead to interspecific interactions, although the probability of an interaction would vary considerably depending on the numbers of each predator and the amount of prey (Spitz *et al.*, 2006).

A study of diet variability in harbour porpoises that stranded dead for various causes in Scotland found that sandeels were most important and *Trisopterus* species were least important in the diets of porpoises attacked by bottlenose dolphins (Santos *et al.*, 2004). The current study in Wales further supports the results found by Santos *et al.*(2004) as GLMM results show that when sandeel abundance was high, more attacks occurred (Table 8, Figure 28). Whether, this is due to a high density of sandeels in a small area, causing bottlenose dolphins and harbour porpoises to come into contact more often and resulting in these often fatal interactions; or if this is due to sandeels being abundant at a time of reduced resources and therefore becoming an important prey temporally for both cetaceans (Santos *et al.*, 2001), is unclear. The relationship between attacks and sandeel abundance is further supported by the decrease in attacks in July, the month in which adult sandeels are known to retreat into the sediment (Winslade, 1974). However, the increase in strandings in September, when sandeel abundance is low, may be due to the increased presence of and competition for Sprat which are seasonally abundant in August and September (Anderwald *et al.*, 2012) and are fed on by both cetaceans (Table 6).

Sandeels are site-specific demersal spawners (Ellis *et al.*, 2012) and tend to inhabit shallow turbulent waters, with sandy to gravelly sediments, at depths of 20-70 metres (Greenstreet *et al.*, 2010). They also exhibit high site fidelity due to their habitat preference (Ellis *et al.*, 2012). They emerge from the sediment between April and September to feed in the water column (Scottish Government, 2010). In Wales, this preferred sediment type and emergence period corresponds to the coast where bottlenose dolphins are known to reside (Figure 45).

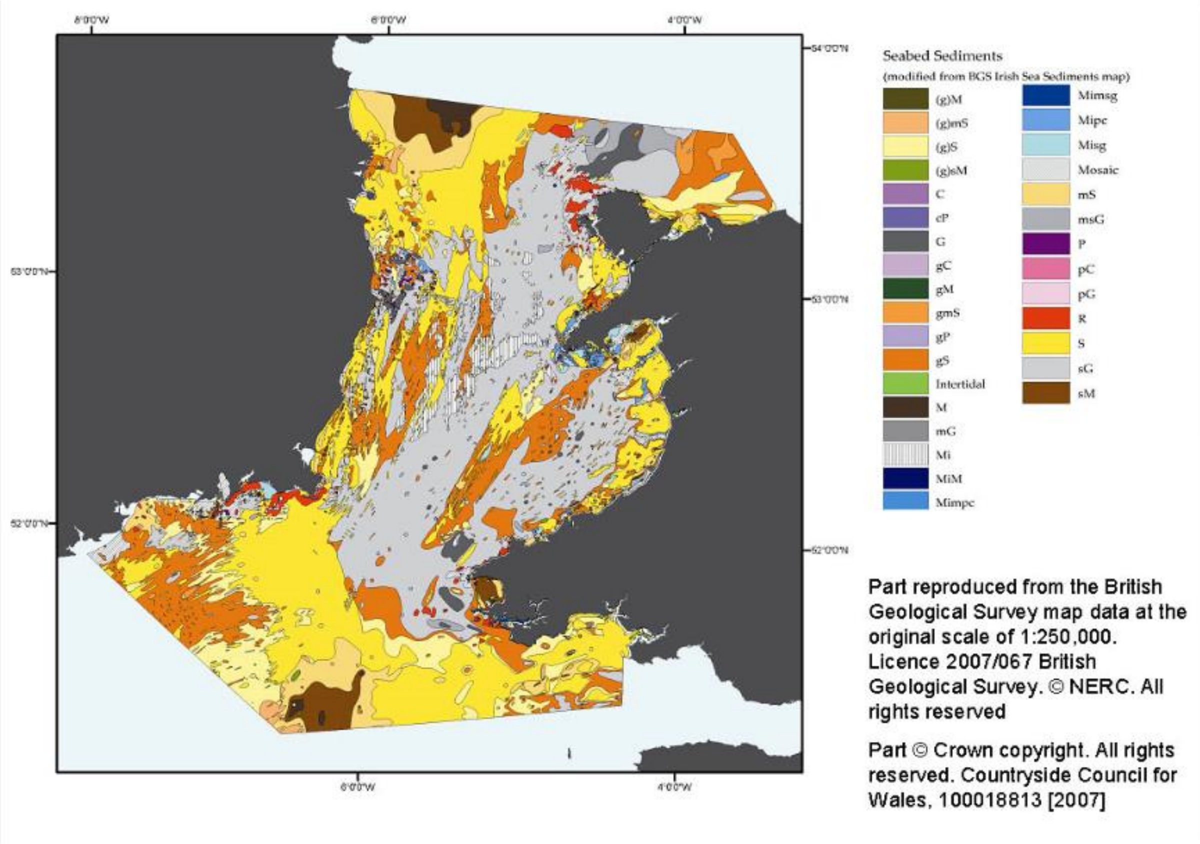


Figure 45. Seabed sediment types in the Irish Sea. Preferred sandeel sediment is in yellow (sand) and gravelly sand (orange-brown) (Robinson *et al*., 2011)

Sandeels are also an important prey for a number of commercially important fish species, such as whiting, cod and haddock (Holland *et al*., 2005). These predatory fish species are important prey for both bottlenose dolphins and harbour porpoises. These predatory fish may follow sandeels to feed on them. Shoals of whiting and cod may lead to bottlenose dolphins aggregating to feed, and so any porpoises that were following and feeding on the sandeels may come into contact with the dolphins, resulting in some aggressive interactions. However, as sandeel abundance has decreased, competition for other species such as whiting and herring may result in an increase in encounters and conflict as both species feed on the same prey. The relationship between the abundance of species such as whiting and the number of attacked porpoises is weak. Haddock abundance was found to increase during the summer when there is high co-occurrence of the cetacean species but low strandings, suggesting that this increase in haddock abundance may reduce food competition between the cetaceans. The importance of sandeels as a prey species for harbour porpoises is further supported by the increase in cases of starvation of porpoises as sandeel abundance has decreased over time (Figure 27).

Despite dietary overlap between the species from documented studies, the diet of each species often varies with locality due to differences in environmental conditions and habitat available for the fish and their prey. Habitats in Welsh waters are likely to vary considerably compared with those elsewhere and so available fish species and abundance are also likely to vary. Therefore, dietary overlap between these cetaceans in Wales may be quite different to that in studies elsewhere. The importance of changes in prey abundance within the area may cause an increase in competition between the species and could therefore increase the likelihood of attacks. Since 1988, the temperature of the water in the Celtic Sea has been increasing compared with previous decades, coinciding with a decrease in the abundance of cod and haddock in the area (Pinnegar *et al.*, 2002). Many of the fish species that prefer warm waters, such as sprat, feed at lower trophic levels. Therefore, the increase in sea temperature can augment the decline in trophic levels caused by fishing (Pinnegar *et al.*, 2002), whilst nutritionally important species such as sandeels are being negatively affected.

Though affected by economics, there has been an overall decrease in landings of commercially important fish species in Wales since 1993, many of which are also important prey for bottlenose dolphins and harbour porpoises. Starvation of harbour porpoises has been increasing over time, likely due to the reduction in fish species abundance. This may also be the case for bottlenose dolphins. The changes in fish species abundance is likely to be augmented by changes in climate and could increase competition between cetaceans as resources are reduced leading to further aggressive interactions.

In other regions, such as Scotland and California, the diet of bottlenose dolphins has been found to significantly overlap with that of other species, including harbour seals and California sea lions (Cotter *et al.*, 2011). However, there is no evidence of attacks between these species. This may be due to abundant prey resources in the area or these species may have well-developed niche partitioning either spatially or temporally.

4.3 Object-oriented play

There have been no known cases of bottlenose dolphins stranded-attacked by conspecifics in Wales, at least between 1990 and 2014. Therefore, it seems unlikely that object-oriented play is a cause of these interspecific interactions in Wales. However, strandings investigations in Scotland have found five bottlenose dolphin calves that were killed by conspecifics, which along with a number of direct observations (Robinson, 2014) suggests that infanticide may be a reason for the interactions in that area (Patterson *et al.*, 1998). The injuries found on the calves are the same as has been reported previously on harbour porpoises attacked by bottlenose dolphins. These include bruising around the head and thorax, fractured ribs, haemorrhaging, lungs ruptured by broken ribs, and tooth rake marks (Patterson *et al.*, 1998). Another similarity to the attacked harbour porpoises is that these calves were not eaten. The size range of the calves killed by bottlenose dolphins was similar to that of attacked harbour porpoises (Figure 39), suggesting that the interspecific interactions of the species in this area may be due to practice for infanticide (Ross and Wilson, 1996; Patterson *et al.*, 1998; Robinson, 2014). In Florida, direct observations of bottlenose dolphins attacking a conspecific calf (Kaplan, 2009) in a similar way to observed attacks on harbour porpoises, also suggests infanticide practice as a cause. However, it may be that this method of killing another animal is simply very effective. In Wales, the harbour porpoises attacked were found to be within a similar size range in body length to those bottlenose dolphins attacked in Scotland (Figure 40) suggesting that infanticide cannot be excluded as a possible explanation for the attacks in Wales. Despite the lack of stranded-attacked bottlenose dolphins in Wales, it is possible that this occurs more often than documented, as these fatal interactions take place at sea and few direct observations have occurred. However, without any bottlenose dolphin strandings due to intra-specific aggression, it is not likely to be a cause in Wales.

Extensive documentation of fighting between male bottlenose dolphins globally (Connor *et al.*, 2001; Herzing *et al.*, 2003; Coscarello and Crespo, 2009), usually to gain access to females, suggests that aggressive behaviour towards conspecifics is likely to occur in the Welsh population. Therefore, practice-fighting may be a potential causal factor in such fatal interactions between bottlenose dolphins and harbour porpoises.

4.4 Sex ratio and elevated testosterone

Most strandings of attacked harbour porpoises occurred in the summer months from April to September. During this time, the main bottlenose dolphin breeding period occurs, with calving and mating between July and September. Suggesting that hormone levels within the bottlenose dolphin population will be high. These summer months during breeding relate to a time of high co-occurrence and higher strandings rate, possibly due to attacks from females protecting their calves or due to males that may be defending their access to females. During this period, males are known to fight each other, competing for females and harassing them. Young males may be sexually frustrated due to their inability to gain access to females. All these factors may result in heightened aggression, which could then be directed towards porpoises in the vicinity. In Wales, identified attackers are all males (Evans, *pers. comm.*). In this study, a larger proportion of male harbour porpoises were attacked by bottlenose dolphins than females, although this was not significant. It is unlikely that the dolphins are attacking a specific sex, and is more likely a random occurrence.

4.5 Other cases of attacks

Bottlenose dolphins are one of the few mammal species to direct lethal, non-predatory aggression towards other marine mammal species (Connor *et al.*, 2000). These fatal interactions do not result in the consumption of the mammal by the bottlenose dolphins. Only pursuit, injury and death result. Documented behaviour of this kind in the animal kingdom is quite rare, although similar behaviour is known between lions and hyenas (Kruuk, 1972; Trinkel and Kastberger, 2005) in which food competition is the cause of violent interactions, in which death of either animal can occur. However, in the case of bottlenose dolphins and harbour porpoises, the interaction is unequal with the smaller porpoise always being the injured or killed party.

Therefore, in areas of high co-occurrence, it is necessary for porpoises to avoid bottlenose dolphins either through niche partitioning or by out-manoeuvring them. Both visual and acoustic evidence from a number of studies, show that harbour porpoises avoid bottlenose dolphins (Simon *et al.*, 2010; Evans *et al.*, 2015; Jacobson *et al.*, 2015). Bottlenose dolphins are also known to engage in aggressive attacks with other cetacean species (Table 1).

Fatal interactions between bottlenose dolphins and harbour porpoises have been recorded in other areas, including Scotland, Cornwall and Devon (Figure 46), California and the French coast of the Bay of Biscay. In the Moray Firth, Scotland, bottlenose dolphins attacks account for 63% of harbour porpoise strandings (Ross and Wilson, 1996) and are thought to be due to multiple factors, including infanticide practice (Robinson, 2014). In Cornwall and Devon, harbour porpoises were first identified as attacked by bottlenose dolphins in 2001 (Barnett *et al.*, 2009). Since then, a number of other cetacean species (common dolphins, striped dolphin and Risso's dolphin) have stranded with injuries likely caused by bottlenose dolphins (Barnett *et al.*, 2009).

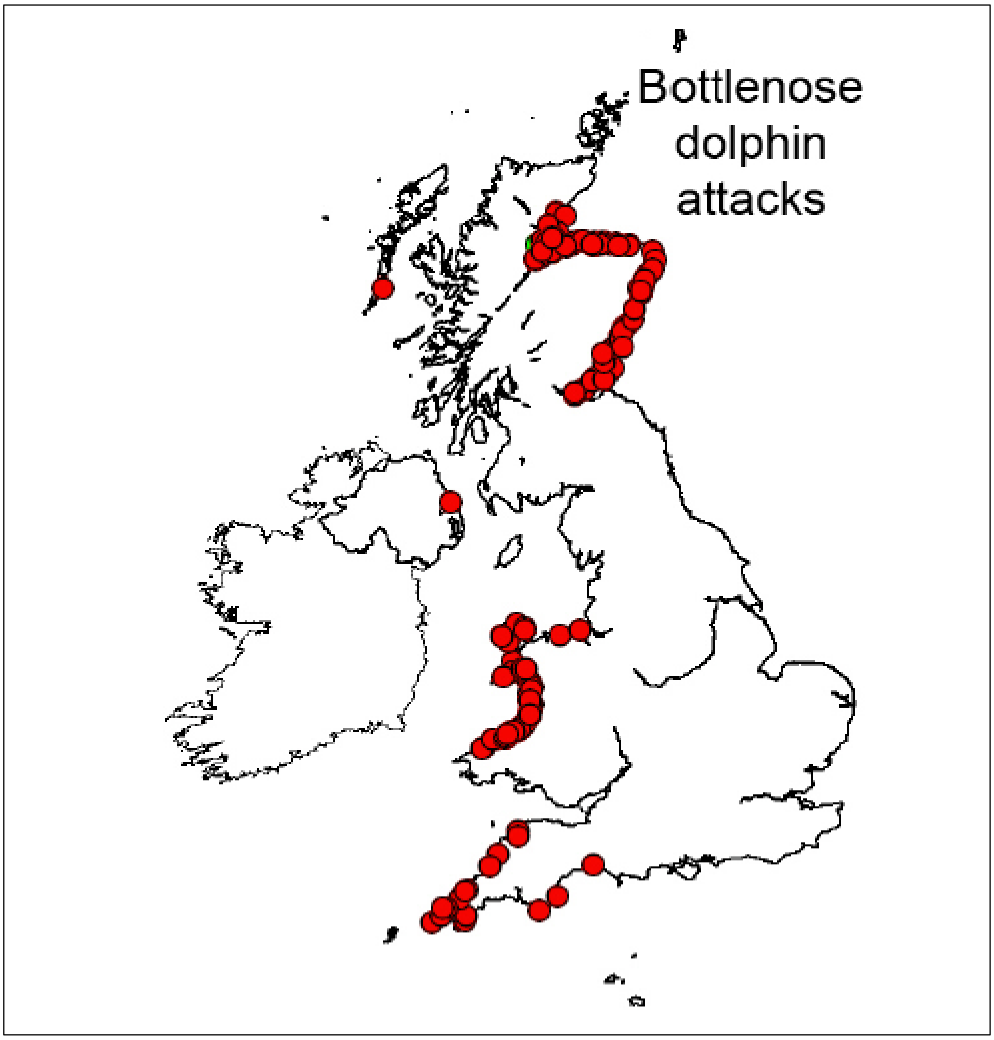


Figure 46. Harbour porpoises stranded-attacked by bottlenose dolphins around the UK, 1991-2010 (Deaville and Jepson, 2011)

Retrospective analysis of photographs of stranded common dolphins, taken in 1992, on the Isles of Scilly has identified rake marks consistent with those caused by bottlenose dolphins (Barnett *et al.*, 2009). At least five bottlenose dolphins in South-West England have also been found with lesions resulting from intraspecific aggression (Barnett *et al.*, 2009). Many animals documented as attacked by bottlenose dolphins were juveniles, which may be significant in terms of causation. However, their smaller size and naivety may make them more vulnerable. Currently, the range of cetacean species found attacked by bottlenose dolphins in South-West England suggests that multiple factors (such as infanticide, practice-fighting, sexual frustration and interference competition for prey), may cause this aggression (Barnett *et al.*, 2009).

Between 2005 and 2009, in California, 44 harbour porpoise deaths were due to attacks by bottlenose dolphins (35%) (Cotter *et al.*, 2011). In this area, competition for resources is believed to be weak causation, since in this region there is little dietary overlap, and the species distribution patterns differ. However, infanticide and practice-fighting are thought to be likely causes, although the majority of attacks (64%) occurred during peak breeding season when elevated testosterone and sexual frustration may be contributing factors (Cotter *et al.*, 2011). In the Bay of Biscay, Spitz *et al.*, (2006) found that bottlenose dolphins and harbour porpoises show partial dietary overlap, which may cause interference competition.

4.6 Attacks on porpoises by grey seals

Recent studies have found that attacks on harbour porpoises by grey seals (*Halichoerus grypus*) are becoming more common (Leopold *et al.*, 2014; Leopold *et al.*, 2015). Studies on these attacks have found that they are predatory, with grey seals targeting the energy rich blubber of harbour porpoises. Such predatory attacks are likely due to prey competition and a shortage of food common to both species.

5. Conclusions

Intra- and inter-specific interactions are often costly, though a superior species may have a particular advantage over the inferior, with some benefits being gained from the interaction. However, the causal factors and the advantages gained may vary depending on location.

From this study it was found that periods of high co-occurrence correspond to increases in stranded-attacked porpoises, and that prey competition and reduced resources are the most likely causal factors of the aggressive interactions in Wales. Multiple other factors are likely to influence the attacks, particularly heightened aggression between July and September, when mating and calving of bottlenose dolphins occur in Cardigan Bay. Current low fish stocks, due to overfishing, are likely to be affected further by climate change and habitat degradation, leading to further resource reductions and an increase in competition. With further declines in fish species causing increased starvation, populations of harbour porpoise such as those in Wales, which are regularly attacked by bottlenose dolphins, are likely to be reduced, leading to a change in ecosystem functioning. It is therefore important that management takes into consideration all variables involved to reduce any loss of porpoises.

Current management in Welsh waters for these cetaceans varies, with two SACs in Cardigan Bay established to conserve the resident bottlenose dolphin population. However currently, there are a number of sites proposed as SACs for the protection of harbour porpoises around the Welsh coast. The areas currently under consultation include North Anglesey, Cardigan Bay and West Pembrokeshire, and the outer Bristol Channel. These areas were identified and presented to the European Commission in March 2015, and boundaries will be refined by December 2015 (Natural Resources Wales, 2015). Further management of bycatch and boat activity is important to reduce cetacean mortality and displacement in Wales.

Further studies on the sex, age and hormone levels of participating bottlenose dolphin individuals may help to distinguish whether the interactions can be related to infanticide, practice-fighting or a skewed operational sex ratio. Stomach contents' analysis would be extremely beneficial to gain further knowledge of differences in diet between individual harbour porpoises that have died from different causes. In general, the majority of studies that have taken place worldwide show that delphinids and porpoises will tend to avoid any direct competition if possible by using dietary, physiological, behavioural and habitat use specialisations to fulfil a particular niche.

5.1 Limitations

There are little available data on fish species' abundance and so it has not been possible to investigate changes in seasonal distribution or abundance of some species, which may have an effect on the interactions between bottlenose dolphins and harbour porpoises. Further studies of fish abundance throughout the year could provide support for the relationship of abundance with attacks of harbour porpoises. Studies by Peltier *et al.* (2013; 2014) have used drift models to give a more accurate position of the origin of a stranded animal. Future studies could develop these drift models for other areas such as the Irish Sea, which would give a better idea of where these interactions are occurring. These could then be further related to specific biotic and abiotic features within the habitat. Due to the limitations in the data, including absence of bottlenose dolphin strandings from attacks by conspecifics, and limited fisheries data, it is not possible to give a definitive cause for the attacks in Welsh waters.

Word count: 10,979

6. References

1. Alonso, J.M., Lopez, A., Gonzalez, A.F. and Santos, M.B. 2000. Evidence of violent interactions between bottlenose dolphins (*Tursiops truncatus*) and other cetacean species in NW Spain. *Proceedings of the 14th Annual Conference of the European Cetacean Society, Cork, Ireland, April 2nd-5th 2000*. Pp. 105-106.
2. Anderwald, P., Evans, P.G.H., Dyer, R., Dale, A., Wright, P.J. and Hoelzel, A.R. 2012. Spatial scale and environmental determinants in minke whale habitat use and foraging. *Marine Ecology Progress Series*, 450: 259-274.
3. Archer, J. 1988. *The behavioural biology of aggression*. Cambridge Studies in Behavioural Biology. Cambridge University Press, New York.
4. Baines, M.E. and Evans, P.G.H. 2012. *Atlas of the Marine Mammals of Wales*. CCW Monitoring Report No. 68. 2nd edition. 139pp.
5. Baines, M.E., Evans, P.G.H. and Shepherd, B. 2000. *Bottlenose dolphins in Cardigan Bay, West Wales*. First report to EU INTERREG and Countryside Council for Wales. Sea Watch Foundation, Oxford.
6. Baird, R.W. 1998. An interaction between Pacific white sided dolphins and a neonatal harbour porpoise. *Mammalia*, 62 (1), 129-134.
7. Baird, R.W., Ligon, A.D., Hooker, S.K. and Gorgone, A.M. 2001. Subsurface and nighttime behaviour of pantropical spotted dolphins in Hawai'i. *Canadian Journal of Zoology*, 79: 988-96
8. Barnett, J., Davidson, N., Deaville, R., Monies, R., Loveridge, J., Treganza, N. and Jepson, P.D. 2009. Postmortem evidence of interactions of bottlenose dolphins (*Tursiops truncatus*) with other dolphin species in South-West England. *Veterinary Record*. 165, 441-444.
9. Baulch, S. 2012. *Fine scale spatio-temporal variation and habitat partitioning in bottlenose dolphins and harbour porpoises*. MSc Thesis, University of Bangor.
10. Bearzi, M. 2005. Dolphin sympatric ecology. *Marine Biology Research*, 1, 165-175.
11. Bjørge, A. and Tolley K.A. 2009. Harbour porpoise, *Phocoena phocoena*. In: W.F. Perrin, B. Wursig and J.G. Thewissen, *Encyclopedia of Marine Mammals*, second edition, pp. 530-533. London, Elsevier.
12. Bjorge, A. and Tolley, K.A. 2004. Harbour porpoise. In: *Encyclopedia of Marine Mammals*. Academic Press, London and New York.

13. Browne, E. 1999. The diet of the harbour porpoise, *Phocoena phocoena*, in Irish waters. MSc thesis. University College Cork.
14. CCW (Countryside Council for Wales). 2009. Cardigan Bay, Euopean Marine Site. Regulation 33.
15. CCW (Countryside Council for Wales). Species Series. 2013. http://www.ccgc.gov.uk/landscape--wildlife/habitats--species/priority-species/harbour-porpoise.aspx
16. Clua, E. and Grosvalet, F. 2001. Mixed-species feeding aggregations of dolphins, large tunas and seabirds in the Azores. *Aquatic Living Resources*, 14, 11-18.
17. Connor, R.C. Heithaus, M. and Barre, L. 2001. Complex social structure, alliance stability and mating access in a bottlenose dolphin 'super-alliance'. *Proceedings of the Royal Society London B*, 268, 263-267.
18. Connor, R.C., Richards, A.F., Smolker, R.A. and Mann, J. 1996. Patterns of female attractiveness in Indian Ocean bottlenose dolphins. *Behaviour*, 133, 37-69.
19. Coscarella, M.A. and Crespo, E.A. 2009. Feeding aggregation and aggressive interaction between bottlenose (*Tursiops truncatus*) and Commerson's dolphins (*Cephalorhynchus commersonii*) in Patagonia, Argentina. *Journal of Ethology*, 28, 83-187.
20. Cotter, M.P., Maldini, D. and Jefferson, T.A. 2011. 'Porpicide' in California: killing of harbor porpoises (Phocoena phocoena) by coastal bottlenose dolphins (Tursiops truncatus). *Marine Mammal Science*, 28 (1), 1-15.
21. CSIP. 2013. http://ukstrandings.org/csip-reports/
22. Darkes, G. 2008. How long is the UK coastline? The British Cartographic Society. http://www.cartography.org.uk/default.asp?contentID=749
23. Deaville, R. 2014. UK Cetacean Strandings Investigation Programme. Annual Report for the period 1st January – 31st December 2012. *Report to DEFRA.* 68pp.
24. De Stephanis, R.D., Gimenez, J., Esteban, R., Gauffier, P., Garcia-Tiscar, S., Sinding, M-H.S. and Verborgh, P. 2014. Mobbing- like behaviour by pilot whales towards killer whales: a response to resource competition or perceived predation risk? *Acta Ethologica*.
25. Dunn, D.G., Barco, S.G., Pabst, D.A. and McLellan, W.A. 2002. Evidence for infanticide in bottlenose dolphins of the Western North Atlantic. *Journal of Wildlife Disease*. 38 (3), 505-510
26. Ellis, J.R., Milligan, S.P., Readdy, L., Taylor, N. and Brown, M.J. 2012. Spawning and nursery grounds of selected fish species in UK waters. *Science Series Technical Report*, Cefas Lowestoft, 147: 56pp

27. Evans, P.G.H., Anderwald, P. and Baines, M.E. 2003. *UK Cetacean Status Review*. Report to English Nature and Countryside Council for Wales.
28. Evans, P.G.H. and Hintner, K. 2010. A Review of the Direct and Indirect Impacts of Fishing Activities on Marine Mammals in Welsh Waters. *CCW Policy Research Report* No. 104. 160pp.
29. Evans, P.G.H. 2012. *Recommended Management Units for Marine Mammals in Welsh Waters*. CCW Policy Research Report No. 12/1. 69pp
30. Evans, P.G.H., Pierce, G.J., Veneruso, G., Weir, C.R., Gibas, D., Anderwald, P. and Begoña Santos, M. 2015. Analysis of long-term effort-related land-based observations to identify whether coastal areas of harbour porpoise and bottlenose dolphin have persistent high occurrence & abundance. *JNCC report* No. 543, JNCC, Peterborough.
31. Feingold, D. and Evans, P.G.H. 2014. Bottlenose Dolphin and Harbour Porpoise Monitoring in Cardigan Bay and Pen Llyn a'r Sarnau Special Areas of Conservation 2011- 2013. *Natural Resources Wales Evidence Report Series* No. 4. 124pp.
32. Flores, P.A.C. and Fontoura, N.F. 2006. Ecology of marine tucuxi, *Sotalia guianensis*, and bottlenose dolphin, *Tursiops truncatus*, in Baía Norte, Santa Catarina state, southern Brazil. *Latin American Journal of Aquatic Mammals*. 5 (2), 105-115.
33. Forestell, P.H., Wright, A.M., DiBerardinis, A., Larkin, S. and Schott, V. 1999. Sex and the single tucuxi: Observations of interspecies mating between free ranging bottlenose (*Tursiops truncatus*) and tucuxi (*Sotalia fluviatilis*) dolphins in Costa Rica. 13th Biennial Conference on the Biology of Marine Mammals, Maui, Hawaii.
34. Frantzis, A. and Herzing, D. 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), 188-197.
35. Gentle, L.K. and Gosler, A.G. 2001. Fat reserves and perceived predation risk in the great tit *Parus major*. *Proceedings of the Royal Society of Biological Sciences*, 268, 487-491.
36. Gibson, R.N. 2003. Go with the flow: tidal migration in marine animals. *Hydrobiologia*, 503, 153-161
37. Greenstreet, S.P.R., Holland, G.J., Guirey, E.J., Armstrong, E., Fraser, H.M., and Gibb, I.M. 2010. Combining hydroacoustic seabed survey and grab sampling techniques to assess "local" sandeel population abundance. *ICES Journal of Marine Science*, 67, 971–984.

38. Hammond, P.S., Berggren, P., Benke, H., Borchers, D.L., Collet, A., Heide-Jorgensen, M.P., Heimlich, S., Hiby, A.R., Leopold, M.F. and Oiens, N. 2002. Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent waters. *Journal of Applied Ecology*, 39, 361-376.
39. Haelters, J. and Everaarts, E. 2011. Two cases of physical interaction between white beaked dolphin (*Lagenorhynchus albirostris*) and juvenile harbour porpoises (*Phocoena phocoena*) in the Southern North Sea. Aquatic Mammals, 37 (2), 198-201.
40. Herzing, D.L. and Johnson, C.M. 1997. Interspecific interactions between spoteed dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) in the Bahamas, 1985-1995. *Aquatic Mammals*, 23, 85-99.
41. Herzing, D.L., Moewe, K. and Brunnick, B.J. 2003. Interspecific interactions between Atlantic spotted dolphins (*Stenella frontalis*) and Bottlenose dolphins (Tursiops truncatus) on Great Bahama Bank, Bahamas. *Aquatic Mammals*, 23, 335-341
42. Higgins, L.V. and Tedman, R.A. 1990. Effects of attacks by male Australian sea lions, Neophoca cinerea, on mortality of pups. *Journal of Mammalogy*, 71 (4):617-619.
43. Holland, G. J., Greenstreet, S. P. R., Gibb, I. M., Fraser, H. M., and Robertson, M. R. 2005. Identifying sandeel *Ammodytes marinus* sediment habitat preferences in the marine environment. *Marine Ecology Progress Series*, 303, 269–282.
44. IUCN. 2013. Hammond, P.S., Bearzi, G., Bjørge, A., Forney, K., Karczmarski, L., Kasuya, T., Perrin, W.F., Scott, M.D., Wang, J.Y., Wells, R.S. and Wilson, B. 2008. *Phocoena phocoena*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.2. <www.iucnredlist.org>. Downloaded on **04 May 2014**.
45. IUCN. 2013a. Hammond, P.S., Bearzi, G., Bjørge, A., Forney, K.A., Karkzmarski, L., Kasuya, T., Perrin, W.F., Scott, M.D., Wang, J.Y., Wells, R.S. and Wilson, B. 2012. *Tursiops truncatus*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.2. <www.iucnredlist.org>. Downloaded on **04 May 2014**.
46. IUCN, 2014. Hammond, P.S., Bearzi, G., Bjørge, A., Forney, K., Karczmarski, L., Kasuya, T., Perrin, W.F., Scott, M.D., Wang, J.Y., Wells, R.S. and Wilson, B. 2008. *Phocoena phocoena (Baltic Sea subpopulation)*. The IUCN Red List of Threatened Species. Version 2014.3. <www.iucnredlist.org>. Downloaded on 04 February 2015
47. Jacobson, E.K., Forney, K.A. and Harvey, J.T. 2015. Acoustic evidence that harbour porpoises (*Phocoena phocoena*) avoid bottlenose dolphins (*Tursiops truncatus*). *Marine Mammal Science*, 31 (1), 386-397.

48. Jepson, P.D. and Baker, J.R. 1998. Bottlenosed dolphins (*Tursiops truncatus*) as a possible cause of acute traumatic injuries in porpoises (*Phocoena phocoena*). *Veterinary Record*, 143, 614-615.
49. Johnston, D.W., Westgate, A.J. and Read, A.J. 2005. Effects of fine scale oceanographic features on the distribution and movements of harbour porpoises Phocoena phocoena in the Bay of Fundy. *Marine Ecology Progress Series*, 295, 279-293.
50. Kaplan, J.D., Lentell, B.J. and Lange, W. 2009. Possible evidence for infanticide among bottlenose dolphins (*Tursiops truncatus*) off St. Augustine, Florida. *Marine Mammal Science*. 25 (4), 970-975.
51. Larrat, S., Measures, L.N. and Lair, S. 2012. Rake Marks on a Harbour Porpoise (*Phocoena phocoena*) Calf Suggestive of a Fatal Interaction with an Atlantic White-Sided Dolphin (*Lagenorhynchus acutus*). *Aquatic Mammals*. 38 (1): 86-91.
52. Le Boeuf, B.L. and Campagna, C. 1994. Protection and abuse of youg in pinnipeds. Pp. 257-276. In: Parmigiani and S. Vom Saal, F. *Infanticide and parental care*. Harwood Academic Publishers, London.
53. Leopold, M.F., Begeman, L., Bleijswijk, J.D.L.V., Ijsseldijk, L.L, Witte, H.J. and Grone, A. 2015. Exposing the grey seal as a major predator of harbour porpoises. *Proceedings of the Royal Society London Biological Sciences*, 282, 2429.
54. Leopold, M.F., Begeman, L., Hebe, E., Hiele, J.V.D., Hiemstra, S., Keijl, G., Meesters, E.H., Verheyen, D. and Grone, A. 2014. Porpoises: from predators to prey. *Journal of Sea Research*, 97, 14-23.
55. Lockyer, C. 1995. Investigation of aspects of the life history of the harbour porpoise, *Phocoena phocoena*, in British waters. In Special Issue, 16: *Biology of Phocoenids*, A. Bjørge & G. P. Donovan (eds). Cambridge: International Whaling Commission, 189–197.
56. MacLeod, C.D., Begona Santos, M., Reid, R.J., Scott, B.E. and Pierce, G.J. 2007. Linking sandeel consumption and the likelihood of starvation in harbour porpoises in the Scottish North Sea: could climate change mean more starving porpoises? *Biology Letters*, 3, 185-188.
57. Natural Resources Wales, 2015. Special Areas of Conservation. Downloaded on 15/03/2015. http://naturalresourceswales.gov.uk/content/docs/pdfs/our-work/Policy-advice-and-guidance/marine-and-freshwater-fisheries/possible-new-marine-special-areas-of-conservation-and-special-protection-areas-in-wales-faqs.pdf?lang=en

58. Norrman, E., Dussan-Duque, S., and Evans, P.G.H. 2015. *Bottlenose dolphins in Wales: systematic mark-recapture surveys in Welsh waters.* Natural Resources Wales Evidence Report Series. 84pp.
59. Olivier, B. and Young, L.J. 2002. Animal models of aggression. *Neuropsychopharmacology: the fifth generation of progress*. 1699-1708.
60. Patterson, I.A.P., Reid, R.J., Wilson, B., Grellier, K., Ross H.M. and Thompson P.M. 1998. Evidence for infanticide in bottlenose dolphins: an explanation for violent interactions with harbour porpoises? *Proceeding of the Royal Society London*, 265, 1167-1170.
61. Peltier, H., Baagøe, H., Camphuysen, K., Czeck, R., Dabin, W., Daniel, P., Deaville, R., Haelters, J., Jauniaux, T., Jensen, L., Jepson, P., Keiji, G., Siebert, U., Van Canneyt, O. and Ridoux, V. 2013. The Stranding Anomaly as Population Indicator: the Case of Harbour Porpoise *Phocoena phocoena* in North-Western Europe. *PLoS One* 8(4):e62,180,
62. Peltier, H., Jepson, P., Dabin, W., Deaville, R., Daniel, P., Van Canneyt, O. and Ridoux, V. 2014. The Contribution of Stranding Data to Monitoring and Conservation Strategies for Cetaceans: Developing Spatially Explicit Mortality Indicators for Common Dolphins (*Delphinus delphis*) in the Eastern North-Atlantic. *Ecological Indicators* 39:203–214
63. Penrose, R. 2006. *Marine mammal and marine turtle strandings (Welsh coast). Annual Report 2005.* Marine Environmental Monitoring. www.strandings.com
64. Pesante, G., Evans, P.G.H., Anderwald, P., Powell, D. and McMath, M. 2008a. Connectivity of bottlenose dolphins in Wales: North Wales photo-monitoring. *CCW Marine Monitoring Report No. 62*, 1-42.
65. Pesante, G., Evans, P.G.H., Baines, M.E. and McMath, M. 2008b. Abundance and life history parameters of bottlenose dolphin in Cardigan Bay: Monitoring 2005-2007. *CCW Marine Monitoring Report* no. 61, 1-75.
66. Pinnegar, J.K., Jennings, S., O'Brien, C.M. and Polunin, N.V.C. 2002. Long-term changes in the trophic level of the Celtic Sea fish community and fish market price distribution. *Journal of Applied Ecology*, 39, 377-390.
67. Polis, G.A., Myers, C.A. and Holt, R.D. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology, Evolution and Systematics*, 20, 297-330.

68. Psarakos, S., Herzing, D.L. and Marten, K. 2003. Mixed species associations between pantropical spotted dolphins (Stenella attenuate) and Hawaiian spinner dolphins (Stenella longirostris) off Oahu, Hawaii. *Aquatic Mammals*, 29 (3), 390-395.
69. R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.
70. Reid, J.B., Evans, P.G. and Northridge, S.P. 2003. *Atlas of cetacean distribution in north-west European waters*. JNCC.
71. Robinson, K.P. 2014. Agonistic intraspecific behaviour in free- ranging bottlenose dolphins: Calf directed aggression and infanticidal tendencies by adult males. *Marine Mammal Science*, 30, 1.
72. Robinson, K., Ramsay, K., Lindenbaum, C., Walker, P., Frost, N., Vittorio, M. and Wright, A. 2011. Habitat Mapping for Conservation and Management of the Southern Irish Sea (HABMAP). III: Modelling and mapping extension study. *CCW Science Report No.951*. 102pp + Appendices.
73. Rose, N.A., Deutsch, C.J. and Le Boeuf, B.J. 1991. Sexual behaviour of male northern elephant seals: III. The mounting of weaned pups. *Behaviour*, 19, 171-192.
74. Ross, H.M. and Wilson, B. 1996. Violent interactions between bottlenose dolphins and harbour porpoises. *Proceedings of the Royal Society Biological Sciences*, 263 (1368), 283-286.
75. SAMBAH, 2014. Press release on 10th of December 2014 from SAMBAH project. www.sambah.org
76. Santos, M.B., Pierce, G.J., Reid, G.J., Patterson, I.A., Ross, H.M. and Mente, E. 2001. Stomach contents of bottlenose dolphins (*Tursiops truncatus*) in Scottish waters. *Journal of the Marine Biological Association of the United Kingdom*, 81, 873-878.
77. Santos, M.B., Pierce, G.J., Learmonth, J.A., Reid, R.J., Ross, H.M., Patterson, I.A.P., Reid, D.G. and Beare, D. 2004. Variability in the diet of harbour porpoises (*Phocoena phocoena*) in Scottish waters 1992-2003. *Marine Mammal Science*, 20, 1-27
78. Scottish Sea Fisheries Statistics. 2009. http://www.scotland.gov.uk/Publications/2010/09/15155811/48
79. Scottish Government, 2010. http://www.gov.scot/Topics/marine/marine-environment/species/fish/sandeels
80. Sea Watch Foundation. 2012. *The Harbour porpoise in UK waters*. Fact sheet.

81. Sekiguchi, K. 1995. Occurrence, behaviour and feeding habits of harbour porpoises (Phocoena phocoena) at Pajaro Dunes, Monterey Bay, California. *Aquatic Mammals*, 21, 91-103.

82. Shane, S.H. 1995. Relationship between pilot whales and Risso's dolphins at Santa Catalina Island, California, USA. *Marine Ecology Progress Series*, 123, 5-11.

83. Simon, M., Nuuttila, H., Reyes-Zamudio, M. M., Ugarte, F., Verfuss, U. and Evans, P.G.H. 2010. Passive acoustic monitoring of bottlenose dolphins 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(08), 1539–1545.

84. Spitz, J., Rosseau, Y. and 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: 259-270.

85. Thompson, P., White, S. and Dickson, E. 2004. Co-variation in the probabilities of sighting harbor porpoises and bottlenose dolphins. *Marine Mammal Science*, 20 (2), 322-328.

86. Trinkel, M. and Kastberger, G. 2005. Competitive interactions between spotted hyenas and lions in the Etosha National Park, Namibia. *African Journal of Ecology*.,43, 220-224.

87. Vitiello, M.D. and Stoff, D.M. 1997. Subtypes of aggression and their relevance to child psychiatry. *Journal of the American Academy of Child and Adolescent Psychiatry*, 36, 3, 307-315.

88. Wedekin, L.L., Daura-Jorge, F.G. and Simoes-Lopes, P.C. 2004. An aggressive interaction between Bottlenose dolphins (*Tursiops truncatus*) and estuarine dolphins (*Sotalia Guianensis*) in Southern Brazil. *Aquatic Mammals*, 30 (3), 391-397.

89. Wells, R. and Scott, M. 2002. "Bottlenose Dolphins". In Perrin, W.; Wursig, B. and Thewissen, J. *Encyclopedia of Marine Mammals*. Academic Press. pp. 122–127.

90. Wilson, B. 2008. Bottlenose dolphin. In: S. Harris and D.W. Yalden, *Mammals of the British Isles: Handbook*, 4^{th} Edition, pp. 709-715. The Mammal Society, Corby.

91. Winslade, P. 1974. Behavioural studies on the Lesser Sandeel Ammodytes marinus (Raitt). *Journal of Fish Biology*, 6: 565–599.

92. Wolff, J.O. 1997. Population regulation in mammals: an evolutionary perspective. *Journal of Animal Ecology*, 66, 1-13.

7. Appendix 1

Final maps of harbour porpoise stranded killed by bottlenose dolphins, and distribution and abundance of both species, corrected for effort, over the study period by both month and year. The maps that include strandings data, use only those data that correspond to the months within each year that co-occurrence (overlap) could be analysed.

7.1 Stranding maps

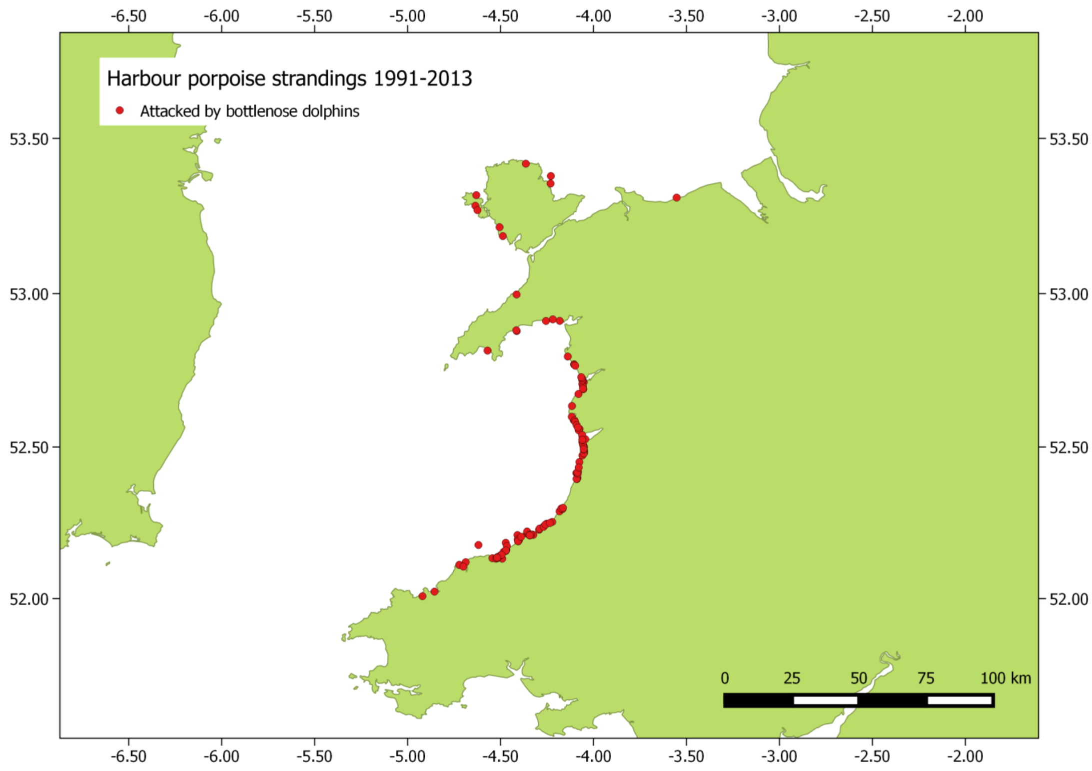


Figure 1. Map of the distribution of stranded-attacked porpoises around the Welsh coast

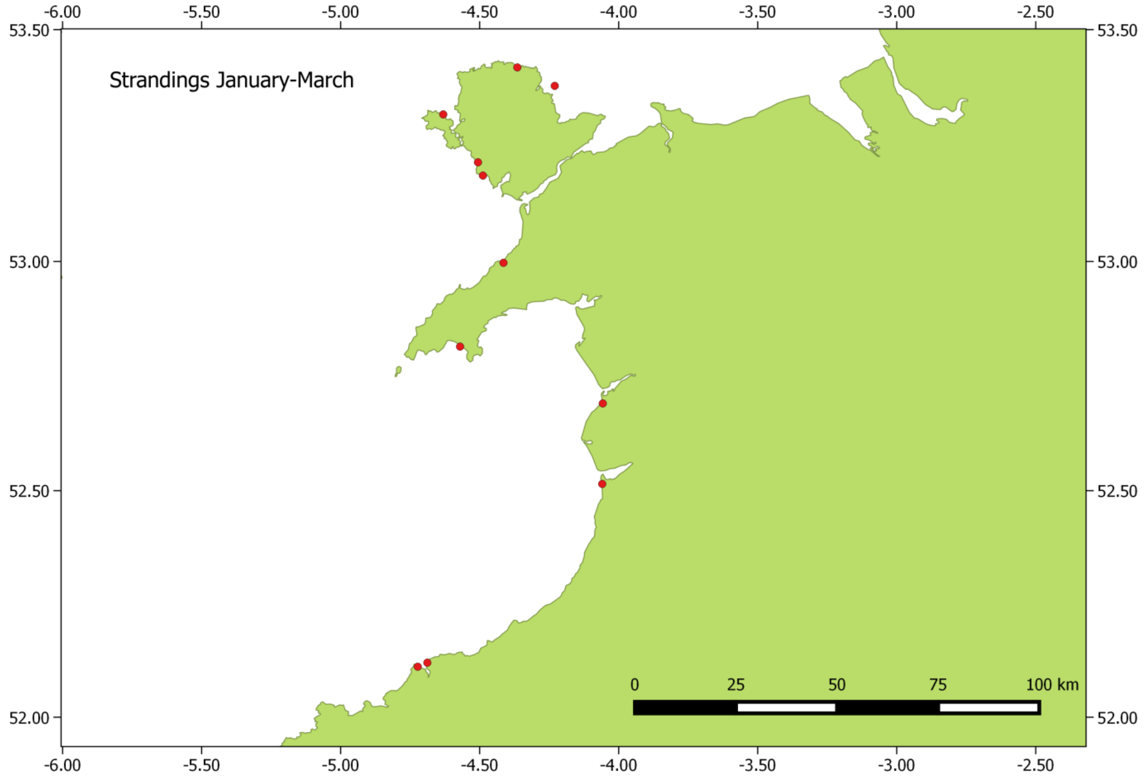


Figure 2. Map of stranded-attacked porpoises from January-March along the Welsh coast

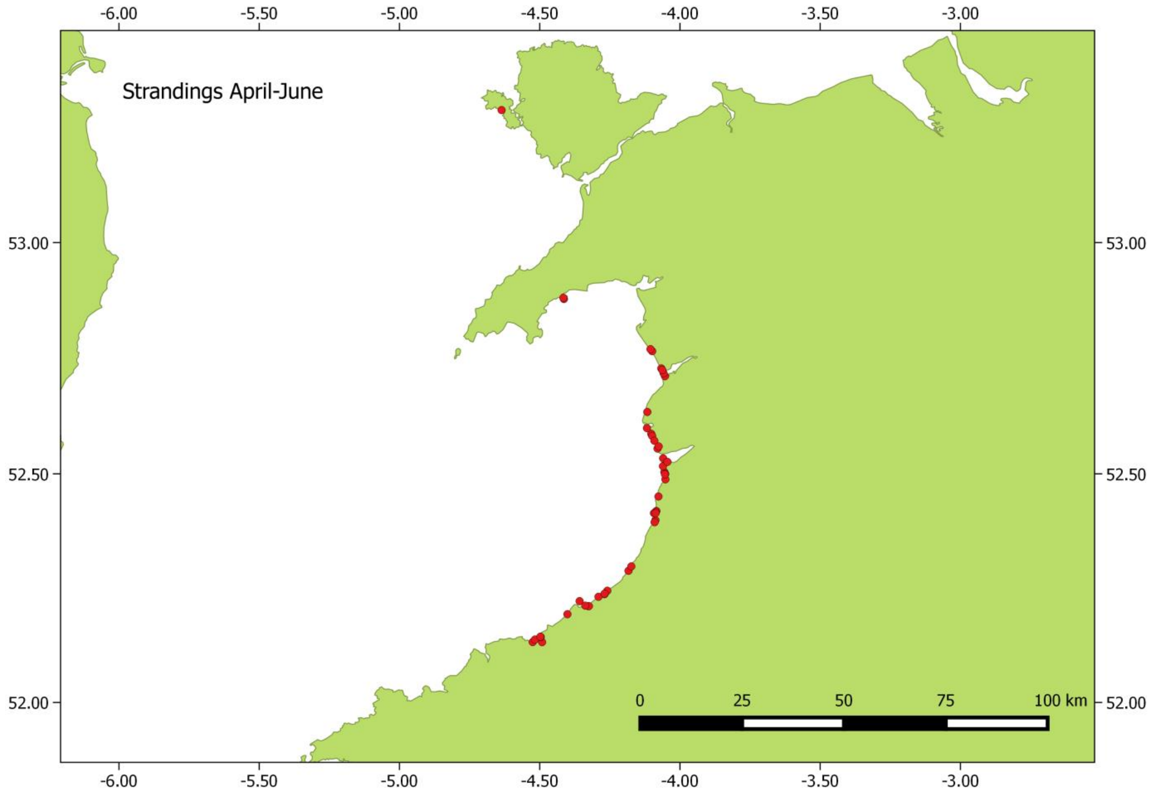


Figure 3. Map of stranded-attacked porpoises from April-June along the Welsh coast

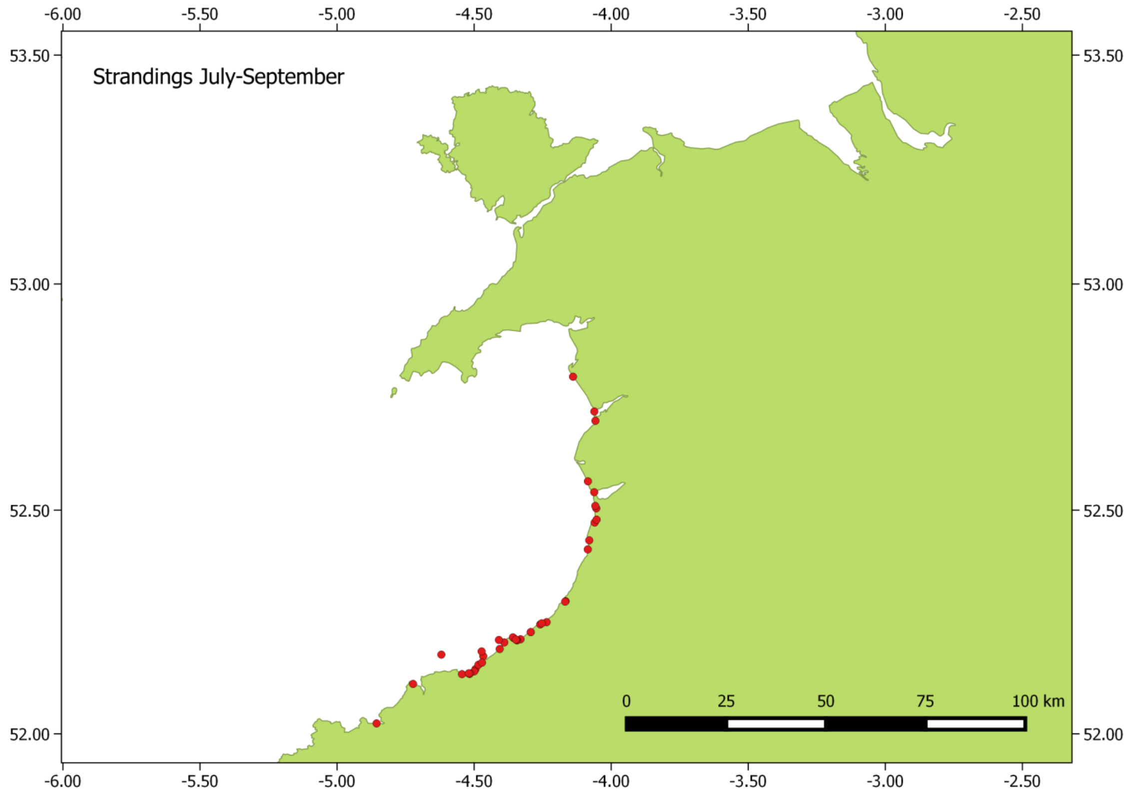


Figure 4. Map of stranded-attacked porpoises from July-September along the Welsh coast

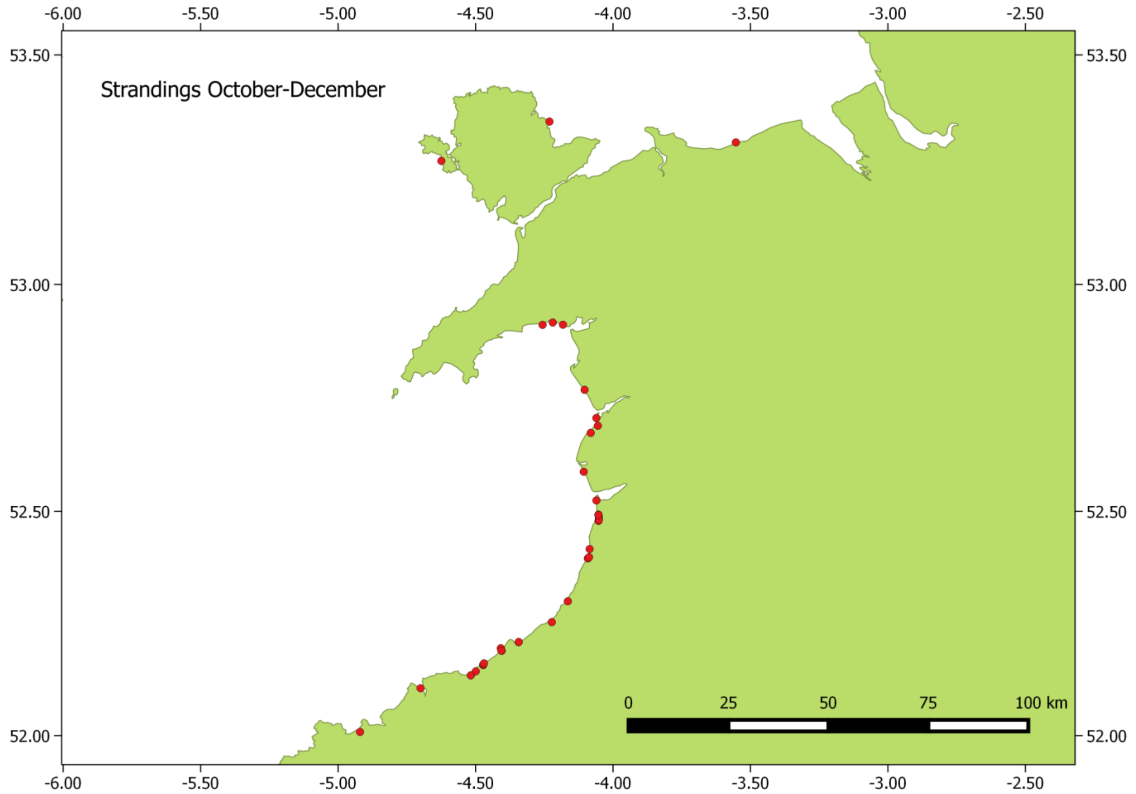


Figure 5. Map of stranded-attacked porpoises from January-March along the Welsh coast

7.2 Sightings maps

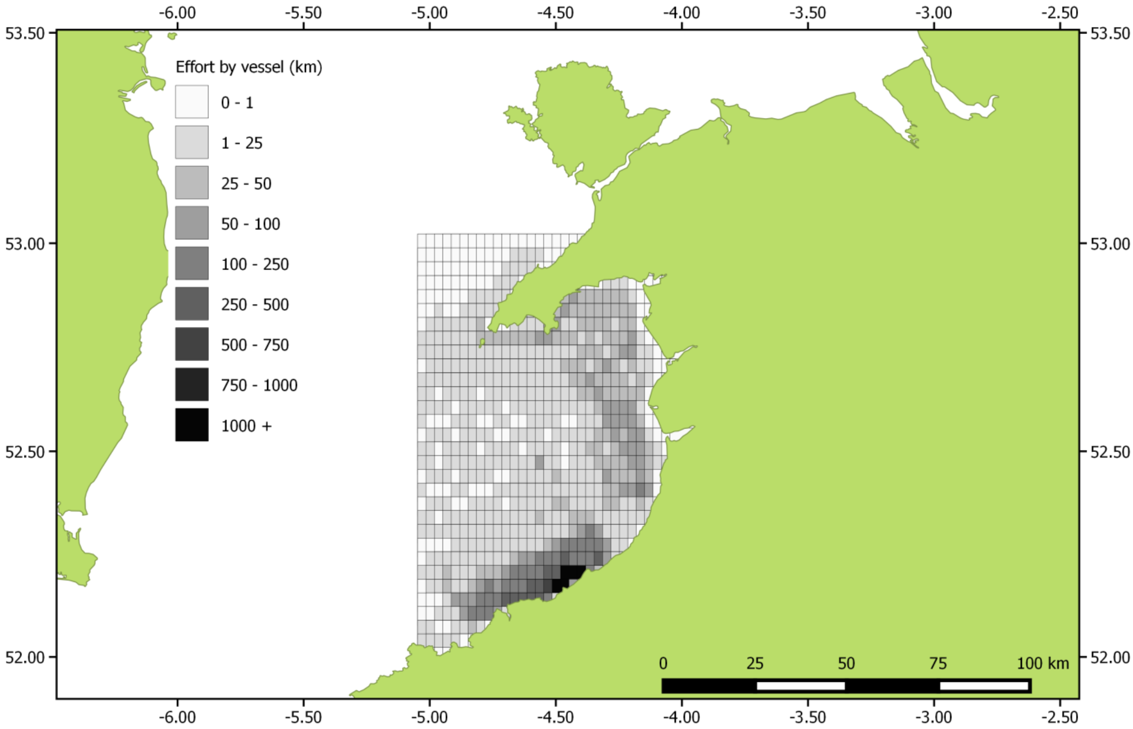


Figure 6. Map of total vessel effort (km) per cell in Cardigan Bay between 2001-2014

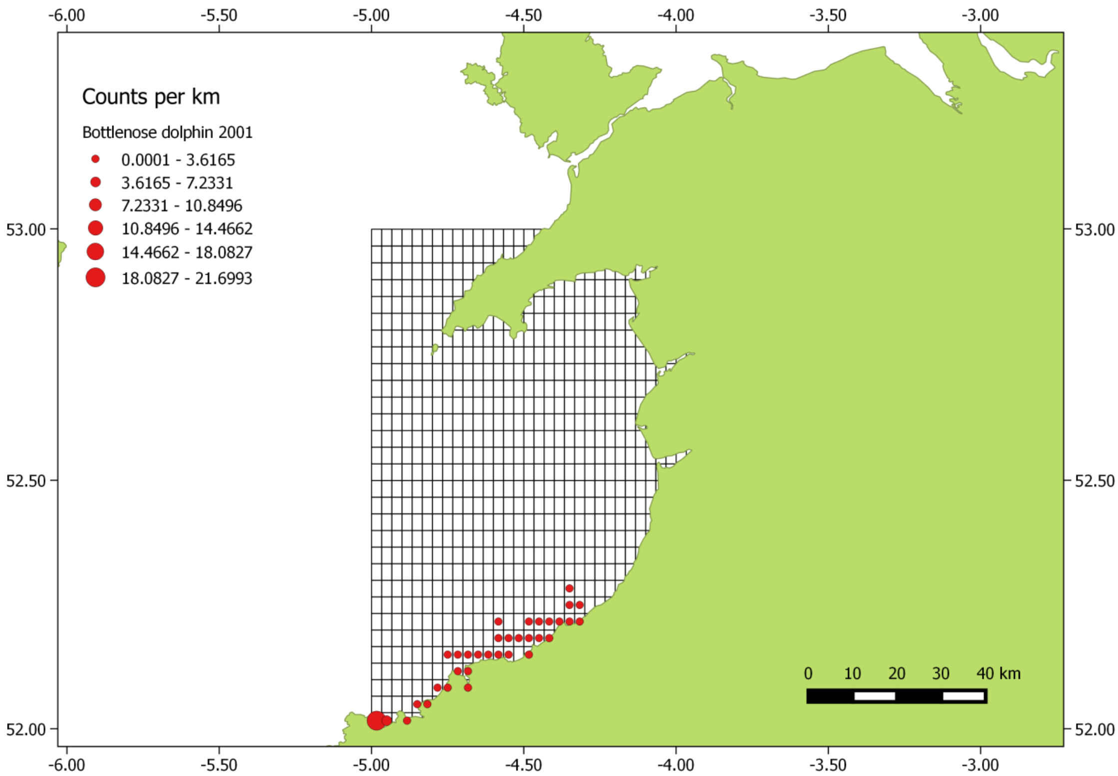


Figure 7. Map of bottlenose density (count per km) corrected for effort in 2001

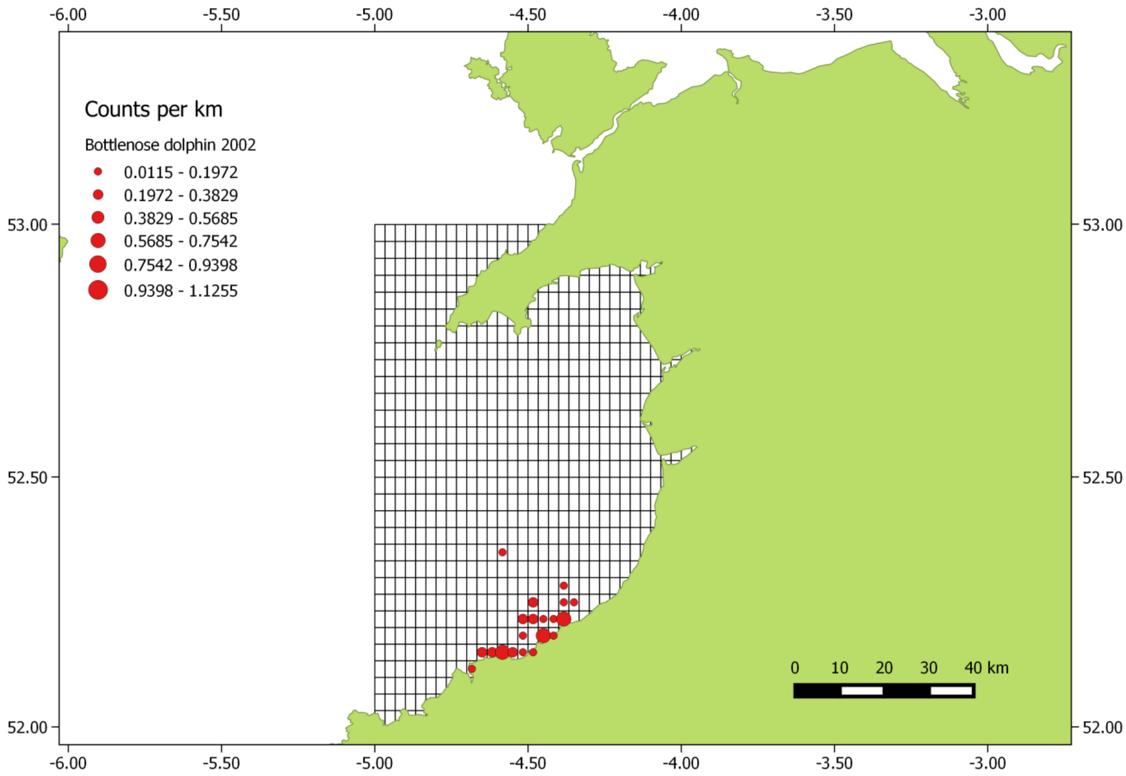


Figure 8. Map of bottlenose density (count per km) corrected for effort in 2002

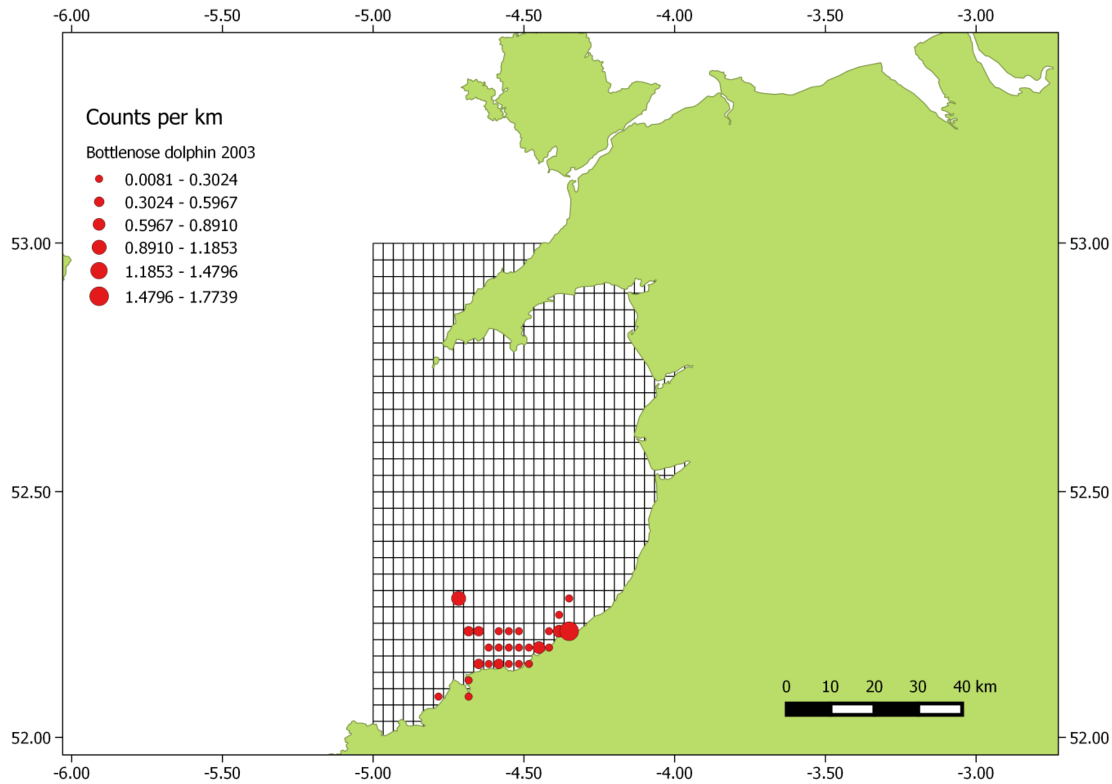


Figure 9. Map of bottlenose density (count per km) corrected for effort in 2003

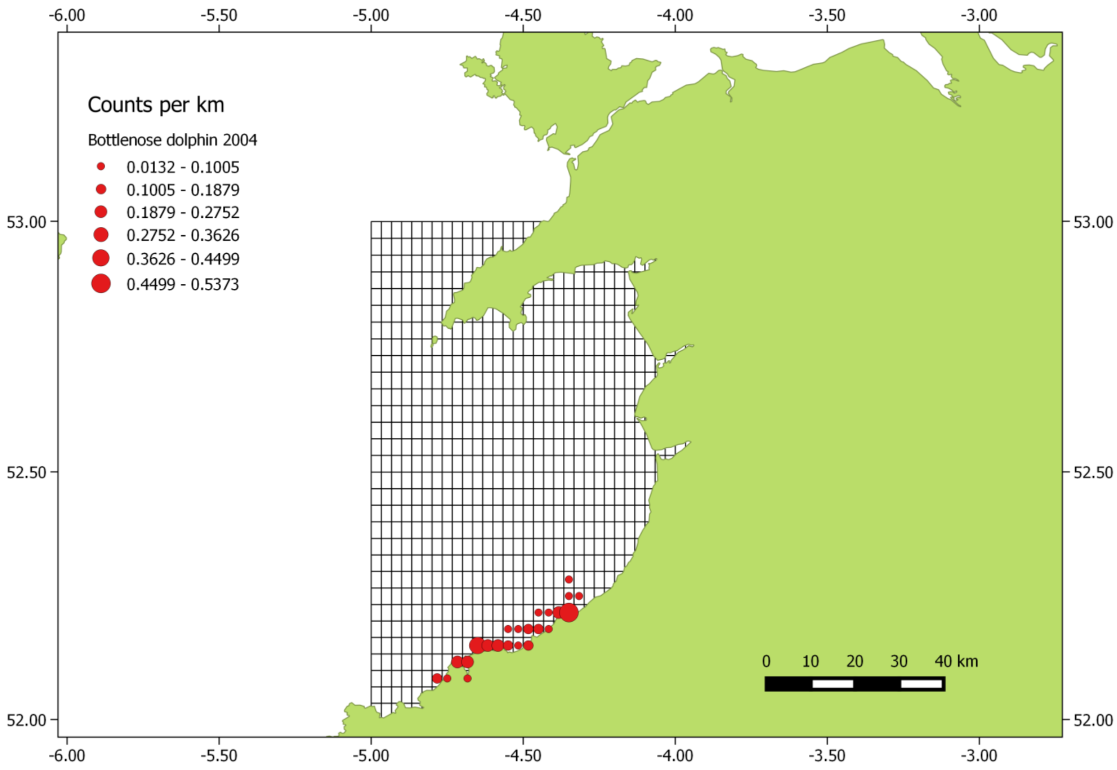


Figure 10. Map of bottlenose density (count per km) corrected for effort in 2004

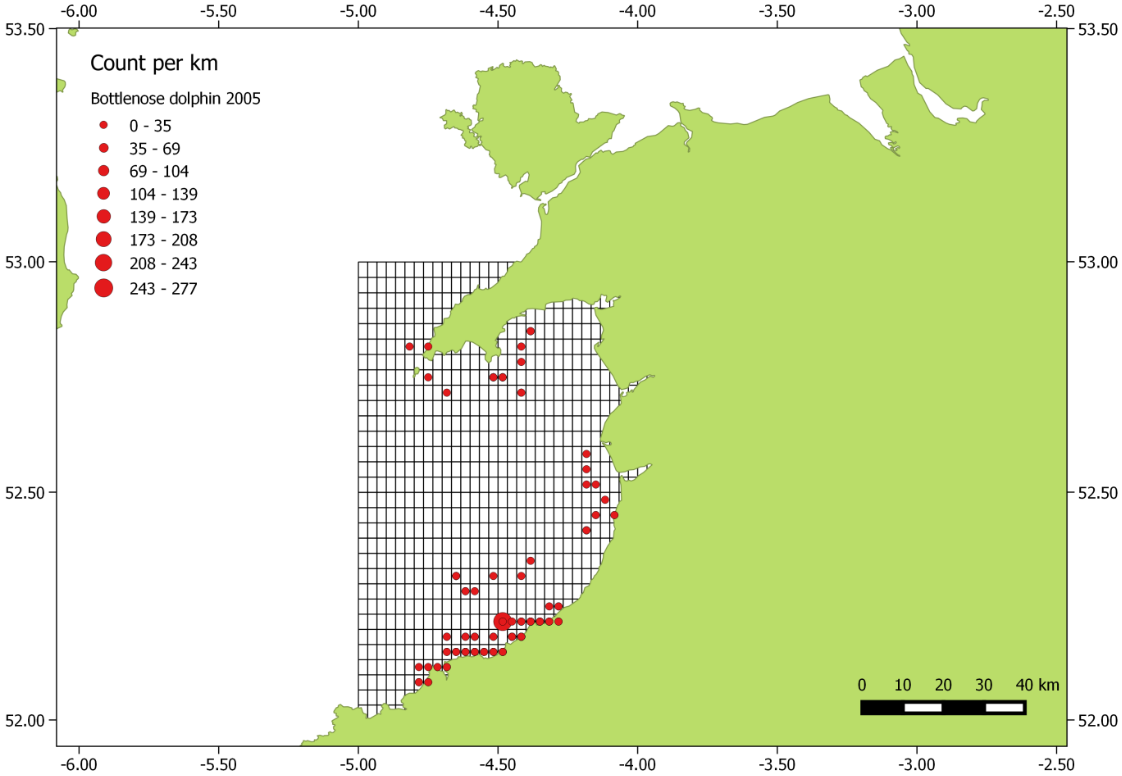


Figure 11. Map of bottlenose density (count per km) corrected for effort in 2005

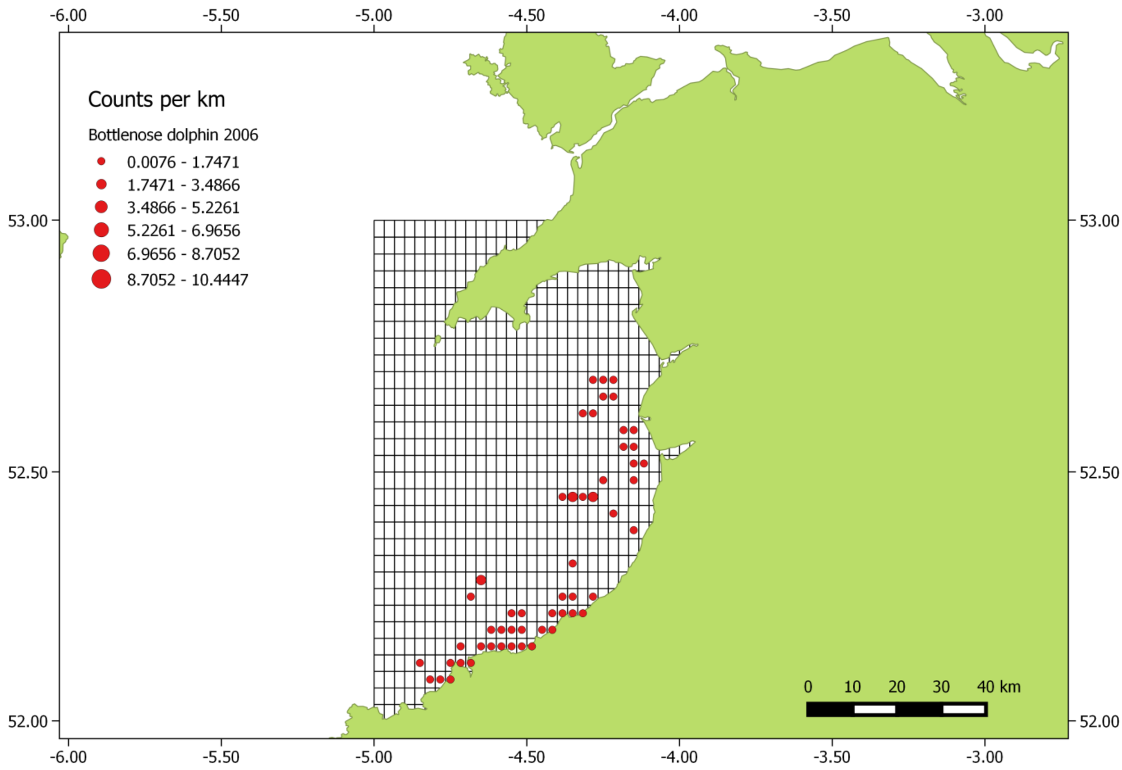


Figure 12. Map of bottlenose density (count per km) corrected for effort in 2006

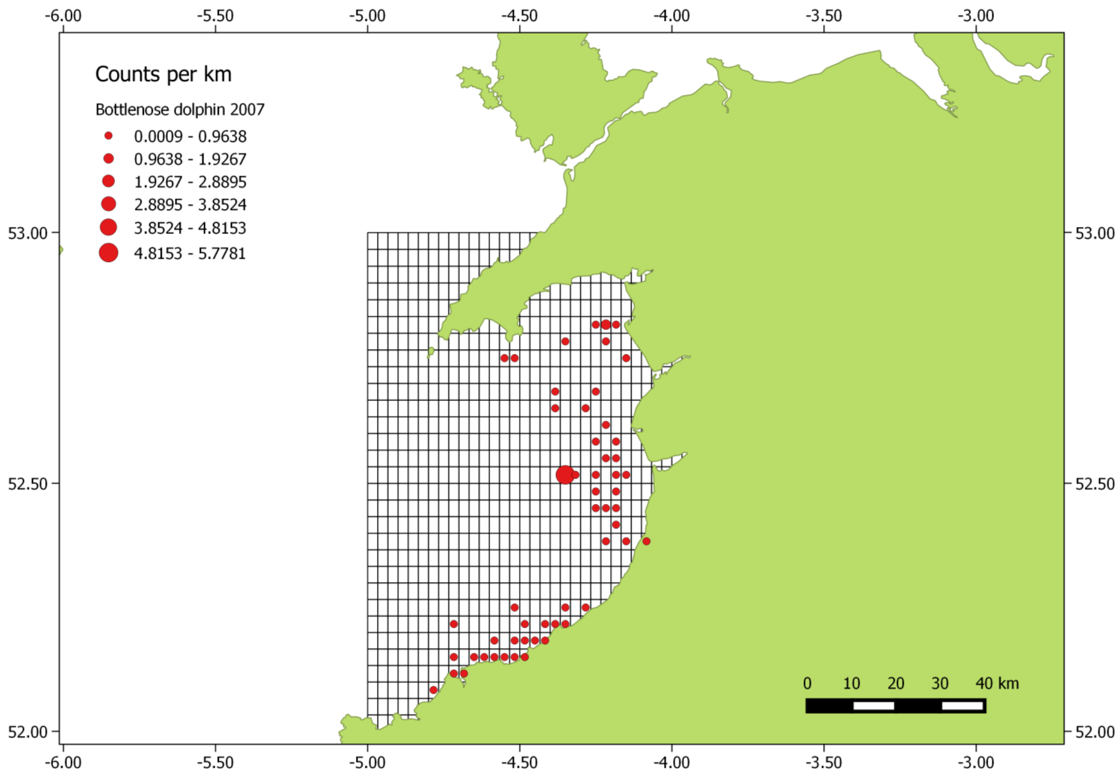


Figure 13. Map of bottlenose density (count per km) corrected for effort in 2007

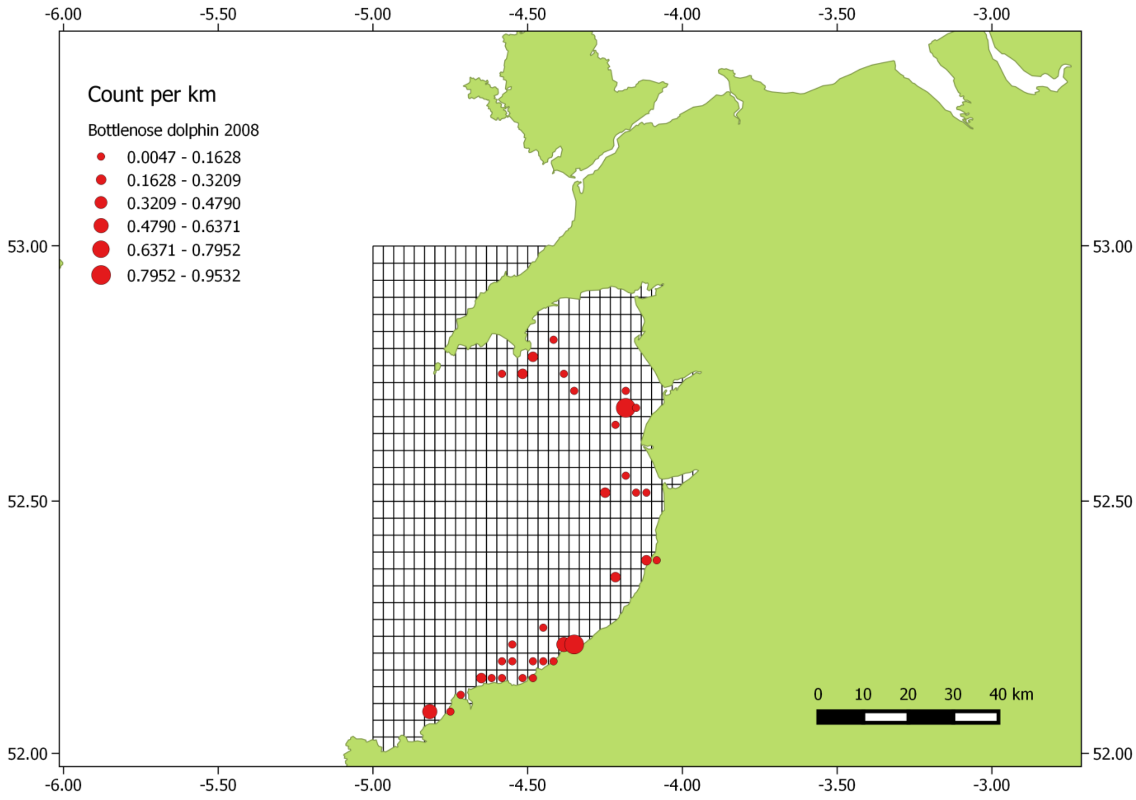


Figure 14. Map of bottlenose density (count per km) corrected for effort in 2008

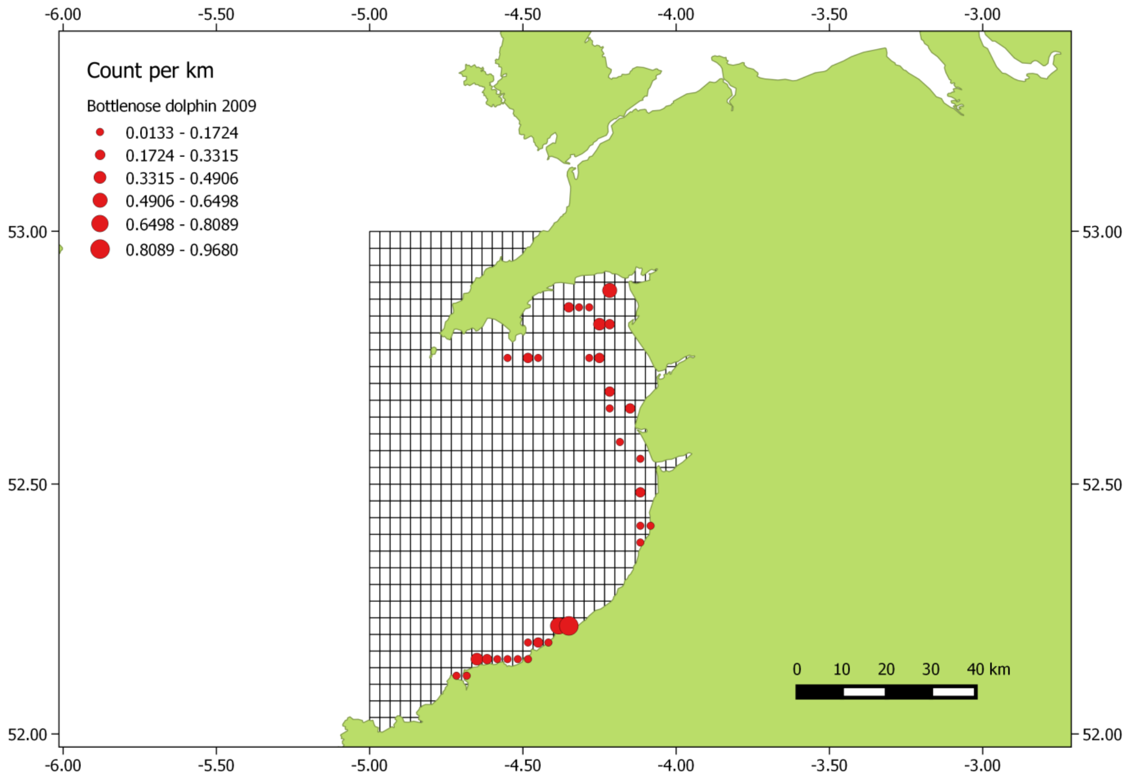


Figure 15. Map of bottlenose density (count per km) corrected for effort in 2009

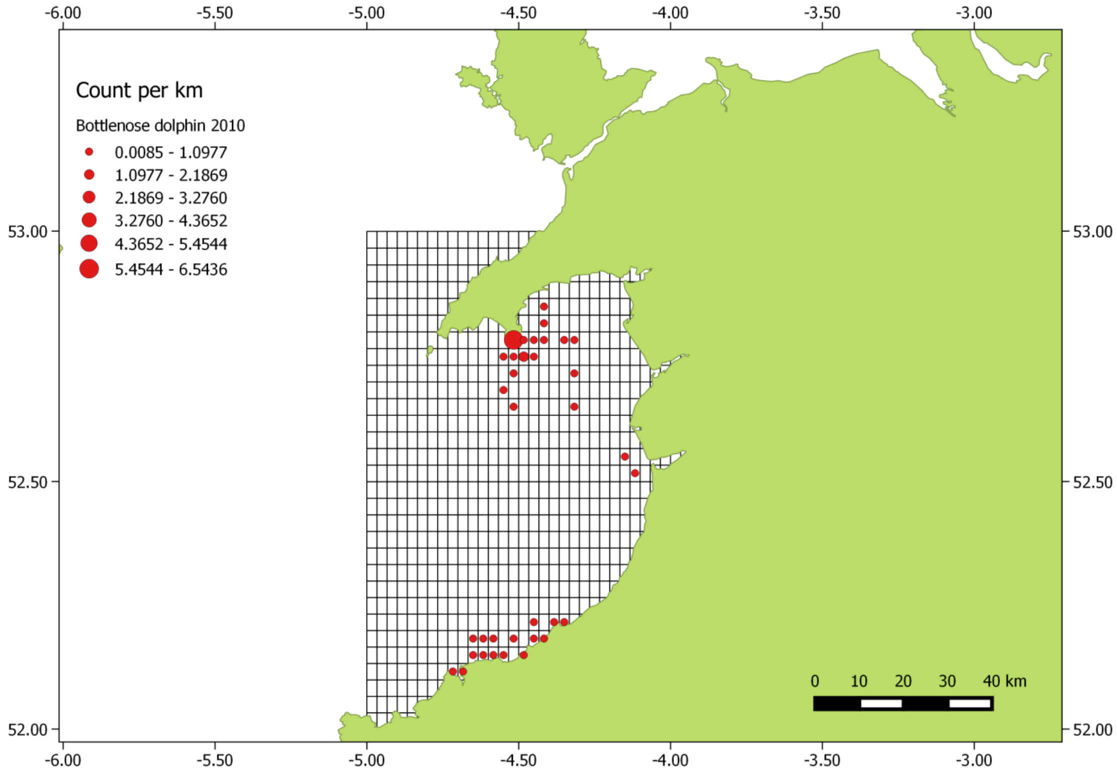


Figure 16. Map of bottlenose density (count per km) corrected for effort in 2010

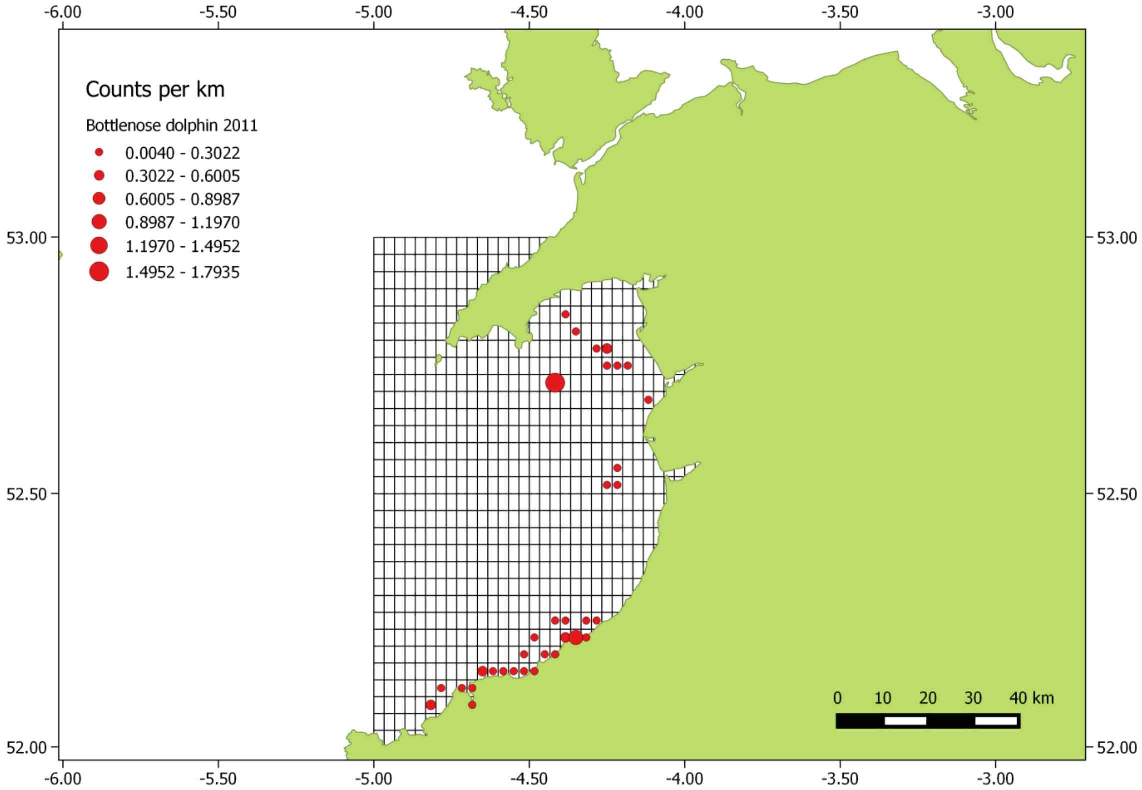


Figure 17. Map of bottlenose density (count per km) corrected for effort in 2011

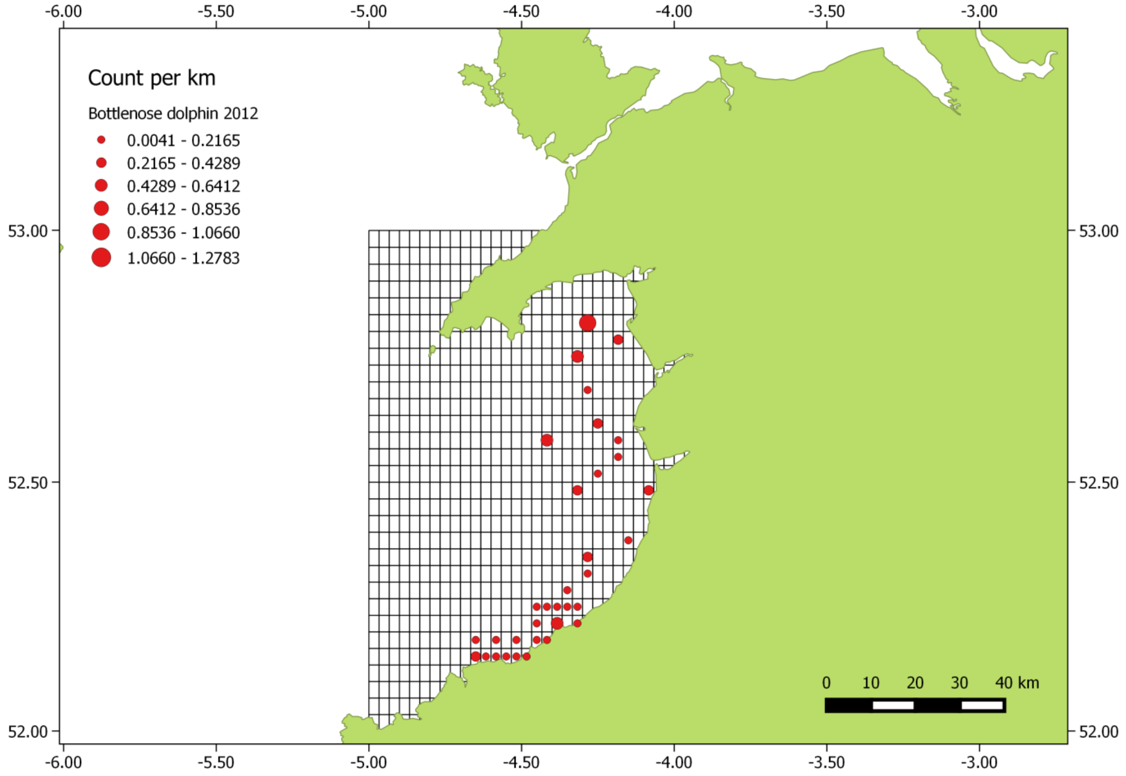


Figure 18. Map of bottlenose density (count per km) corrected for effort in 2012

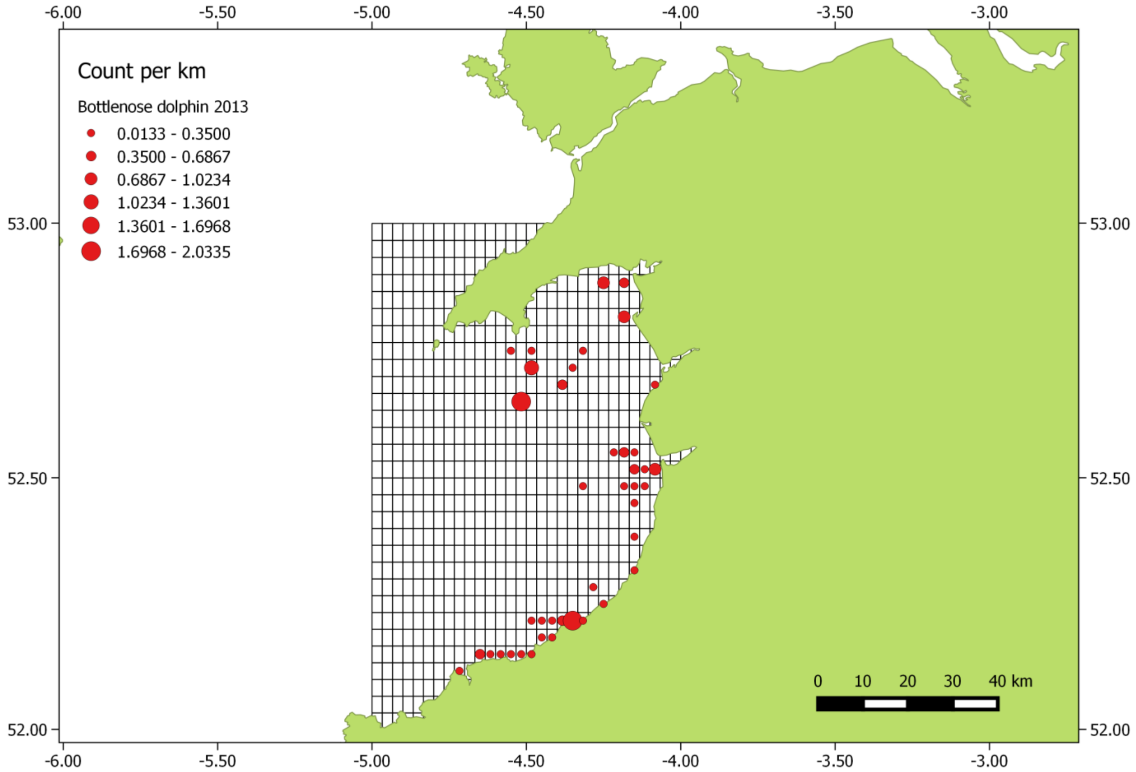


Figure 19. Map of bottlenose density (count per km) corrected for effort in 2013

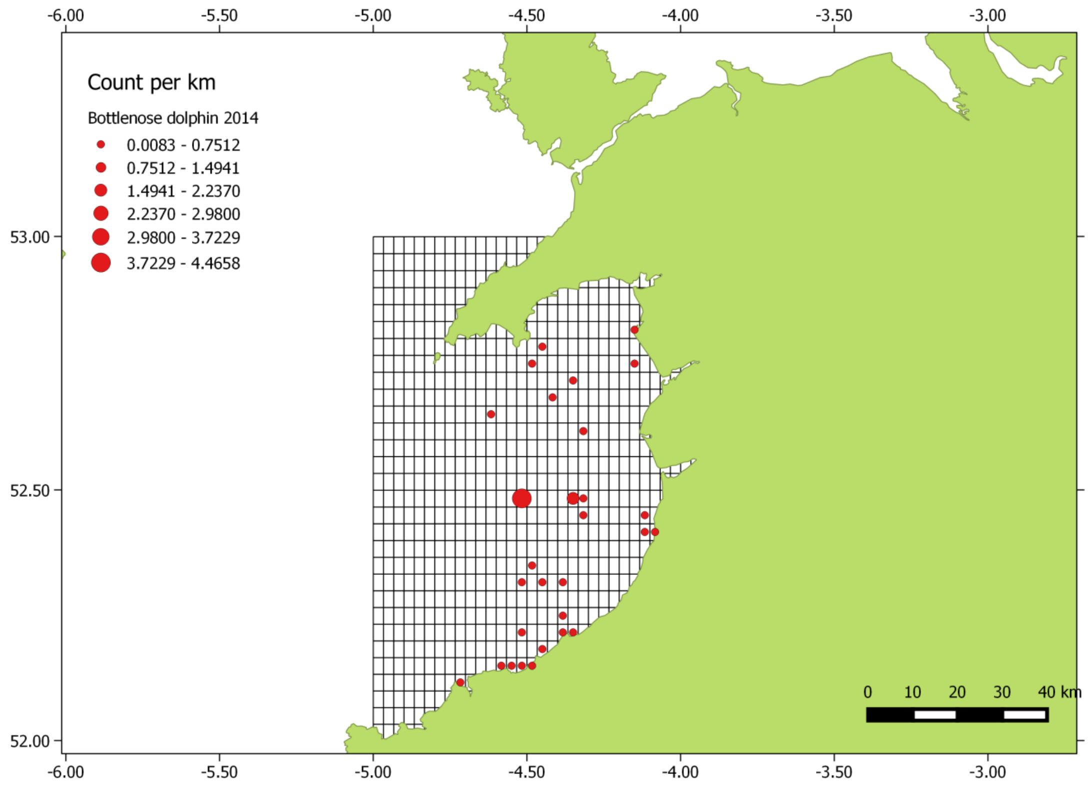


Figure 20. Map of bottlenose density (count per km) corrected for effort in 2014

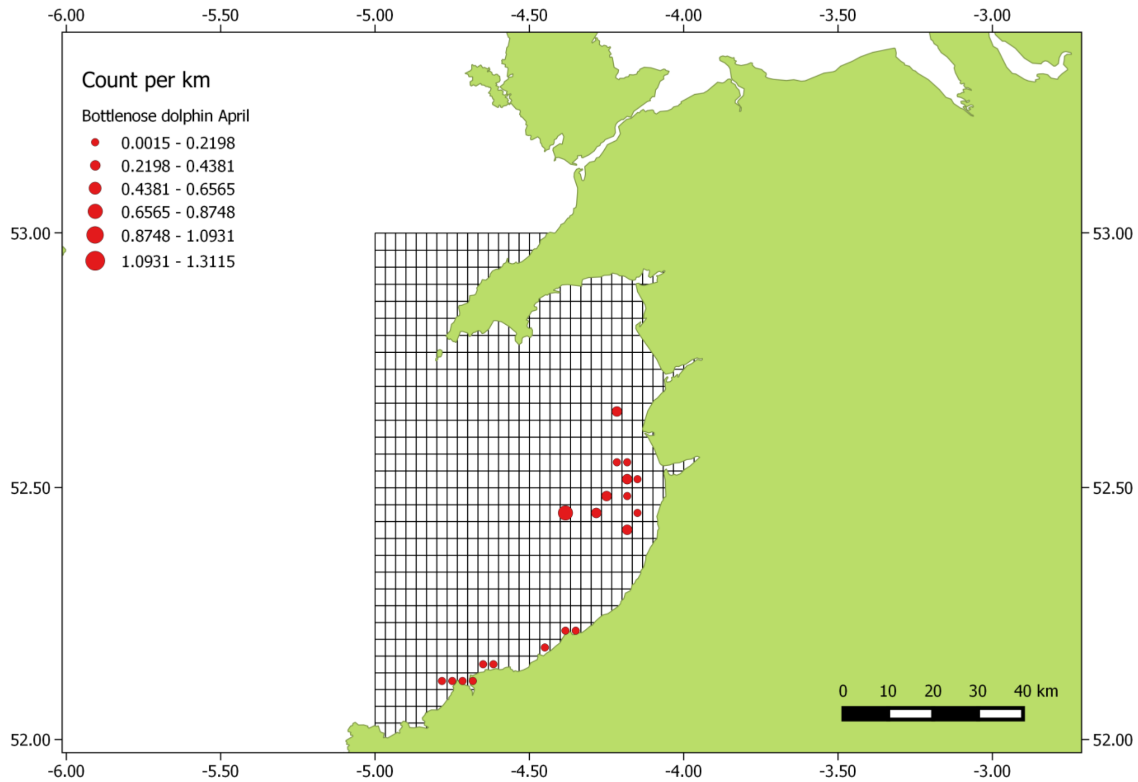


Figure 21. Map of bottlenose density (count per km) corrected for effort in April

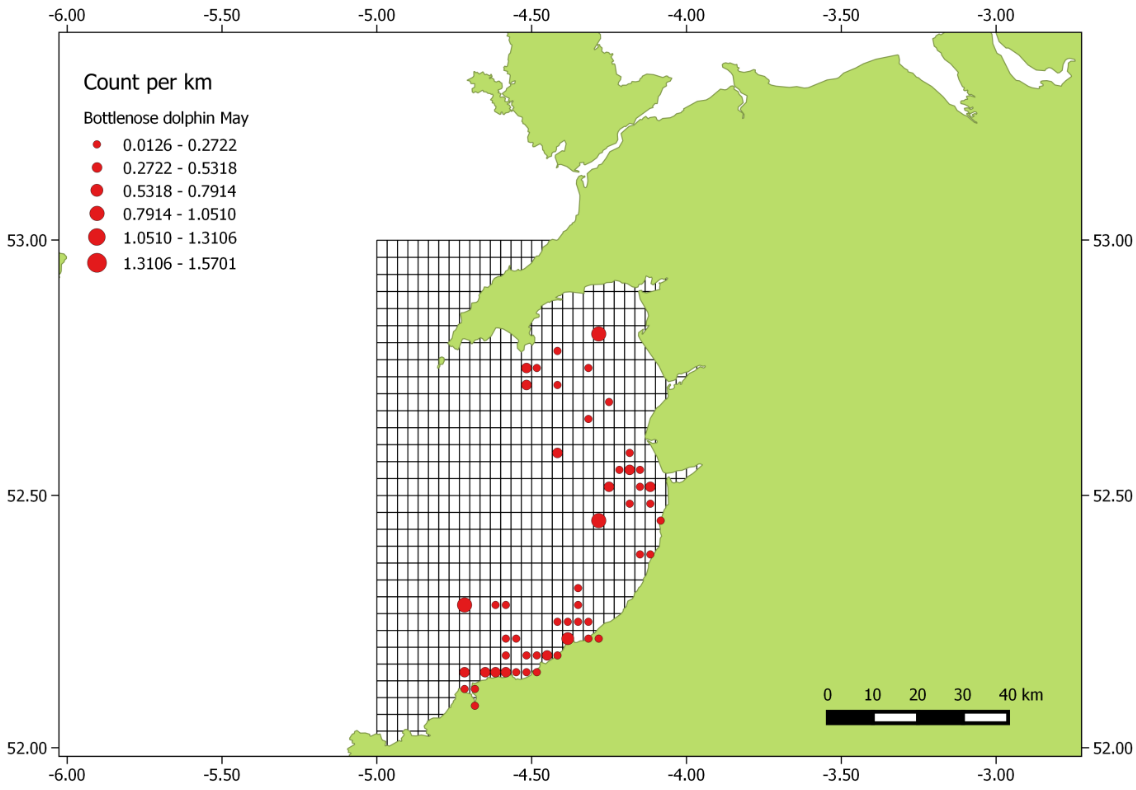


Figure 22. Map of bottlenose density (count per km) corrected for effort in May

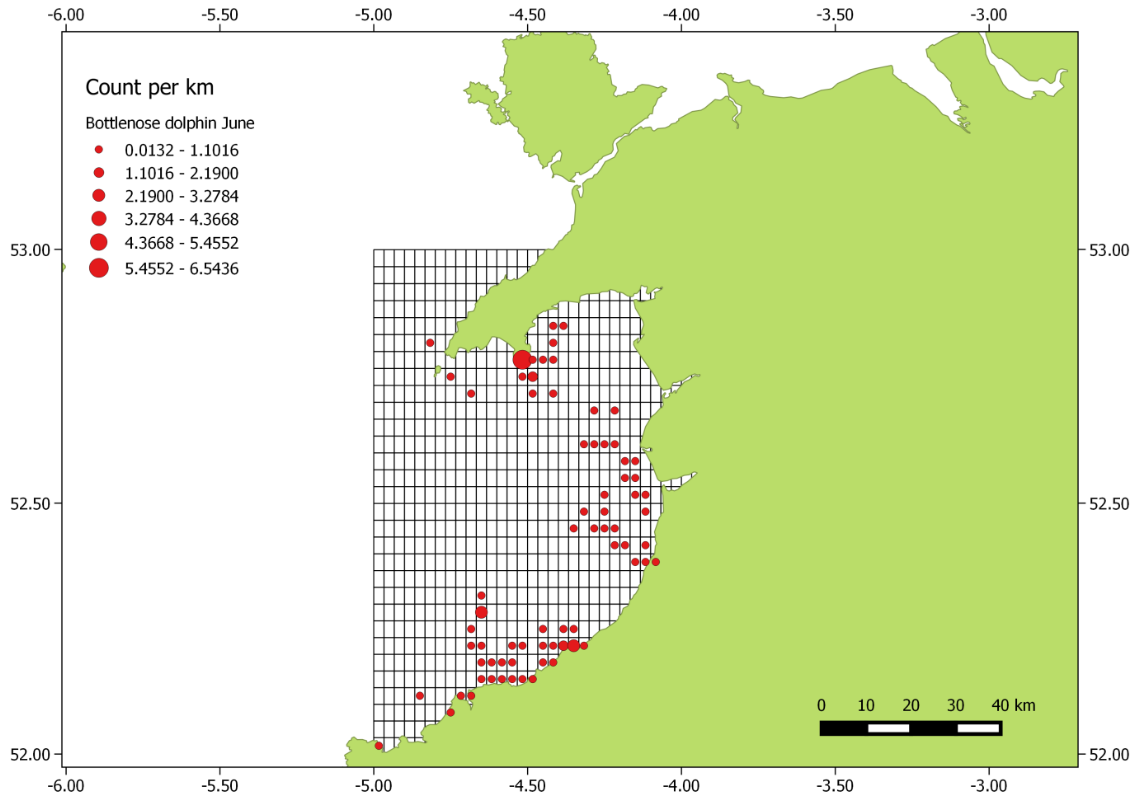


Figure 23. Map of bottlenose density (count per km) corrected for effort in June

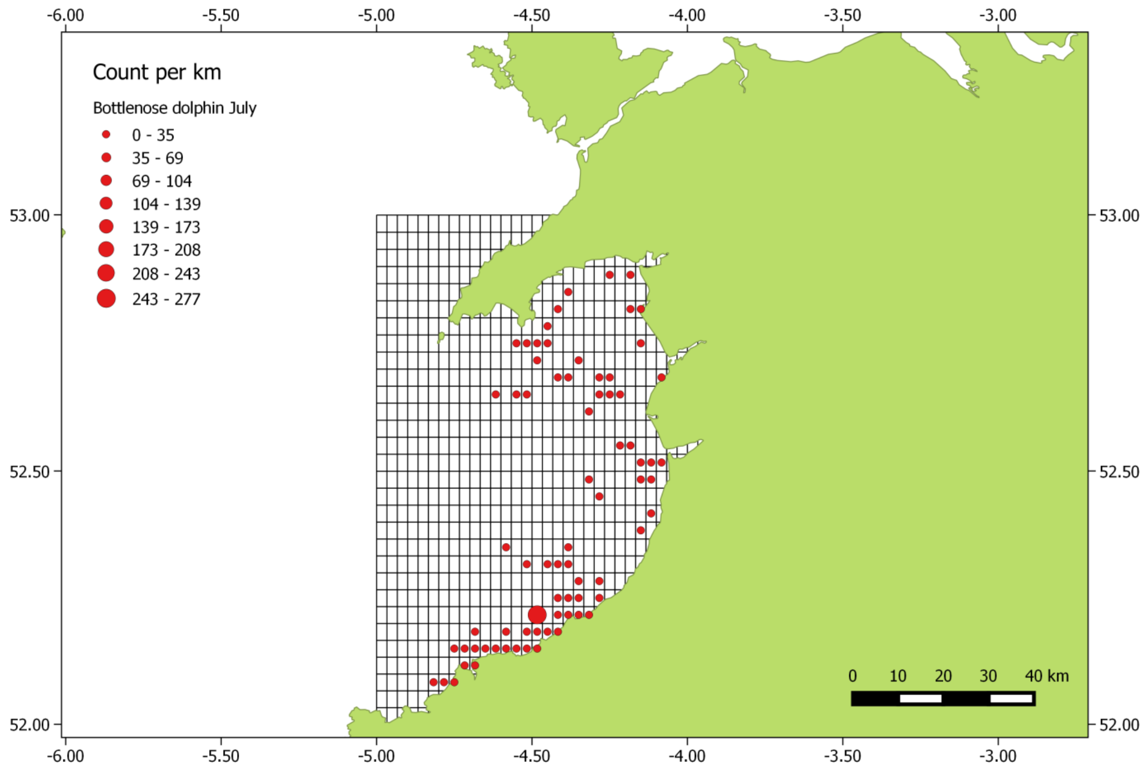


Figure 24. Map of bottlenose density (count per km) corrected for effort in July

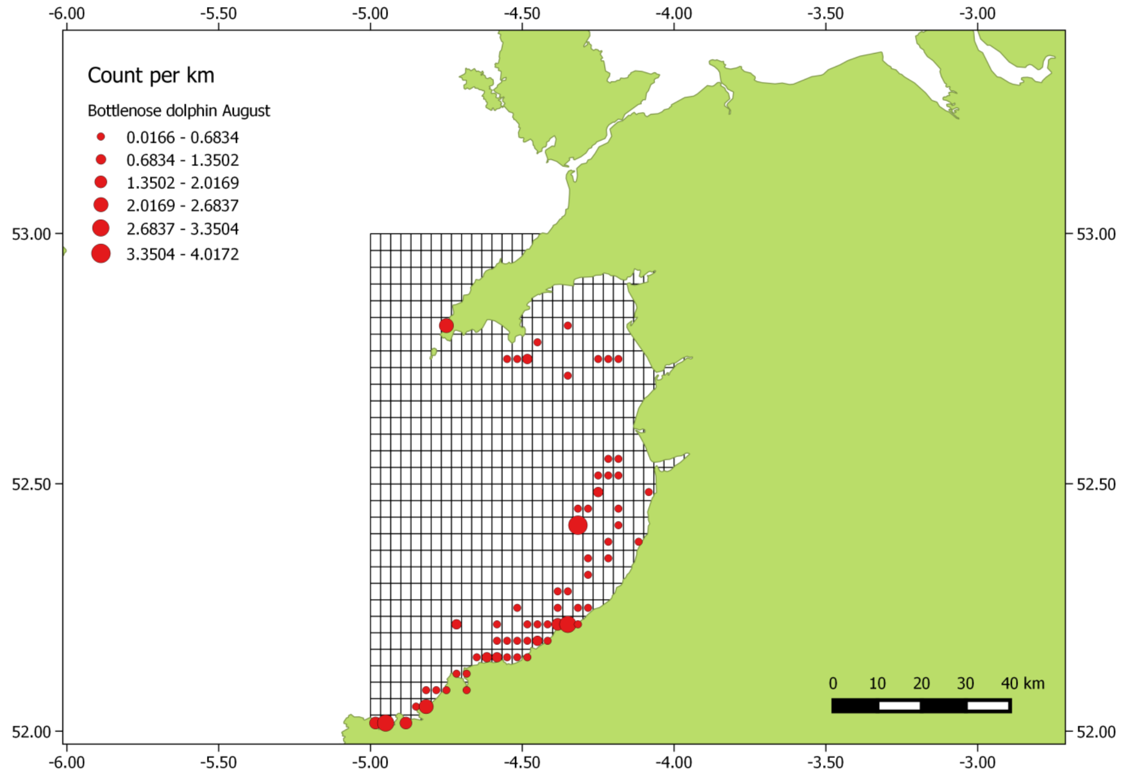


Figure 25. Map of bottlenose density (count per km) corrected for effort in August

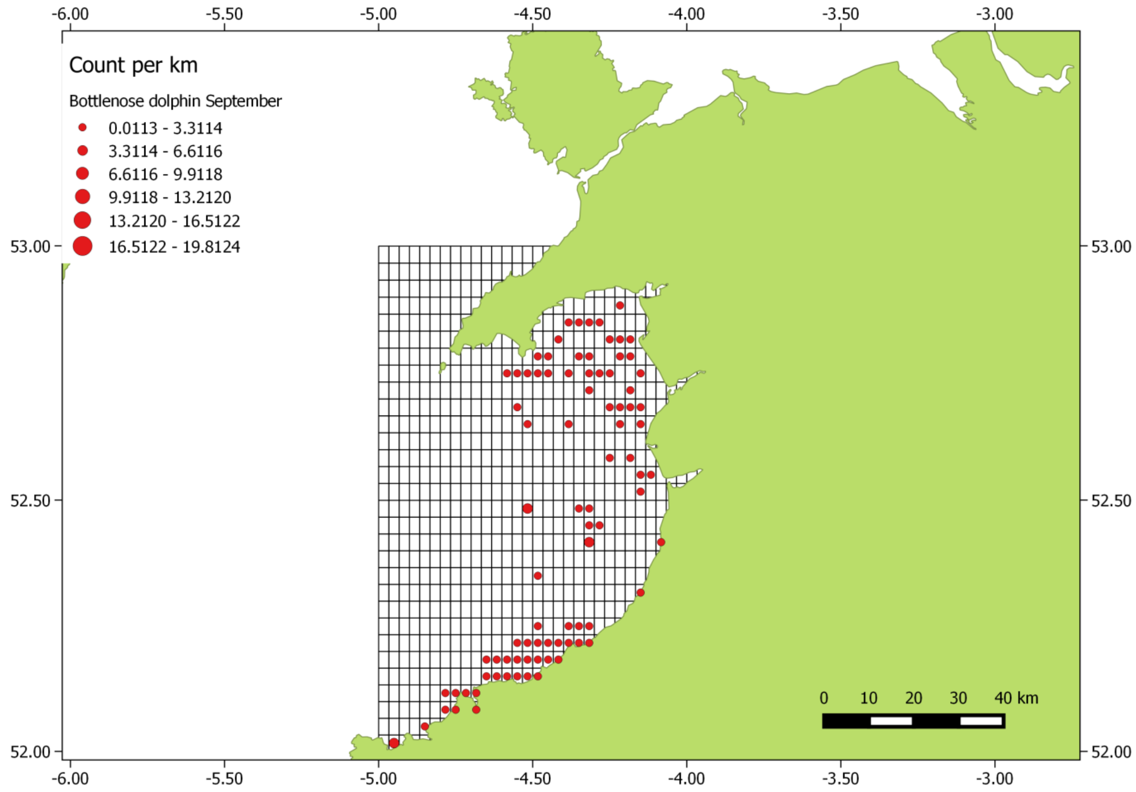


Figure 26. Map of bottlenose density (count per km) corrected for effort in September

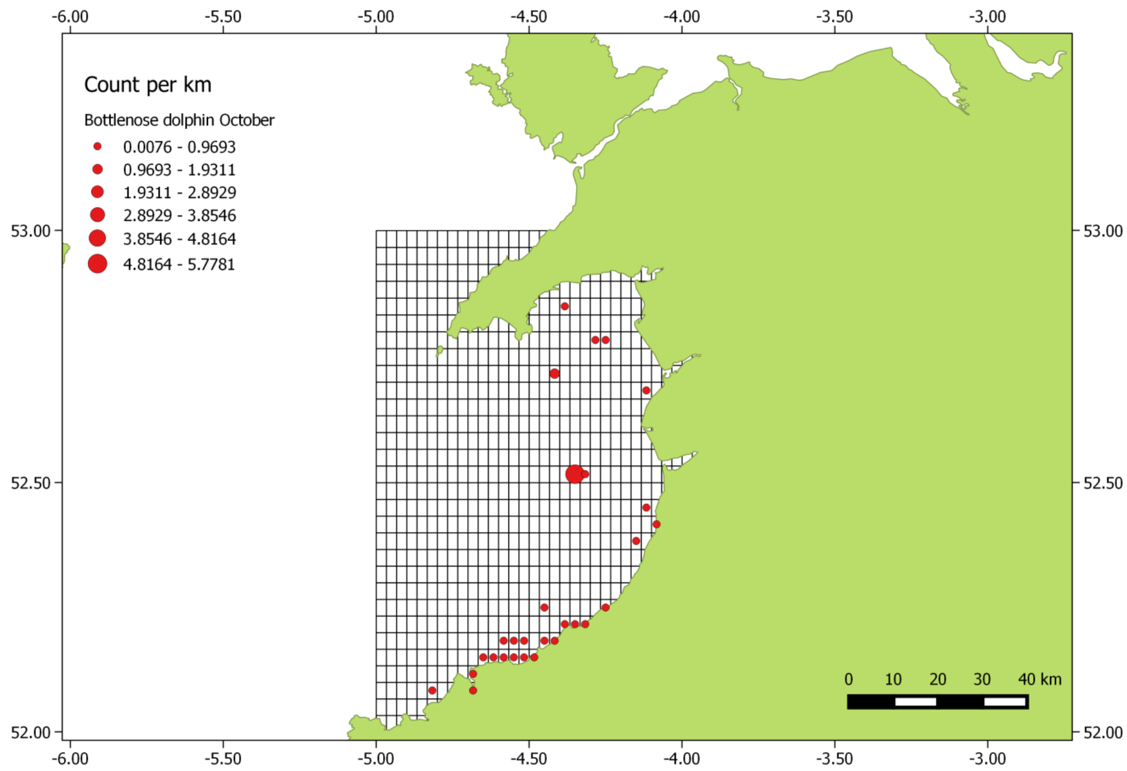


Figure 27. Map of bottlenose density (count per km) corrected for effort in October

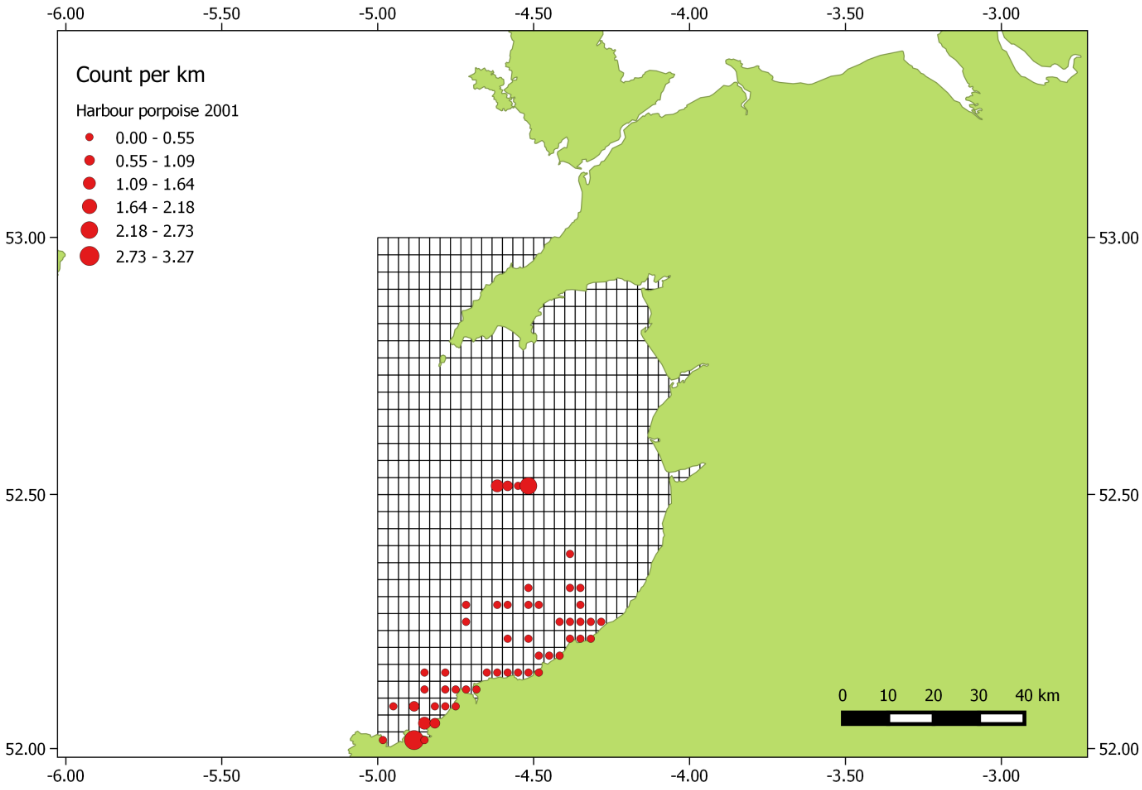


Figure 28. Map of harbour porpoise density (count per km) corrected for effort in 2001

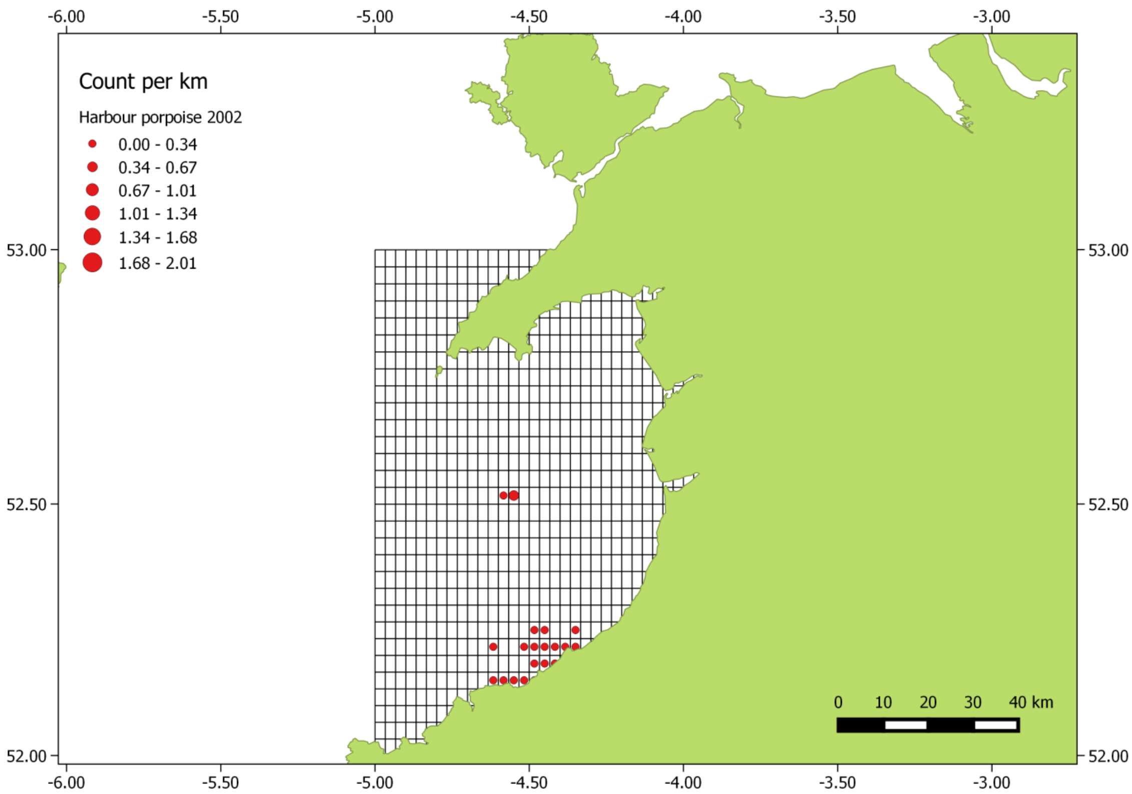


Figure 29. Map of harbour porpoise density (count per km) corrected for effort in 2002

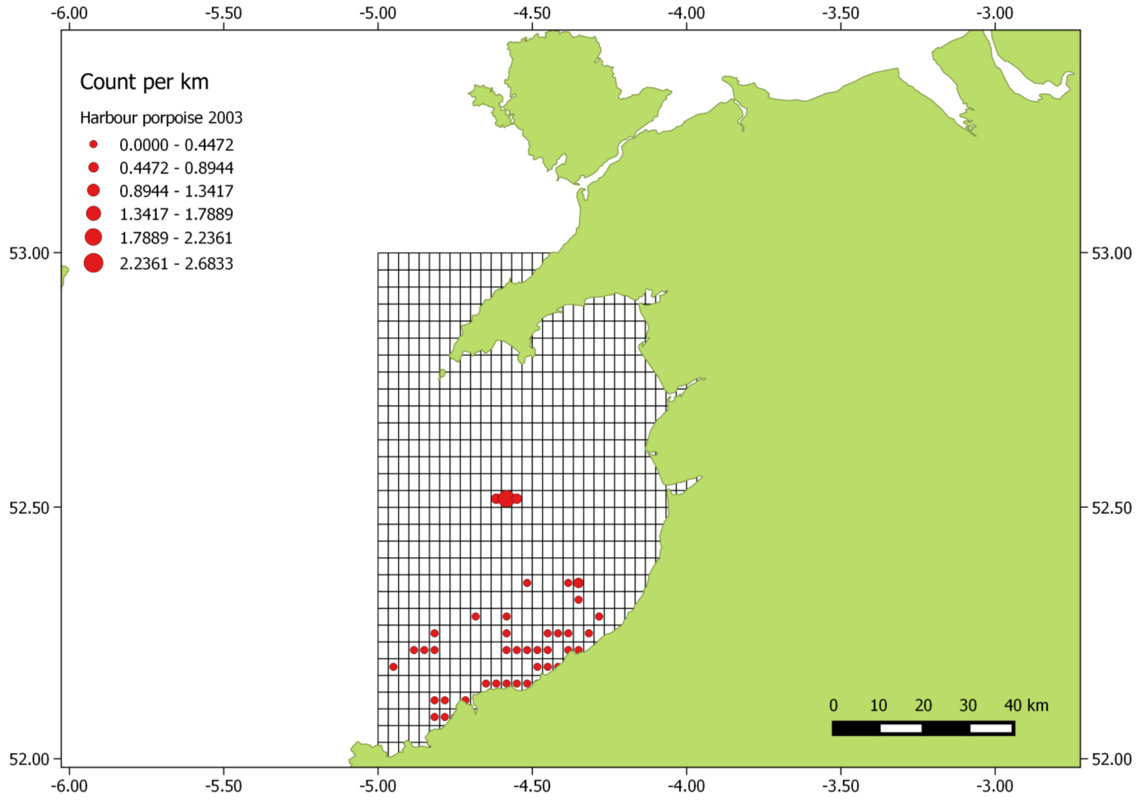


Figure 30. Map of harbour porpoise density (count per km) corrected for effort in 2003

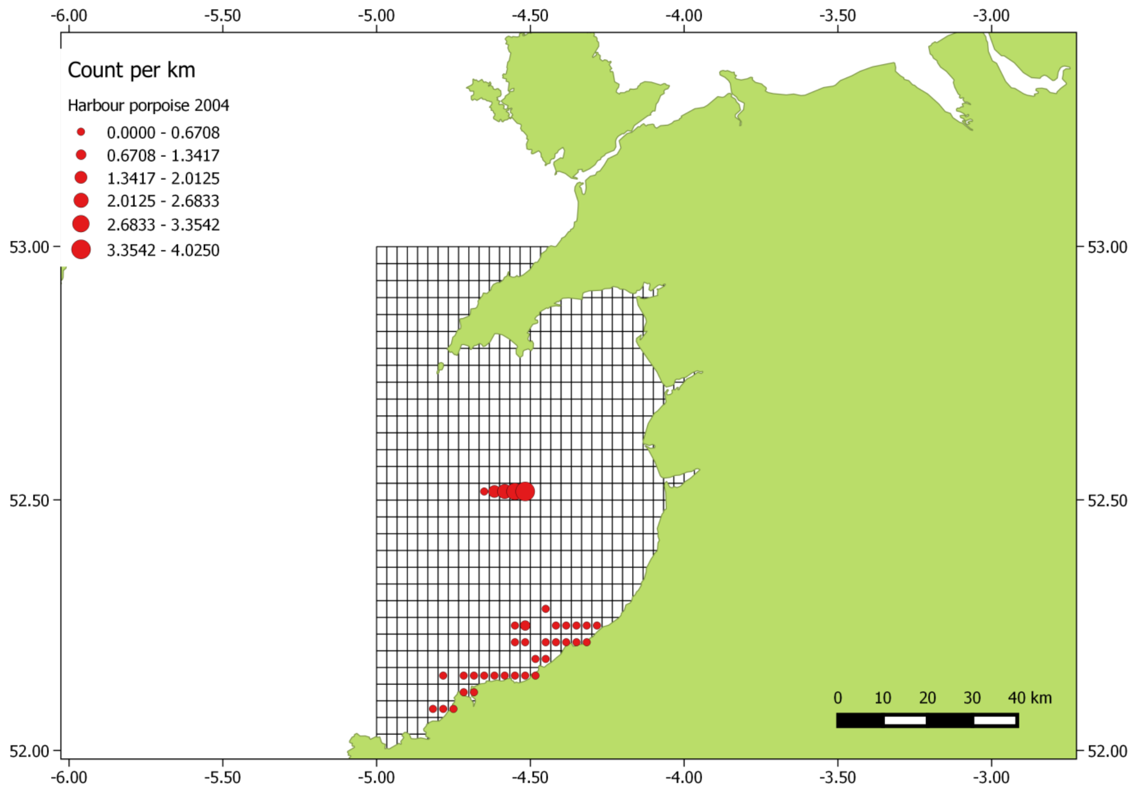


Figure 31. Map of harbour porpoise density (count per km) corrected for effort in 2004

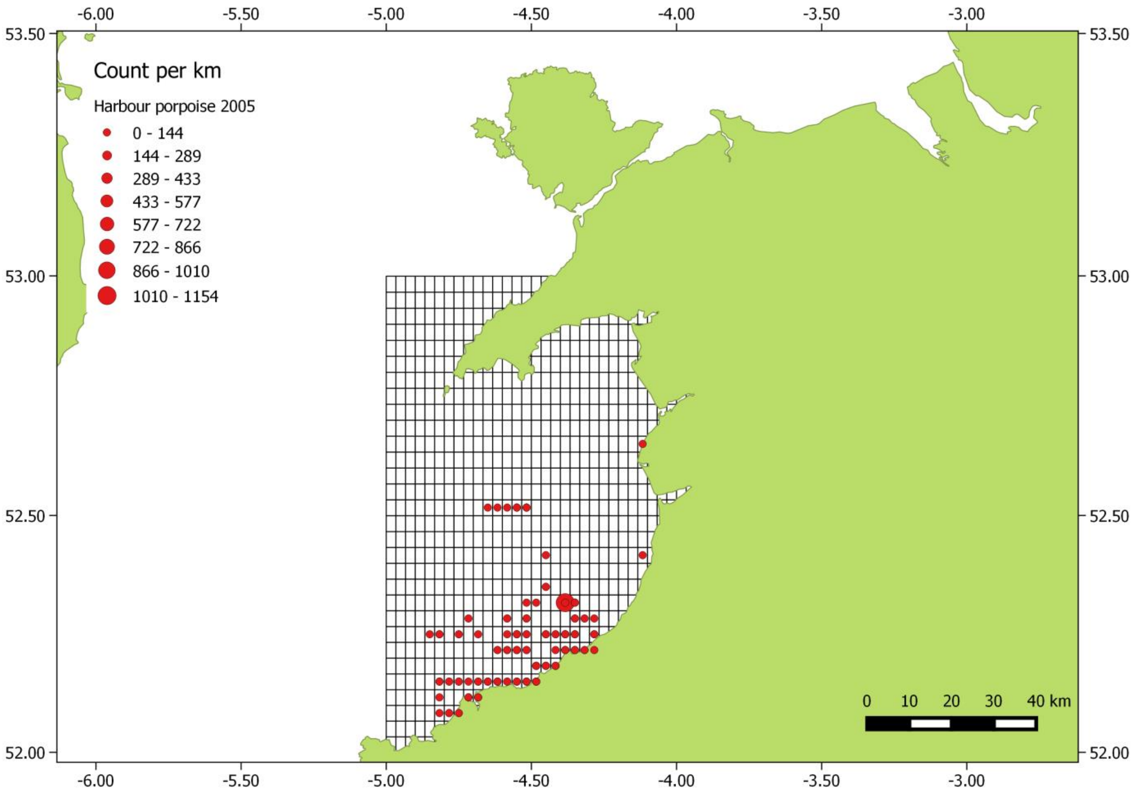


Figure 32. Map of harbour porpoise density (count per km) corrected for effort in 2005

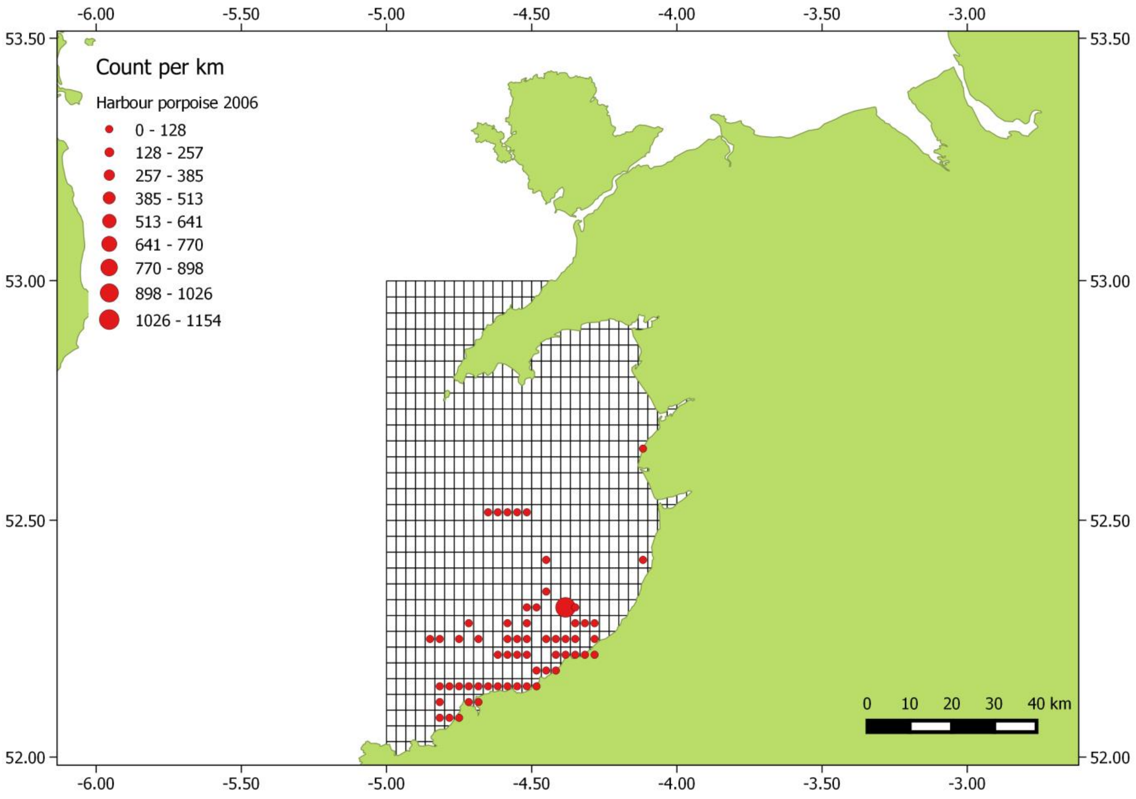


Figure 33. Map of harbour porpoise density (count per km) corrected for effort in 2006

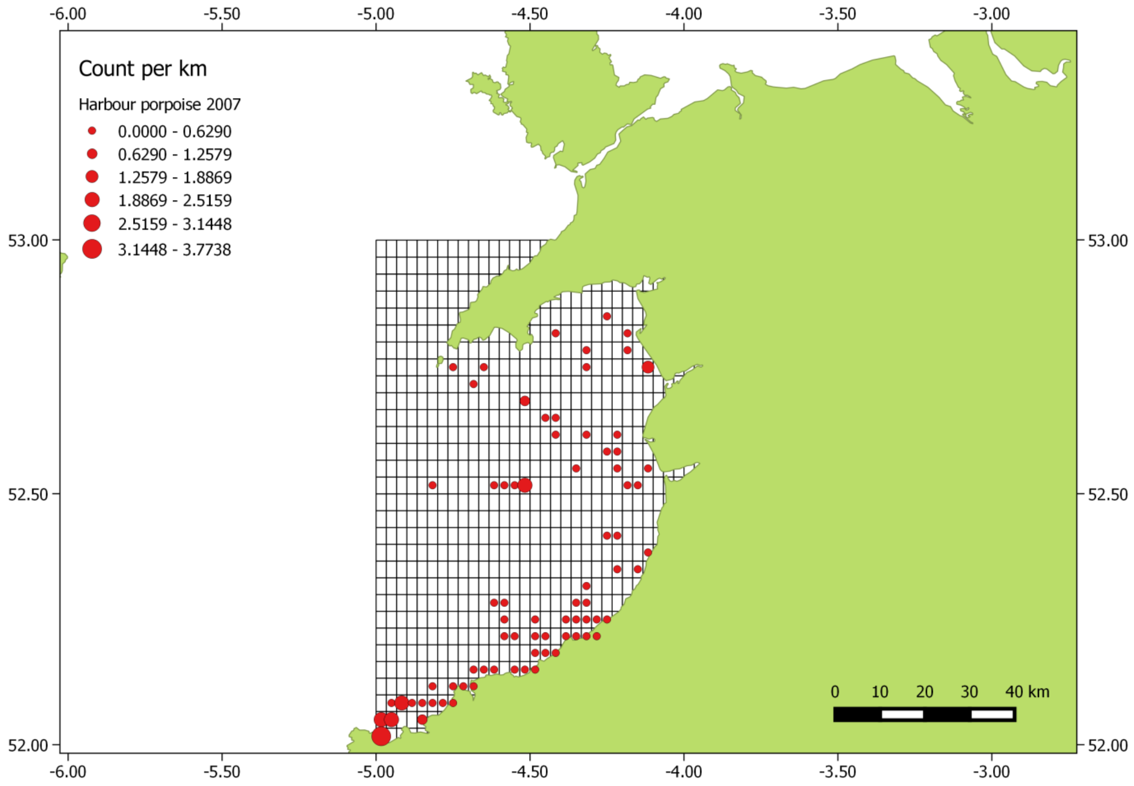


Figure 34. Map of harbour porpoise density (count per km) corrected for effort in 2007

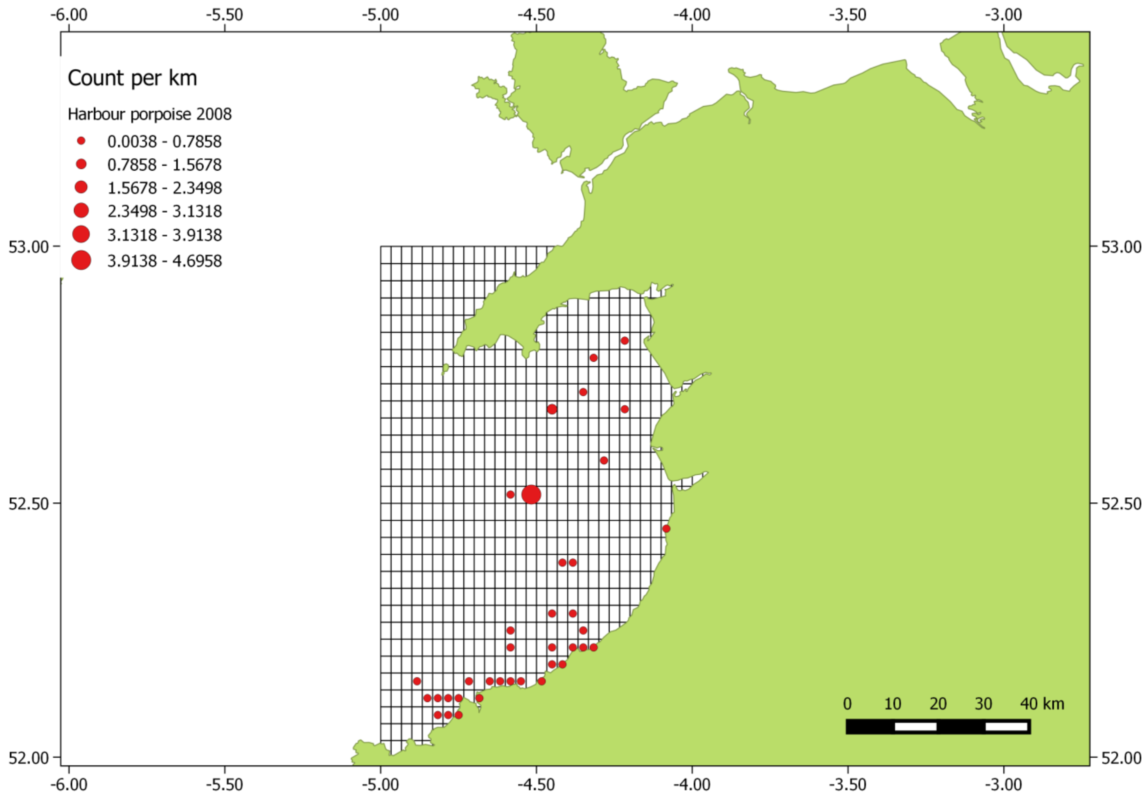


Figure 35. Map of harbour porpoise density (count per km) corrected for effort in 2008

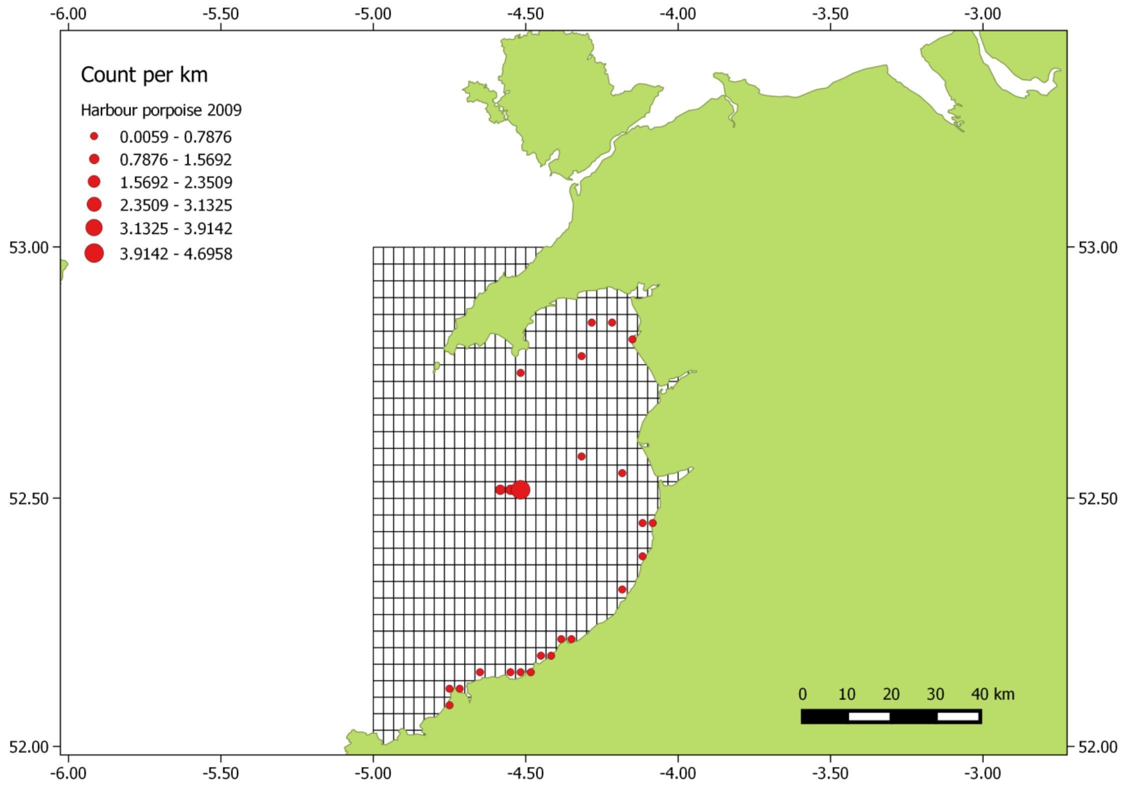


Figure 36. Map of harbour porpoise density (count per km) corrected for effort in 2009

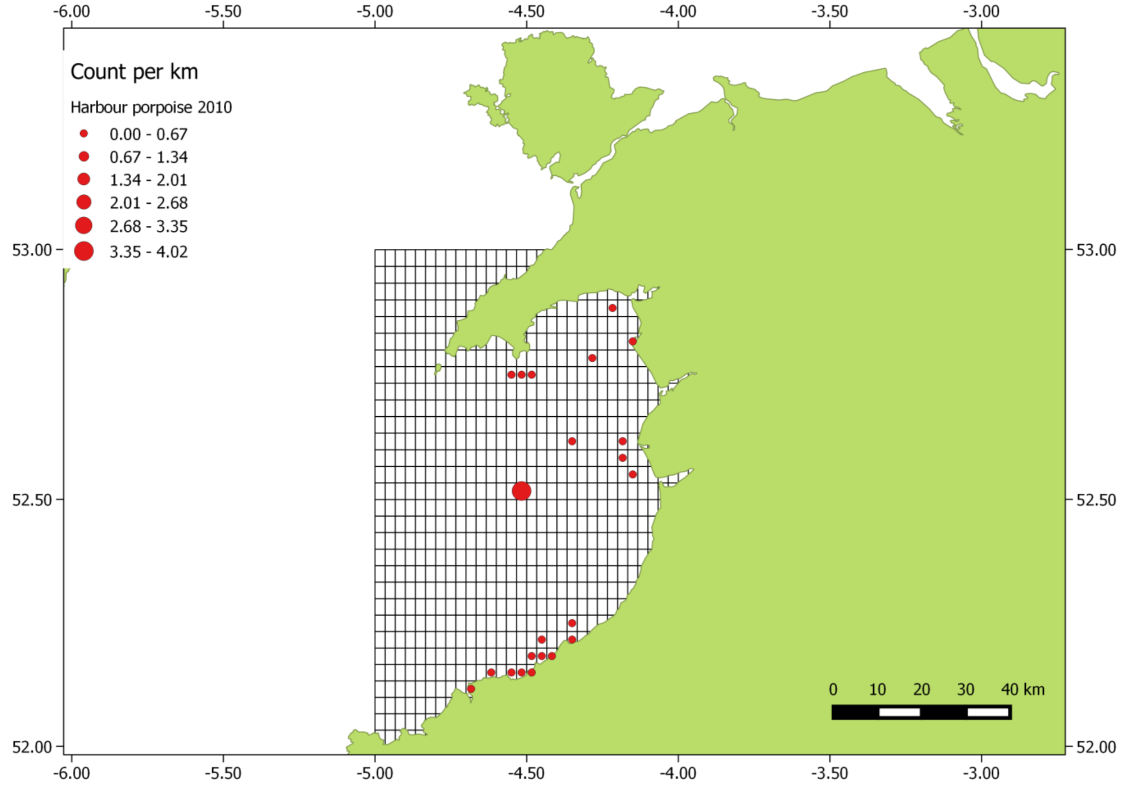


Figure 37. Map of harbour porpoise density (count per km) corrected for effort in 2010

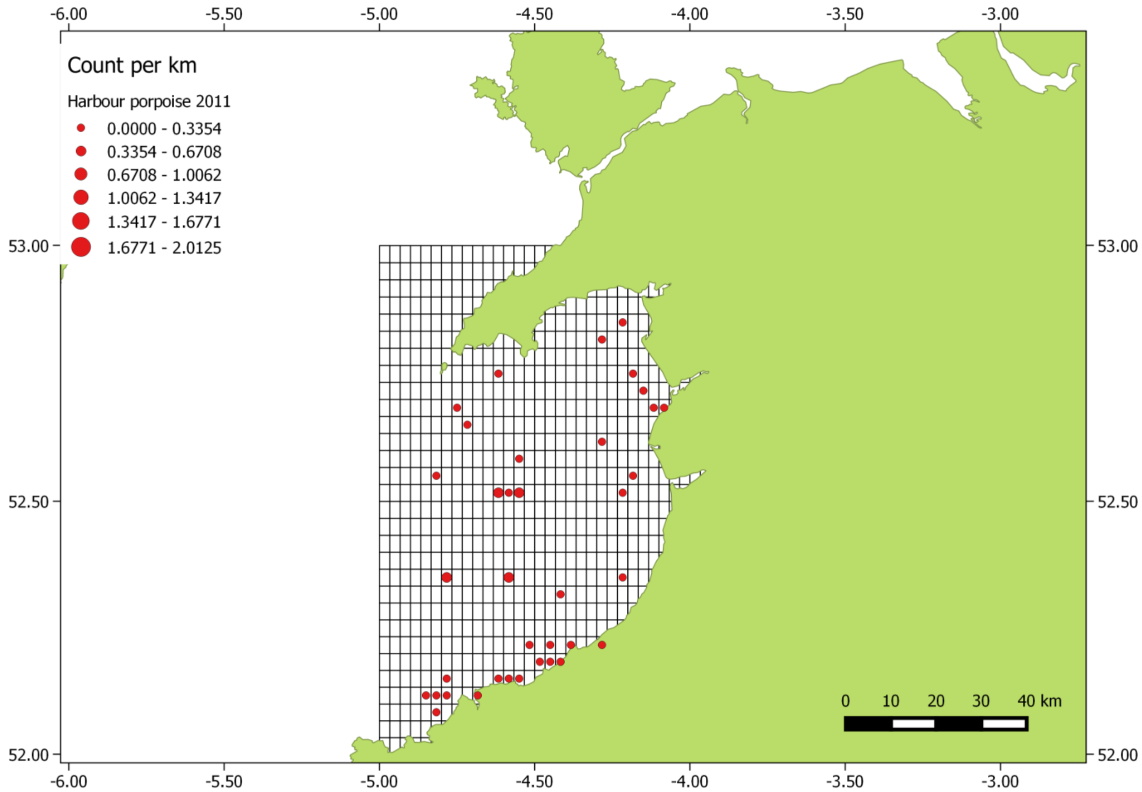


Figure 38. Map of harbour porpoise density (count per km) corrected for effort in 2011

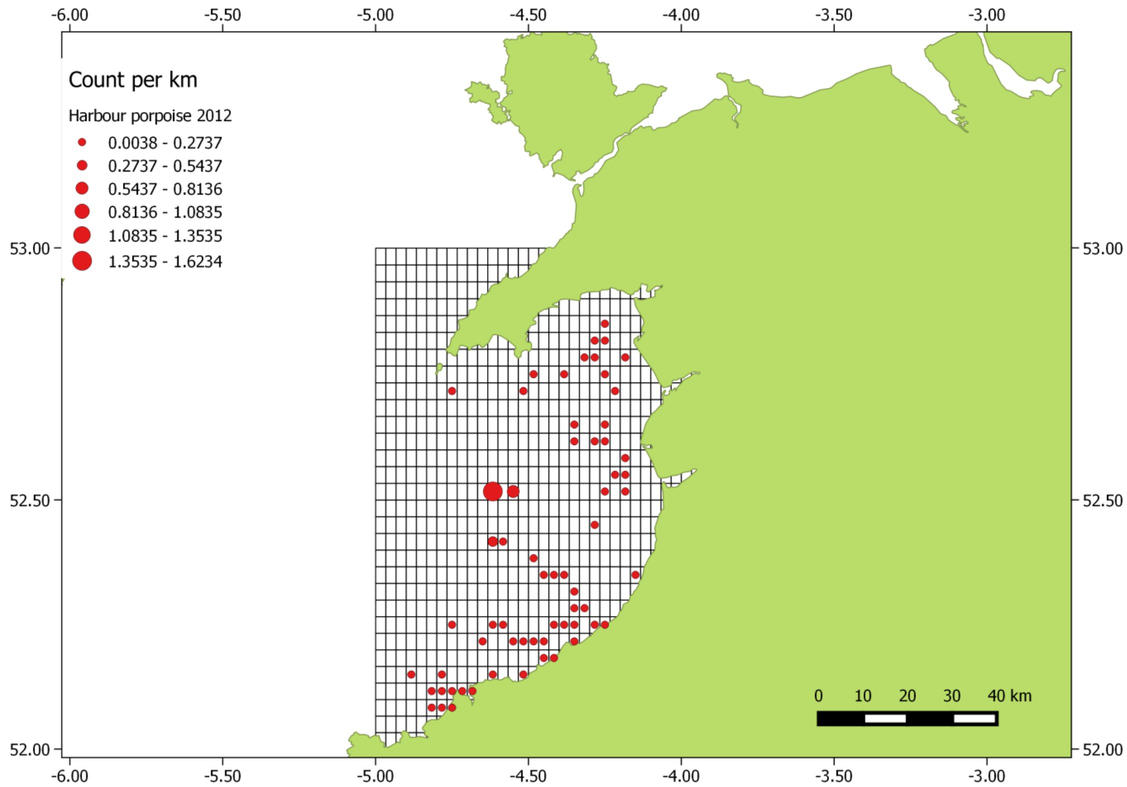


Figure 39. Map of harbour porpoise density (count per km) corrected for effort in 2012

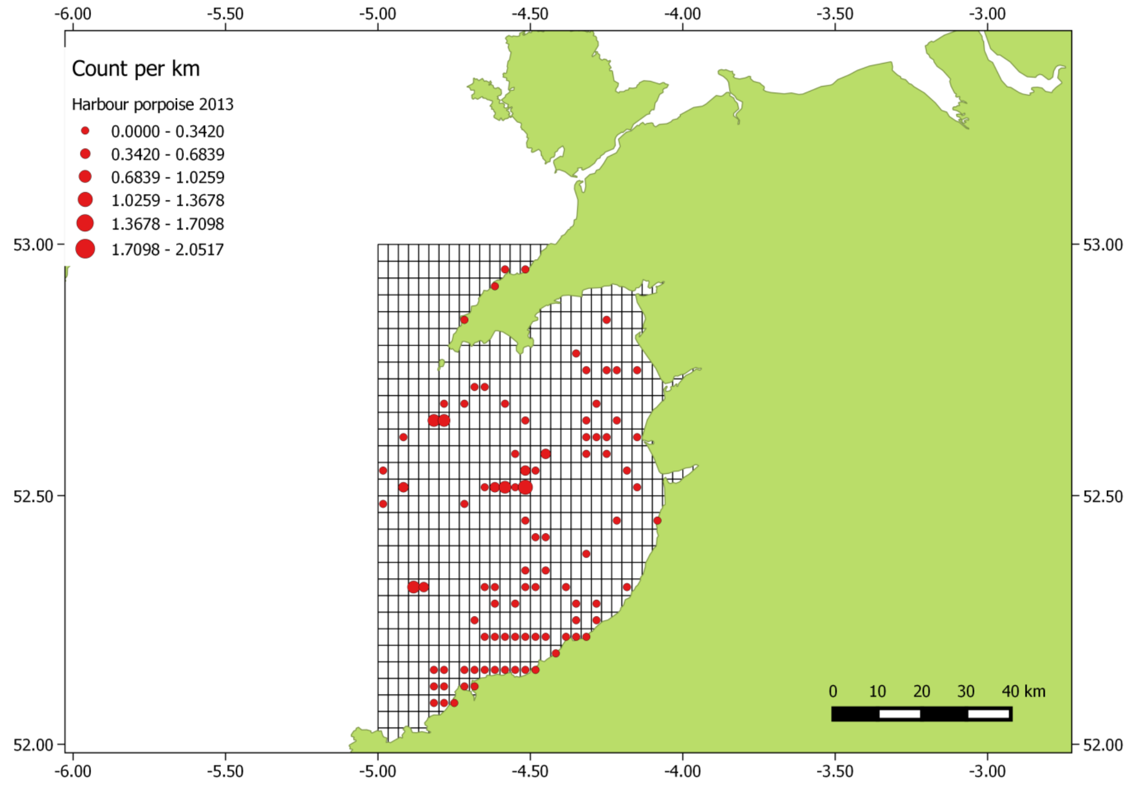


Figure 40. Map of harbour porpoise density (count per km) corrected for effort in 2013

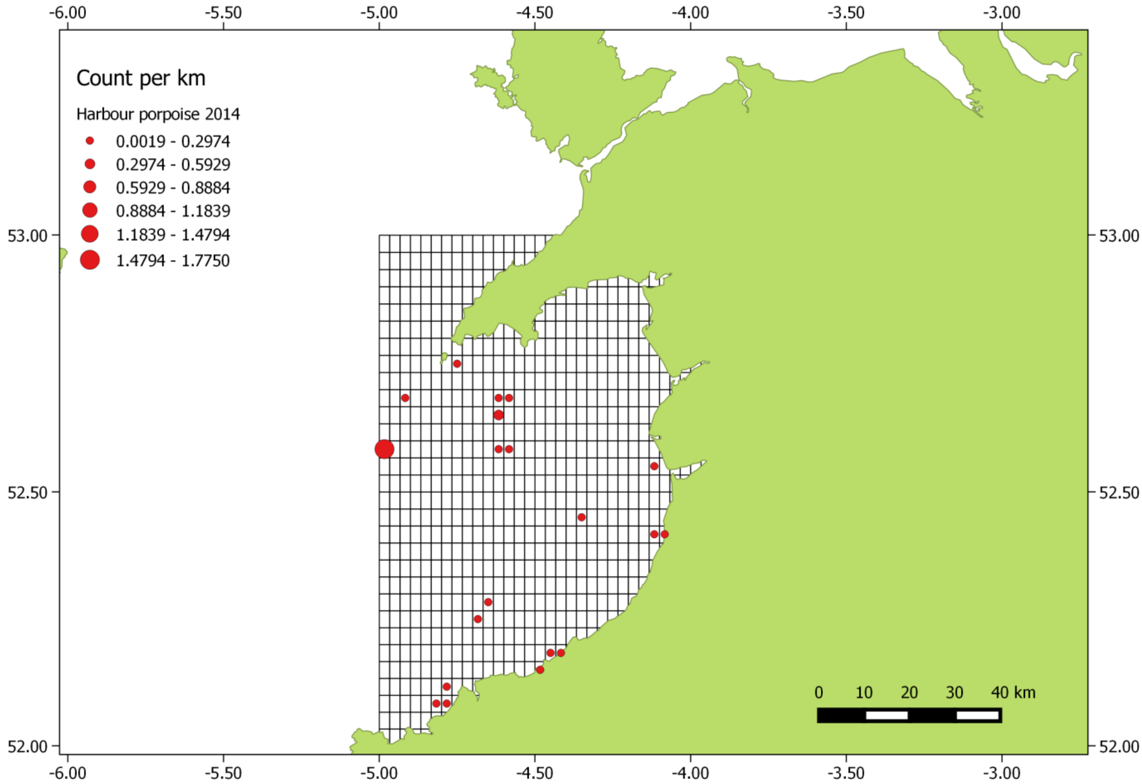


Figure 41. Map of harbour porpoise density (count per km) corrected for effort in 2014

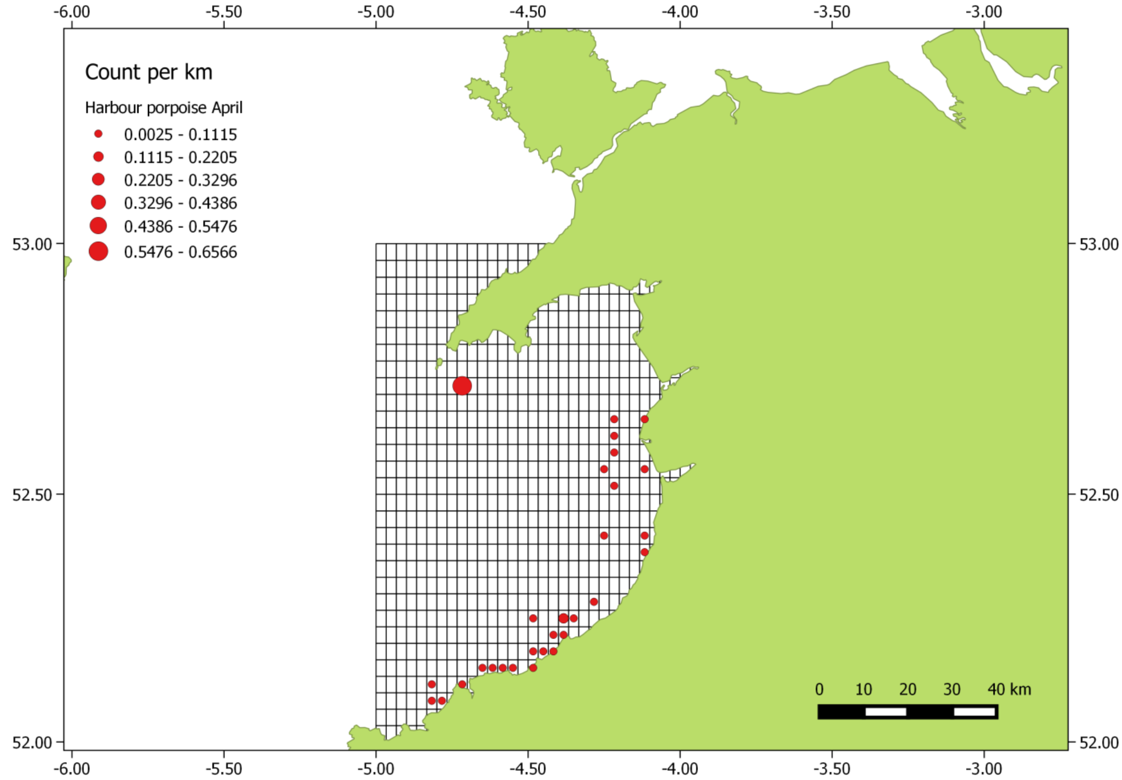


Figure 42. Map of harbour porpoise density (count per km) corrected for effort in April

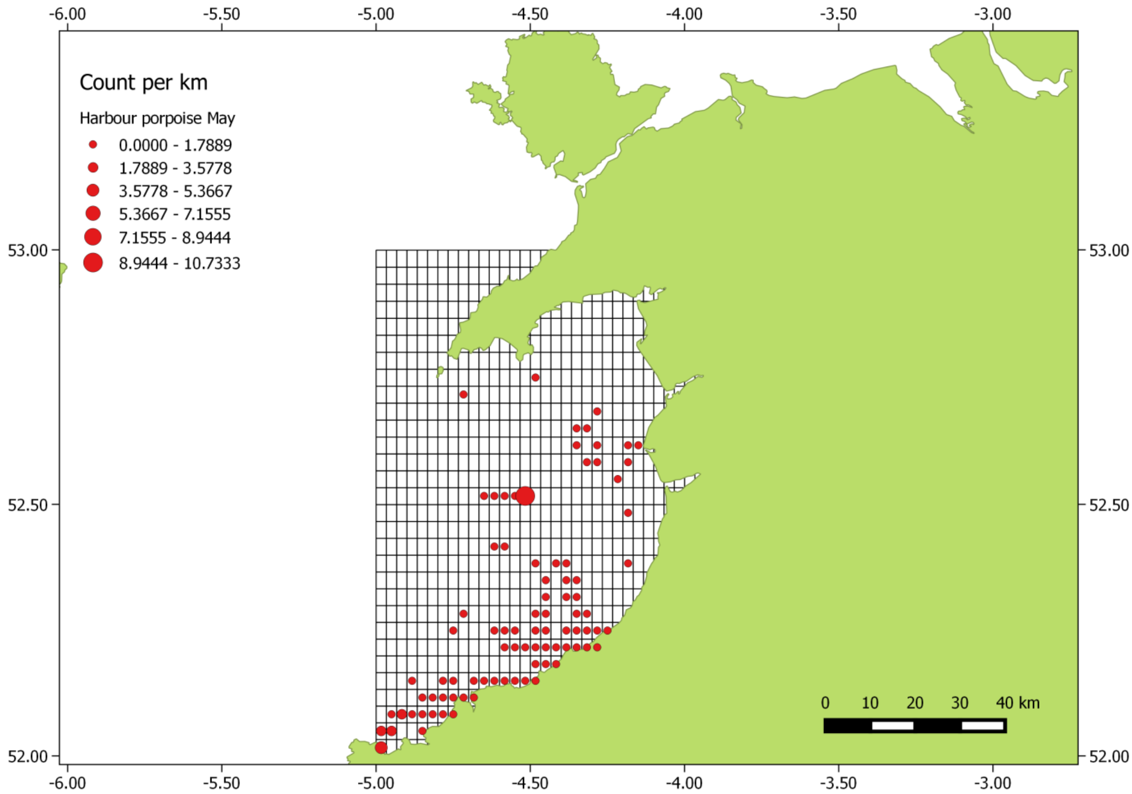


Figure 43. Map of harbour porpoise density (count per km) corrected for effort in May

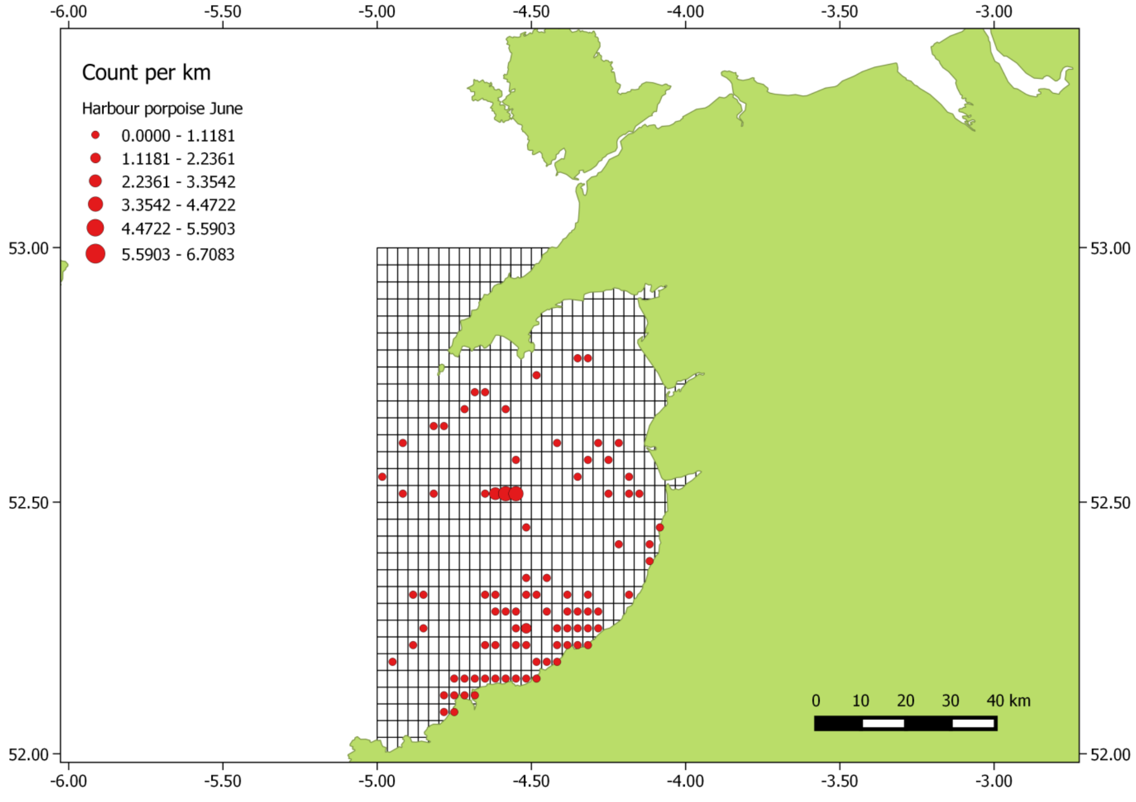


Figure 44. Map of harbour porpoise density (count per km) corrected for effort in June

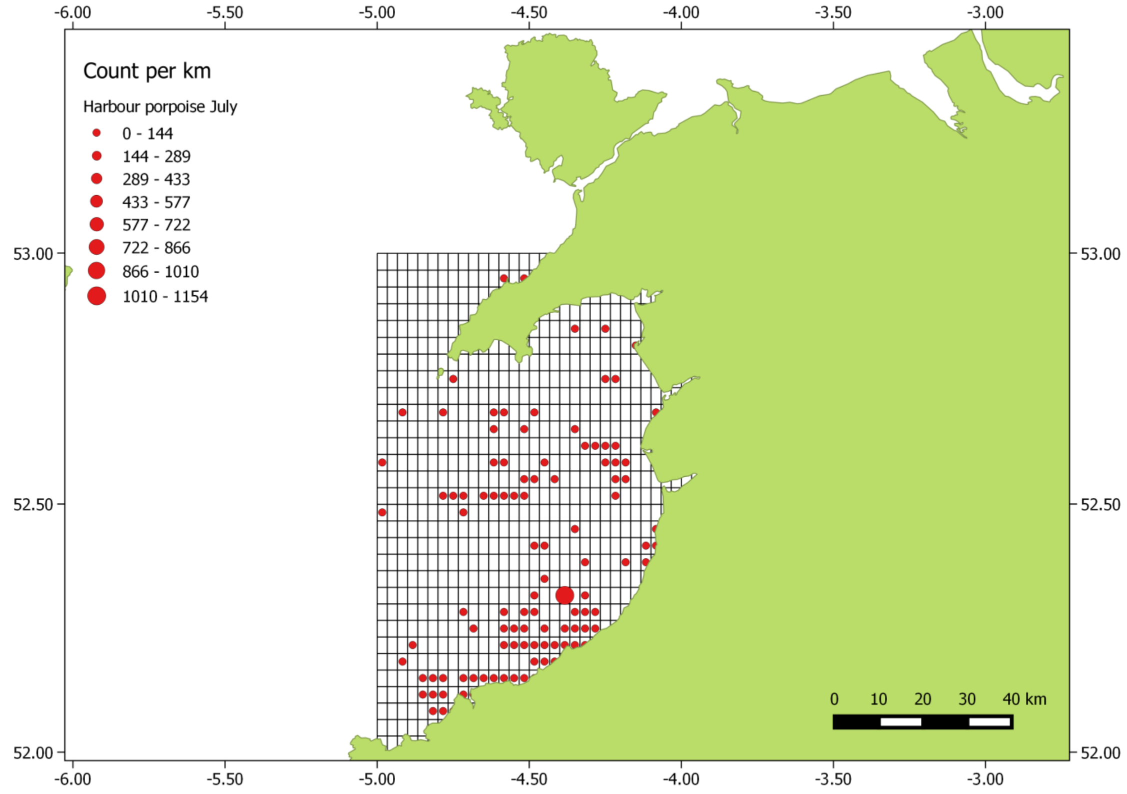


Figure 45. Map of harbour porpoise density (count per km) corrected for effort in July

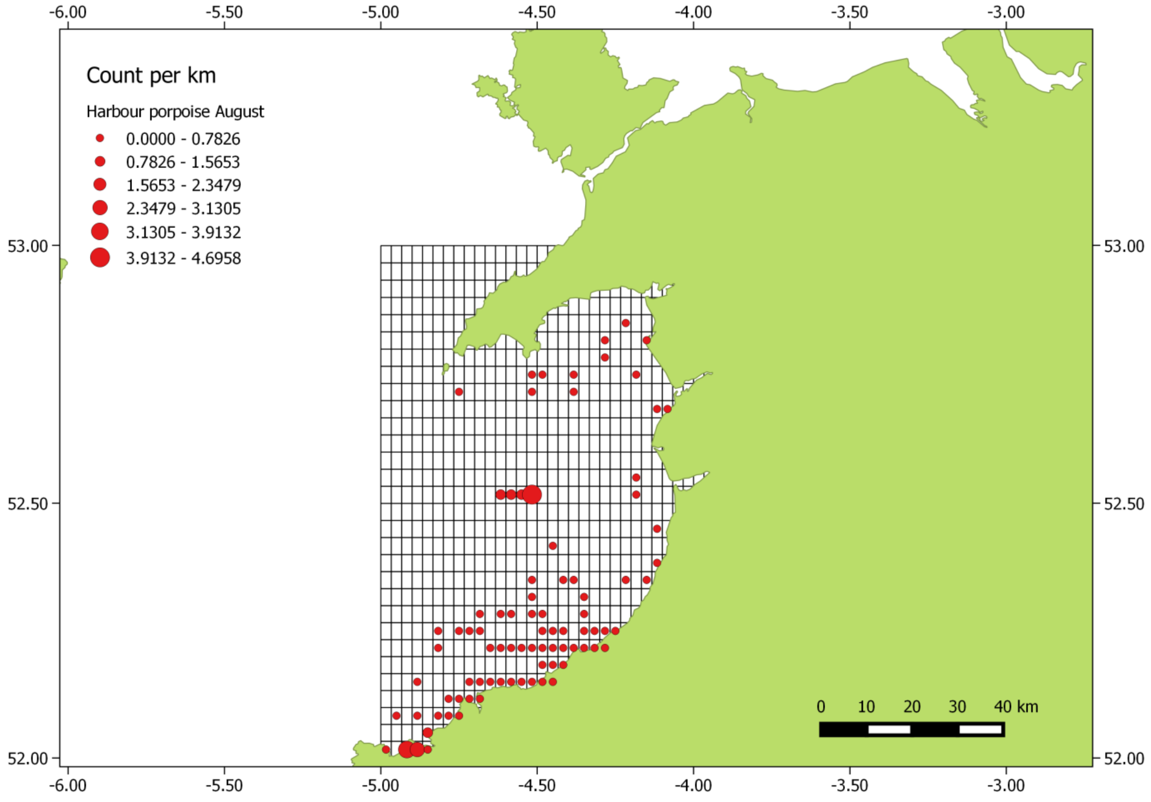


Figure 46. Map of harbour porpoise density (count per km) corrected for effort in August

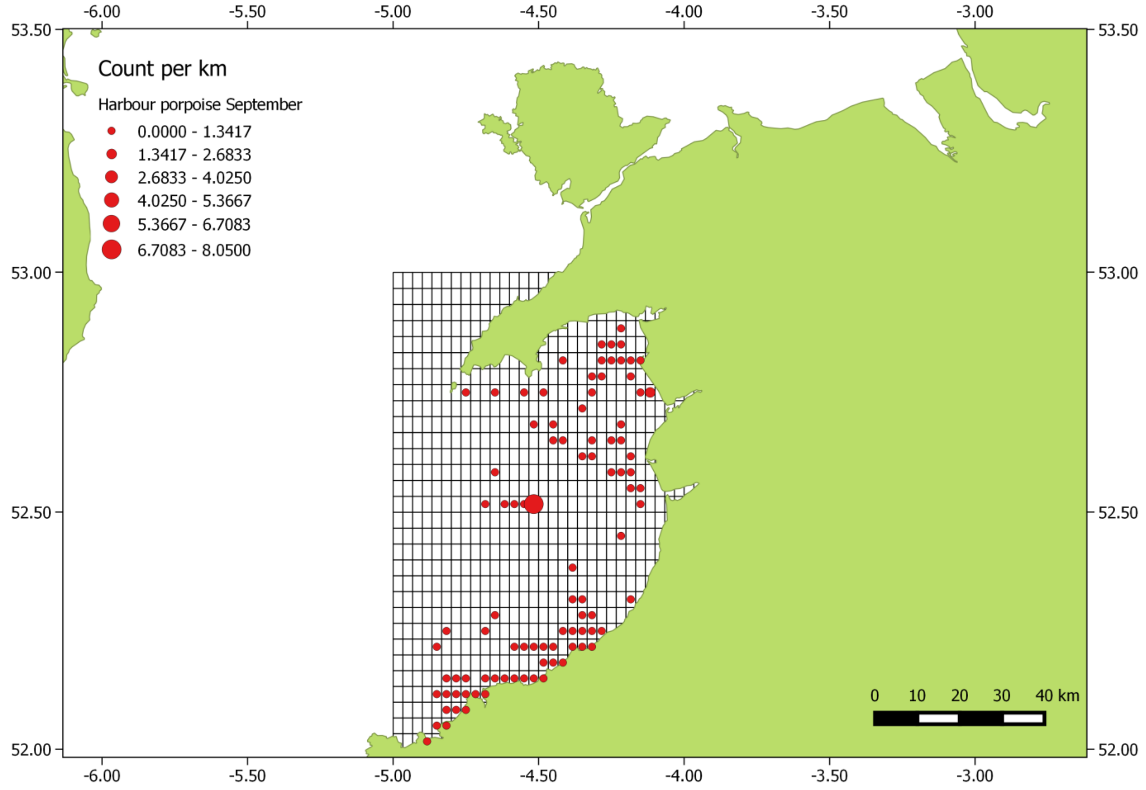


Figure 47. Map of harbour porpoise density (count per km) corrected for effort in September

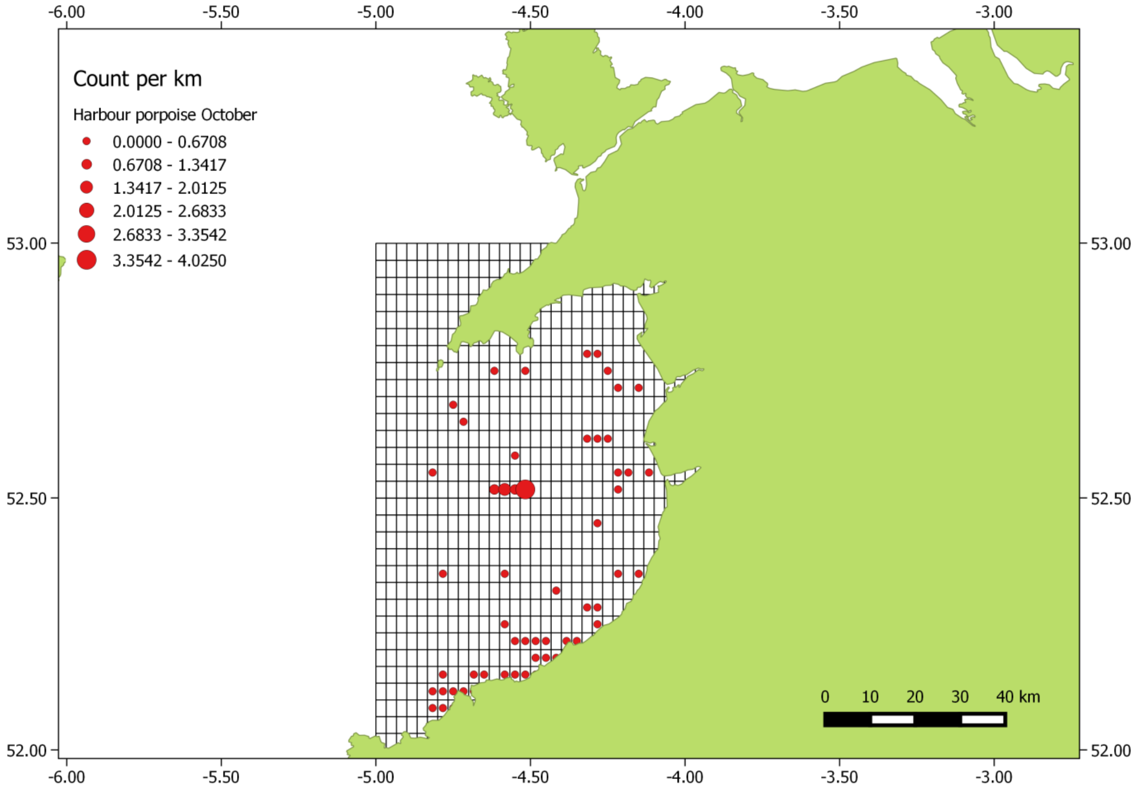


Figure 48. Map of harbour porpoise density (count per km) corrected for effort in October

7.3 Co-occurrence (overlap) maps

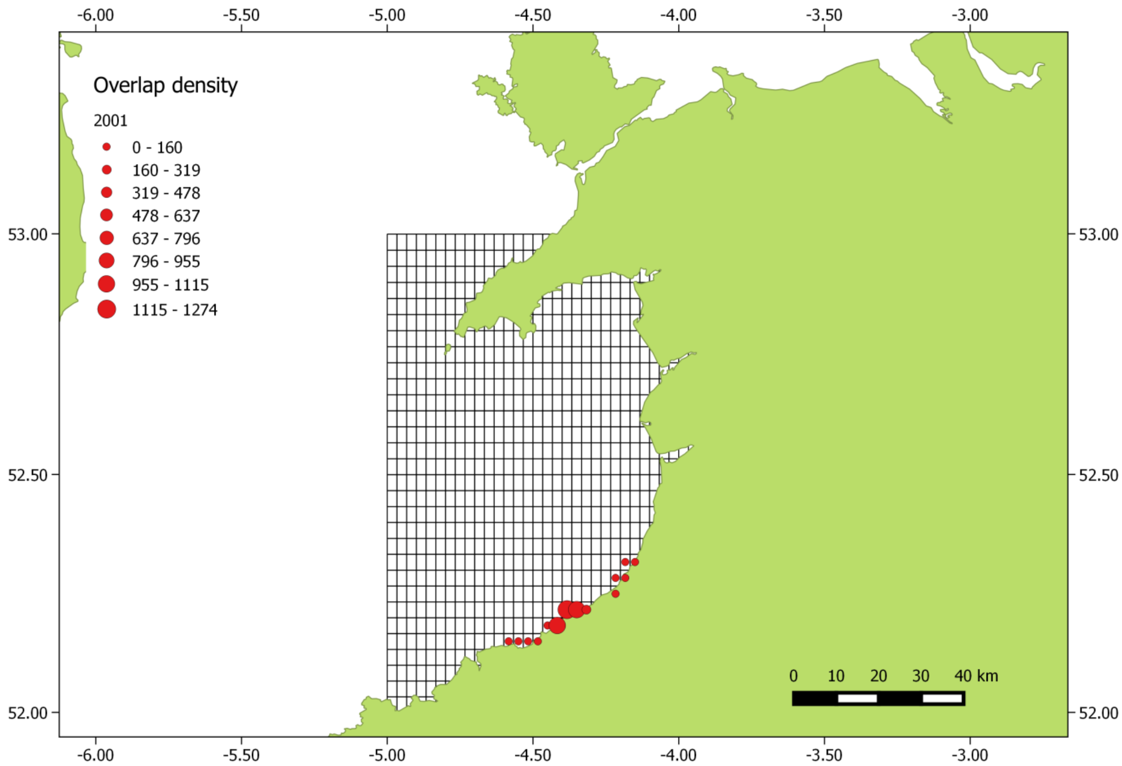


Figure 49. Map of overlap density (count per km) corrected for effort in 2001

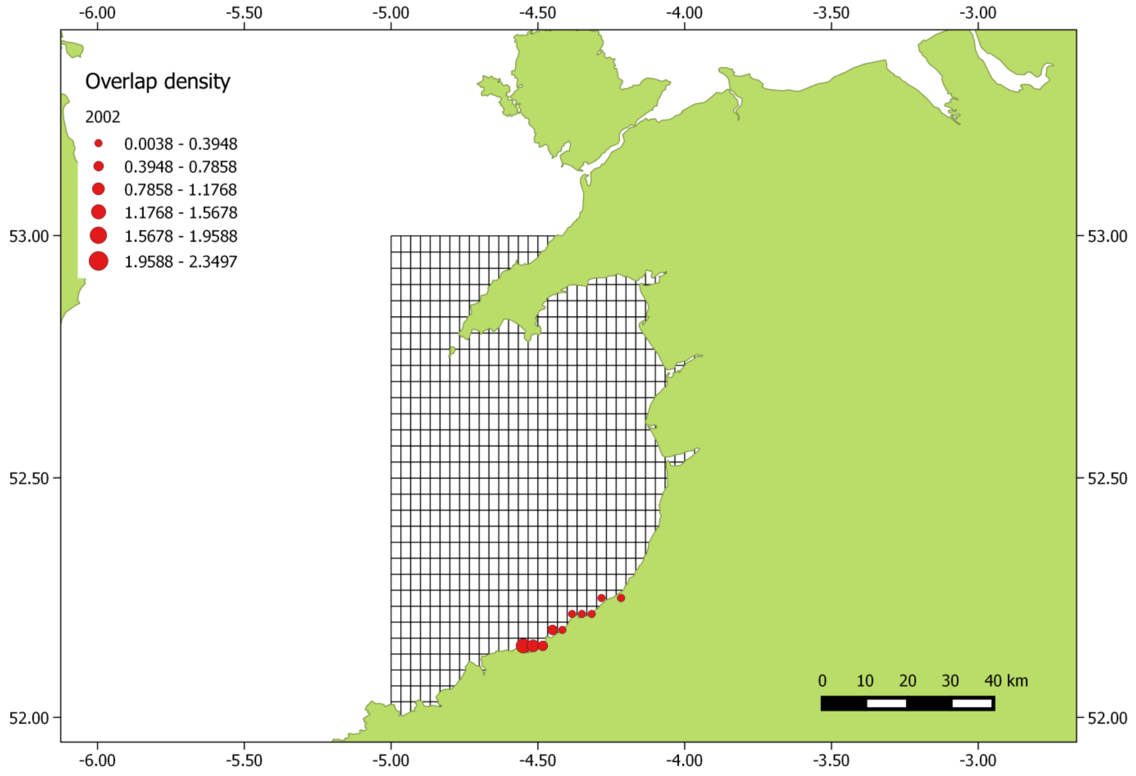


Figure 50. Map of overlap density (count per km) corrected for effort in 2002

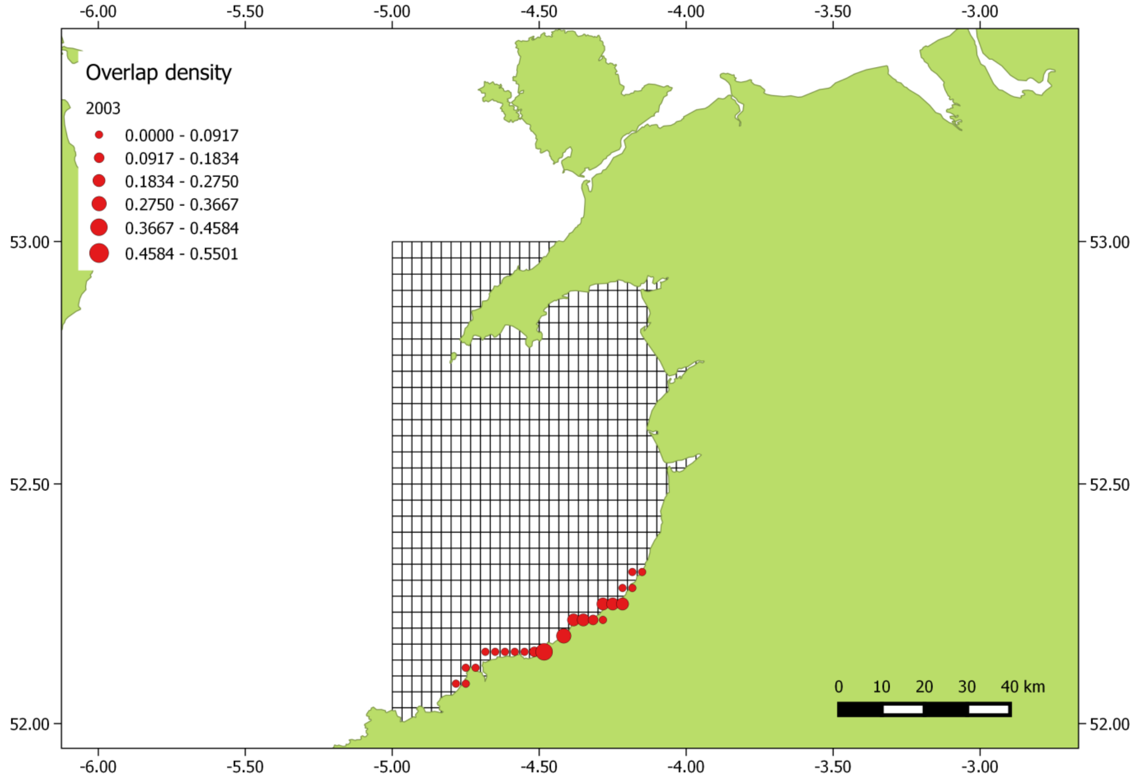


Figure 51. Map of overlap density (count per km) corrected for effort in 2003

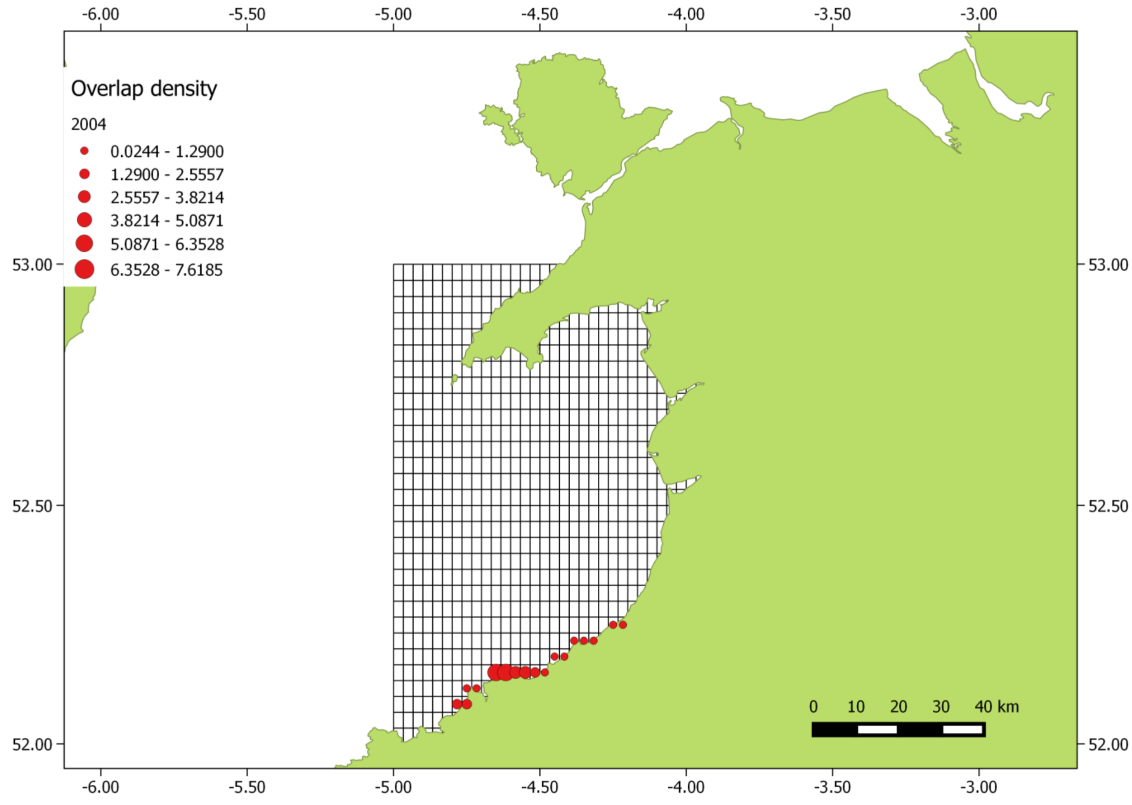


Figure 52. Map of overlap density (count per km) corrected for effort in 2004

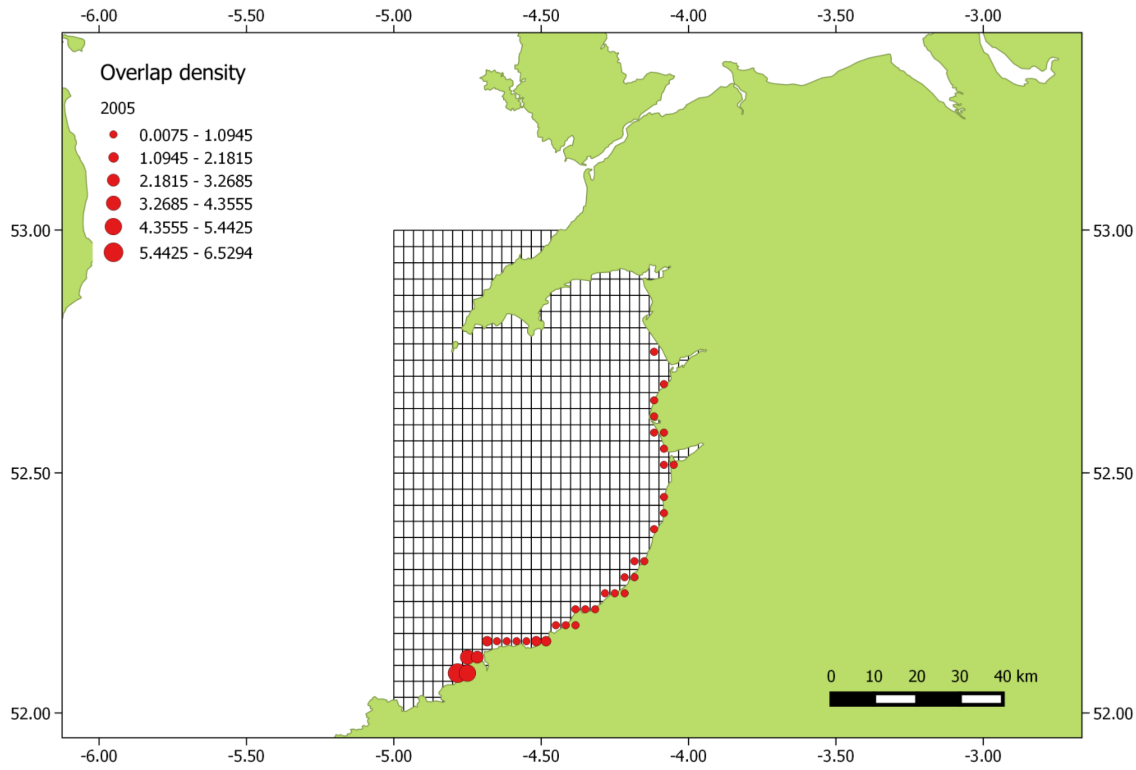


Figure 53. Map of overlap density (count per km) corrected for effort in 2005

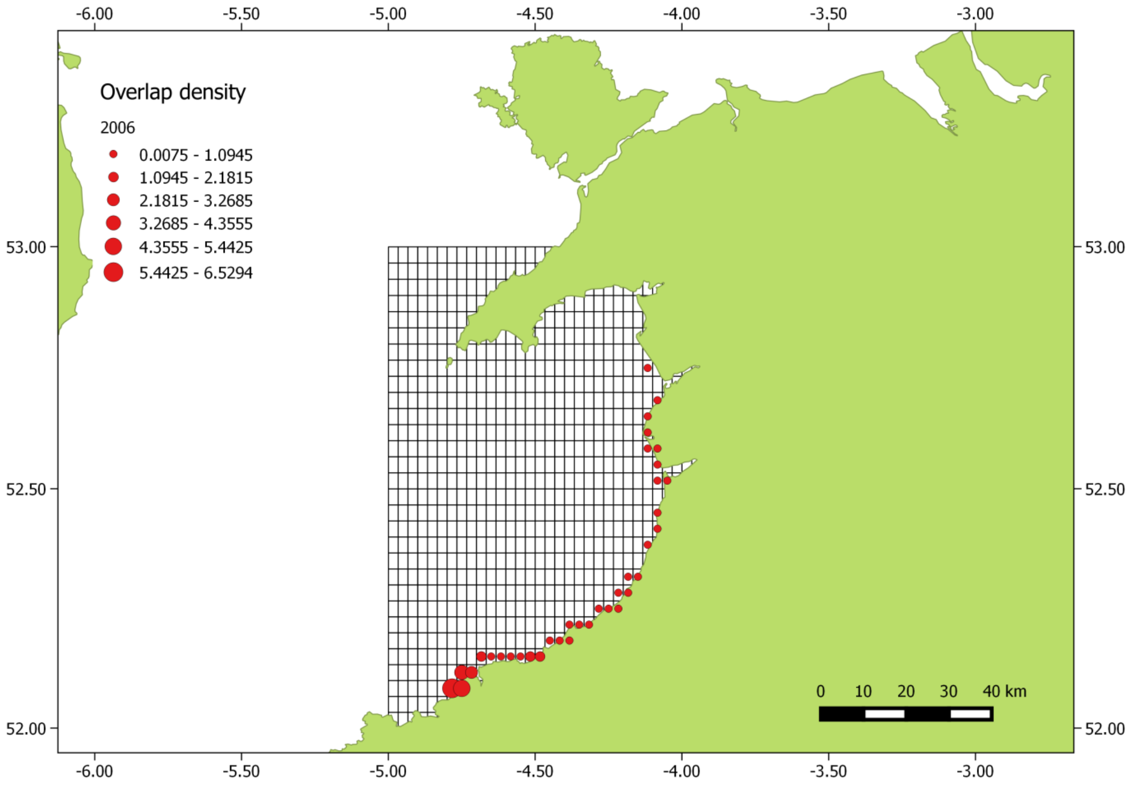


Figure 54. Map of overlap density (count per km) corrected for effort in 2006

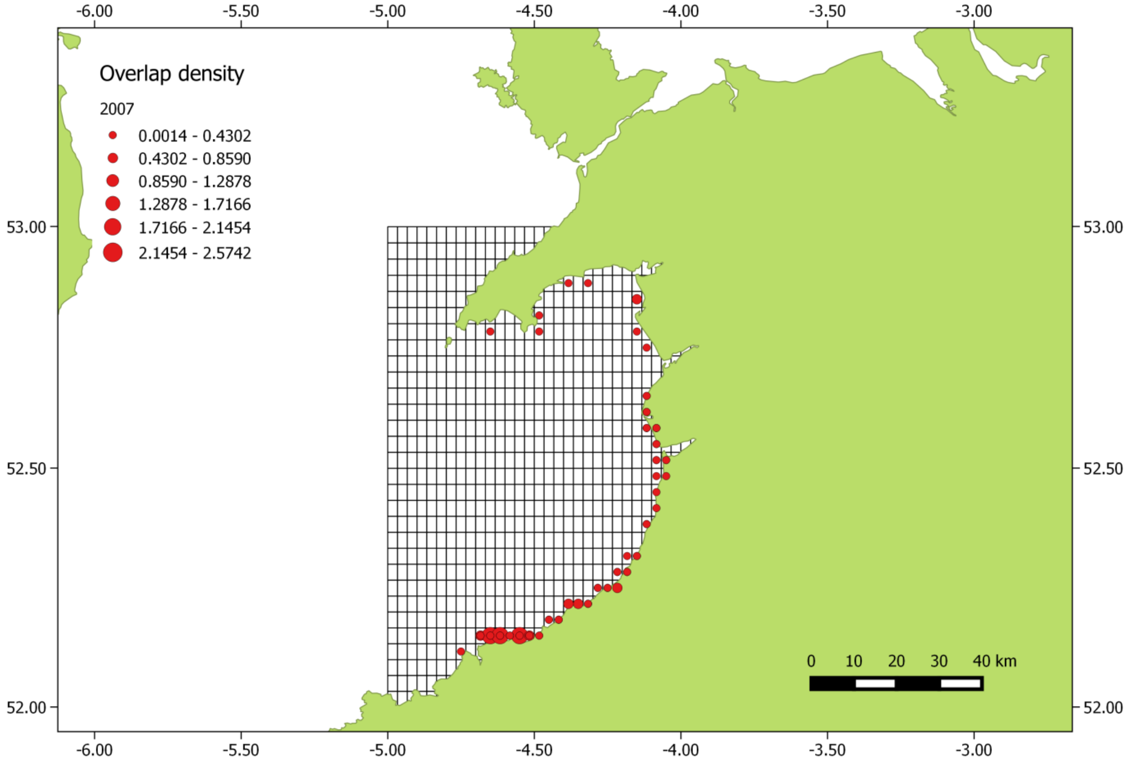


Figure 55. Map of overlap density (count per km) corrected for effort in 2007

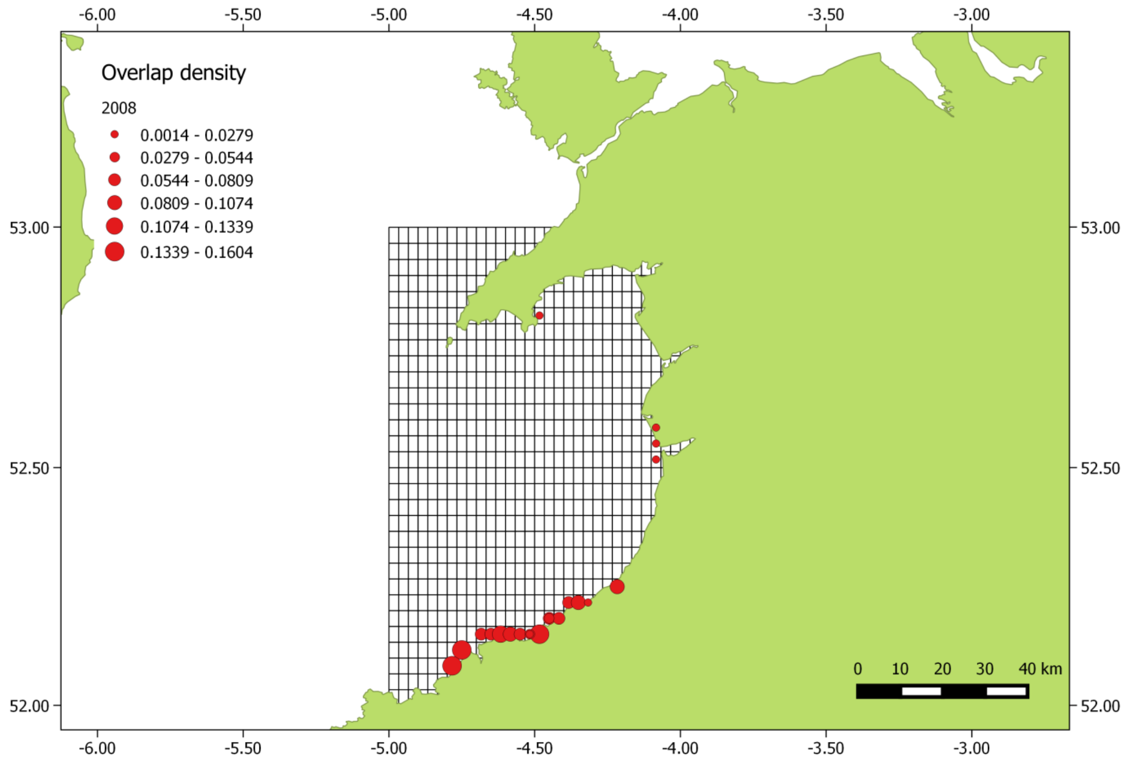


Figure 56. Map of overlap density (count per km) corrected for effort in 2008

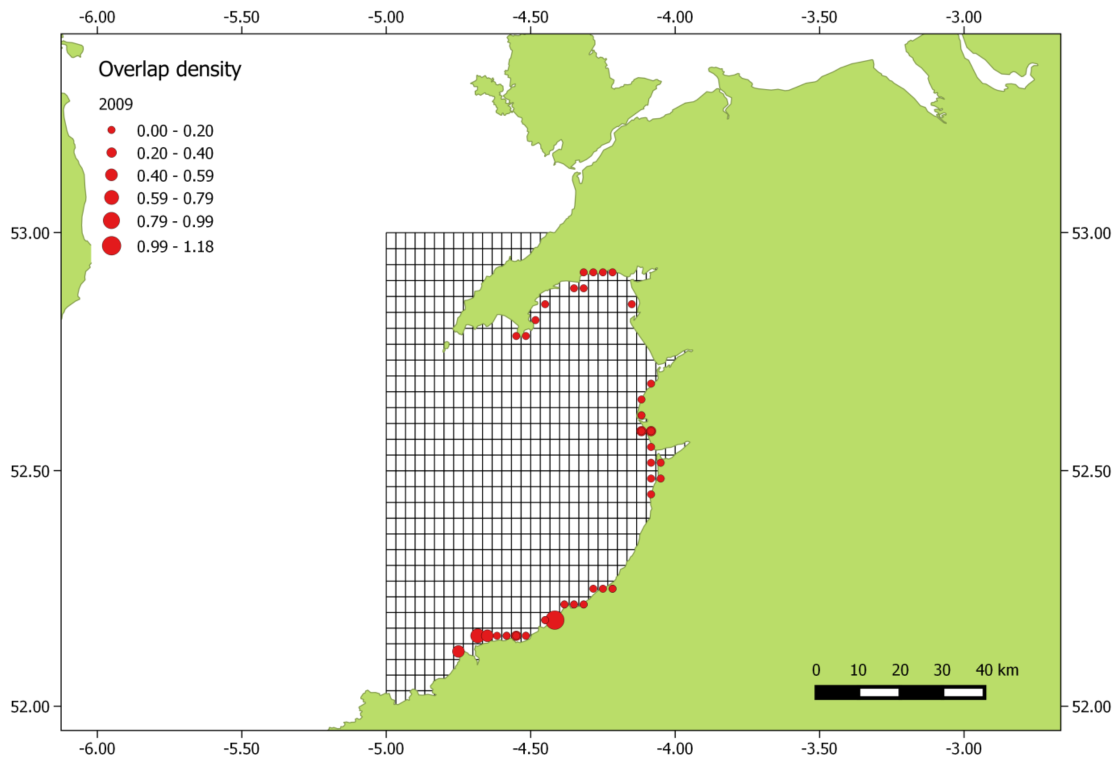


Figure 57. Map of overlap density (count per km) corrected for effort in 2009

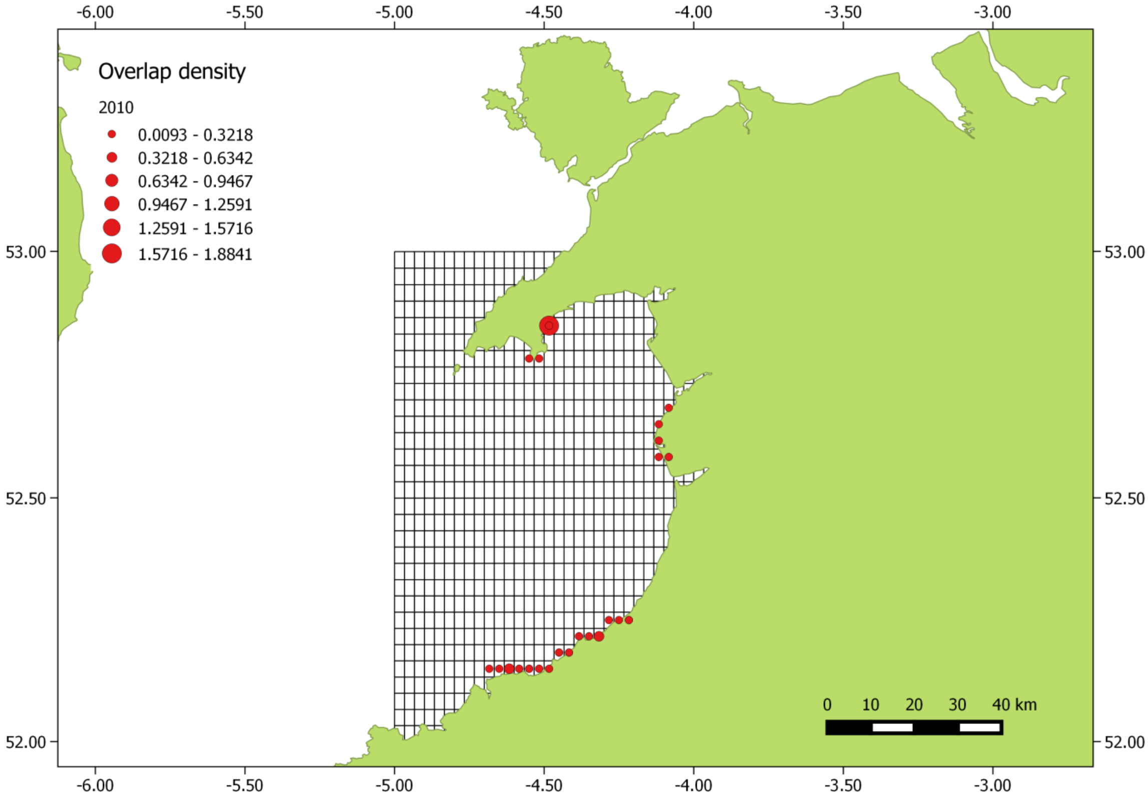


Figure 58. Map of overlap density (count per km) corrected for effort in 2010

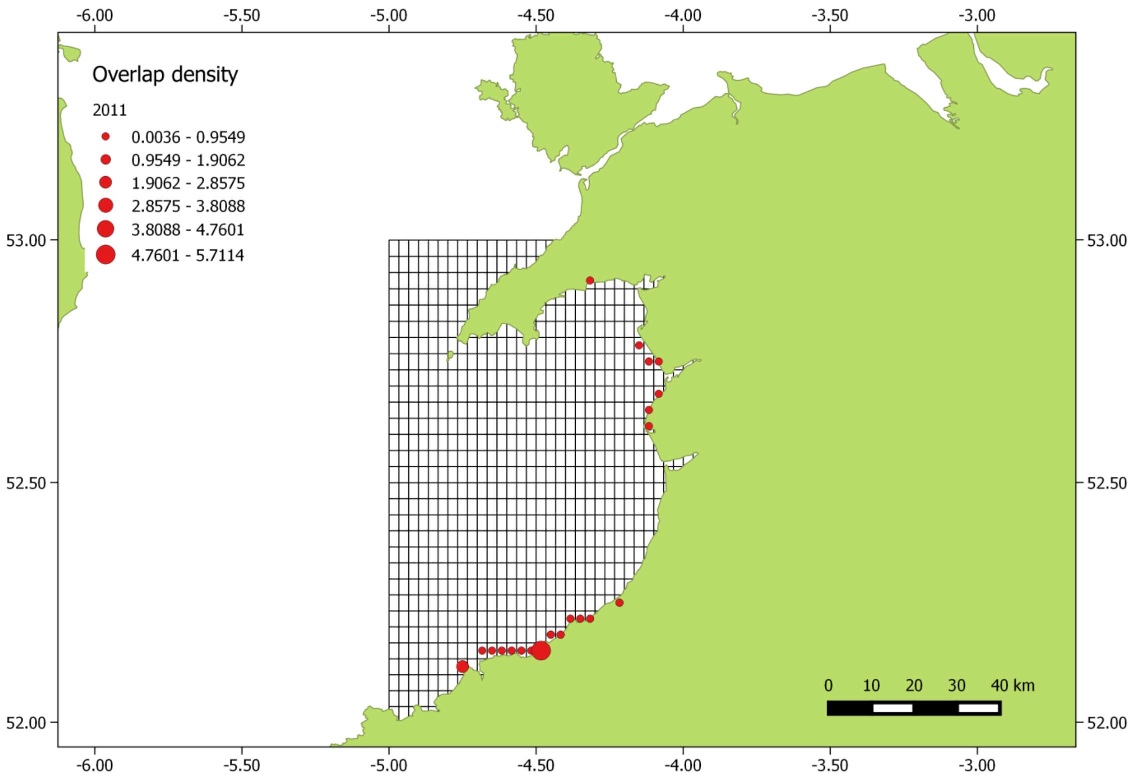


Figure 59. Map of overlap density (count per km) corrected for effort in 2011

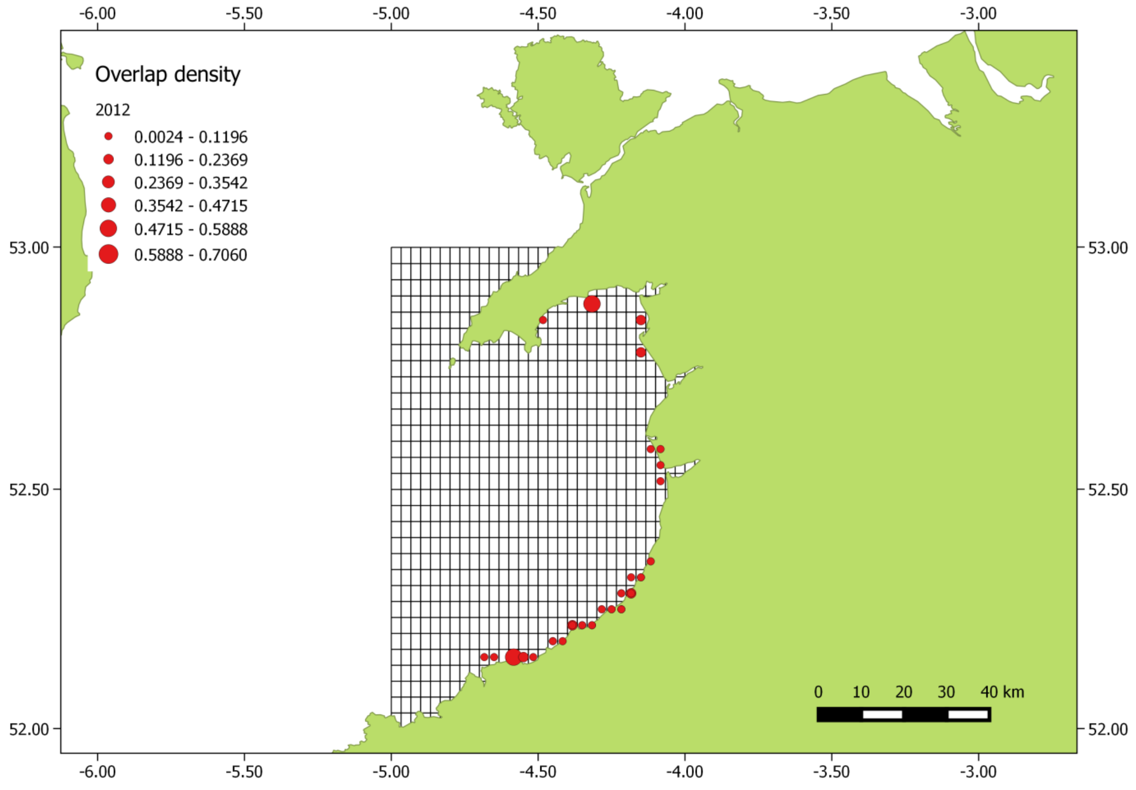


Figure 60. Map of overlap density (count per km) corrected for effort in 2012

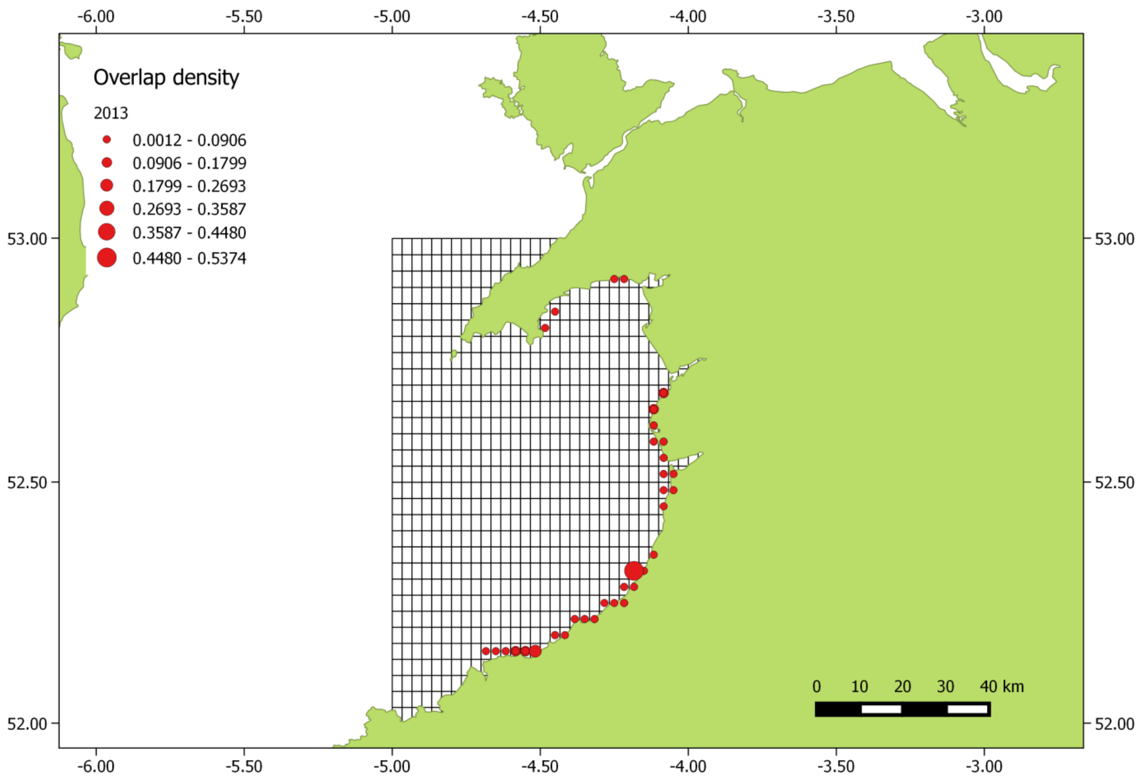


Figure 61. Map of overlap density (count per km) corrected for effort in 2013

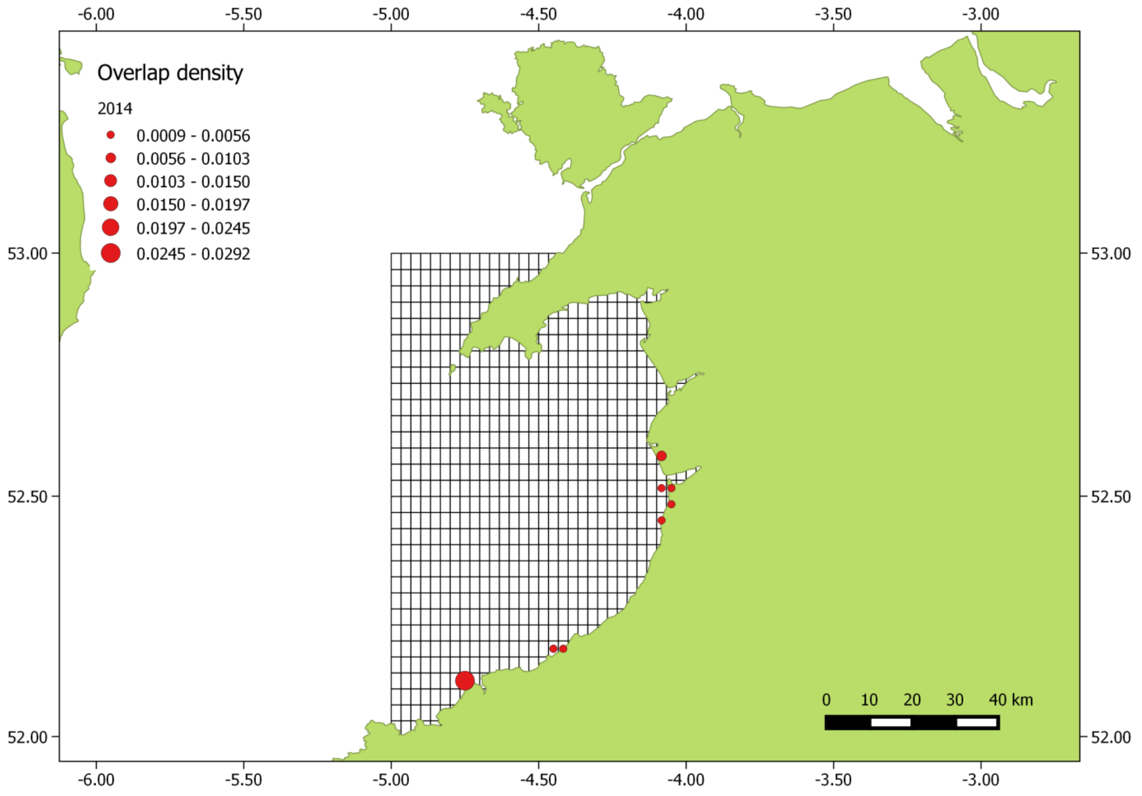


Figure 62. Map of overlap density (count per km) corrected for effort in 2014

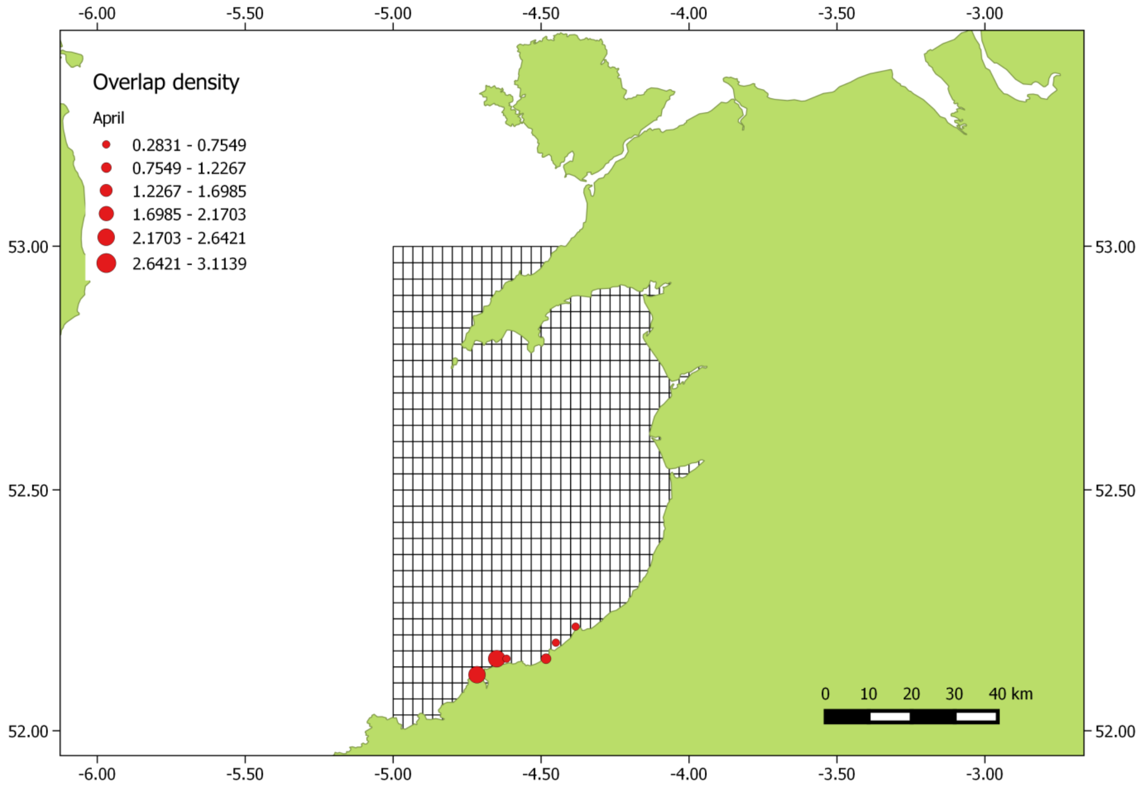


Figure 63. Map of overlap density (count per km) corrected for effort in April

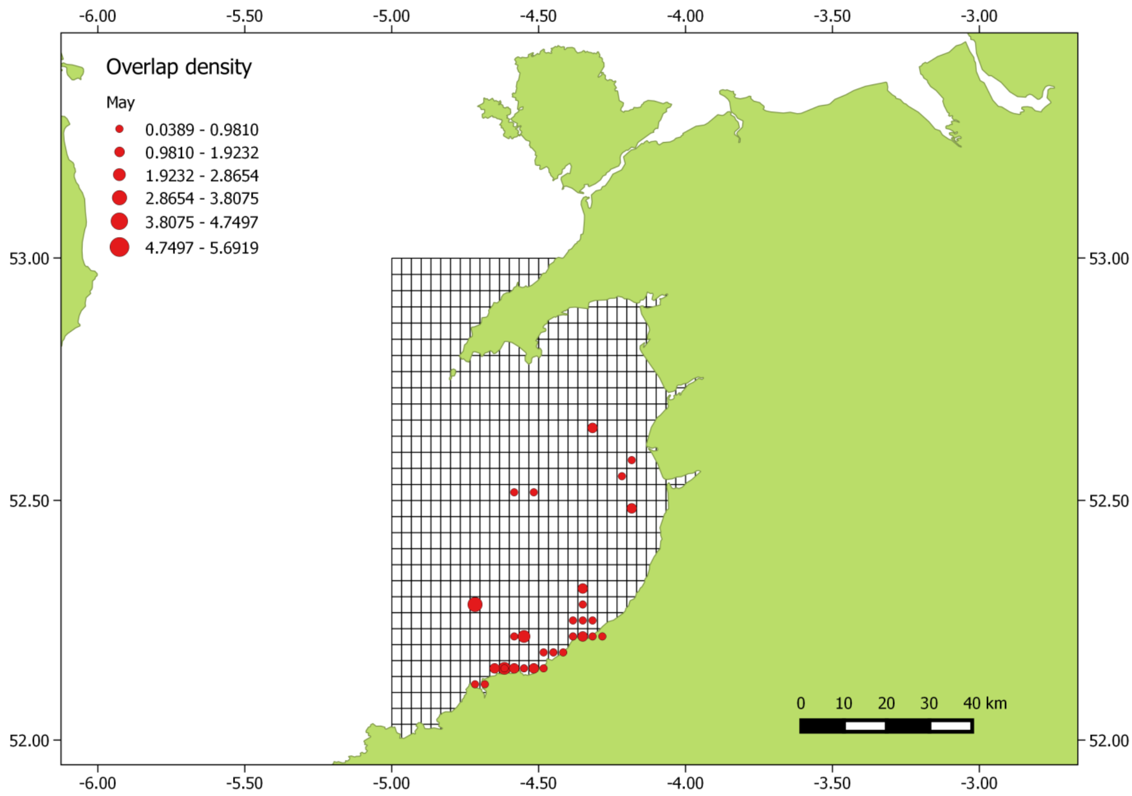


Figure 64. Map of overlap density (count per km) corrected for effort in May

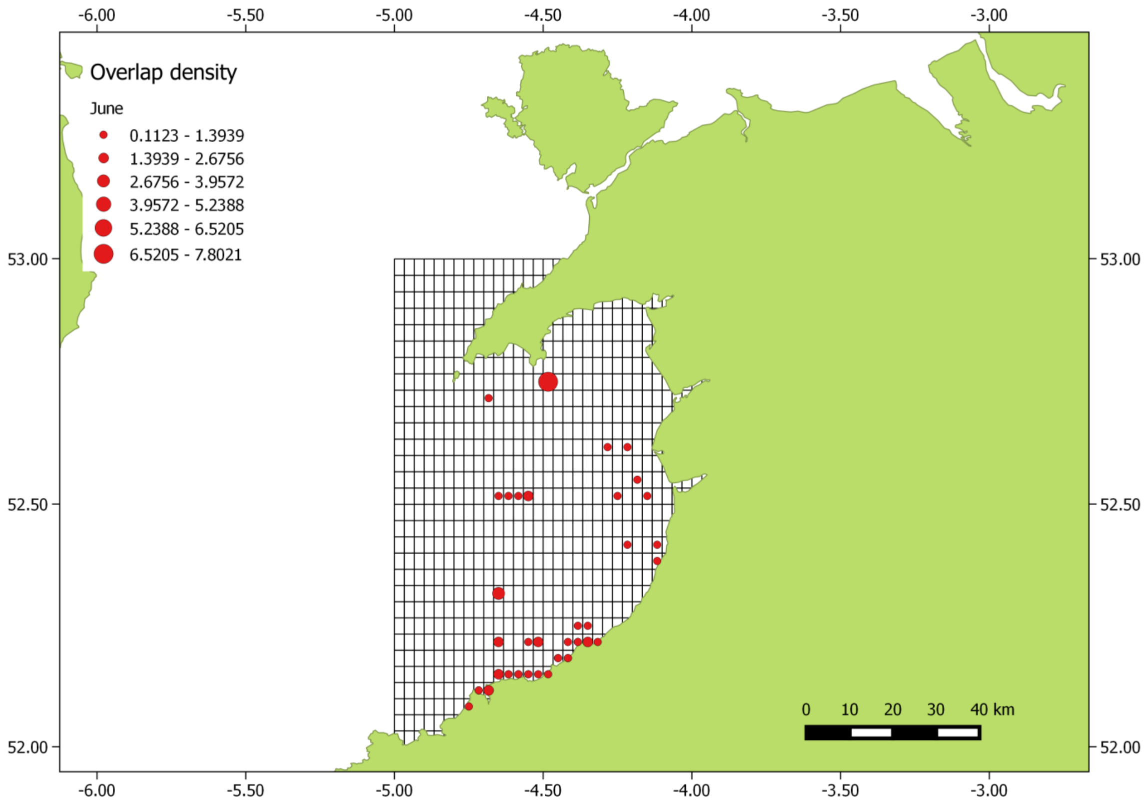


Figure 65. Map of overlap density (count per km) corrected for effort in June

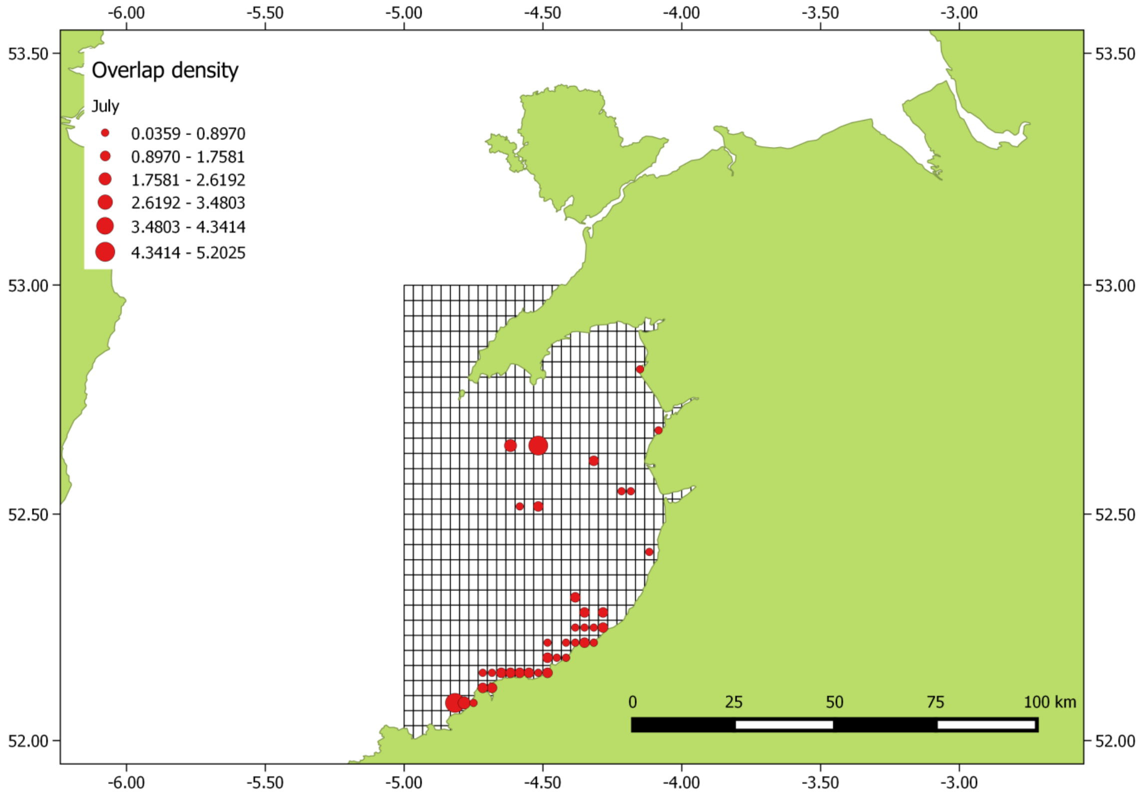


Figure 66. Map of overlap density (count per km) corrected for effort in July

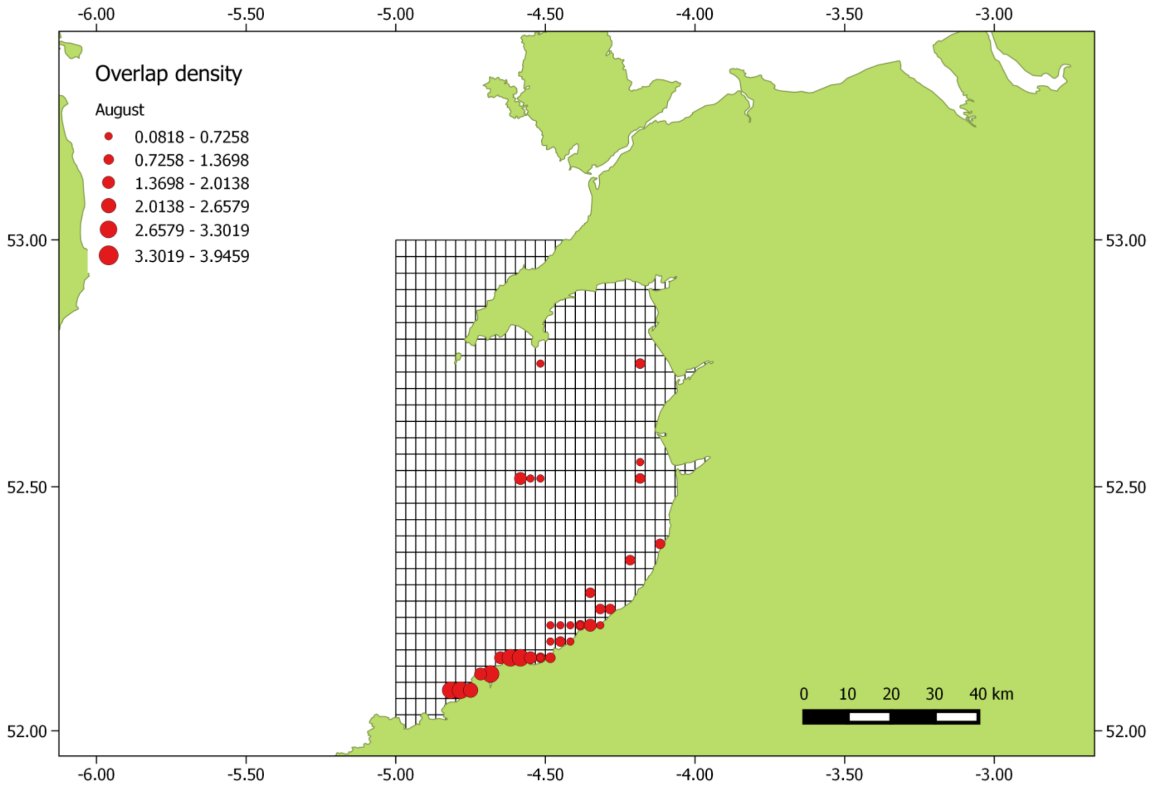


Figure 67. Map of overlap density (count per km) corrected for effort in August

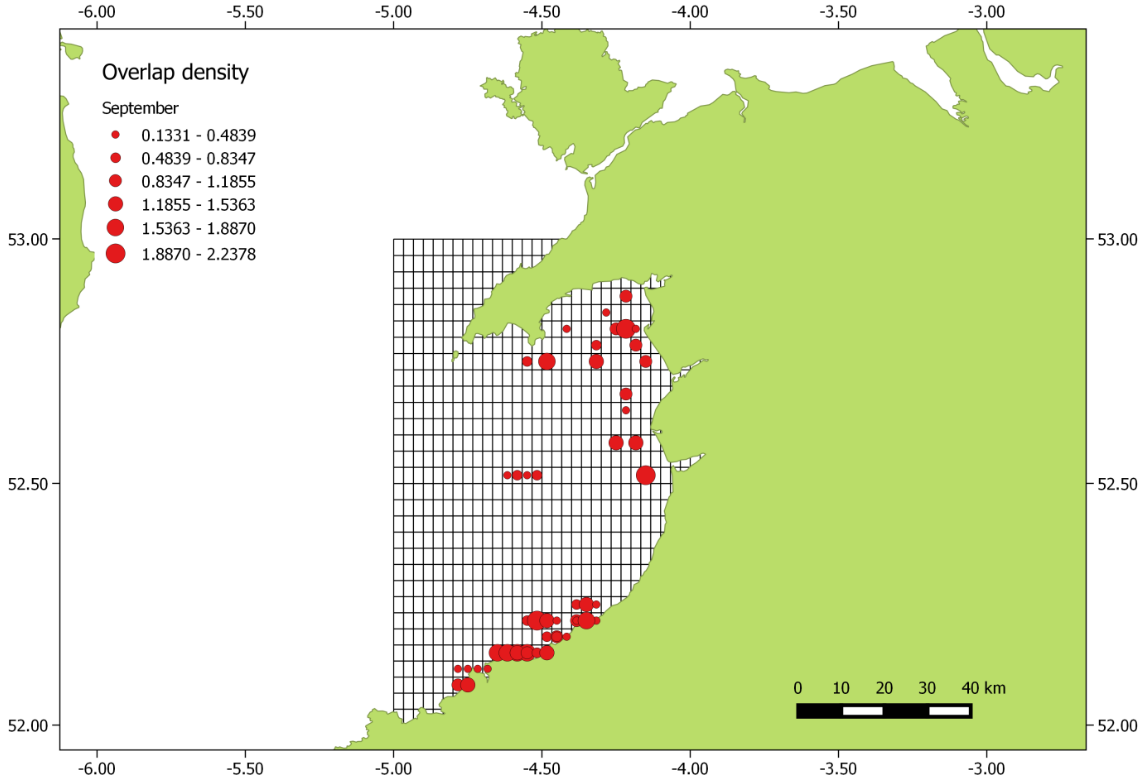


Figure 68. Map of overlap density (count per km) corrected for effort in September

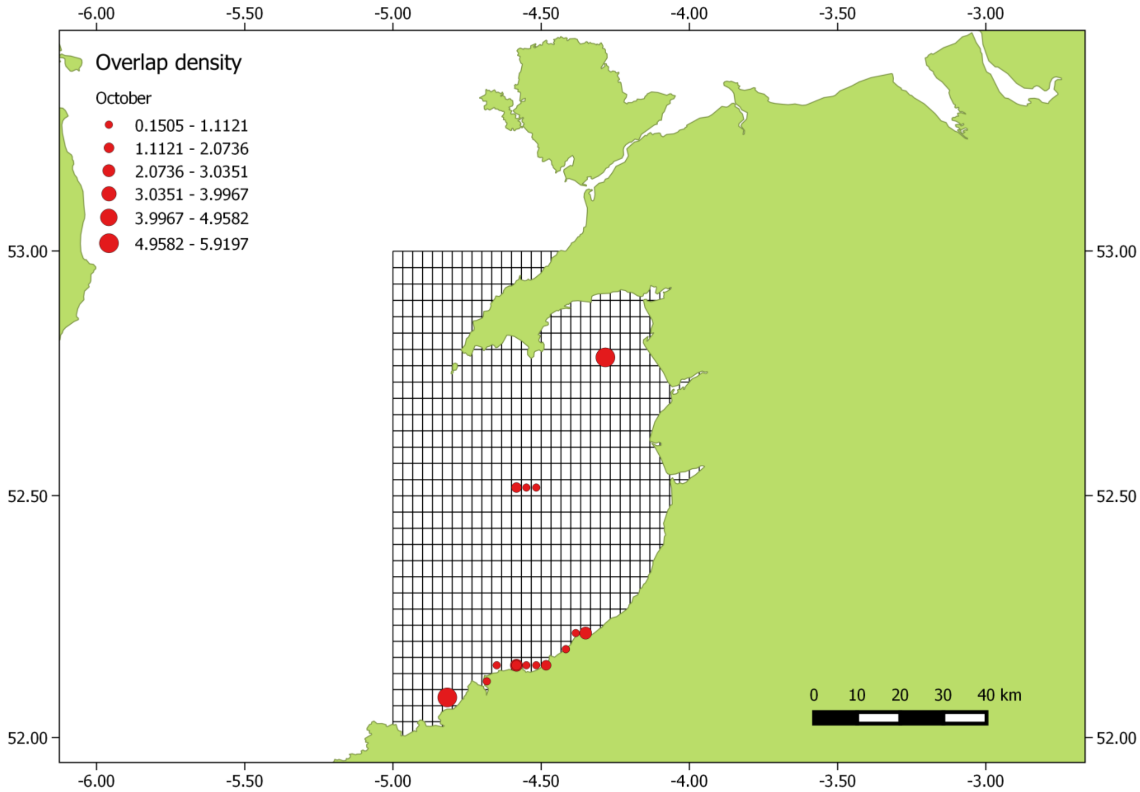


Figure 69. Map of overlap density (count per km) corrected for effort in October

7.4 Overlap and strandings

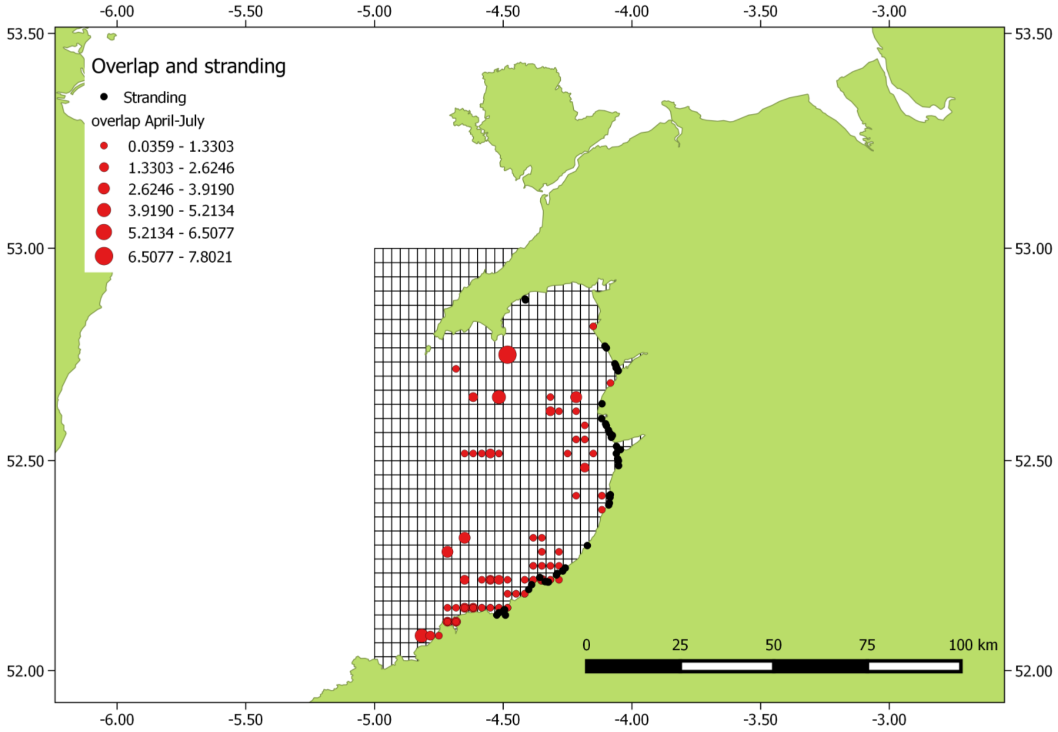


Figure 70. Map of overlap density (count per km) corrected for effort and strandings, April-July

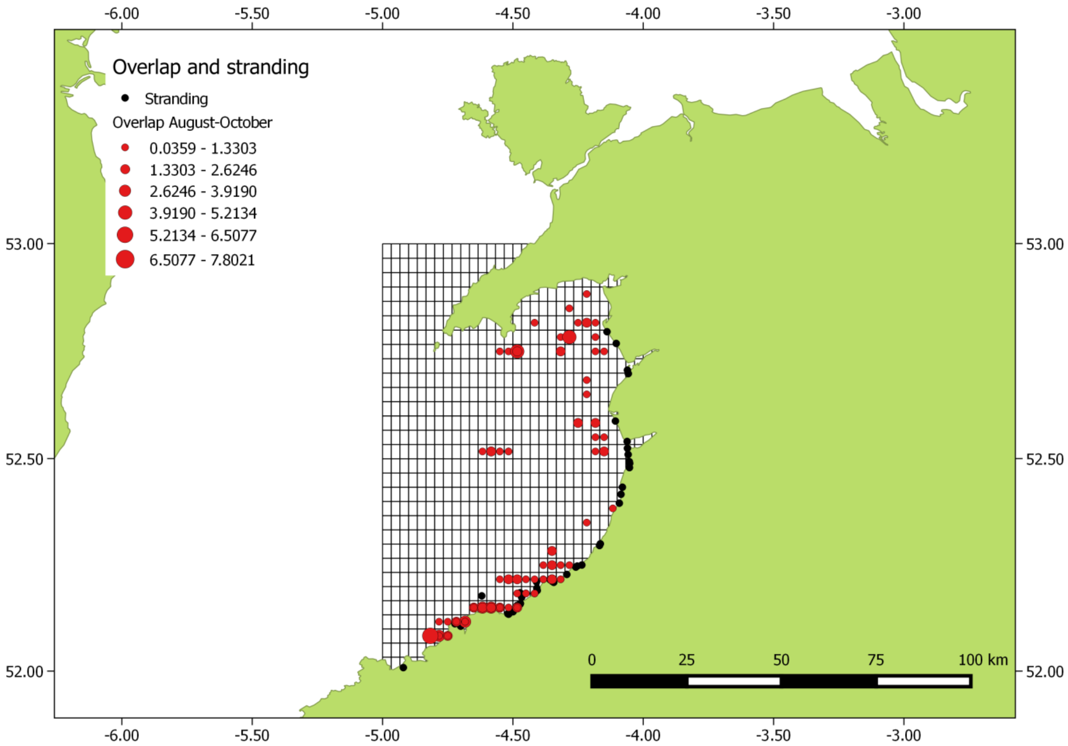


Figure 71. Map of overlap density (count per km) corrected for effort and strandings in August-October

7.5 Marine mammal atlas sightings maps

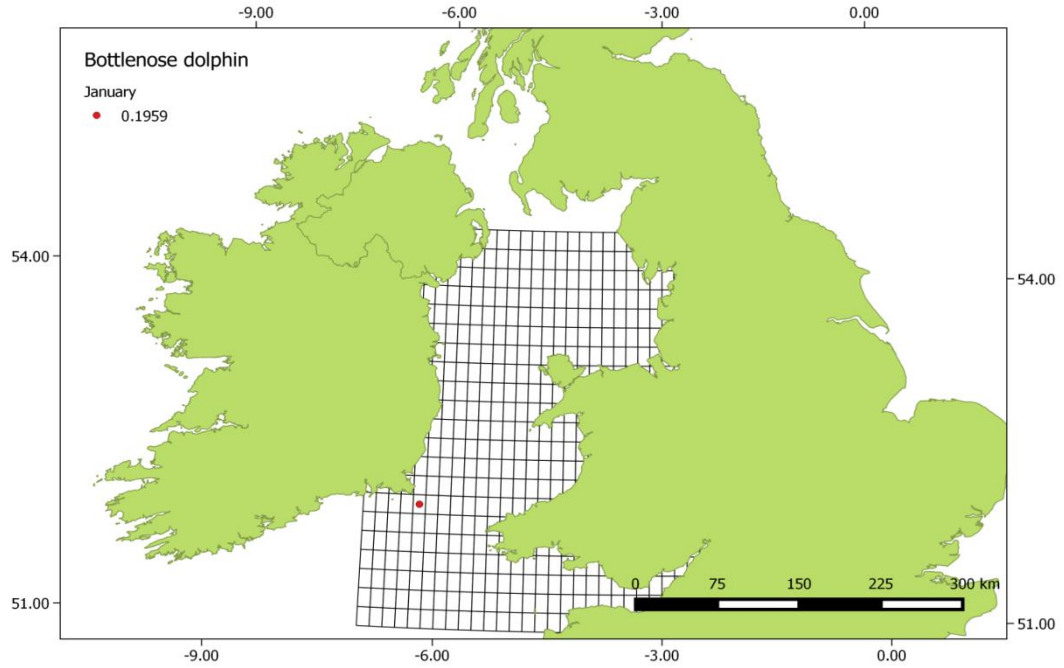


Figure 72. Map of bottlenose dolphin density (count per km) corrected for effort in January

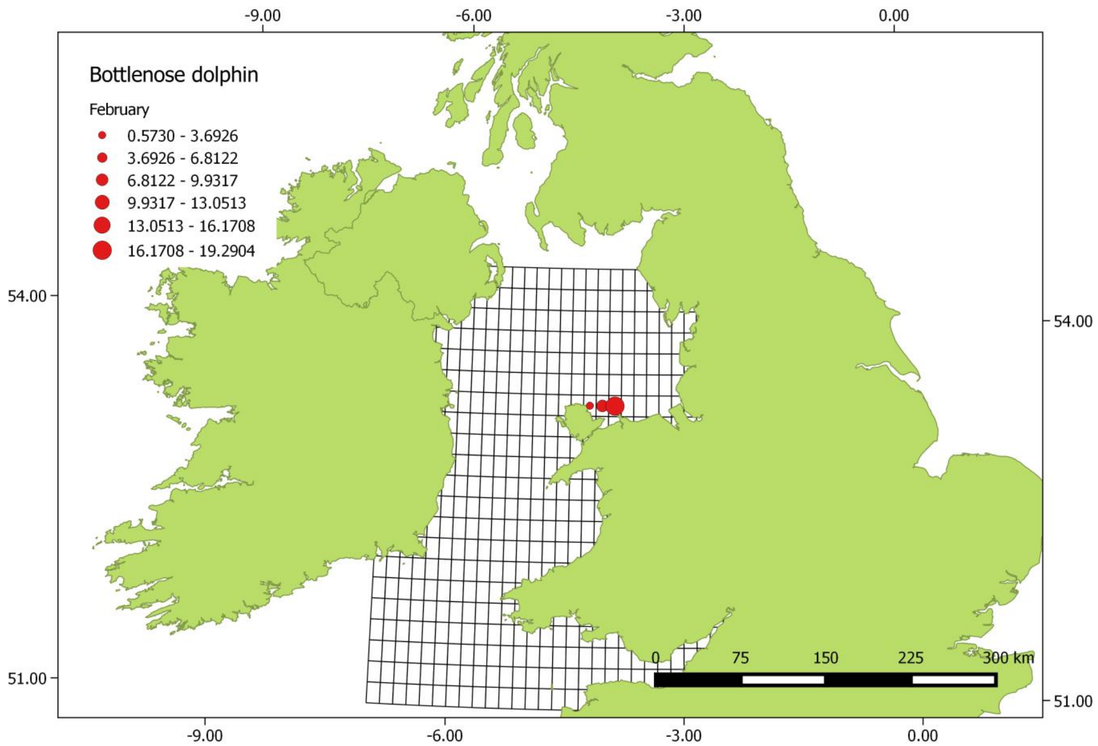


Figure 73. Map of bottlenose dolphin density (count per km) corrected for effort in February

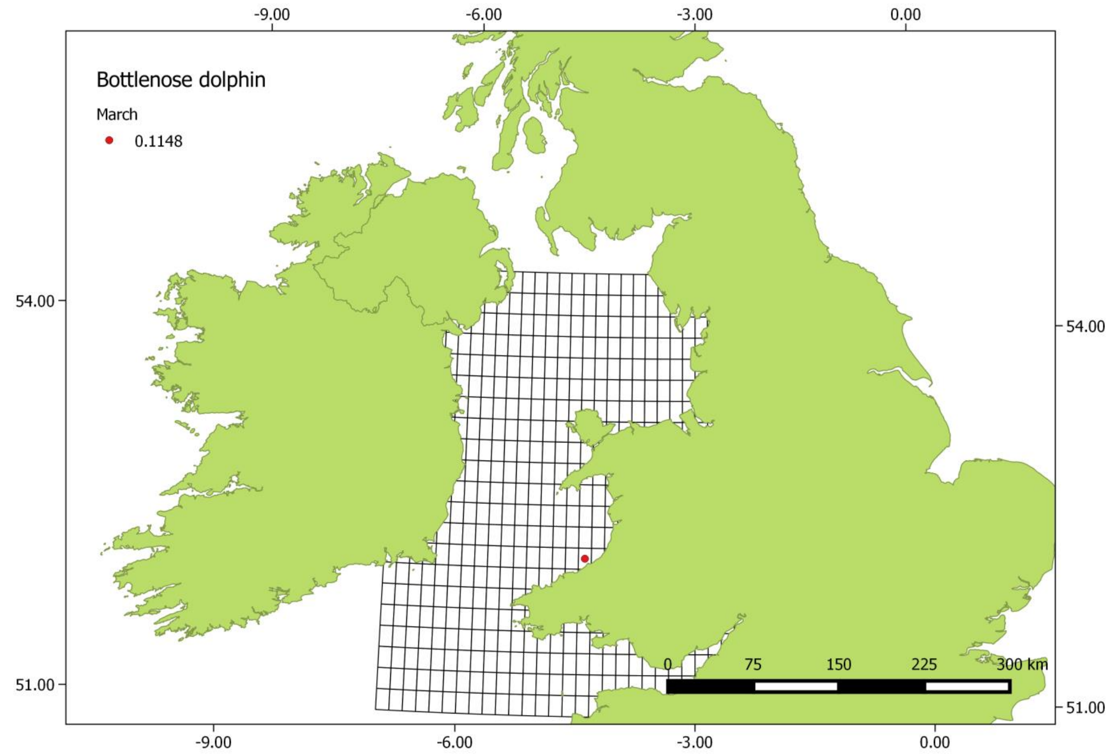


Figure 74. Map of bottlenose dolphin density (count per km) corrected for effort in March

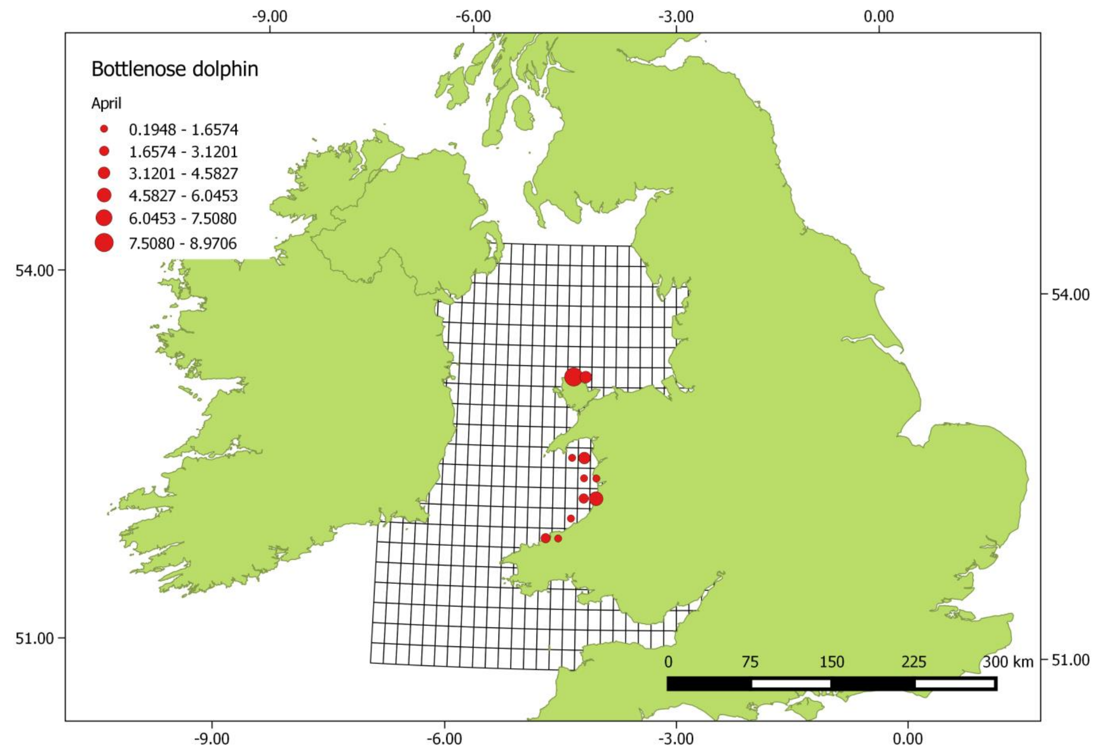


Figure 75. Map of bottlenose dolphin density (count per km) corrected for effort in April

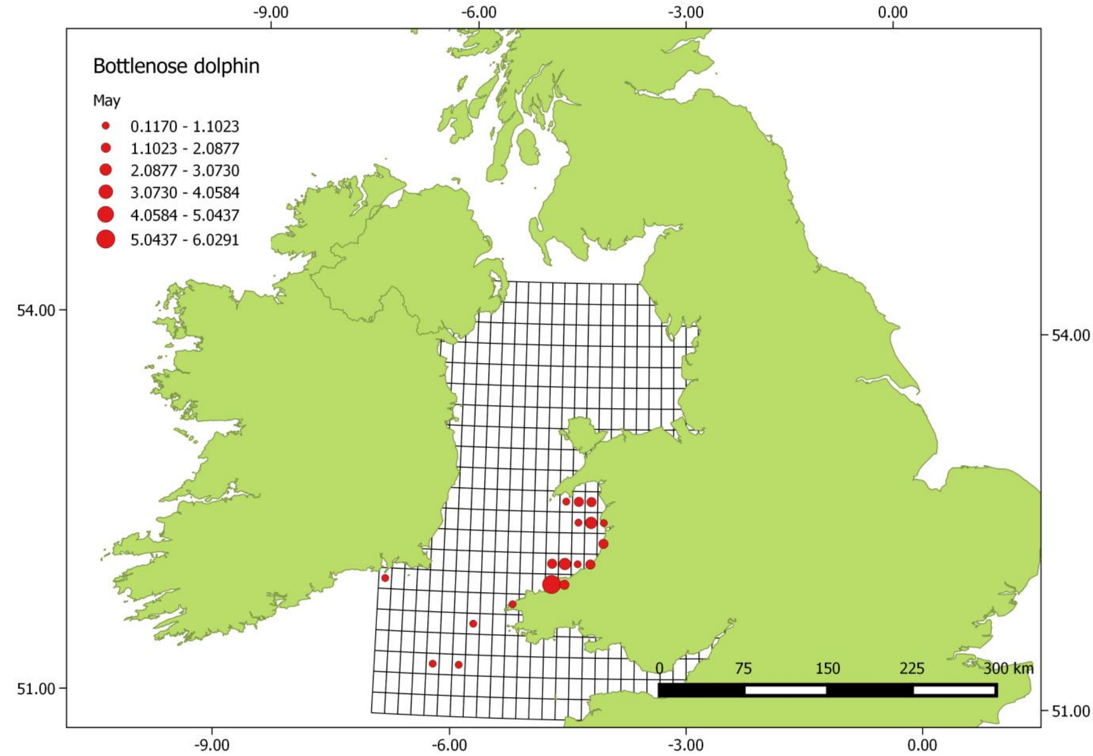


Figure 76. Map of bottlenose dolphin density (count per km) corrected for effort in May

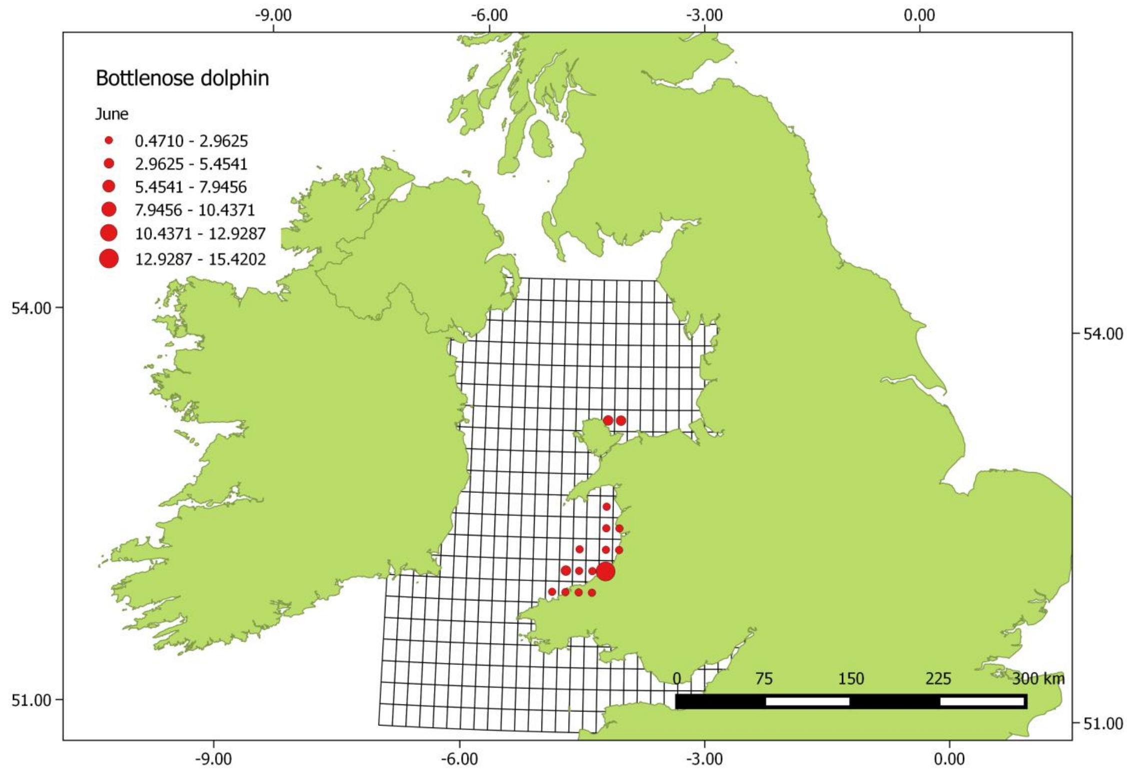


Figure 77. Map of bottlenose dolphin density (count per km) corrected for effort in June

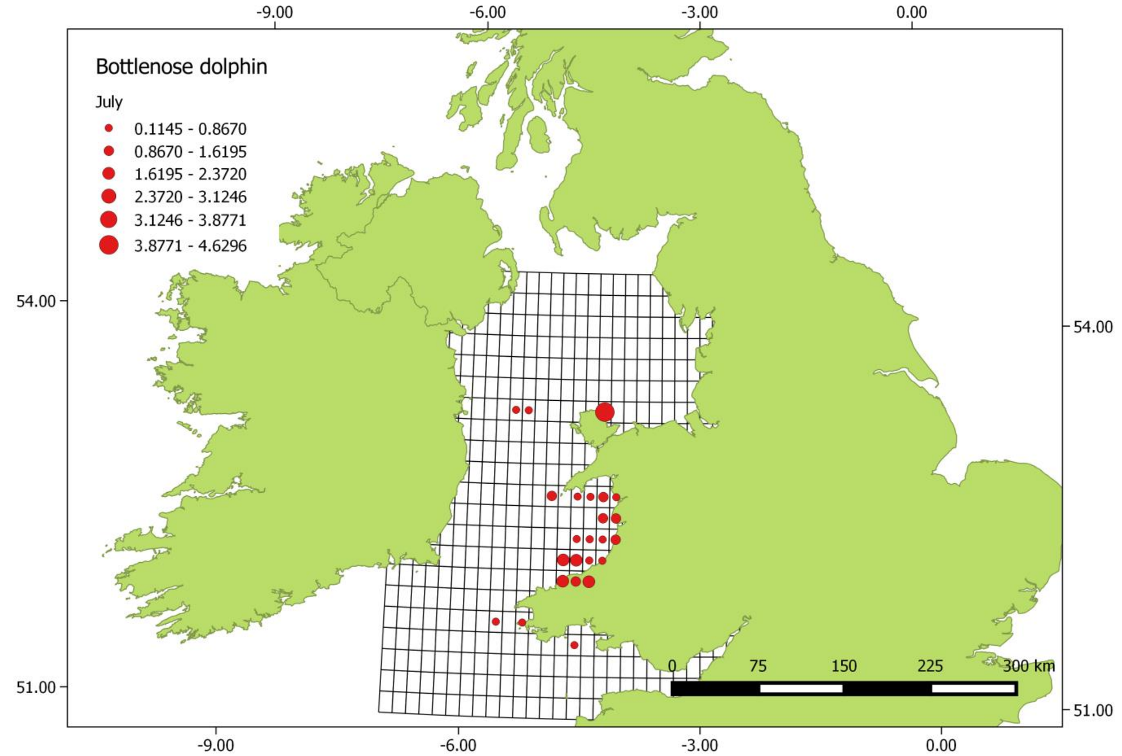


Figure 78. Map of bottlenose dolphin density (count per km) corrected for effort in July

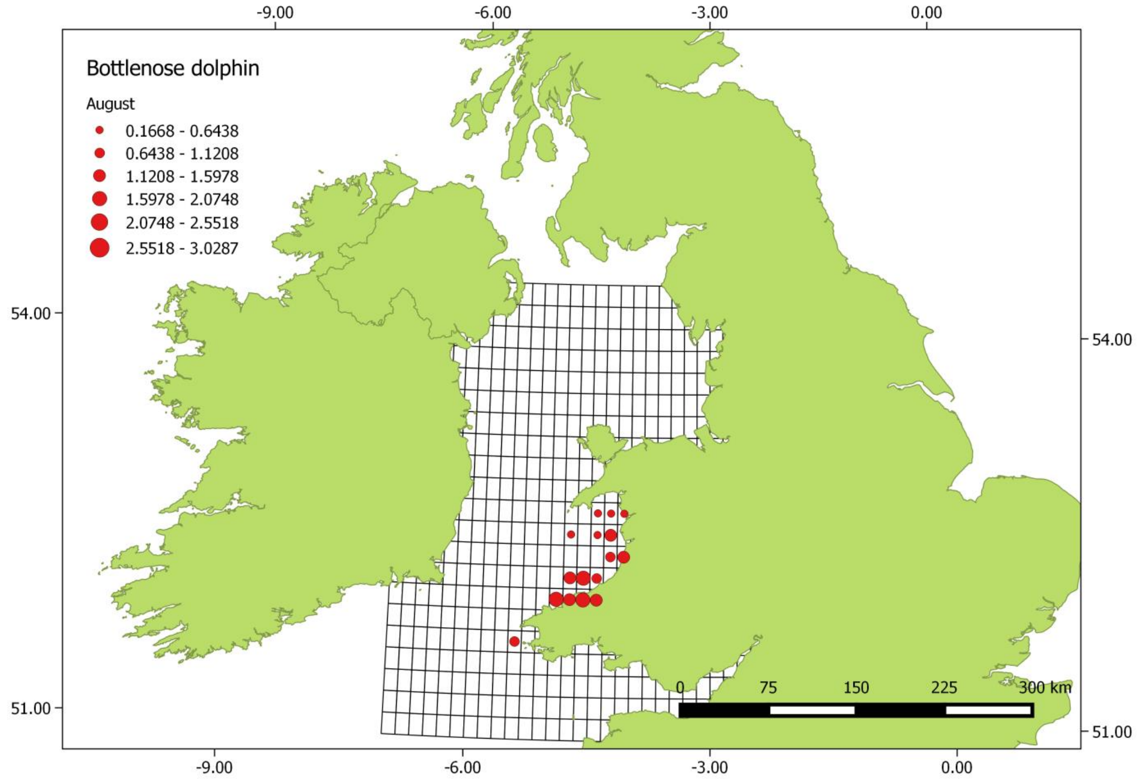


Figure 79. Map of bottlenose dolphin density (count per km) corrected for effort in August

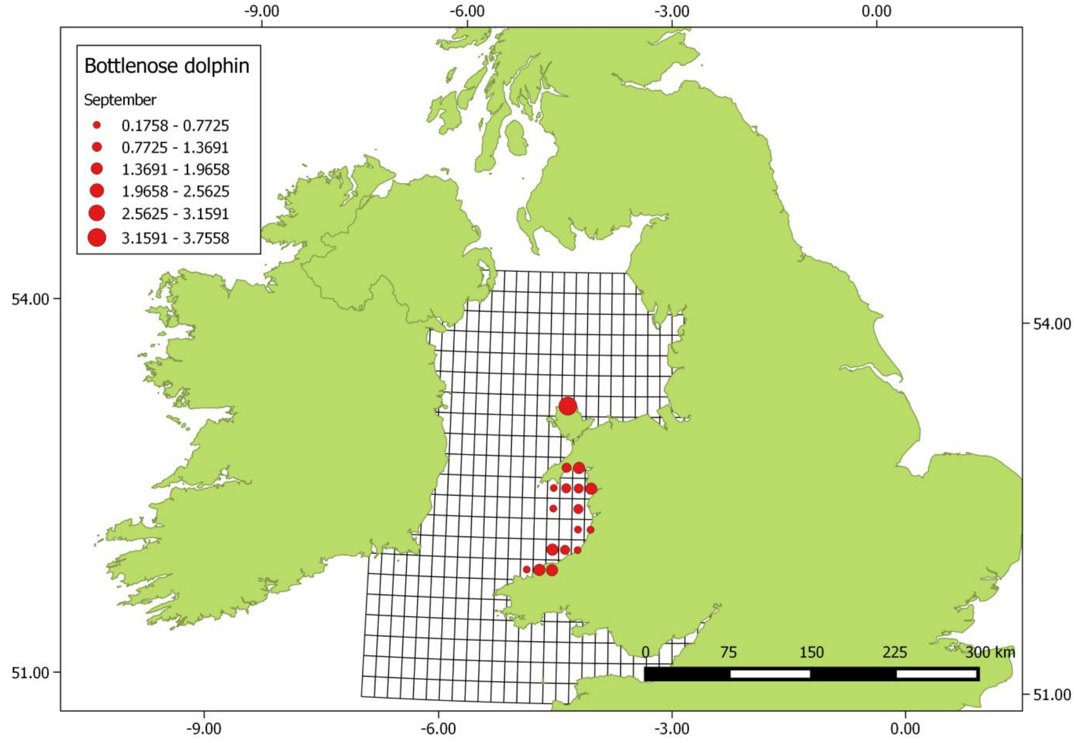


Figure 80. Map of bottlenose dolphin density (count per km) corrected for effort in September

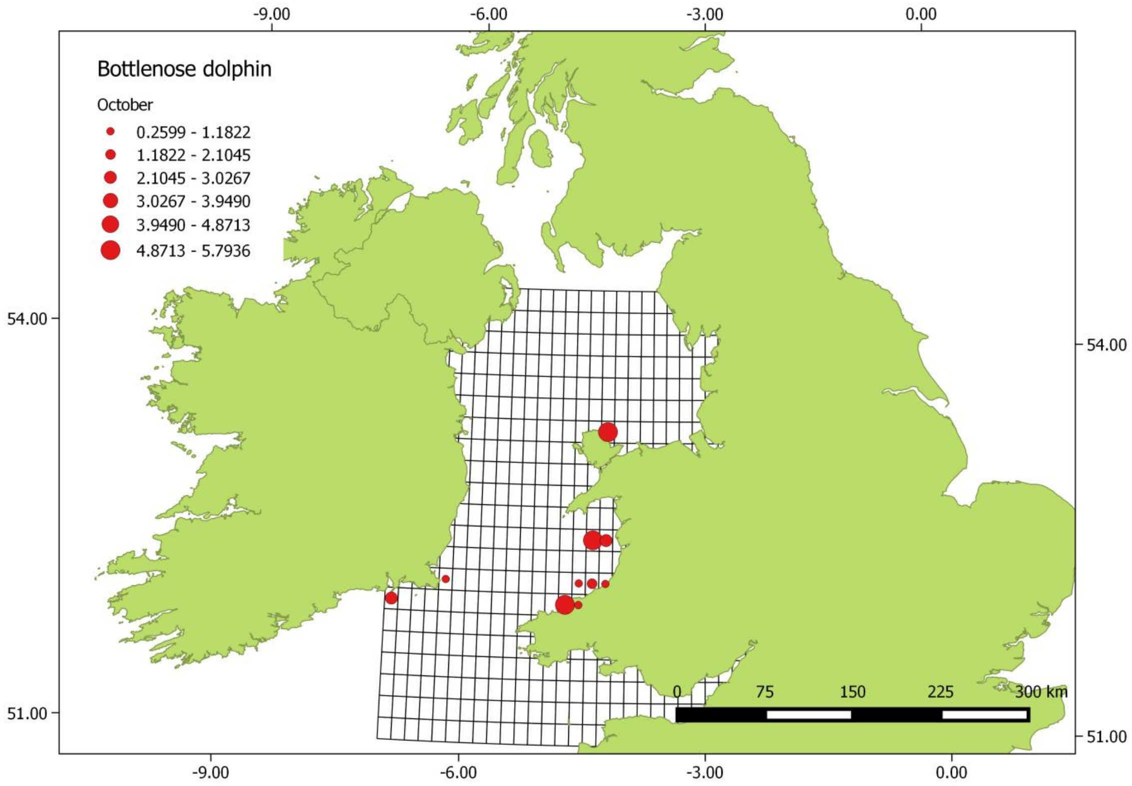


Figure 81. Map of bottlenose dolphin density (count per km) corrected for effort in October

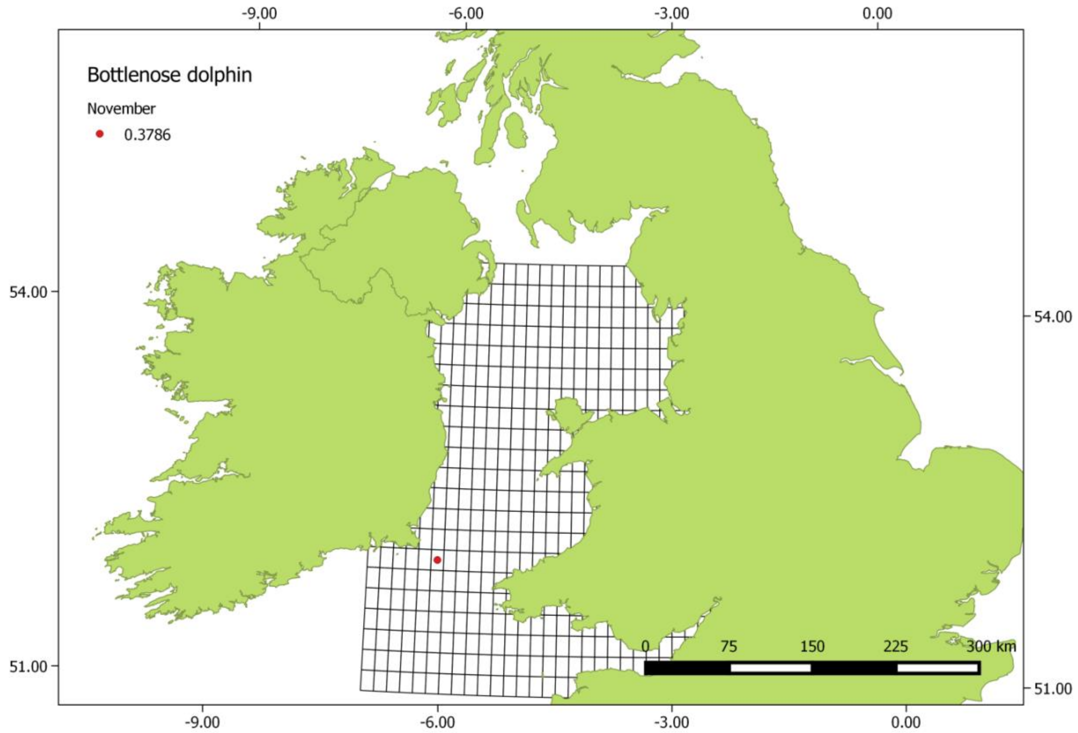


Figure 82. Map of bottlenose dolphin density (count per km) corrected for effort in November

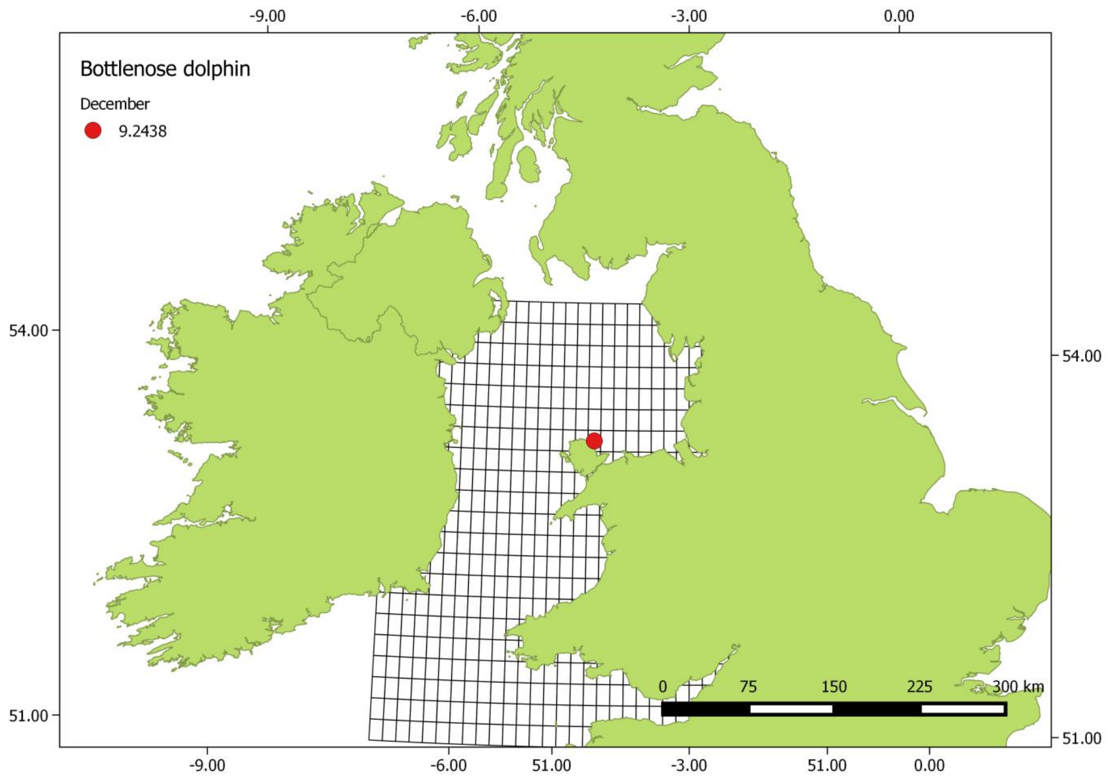


Figure 83. Map of bottlenose dolphin density (count per km) corrected for effort in December

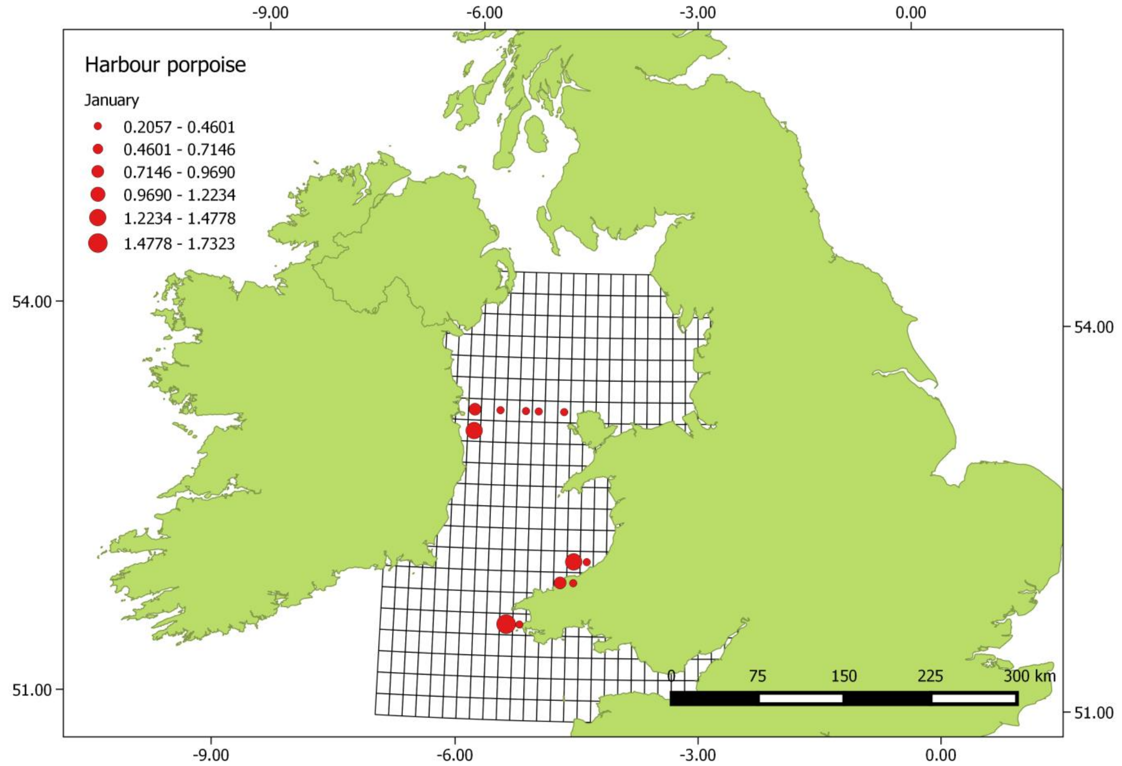


Figure 84. Map of harbour porpoise density (count per km) corrected for effort in January

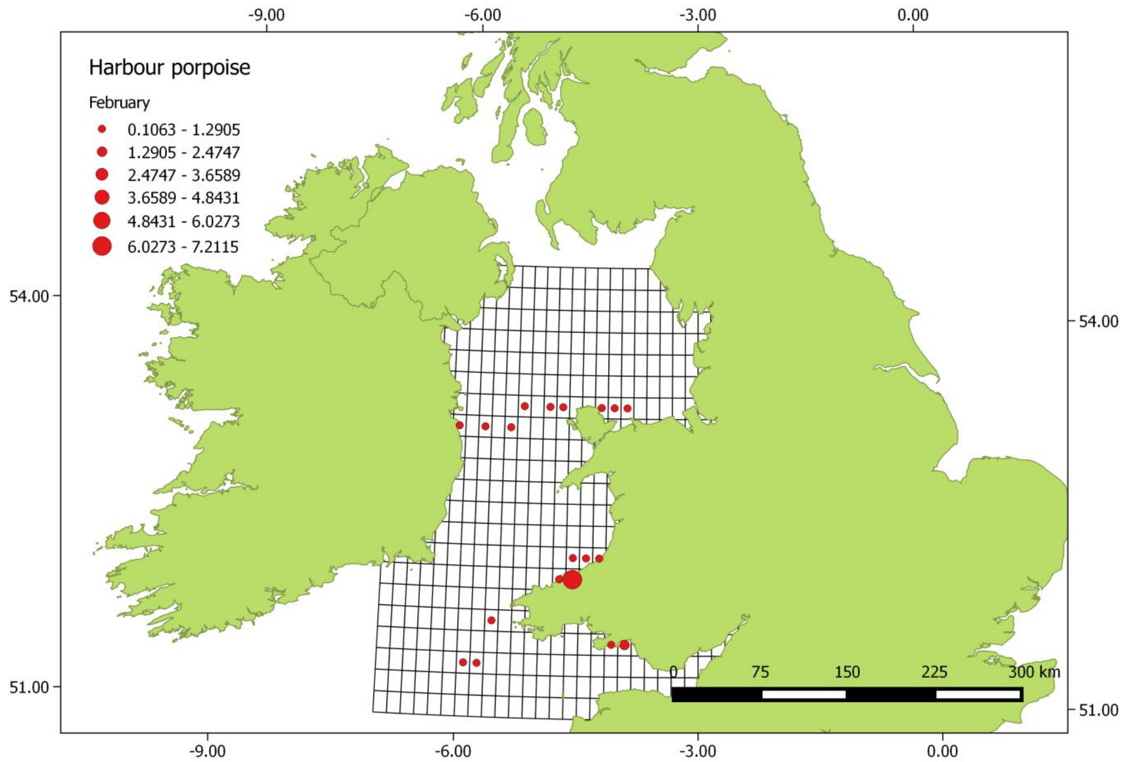


Figure 85. Map of harbour porpoise density (count per km) corrected for effort in February

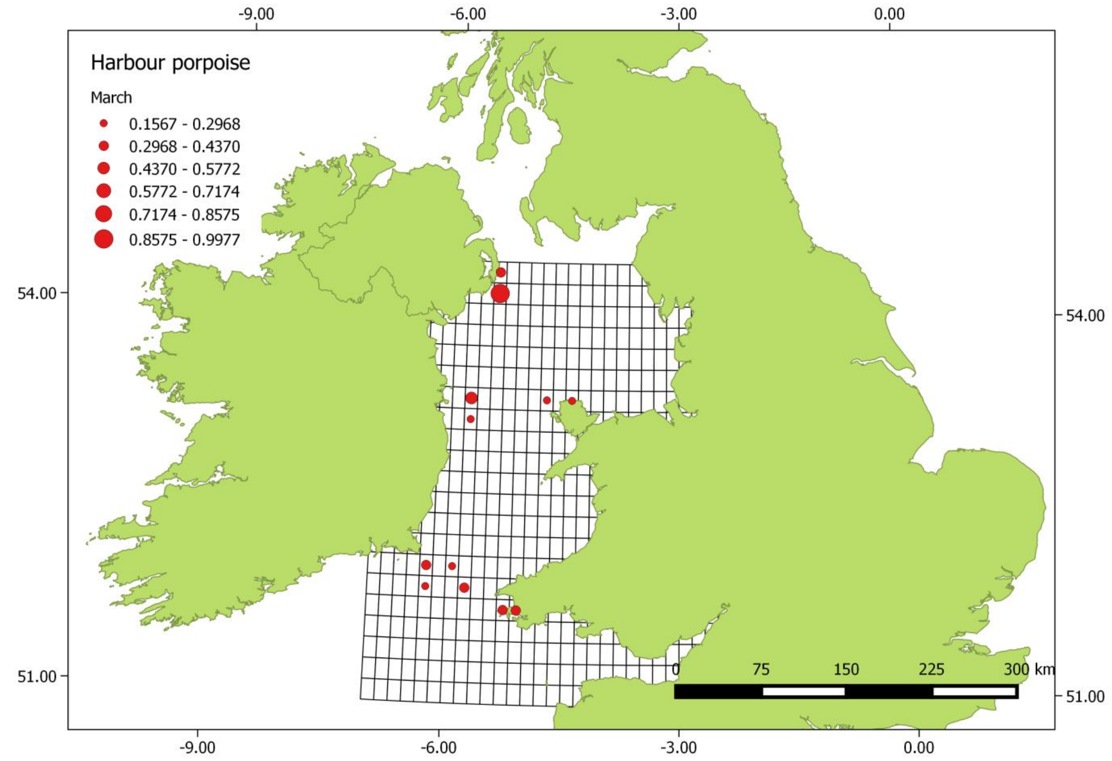


Figure 86. Map of harbour porpoise density (count per km) corrected for effort in March

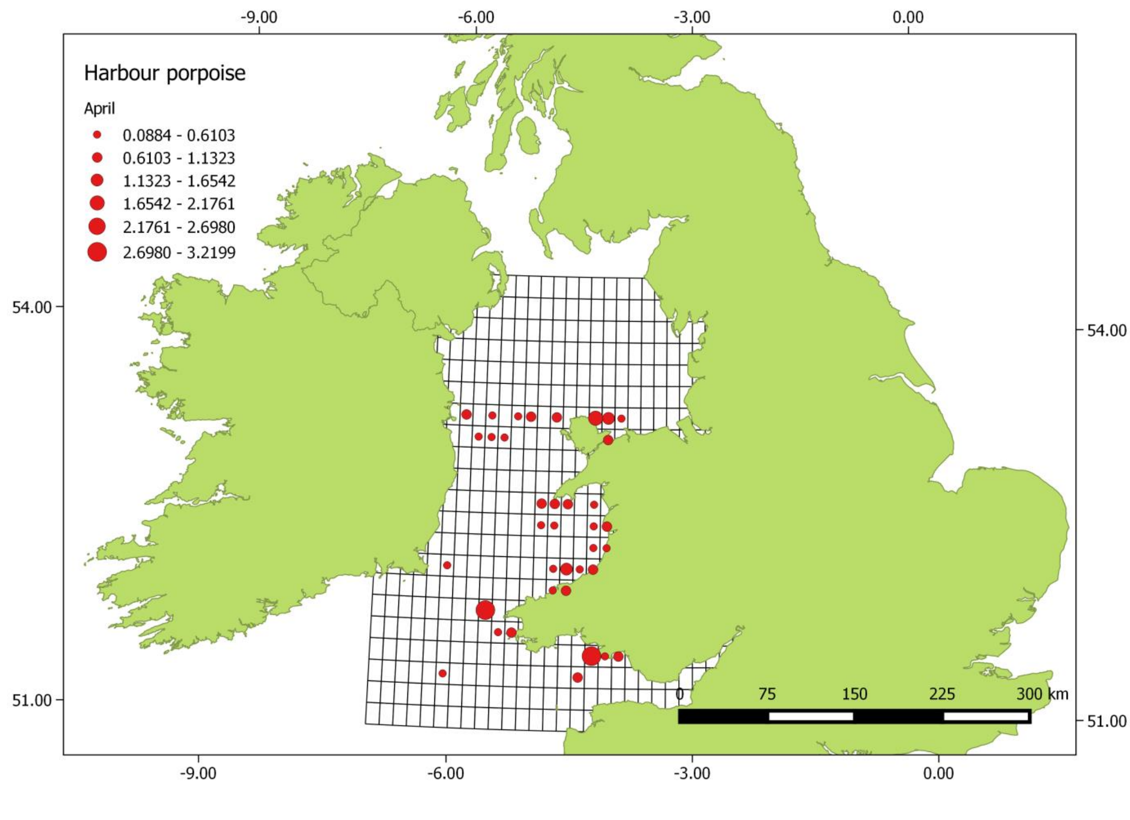


Figure 87. Map of harbour porpoise density (count per km) corrected for effort in April

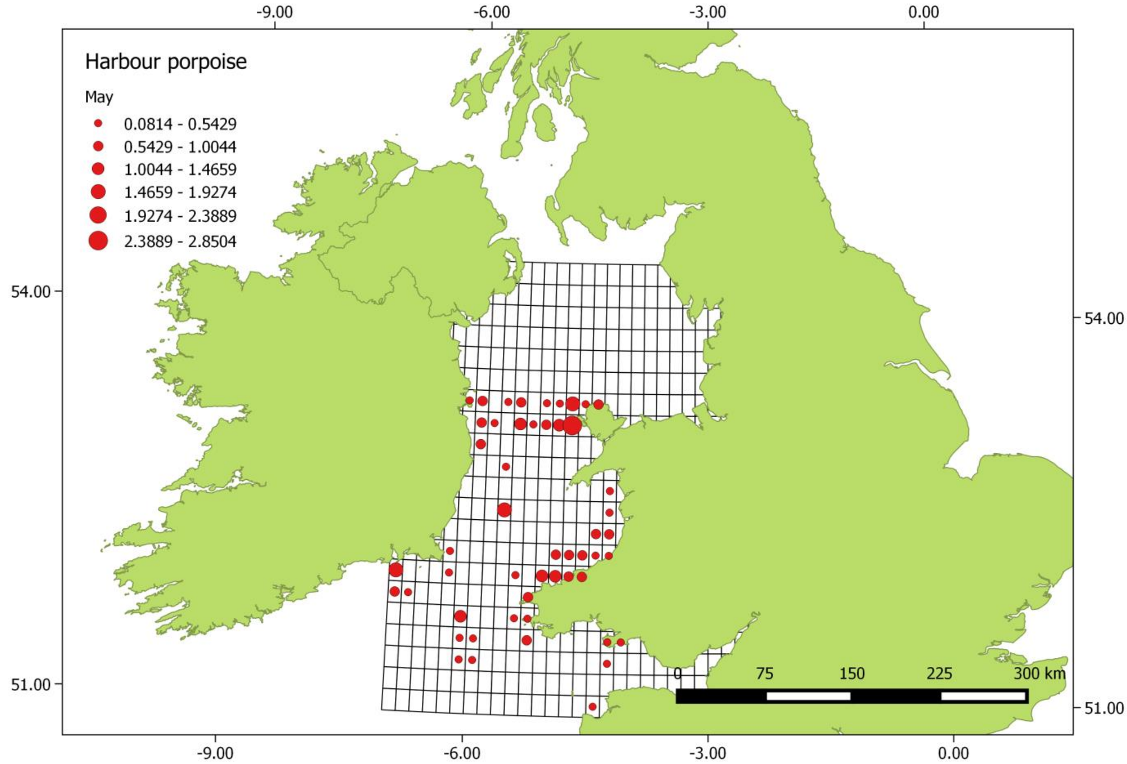


Figure 88. Map of harbour porpoise density (count per km) corrected for effort in May

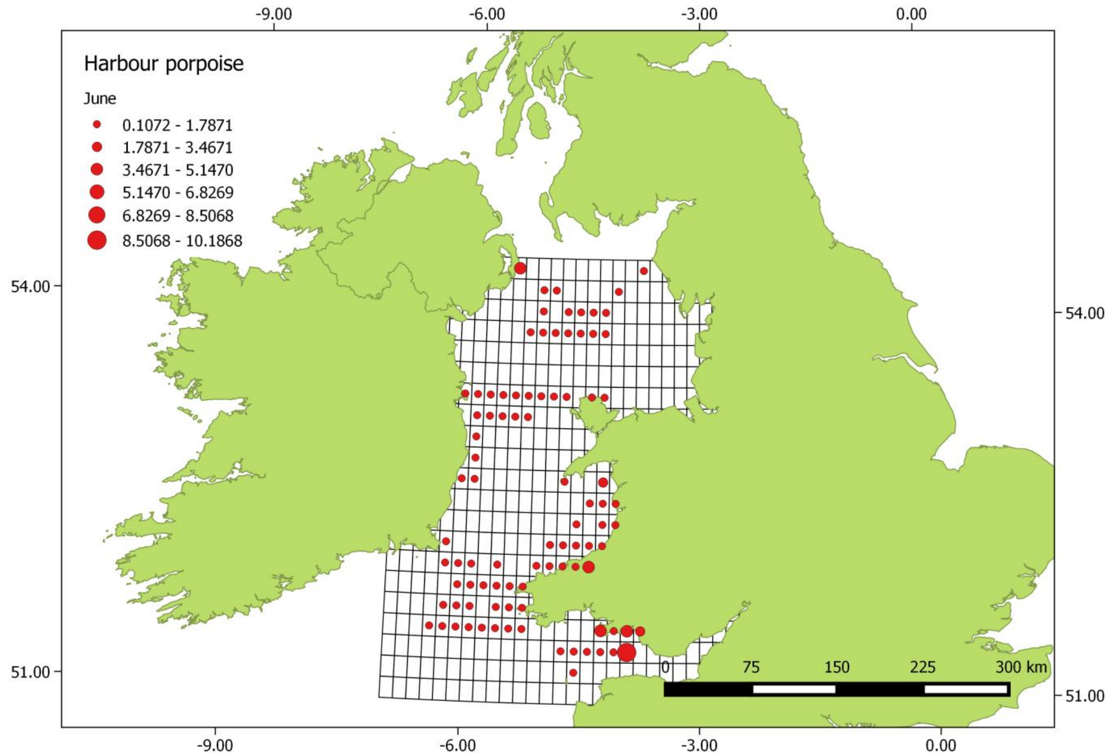


Figure 89. Map of harbour porpoise density (count per km) corrected for effort in June

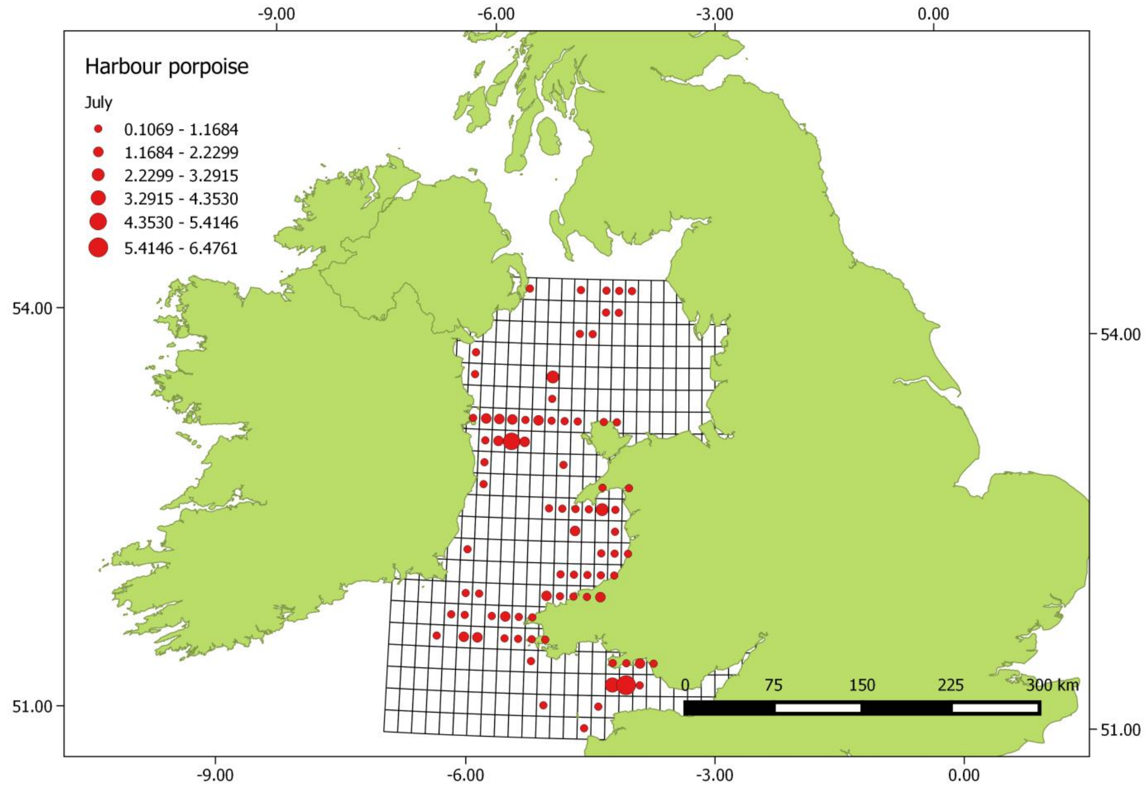


Figure 90. Map of harbour porpoise density (count per km) corrected for effort in July

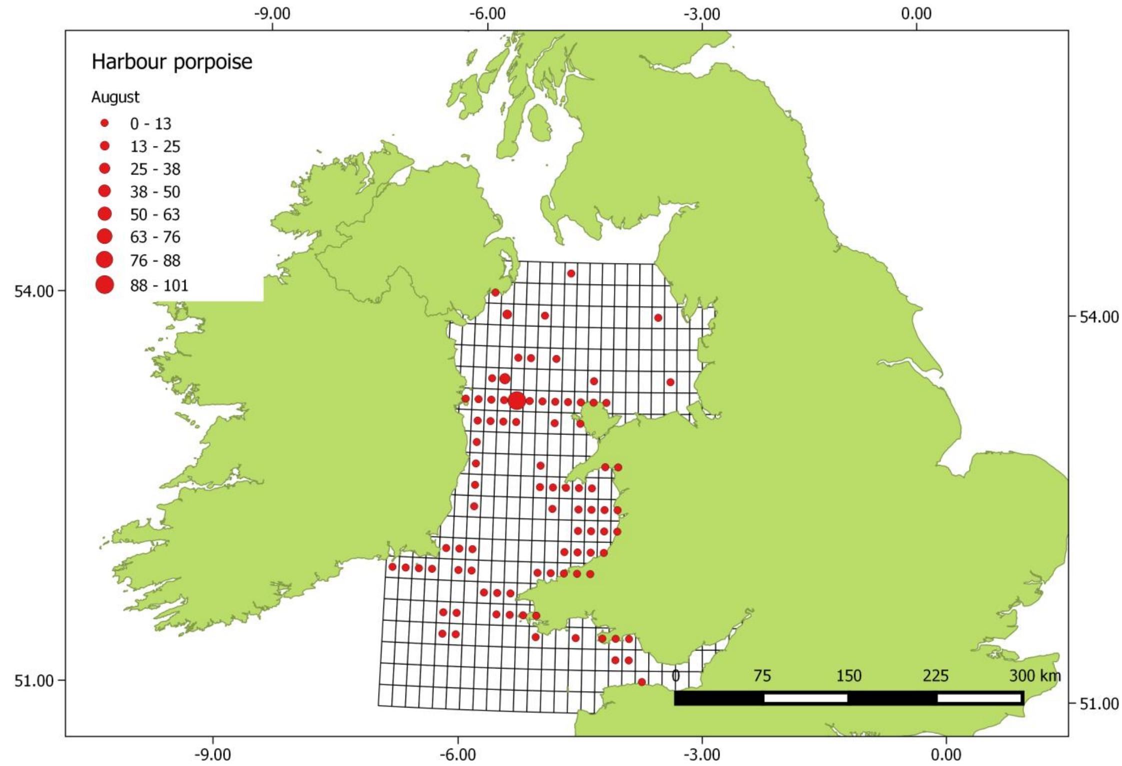


Figure 91. Map of harbour porpoise density (count per km) corrected for effort in August

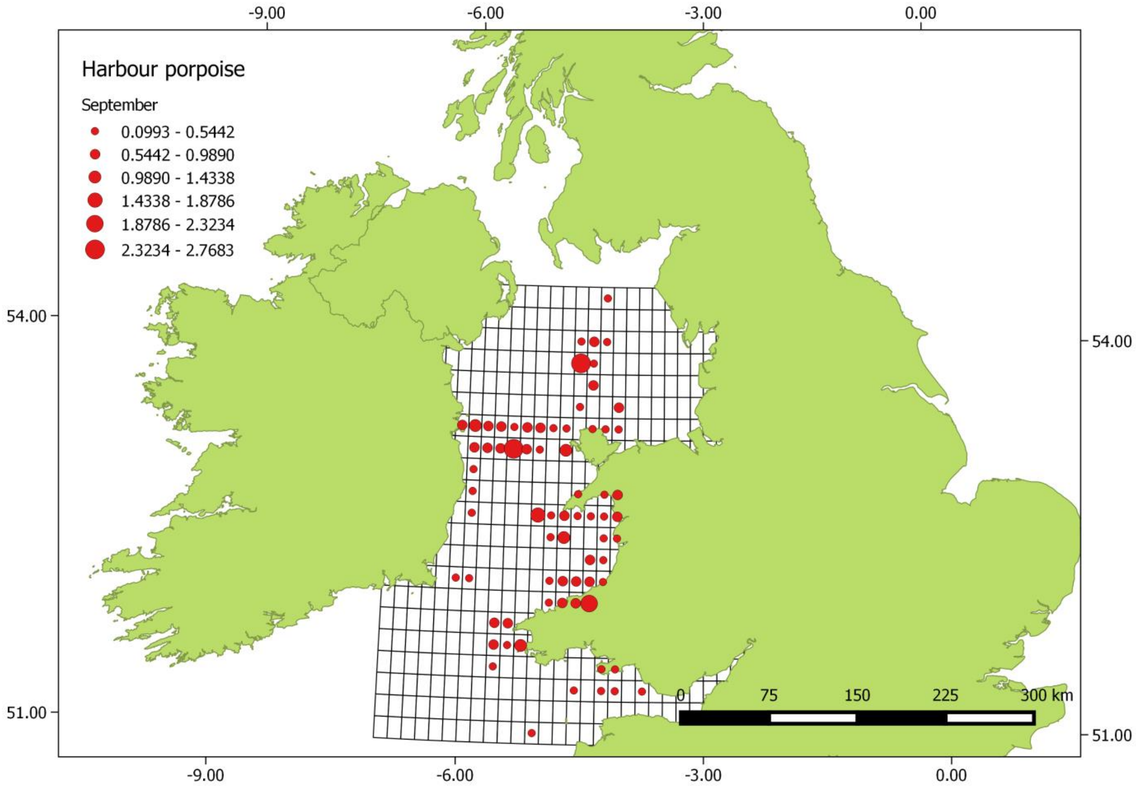


Figure 92. Map of harbour porpoise density (count per km) corrected for effort in September

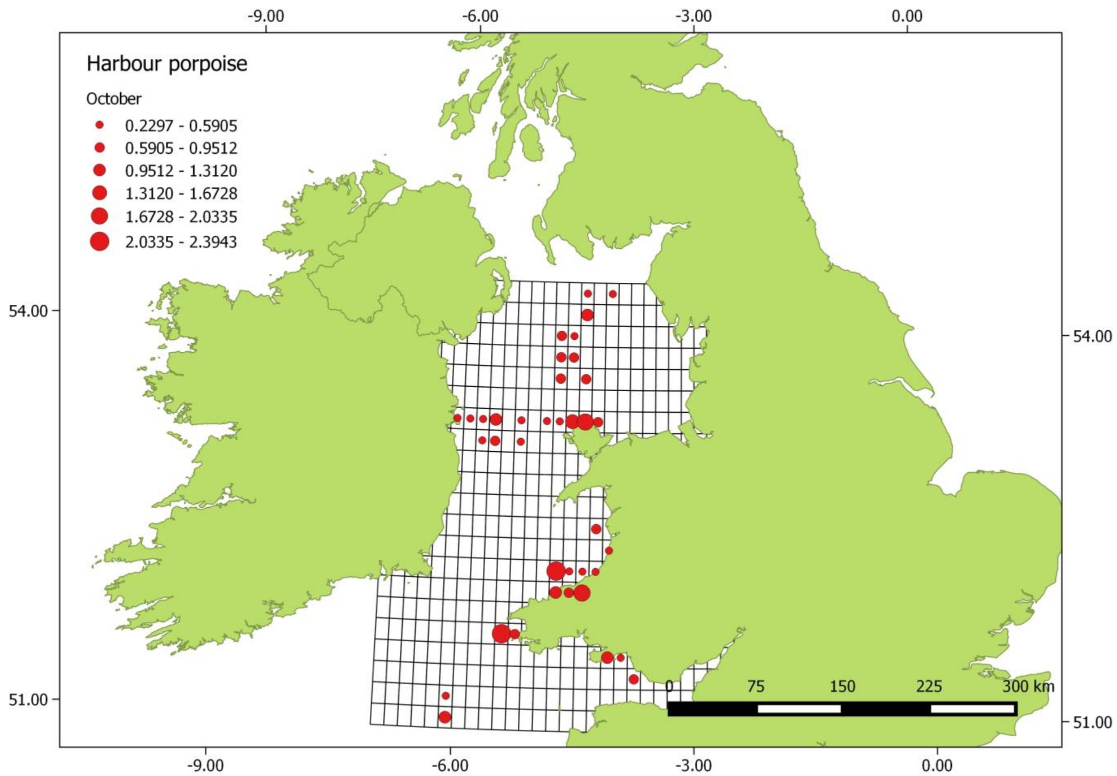


Figure 93. Map of harbour porpoise density (count per km) corrected for effort in October

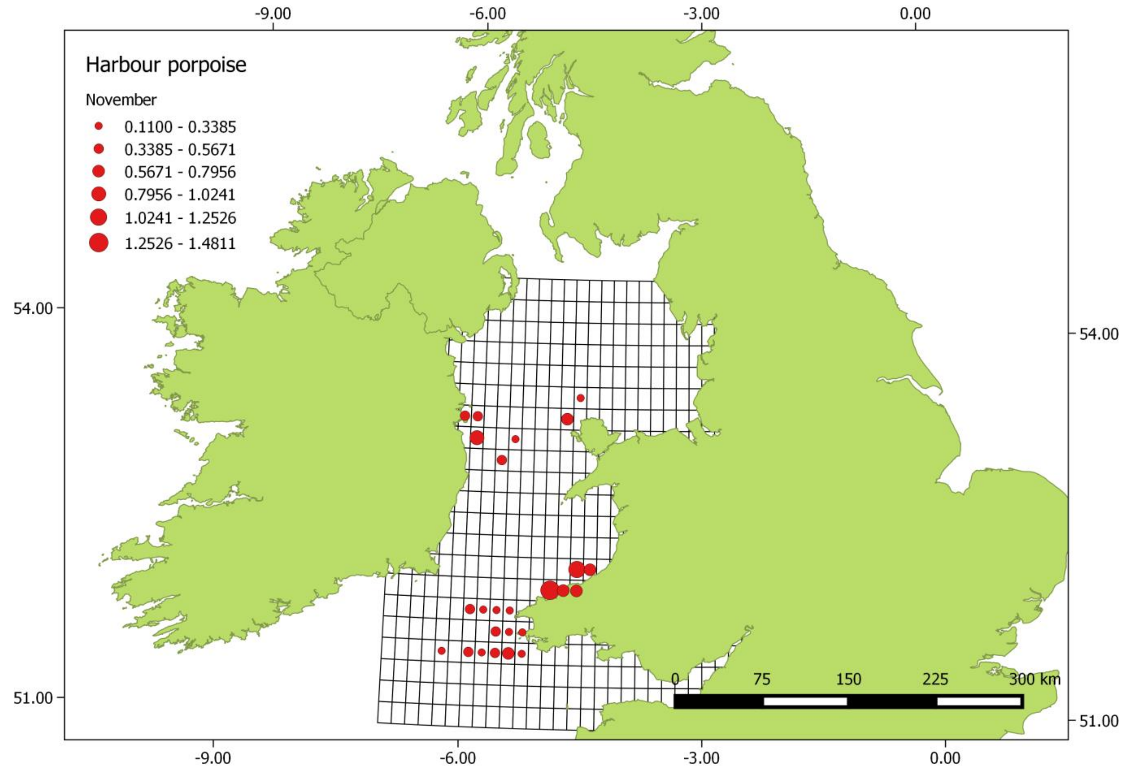


Figure 94. Map of harbour porpoise density (count per km) corrected for effort in November

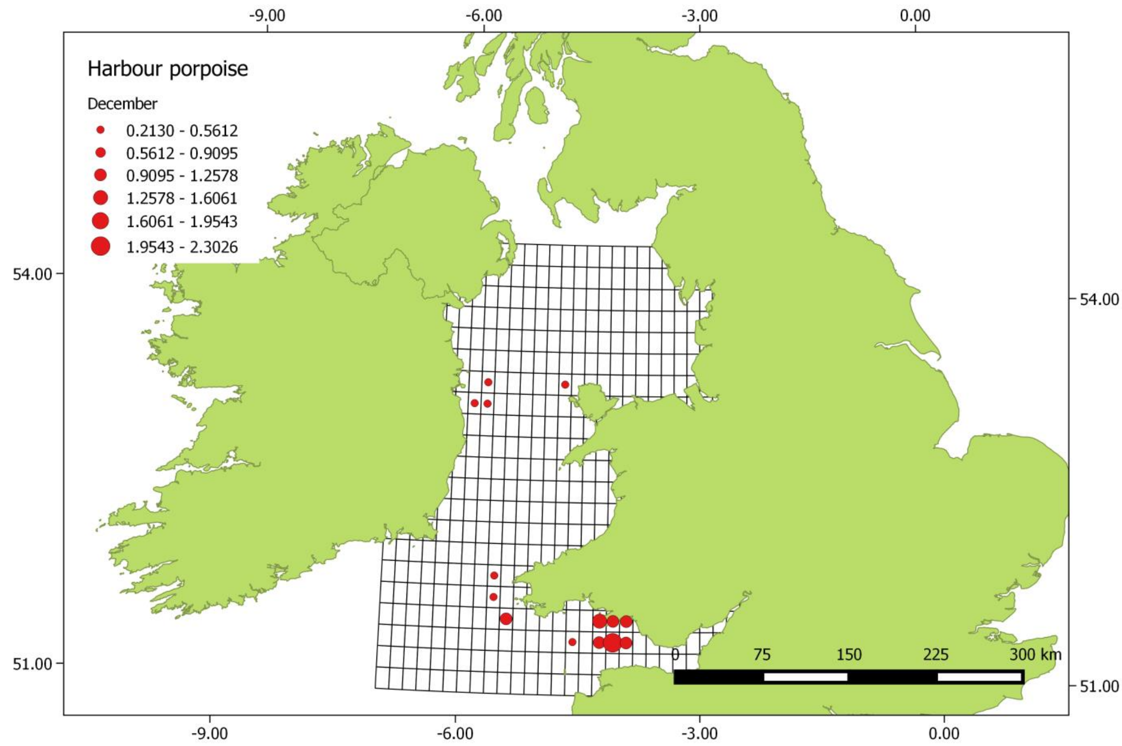


Figure 95. Map of harbour porpoise density (count per km) corrected for effort in December

7.6 Co-occurrence (overlap) maps

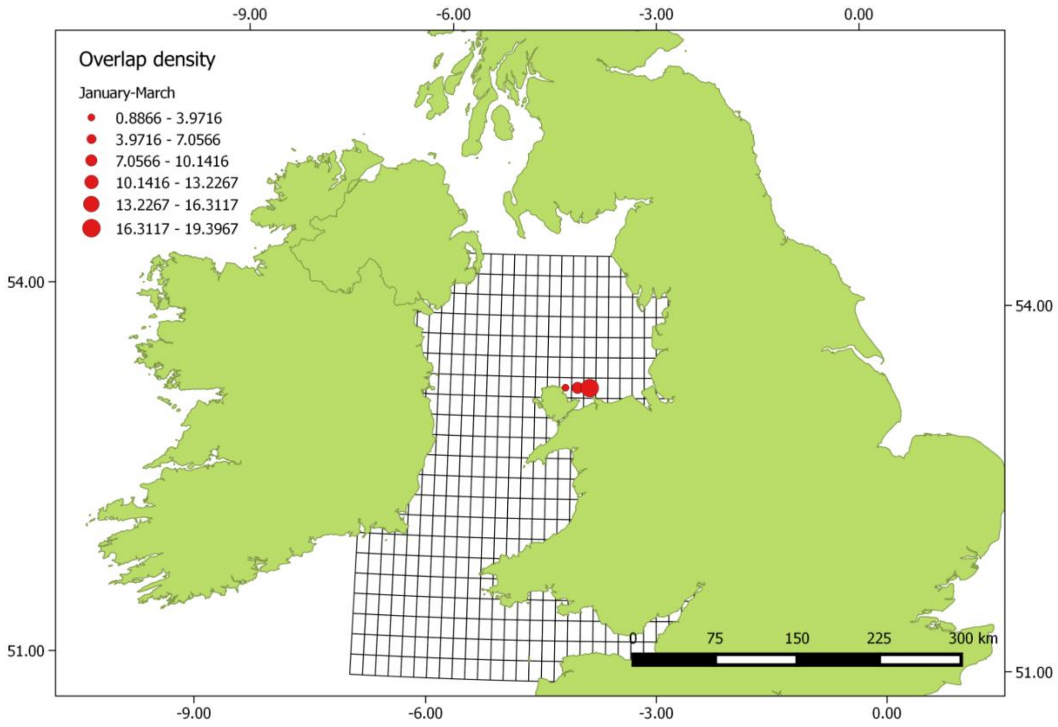


Figure 96. Map of overlap density (count per km) corrected for effort in January-March

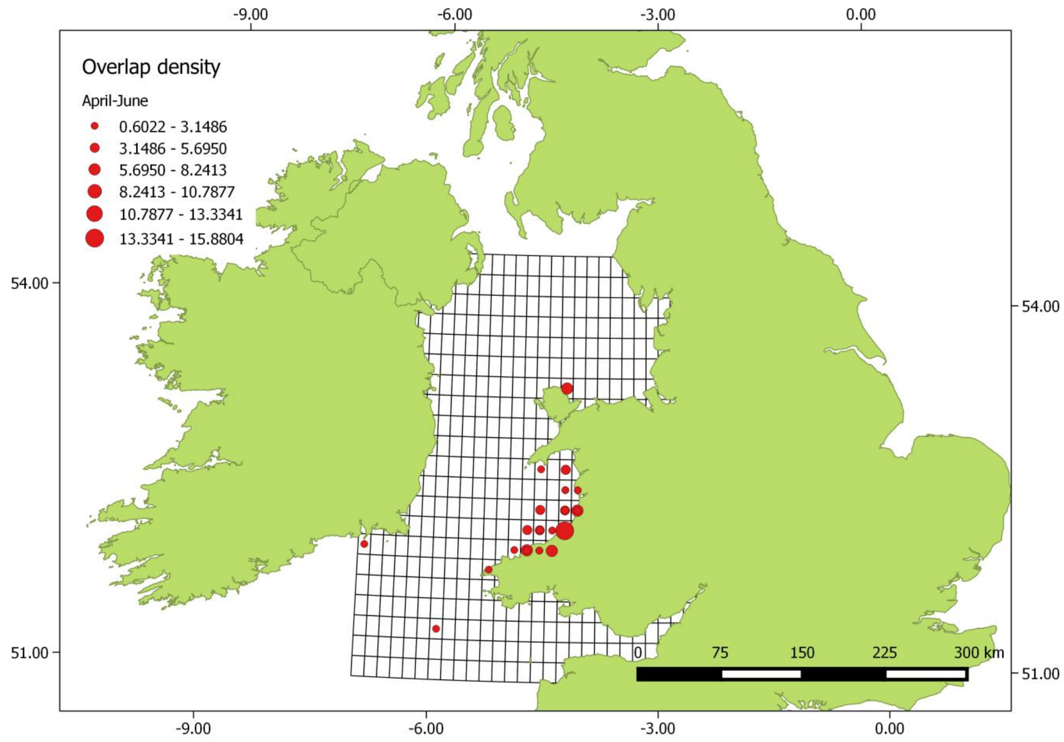


Figure 97. Map of overlap density (count per km) corrected for effort in April-June

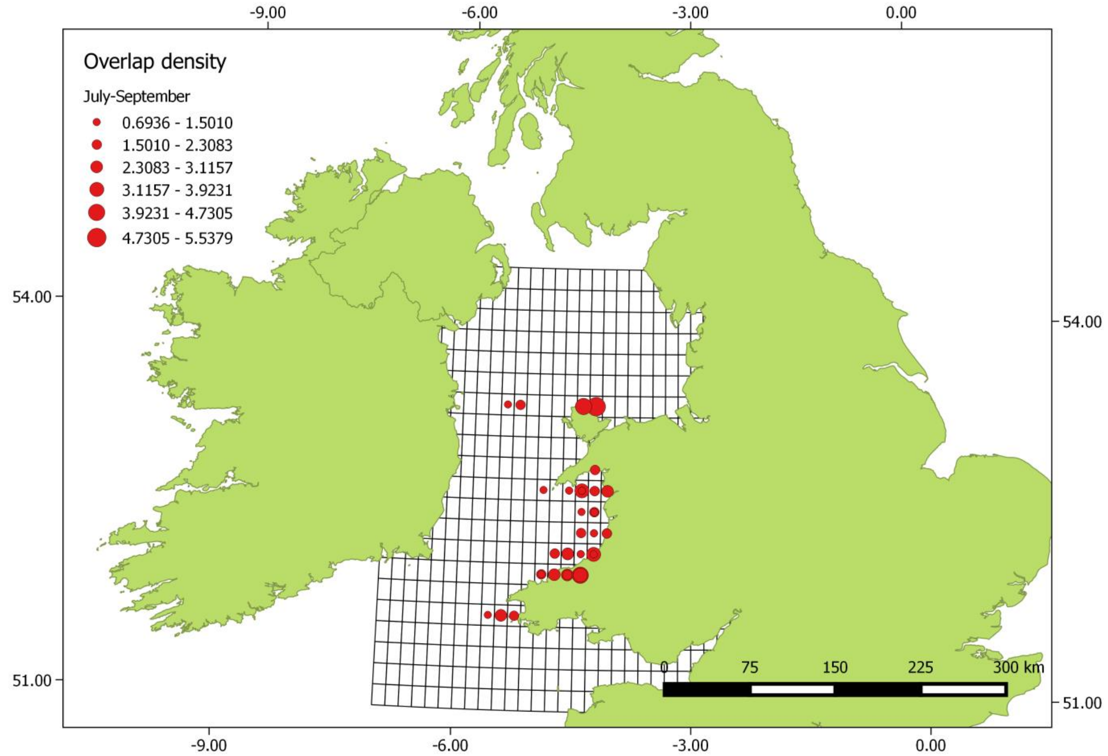


Figure 98. Map of overlap density (count per km) corrected for effort in July-September

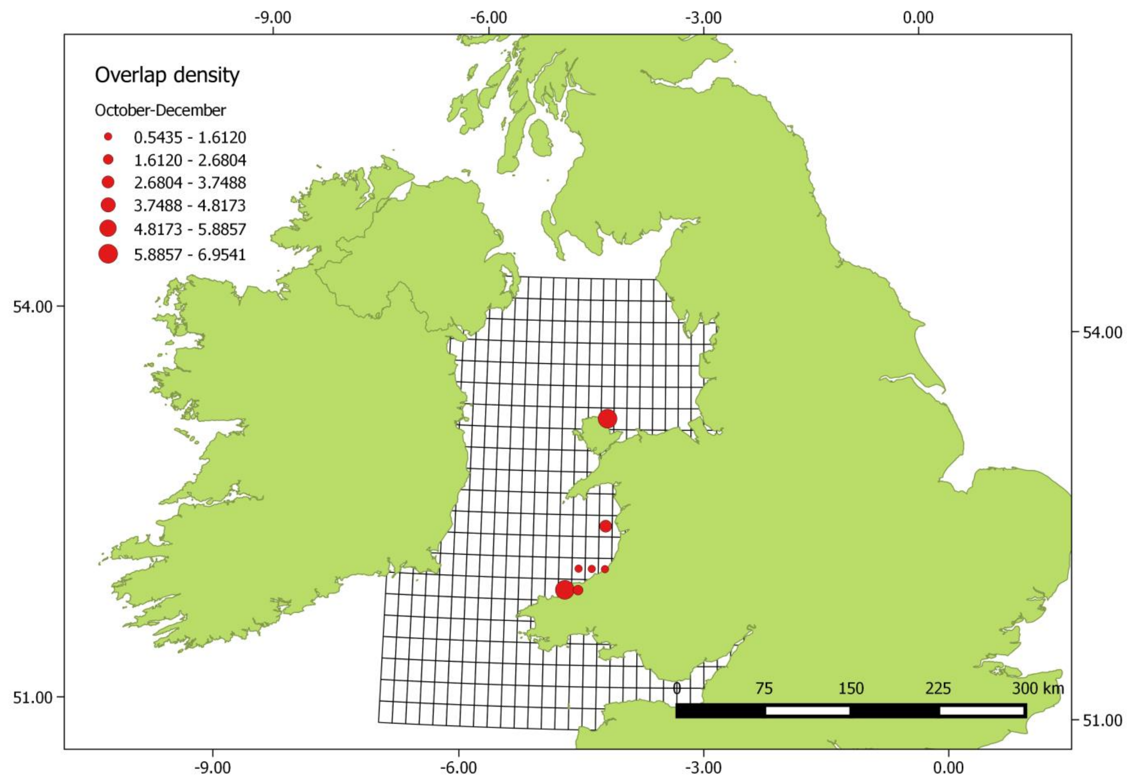


Figure 99. Map of overlap density (count per km) corrected for effort in October-December

8. Appendix 2

R script used to run GLMM

```
sfe<-read.csv("data_for_analysis2.csv", header=T)

names(sfe)

head(sfe)

table(sfe$stranding)

sfe[sfe == "-1" ] = NA

sfe<-subset(sfe,effort!="NA")

sfe<-subset(sfe,id!="NA")

sfe$bnd_group[is.na(sfe$bnd_group)] <- 0

sfe$hp_group[is.na(sfe$hp_group)] <- 0

sfe$bnd_dens<-sfe$bnd_group/sfe$effort

sfe$hp_dens<-sfe$hp_group/sfe$effort

sfe$ratio2<-sfe$bnd_dens/sfe$hp_dens

summary(sfe)

sfe$ratio2[is.na(sfe$ratio2)] <- 0

sfe$overlap[is.na(sfe$overlap)] <- 0

sfe$Ammodytidae[is.na(sfe$Ammodytidae)] <- 0

sfe$group_ratio<-sfe$bnd_group/sfe$hp_group

sfe$group_ratio[is.na(sfe$group_ratio)] <- 0

str(sfe)

panel.cor <- function(x, y, digits = 2, prefix = "", cex.cor, ...)

{
```

```
  usr <- par("usr"); on.exit(par(usr))
  par(usr = c(0, 1, 0, 1))
  r <- abs(cor(x, y))
  txt <- format(c(r, 0.123456789), digits = digits)[1]
  txt <- paste0(prefix, txt)
  if(missing(cex.cor)) cex.cor <- 0.8/strwidth(txt)
  text(0.5, 0.5, txt, cex = cex.cor * r)
}
pairs(sfe[7:22], lower.panel = panel.smooth, upper.panel = panel.cor)
str(sfe)
library(nlme)
summary(sfe)
#sfe$Total_scaled<-sfe$Total_fish/10000
#sfe$year_new<-sfe$year-2000
sfe$fmonth<-as.factor(sfe$month)
library(AICcmodavg)
Cand.models <- list( )
Cand.models[[1]]<-lme(stranding ~ overlap + year + bnd_group + Total_fish,  random=~1|cell, method="ML", data=sfe, na.action=na.omit)
Cand.models[[2]]<-lme(stranding ~ overlap + fmonth + year + bnd_group + Total_fish, random=~1|cell, method="ML", data=sfe, na.action=na.omit)
Cand.models[[3]]<-lme(stranding ~ overlap + fmonth + year + bnd_group + Ammodytidae, random=~1|cell, method="ML", data=sfe, na.action=na.omit)
```

Cand.models[[4]]<-lme(stranding ~ overlap + fmonth + year + bnd_group + Melanogrammus, random=~1|cell, method="ML", data=sfe, na.action=na.omit)

Cand.models[[5]]<-lme(stranding ~ overlap + fmonth + year + bnd_group + Merlangius, random=~1|cell, method="ML", data=sfe, na.action=na.omit)

Cand.models[[6]]<-lme(stranding ~ overlap + fmonth + year + bnd_group + Trisopterus, random=~1|cell, method="ML", data=sfe, na.action=na.omit)

Cand.models[[7]]<-lme(stranding ~ overlap + year + bnd_group + Ammodytidae, random=~1|cell, method="ML", data=sfe, na.action=na.omit)

Cand.models[[8]]<-lme(stranding ~ overlap + year + bnd_group + Melanogrammus, random=~1|cell, method="ML", data=sfe, na.action=na.omit)

Cand.models[[9]]<-lme(stranding ~ overlap + year + bnd_group + Merlangius, random=~1|cell, method="ML", data=sfe, na.action=na.omit)

Cand.models[[10]]<-lme(stranding ~ overlap + year + bnd_group + Trisopterus, random=~1|cell, method="ML", data=sfe, na.action=na.omit)

Cand.models[[11]]<-lme(stranding ~ overlap + fmonth + year + bnd_group + Merlangius + overlap*Merlangius, random=~1|cell, method="ML", data=sfe, na.action=na.omit)

Cand.models[[12]]<-lme(stranding ~ overlap + fmonth + year + bnd_group + Total_fish + overlap*Total_fish, random=~1|cell, method="ML", data=sfe, na.action=na.omit)

Cand.models[[13]]<-lme(stranding ~ overlap + fmonth + year + bnd_group + Ammodytidae + overlap*Ammodytidae, random=~1|cell, method="ML", data=sfe, na.action=na.omit)

Modnames <- paste("mod", 1:length(Cand.models), sep = " ")

aictab(cand.set=Cand.models,modnames=Modnames,sort=TRUE)

summary(Cand.models[[7]])