The possible reasons for bottlenose dolphins (*Tursiops truncatus*) participating in non-predatory aggressive interactions with harbour porpoises (*Phocoena phocoena*) in Cardigan Bay, Wales

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Abstract

Between 1991 and 2011, 137 harbour porpoises (*Phocoena phocoena*) died as a result of attacks by bottlenose dolphins (*Tursiops truncatus*) in Cardigan Bay. The suggested reasons for these non-predatory aggressive interactions include: aberrant behaviour, geographic overlap, dietary overlap, object-oriented play for infanticide practice or for fighting practice, elevated testosterone levels during the breeding season of bottlenose dolphins or skewed operational sex ratio of the bottlenose dolphins (the number of sexually available males relative to sexually available females).

Geographic overlap and object-oriented play for infanticide practice and fighting practice were investigated using boat survey data (2005-2011) from the Cardigan Bay Marine Wildlife Centre and strandings data (1994-2011) from the Cetacean Strandings Investigation Program. Dietary overlap was examined by reviewing literature based on stomach samples taken from the two study species located in the British Isles. The remaining factors were not investigated due to time and equipment constraints, and aberrant behaviour was dismissed, as there is widespread documentation of non-predatory aggressive behaviour between bottlenose dolphins and harbour porpoises.

Results showed that there was a minor geographic overlap; under a fifth of each speciesô area coverage, and thus it was unlikely to cause the attacks. There was a dietary overlap; although the extent of the overlap is uncertain, so dietary overlap remains a possible cause of the non-predatory aggression. Object-oriented play for infanticide practice seems to be unlikely, as only three bottlenose dolphin calves died

(with unknown cause of death) over 18 years, indicating that either infanticide is not occurring or it is extremely rare. Object-oriented play for fighting practice was supported by literature but the results were inconclusive, therefore, it is also considered a possible reason for the attacks on harbour porpoises. Further investigation is required to determine which of these possible reasons is the definitive cause of the non-predatory aggression.

Introduction

Aggression is determined as any overt behaviour that produces repellent or harmful stimuli or physical injury to another organism (Olivier & Young, 2002). Often it results in resolving status, priority, or access to an object or a space (Hinde, 1970). Animal aggression is commonly categorized into two types: offensive or defensive, each type is associated with different areas of the brain: defensive aggression involves the amygdala and medial hypothalamus whereas offensive aggression is linked to the medial amygdala, the orbital prefrontal, and the anterior and fronto-medial hypothalamus. If an animal initiates intentional harm to another organism it is exhibiting offensive behaviour, this includes territorial aggression and inter-male aggression. In contrast, an animal inflicting harm as a response to a threat is behaving defensively, such as maternal aggression and fear-induced aggression. (Vitiello & Stoff, 1997). Predatory aggression is usually classified separately from offensive and defensive aggression, as it appears to be predominantly determined by appetite mechanisms (associated with the lateral hypothalamus), linking to a different brain system (Olivier & Young, 2002). Offensive and defensive behaviour can thus be classified as non-predatory aggressive behaviour. Non-predatory and predatory aggression are found extensively throughout the animal kingdom: predatory aggression occurs inter-specifically and non-predatory aggression takes place inter and intra-specifically.

There is widespread documentation of aggressive non-predatory interactions that occur between sympatric species of odontoceti (Shane, 1995; Orr & Harwood, 1998; Wedekin et al., 2004). A majority of aggressive non-predatory interactions among odontoceti interactions involve bottlenose dolphins (*Tursiops truncatus*), which are

one of the few odontoceti known to direct lethal, non-predatory aggression on other members of this suborder (Connor et al., 2000). Bottlenose dolphins have been reported to interact aggressively with estuarine dolphins (*Sotalia guianensis*), Atlantic spotted dolphins (*Stenella frontalis*), short-beaked common dolphins (*Delphinus delphis*), harbour porpoises (*Phocoena phocoena*), striped dolphins (*Stenella coeruleoalba*), juvenile long-finned pilot whales (*Globicephala melas*), and Rissoôs dolphins (*Grampus griseus*) (Barnett et al., 2009; Cotter et al., 2012). There have also been recordings of bottlenose dolphins committing infanticide in Scotland (Patterson et al., 1998) and on the East Coast of the United States (Dunn et al., 2002).

Bottlenose dolphin attacks on harbour porpoises are commonly recorded on the East and West coasts of the Unites States (Cotter et al., 2012) and along the United Kingdom coastline: North east Scotland (Ross & Wilson, 1996; Patterson et al., 1998), Wales and South-western England (Jepson & Baker, 1998). There have been very few direct observations of these attacks, and even fewer have officially been documented e.g. Ross & Wilson (1996), thus there is limited data on the factors influencing the attacks. Most of the evidence of bottlenose dolphins attacks on harbour porpoises is obtained through post-mortem investigations of stranded harbour porpoises. This means that there is potentially a far greater number of aggressive interactions between bottlenose dolphins and harbour porpoises, than is represented by current data.

From the few direct observations that have been recorded it appears that often more than one dolphin is involved in the attack of a harbour porpoise. During such attacks the dolphins exhibit aggressive behaviours including sandwiching (trapping the porpoise between two dolphins), drowning, tossing and ramming (Cotter et al., 2012).

The injuries sustained from these behaviours are often fatal or may reduce the longevity of the animal: rake and bite marks, haemorrhagic cavities, skeletal fractures, and damaged internal organs.

The purpose of this investigation is to examine why the attacks by bottlenose dolphins on harbour porpoises occur. The reasons for these non-predatory aggressive interactions remain unclear and may be due to a number of complex factors. The primary issue is that there are a limited number of documented observations of the aggressive interactions and thus there is a lack of information about the dolphins and porpoises involved in these attacks, which is key to understanding why the bottlenose dolphins attack the harbour porpoises. The existence of both harbour porpoises and bottlenose dolphins in Cardigan Bay and the documented evidence of attacks (137 harbour porpoise deaths due to bottlenose dolphins between 1991 and 2011 recorded by the Cetacean Strandings Investigation Programme on the Welsh coastline) and the historical data associated with the co-existence of these different species (from the Cardigan Bay Marine Wildlife Centre database) provide a sufficient body of data to investigate the possible reasons for these aggressive interactions within Cardigan Bay.

In various literature a number of reasons for attacks on harbour porpoises by bottlenose dolphins have been proposed, these include: aberrant behaviour (this is unlikely due to widespread documentation of similar behaviours- Cotter et al., 2012), inter-species territoriality (Sekiguchi, 1995; Spitz et al., 2006), involving competitive behaviour caused by geographic and dietary overlap (evidence of dietary overlap and lack of geographic overlap), object-oriented play either for infanticide practice

(Patterson et al., 1998; Ross & Wilson, 1996; Jepson & Baker, 1998) or fighting practice, elevated testosterone levels of male bottlenose dolphins during the breeding season (Higgins & Tedman, 1990; Rose et al., 1991), and any skewed operational sex ratio (Le Boeuf & Campagna, 1994), which is the number of sexually available males relative to sexually available females.

Bottlenose dolphins have been documented directing non-predatory aggressive behaviour towards harbour porpoises and other cetacean species in many locations (Ross & Wilson, 1996; Jepson & Baker, 1998; Dunn et al., 2002; Wedekin et al., 2004), dismissing aberrant behaviour as a potential cause of the attacks on harbour porpoises in Cardigan Bay.

Sekiguchi (1995) found evidence of aggressive interactions between bottlenose dolphins and harbour porpoises occurring when harbour porpoise population densities were highest within their geographic range, indicating that bottlenose dolphins may direct territorial aggression towards harbour porpoises. Spitz et al. (2006) suggested that the attacks on harbour porpoises could be attributed to competition resulting from geographic and dietary overlap. However, there is no documentation of aggressive interactions with cetacean species such as the California sea lion (*Zalophus californianus*) or the harbour seal (*Phoca vitulina*), which are in direct competition with bottlenose dolphins for food resources.

Male bottlenose dolphins may commit infanticide as a strategy to increase their individual reproductive fitness (Pusey & Packer, 1994): female bottlenose dolphins typically calve only every two to four years, but a few days after losing a calf they become receptive to males (Connor et al., 1996). It is also possible that a female will

kill another motherôs calf when resources are limited, helping reduce competition for food and thus increase her offspringôs fitness (Wolff, 1997). Patterson et al. (1998) proposed that bottlenose dolphin attacks on harbour porpoises were attributed to the small size of harbour porpoises, as they are a similar size to bottlenose dolphin calves. This hypothesis is supported by records of harbour porpoise strandings in the United Kingdom, which show that the majority of the harbour porpoises killed by bottlenose dolphins measured between 1 m and 1.5 m long (Ross & Wilson, 1996; Jepson & Baker, 1998).

Fighting amongst bottlenose dolphins is either the result of inter-sexual competition (Clutton-Brock & Parker, 1995), including sexual coercion (Smuts & Smuts, 1993), or intra-sexual competition (Cummingham & Birkhead, 1998). Male sexual aggression is the most common in the polygynous species such as bottlenose dolphins (Conner et al., 1996): males will fight one another for access to a female in order to increase their reproductive success. It is possible that harbour porpoises are used to practice fighting skills, as the bottlenose dolphins will benefit by developing their fighting skills without suffering the costs of fighting a conspecific: the small size of the harbour porpoises means that the risk of injury to the bottlenose dolphin is minimal (Cotter et al., 2012).

It has been suggested that high testosterone levels trigger the aggressive behaviour directed at harbour porpoises by the bottlenose dolphins (Higgins & Tedman, 1990; Rose et al., 1991). These high testosterone levels occur during the breeding season of the bottlenose dolphin, however, in the United Kingdom there is no evidence of seasonality in the frequency of harbour porpoise strandings related to attacks by bottlenose dolphins. Le Boeuf & Campagna (1994) suggested that a skewed male-

female sex ratio, where the number of sexually available males outnumbers the number of sexually available females, might result in increased aggression in male bottlenose dolphins due to increased frustration by low ranking or inexperienced males at the inability to acquire a mate.

In order to investigate the potential reasons for the non-predatory aggressive interactions between bottlenose dolphins and harbour porpoises in Cardigan Bay, Cetacean Strandings Investigation Programme (CSIP) records for the Welsh coastline (dating from 1994 until 2011) and Cardigan Bay Marine Wildlife Centreôs (CBMWC) boat survey data (dating from 2005 until 2011) were used.

Methods

Study species

The harbour porpoise is a small marine mammal, measuring up to a maximum of two metres in length, it is found throughout the Northern Hemisphere in temperate waters (Rogan et al., 2001). Usually harbour porpoises do not exceed 1.5 metres and the females are marginally larger than the males (Shirihai & Jarrett, 2006). The harbour porpoise is one of the most common cetaceans in northwest Europeôs shelf waters (Hammond et al., 2002); nevertheless it is a threatened species, primarily as a result of fishery by-catch (Santos & Pierce, 2003). Within shelf waters harbour porpoises are usually found near headlands, in bays, estuaries or tidal channels (Alford, 2006). They are thought to be restricted to shallower depths due to limitations in their diving abilities and their feeding habits (their prey feed and live on the sea bed) (Read, 1999). Harbour porpoises feed on non-spiny fish such as whiting, pollock, cod, herring, and sardines and also cephalopods such as squid. They consume large amounts of food relative to their size: around 10% of their body weight every day. (Bjorge & Tolley, 2008).

The common bottlenose dolphin (*Tursiops truncatus*) is a larger marine mammal than the harbour porpoise, measuring up to a maximum length of four metres; it is widely distributed, inhabiting both tropical and temperate waters (Wiley et al., 1994). Adult bottlenose dolphins usually measure between 2.5 and 3.8 m, with males being significantly larger than the females. Newborn calves, nurse for 12 to 18 months and tend to measure around 0.8 m to 1.4 m long but the calves may remain with their mothers for three to six years. (Shirihai & Jarrett, 2006). Bottlenose dolphins have an

extremely varied diet and habitat but they are often found inshore where there are deep narrow channels with steep sloping seabeds and strong tidal currents (Wells & Scott, 1999). They feed primarily on fish, and sometimes squid, and crustaceans, and can consume up to 5% of their body weight in food every day (Wells & Scott, 2002).

Study area

Cardigan Bay is one of the largest bays in the British Isles: it is an inlet of the Irish Sea with around 200km of coastline (Countryside Council for Wales, 2009). One of three resident populations of bottlenose dolphins found within British and Irish waters inhabits this coastline, the other two are found in the Shannon Estuary in south-west Ireland and the Moray Firth in north-east Scotland (Alford, 2005). Within Cardigan Bay, a Special Area of Conservation was designated (approximately 968 km^2) between Ceibwr Bay (North Pembrokeshire, and Aberarth (South Ceredigion) by the European Union Habitats and Species Directive in 2004 (Countryside Council for Wales, 2009), to protect a range of habitats and species, primarily the resident bottlenose dolphin population.

Methods of data collection

From the literature discussed in the introduction it can be established that the non-predatory aggressive interactions between bottlenose dolphins and harbour porpoises cannot be contributed to aberrant behaviour. Therefore, in this investigation no further examination was required to eliminate aberrant behaviour as a possible reason for the attacks in Cardigan Bay.

To investigate the presence of geographic overlap as a possible reason for the non-predatory aggressive interactions, the geographical distribution of each species population was identified. The Cardigan Bay Marine Wildlife Centre carried out boat-based surveys along a 90 km stretch of Cardigan Bayôs coastline (from Llan-non to Fishguard: within the Special Area of Conservation). On these boat surveys the Cardigan Bay Marine Wildlife Centre researchers recorded the distance of the animal sighted from the boat (in metres), the angle of the animal from the boat, the boat course (in degrees), and the GPS co-ordinates of the boat at the time of the sighting. This data was then used to calculate the co-ordinates of the bottlenose dolphins and harbour porpoises using equations from a Cardigan Bay Marine Wildlife Centre excel spreadsheet (see appendix). Data collected between 2005 and 2011 has been compiled to gain an accurate representation of each speciesô geographical distribution. By establishing whether there is a significant geographical overlap of the two species, the aggressive interactions could possibly be attributed to territorial behaviours.

The stomach contents of bottlenose dolphins and harbour porpoises were not recorded by the Cetacean Strandings Investigation Programme during post-mortem, except when unusual contents were discovered. Thus to investigate the presence of dietary overlap it was necessary to review past studies on each speciesô diet. Currently there is no literature on the diets of these two species specifically within the Cardigan Bay area, therefore it was necessary to review literature based on bottlenose dolphins and harbour porpoises found around the British Isles. If there is a significant dietary overlap between the two species, the attacks could potentially be attributed to competition for food.

To implicate infanticide object-oriented play as a possible cause of the non-predatory

aggressive interactions, Cetacean Strandings Investigation Programme records were assessed to investigate whether there were any bottlenose dolphin calves (measuring between 0.8 m and 2 m) found stranded in Cardigan Bay, and if there was any evidence to indicate their cause of death was an attack by a bottlenose dolphin i.e. infanticide. Evidence of infanticide occurring within the Cardigan Bay bottlenose dolphin population could suggest that the attacks on the harbour porpoises are practice for killing bottlenose dolphin calves, which are a similar size to harbour porpoises, making them a suitable target for practice.

To investigate whether practice fighting object-oriented play is a possible reason for the attacks on the harbour porpoises, Cetacean Strandings Investigation Programme records were examined to establish whether there were any adult male bottlenose dolphins (measuring more than 2.5 m long) found stranded in Cardigan Bay, and if the cause of death was identified as an attack by a conspecific. If fighting amongst male bottlenose dolphins in Cardigan Bay result in death, it is possible that male bottlenose dolphins practising their fighting skills cause the aggressive interactions with harbour porpoises, as there is minimal risk of harm.

It was not possible to investigate the operational sex ratio of the bottlenose dolphin population due to time and equipment constraints that prevented the Cardigan Bay Marine Wildlife Centre from examining the genital slits of the bottlenose dolphins, which is the accurate method of sex identification. Bottlenose dolphin breeding seasons could not be investigated as a possible reason for non-predatory aggressive reactions due to the Cetacean Strandings Investigation Programme not recording the estimated time of death of the stranded harbour porpoises: potential connections could not be drawn between the bottlenose dolphin-breeding season and the attacks on

harbour porpoises.

Due to limitations in the information obtained in data collection for the Cardigan Bay Marine Wildlife Centre and Cetacean Strandings Investigation Programme it was only possible to investigate geographical distribution, dietary overlap and object-oriented play as possible reasons for the non-predatory aggressive interactions between bottlenose dolphins and harbour porpoises.

Methods of data analysis

A Geographic Information System program called ArcMap was used to plot the co-ordinates of the bottlenose dolphin and harbour porpoise sightings onto a map of the Cardigan Bay coastline, generating a visual representation of the geographical distributions of the two species. Any plots that resided on land or outside of the survey area were noted and erased from the data set. To provide the proportion of the overlap of the two speciesô populations, a statistical computing program called R was used, which took the Cardigan Bay Marine Wildlife Centre co-ordinates of the two speciesô populations and calculated the proportion of the area coverage of the harbour porpoise sightings that overlapped with the area coverage of the bottlenose dolphin sightings and vice versa. In the investigation of dietary overlap, literature was reviewed and no further analysis was required. The Cetacean Strandings Investigation Programme bottlenose dolphin strandings were examined and charts were composed to assess whether there was any evidence of infanticide or fighting.

Results

Geographical distribution

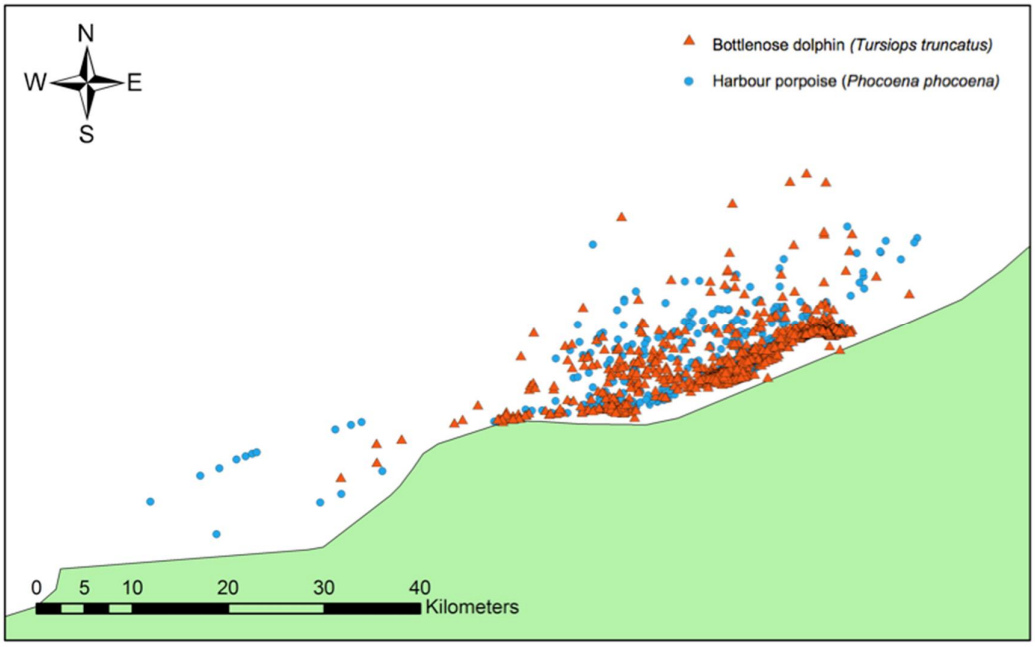

Figure 1. The geographical distribution of harbour porpoise and bottlenose dolphin sightings between Llan-non and Fishguard plotted using ArcMap.

In figure 1 it can be seen that there is an overlap between the bottlenose dolphin and harbour porpoise sightings. The harbour porpoises appear to be more sparsely distributed than the bottlenose dolphins, which is supported by the area coverage of each species (calculated using the R statistical program): harbour porpoises were distributed across 31.71 km^2 of ocean and the bottlenose dolphins were sighted across 26.71 km^2. The bottlenose dolphin sightings seem to cluster closer to the shore, whereas the harbour porpoises appear to be located further from the shore. There is a small portion of each speciesô sightings which overlapped with one another: 17.95% of the bottlenose dolphin sightings overlapped with the harbour porpoises, and 14.64% of the harbour porpoise sightings overlapped with the bottlenose dolphins.

There are also a greater number of bottlenose dolphin sightings than harbour porpoise sightings (2288: 505).

Object-oriented play

Of the 38 bottlenose dolphin strandings recorded by Cetacean Strandings Investigation Programme (between 1994 and 2011), only four were suitable for post-mortem. The cause of death was established in three out of four of the post-mortems: two dolphins died from a generalized bacterial infection, one dolphin died due to trauma resulting from by-catch, and one dolphinôs cause of death could not be established. Overall there are 35 bottlenose dolphin strandings with an unknown cause of death (34 of these were too decomposed to enable a post-mortem). There appears to be a relatively small number of bottlenose dolphin strandings compared to that of harbour porpoise strandings (136 harbour porpoise strandings caused by bottlenose dolphin attacks out of 1428 total harbour porpoise strandings between 1994 and 2011). As cause of death is unknown for the 35 bottlenose strandings it is possible that some of the bottlenose dolphins died due to conspecific attacks. Therefore the sex and length of the 35 stranded bottlenose dolphins were assessed to find any possible indication of infanticide (strandings of bottlenose dolphins measuring 0.8-2.4 m) or fighting (strandings of bottlenose dolphins measuring more than 2.4 m and that are male).

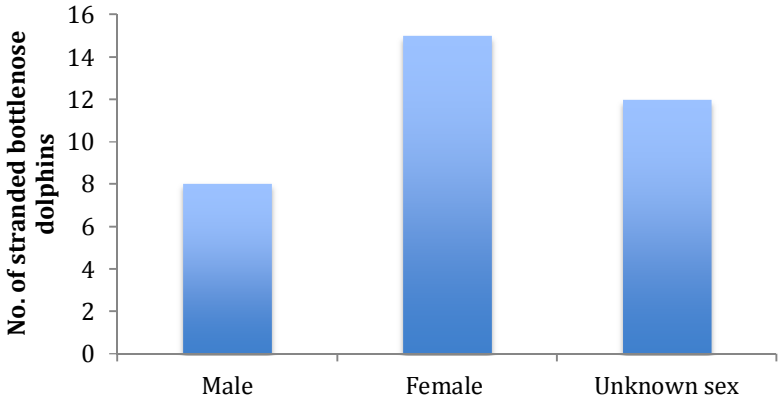

Figure 2. The frequency distribution of the sexes of bottlenose dolphin found stranded (with an unknown cause of death) in Cardigan Bay between 1994 and 2011.

Figure 2 shows that out of the strandings for which sex was identified there is a greater frequency of female bottlenose dolphins found stranded (65% of sex identified bottlenose strandings and 43% of total strandings) than males (35% of sex identified bottlenose dolphin strandings and 23% of total strandings). However, 34% of the total strandings did not have their sex identified.

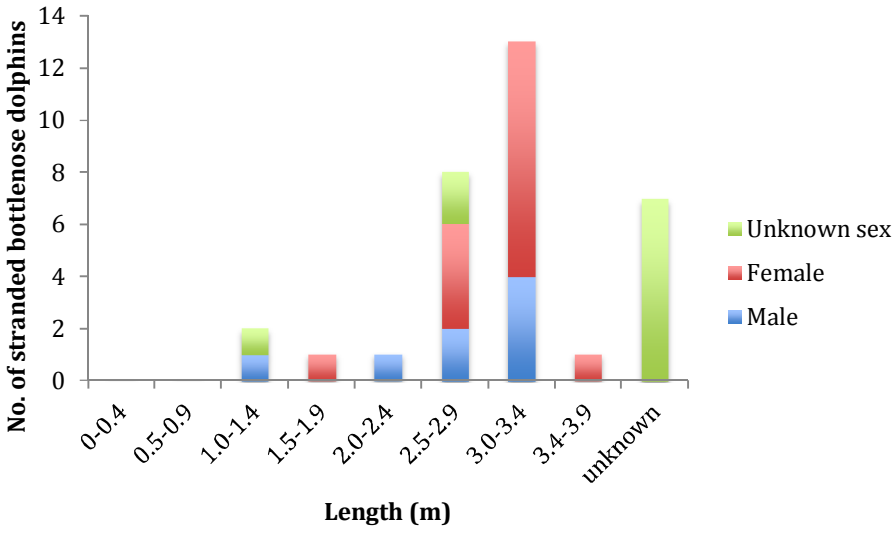

Figure 3. The length frequency distribution of bottlenose dolphin strandings (with an unknown cause of death) found in Cardigan Bay between 1994 and 2011.

Figure 3 shows the number of strandings that measured within certain size categories. 8% of the bottlenose dolphin strandings appear to fall within the 1 m to 1.9 m size range. The majority of the bottlenose strandings (72%) measure between 2 m and 3.9 m. The remaining 20% were not given a measurement. Seven out of the eight male bottlenose strandings measured within the 2 m to 3.4 m size range, a narrower size range, and the sizes were smaller compared to the 14 of the 15 female bottlenose strandings that measured between 2.5 m and 3.9 m.

Discussion

Geographical distribution

The results show that there is an overlap between the bottlenose dolphin and harbour porpoise sightings, however, the overlap comprises only a small proportion (under a fifth) of area coverage of each speciesô sightings. The calculation of the overlap using the R statistical computing program did not address the times of the sightings; therefore the overlap of the two species is possibly even smaller than is represented in the results. For example, a bottlenose dolphin may have been sighted at the same location but at a different time to a harbour porpoise and should not contribute to the overlap proportion. Nevertheless, the extent of the overlap between the two species does not seem great enough to cause the bottlenose dolphins to direct territorial aggression towards harbour porpoises.

The harbour porpoises have greater area coverage than bottlenose dolphins, despite there being a larger number of bottlenose dolphin sightings: the bottlenose dolphin sightings are clustered around shallower depths (demonstrated by ArcMap plots closer to the shore), and the harbour porpoises are mostly found at deeper depths (demonstrated by ArcMap plots located further from the shore), which is supported by various literature (Defran & Weller, 1999; Caretta et al., 2001). If the two species are usually distributed at differing depths, significant overlap between the two species is even less likely. In addition, the harbour porpoises are often solitary or are found in smalls groups, and they have small body sizes, making them a very unlikely threat to bottlenose dolphins (Cotter et al., 2012). The results and the literature seem to indicate that geographic overlap, and thus inter-species territoriality, is not a potential

cause for the non-predatory aggressive interactions between bottlenose dolphins and harbour porpoises.

Object-oriented play

There was a low number of bottlenose dolphin strandings between 1994 and 2011, especially in comparison to the number of harbour porpoise strandings. It is very unlikely that all of the bottlenose dolphin deaths can be attributed to attacks by conspecifics, thus the number of possible deaths caused by bottlenose dolphin attacks may be very low or none at all. The bottlenose dolphin strandings from the Cetacean Strandings Investigation Programme are the only indicators of potential infanticide or fighting occurring within the bottlenose dolphin population in Cardigan Bay, due to the lack of documented direct observations. Nevertheless, these strandings may be a poor representation of bottlenose dolphin deaths as it is possible there are many dolphin carcasses that have not been discovered and documented. Unfortunately, all but four of the 38 bottlenose dolphin strandings were unsuitable for post-mortem and thus did not have their cause of death identified. Due to this limitation, all of the bottlenose dolphins with unknown cause of death were considered in the investigation for potential object-oriented play: any calf or adult male deaths were considered as possible victims of infanticide or fighting.

It was found that only three of the strandings were calves and the majority (24) were adults. The three calves could have died from a number of causes including trauma from by-catch and generalised bacterial infection (the causes of death in three of the necropsied stranded bottlenose dolphins). However, if the deaths of the calves were the result of infanticide, it would appear to occur very rarely as only three calves were

found stranded over 18 years. In comparison, Patterson et al. (1998) documented five bottlenose dolphin calf deaths caused by infanticide over six years in Moray Firth, and Dunn et al. (2002) recorded nine over two years in the western North Atlantic. Despite there being evidence of infanticide in bottlenose dolphin populations in the British Isles (Patterson et al., 1998) and other locations (Dunn et al., 2002), it does not appear to be likely in Cardigan Bay. Therefore, object-oriented play aimed at practising skills used in infanticidal attacks does not seem to be a potential cause of bottlenose dolphin attacks on harbour porpoises.

Results show that there was a greater number of female adult bottlenose dolphins found stranded than male adults. However, a significant proportion of the stranded adult bottlenose dolphins did not have their sex identified, meaning the sex ratio of the strandings is not accurately represented. The cause of death for 21 out of 24 of the adult strandings remained unidentified; therefore it is difficult to ascertain from this data set, whether fighting occurs amongst the bottlenose dolphins in Cardigan Bay. However, literature suggests that fighting between males is relatively common in bottlenose dolphins, especially when there is high mate competition (Conner et al., 2000; Scott et al., 2005). Limitations in the data collected have led to a lack of evidence for fighting in bottlenose dolphins in Cardigan Bay. Nevertheless, widespread documentation of inter-male fighting in bottlenose dolphins suggests that practice fighting may be a potential cause of non-predatory aggressive interactions between bottlenose dolphins and harbour porpoises.

Diet

There is scarce literature on the diets of bottlenose dolphins and harbour porpoises located within the British Isles: only three articles were reviewed (Browne, 1999; Santos et al., 2001; Santos et al., 2004). These articles documented the stomach contents of stranded bottlenose dolphins (Santos et al., 2001) and harbour porpoises (Santos et al., 2004) in Scottish waters, and of stranded harbour porpoises in the Irish Sea (Browne, 1999). After assessing all three articles it was clear that fish are the predominant food source of both species (comprising around 90% of prey species found in stomach contents). Whiting (*Merlangius merlangus*) is a major constituent of both speciesô diets (accounting for 33% to 51% of prey species). Other fish species found in both bottlenose dolphin and harbour porpoise stomachs include: sandeels (family Ammodytidae: found only in the study species located in Scottish waters: over 10% of prey species), pollack (*Pollachius pollachius* and *Pollachius virens*), and haddock (*Melanogrammus aeglefinus*). A small portion of both bottlenose dolphin and harbour porpoise diets comprised of squid and crustaceans such as shrimp.

Although there appears to be an overlap in the diets of the two species, the extent of the overlap is uncertain. Diet can also vary depending on locality (Barros & Odell, 1990): the documented stomach contents that were assessed for this investigation were sampled from the study species stranded within the British Isles but not specifically Cardigan Bay. The habitats found within Cardigan Bay may differ considerably from other locations and thus it is likely that the type and abundance of prey species may also differ. This means bottlenose dolphins and harbour porpoises in Cardigan Bay may have different diets, and therefore a differing level of dietary overlap compared to that which has been found in the literature.

In addition to dietary overlap it is important to take into consideration the type and abundance of the prey species within Cardigan Bay. If prey population numbers were low this could possibly cause intense competition for food, to the extent that bottlenose dolphins attack harbour porpoises. Cardigan Bay has a designated Special Area of Conservation and thus it is likely that the prey populations of the bottlenose dolphin and harbour porpoise are relatively stable and that food competition is not severe enough to result in attacks on harbour porpoises. In Scottish waters it has been documented that bottlenose dolphins have many prey species in common with harbour seals (*Phoca vitulina*) (Tollit & Thompson, 1996), which would suggest direct competition, yet there appears to be no records of harbour seal deaths attributed to attacks by bottlenose dolphins. This example further weakens the hypothesis that dietary overlap is a possible cause of attack on harbour porpoises.

Non-predatory aggressive interactions between bottlenose dolphins and harbour porpoises in the North Atlantic have been attributed to competition associated with the extent of geographic and dietary overlap (Spitz et al., 2006). In contrast, in the Pacific, bottlenose dolphins and harbour porpoises do not appear to have a significant overlap in diets: bottlenose dolphins have a wider variety of prey than harbour porpoises and harbour porpoises have a greater foraging depth range (Cotter et al., 2012). Literature is contradictory about dietary overlap attributing to the attacks and so without further investigation into the type of abundance of the prey species of bottlenose dolphins and harbour porpoises found in Cardigan Bay, it is difficult to know whether dietary overlap is potentially responsible for the attacks on harbour porpoises. With conflicting literature and uncertainty about the diets of the study species in Cardigan Bay, dietary overlap should not be eliminated as a potential reason for non-predatory aggressive interactions between bottlenose dolphins.

Conclusion

It was only possible to investigate geographic overlap, object-oriented play (for infanticide practice or fighting practice), and dietary overlap as the potential reasons for the non-predatory aggressive interactions between bottlenose dolphins and harbour porpoises in Cardigan Bay. Literature indicates that object-oriented play for practice fighting is a possible cause of the attacks on the harbour porpoises in Cardigan Bay: the data collected provided inconclusive results. The literature review of the two speciesô diets indicated that dietary overlap might also be a potential cause of the non-predatory aggression directed at harbour porpoises.

The results from the geographic distribution of the two species indicated that geographic overlap was not likely to be the cause of the attacks, and this was supported by the literature. The data regarding object-oriented play for practising infanticidal skills implicated that it was an unlikely reason for non-predatory aggression; however, the literature indicated it is a possibility in other locations.

The conclusions for object-oriented play and dietary overlap were drawn from a review of literature rather than the data collected, which was inconclusive. To establish whether there is a significant dietary overlap between the two species, stomach samples should be taken and the contents documented. It would also be helpful to measure the abundance and type of prey species found in Cardigan Bay as this may impact the competition for food and thus the effect of dietary overlap on bottlenose dolphin aggression.

The harbour porpoise is a threatened species and thus it is important to look at all factors affecting its populationsô trends. A substantial number of harbour porpoise deaths can be attributed to bottlenose dolphin attacks and it is possible that humans may be indirectly influencing these attacks, for example depleting fish stocks, and thus increasing competition for food. Therefore, it is important to instigate a thorough investigation into the cause of the bottlenose dolphins attacks on the harbour porpoises, to establish whether human management can play a role in better conserving the harbour porpoise.

Acknowledgements

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Appendix

CBMWC sightings form:

Sightings Form.

Organisation/Individual: CBMWC
Boat & Skipper: ____
Person Responsible for data: ____
Crew: ____

Date (DD/MM/YY): ____
Start Time(24hr): ____
End Time(24hr): ____
Page: ___ of ___

Survey Type:
TR ☐ NTR ☐ ID ☐
DIVE ☐ F ☐OTHER ☐

Entered onto Database ☐
Checked on Database ☐

No. of observers ☐

Sighting No.	* Time 24hr	* Latitude	* Longitude	Angle from boat * P left	Angle from boat * S right	Distance (m) *	Species Seen		Numbers Seen Total	A	J	C	NB	Behaviour (see key) Travelling dir'n (compass point or VAR)	Bird Species				Approx. no. seen	Bird behaviour		Sighting seen By	Notes
		N52°	W004°				BND	HP							HG	K	GT	MS		T	R		
							GS								R	G	MG			F	A		
		N52°	W004°				BND	HP							HG	K	GT	MS		T	R		
							GS								R	G	MG			F	A		
		N52°	W004°				BND	HP							HG	K	GT	MS		T	R		
							GS								R	G	MG			F	A		
		N52°	W004°				BND	HP							HG	K	GT	MS		T	R		
							GS								R	G	MG			F	A		
		N52°	W004°				BND	HP							HG	K	GT	MS		T	R		
							GS								R	G	MG			F	A		
		N52°	W004°				BND	HP							HG	K	GT	MS		T	R		
							GS								R	G	MG			F	A		
		N52°	W004°				BND	HP							HG	K	GT	MS		T	R		
							GS								R	G	MG			F	A		
		N52°	W004°				BND	HP							HG	K	GT	MS		T	R		
							GS								R	G	MG			F	A		
		N52°	W004°				BND	HP							HG	K	GT	MS		T	R		
							GS								R	G	MG			F	A		
		N52°	W004°				BND	HP							HG	K	GT	MS		T	R		
							GS								R	G	MG			F	A		
		N52°	W004°				BND	HP							HG	K	GT	MS		T	R		
							GS								R	G	MG			F	A		
		N52°	W004°				BND	HP							HG	K	GT	MS		T	R		
							GS								R	G	MG			F	A		
		N52°	W004°				BND	HP							HG	K	GT	MS		T	R		
							GS								R	G	MG			F	A		

Guide to the Sightings Form

Before the survey starts:

- Please fill in the boxes at the top of the form. This includes:
  - Organisation/individual: CBMWC
  - Boat & Skipper
  - Person responsible for data: (One member of CBMWC team)
  - Crew: (All CBMWC team onboard)
  - Date: DDMMYY
  - Total no. of observers at any one time (i.e. you & skipper or you, skipper & other CBMWC volunteer/s).

When you have a sighting!
Your effort form should be kept up to date so when you have a sighting you can immediately fill in the sightings form. If your effort changes when you have the sighting (i.e. you slow down) please record the core sightings data, indicated on the form by an *, before recording a new effort line.

Please record the following immediately upon confirmation of sighting:

- **Time:** 24 hour, the time should be taken from the hand held GPS.
- **Latitude / longitude:** For surveys by CBMWC the latitude is usually N52° which is already on the form. The longitude is usually W004°; this is again already present on the form. You only need to record the minutes & decimal minutes (two digits followed by three decimals. E.g. 12.345 & 21.234). Taken from handheld GPS.
  N.B. The full latitude & longitude figures **MUST** be recorded prior to other data. Please write the last 3 digits first as these change constantly.

- **Angle from boat:** This is either P, port (left) or S, starboard (right) of the boat. The angle to the animal can be obtained from the laminated protractor (0-180º) from port or starboard. If the animal is directly on the bow (in front) of the boat, enter 0° in one of the boxes and if it is directly astern (behind) of the boat, enter 180º in one of the boxes.

- **Distance:** Best estimate in metres of the distance to the animal. Avoid rounding. If in doubt, ask. As a guide remember Sulaire is approximately 10 metres in length.

The above information must all be recorded at the same time as they relate to each other.

The following information can be recorded once you have established the details:

- **Species:** circle one of the following:
  BND = Bottlenose dolphin; HP = Harbour porpoise; GS = Grey seal, there is an empty box for any other species. Don't assume it is one of the big three; we do have sightings of other species occasionally. If you are unsure – ASK.

- **Total no:** Best estimate of the total number of animals, (minimum number sighted).

- **Adults:** Best estimate for the number of adults.

- **Juveniles:** Best estimate for the number of juveniles.

- **Calves:** Best estimate for the number of calves.

- **New Born (NB):** Best estimate for the number of New Borns.

- **Behaviours/Direction of travel**: Please note the behaviour of the animal when first seen (top line) and subsequent behaviours observed, please include the direction of travel (compass direction travelling to).
  VAR = variable; compass direction can be obtained from the compass or the compass function on the hand-held GPS if on the roof.

Behaviours: Travel (T), fast travel (FT), Foraging (FO), feeding-fish seen (FF), leaping (L), tail slap (TS), rest (R), milling (M), sex (S), bow ride (BR), wake ride (WR), calf suckling (CS), socialising (SO), close contact (CC), loose group (LG), unknown (U), Other (O)

GS & other: Hauled out (H), in water (W), swimming (S), other (O)

CBMWC excel spreadsheet equations:

STEP 1:

	A	B	C	D
	Lat 1 (deg)	**Lon 1 (deg)**	**Brng (deg)**	**Dist (km)**
1	Latitude	Longitude	Bearing of animal	Distance from boat

The bearing of the animal is calculated from the angle of the animal from the boat (0-180°) and which side of the boat it is was sighted (port or starboard). Using a compass subtract the angle of the animal from 360° if it was sighted on the port side and add it to 360° if it was sighted on the starboard side.

STEP 2:

	E	F	G
	Lat 2 (rad)	**Lon 2 (rad)**	**Brng (rad)**
1	=RADIANS(A1)	=RADIANS(B1)	=RADIANS(C1)

STEP 3:

	H	I
	Lat 2 (rad)	**Lon 2 (rad)**
1	=ASIN(SIN(_lat1)*COS(d/ER) + COS(_lat1)*SIN(d/ER)*COS(brng))	=_lon1 + ATAN2(COS(d/ER)- SIN(_lat1)*SIN(_lat2), SIN(brng)*SIN(d/ER)*COS(_lat1))

STEP 4:

	J	K
	Lat 2 (deg)	**Lon 2 (deg)**
1	=DEGREES(H1)	=DEGREES(I1)