Fine-scale spatio-temporal variation and habitat partitioning in bottlenose dolphins and harbour porpoises

Abstract

1. Coastally distributed cetacean species face many threats from anthropogenic activities. However, owing to high temporal and spatial variability in the distribution of marine mammals, impacts can be difficult to detect, and long-term monitoring is required to detect changes in populations' distributions and habitat use. Understanding of these spatio-temporal changes in distribution and abundance of marine mammals is essential for successful conservation and management, as it allows mitigation measures to be targeted to critical times and habitats.
2. Fine-scale variation in the spatial and temporal distribution of bottlenose dolphins and harbour porpoises was examined in Cardigan Bay, West Wales, using acoustic monitoring. Static omni-directional hydrophones, known as T-PODs, were deployed at ten sites within the bay, for two years, providing a continuous means of monitoring rates of occurrence of both species.
3. Acoustic detections indicated large seasonal changes in the relative abundance of harbour porpoises and bottlenose dolphins in Cardigan Bay and revealed seasonal variation in habitat use within the bay. Both species exhibited consistent seasonal changes in distribution from one year to the next, but relatively little variation in presence between diel periods, though finer-scale temporal variation was evident.
4. In addition, both species displayed fine-scale fluctuations in occurrence over the tidal cycle, consistent across sites, seasons and years. Variation in harbour porpoise and bottlenose dolphin presence over the tidal cycle was strongly negatively correlated. This, in conjunction with differences in seasonal presence, and low rates of co-occurrence despite interspecific similarities in habitat preferences, provides evidence of fine-scale spatio-temporal habitat partitioning between harbour porpoises and bottlenose dolphins.
5. This is, to our knowledge, some of the first evidence of habitat partitioning between these two species. Not only does this mean that the two species may require different management actions but is particularly interesting considering the marked increase in porpoise deaths as a result of bottlenose dolphin attacks in the last decade, which are suggestive of an increase in interspecific competition, whether as a result of changes in abundance or distribution of bottlenose dolphins or harbour porpoises, or increased competition for less prey.

Introduction

Bottlenose dolphin (*Tursiops truncatus)* and harbour porpoise *(Phocoena phocoena)* populations have contracted in range across Europe in the last century (Evans, 1990). Within UK waters, bottlenose dolphins disappeared from areas such as the Bristol Channel, the Severn Estuary and the South-West English coast (de Boer & Simmonds, 2003), while harbour porpoise populations also declined significantly, particularly in the North Sea and the English Channel, though both species have since returned to some localities (Evans *et al*., 2003; Eisfeld, 2005). Anthropogenic actions are thought to be largely responsible for historical changes in the distribution and abundance of cetaceans, with prey depletion, coastal development, bycatch and pollution all possible factors in their decline (Evans, 1980; Sini *et al*., 2005). Notwithstanding concern over the status of these species, their position as apex predators makes them key indicators of ecosystem health (Ballance *et al*., 2006). However, as K-selected species, their long lifespan often buffers them from impacts, with environmental perturbations and anthropogenic disturbances likely to result in changes in distribution and reproductive success rather than survival (Ballance *et al*., 2006).

Within their population range bottlenose dolphins and harbour porpoises show high temporal variability in their distribution, with seasonal and diel fluctuations in distribution (Wilson *et al*., 1997; Verfuss *et al*., 2007). With cetaceans continuing to face threats such as bycatch, prey depletion and climate change, an understanding of spatio-temporal changes in abundance and distribution and current habitat use is essential for management, allowing mitigation measures to be targeted to critical areas and times of peak abundance. Here, spatio-temporal fluctuations in the distribution and relative abundance of bottlenose dolphins and harbour porpoises are analysed, within Cardigan Bay, Wales. In particular, I examine fine-scale seasonal, tidal and diel changes in the relative abundance and distribution of bottlenose dolphin and harbour porpoise, through the use of static passive acoustic monitoring.

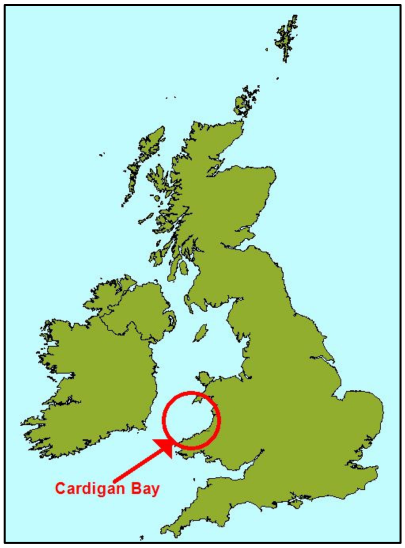
Seasonal changes in the distribution of bottlenose dolphins and harbour porpoises appear normal in populations around the UK and typically correspond with the seasonal occurrence of prey species (Northridge *et al*., 1995; Wilson *et al*., 1997; Evans *et al*., 2003). However, although studies of seasonal shifts in bottlenose dolphin distributions have been relatively extensive (Wilson *et al*., 1997; Evans *et al*., 2003), less is known about their habitat use during the winter, due to the difficulty of conducting visual surveys in poor weather (Simon *et al. manuscript in progress*). For harbour porpoise populations there is greater uncertainty concerning their seasonal movements, with suggestions of north-south, east-west and inshore and offshore migrations (Northridge *et al*., 1995). Similarly, relatively little is known about local diel changes in habitat use and activity of bottlenose dolphins and harbour porpoises, particularly nocturnal activity, with other populations showing differing degrees of diel variation (Brager, 1993; Gregory & Rowden, 2001; Carlstrom, 2005; Ingram *et al*., 2005; Philpott *et al*., 2007).

Acoustic monitoring is a useful tool for examining fine-scale changes in the distribution and relative abundance of cetaceans. While visual surveys are limited by weather conditions and visibility, acoustic monitoring allows fine-scale habitat use of cetaceans to be monitored continuously, independent of weather and over the entire diel period. The application of static omni-directional hydrophones, known as T-PODs, has been relatively recent (Gordon & Tyack, 2002), although they have already been used to assess impacts of wind farm construction and to track changes in seasonal and diel distribution of cetaceans (Fisher & Tregenza, 2003; Carlstrom, 2005; Leeney & Tregenza, 2006; Verfuss *et al*., 2007). T-PODs detect echolocation click trains produced by bottlenose dolphins and harbour porpoises. Both species use echolocation for detection and differentiation of prey, with echoes providing information on the range of targets and allowing them to detect objects outside their visual range (Au *et al*., 2000). However, while harbour porpoises echolocate almost continuously (Akamatsu *et al*., 2007), and may use echolocation not only in foraging and navigation but also possibly for communication, bottlenose dolphins use echolocation principally for foraging, using whistles and burst-pulsed vocalisations for social communication (Au *et al*. 2000). Echolocation signals of bottlenose dolphins and harbour porpoises have distinct characteristics and can be distinguished on the basis of peak frequencies and bandwidth, allowing both species to be monitored simultaneously. Acoustic detection rates are thought to be related to the rate of occurrence of species (Carstensen *et al*., 2006; Verfuss *et al*., 2007), and although data cannot be used to estimate actual abundance, it gives an indication of the relative abundance of cetaceans at different times and locations (Leeney & Tregenza, 2006).

Methods

Study Site

Cardigan Bay is a shallow, sheltered bay of 5,500 km^2, covering a gentle shelf, less than 50 m in depth (Baines *et al*., 2000). Tidal currents are semi-diurnal and relatively weak with a moderate tidal range (Baines *et al*., 2000). Sea surface temperatures range from 5 ºC in February to 20 ºC in July–August, and as a result of the weak tidal currents seasonal stratification of the water body occurs in shallower areas of the bay in the summer (Baines *et al*., 2000). Cardigan Bay Special Area of Conservation (SAC) is in the South of Cardigan Bay, covering 1040 km^2, and was formally designated an SAC under the EU Habitats Directive to protect concentrations of bottlenose dolphins found there. Ten T-PODs were deployed within Cardigan Bay SAC at depths of 12-25 m, with two T-PODs deployed at each of three locations, one inshore (approximately 300 m from the coast) and one further off-shore (800 m - 1 km from the coast), while the remaining T-PODs were deployed at Ynys Lochtyn, Cardigan Island and two within New Quay Bay (Fig. 1).



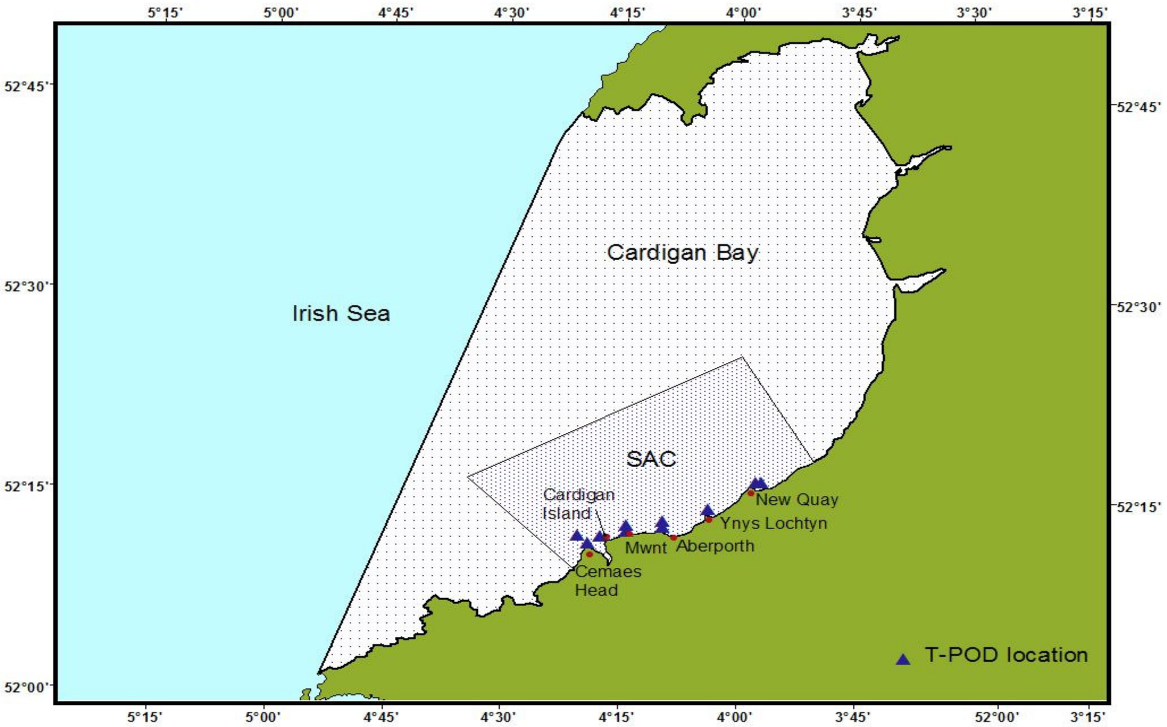


Figure 1: Deployment sites of the ten T-PODs within Cardigan Bay SAC. From the left: Cemaes Head, Cardigan Island, Mwnt, Aberporth, Ynys Lochtyn and New Quay.

T-Pods

Echolocation signals were recorded using passive acoustic click detectors (T-PODS, Chelonia Ltd. Cornwall, UK). These are statically-moored omni-directional hydrophones, which automatically log the time and duration of click trains that resemble those of target species, scanning through six frequency channels per minute. Three channels were set to detect bottlenose dolphin clicks and three for detection of harbour porpoises. Bottlenose dolphin echolocation has a peak frequency of 60-140 kHz, whereas harbour porpoises produce clicks between 120-150 kHz (Au *et al*., 2000). Although there is some overlap in the frequencies used by bottlenose dolphins and harbour porpoises, by comparing the output of two filters on each channel it is possible to differentiate the two species. For bottlenose dolphins, target filters are set to 50 kHz with the reference filter at 70 kHz, resulting in peak sensitivity at 50 kHz, which falls to zero beyond 60 kHz. Therefore, only frequencies falling below 60 kHz are logged, eliminating any false positive detection of harbour porpoises on bottlenose dolphin channels. Harbour porpoise channels have a target filter frequency of 130 kHz and a reference filter at 92 kHz, causing all frequencies below 110 kHz to be filtered out. Although there is a chance of false positive detections of harbour porpoises, due to occasional high frequency echolocation by bottlenose dolphins, use of a narrow bandwidth setting eliminates the vast majority of these, while any remaining false positives are unlikely to influence results due to large sample sizes. T-PODs were deployed from May 2005 until January 2007 at ten locations within Cardigan Bay SAC. They have a detection range of up to 1250 m (Philpott *et al*., 2007), but the majority of acoustic detections occur within 500 m, with detection rates decreasing with increasing distance (Reyes Zamudio, 2005; Tougaard *et al*. 2006). T-POD hydrophones were calibrated to a sensitivity of ± 2 dB (*re* 1µPa) before being deployed, and settings were later validated with a field calibration (Simon *et al*., 2006 *in prep.*). Data were logged continuously for 5-6 weeks before being downloaded and the T-PODs re-deployed.

Data Analysis

Acoustic data were analysed with the software T-POD.exe (version 8.17; Chelonia Ltd. Cornwall, UK) which classifies click trains as having a 'high', 'low' or 'doubtful' probability of being of cetacean origin according to the regularity of the click train, as interclick intervals within cetacean click trains are less variable than those from boat sonar, propellers or other biological sources (Tregenza, 2007). Both 'high' and 'low' probability classified trains are typically considered as being of cetacean origin; therefore both were used for analysis, while doubtful trains were excluded (Tregenza, 2007). Although T-PODs record details such as the time and duration of click trains, interclick intervals and pulse repetition frequency, only data on the number of minutes per hour in which there were positive detections, referred to as detection positive minutes (DPM), were used. Data on time of sunrise and sunset for each day of the year were obtained from the U.S. Naval Observatory (Astronomical Applications Dept. Nautical Twilight Times, http://aa.usno.navy.mil/). Differences between daylight times for different T-POD locations were minimal, being less than two minutes; therefore daylight times for Aberporth were used for all locations. Tidal data were obtained from Ceredigion County Council and tide times were adjusted for each T-POD location.

Statistical analysis

Data were non-parametric and could not be transformed to a normal distribution. Therefore, differences in detection rates between years, seasons, sites, times of day and different parts of the tidal cycle were determined using the Kruskal-Wallis test and the Scheirer-Ray-Hare extension of the Kruskal-Wallis test. *Post-hoc* Mann-Whitney *U* tests were carried out to determine which sites, times of day or seasons were significantly different from each other, applying the Bonferroni correction for multiple comparisons.

Results

Site preferences

All monitored sites in Cardigan Bay SAC had significantly different occurrence rates of harbour porpoises (Scheirer-Ray-Hare extension of the Kruskal-Wallis test: $H_{9,116273}=706.3$, $P<0.0001$) and of bottlenose dolphins ($H_{9,116273}=363.6$, $P<0.0001$; Fig. 2). Occurrence of bottlenose dolphins was significantly higher offshore from Aberporth than at any other site, with approximately twice the number of detection positive minutes (DPM) per hour, while their occurrence was lowest offshore from Cemaes Head, with a mean of only 0.3 DPM per hour (Fig. 2). Similarly, harbour porpoise detections were significantly higher offshore from Aberporth, and lowest inshore at Cemaes Head (Fig. 2). Although there appears to be some concurrence between the relative use of sites by bottlenose dolphins and harbour porpoises, there was no significant correlation between their relative occurrence at each site on an hourly basis (Spearman's rank correlation: r=-0.004, P=0.187). Relative occurrence of harbour porpoises was negatively correlated with that of bottlenose dolphins at each site on a daily basis (r=-0.10, P<0.0001), but only 1% of the variation in occurrence of one species was explained by that of the other. At sites at which both inshore and offshore locations were monitored, relative occurrence of harbour porpoises was significantly higher offshore than inshore. For bottlenose dolphins inshore and offshore sites had significantly different detection rates at Aberporth and Cemaes Head, but in no consistent direction (Fig. 2).

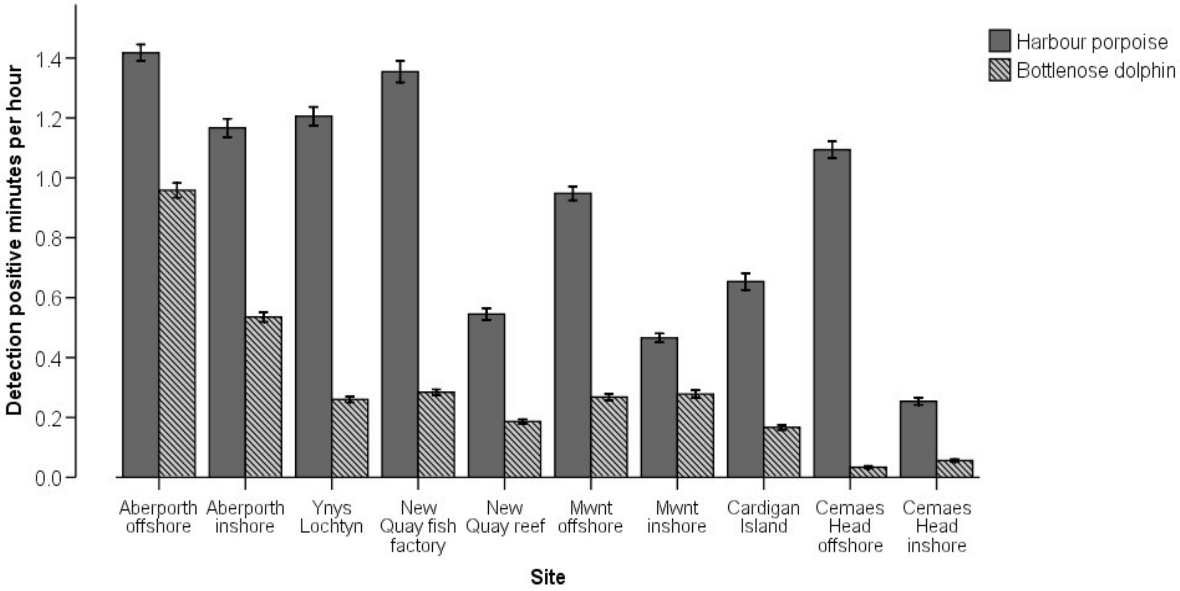


Figure 2: Number of detection positive minutes per hour of bottlenose dolphins and harbour porpoises at each site. Data represent means ± 1 standard error.

Inter-annual variation

Detection rates of bottlenose dolphins were significantly lower in 2006 than 2005 (Mann-Whitney: U=1356169986, P<0.0001; Fig. 3), although summer occurrence in 2006 exceeded that in 2005 at several sites. Conversely, detection rates of harbour porpoises were significantly higher in 2006 than 2005 (Mann-Whitney: U=1397184154, P<0.0001), except in winter (Fig. 3). Harbour porpoises were detected at significantly higher rates than bottlenose dolphins (Scheirer-Ray-Hare: $H_{1,180526}$=732.4, P<0.0001), at all sites, in all diel periods, and in all seasons except summer. In summer, detection rates of bottlenose dolphins significantly exceeded those of harbour porpoises at all sites except Cemaes Head and offshore from Mwnt, where detection rates remained below those of harbour porpoises throughout the year.

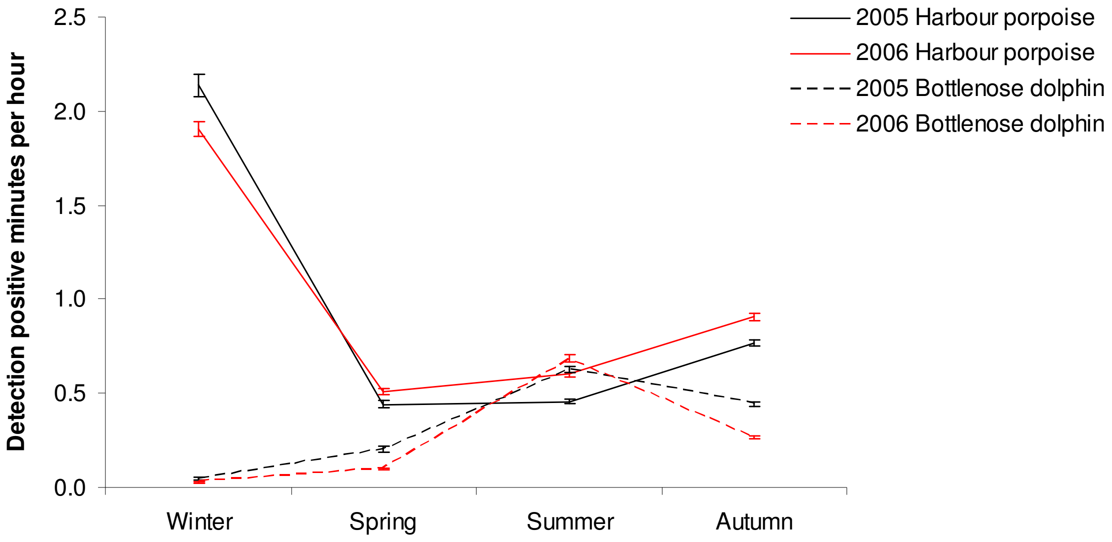


Figure 3: Mean number of detection positive minutes per hour of bottlenose dolphins and harbour porpoises in 2005 and 2006. Data represent means ± 1 standard error.

Seasonal variation

Relative abundance of bottlenose dolphins differed significantly between all seasons (Scheirer-Ray-Hare: $H_{3,116273}$=453.8, P<0.0001), with a significantly higher number of detection positive minutes per hour in summer than in any other season (0.66 DPM per hour). Detection rates increased from April, peaking in July and then falling throughout the following months, with relative occurrence 83% lower in autumn (0.36 DPM per hour), though this exceeded occurrence in spring (0.12 DPM per hour) and winter (0.03 DPM per hour; Fig. 4). Relative abundance of harbour porpoises also differed significantly between all seasons (Scheirer-Ray-Hare: $H_{3,116273}$=572.9, P<0.0001), but with a significantly higher number of detections in winter, with more than double the number of positive detections per hour of any other season (Fig. 5). Relative occurrence was progressively lower in autumn (0.83 DPM per hour), summer (0.54 DPM per hour) and spring (0.50 DPM per hour), respectively.

Seasonal changes in relative abundance of bottlenose dolphins and harbour porpoises were the same in both years. However, not all sites showed the same pattern of seasonal variation (Scheirer-Ray-Hare, interaction: $H_{27,116273}$=268.8, P<0.0001). At the majority of sites, bottlenose dolphins showed the aforementioned seasonal trend, being most abundant in summer and least in winter (Fig. 4). However, at New Quay sites relative abundance of bottlenose dolphins was significantly higher in autumn than in any other season (Fig. 4). Seasonal variations in relative abundance of harbour porpoises were also site-specific (Scheirer-Ray-Hare, interaction: $H_{27,116273}$=548.8, P<0.0001; Fig. 5). Although the majority of sites had significantly higher occurrence in winter and lowest in spring or summer, offshore from Aberporth and inshore at Cemaes Head relative abundance was lowest in winter, with detection rates significantly highest in autumn and summer, respectively (Fig. 5). Indeed, relative use of sites differed between seasons. Occurrence of both bottlenose dolphins and harbour porpoises was higher at New Quay fish factory than at any other site during winter, whereas in all other seasons, Aberporth had the highest occurrence of both species, with detection rates particularly elevated above those of other sites in summer and autumn (Fig. 4 & 5).

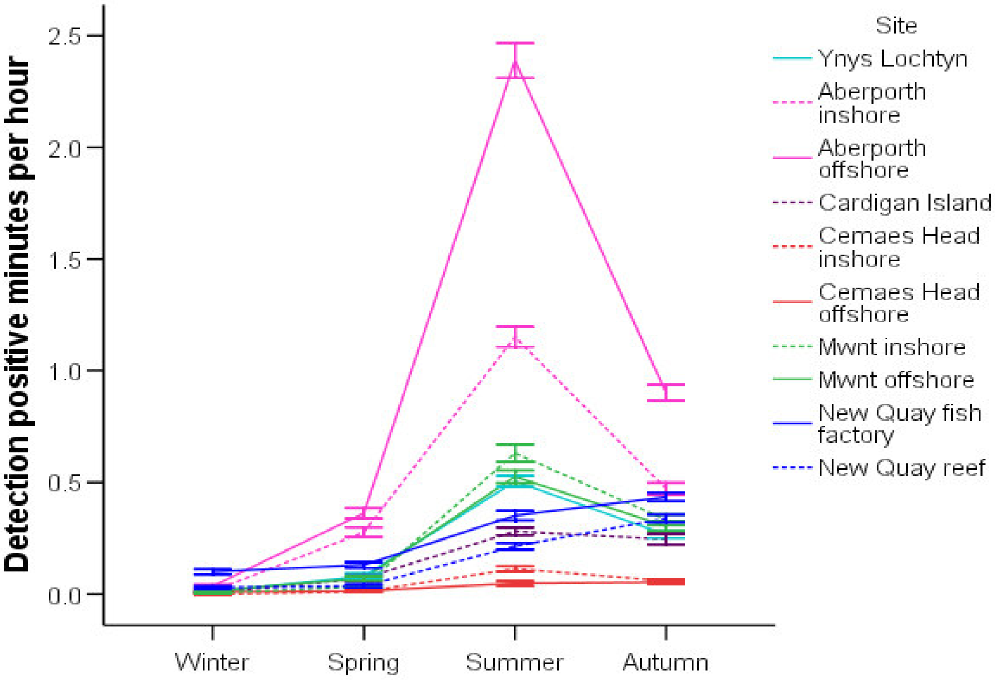


Figure 4: Mean number detection positive minutes per hour of bottlenose dolphins at each site in winter, spring, summer and autumn. Data represent means ± 1 standard error.

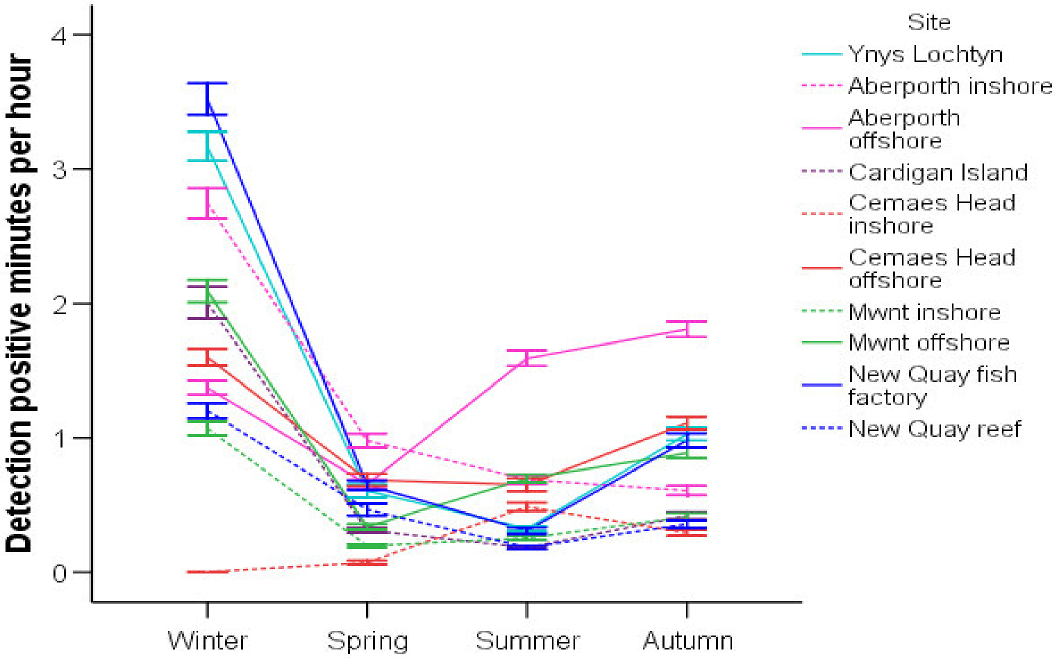


Figure 5: Mean number of detection positive minutes per hour of harbour porpoises at each site in winter, spring, summer and autumn. Data represent means ± 1 standard error.

Diel variation

There was no significant diel variation in relative occurrence of bottlenose dolphins across all sites, years or seasons (Kruskal-Wallis: H=0.739, df=3, P=0.864; Fig. 6). However, at individual sites they did show year and season specific differences in diel presence. For example, in autumn of 2005 and 2006 relative occurrence of dolphins was significantly higher during the day than at night offshore from Aberporth, although at all other sites there were no significant differences between diel periods. However, although relative occurrence did not often differ significantly between diel periods, significant changes could be seen throughout a 24-hour period (Kruskal-Wallis: H=727.3, df=26, P<0.0001). Occurrence of bottlenose dolphins was relatively low throughout the night but increased prior to dawn, and continued to rise after sunrise, increasing by 37% in the first hour after dawn and reaching a peak 2-3 hours after sunrise. Throughout the rest of the day detection rates decreased progressively until 16:00 hours when there was a slight increase, coinciding with sunset (Fig. 7).

Diel occurrence of harbour porpoises differed significantly (Kruskal-Wallis: H=24.3, df=3, P<0.0001), but only in autumn and summer, with significantly higher occurrence at night than in the day in summer, at Aberporth and inshore at Mwnt, and significantly higher occurrence in the day in autumn at Cardigan Island, New Quay fish factory and offshore from Cemaes Head. In addition, relative abundance changed significantly throughout the 24-hour cycle (Kruskal-Wallis: H=171.3, df=18, P<0.0001). Peak detections occurred after midnight, with large decreases in occurrence at five hours before sunrise and at sunrise itself (Fig. 7). Relative abundance remained relatively low throughout the day until approximately 19:00 hours, the average time of sunset, where it increased (Fig. 7). Changes in relative abundance of harbour porpoises mirrored those of bottlenose dolphins, with increases in occurrence of bottlenose dolphins concurrent with decreases in relative abundance of harbour porpoises, though they were not significantly correlated (Fig. 7).

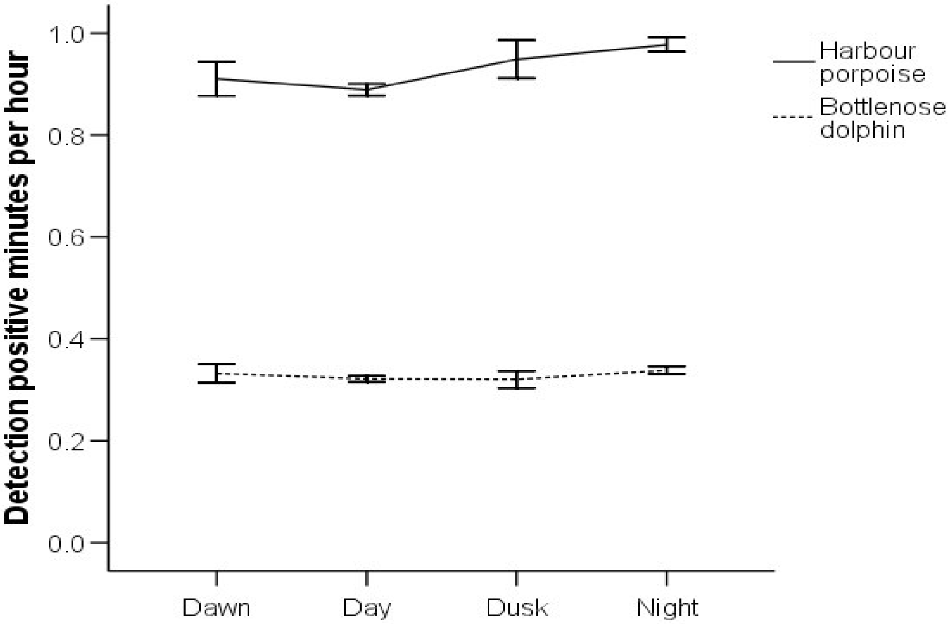


Fig. 6: Mean number of detection positive minutes per hour of bottlenose dolphins and harbour porpoises at dawn, day, dusk and night. Data represent means ± 1 standard error.

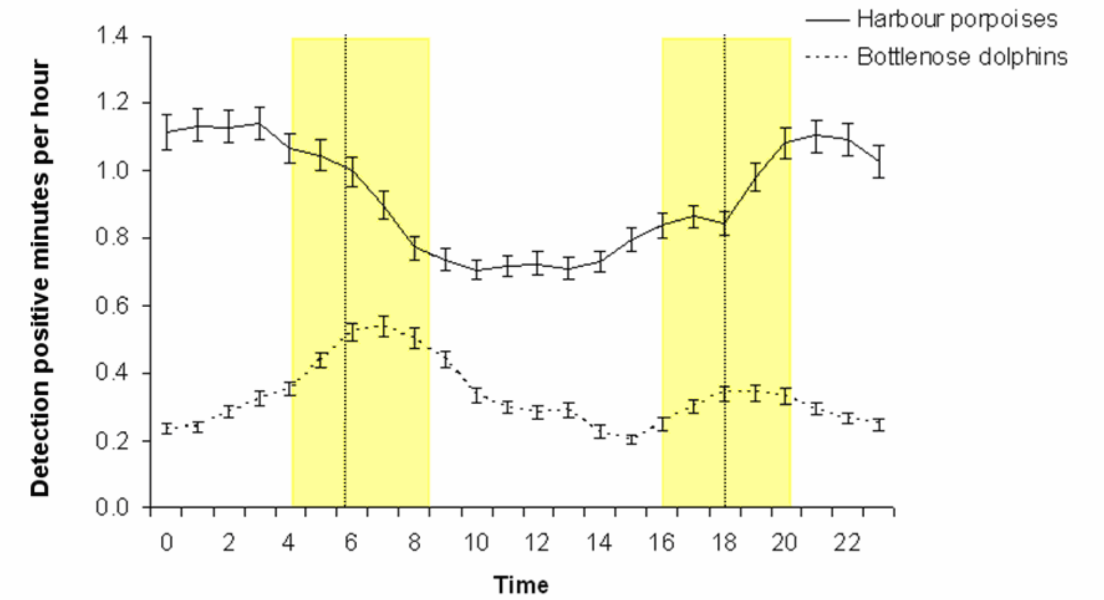


Fig. 7: Mean number of detection positive minutes per hour of bottlenose dolphins and harbour porpoises at each hour of the day. Data represent means ± 1 standard error. Shaded areas represent range of sunrise and sunset times, with vertical dotted lines to show average sunrise and sunset times.

Tidal variation

Relative abundance of bottlenose dolphins and harbour porpoises changed significantly during the tidal cycle (Kruskal-Wallis, bottlenose dolphins: H=87.5, df=11, P<0.0001; harbour porpoises: H=148.3, df=11, P<0.0001). Detection rates of harbour porpoises were significantly higher during the ebb phase of the tidal cycle (Mann-Whitney: U=1227258214.5*,* P=0.001), whereas bottlenose dolphins were significantly higher during the flood (Mann-Whitney: U=1217371873.0*,* P<0.0001). In addition, occurrence rates fluctuated within the flood and ebb phases (Fig. 8). Occurrence of bottlenose dolphins peaked at low water and 2-3 hours before high water, falling to a minimum 2 hours after high water, and then increasing as low water was approached, 3-5 hours after high water (Fig. 8). Changes in the relative abundance of harbour porpoises mirrored those of bottlenose dolphins, with a peak four hours before and 2-3 hours after high water, and a dip in detection rates in the period of slack water at the turn of the tide and at low water (Fig. 8). Indeed, there was a significant negative correlation between the relative occurrence of bottlenose dolphins and harbour porpoises over the tidal cycle (Spearman's rank correlation: r=-0.629, n=12, P=0.028), with 40% of the variation in occurrence of one species explained by that of the other.

Changes in relative abundance of bottlenose dolphins and harbour porpoises over the tidal cycle were consistent across years and different diel periods. In addition, tidally-related occurrence was similar across seasons, although in winter there was little change in bottlenose dolphin detection rates over the tidal cycle, and a greater magnitude of variation in harbour porpoise occurrence. Furthermore, patterns of variation over the tidal cycle were consistent across the majority of sites. However, at Cemaes Head there was very little change in detection rates of bottlenose dolphins or harbour porpoises over the tidal cycle, while New Quay sites and inshore at Mwnt also showed some divergence from the average pattern. Nevertheless, despite heterogeneity between sites in the timing and magnitude of changes in occurrence over the tidal cycle, at the majority of sites changes in bottlenose dolphin and harbour porpoise presence still mirrored each other, although this was not clear in winter, when relative abundance of bottlenose dolphins is at its lowest, or inshore at Mwnt, where both species generally showed parallel changes in abundance over the tidal cycle. Relative use of sites also altered during the tidal cycle. During the three hours before low water, the presence of bottlenose dolphins inshore at Mwnt and of harbour porpoises at New Quay fish factory exceeded that at Aberporth, where relative abundance was typically highest at all other times.

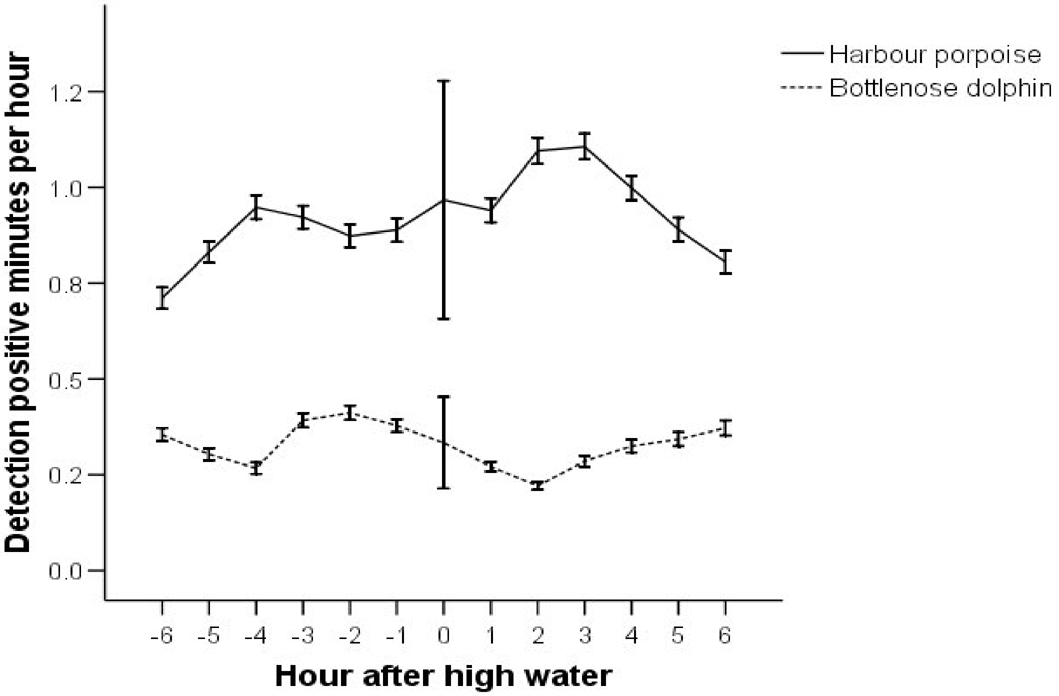


Fig. 8: Mean number of detection positive minutes per hour of bottlenose dolphins and harbour porpoises at each hour of the tidal cycle. Data represent means ± 1 standard error.

Co-occurrence of bottlenose dolphins and harbour porpoises

Bottlenose dolphins and harbour porpoises were rarely both detected within the same hour, with only 2.72 % of hourly detections being positive for both species. Co-occurrence was most common in the summer (51% of co-detections), though 36% of co-detections occurred in autumn. Simultaneous detections of both species were unevenly distributed across sites, with 37.2% occurring offshore from Aberporth, while approximately 10% or less occurred at each of the other sites. Similar proportions of simultaneous detections of dolphins and porpoises occurred during the day (51%) and at night (37%), while 6.1% and 5.6% occurred at dawn and dusk, respectively.

Discussion

Site preferences

Inshore and offshore sites at Aberporth were hotspot locations for bottlenose dolphins, with over 48% more detections per hour than any other site; while offshore Aberporth and New Quay fish factory were favoured by harbour porpoises (Fig. 2). Harbour porpoises showed a marked preference for offshore rather than inshore sites, while bottlenose dolphins displayed no consistent preference. For harbour porpoises, which echolocate almost continuously (Akamatsu *et al.*, 2007), this is likely to be good reflection of their overall distribution between these sites. However, as bottlenose dolphins use echolocation only when feeding or travelling (Au *et al.*, 2000), this indicates that these locations are likely to be foraging hotspots. Their use of sites for other activities, such as socialising, is not detected by acoustic monitoring, but as bottlenose dolphins spend 90-97 % of their time engaged in foraging and travelling (Beddier*, pers. comm.*), and with prey distribution thought to be the primary determinant of their distribution (Sini *et al.*, 2005), acoustic detections are likely to be a good indication of their overall distribution. Indeed, visual surveys have also identified Aberporth as a favoured feeding site for bottlenose dolphins, in addition to others such as Ynys Lochtyn, New Quay and Mwnt (Baines *et al.*, 2000).

Inter-annual variation

Acoustic detection rates of bottlenose dolphins were significantly lower in 2006 than 2005, although they differed by only 0.14 DPM per hour. This concurs with trends in abundance estimates from photo-ID, which estimated a population decrease of 8 animals in 2006, although line-transect estimates showed the opposite trend (Pesante *et al.,* 2007). Acoustic detections of porpoises increased in 2006 by 0.16 DPM per hour, concurring with line-transect estimates of the population, although 2005 and 2006 estimates differed by only 3 animals (Pesante *et al.*, 2007). Changes in relative abundance of harbour porpoises and bottlenose dolphins may be related to inter-annual changes in fish stocks, with sand eels (Poloczanska *et al., 2004*), bass (Henderson & Corps, 1997), and herring (Toreson & Ostvedt, 2000) all showing high inter-annual variability in abundance. However, further data are required to determine the efficacy of acoustic monitoring for detecting long-term trends in populations, as acoustic trends are not consistent with those from line-transect bottlenose dolphin estimates, though it must be remembered that the coastal location of the T-PODs may limit their ability to reflect trends in abundance in the whole SAC, which extends 12 miles offshore. Acoustic detections of harbour porpoises exceeded those of bottlenose dolphins in all seasons except summer. However, population estimates of harbour porpoises and bottlenose dolphins generally fall within a similar range and differences in detection rates are likely to reflect differences in echolocation rates, with porpoises echolocating almost continuously and bottlenose dolphins only when foraging and travelling (Au *et al.* 2000; Akamatsu *et al.*, 2007), rather than solely indicating differences in relative abundance of the two species.

Seasonal variation

Acoustic detection rates of bottlenose dolphins and harbour porpoises in Cardigan Bay changed markedly between seasons, with highest detections of bottlenose dolphins during the summer and porpoises during the winter, in accordance with trends from visual surveys (Baines *et al*., 2000). For both species, availability and distribution of prey is a primary determinant of their distribution (Wilson *et al*., 1997) and the summer increase in numbers of bottlenose dolphins corresponds with seasonal concentrations of mackerel and salmonids in Cardigan Bay (Baines *et al*., 2000). However, the increase in bottlenose dolphin presence also coincides with their calving season, which extends from May-September, peaking in July and August (Evans *et al*., 2003). Although abundance of prey must be vital, it is possible that the seasonal increase in presence is due to the advantages of Cardigan Bay as a calving area, with a similar seasonal increase in bottlenose dolphin presence seen inshore in the Moray Firth, again coinciding with the seasonal migration of anadromous fish and the calving season (Wilson *et al*., 1997; Hastie *et al*., 2003). Indeed, in Australia, reproductive success of bottlenose dolphins is predicted by water depth, with a shift to shallower waters observed during the calving season (Mann *et al*., 2000). Though this is thought to be for protection from shark predation which is not a threat to dolphins in temperate waters, decreased depth may facilitate protection of calves from infanticide, aiding detection of male conspecifics, allowing mothers not to leave calves unprotected for extended periods while foraging, and potentially reducing the energetic costs of foraging (Mann *et al*., 2000). In addition, increased summer temperatures inshore compared to offshore may be more thermally efficient for mothers and calves (Mann *et al*., 2000), while the topography of the bay also provides protection from strong currents and tides (Baines *et al*., 2000). However, while depth, shelter and increased sea temperatures may all factor in the increased prevalence of bottlenose dolphins within Cardigan Bay in summer, food availability is likely to be of primary importance, as pregnant and lactating mothers increase their food intake by up to 50% (Cheal & Gales, 1992). Indeed, it is possible that reproduction is timed to take advantage of increased food availability arising from the inshore migrations of shoaling prey species (Grellier *et al*., 1995).

The reduction in relative abundance of dolphins within Cardigan Bay in winter is likely to be driven by changes in prey availability. However, although the prey of harbour porpoises overlaps considerably with that of bottlenose dolphins (Santos & Pierce, 2003), porpoises show markedly different seasonal variation in abundance, with highest detection rates in winter. Both species prey on Atlantic herring (*Clupea harengus*), mackerel (*Scomber scombrus*), sandeels (*Ammodytidae*), cod (*Gadus morhua*) and sprat (*Sprattus sprattus*), although dolphins also feed on sea bass (*Dicentrarchus labrax*) and grey mullet (*Chelon labrosus*) (Evans *et al*., 2000; Santos *et al*., 2001; Santos & Pierce, 2003). However, differences in seasonal distributions of bottlenose dolphins and harbour porpoises suggest that they show different prey preferences. Increases in porpoise densities in winter coincide with concentrations of herring, typically their major prey species (Aarefjord *et al*., 1995, Gannon *et al*.,. 1998, Borjesson *et al*., 2003), which occur in Cardigan Bay in autumn and winter (Evans *et al*., 2000). However, the seasonal change in distribution of porpoises may also arise as a result of the change in relative abundance of bottlenose dolphins, with more porpoises migrating into the area when bottlenose dolphin densities are low, due to decreased competition for food or lower levels of interspecific aggression (Patterson *et al.*, 1998). Although, harbour porpoises also calve in summer, this does not lead to a similar increase in detection rates as for bottlenose dolphins, and preferred calving areas appear to be further south in Pembrokeshire (Baines & Earl, 1999).

Seasonal changes in the relative abundance of bottlenose dolphins and harbour porpoises were consistent across both recorded years and the majority of sites, suggesting that seasonal changes in prey abundance are also consistent from one year to the next and occur across the whole of Cardigan Bay. However, at some sites patterns of seasonal variation differed, presumably due to seasonal local abundances of prey. In addition, site preferences changed between seasons, with offshore Aberporth the primary foraging hotspot for harbour porpoises and bottlenose dolphins in spring, summer and autumn, but New Quay fish factory having the highest abundance of both species in winter. This could result from seasonal shifts in prey distribution with ocean currents, or from differences in habitat preferences of seasonally abundant prey. However, fine-scale spatio-temporal distribution of prey species is not well known in Cardigan Bay (Bailey & Thompson, 2006), and must be mapped before it is possible to determine the strength of fine-scale association between predator and prey.

Diel variation

Detection rates of bottlenose dolphins and harbour porpoises exhibited little variation between diel periods, although there were site, season and year specific differences between day and night-time occurrence. Diel occurrence varied most frequently in autumn, with significantly higher daytime occurrence of bottlenose dolphins and harbour porpoises at several sites, whereas in summer, harbour porpoises were detected more at night inshore at Mwnt. While differences in diel detection rates may reflect changes in occurrence at monitored sites, it is also possible that echolocation rates differ between diel periods. Increased echolocation has been documented at night in harbour porpoises (Carlstrom, 2005; Cox *et al.*, 2001; Teilmann, 2002) and in a single captive bottlenose dolphin (Akamtsu *et al.*, 1992), and has been proposed to compensate for loss of visual cues (Carlstrom, 2005). However, here, elevated nocturnal echolocation occurred relatively rarely, with daytime detection rates often exceeding those at night. Nonetheless, increases and decreases in detection rates of harbour porpoises coincided with sunset and sunrise, respectively, suggesting that echolocation rates may change between diel periods but that this is masked by finer-scale variation within diel periods. Indeed, the overall lack of variation in bottlenose dolphin and harbour porpoise presence between diel periods may be due to significant variation at a finer temporal scale (Fig. 7). Detection rates of bottlenose dolphins, for example, peak between 7:00 and 10:00 a.m., as observed in visual surveys in Cardigan Bay (Gregory & Rowden, 2001), but are low throughout the rest of the day, possibly as a result of disturbance from increasing boat traffic, which can significantly affect habitat use (Corkeron, 1995), and behavioural budgets of cetaceans (Lusseau, 2003).

Alternatively, differences in detection rates between diel periods may solely reflect changes in occurrence at monitored sites between diel periods, presumably in relation to cycles in prey activity. Many prey species have diurnal or nocturnal peaks in activity: herring, mackerel and sprats for example, spend the day close to the sea bed, dispersing at night to feed at the surface (Cardinale *et al*., 2003). Hence, autumn increases in daytime detection rates may occur as a result of seasonal concentrations of herring, with increased daytime foraging to target fish when they are aggregated at depth, maximising feeding efficiency. Alternatively, some nocturnal prey may be more conspicuous at night causing the elevated night-time presence of harbour porpoises in summer at Mwnt.

Tidal variation

Bottlenose dolphins and harbour porpoises exhibited significant variation in occurrence over the tidal cycle. Whereas bottlenose dolphins were most abundant in the tidal flood, harbour porpoises were detected at higher rates during the ebb. However, within these tidal phases there was significant finer-scale variation in their presence, with peaks in occurrence of harbour porpoises four hours before and 2-3 hours after high water, and low occurrence at the turn of the tide and low water. Bottlenose dolphins showed the converse pattern, being abundant at low water and two hours before high water, with minima at fours before and two hours after high water, as documented visually by Lamb (2004). Patterns of variation in occurrence over the tidal cycle were the same from one year to the next, across different times of day and largely across seasons. The consistency of these tidally-related patterns in occurrence suggests that they are related to predictable concentrations of prey occurring at specific stages of the tidal cycle. Prey are thought to accumulate at tidal fronts, due to active or passive transport on tidal currents (Aprahamian *et al*., 1998), with species such as plaice, flounder and turbot, migrating in and off-shore with the tidal cycle to take advantage of intertidal prey (Gibson *et al*., 1996). This may enable cetaceans to increase foraging efficiency by targeting these areas. Indeed, bottlenose dolphins in the Moray Firth are spatially associated with tidal fronts (Mendes, 2002).

In addition, cetaceans may use tidal currents to minimise the energetic costs of foraging and travelling (Williams *et al*., 1996). Bottlenose dolphins had the highest detection rates at times when there was least water movement, and have been observed to move in the same direction as the tidal flow or in slack periods when there is least tidal resistance (Gregory & Rowden, 2001). Harbour porpoises on the other hand, were detected most mid-way through the flood and ebb, when tidal currents are strongest. However, whether this is because porpoises are orientating themselves against the tidal flow to forage, as in the Shetland Islands (Evans, 1996), or travel with them, using currents to minimise the energetic costs of foraging (Williams *et al*., 1996), cannot be determined without visual observations. However, it is also possible that differences in detection rates between seasons, diel and tidal phases may reflect changes in echolocation behaviour rather than relative occurrence, with echolocation rates influenced by behaviour, group size and possibly visibility (Jones and Sayigh, 2002). However, correspondence of acoustic trends with visual observations suggests that detection rates are a good indication of relative occurrence, at least for seasonal and tidal changes, though diel changes are more doubtful.

Spatio-temporal habitat partitioning

Although there is considerable overlap in the prey spectrum of harbour porpoises and bottlenose dolphins (Santos & Pierce, 2003), seasonal distributions of the two species differed markedly, suggesting significant differences in prey preferences. In addition, bottlenose dolphins and harbour porpoises showed fine-scale spatio-temporal partitioning over the tidal cycle, with a strong negative correlation between their relative occurrence, with 40% of the variation in occurrence in one species explained by the other. Site preferences show some congruence, both species typically having the highest abundance at Aberporth and lowest at Cemaes Head, and preferring New Quay to any other site during the winter. However, there was little or no correlation between their detection rates at each site on a daily or hourly basis, and only 2.7% of hourly detections were positive for both species. Similarities in site preferences are therefore presumably a result of aggregation of different prey species in areas of high productivity, with observed temporal differences in bottlenose dolphin and harbour porpoise habitat use related to differences in temporal behaviour of their respective prey or avoidance of interspecific competition.

With prey distribution thought to be the primary factor influencing the spatio-temporal distribution of cetaceans, it is probable that although there is some overlap in the prey spectrum of bottlenose dolphins and harbour porpoises, prey specialisation of the two species has driven a divergence in seasonal, diel and tidal occurrence (Bearzi, 2005). Such habitat partitioning is likely to have occurred as a result of selection to minimise competition for resources between these two sympatric species, leading to a divergence in ecological niches. This is the some of the first evidence of habitat partitioning between these two species and its evolutionary history is therefore unknown. However, increasing mortality rates of harbour porpoises as a result of aggressive encounters with bottlenose dolphins, may be evidence of continued and increasing competition between these species for food and space, with a doubling in mortality rates over the last ten years (Bennett *et al*., 1995; Deaville & Jepson, 2006). Such changes in the level of interspecific competition could result from changes in the distribution or abundance of one or both species, or may be a consequence of recent local declines in stocks of many major prey species, due to overfishing (Pinnegar *et al*., 2002). Alternatively, these fatal attacks may result from bottlenose dolphins practicing infanticidal or aggressive behaviours (Ross & Wilson, 1996; Patterson *et al*., 1998), either way this would act as an additional selective force for divergence in the spatio-temporal distribution of the two species.

Recommendations for Management

Temporal and spatial use of the SAC by bottlenose dolphins and harbour porpoises differs significantly and it is important that management plans reflect this. Fine-scale habitat use is dynamic, with site preferences changing between seasons and even different stages of the tidal cycle and the full temporal range of habitat use must be protected. Aberporth and New Quay appear to be critical areas for both bottlenose dolphins and harbour porpoises and zonation of the SAC into different levels of protection may help further conserve these critical habitats. In particular, limits on fishing activity and an extension of the code of conduct for boat users, to locations other than New Quay, may particularly minimise detrimental impacts on dolphin and porpoise populations as bycatch is the largest cause of mortality on Welsh coasts (Bennett *et al*., 2000), while boat activity can also significantly affect habitat use (Corkeron, 1995), and behavioural budgets of cetaceans (Lusseau, 2003).

Acknowledgements

I would like to thank all staff and volunteers at Seawatch Foundation for their help with this project. I would particularly like to thank Hanna Nuuttila for her ideas, advice and support throughout the project and Peter Evans for his suggestions and comments on an earlier draft of this manuscript.

References

Aarefjohr, H., Bjorge, A., Kinzea, C.C., & Lindsted, I. (1995) Diet of harbour porpoise *(Phocoena phocoenu)* in Scandinavian waters. *Report of the International Whaling Commission*, **16**, 211-222.

Aprahamian, M.W., Jones, G.O., Gough, P.J. (1998) Movement of adult Atlantic salmon in the Usk estuary, Wales. *Journal of Fish Biology*, **53**, 221–225

Akamatsu, T., Teilmann, J., Miller, L., Tougaard, J., Dietz, R., Wang, D., Wang, K., Siebert, U. & Naito, Y. (2007) Comparison of echolocation behaviour between coastal and riverine porpoises. *Deep-Sea Research*, **54**, 290-297.

Au, W., Popper, A. & Fay, R. (2000) Hearing by Whales and Dolphins. Springer Verlag.

Bailey, H. & Thompson, P. (2006) Quantitative analysis of bottlenose dolphin movement patters and their relationship with foraging. *Journal of animal ecology,* **75**, 456-465.

Baines, M. & Earl, S. (1999) Analysis of sightings data for indications of harbour porpoise breeding off the Welsh coast. Contract Science Report. No. 379. *Marine Environmental Monitoring*. 19pp.

Baines, M.E., Evans, P.G.H., and Shepherd, B. (2000) *Bottlenose Dolphins in Cardigan Bay, West Wales.* First Report to EU INTERREG & Countryside Council for Wales. Sea Watch Foundation, Oxford.

Ballance, L. T., Pitman, R. L. & Fiedler, P. C. (2006) Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: A review. *Progress in Oceanography*, **69**, 360-390.

Bearzi, M. (2005) Habitat Partitioning by Three Species of Dolphins in Santa Monica Bay, California. *Bulletin of the Southern California Academy of Sciences*, **104**, 113–124

Bennett, P. M., Jepson, P. & Deaville, R. (2000) Cetacean strandings investigation: England and Wales and Poseidon database. Final report on contract CR0177. Conducted for the Department of the Environment, Transport and the Regions.

Borjesson, P., Berggren, P., & Ganning, B. (2003) Diet of harbour porpoises in the Kattegat and Skagerrak Seas: Accounting for individual variation and sample size. *Marine Mammal Science,* **19**, 38-58.

Bräger, S. (1993). Diurnal and seasonal behavior patterns of bottlenose dolphins (*Tursiops truncatus*). *Marine Mammal Science*, **9**, 434-438.

Cardinale, M., Casini, M., Arrhenius, F. & Hakansson, N. (2003) Diel spatial distribution and feeding activity of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the Baltic Sea. *Aquatic Living Resources*, **16**, 283-292.

Carlström, J. (2005) Diel variation in echolocation behaviour of wild harbor porpoises. *Marine Mammal Science*, **21**, 1-12.

Carstensen, J., Henriksen, O.D., Teilmann, J., (2006). Impacts on harbour porpoises from offshore wind farm construction: acoustic monitoring of echolocation activity using porpoise detectors (T-PODs). *Marine Ecology Progress Series,* **321**, 295–308.

Cheal, A. J. & Gales, N. J. (1992) Growth, sexual maturity and food intake of Australian Indian Ocean bottlenose dolphins, *Tursiops truncates*, in captivity. *Australian Journal of Zoology*, **40**, 215-223.

Corkeron, P. J. (1995) Humpback whales (Megaptera novaeangliae) in Hervey Bay, Queensland: Behaviour and responses to whalewatching vessels. *Canadian Journal of Zoology*, **73**, 1290–1299.

Cox, T.M., Read, A.J., Solow, A., & Tregenza, N. (2001) Will harbour porpoises *(Phocoena phocoena)* habituate to pingers? *Journal of Cetacean Research & Management,* **3**, 81–86

de Boer, M. N. & Simmonds, M. P. (2003) Small cetaceans along the coasts of Wales and Southwest England. WDCS/Greenpeace Survey Report.

Deaville, R. & Jepson, P. D. (2006) UK cetacean strandings investigation programme. Annual Report to DEFRA for the periods 1st January -31st December 2006.

Eisfeld, S.M. & Kock, K. H. (2006) Expert Paper to the ASCOBANS Conservation Plan for Harbour Porpoises (*Phocoena phocoena* L.) in the North Sea. Working Paper. Doc.

MOP5 Doc. 18 (S). ASCOBANS 5th Meeting of the Parties, Egmond aan Zee, Netherlands, 18-22 September 2006. 69pp.

Evans, P.G.H. (1980) Cetaceans in British waters. *Mammal Review*, **10**, 27-52.

Evans, P.G.H. (1990) European cetaceans and seabirds in an oceanographic context. *Lutra*, **33**, 95-125.

Evans, P.G.H. (1996) Temporal and spatial distributions of harbour porpoises in Shetland waters, 1990-1995. The Shetland Cetacean Report, 1995. Published by the Shetland Sea Mammal Group, August 1996.

Evans, P. G. H., Baines, M. E. & Sheperd, B. (2000). Bottlenose dolphin prey and habitat sampling trials. *Report to the Countryside Council for Wales.* Sea Watch Foundation, Oxford, pp.65.

Evans, P.G.H., Anderwald, P. & Baines, M.E. (2003) UK cetacean status review. *Report to English Nature and Countryside Council for Wales*. Sea Watch Foundation, Oxford. 160 pp.

Fisher, P. & Tregenza, N. (2003) An assessment of the effect of a tidal power generator on porpoise habitat use and an evaluation of the acoustic methods employed, August - October 2003. A report to the Highlands and Islands Enterprise, Shetland Islands Council, The Crown Estate & The Engineering Business Ltd.

Gannon, D.P., Craddock, J.E., & Read, J. A. (1998) Autumn food habits of harbour porpoises *(Phocoena phocoena)* in the Gulf of Maine. *Fishery Bulletin, U.S.*, **96**, 428-437.

Gibson, R. N., Robb, L., Burrows, M.T. & Ansell, A.D. (1996) Tidal, diel and longer term changes in the distribution of fishes on a Scottish sandy beach. *Marine Ecology Progress Species*, **130**, 1-17.

Gordon, J. & Tyack, P.L. (2002) Acoustic Techniques for Studying Cetaceans. Pp. 293-324. In: Evans, P.G.H. and Raga, J.A. (Editors) *Marine Mammals: Biology and Conservation.* Kluwer Academic/Plenum Press, New York & London. 630pp.

Gregory, P. R. & Rowden, A. A. (2001) Behaviour patterns of bottlenose dolphins *(Tursiops truncatus*) relative to tidal state, time-of-day, and boat traffic in Cardigan Bay, West Wales. Aquatic Mammals, **27**, 105-113.

Grellier, K., Arnold, H., Thompson, P.M., Wilson, B. and Curran, S. (1995)
Management recommendations for the Cardigan Bay bottlenose dolphin population. *Report to the Countryside Council for Wales* (CCW Contract Science Report No 134).

Hastie, G.D., Wilson, B., Thompson, P.M. (2003) Fine-scale habitat selection by coastal bottlenose dolphins: application of a new land-based video-montage technique. *Canadian Joural of Zoology*, **81**, 469-478.

Henderson, P. A. & Corps, M. (1997) The role of temperature and cannibalism in interannual recruitment variation of bass in British waters. *Journal of Fish Biology*, **50**, 280-295.

Jones, J.G. & Sayigh, L.S. (2002) Geographic variation in rates of vocal production of free-ranging bottlenose dolphins. *Marine Mammal Science*, **18**, 374-393.

Lamb, J. (2004) Relationships between presence of bottlenose dolphins, environmental variables and boat traffic; visual and acoustic surveys in New Quay Bay, Wales. MSc Thesis, University of Wales, Bangor, UK.

Leeney, R.H. and Tregenza, N.J.C. (Editors) (2006) Static Acoustic Monitoring of Cetaceans. Proceedings of workshop held at 26th Annual Conference of European Cetacean Society, Gdynia, Poland, 2 April 2006. European Cetacean Society Special issue No. 46, Kiel, Germany

Lusseau, D. (2003) The effects of tour boats on the behavior of bottlenose dolphins: Using Markov chains to model anthropogenic impacts. *Conservation Biology*, **17**, 6.

Mann, J., Connor, R., Barre, L. & Heithaus, M. (2000) Female reproductive success in bottlenose dolphins: life history, habitat provisioning, and group-size effects. *Behavioural Ecology*, **11**, 210-219.

Mendes, S., Turrell, W.R., Lutkebohle, T., & Thompson, P.M. (2002) Influence of the tidal cycle and a tidal intrusion front on the spatio-temporal distribution of coastal bottlenose dolphins. *Marine Ecology Progress Series,* **239**, 221–229.

Northridge, S.P., Tasker, M.L., Webb, A. & Williams, J.M. (1995) Distribution and reletive abundance of harbour porpoises (*Phocoena phocoena* L.), white-beaked dolphins (*Lagenorhynchus albirastris* Grey), and minke whales (*Balaenoptera acutorastrata* Lacepede) around the British Isles. *ICES Journal of Marine Science,* **52**, 55-66.

Patterson, I., Reid, R., Wilson, B., Grellier, K., Ross, H. & Thompson, P. (1998) Evidence for infanticide in bottlenose dolphins: an explanation for violent interactions with harbour porpoises? *Proceedings of the Royal Society*, *London*, **265**, 1167-1170.

Pesante, G., Baines, M. E., Felce, T. H., Ugarte, F. & Evans, P. G. H. (2007) Trends of abundance of bottlenose dolphins and harbour porpoises in the Cardigan Bay Special Area of Conservation, Wales (2001-2006). 21st conference of the European Cetacean Society.

Philpott, E., Englund, A., Ingram, S. & Rogan, E. (2007) Using T-PODs to investigate the echolocation of coastal bottlenose dolphins. *Journal of the Marine Biological Association*, **87**, 11-17.

Pinnegar, J. K., Jennings, S., O'Brien, C. M. & 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.

Poloczanska, E.S., Cook, R.M., Ruxton, G.D., & Wright, P.J. (2004) Fishing vs. natural recruitment variation in sandeels as a cause of seabird breeding failure at Shetland: a modelling approach. *ICES Journal of Marine Science,* **61**, 788-797.

Ross, H. M. & Wilson, B. (1996) Violent interactions between bottlenose dolphins and harbour porpoises. *Proceedings of the Royal Society*, *London*, **263**, 283-286.

Santos, M. B. & Pierce, G. J. (2003) The diet of harbour porpoise in the Northeast Atlantic. *Oceanography and Marine Biology: an Annual Review*, **41**, 355-390.

Santos, M. B., Pierce, G. J., Reid, R. J., Patterson, I., Ross, H. M. & Mente, E. (2001) Stomach contents of bottlenose dolphins in Scottish waters. *Journal of the Marine Biological Association*, **81**, 873-878.

Sini, M. I., Canning, S. J., Stockin, K. A. & Pierce, G. J. (2005) Bottlenose dolphins around Aberdeen harbour, north-east Scotland: a short study of habitat utilization and the potential effects of boat traffic. *Journal of the Marine Biological Association*, **85**, 1547-1554.

Teilmann, J., Henriksen, O.D., Cartensen, J.and Skov, H. (2002) Monitoring effects of offshore windfarms on harbour porpoises using PODs (porpoise detectors). Ministry of the Environment, Denmark.

Toresen R., Østvedt O.J. (2000) Variation in abundance of Norwegian spring-spawning herring (*Clupea harengus*, Clupeidae) throughout the 20th century and the influence of climatic fluctuations. *Fish and Fisheries*, **1**, 231-256.

Tougaard, J., Poulsen, L., Amundin, M., Larsen, F., Rye, J. & Teilman, J. (2006) Detection function of T-PODs and estimation of porpoise densities. Proceedings of the workshop Static Acoustic Monitoring of Ceatceans, 20th Annual Meeting of the European Cetacean Society, Poland.

Tregenza, N. (2007). *T-POD online help pages.* http://www.chelonia.co.uk/html/pod.html

Verfuss, U. K., Honnef, C. G., Meding, A., Dahne, M., Mundry, R. & Benke, H. (2007) Geographical and seasonal variation of harbour porpoise (*Phocoena phocoena*) presence in the German Baltic Sea revealed by passive acoustic monitoring. *Journal of the Marine Biological Association*, **8**, 165-176.

Williams, T., Shippee, S., Rothe, M. (1996) Strategies for reducing foraging costs in dolphins. In: Greenstreet, S., Tasker, M. (eds) Aquatic predators and their prey. Fishing News Books, University Press, Cambridge, pp 4–9.

Wilson, B., Thompson, P.M., Hammond, P.S. (1997) Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. *Journal of Applied Ecology*, **34**, 1365–1374

Winslade, P., (1974) Behavioural studies of the Lesser Sandeel (*Ammodytes marinus)* (Raitt). II. The effect of light intensity on activity. *Journal of Fish Biology,* **6**, 577-586

Word count: 5641