The occurrence and foraging activity of bottlenose dolphins and harbour porpoises in Cardigan Bay SAC, Wales.

by

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SEA WATCH
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Declaration

This work has not been accepted in substance for any degree and is not being currently submitted for any degree.

This dissertation is being submitted in partial fulfilment of the requirements of M.Sc. Marine Biology.

This dissertation is the result of my own independent work / investigation, except where otherwise stated.

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Abstract

Ten cetacean click detectors (T-Pods) were deployed at set locations within Cardigan Bay SAC. From sounds recorded between March 2005 and February 2006, bottlenose dolphin and harbour porpoise click trains were determined to allow for investigation into the occurrence and foraging activity of the two species. In doing so, the study would build on current knowledge of use of the SAC by these two species using both visual and acoustic methods.

Clear patterns in occurrence were determined, with bottlenose dolphin abundance reaching a maximum in September and October 2005, and harbour porpoises in December 2005. Spatial shifts between T-Pod locations were not detected, however. Occurrence was further influenced by the spring/neap tidal cycle with bottlenose dolphins showing a trend of increased detection with increased tidal height and harbour porpoises a trend of decrease. It was assumed that changes in abundance were most likely related to prey availability.

Using click train characteristics to determine those trains involved specifically in foraging, two peaks in foraging activity were revealed. The first occurred during the late summer and early autumn, but was only observed at offshore Aberporth. A second peak occurred during winter months at the majority of T-Pod locations and was believed to be a consequence of increased foraging requirements, declines in prey abundance or due to a reduction in boat activity. The analysis of foraging clicks did not distinguish between bottlenose dolphins and harbour porpoises, and so it was not possible to link foraging to a particular species.

Foraging was found to be unrelated to time of day at the majority of locations, although nocturnal foraging was revealed at Cardigan Island and offshore Aberporth. Tidal state was further found to affect foraging activity, with most foraging occurring during the first half of the ebb or first half of the flood. Velocity did not appear to affect foraging activity.

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Abbreviations

Throughout, abbreviations of the names of T-Pod locations and tidal states are used on graphs. These include:

T-Pod Locations

AB in – inshore Aberporth
AB out – offshore Aberporth
CA – Cardigan Island
CH in – inshore Cemaes Head
CH out – offshore Cemaes Head
MW in – inshore Mwnt
MW out – offshore Mwnt
NQ f – New Quay fish factory
NQ r – New Quay reef
YN – Ynys Lochtyn

Tidal States

1st Flood – the first half of the flood tide
2nd Flood – the second half of the flood tide
1st Ebb – the first half of the ebb tide
2nd Ebb – the second half of the ebb tide

1. Introduction

The southern region of Cardigan Bay (Wales) is a 'Special Area of Conservation' as a consequence of the resident bottlenose dolphin population, with the region believed to be an important feeding and breeding area for the species (Countryside Council for Wales *et al.*, 2001). Also home to a population of harbour porpoises, the region is subject to visual monitoring programmes. In 2005, hydrophone acoustic monitoring by Sea Watch Foundation extended the studies of distribution, abundance and habitat use by the two species within the SAC. This study focused on information obtained from hydrophones deployed in the SAC to develop a better understanding of how the two main cetacean species inhabiting the SAC used the coastal zone, and to examine aspects of this relatively new monitoring method.

1.1 The study species: the bottlenose dolphin and harbour porpoise

The bottlenose dolphin is the best known of all cetacean species (Wells & Scott, 1999). Until recent molecular studies it was believed that the bottlenose dolphin formed one species with two separate types, although they are now classified as separate species: the Atlantic bottlenose dolphin (*Tursiops truncatus*) and the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) (Morisaka *et al.*, 2005). The Atlantic bottlenose dolphin has been studied more intensively than any other species of Delphinidae (Saayman *et al.*, 1973), and probably more than any cetacean species (Wells & Scott, 1999). Widely distributed, the bottlenose dolphin inhabits both tropical and temperate marine waters (Shane, 1980; Wiley *et al.*, 1994). Their diet and habitats are extremely varied (Ballance, 1992), although they are most often concentrated in inshore locations (Wells & Scott, 1999), hence their ease of study in comparison to many other cetaceans.

The harbour porpoise has a less extensive distribution than the bottlenose dolphin, and is confined to the temperate waters of the northern hemisphere (Gaskin *et al*., 1993; Read & Westgate, 1997). It is one of the commonest cetaceans found in British waters (Evans, 1990; Hammond *et al*., 2002; Evans *et al*., 2003; Reid *et al*., 2003), and one of the most studied of the phocoenids (Boran *et al*., 2001). The harbour porpoise is typically a species of shelf seas, and in the region, often inhabits the waters off headlands, and in bays, estuaries and tidal channels (Baines & Earl, 1999). Their restriction to the continental shelf is probably a consequence of their limited diving ability and demersal feeding habits (Read, 1999).

1.1.1 Diet and foraging behaviour

Bottlenose dolphins consume a wide variety of fish and invertebrate species (Irvine *et al*., 1981; Ballance, 1992; Santos *et al*., 2001). Regardless of location, bottlenose dolphins display a preference for sciaenids, scombrids and mugilids, although proportions in the diet depends on the local abundance of these prey species (Wells & Scott, 1999). The harbour porpoise feeds on a variety of small schooling fish such as clupeids and gadoids (Read, 1999; Santos *et al*., 2004), exploiting seasonally abundant prey (C. Pierpoint, pers. comm.).

Bottlenose dolphins generally forage as solitary individuals in coastal waters, although the cooperative herding of prey by larger groups has occasionally been observed (Wilson *et al*., 1997; Wells & Scott, 1999). It has been suggested that foraging in deeper waters requires group cooperation often involving over 15 individuals. Collaborative strategies include combined echolocation to expedite prey detection, precise group positioning and the entrapment of prey between groups (Saayman *et al*., 1973; Würsig & Würsig, 1979). Cooperative feeding has been reported in the harbour porpoise but usually only for catching schooling prey. Observations of harbour porpoises have described individuals maintaining position for long periods of time against strong tidal currents. This behaviour has been interpreted as the harbour porpoises ambushing prey which may be carried and concentrated by the current and benthic topography (Evans, 1997; C. Pierpoint, pers. comm). However, actual observation of the concentration of prey and the ambush by harbour porpoises is lacking. One study in the Bay of Fundy, Canada did identify aggregations of prey species along localized fronts using acoustic and remote sensing techniques and suggested that areas of vortices and increased current strength such as around headlands and islands could potentially lead to prey aggregation (Johnston *et al*., 2005). In Shetland, Scotland, echosounder surveys revealed harbour porpoises to be associated with concentrations of sandeels, with porpoises positioning themselves at the head of a basin in Mousa Sound at times of increasing tidal strength (Evans, 1997).

Bottlenose dolphins often forage around characteristic topographic features, for example deep, narrow channels with steep sloping sea beds and strong tidal currents. Reports of such areas being used by bottlenose dolphin populations come from geographically distinct areas, for example, off the north east of Scotland (Wilson *et al*., 1997; Hastie *et al*., 2004), in Cardigan Bay (Evans & Lewis,1993), and in the Shannon estuary, Ireland, (Ingram & Rogan, 2002). Wilson *et al*. (1997) suggested that the topographic features may increase foraging efficiency by creating a bottleneck for migratory fish, a theory later endorsed, but without substantial evidence, by Hastie *et al*. (2004). Harbour porpoise populations in Shetland, Scotland (Evans, 1997), off the coast of West Wales (Pierpoint *et al*., 1998) and in the Bay of Fundy, Canada, (Johnston *et al*., 2005) have also been observed foraging in areas of strong tidal currents, which were again thought to concentrate prey species (Evans, 1997; Johnston *et al*., 2005). In contrast, the foraging habitats of bottlenose dolphin populations in Sarasota Bay, Florida (Barros & Wells, 1998) and the Gulf of California (Ballance, 1992) include shallow sea grass and estuarine areas with high nutrient levels which consequently support an abundance of zooplankton and fish (Balance, 1992).

Incidences of foraging and feeding by bottlenose dolphins and harbour porpoises have been associated with the time of day and stage of the tidal cycle. Off the coasts of Africa (Saayman *et al*., 1973) and Texas (Bräger, 1993), feeding activity peaks in the morning with a secondary peak occurring in late afternoon. Off the Florida coast, foraging activity peaks at dawn and progressively decreases throughout the day (Allen *et al*., 2001). In contrast, off the Argentine coast, peak feeding activity is reached in the afternoon (Würsig & Würsig, 1979). In all cases, the ultimate factor creating the observed patterns is most likely the diurnal patterns and availability of prey species.

Associations between foraging activity and tidal cycles have been observed for bottlenose dolphins inhabiting the Shannon Estuary, Ireland, with foraging twice as frequent on flowing tidal states as opposed to during slack water (Ingram & Rogan, 2002). Harbour porpoises at particular sites within Cardigan Bay are reported to forage almost entirely on the ebb tides (C. Pierpoint, pers. comm.). Off the coast of New Quay (Cardigan Bay), bottlenose dolphin foraging was observed to occur mainly during the first half of the ebb (Gregory & Rowden, 2001).

At Ynys Lochtyn (Cardigan Bay, south of New Quay), foraging was concentrated during the first half of the ebb and the second half of the flood (Gregory & Rowden, 2001). Peak foraging activity appears, therefore, to vary over even a small distance of a few kilometres suggesting that different areas could provide rewarding foraging grounds depending on the tidal state. Foraging and feeding behaviours of bottlenose dolphins and harbour porpoises will have direct consequences on observed daily and seasonal migration and habitat usage by the two species. An understanding of foraging and feeding will therefore aid the interpretation of observed habitat usage and migrations over daily to seasonal timescales.

1.1.2 Seasonal migration and daily movement

Long-term tagging and monitoring programmes have greatly increased our knowledge of the ranges and movement exhibited by small toothed whales. For example, populations of coastal bottlenose dolphins have been documented to exhibit permanent home ranges and seasonal migrations (Wells & Scott, 1999). The extent of seasonal migration exhibited by bottlenose dolphins and harbour porpoises can vary greatly between populations, with some exhibiting little or no seasonal migration such as those in Argentine Bay (Würsig, 1978) and Florida (Irvine *et al*., 1981) and others displaying movements of up to hundreds of kilometres such as the Moray Firth population where individuals may range as far south as the Northumberland coast (Evans *et al*., 2003). The extent of movement by a population has likely implications for management, with management of populations displaying localised movements being focused into smaller regions, demanding fewer resources and potentially proving more effective than the management of populations undergoing extensive migrations.

Seasonal movements may relate to the distribution and abundance of prey species, or water temperature which may possibly cause migration directly or indirectly through redistributing the prey. Within the Moray Firth, Scotland, movement is associated with the migration of prey species, the Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*), through the inner Moray Firth to spawn in the spring and summer months (Wilson *et al*., 1997). Off the coast of Western Florida, bottlenose dolphin movement into the Gulf of Mexico is associated with the movement and spawning activity of the striped mullet (*Mugil cephalus*) (Irvine *et al*., 1981). Seasonal migrations of harbour porpoises are less clearly understood (Read, 1999), although they also appear to be food related. For example, the migration of harbour porpoises into Fish Harbour, Canada, coincides with the arrival of juvenile herring (*Clupea harengus*) (Gaskin & Watson, 1985). The density of prey species will obviously affect the extent of local movement, with cetaceans feeding on localised but densely aggregated prey displaying smaller ranges than populations feeding on more dispersed and less densely aggregated prey species (Würsig and Würsig, 1979).

Movement of the bottlenose dolphin and harbour porpoise over a daily timescale has been associated with the tidal cycle for numerous populations. However the ultimate cause is most likely the occurrence of prey species, with certain tidal states optimising foraging techniques or by the movement of prey species being tidally related and cetacean movement being indirectly related to the tidal cycle as a consequence. Off the Texas coast, bottlenose dolphins swim consistently against the ebb and occasionally against the flood tide and this is suggested to be a consequence of greater fish numbers moving through the area on an ebbing tide (Shane, 1980). Off the Florida coast, bottlenose dolphin movement occurred mainly against the tide, with dolphins frequently moving against strong tidal currents (Irvine *et al.*, 1981). In contrast, bottlenose dolphins in Cardigan Bay, Wales, often move with the tidal flow or during slack water, suggested to decrease the energetic cost of swimming (Gregory & Rowden, 2001).

The daily ranging of harbour porpoises, like bottlenose dolphins, have also been associated with the tidal cycle and current strength. Off the Canadian coast, radio tagged harbour porpoises moved inshore with the flood tide and offshore with the ebb tide (Read & Gaskin, 1985). Off Ramsey Sound in West Wales, harbour porpoises travel to foraging sites on prevailing tidal currents suggested to decrease the energetic cost of movement and foraging (C. Pierpoint, pers. comm.).

Knowledge of the movement, range and habitats utilised by bottlenose dolphins and harbour porpoises is integral to the successful management and protection of both the species and the habitats in which they are found. An understanding of how habitat utilisation is impacted by season, time of day, tide and benthic topography is important for focused management so as to maximise returns from the finite inputs of capital, manpower and time, and allow for successful conservation.

1.1.3 Echolocation

The vocalisations of small toothed whales can be separated into distinct structural types: the long duration narrow-band whistles used for intraspecific communication, and the short duration broadband burst pulse sounds and echolocation clicks (Reyes Zamudio, 2005; Wells & Scott, 1999). Echolocation is suggested to have evolved to overcome problems associated with self orientation and object location in poorly illuminated conditions. It is thought to have arisen independently in five mammalian groups (Berta & Sumich, 1999). Echolocation can be defined as the ability to produce high frequency sounds or ‘clicks’ of short duration and to detect the resultant echoes that bounce off targets, and has become highly specialized in odontocete species (Berta & Sumich, 1999; Tyack, 2000).

The source of echolocation sound production is the ‘monkey lips/dorsal bursae’ (MLDB complex) associated with the upper nasal passages. The periodic opening of the monkey lips breaks up the air flow passing through the lips, determining the click repetition rate, with the melon acting to focus the resultant sound (Berta & Sumich, 1999). Echolocation in bottlenose dolphins typically employs pulses within the range of 40-130 kHz and harbour porpoises within the range of 120-150 kHz (Wells & Scott, 1999; Tyack, 2000). The faint high frequency echoes are perceived by the ear and lower jaw which are anatomically specialised to amplify the echoes and enhance sound detection, for example, fat pads in the lower jaw which conduct sound to the middle ear where it is detected (Berta & Sumich, 1999).

Sounds produced by bottlenose dolphins and harbour porpoises can be recorded using deployed hydrophones. With an understanding of the sounds produced by the species, the recordings can be used to monitor occurrence and habitat usage by the species. Information on the distinct characteristics of echolocation sounds used specifically in foraging and food capture can allow for identification of foraging and feeding events. Monitoring bottlenose dolphin and harbour porpoise foraging and feeding will enable identification of the locally important areas for the species, which will further aid the successful management of the species.

1.2 The *Tursiops* and Porpoise Detector (T-Pod)

The T-Pod (Chelonia Marine Research) is a self contained submersible acoustic data logger which continuously records sounds including those made by harbour porpoises and bottlenose dolphins. T-Pod units will also record environmental parameters such as current strength, temperature and salinity (Evans & Hammond, 2004).

Originally called a POD or porpoise detector, the POD was developed to monitor the effectiveness of acoustic alarms for decreasing porpoise by-catch by commercial fishing activities (Tregenza & Northridge, 1999). The later version, the T-Pod or *Tursiops* and porpoise detector, detects and records the vocalisations of both harbour porpoises and bottlenose dolphins.

The deployment of T-Pods is a particularly useful method when studying the harbour porpoise, which at the surface is rather inconspicuous, but is extremely vocal (Evans & Hammond, 2004). Traditional visual observation techniques from land or boat-based surveys used to monitor cetaceans often provide limited coverage, being restricted to surface behaviour, and are dependent on sea and wind state. The accuracy of results obtained from such observational techniques are also dependent upon characteristics of the observers, for example, the number present, eye height, experience and ability, and characteristics of the study species such as school size and behaviour which will affect level of conspicuousness (Evans & Hammond, 2004). The use of T-Pods has the potential to allow more continuous, longer term studies into the movement and foraging behaviour of bottlenose dolphins and harbour porpoises that are less constrained by weather conditions. However, at present, acoustic monitoring is more difficult to interpret than visual monitoring due to a lack of knowledge and understanding of cetacean vocalisation rates (Gordon & Tyack, 2002).

1.3 The Study Area

Cardigan Bay is the largest bay in the British Isles, enclosing an area of approximately 5,500km^2 and comprising around 200km of coastline (Countryside Council for Wales *et al.*, 2001) from St David's Head in the south to the Llyn

Peninsula in the north. It is home to one of three resident populations of bottlenose dolphins found within British and Irish waters, with the other two populations inhabiting the Shannon Estuary in south-west Ireland and the Moray Firth in north-east Scotland.

The study area, the southern end of Cardigan Bay, experiences a mean spring tidal range of 4-5m with tidal currents around 1.8 knots. The tide enters Cardigan Bay via St George's Channel and runs north during the flood and south during the ebb. Tides are semi-diurnal with 12 hours 25 minutes between two successive high or low waters (Baines *et al.*, 2000) which could have implications on observed daily migrations of bottlenose dolphins and harbour porpoises indirectly through redistribution of prey species.

In 2004, Cardigan Bay was designated a Special Area of Conservation (SAC) under Annex II of the EU Habitats and Species Directive (Countryside Council for Wales *et al.*, 2001) as a direct consequence of the resident bottlenose dolphin population. Cardigan Bay SAC covers an area of approximately 968km^2 (Hoyt, 2005) with the boundary running along the coast at mean high water mark from Aberath, Ceredigion, (52° 15' 4"N, 4° 13' 50"W), to the South of the Teifi Estuary, Pembrokeshire, (52° 4' 5"N, 4° 46' 10"W) (Reyes Zamudio, 2005).

Since 1980, 14 species of cetacean have been reported in Cardigan Bay, although the six most regularly encountered species were the bottlenose dolphin (*Tursiops truncatus*), harbour porpoise (*Phocoena phocoena*), common dolphin (*Delphinus delphis*), Risso's dolphin (*Grampus griseus*), killer whale (*Orcinus orca*), and long finned pilot whale (*Globicephala melas*) (Evans, 1995). Aside from cetacean species, Cardigan Bay is further regarded important due to the Atlantic grey seal (*Halichoerus grypus*), sea lampreys (*Petromyzon marinus*), river lampreys (*Lampetra fluvialtilis*) and features such as subtidal sandbanks, reefs and submerged and partially submerged sea caves (Countryside Council for Wales, 2005).

The importance of Cardigan Bay SAC to both bottlenose dolphins and harbour porpoises has led to efforts being made to protect the species through the management of the region. Monitoring of the species is a necessity if management is to be successful. At present, visual observation techniques are the most common form of monitoring in Cardigan Bay SAC. Weather permitting, daily land and boat based surveys are conducted by Sea Watch Foundation and Cardigan Bay Marine Wildlife Centre throughout the summer months.

More recently, in March 2005, T-Pods were deployed by Sea Watch Foundation to acoustically monitor bottlenose dolphins and harbour porpoises at ten locations along the length of coastline within the SAC. Once a greater understanding of acoustic methods is developed, acoustic monitoring has the potential to provide longer term studies into the bottlenose dolphins and harbour porpoises inhabiting the coastal strip of Cardigan Bay SAC, with increased knowledge of the species allowing for more effective management of the species and the SAC.

1.4 Aims and Objectives

The focus of the research was to assess cetacean occurrence and foraging behaviour along the coast within Cardigan Bay 'Special Area of Conservation' using acoustic techniques. Using T-Pod computer software, cetacean presence/absence and foraging click train information was determined over time periods of up to 11 months depending on the extent of data available.

The main objectives of the study were:

- To acoustically differentiate between harbour porpoise and bottlenose dolphin presence.
- To determine if harbour porpoise and bottlenose dolphin presence/absence is related to variables including the spring/neap tidal cycle and month of the year, and to quantitatively describe how cetacean presence varies throughout the study period, from which movement patterns can be inferred.
- To investigate how occurrence of foraging is related to factors such as location, time of day, month of the year, tidal state and current strength.

2. Materials and methods

2.1 T-Pod deployment

Sounds were recorded in Cardigan Bay SAC using a total of ten T-Pods. Deployment was conducted by Sea Watch Foundation at various coastal locations within Cardigan Bay SAC, from New Quay reef in the north to Cemaes Head in the south (see Figure 1) to monitor the presence and movement of the two species within the SAC. Deployment locations were chosen from observations of habitat usage by bottlenose dolphins and harbour porpoises with greater numbers of individuals observed within 15km of the coastline in the areas of T-Pod deployment (Evans, 1995; Baines *et al.*, 2000). V3 model T-Pods were deployed at locations offshore Aberporth, offshore Mwnt, Cardigan Island and offshore Cemaes Head, and the V4 model at locations New Quay reef, New Quay fish factory, Ynys Lochtyn, inshore Aberporth, inshore Mwnt and inshore Cemaes Head. T-Pods were systematically deployed with V4 model T-Pods at inshore locations and V3 at offshore locations. The systematic deployment was chosen because of the increased reliability of the current V4 model and due to the monitoring of inshore waters being of greater interest to Sea Watch Foundation (Sea Watch Foundation, pers. comm.).

The T-Pods were collected, the data downloaded, and the T-Pods then re-deployed every 4-6 weeks with the help of local fishermen (Simon & Evans, 2005). Data recording was continuous once the T-Pod was deployed. The data used for the current study were collected from March 2005 to February 2006.

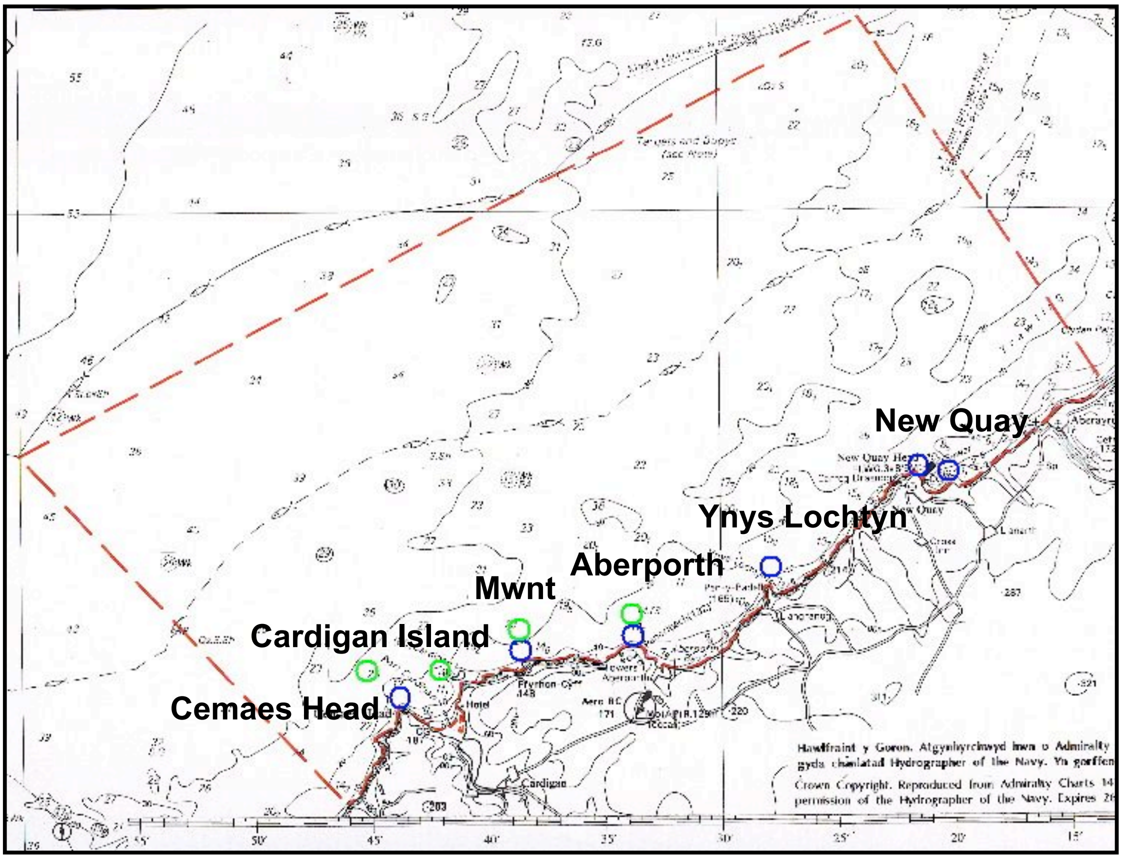


Figure 1 The locations of the T-Pods deployed within Cardigan Bay SAC with green circles representing the V3 model and the blue circles the V4 model. The SAC boundary is shown by the dashed red line. (Map courtesy of Sea Watch Foundation).

2.2 T-Pod settings

The T-Pod has six channels or scans that log click trains for 9.3 seconds. During the current deployment, three non consecutive channels were tuned to a lower frequency range (target filter frequency 50 kHz, bandwidth 5) to detect bottlenose dolphins and the remaining three channels to a higher frequency range (target filter frequency 130 kHz, bandwidth 3) to detect harbour porpoises (Sea Watch Foundation, pers. comm.). Bottlenose dolphins, however, occasionally emit sounds at the higher frequency characteristic of the harbour porpoise and as a consequence the higher frequency scans may sometimes record both species. The scan settings used during the study were selected by Sea Watch Foundation following pool calibration tests conducted at the Oceanographic Museum in Stralsund (Germany), and sea calibration tests to allow for comparison of data recorded on different T-Pods (Simon & Evans, 2005). From calibration experiments the optimal bandwidth settings of 5 for bottlenose dolphins and 3 for harbour porpoises were determined to decrease false detection of bottlenose dolphin sounds on the scan channels set to detect harbour porpoises (Simon & Evans, 2005).

2.3 Acoustic data processing

Downloaded data were analysed using the custom written T-Pod software (v. 7.48), obtainable from http://www.chelonian.demon.co.uk/PODhome.html. The software produces useable data in a two stage process. Firstly, the hydrophone recordings are scanned for recognisable sounds or 'clicks'. Next, data are scanned for detectable strings of clicks known as 'trains'. The software then attempts to classify the trains as cetacean or otherwise produced based on past experience of known cetacean sound emissions. Thomsen *et al.* (2005) describe in detail the process of data classification and integration and their recommendations have been followed for this study. In the current study, click trains in the most likely cetacean sound category were used for the analysis. There was insufficient time to investigate 'doubtful' clicks (Thomsen *et al.*, 2005). Once click trains were identified, they could be examined over time scales ranging from micro seconds to weeks.

The number of detection positive minutes (DPM), the number of minutes within a specified time period in which cetaceans were detected, was exported with a time base from the raw train data. DPM time series were created for largely bottlenose dolphins by summing the trains occurring from the 3 low frequency scans and for largely harbour porpoises from the trains occurring from the 3 high frequency scans. When required, DPM per week were calculated by combining DPM per day recorded in a one week period (from Monday through to Sunday) and were assigned the month in which the DPM were recorded. If a week fell between two months, the calculated DPM per week was assigned the month in which most DPM per days were from. Combining the data in this way produced up to five replicate DPM per week values for each month of the study period.

Click train information for the most likely cetacean noises was extracted to give the train duration, number of clicks in the train, inter-click interval (ICI) and the time and date when the train was recorded. Foraging click trains were defined as trains containing up to and including 70 clicks and possessing maximum inter click intervals (ICI) of less than or equal to 350_m which were suggested by Reyes Zamudio (2005) for bottlenose dolphins, following comparisons between visual observations and acoustic data sets within Cardigan Bay SAC.

Additional tidal information was obtained from Pwllheli tide tables for 2005 and 2006. Times of high and low tide at New Quay and Cardigan throughout the study period were obtained by subtracting 23 minutes for New Quay tide times and 49 minutes for Cardigan. New Quay fish factory, New Quay reef and Ynys Lochtyn were allocated tidal times calculated for New Quay. Inshore and offshore Aberporth, Mwnt, Cemaes Head and Cardigan Island were allocated tidal times calculated for Cardigan. Tidal height information was also obtained from the Pwllheli tide tables. Although not exact values for the study area, tidal height for the study area would have followed the same pattern throughout the course of high to low tide, spring to neap tide during the study period. Pwllheli tidal height would therefore provide a reliable indication of spring and neap tide occurrence.

POLCOMS current data were kindly provided by Dr Simon P. Neill from the Centre of Applied Marine Sciences (University of Wales, Bangor) from a model run for a complete spring and neap tidal cycle for New Quay, Ynys Lochtyn, Aberporth, Mwnt, Cardigan Island and Cemaes Head coordinates. Data were in the form of eastward velocity and northward velocity, from which the vector velocity was calculated using Pythagoras theorem.

The number of believed cetacean foraging click trains recorded per hour was calculated for each location over the ten-month study period. Values of foraging click trains per hour for each location were allocated a stage of the tidal cycle depending on when the trains were recorded in relation to high and low tide, using categories previously adopted by Gregory and Rowden (2001). The allocation of tidal states was repeated twice and compared so as to prevent mistakes. Values of foraging click trains per hour were further allocated a velocity value calculated from the current data set.

3. Results

3.1 Cetacean Presence

3.1.1 Separating bottlenose dolphin and harbour porpoise recorded click trains

DPM per day from channels set to detect higher frequency sounds and those set to detect lower frequency sounds for each T-Pod location are shown in figure 2.

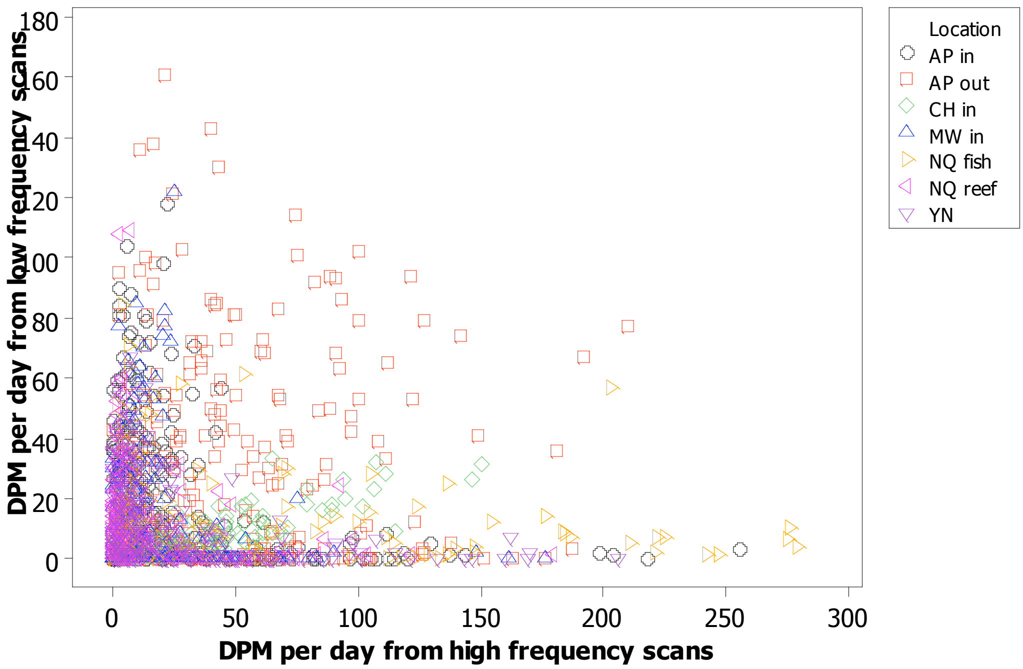


Figure 2 Detection positive minutes per day from high frequency scans against detection positive minutes per day from low frequency scans for each T-Pod location (N=1513).

The graph reveals clear L - shaped distributions for most locations, indicating that recorded sounds were picked up on either the channels set to detect the low frequency sounds or on the channels set to detect the higher frequency sounds, but rarely on both channels simultaneously. However, data collected at offshore

Aberporth do not show an L – shaped distribution with recorded sounds commonly being detected on both the scan channels set to detect high frequency sounds and those set to detect low frequency sounds. Data collected at inshore Cemaes Head also do not conform to an L – shaped distribution with the data appearing to follow a positive correlation between DPM per day recorded on channels set to detect high frequency sounds and channels set to detect low frequency sounds.

Pearson's correlation coefficients were calculated for DPM1 *versus* DPM2 to determine if the higher frequency scans were picking up solely harbour porpoise vocalisations or both harbour porpoise vocalisations and high frequency bottlenose dolphin sounds. A significant negative correlation between DPM1 and DPM2 would indicate that the channels set to the higher frequency were detecting harbour porpoises and that both cetacean species used the area, although at different times. A significant positive correlation between DPM1 and DPM2 would indicate both high and low frequency vocalisations were being detected together and that either both species were co-occurring or that the channels set to the higher frequency were detecting bottlenose dolphins emitting a high frequency. A lack of correlation between DPM1 and DPM2 would suggest that the channels set to the higher frequency were occasionally detecting harbour porpoises and occasionally bottlenose dolphins, with both species co-occurring, preventing partition of bottlenose dolphins and harbour porpoises. The results of the correlation analysis are show in table 1.

Table 1 Pearson's correlation coefficients, degrees of freedom (df) and associated probabilities for correlations between detection positive minutes (DPM) per day number 1 (detected by scan channels set to the lower frequency) and DPM 2 (detected by scan channels set to the higher frequency) for each T-Pod location. Significant correlations are shown in bold.

T-Pod Location	Pearson's Correlation	df	p
Inshore Cemaes Head	**0.876**	207	**p<0.001**
Inshore Mwnt	**-0.233**	241	**p<0.001**
Inshore Aberporth	**-0.303**	250	**p<0.001**
Offshore Aberporth	0.019	230	p=0.777
Ynys Lochtyn	**-0.371**	218	**p<0.001**
New Quay Fish Factory	**-0.187**	165	**p=0.015**
New Quay Reef	**-0.209**	188	**p=0.004**

DPM per day recorded at the offshore T-Pod deployed at Aberporth revealed no significant correlation between DPM1 and DPM2 (Pearson's correlation 0.019, df = 230 p = 0.777), although on examination of the scatterplot a negative correlation was suggested at the upper range of DPM1 which could have been masked by the large proportion of data points with DPM1 values of zero. It was decided to divide DPM2 into bands of 0-50, 51-100, 101-150, 151+ DPM per day and within each band take the top 25% with respect to DPM1 and re-test for a significant correlation. On removal of the lowest 75% in each band the correlation still proved non-significant (Pearson's correlation -0.214, df = 56 p = 0.107). It must be presumed that the scans set to the higher frequency, giving rise to DPM2, were sometimes detecting harbour porpoises and other times bottlenose dolphins emitting higher frequency sounds. As a consequence, DPM for harbour porpoises and bottlenose dolphins recorded at offshore Aberporth could not be partitioned and further analysis examined the two species combined as 'all cetaceans'.

The data set from inshore Cemaes Head revealed a significant positive correlation between DPM1 and DPM2 (see Table 1), suggesting that either harbour porpoises and bottlenose dolphins were occurring both spatially and temporally together or bottlenose dolphins were emitting high frequency sounds in addition to lower frequency sounds and as a consequence were being detected on both channels. As with data from the offshore T-Pod at Aberporth, harbour porpoises and bottlenose dolphins could not be partitioned and further analysis examined both species combined as ‘all cetaceans’.

DPM per day recorded at Ynys Lochtyn, New Quay fish factory, New Quay reef and the inshore sites at Mwnt and Aberporth revealed significant negative correlations between DPM1 and DPM2 (see Table 1). The significant negative correlations between higher frequency sounds and lower frequency sounds detected by the T-Pods suggest that channels set to the lower frequency were detecting bottlenose dolphins and channels set to the higher frequency harbour porpoises. DPM1 therefore represented bottlenose dolphin detections and DPM2 harbour porpoise detections, and as a consequence the two species could be examined individually in further analysis.

3.1.2 Variation in relation to tidal height

Detection positive minutes per day were used as an indicator of cetacean presence and correlated with daily average high tidal height using Pearson’s correlation. The test would determine possible relationships between cetacean presence and tidal height and, indirectly, relationships with velocity and the spring and neap tidal cycle. For the T-Pod locations offshore Aberporth and inshore Cemaes Head DPM1 and DPM2 were combined to examine all cetacean presence. As explained above, DPM1 and DPM2 were analysed individually to examine bottlenose dolphin and harbour porpoise presence for the records made at Ynys Lochtyn, New Quay fish factory, New Quay reef, inshore Mwnt and inshore Aberporth.

Bottlenose dolphin and harbour porpoise combined DPM per day for the locations offshore Aberporth and inshore Cemaes Head showed no significant correlation with average daily tidal height for each month of the study period, the results of which are shown in Table 2.

Table 2 Pearson's correlation coefficients, degrees of freedom (df) and associated probabilities for correlations between average daily tidal height and harbour porpoise and bottlenose dolphin detection positive minutes per day combined for the locations offshore Aberporth and inshore Cemaes Head for each month between the period June to December 2005.

Location	**Aberporth offshore**			**Cemaes Head inshore**		
Month	Correlation	df	p	Correlation	df	p
All	-0.032	180	0.672	-0.033	169	0.666
June	0.120	8	0.740			
July	-0.369	22	0.076	-0.278	29	0.130
August	-0.246	28	0.190	0.148	27	0.444
September	0.091	27	0.638	0.196	24	0.336
October	0.273	27	0.152	-0.194	28	0.305
November	-0.008	28	0.968	0.307	27	0.105
December	0.290	28	0.120	0.149	21	0.498

For data collected at locations Ynys Lochtyn, New Quay fish factory, New Quay reef, inshore Mwnt and inshore Aberporth, bottlenose dolphin and harbour porpoise DPM per day were analysed independently for each month in which data sets were available, the results of which are shown in Table 3. Significant negative correlations between bottlenose dolphin detection and average daily tidal height were rare, with two proving to be significant out of 10 negative correlations (at inshore Mwnt during May and August 2005). 15 of the remaining 29 positive correlations proved significant. In contrast, significant positive correlations between harbour porpoise detection and average daily tidal height were rare, with one being significant out of 12 positive correlations (at inshore Mwnt during December 2005). Of the remaining 23 negative correlations, five proved significant.

Table 3 Pearson's correlation values, degrees of freedom (df) and associated probabilities for correlations between average daily tidal height and detection positive minutes per day for each month between the period June to December 2005. Table I. bottlenose dolphin DPM per day. Table II. harbour porpoise DPM per day analysed separately for locations Ynys Lochtyn, New Quay fish factory, New Quay reef, inshore Mwnt and inshore Aberporth. Significant correlations are shown in bold.

I.

Location	**Ynys Lochtyn**			**New Quay Fish Factory**			**New Quay Reef**			**Mwnt Inshore**			**Aberporth Inshore**		
Month	Correlation	df	p	Correlation	df	p	Correlation	df	p	Correlation	df	p	Correlation	df	p
All	**0.270**	214	**<0.001**	**0.268**	149	**0.001**	**0.302**	172	**<0.001**	-0.110	191	0.127	0.148	231	0.024
May	**0.030**	29	**0.030**							**-0.364**	29	**0.044**	0.297	29	0.104
June	0.627	8	0.052							0.128	19	0.579	0.161	28	0.396
July	**0.429**	22	**0.035**				0.336	21	0.117				-0.068	29	0.717
August	**0.438**	28	**0.015**	-0.127	28	0.505	-0.058	28	0.762	**-0.576**	19	**0.006**	0.370	21	0.082
September	**0.443**	27	**0.016**	**0.400**	28	**0.028**	**0.365**	28	**0.048**	0.366	27	0.051	**0.378**	27	**0.043**
October	0.300	29	0.101	**0.487**	29	**0.005**	**0.522**	29	**0.001**	0.002	29	0.992	0.228	27	0.235
November	**0.402**	28	**0.028**	**0.369**	28	**0.045**	**0.369**	28	**0.045**	0.132	27	0.495	0.085	28	0.655
December	-0.085	29	0.649	-0.017	28	0.928	0.032	28	0.865	-0.254	17	0.294	-0.271	28	0.148

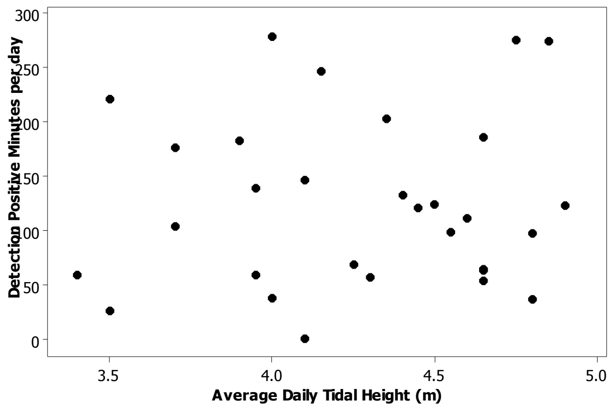
II.

Location	**Ynys Lochtyn**			**New Quay Fish Factory**			**New Quay Reef**			**Mwnt Inshore**			**Aberporth Inshore**		
Month	Correlation	df	p	Correlation	df	p	Correlation	df	p	Correlation	df	p	Correlation	df	p
All	-0.117	214	0.086	0.049	149	0.553	0.042	172	0.580	0.007	191	0.922	-0.068	231	0.298
May	-0.174	29	0.349							0.007	29	0.970	-0.169	29	0.364
June	-0.120	8	0.741							-0.383	19	0.086	-0.202	28	0.284
July	-0.315	22	0.134				-0.300	21	0.164	-0.327	10	0.299	**-0.595**	29	**<0.001**
August	-0.301	28	0.106	-0.058	28	0.760	0.008	28	0.966	-0.261	19	0.253	**-0.715**	20	**<0.001**
September	**-0.497**	27	**0.006**	0.090	28	0.635	-0.202	28	0.284	-0.337	27	0.074	-0.170	27	0.378
October	-0.272	29	0.139	-0.004	29	0.981	0.029	29	0.877	**-0.500**	29	**0.004**	-0.274	27	0.151
November	0.077	28	0.687	0.128	28	0.502	-0.019	28	0.919	0.177	27	0.359	0.126	28	0.506
December	**-0.550**	29	**0.001**	0.062	28	0.744	0.352	28	0.056	**0.529**	17	**0.020**	0.104	28	0.584

Results suggest a trend of increased bottlenose dolphin detection with increasing tidal height, indicating greater detection during times of spring tide in relation to neap tides. This could be a consequence of greater dolphin vocalisation during spring tides or increased numbers of dolphins occurring in the area of T-Pod deployment during spring tides, leading to greater rates of detection. In contrast to bottlenose dolphins, harbour porpoises appeared to show trends of decreased detection with increased tidal height, with detection greatest during neap tide, although supported by a smaller number of significant correlations than for bottlenose dolphins.

Three sample graphs are displayed in Figure 3 to illustrate the data patterns. The first shows a month in which no correlation was observed between DPM per day and average daily tidal height, the second a month in which a significant positive correlation was observed between bottlenose dolphin DPM per day and average daily tidal height and the third a month in which a significant negative correlation was observed between harbour porpoise DPM per day and average daily tidal height.

I.



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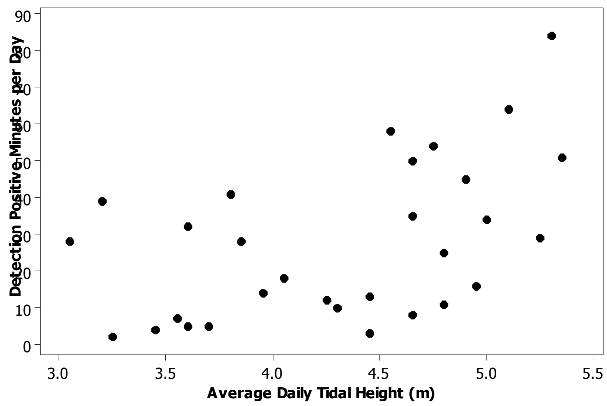

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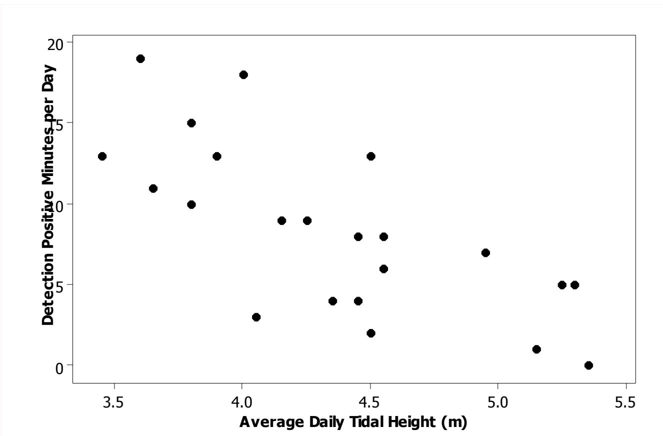


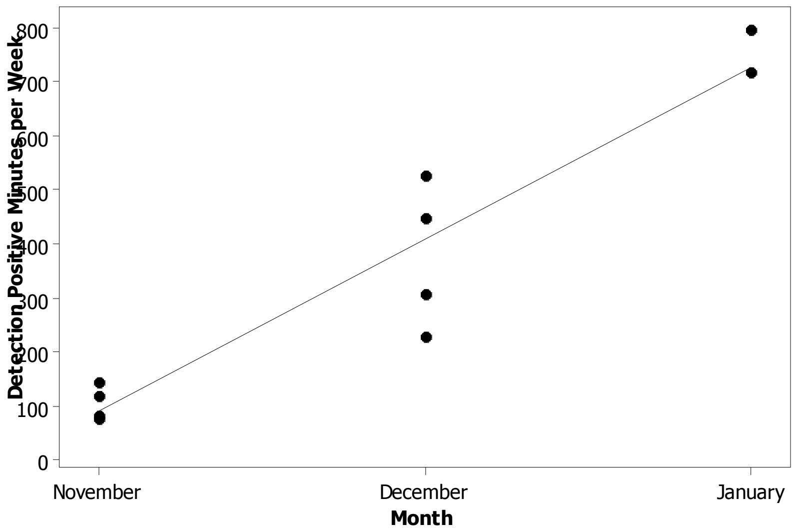
Figure 3 Graphs showing the patterns of no, positive and negative correlation obtained when Pearson's correlation analysis was conducted on detection positive minutes per day and average daily tidal height. I. No correlation obtained at New Quay fish factory for harbour porpoise detection positive minutes per day during December 2005. II. Significant positive correlation obtained at New Quay fish factory for bottlenose dolphin detection positive minutes per day during October 2005 with a clear positive correlation evident at high tidal heights. III. Significant negative correlation obtained at inshore Aberporth for harbour porpoise detection positive minutes per day during August 2005.

To determine if the correlations detected were indicative of an effect of tide on cetacean presence, the number of correlations that were i. significantly positive ii. showed no correlation or iii. significantly negative were recorded for each of the two species. Significance was equated to the 10% rather than the 5% level, given the high variability and relatively low number of observations. A chi-squared test of independence indicated a significant difference between the distributions of correlations for bottlenose dolphins and harbour porpoises ($\chi^2 = 16.453$, df=2, $p<0.001$). Of 34 correlations for bottlenose dolphin presence with average tidal height, 16 proved significantly positively correlated (at the 10% level), 16 showed no correlation and two proved significantly negatively correlated. Of 35 correlations of harbour porpoise presence with average tidal height, two proved significantly positively correlated (at the 10% level), 25 showed no correlation and eight proved significantly negatively correlated. The highest chi-square contribution was obtained from the positive correlations, suggesting the greatest cause of difference between the distributions was the greater than expected number of bottlenose dolphin correlations displaying significant positive correlations with tidal height and lower than expected for harbour porpoises. From the analysis it is evident that bottlenose dolphin presence either shows no relationship with average tidal height or shows a positive correlation with DPM per day increasing with average tidal height. Harbour porpoise DPM per day most frequently displayed no relationship with average tidal height, although a decrease in presence as average tidal height increases was indicated.

3.1.3 Variation between T-Pod deployment locations and months of the year

Values of DPM per week for each T-Pod location were plotted against month of the year and examined to see where patterns of increasing or declining detection positive minutes per week existed, examples of which are shown in Figure 4. As explained above, DPM1 and DPM2 were combined for locations offshore Aberporth and inshore Cemaes Head. For the remaining locations, DPM1 and DPM2 were examined separately.

I.



II.

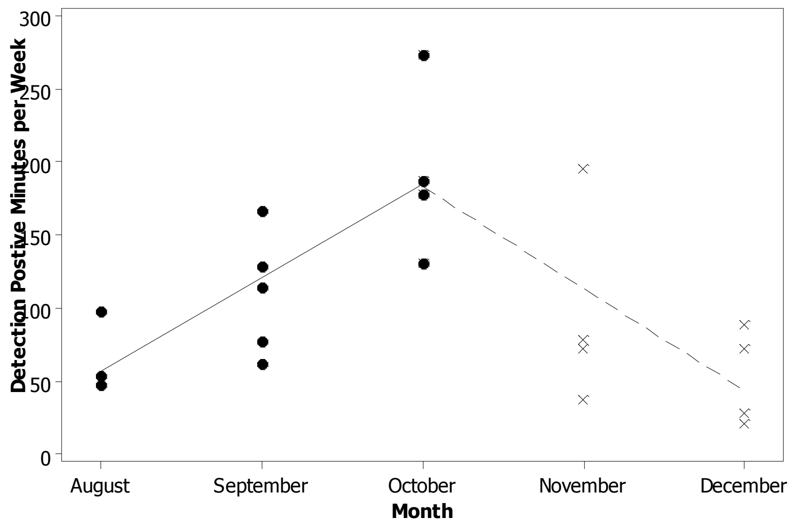


Figure 4 An example of the patterns of changing DPM per week per month observed for I. harbour porpoises II. bottlenose dolphins on which regression analysis of variance was performed. I. Harbour porpoise DPM per week at inshore Aberporth between November 2005 to January 2006. II. Bottlenose dolphin DPM per week at New Quay fish factory between August to December 2005.

Combined bottlenose dolphin and harbour porpoise DPM per week obtained at both inshore Cemaes Head and offshore Aberporth proved to be significantly negatively correlated with time from September to November 2005 (Pearson's correlation -0.895, df = 6, $p<0.001$ and Pearson's correlation -0.890, df = 9, $p<0.001$ respectively). Table 4 shows an analysis of variance, with time as a covariate, for weekly average DPM. During the period of September to November 2005, DPM per week at offshore Aberporth declined by 297.25 minutes per month, i.e. approximately 5 hours per month, over the three-month period. At inshore Cemaes Head, DPM per week declined by 161.99 minutes per month, hence nearly 3 hours, over the same three-month period. The rate of decline in detection was significantly greater for offshore Aberporth than inshore Cemaes Head (see Table 4 (II), Interaction $F_{1,17} = 5.01$, $p = 0.039$). Table 4 (I) shows that the initial level of detection (DPM per week) was 2.7x greater at offshore Aberporth than inshore Cemaes Head.

Table 4 The results of regression analysis for "all cetacean" detection positive minutes per week for offshore Aberporth and inshore Cemaes Head.

I. Predicted start values for September 2005 with associated 95% confidence intervals and slopes from regression analysis of all cetacean detection positive minutes per week against month of the year between September to November 2005. Slopes significantly differ.

T-Pod Location	Predicted Initial Detection (DPM wk^{-1})	95 % CI	Slope (DPM wk^{-1} mth^{-1})
Offshore Aberporth	934.70	784.00 - 1085.40	-297.25
Inshore Cemaes Head	347.10	266.40 - 427.80	-161.99

II. Analysis of variance table with month of the year as the covariate, Seq = sequential Adj = adjusted for entry order into the model.

Source	df	Seq SS	Adj SS	Adj MS	F	P
Season & Location	1	996447	121137	121137	8.95	**0.008**
Month	1	820129	781311	781311	57.72	**<0.001**
Interaction	1	67783	67783	67783	5.01	**0.039**
Error	17	230109	230109	13536		
Total	20	2114468				

Harbour porpoise DPM per week obtained at inshore Aberporth, inshore Mwnt, New Quay fish factory, New Quay reef, and Ynys Lochtyn all showed highly significant positive correlations against month between periods ranging from September 2005 to January 2006 (see Table 5). All positive correlations fell within the range of 0.775 and 0.946, with associated probabilities of 0.005 or less.

Bottlenose dolphin DPM per week obtained at inshore Aberporth, inshore Mwnt, New Quay fish factory and New Quay reef all showed significant positive correlations against month of the year for summer months between May to October 2005, with positive correlations ranging between 0.442 and 0.765 and associated probabilities of 0.045 or less. Following that summer to autumn increase, negative correlations ranging from -0.752 to -0.869 with associated probabilities of 0.005 or less, were obtained (see Table 5).

Table 5 Pearson's correlation values, degrees of freedom (df) and associated probabilities for correlations between harbour porpoise and bottlenose dolphin detection positive minutes per week and month of the year. The months over which the significant correlations were found are given in brackets.

Species	**T-Pod Location**	**Pearson's Correlation**	**df**	**p**
Harbour porpoises:	Inshore Aberporth (Nov 2005 - Jan 2006)	**0.946**	8	**<0.001**
	Inshore Mwnt (Sept 2005 - Jan 2006)	**0.813**	17	**<0.001**
	New Quay Fish Factory (Oct - Dec 2005)	**0.807**	9	**0.003**
	New Quay Reef (Oct - Dec 2005)	**0.775**	9	**0.005**
	Ynys Lochtyn (Sept - Dec 2005)	**0.793**	14	**<0.001**
Bottlenose dolphins	Inshore Aberporth (May - Sept 2005)	**0.442**	19	**0.045**
	Inshore Aberporth (Sept - Dec 2005)	**-0.818**	13	**<0.001**
	Inshore Mwnt (May - Oct 2005)	**0.730**	16	**0.001**
	Inshore Mwnt (Oct - Dec 2005)	**-0.836**	8	**0.003**
	New Quay Fish Factory (Aug - Oct 2005)	**0.765**	10	**0.004**
	New Quay Fish Factory (Oct - Dec 2005)	**-0.752**	10	**0.005**
	New Quay Reef (Jul - Oct 2005)	**0.576**	13	**0.024**
	New Quay Reef (Oct - Dec 2005)	**-0.855**	10	**<0.001**

Prior to regression analysis, three consecutive values of 5 DPM per week were removed from the bottlenose dolphin data set for inshore Aberporth in June due to failure to follow observed patterns. Data points preceding and following the removed points were showing DPM per week values greater than 100 leading to the conclusion that during the consecutive three weeks either a T-Pod failure occurred, an event which masked detection, or there was an event which caused bottlenose dolphins to uncharacteristically leave the area.

Due to lack of homogeneity of residual variance (Bartlett's statistic = 79.99, $p<0.001$), the dependant variable was log transformed to stabilise the variance (resultant Bartlett's statistic = 13.65, $p=0.324$). Comparisons between regressions for all relationships at locations listed in Table 5 were undertaken. Table 6 details the comparisons.

Table 6 The results of regression comparisons for the relationships between harbour porpoise and bottlenose dolphin detection positive minutes (DPM) per week and time (month) at inshore Aberporth, inshore Mwnt, New Quay fish factory, New Quay reef and Ynys Lochtyn.

I. Predicted start values with associated 95% confidence intervals and slopes from regression analysis of harbour porpoise and bottlenose dolphin detection positive minutes per week against month of the year. The months over which regression analysis of variance was conducted are shown in brackets. Letter subscripts indicate slopes that do not significantly differ.

	T-Pod Location	Predicted initial Detection (DPM wk^{-1})	95 % CI	Slope (DPM wk^{-1} mth^{-1})
Harbour porpoises	Aberporth Inshore (Nov 2005 - Jan 2006)	109.12	76.88 - 154.85	0.453 a,b
	Mwnt Inshore (Sept 2005 - Jan 2006)	43.43	26.68 - 70.70	0.225 d,e
	New Quay Fish Factory (Oct - Dec 2005)	57.35	31.23 - 105.27	0.578 a
	New Quay Reef (Oct - Dec 2005)	17.18	8.68 - 34.02	0.536 a,b
	Ynys Lochtyn (Sept - Dec 2005)	48.65	28.70 - 82.19	0.327 a,b,e
Bottlenose dolphins	Aberporth Inshore (May - Sept 2005)	134.93	81.40 - 223.62	0.078 f
	Aberporth Inshore (Sept - Dec 2005)	313.184	186.64 - 525.41	-0.380 c
	Mwnt Inshore (May - Oct 2005)	40.34	27.51 - 59.14	0.119 d,f
	Mwnt Inshore (Oct - Dec 2005)	213.60	109.42 - 416.87	-0.480 c,g
	New Quay Fish Factory (Aug - Oct 2005)	61.17	41.34 - 90.41	0.237 d,e,f
	New Quay Fish Factory (Oct - Dec 2005)	177.91	100.16 - 316.08	-0.313 c
	New Quay Reef (Jul - Oct 2005)	62.99	35.10 - 113.06	0.128 d,e,f
	New Quay Reef (Oct - Dec 2005)	256.15	116.71 - 562.21	-0.638 g

II. Analysis of variance table with month of the year as the covariate, Seq = sequential Adj = adjusted for entry order into the model.

Source	df	Seq SS	Adj SS	Adj MS	F	P
Season & Location	12	5.9142	17.2250	1.4354	22.82	**<0.001**
Month	1	1.9753	0.6081	0.6081	9.67	**0.002**
Interaction	12	18.0324	18.0324	1.5027	23.88	**<0.001**
Error	152	9.5630	9.5630	0.0629		
Total	177	35.4849				

From the lines fitted during regression analysis, it is evident that predicted bottlenose dolphin and harbour porpoise DPM per week values were of a similar magnitude prior to the autumn increase exhibited by bottlenose dolphins and the early winter increase exhibited by harbour porpoises. The increase in DPM per week estimated for harbour porpoises, be it due to increased occupancy or activity levels, was greater than that estimated for bottlenose dolphins, being in the range of eight to fourteen fold as opposed to two to four fold.

In the autumn of 2005, bottlenose dolphin DPM per week values were estimated to increase two fold at inshore Aberporth and New Quay reef, three fold at New Quay fish factory, and four fold at inshore Mwnt, from initial DPM per week values between 40.34 (estimated for inshore Mwnt) and 134.93 (estimated for inshore Aberporth). Following peaks in DPM per week, declines were estimated at approximately four fold at New Quay fish factory, nine fold at inshore Mwnt, thirteen fold at inshore Aberporth, and nineteen fold at New Quay reef. Predicted final DPM per week values were between 13.58 (estimated for New Quay reef) and 42.17 (estimated for New Quay fish factory). During the winter months of 2005 and 2006, harbour porpoise DPM per week values were estimated to increase eight fold at inshore Aberporth and inshore Mwnt, ten fold at Ynys Lochtyn, twelve fold at New Quay fish factory, and fourteen fold at New Quay fish factory from estimated initial values in the region of 17.18 (estimated for New Quay reef) and 109.12 (estimated for inshore Aberporth).

The analysis of variance clearly indicated significant differences between slopes (see Table 6 I), Interaction $F_{12,152} = 23.88$, $p<0.001$). Differences between individual slopes were analysed by T-test using a Bonferroni procedure to adjust significance levels to the number of comparisons. Slopes which did not differ significantly are indicated in Table 6 using letter subscripts. Rates of increase of harbour porpoise DPM per week per month were greater than for bottlenose dolphins. However, the rate of increase of harbour porpoise DPM per week per month proved only significantly greater at the locations inshore Aberporth, New Quay fish factory, New Quay reef, and Ynys Lochtyn, at which the greatest overall rate of increase was observed with an average slope of 0.474 DPM wk^{-1} mth^{-1}. The lowest significant overall rate of increase occurred at inshore Mwnt, inshore Aberporth, New Quay fish factory and New Quay reef for bottlenose dolphin DPM per week per month with an average slope of 0.141 DPM wk^{-1} mth^{-1}. Bottlenose dolphin declines in DPM per week per month occurred at the greatest rate at locations inshore Mwnt and New

Quay reef with an average slope of -0.559 DPM wk^{-1} mth^{-1}. Rate of decline at locations inshore Aberporth, inshore Mwnt and New Quay fish factory for bottlenose dolphin DPM per week per month occurred on average at a lower rate with an average slope of -0.391 DPM wk^{-1} mth^{-1}. For bottlenose dolphin DPM per week per month, the rate of increase at all locations was slower than the rate of decrease.

3.2 Incidence of foraging

Over the deployment both in space and time, a total of 161,266 click trains were classified by the software as either high or low probability cetacean noises. According to the criterion adopted (see methods), 2,428 were considered click trains potentially indicating foraging, i.e. 1.5% of the total. Of those indicating foraging, only 251 (10%) were potentially bottlenose dolphins (low frequency scans). As a consequence, all the data were analysed together as ‘cetacean’ although for a number of locations, the great proportion of recorded foraging click trains were likely to have been produced by harbour porpoises.

3.2.1 Time of year

The total number of foraging click trains recorded per month at each T-Pod location was calculated. The number of days over which the totals were calculated varied between months and locations, primarily due to times of T-Pod collection and re-deployment, or T-Pod failure. Values were standardised to allow for comparison by dividing the total number of foraging click trains recorded per month by the total number of days that the T-Pod was recording. Figure 5 shows the standardised values of foraging click trains recorded per month over the study period, for each location.

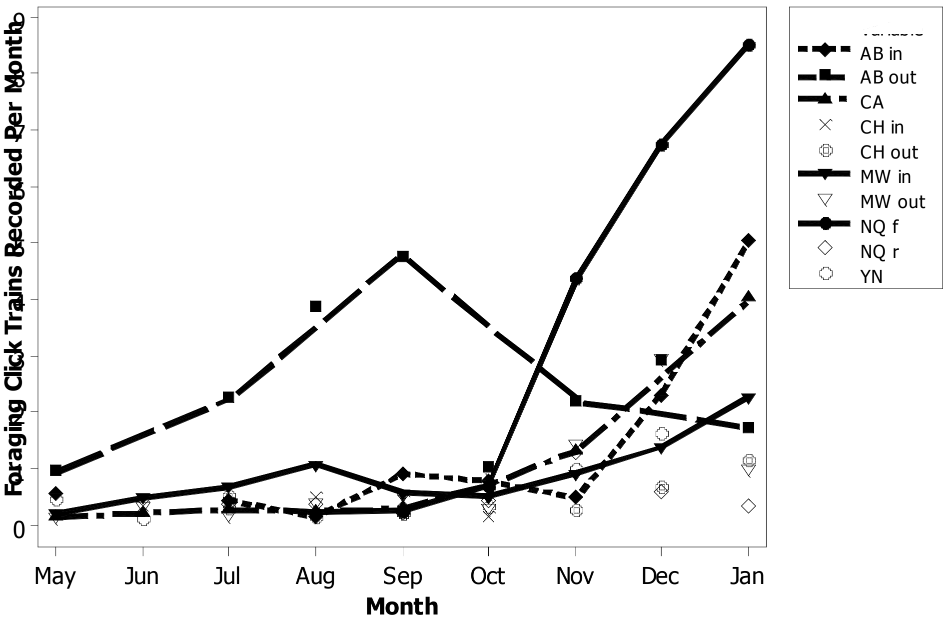


Figure 5 Standardised values of foraging click trains recorded per month at each T-Pod location between May 2005 to January 2006. Lines connect monthly totals for sites showing more than 1 or 2 trains per month.

From the graph it is evident that relatively few suspected foraging trains were detected per month throughout the study period. The number of foraging click trains recorded per month at offshore Aberporth increased during the late summer months and subsequently declined during winter months. That pattern was unique to offshore Aberporth, which also had the greatest numbers of foraging click trains recorded during the summer months. Foraging click trains declined at offshore Aberporth following the September maximum, whereas at New Quay fish factory, inshore Aberporth, Cardigan Island, and to a lesser extent inshore Mwnt, evidence of foraging increased through the winter months (Figure 5). Potential foraging at New Quay fish factory increased to the highest level displayed at any location (nearly 9 'trains' per month, in January 2006, Figure 5). All remaining locations show consistently low levels of recorded foraging click trains per month, with minor fluctuations.

3.2.2 Time of day

The summed total of foraging click trains recorded per hour across all months of the year and T-Pod locations was calculated and analysed using spectral analysis. Day length will vary somewhat throughout the year although if a nocturnal or diurnal foraging preference occurs, it will be revealed by the analysis without the need to account for the changing day length. Figure 6 displays the time series. The cumulative periodogram indicated a significant cyclical trend. The number of foraging click trains recorded declined during the day and reached a maximum at night. Both autocorrelation and partial autocorrelation for the time series indicated a periodic function with a single autoregressive parameter. A single parameter autoregressive ARIMA was fitted to the data, and a spectral "check" (Diggle 1990) used to confirm the significance of the cyclical trend (autoregressive parameter = 0.3224, model variance = 488.0).

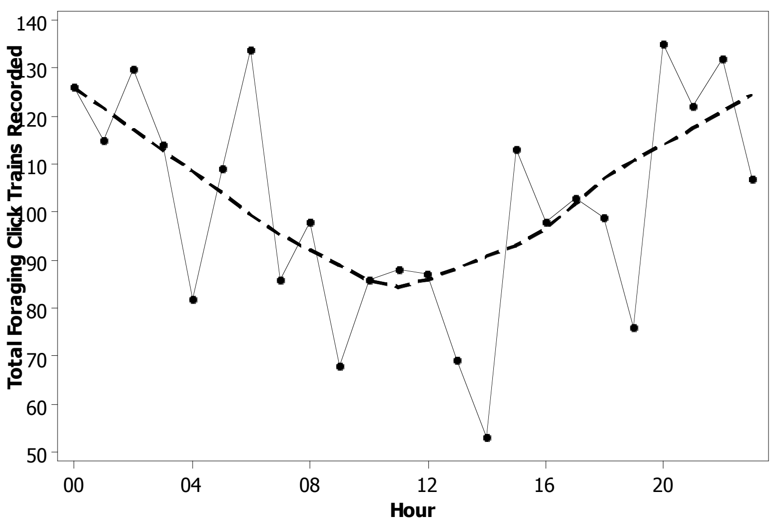
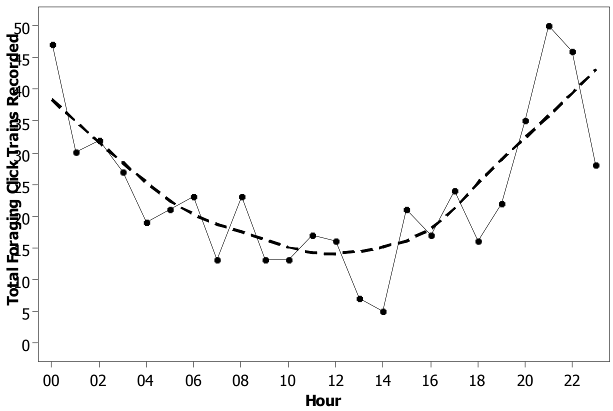


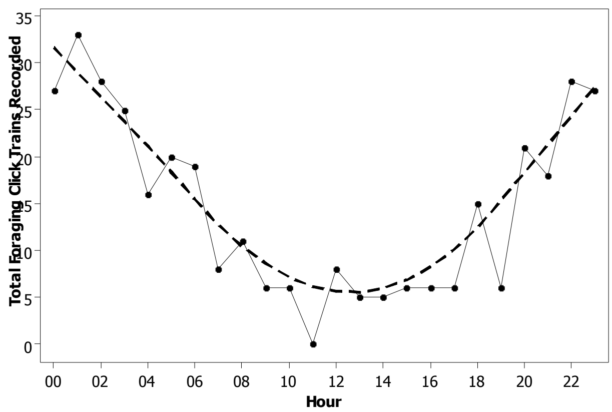
Figure 6 Total foraging click trains recorded in each hour of the day over the whole sampling area and time period. A Lowess smoother has been fitted.

The data were subdivided by location, and investigated for rhythmic trends in potential foraging. T-Pod locations inshore Aberporth, inshore Cemaes Head, offshore Cemaes Head, inshore Mwnt, offshore Mwnt, New Quay reef and Ynys Lochtyn all revealed no significant cyclical trends. Potential foraging events occurred randomly throughout the day and night. At offshore Aberporth and Cardigan Island, a significant nocturnal periodicity was confirmed (offshore Aberporth autoregressive parameter = 0.7440, model variance = 74.87; Cardigan Island autoregressive parameter = 0.8328, model variance = 38.58) (see Figure 7). Potential foraging at New Quay fish factory appeared to show a diurnal activity pattern with clear decline throughout the night (see Figure 7). However, spectral analysis could not detect a significant periodicity at New Quay fish factory.

I.



II.



III.

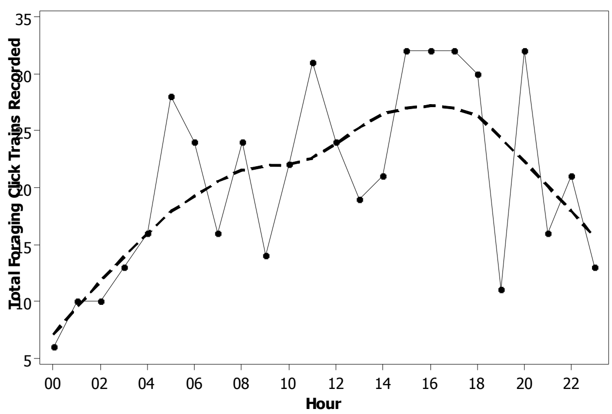


Figure 7 Total foraging click trains recorded per hour of the day between March - June 2005 and January - February 2006 at I. offshore Aberporth, II. Cardigan Island and III. New Quay fish factory. Lowess smoother lines have been fitted to illustrate the periodicity. I. and II. reveal significant nocturnal periodicity. The diurnal periodicity shown in III. proved non-significant.

3.2.3 Tidal State

Total values of foraging click trains recorded were calculated for each location for each of the four tidal stages throughout the study period (see Table 7).

Table 7 The percentage number of foraging click trains recorded per quarter of a complete tidal cycle for each T-Pod location. The total number of foraging click trains recorded at each T-Pod location and stage of the tidal cycle are shown in bold (N=2430).

Tidal State	1st Flood	2nd Flood	Ist Ebb	2nd Ebb	Total
Location					
Inshore Aberporth	28	17	43	12	**275**
Offshore Aberporth	27	17	32	24	**565**
Cardigan Island	35	8	28	29	**350**
Inshore Cemaes Head	16	14	37	33	**43**
Offshore Cemaes Head	17	14	40	30	**96**
Inshore Mwnt	28	14	26	32	**218**
Offshore Mwnt	23	18	34	25	**164**
New Quay Fish Factory	21	35	30	14	**497**
New Quay Reef	30	23	23	23	**98**
Ynys Lochtyn	18	16	45	21	**124**
Total	**628**	**466**	**792**	**544**	

A chi-squared goodness of fit test gave χ^2 = 197.568 for 27 df, and p<0.001, revealing that the frequency distribution across tidal states differed significantly between at least two locations. Across all locations, the greatest number of foraging click trains was recorded during the first half of the ebb (792 trains recorded) and the first half of the flood (628 trains recorded). The least number of foraging click trains was recorded during the second half of the flood (466 trains recorded). Across all tidal states, the T-Pod locations at which the most foraging click trains were recorded were offshore Aberporth, New Quay fish factory and Cardigan Island (565, 497 and 350 click trains recorded respectively). T-Pod locations inshore Aberporth, inshore Mwnt, offshore Mwnt and Ynys Lochtyn had values of 275, 218, 164 and 124 recorded foraging click trains respectively. The lowest numbers of foraging click trains were recorded at inshore Cemaes Head, offshore Cemaes Head and New Quay reef (43, 96 and 98 recorded click trains respectively).

Inshore Aberporth had greater numbers of recorded foraging click trains during the first half of the ebb tide (118 recorded click trains, far greater than expected). A high contribution to chi-square came from the second half of the ebb with 33 recorded click trains (less than expected). Offshore Aberporth had the greatest values of recorded foraging click trains during the first half of the ebb and the first half of the flood (180 and 151 recorded click trains respectively). Cardigan Island provided the second highest chi-square contributor with 28 foraging click trains recorded during the second half of the flood (58% less than expected). Highest levels of recorded foraging click trains at Cardigan Island were experienced during the first half of the flood (124 recorded click trains, 37% more than expected), contributing considerably to chi-square. Numbers of foraging click trains recorded at inshore Cemaes Head were the lowest of all locations, with values ranging between 6 during the second half of the flood and 16 during the first half of the ebb, and consequently providing little information. Offshore Cemaes Head and New Quay reef also showed low numbers of recorded foraging click trains, and provided low contributions to chi square. Inshore Mwnt had greater than expected values of foraging click trains recorded during the second half of the ebb tide, with a large contribution to chi square. Offshore Mwnt, however, showed chi-square contributions of less than 1, with observed values deviating little from expected values. Recorded values of foraging click trains ranged between 30 during the second half of the flood tide and 56 during the first half of the ebb tide. New Quay fish factory provided the largest contributor to chi-square from the second half of the flood tide (173 recorded foraging click trains, 81% greater than expected). Lowest values were recorded during the second half of the ebb (71 recorded foraging click trains, 36% less than expected). Ynys Lochtyn had similar values of recorded foraging click trains throughout all tidal states except during the first half of the ebb when 56 click trains were recorded (39% greater than expected).

Correspondence analysis was used to summarise the differences found between locations, and the resultant graph is shown in Figure 8. 93% of the information is represented in the plot, with 74% from component 1 and 19% from component 2. T-Pod locations inshore Cemaes Head, offshore Cemaes Head and New Quay reef were removed due to values of recorded foraging click trains being less than 100 over the study period, and consequently providing little information. The graph illustrates how recorded foraging click trains at inshore Aberporth and Ynys Lochtyn were associated with the first half of the ebb tide. At New Quay fish factory, recorded foraging click trains were associated with the second half of the flood tide. Foraging click trains recorded at inshore Mwnt were associated with the second stage of the ebb. At Cardigan Island, foraging click trains were recorded mainly during the first half of the flood tide, although also substantially during the ebb, resulting in their positioning on the graph being pulled towards the second half of the ebb. Offshore Mwnt shows little variation between the stages of the tidal cycle, although more foraging click trains were recorded during the ebb, resulting in a central position between the 2nd ebb and 1st ebb. Foraging click trains recorded at offshore Aberporth were associated with the first half of both the flood and the ebb, resulting in a slightly more central positioning.

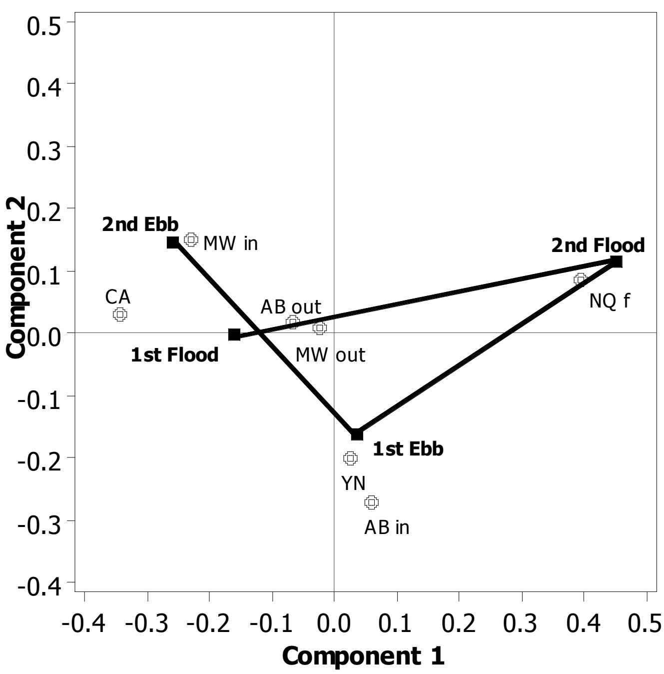


Figure 8 Symmetric row and column plot from correspondence analysis of the total number of foraging click trains recorded at each T-Pod location for stages of the tidal cycle.

3.2.4 Tidal Velocity

Table 8 shows the Pearson's product moment correlation coefficients for the number of potential foraging click trains per hour versus the estimated seawater velocity for each location. At inshore Cemaes Head, two foraging click trains recorded per hour occurred only four times, with all remaining values being of a single foraging click train recorded per hour. Pearson's correlation was consequently not performed on data for inshore Cemaes Head. A significant negative correlation between foraging click trains recorded per hour and vector velocity was found at inshore Aberporth ($r = -0.178$, $df = 173$, $p = 0.018$), and a positive correlation at New Quay fish factory ($r = 0.200$, $df = 281$, $p = 0.001$). The correlations suggested that the number of foraging click trains recorded per hour declined as velocity increased at inshore Aberporth but increased at New Quay fish factory. All remaining locations gave no significant correlations (see Table 8 I).

Despite the large number of data points obtained, most observations were of a single foraging event per hour. The significant correlations were produced largely from a few, much higher, event rates fortuitously located at either high or low current velocities. Given the uncertainty in ascribing trains as "potential foraging events", a large number of single event occurrences could have been no more than random noise. Assuming two or more events are more reliable than one, correlations were ascertained for the remaining foraging events versus tidal velocity after all observations of one event were removed, the results of which are shown in Table 8 II. No significant correlations were obtained and the overall impression of the result confirmed. There was no relationship between tidal velocity (as estimated from the CAMS model) and potential foraging events.

Table 8 Pearson's correlation values, degrees of freedom (df) and associated probabilities for correlations between vector velocity and foraging click trains recorded per hour. I. results of the correlation including values of 1 foraging click train recorded per hour and II. excluding values of 1 foraging click train recorded per hour. Significant correlations are shown in bold.

I.

T-Pod Location	Pearson's Correlation	df	p
Inshore Aberporth	**-0.178**	173	**0.018**
Offshore Aberporth	-0.068	328	0.220
Cardigan Island	0.009	176	0.901
Offshore Cemaes Head	0.103	79	0.361
Inshore Mwnt	-0.001	158	0.985
Offshore Mwnt	0.100	122	0.270
New Quay Fish Factory	**0.200**	281	**0.001**
New Quay Reef	-0.009	59	0.945
Ynys Lochtyn	0.045	95	0.665

II.

T-Pod Location	Pearson's Correlation	df	p
Inshore Aberporth	-0.227	36	0.170
Offshore Aberporth	-0.039	94	0.708
Cardigan Island	0.126	61	0.325
Inshore Mwnt	0.005	38	0.976
Offshore Mwnt	-0.215	25	0.281
New Quay Fish Factory	0.059	99	0.561
New Quay Reef	-0.386	13	0.155
Ynys Lochtyn	0.049	16	0.848

4. Discussion

4.1 Cetacean Presence

4.1.1 Separating bottlenose dolphin and harbour porpoise recorded click trains

Initially, detection positive minutes obtained from T-Pod scans set to detect either bottlenose dolphins or those set for harbour porpoises could not be assumed to be a direct measure of the target species presence and absence. However, interpretation of correlations between DPM from differential scans obtained at locations Ynys Lochtyn, New Quay fish factory, New Quay reef, inshore Mwnt and inshore Aberporth strongly suggested that each unique scan setting was indeed detecting the target species. The scan channels set to the lower frequency were hence detecting bottlenose dolphins and the scan channels set to the higher frequency were detecting harbour porpoises.

Correlation of DPM obtained at the offshore Aberporth T-Pod, however, revealed that, on occasions, the higher frequency scan was not only detecting the target species, harbour porpoises, but also occasionally the non target species, bottlenose dolphins. At the inshore Cemaes Head T-Pod, analysis of DPM correlation revealed that either bottlenose dolphins and harbour porpoises were occurring both spatially and temporally together, or that the higher frequency scans were detecting non-target bottlenose dolphins. Such uncertainty clearly demonstrates the danger of presuming that scans set to detect a target species are indeed detecting the correct species. Future work that aims to investigate the presence and absence of bottlenose dolphins and harbour porpoises as two separate species should first conduct correlation analysis on the data set to determine if the separate scan channels were detecting the target species. If the two channels were indeed detecting the correct target species, further investigation and analysis can thus commence with harbour porpoise and bottlenose dolphin species treated independently.

4.1.2 Variation in relation to tidal height

At the T-Pod locations Ynys Lochtyn, New Quay fish factory, New Quay reef, inshore Mwnt and inshore Aberporth where harbour porpoise and bottlenose dolphin presence could be studied separately, a trend for increased detection with increased tidal height was indicated for bottlenose dolphins. Such a trend would suggest that either bottlenose dolphins were becoming more vocal during times of high tidal height, i.e. during spring tides, or detection was increasing as a consequence of increased numbers of individuals visiting the T-Pod locations during spring tides. Gaskin and Watson (1985) propose that the transportation of small fish would be at a maximum on spring tides, perhaps explaining why bottlenose dolphin detection was greatest during times of spring tide. However, observational evidence supporting maximum transport of prey species in Cardigan Bay on spring tides is lacking and could form the focus of future study.

Harbour porpoise detection displayed a trend of decrease with increased tidal height, although the trend was less apparent than the trend observed for bottlenose dolphins. The finding indicates that either the species was becoming less vocal during times of spring tide or detection was declining as a consequence of harbour porpoises leaving the T-Pod locations during times of spring tides and returning during neap tides. The finding supports a previous study on harbour porpoises inhabiting Fish Harbour, Canada, in which it was found that their abundance was greatest during neap tides (Gaskin & Watson, 1985). Gaskin and Watson (1985) suggest that greater abundance would have been expected on spring tides under the presumption that the transport of small fish into the study area would have been at a maximum. However, Gaskin and Watson (1985) explain the greatest abundance observed during neap tides to be a consequence of harbour porpoises avoiding semi-enclosed areas during times of extreme current velocities.

In the Moray Firth, violent interactions between bottlenose dolphins and harbour porpoises have been reported, often resulting in the death of harbour porpoises (Ross

& Wilson, 1996; Jepson & Baker, 1998). If the two species come into competition in Cardigan Bay it is possible that harbour porpoises avoided the locations during spring tides when bottlenose dolphin occupancy was potentially maximal. Spatial partitioning of harbour porpoises and bottlenose dolphins in Cardigan Bay has been documented by Bristow (1999), Baines *et al*. (2005) and Simon *et al*. (2006), with Bristow 1999 reporting that the two species were rarely seen within 400m of each other.

The presence of harbour porpoises and bottlenose dolphins at the T-Pod locations offshore Aberporth and inshore Cemaes Head were unrelated to tidal height and hence the spring and neap tidal cycle, with "all cetacean" DPM per day showing no significant correlation with average daily tidal height for each month within the study period. Since the two species were not separated from T-Pod records at these sites, and their respective behaviours with respect to the spring neap cycle appear inverse, it is not unexpected to find no correlation when occurrences of both species are combined.

4.1.3 Variation between T-Pod deployment locations and months of the year

At the T-Pod locations inshore Cemaes Head and offshore Aberporth cetacean presence declined between September and November 2005. The predicted detection values indicate higher cetacean abundance at offshore Aberporth compared to inshore Cemaes Head, with cetaceans being detected at offshore Aberporth almost three times more often during a one week period. If DPM values are taken as indicators of cetacean presence and regularity of habitat use as opposed to possible changes in levels of vocalisation, it can be suggested that either offshore Aberporth was visited by a large number of cetaceans with each individual visiting occasionally, or that a smaller number of cetaceans were using the area repeatedly, either scenario suggesting regularity of habitat use. The most likely situation is probably somewhere between the two extremes.

During the period of September to November 2005 the number of minutes that cetaceans were detected per week at offshore Aberporth declined by approximately 300 per month over the three month period. At inshore Cemaes Head, detection positive minutes per week declined by approximately 150 per month over the three month period. The rate of decline at offshore Aberporth occurred at approximately double the rate of that recorded at inshore Cemaes Head. The result suggests that either double the number of cetaceans left offshore Aberporth per month between September and November 2005 or that the regularity of return became less frequent with time. It is possible that the result was due to lower levels of cetacean detection at inshore Cemaes Head, suggesting lower numbers of cetaceans, which would have put less pressure on the local food sources. Food sources would have become exhausted after a larger period of time, allowing inshore Cemaes Head to support the cetaceans for longer, preventing a more rapid decline in detection as observed for inshore Aberporth. Future work is required to determine if variation in rates of cetacean decline between locations is a consequence of variation in the abundance of prey species.

4.1.3.1 Bottlenose dolphins

For T-Pod locations inshore Aberporth, inshore Mwnt, New Quay fish factory, New Quay reef and Ynys Lochtyn, harbour porpoise and bottlenose dolphin detection could be studied independently. At all those T-Pod locations except Ynys Lochtyn, an increase in DPM per week was observed for bottlenose dolphins throughout the summer months of May - August through to the autumn months of September - October 2005. The greatest rate of increase of DPM per week was observed for New Quay fish factory and the lowest rate for inshore Aberporth. Although New Quay fish factory displayed the greatest rate of increase and inshore Aberporth the lowest, there was no significant difference between rates at the four locations.

All the locations for which bottlenose dolphin presence could be studied independently of harbour porpoises, excluding Ynys Lochtyn which showed no pattern of seasonal change in DPM, displayed an almost identical pattern of progressive increase in DPM per week through summer to autumn months, although the exact timing of the observed increases varied between locations. The greatest variation was apparent when comparing the months in which increases in DPM per week were first observed, with observed increases at inshore Aberporth and Mwnt beginning in May 2005, and in July and August 2005 at New Quay reef and fish factory respectively. However, such discrepancies are almost certainly a consequence of the availability of T-Pod recordings which did not start until July 2005 for New Quay reef and August 2005 for New Quay fish factory.

Maximum bottlenose dolphin DPM per week were reached in September to October 2005. Bristow and Rees (2001) state that bottlenose dolphin numbers within New Quay Bay were greatest during April to November. However, visual observations by Reichelt (2002) indicated peak numbers within Cardigan Bay to be reached in August to September, only slightly earlier than the current study. An extensive study of seasonal trends in bottlenose dolphin within Cardigan Bay revealed peak numbers to occur earlier again in July and August (Evans et al., 2003). Reichelt (2002) suggested the presence of the cetaceans was linked to the occurrence of seasonally available food such as sea trout and herring.

Peaks in bottlenose dolphin numbers recorded during the summer and autumn have been observed for the population inhabiting the Moray Firth, Scotland, (Wilson *et al.*, 1997). Wilson *et al.* (1997) relate the increase in numbers to the spawning activity of sea trout and Atlantic salmon which migrate into the inner Moray Firth to spawn, resulting in a seasonal increase in food and causing bottlenose dolphin movement inshore. However, the inshore movement of sea trout and salmon occurs from February through to October with numbers peaking in June and July with a subsequent decline throughout August, September and October (A.B. Yule, pers. comm.). It is therefore unlikely that peak dolphin numbers in autumn months within the Moray Firth are a consequence of sea trout and salmon abundance. Bottlenose dolphin numbers off the coast of Southern Texas were observed to reach a maximum in winter months, with recorded numbers being twice as high as those reported in summer months, and were understood to be food dependent (Shane, 1980).

Lamb (2004) suggested that the seasonal increase of bottlenose dolphin numbers in Cardigan Bay could be associated with anticipation of breeding or the rearing of calves. Observational evidence suggests that the number of new born calves and males with fresh wounds (assumed to be the consequence of male aggression involved in mate acquisition) increased in summer months (Lott, 2004).

Over the course of the current study no contemporaneous data on either fish availability or mating behaviour were available. New-born calves within Cardigan Bay can occur in most months of the year, although peak between April and July, and consequently are unlikely to explain the September to October peak in the current study. The timing of the increased bottlenose dolphin abundance in Cardigan Bay most closely approximates prey abundance, with peak sea bass (*Dicentrarchus labrax*) abundance occurring in August and inshore influx of mackerel (*Scomber scombrus*) and herring occurring between July and September (Evans *et al*., 2000; Baines *et al*., 2000, 2005).

All T-Pod locations followed an almost identical pattern of increase DPM per week. None of the studied locations displayed a reverse pattern of declining DPM over the period suggesting that, if DPM values were an indicator of bottlenose dolphin numbers, bottlenose dolphins were arriving in the area from outside the studied T-Pod locations and not shifting along the coast between locations. If bottlenose dolphins were shifting along the coast between T-Pod locations it would be expected that locations experiencing the influx would display a progressive increase in DPM and locations from which the bottlenose dolphins were arriving, would experience a progressive decline in DPM. Such a pattern was not observed indicating that bottlenose dolphins were arriving from outside the area and utilising it all contemporaneously.

Following the summer to autumn increase in bottlenose dolphin DPM per week, an autumn to winter decline occurred. The decline began in October 2005, although it was slightly earlier at inshore Aberporth (September 2005), and reached the lowest point in December 2005 for all four locations. The greatest rate of decline was observed at New Quay reef and the lowest at New Quay fish factory. The rate of decline observed at New Quay reef was found to be significantly greater than that observed at inshore Aberporth and inshore Mwnt, which in turn were not significantly different. The rate of decline observed at New Quay fish factory also did not significantly differ from any location.

Once again, due to the almost identical pattern observed at the various locations (although differing slightly in rate of decline and month of initial decline), it must be presumed that bottlenose dolphins were leaving the areas and moving to other areas rather than altering smaller scale utilisation within the area of study. Bottlenose dolphins off the coast of Cornwall have been observed to spend the winter in waters off southern Cornwall, and move north-east along the coast during the spring and summer (Wood, 1998). Similarly, bottlenose dolphins off the south coast of England move eastward along the coast from spring to summer months, with peak numbers off Dorset recorded in April and May and in Hampshire and Sussex in July and August (Williams *et al*., 1997).

The current, relatively small, study area was clearly utilised in total by bottlenose dolphins rather than systematically through the seasons. Grellier *et al*. (1995) suggest that changes in bottlenose dolphin numbers within Cardigan Bay were a consequence of movement offshore following the seasonal migration of mackerel from inshore to offshore waters in colder months. Movement offshore rather than along the coast would result in the pattern of increase and decline seen within the current study area.

At all locations, the increase of bottlenose dolphin DPM per week occurred at a lower rate than the rate of decline. If values of DPM were representing numbers of bottlenose dolphins, dolphin movement out of the area occurred at a faster rate than that of movement into the area. There were no significant differences between the rates of decline in potential numbers from any of the deployment locations. If the decline in recorded dolphin activity was related to the depletion of a food resource, the end of the breeding season, or a threshold change in temperature, etc, then it occurred across the study area at the same rate. A faster rate of leaving an area than in occupying it initially could be driven by a food resource which accumulates slowly in an area and then disperses or is exhausted much more quickly. Sea trout, for example, accumulate inshore over a protracted period. Accumulation continues until rivers swell sufficiently to allow the trout to journey inland, resulting in a rapid departure of the sea trout if the spat continues (A.B. Yule, pers. comm.).

The greatest predicted value of DPM per week was observed for New Quay fish factory in December 2005. The finding could be interpreted as greater resources resulting in the area supporting relatively more bottlenose dolphins or allowing greater regularity of habitat use. At New Quay, Quay Fresh & Frozen Foods Ltd. is reported to dispose of waste material from processed fish, crustaceans and molluscs directly into the water surrounding the factory, which in turn attracts large numbers of fish such as mackerel (Bristow, 1999). The dumping of fish waste would act to artificially increase bottlenose dolphin prey species in the area, perhaps explaining the slower decline in DPM per week, albeit non-significant, observed at New Quay fish factory and why the location appeared to be able to support dolphin numbers in December.

Observations off the coast of New Quay have reported bottlenose dolphins and harbour porpoises regularly foraging close to the factory outfall fall pipe (Pierpoint & Allan, 2004). Pierpoint and Allan (2004) report that, prior to 2003, approximately 100 kg of whelk meat (*Buccinum undatum*) was discharged per day in addition to crushed shell from the factory. However, following 2003, the disposal of whelk meat ceased, leading to a decline in organic matter entering at New Quay, with the withdrawal of organic matter suggested to have detrimental effects on dolphin numbers in the area (Pierpoint & Allan, 2004). However, it is inconceivable that previous whelk flesh disposal from the factory in 2003 could account for greater bottlenose dolphin occurrence in 2005. On the other hand, artificial nutrient enrichment from wash water could still have been occurring in the surrounding waters, attracting prey species to the area.

At present, the dumping of whelk shell remains continues. In 2004, 2000 tonnes of clean crushed shell waste was dumped into surrounding waters (Pierpoint & Allan, 2004). It was believed that the dumping would have detrimental impacts on benthic prey items, and in turn cause a decline in bottlenose dolphin numbers in the area (Pierpoint and Allan, 2004). The current study does not reveal the predicted low occurrence of bottlenose dolphins off the fish factory. However, Pierpoint and Allan (2004) report that the shell waste was limited to a 50 m radius of the 17 discharge pipes, so never likely to cause a serious environmental issue.

Although New Quay fish factory had the largest DPM per week value of all locations occurring in December 2005, inshore Aberporth had larger predicted values prior to December. If artificial resource enhancement from the fish factory located at New Quay did occur, the result would suggest that the enhancement at New Quay fish factory was only beneficial during winter months when, presumably, resources at the remaining locations had naturally declined or became exhausted. However, little is currently known on the seasonality of resources important to the bottlenose dolphins, making it difficult to link the seasonal activity patterns of bottlenose dolphins to changes in resource levels.

4.1.3.2 Harbour porpoises

At inshore Aberporth, inshore Mwnt, New Quay fish factory, New Quay reef and Ynys Lochtyn, harbour porpoise DPM per week progressively increased between September – November to December 2005 – January 2006, following the reduction in bottlenose dolphin activity. The increase in harbour porpoise DPM per week will, henceforth, be interpreted as increased numbers of harbour porpoises, although the possibility of increased DPM values being a consequence of seasonal changes in vocalisation levels or habitat usage cannot be discounted.

Increases in harbour porpoise numbers in the current study occur later in the year than the seasonal increases reported by Gaskin & Watson (1985) in Fish Harbour (Canada) or by Fisher *et al.* (2003) off the coast of Shetland (Scotland), where increases occur in late August and September. Similar August and September peaks in harbour porpoise numbers are reported off the coast of Ireland, Western and Eastern Scotland and Eastern England (Evans *et al.*, 2003). An extensive study by Evans *et al.* (2003) of harbour porpoise presence in Cardigan Bay reports the occurrence of peak numbers between August to October. In Fish Harbour the seasonal increase in harbour porpoise numbers coincided with increased numbers of juvenile herring appearing in the waters (Gaskin & Watson, 1985) but no similar link was forthcoming for the Shetland porpoises. No obvious trophic links between prey species and porpoises in Cardigan Bay have been identified. If, however, as discussed above, porpoises avoid potentially lethal contact with dolphins they may simply not utilise the area until the dolphins move on.

The greatest rate of increase of DPM per week, presumably reflecting a harbour porpoise influx, was calculated for New Quay fish factory. However, the rate did not differ significantly from those estimated at inshore Aberporth, New Quay reef and Ynys Lochtyn. The rate of potential aggregation at the fish factory was significantly greater than that at inshore Mwnt, the lowest estimated rate. The significance of the fish factory as either a direct source of scavenging or as a concentrator of live prey is still questionable and requires more quantitative evidence.

As with the bottlenose dolphins, the pattern of detection for harbour porpoises was the same across the entire study area with no evidence of a gradual influx progressing up or down the coast. The evidence suggests arrival from offshore which probably would not have been detectable with the T-pod arrays given the short distances between inshore and offshore deployments.

Predicted initial and final values for the changes in harbour porpoise DPM per week over the autumn to winter months were greatest at inshore Aberporth, suggesting greater numbers of harbour porpoises or increased regularity of habitat use. However, towards December, New Quay fish factory experienced increased porpoise numbers. Again, the tempting explanation is that the fish waste disposal offers direct or indirect nourishment in an otherwise fairly barren month but the legislative regulation of neat waste disposal from the factory under the Food and Environment Protection Act (1985) would actually suggest a minimal organic input from that source.

Harbour porpoises tended to arrive in the study area at a faster rate than did the bottlenose dolphins, being statistically significant in several locations. The rate of occupancy may be greater simply because more harbour porpoises come in to Cardigan Bay than bottlenose dolphins, hence their rate of arrival over a comparable time scale must be quicker. Previous abundance estimates within Cardigan Bay using line-transect surveys have estimated harbour porpoise numbers to be 30-40% greater than bottlenose dolphin numbers. Estimates calculated for 2005 were 160 bottlenose dolphins and 215 harbour porpoises (P.G.H. Evans, per. comms.). Alternatively, if the porpoises are excluded from the area until the dolphins start to leave, they may be accumulating on the edges of the study area and hence enter the area apparently more quickly than the dolphins. Evans & Hammond (2004) note that harbour porpoises are more vocally active than dolphins which would lead to a greater increase in detection for each subsequent harbour porpoise that enters the region.

4.2 Incidence of foraging

Only 10% of the total number of potential foraging click trains recorded between May 2005 and February 2006 were detected on scans set to detect bottlenose dolphins, so that the vast majority were derived from scans set to detect harbour porpoises. The low numbers for bottlenose dolphins suggest that the click train characteristics proposed by Reyes Zamudio (2005) are not representative of bottlenose dolphins, and that further work is required to determine characteristics that better define bottlenose dolphin click trains involved in foraging, or alternatively that dolphins rarely feed using echolocation in the area.

4.2.1 Time of year

Potential 'all cetacean' foraging click trains at offshore Aberporth peaked in the late summer months and declined during the winter. Assuming the number of foraging click trains recorded is proportional to cetacean foraging effort, offshore Aberporth appears to be the only location in the study area heavily used for summer-autumn foraging. The marked, late summer increase at offshore Aberporth was not seen at any other location. The peak in potential foraging effort at offshore Aberporth coincides with the bottlenose dolphin influx noted at the inshore locations (see above). A similar, dolphin specific, influx pattern could not be established offshore due to the lack of discrimination between dolphins and porpoises in the detection frequencies.

At offshore Aberporth between October and September 2005, ~26% of all cetacean potential foraging trains could be attributed to bottlenose dolphins. Thus, foraging by harbour porpoises still accounted for the majority of 'all cetacean' foraging click trains recorded even at periods when dolphin detection indicated higher numbers or greater activity and porpoise detection rates were low. Given the very low occurrence of potential dolphin foraging noises throughout the study period it is probable that the wrong criteria have been established to characterise potential foraging in dolphins. Further spectral analysis of the recordings is necessary to unequivocally establish reliable criteria before any more inference is made regarding such data in relation to dolphin behaviour.

Following the decline in the number of foraging click trains recorded at offshore Aberporth, autumn and winter increases beginning in October and November 2005 and continuing into January 2006 were recorded at New Quay fish factory, inshore Aberporth, Cardigan Island and to a lesser extent at inshore Mwnt. New Quay fish factory displayed the largest increase in the number of recorded foraging click trains of all locations, beginning abruptly in October 2005. The observed pattern suggests a shift in foraging intensity from offshore Aberporth in the summer months to New Quay fish factory in the autumn and winter months.

The increase in recorded foraging click trains experienced at the four locations during the autumn and winter months coincides with the increase in harbour porpoise detection (see above). New Quay fish factory experienced the greatest increase in the number of recorded click trains of all T-Pods. The remaining locations, inshore Cemaes Head, offshore Cemaes Head, offshore Mwnt, New Quay reef and Ynys Lochtyn had consistently low levels of recorded foraging click trains throughout the study period.

Walker (2005) attributed low levels of foraging at New Quay to high levels of boat activity. However, if level of boat activity was a factor governing levels of foraging off New Quay, low levels of foraging would also have been expected at the nearby New Quay fish factory. During the present study, New Quay reef exhibited the highest levels of potential foraging of all locations but only in the autumn and winter months. The increase in potential foraging at New Quay fish factory began abruptly also in October 2005 following the end of the tourist season. Bristow (1999) reported that boat traffic around New Quay was concentrated between April to October, with 60% of the annual boat traffic occurring in July and August.

Increased foraging levels observed during the autumn and winter months could be attributed to an increase energy requirement due to declining water temperatures (Bräger, 1993). Bräger (1993) also suggests that declining prey abundance would result in the need for extended times of foraging, increasing levels of foraging observed, which Bräger (1993) related to previous findings on the movement of schooling fish out of the Bay of Galveston, Texas (Gunter, 1945; Nelson 1992). However, little is known about the diet of cetaceans within Cardigan Bay, hence no attempt to link cetacean behaviour patterns to the seasonal migration of prey species can be made (Lamb, 2004). In would also be expected that increased levels of turbidity in winter months would result in an increased reliance on echolocation, leading to high levels of detection and proposed foraging events in autumn and winter months.

4.2.2 Time of day

The number of foraging click trains recorded per hour at offshore Aberporth and Cardigan Island showed a significant periodicity with maximum numbers recorded during night time hours and minimum during daytime hours. The patterns indicate potentially nocturnal foraging behaviour at the two locations. Echolocation would be a necessity at night but an optional extra during daylight. Lamb (2004) found the number of all recorded potential cetacean clicks in the waters of New Quay Bay to increase throughout the night.

A diurnal foraging activity pattern was hinted at for the potential foraging click trains recorded at New Quay fish factory. If boat activity off New Quay harbour was reducing cetacean activity (Walker, 2005) nocturnal behaviour could have been expected. The dumping of fish waste from New Quay fish factory during daylight hours could be expected to result in increased food resources for cetaceans. As a consequence, foraging activity at New Quay fish factory could be expected to show a diurnal pattern as opposed to a nocturnal pattern.

Data from no other T-Pod location showed significant periodicity. Walker (2005) considered foraging within Cardigan Bay to occur throughout the day and night. On the other hand, both Bristow (1999) and Reichelt (2000) indicated that porpoise and dolphin foraging levels peaked in the early morning and late afternoon. However, the conclusions were based on visual observation which would not have continued into hours of darkness. The early morning and late afternoon peaks observed by Bristow

(1999) and Reichelt (2000) could thus form part of an extended nocturnal foraging pattern.

In keeping with the current study, the literature suggests that foraging behaviour patterns are highly variable between locations. In one particular year, Gregory and Rowden (2001) reported bottlenose dolphin foraging regularly throughout the day at New Quay, but mainly in the morning at Ynys Lochtyn. However, once again, the observations were limited to daylight hours. In another part of Cardigan Bay, harbour porpoise activity was found to be predominantly diurnal off the Teifi Estuary but nocturnal in Fishguard Bay, although these patterns varied seasonally (Baines *et al*., 2000). Off the coast of Shetland, Scotland, peak times of harbour porpoise foraging varied seasonally from early morning and evening during summer months to a single evening peak in autumn and winter (Evans, 1997). Off the coast of Texas, bottlenose dolphin foraging and feeding peaked in the late afternoon during the summer with no discernible pattern in the autumn (Bräger, 1993).

4.2.3 Tidal State

Across all locations, the greatest number of foraging click trains was recorded during the first half of the ebb and the first half of the flood, suggesting cetacean foraging to increase following the change in tidal direction. The lowest number of foraging click trains recorded across all locations occurred during the second half of the flood. Within specific locations, where any pattern was discernible, the same basic trend emerged of increased potential foraging following a change in tidal direction.

Previous studies of cetacean foraging in Cardigan Bay have not covered such an extensive stretch of coastline as in this T-Pod study. At Ynys Lochtyn, bottlenose dolphin foraging occurred mainly between the second half of the flood and the first half of the ebb (Gregory & Rowden, 2001). In the current study, greatest levels of foraging occurred during the first half of the ebb as found by Gregory and Rowden (2001), but not during the second half of the flood. Lamb (2004) found greater levels of bottlenose dolphin activity, inclusive of foraging, during the ebb at New Quay. The current study found foraging levels to be greatest at New Quay fish factory during the second half of the flood, which contrasts with Lamb's findings, although high numbers were also observed during the first half of the ebb.

Within the Bay of Fundy, Canada, Johnston *et al*. (2005) observed harbour porpoise numbers to be significantly greater during the flood than the ebb. Using remote sensing, Johnston *et al*. (2005) revealed the occurrence of a cyclonic eddy and frontal system during the flood tide, with greater concentrations of prey species along the localised fronts as a result of increased plankton levels (Wolanski & Hamner, 1988). No such detailed hydrographic study has yet been conducted in Cardigan Bay. It is perhaps to be expected that relationships with tidal state would differ between localities as physiographical factors come into play.

4.2.4 Tidal Velocity

Areas of strong tidal currents, and hence high velocity, have been reported as favoured foraging sites for cetaceans due to greater abundance of prey (Gaskin & Watson, 1985; Evans, 1997; Baines *et al*., 2000; Johnston *et al*., 2005). The current study, however, found no evidence for tidal current speed (albeit estimated from fairly robust tidal models) to have any influence over dolphin or porpoise foraging.

4.3 Limitations

In the current study, cetacean detection positive minute values were used to represent numbers of cetaceans. However, T-Pods are unable to distinguish between a single vocal individual and a larger number of less vocal individuals. As a consequence, the possibility that changes in detection were the result of changes in the vocalisation level of cetaceans cannot be discounted. The T-Pod recordings are therefore unable to provide accurate quantitative values on cetacean numbers, or be used to track specific individuals. However, they can provide an indication of overall cetacean numbers and habitat use.

The use of T-Pods to monitor cetacean activity is further limited by the reliance of the method on the animal being vocal. Even when the animal is vocal, if vocalisations are to be detected, they must be directed towards the T-Pod, within the detection distance and within the detection frequency of the T-Pod. Reyes Zamudio (2005) considered that directionality is less of a problem when studying the foraging behaviour of cetaceans because foraging animals will produce greater numbers of clicks and in differing directions when locating prey species, increasing the likelihood of detection by the T-Pod. The detection of harbour porpoises by T-Pods is more likely to reflect the presence of harbour porpoises than for bottlenose dolphins because harbour porpoises echolocate continuously in contrast to bottlenose dolphins which echolocate more irregularly when foraging and feeding (P.G.H. Evans, pers. comm.). Reyes Zamudio (2005) further reported that cetacean activity was detected within 650m of the T-Pod with detection diminishing with distance. Any cetacean vocalisation outside the distance and frequency ranges of the T-Pod would not be detected.

The current study was also limited by the relatively little previous work conducted on distinguishing particular cetacean activities from click train characteristics. In the study, foraging click train characteristics were obtained from work comparing T-Pod data sets with visual observations and theodolite tracking of bottlenose dolphins, at New Quay fish factory and Mwnt during summer 2005 (Reyes Zamudio, 2005). Due to the low proportion of bottlenose dolphin foraging click trains compared to harbour porpoise foraging click trains distinguished from the characteristics used, it is possible that the characteristics were not representative of bottlenose dolphins. Failure to accurately distinguish click trains used in foraging from set click train characteristics will lead to a loss of data and possible incorporation of incorrectly identified click trains into the data set.

4.4 Recommendations for further study

At present, little information exists on the diet of the bottlenose dolphins and harbour porpoises inhabiting Cardigan Bay. Thus it is difficult to make links between cetacean activity patterns and changes in the distribution and abundance of prey species. Little observational evidence exists on the possible accumulation of particular prey species within Cardigan Bay from eddies, fronts, headlands, and at differing tidal stages. Theories to "explain" differences in cetacean activity can continue to be put forward. However, without more evidence to test these hypotheses, little progress can be made on those particular questions. Future work within Cardigan Bay should focus on the changes in distribution and abundance of prey species over varying spatial and temporal scales. Efforts should also be made to more accurately map both the large scale and small scale hydrography of the Bay in relation to favoured cetacean locations and prey species abundance. Future work is also recommended to more clearly define the characteristics of bottlenose dolphin and harbour porpoise detections and foraging sounds recorded.

References

Allen M.C., Read A.J., Gaudet J., and Sayigh L.S. (2001). Fine-scale habitat selection of foraging bottlenose dolphins *Tursiops truncatus* near Clearwater, Florida. Marine *Ecology Progress Series* **222**, 253-264.

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

Baines M.E., Evans P.G.H., and Shepherd B. (2000). *Bottlenose dolphins in Cardigan Bay, West Wales*. . Report to EU INTERREG & Countryside Council for Wales. Sea Watch Foundation, Oxford. 35pp.

Baines, M.E., Reichelt, M., and Evans, P.G.H. (2005) Investigation of harbour porpoise and bottlenose dolphin ecology in Cardigan Bay, UK, using model based spatial analysis. Page 34. In: *Abstracts, 19th Annual Conference of the European Cetacean Society, La Rochelle, France, 2-7 April 2005.*

Ballance L.T. (1992). Habitat use patterns and ranges of the bottlenose dolphin in the Gulf of California, Mexico. *Marine Mammal Science* **8**, 262-274.

Barros N.B., and Wells R.S. (1998). Prey and feeding patterns of resident bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Journal of Mammalogy* **79**, 1045-1059.

Berta A., and Sumich J.L. (1999). Sound production for communication, echolocation, and prey capture. Pp. 255-289. In: *Marine Mammals evolutionary biology*. Academic Press, New York. 494pp.

Boran J.R., Evans P.G.H., and Rosen M.J. (2001) Behavioural ecology of cetaceans. Pp. 197-243. In: P.G.H. Evans and J.A. Raga (Eds.) *Marine mammals; biology and conservation*. Kluwer Academic/ Plenum Publishers, New York & London. 630pp.

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

Bristow T. (1999). *Activity and behaviour of bottlenose dolphins (Tursiops truncatus) in Cardigan Bay*. M.Phil thesis University of Wales, Bangor.

Bristow T., and Rees E.I.S. (2001). Site fidelity and behaviour of bottlenose dolphins (*Tursiops truncatus*) in Cardigan Bay, Wales. *Aquatic Mammals* **27**, 1-10.

Countryside Council for Wales (2005). *Entry in the register of European sites for Wales (Regulation 11.2*). 2pp.

Countryside Council for Wales (CCW), Ceredigion County Council, Environment Agency Wales, North Western and North Wales Sea Fisheries Committee, Pembrokeshire Coast National Park Authority, Pembrokeshire County Council, South Wales Sea Fisheries Committee, Trinity House and Dwr Cymru Welsh Water. (2001).*Cardigan Bay Special Area of Conservation Management Plan*, 190pp.

Diggle P. J. (1990). *Time Series, A Biostatistical Introduction*. Clarendon Press, Oxford.

Evans, P.G.H. (1990) Whales, Dolphins and Porpoises. The Order Cetacea. Pp. 299-350. In: *Handbook of British Mammals*. (Eds. G.B. Corbet & S. Harris). Blackwell, Oxford. 588pp.

Evans P.G.H. (1995). Whales, dolphins and porpoises. Pp. 137-140. In: J.H. Barnes, C.F. Robson, S.S. Kaznowska and J.P Doody (Eds.) Coasts and seas of the United Kingdom, region 12 Wales: Margam to Little Orme. Joint Nature Conservation Committee, Peterborough, U.K.

Evans P.G.H. (1997). *Ecological studies of the harbour porpoise in Shetland, North Scotland*. Report to WWF-UK. Sea Watch Foundation, Oxford.106pp.

Evans P.G.H., and Hammond P.S. (2004). Monitoring cetaceans in European waters. *Mammal Review* **34**, 131-156.

Evans, P.G.H. and Lewis, E. (1993) Comparative ecology of bottlenosed dolphins (*Tursiops truncatus*) in Cardigan Bay and the Moray Firth. Pp. 57-62. In: P.G.H. Evans (Eds) *European Research on Cetaceans - 7.* European Cetacean Society, Cambridge, England. 306pp.

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

Evans, P.G.H., Baines, M.E., and Shepherd, B. (2000). Bottlenose dolphin prey and habitat sampling trials. *Report to the Countryside Council for Wales* (CCW Contract Science Report No 679).

Fisher, P.R., Tregenza, N., Hanton, E., Lomax, C., and Evans, P.G.H. (2003) Acoustic monitoring and visual observations of Harbour Porpoise *Phocoena phocoena* in Yell Sound, Shetland. *The Shetland Sea Mammal Report 2001 & 2002: 20-25.*

Gaskin D.E., and Watson A.P. (1985). The harbour porpoise, *Phocoena phocoena*, in Fish Harbour, New Brunswick, Canada: Occupancy, distribution, and movements. *Fishery Bulletin* **83**, 427-442.

Gaskin D.E., Yamamoto S., and Kawamura A. (1993). Harbour porpoise, *Phocoena phocoena* (L.), in the coastal waters of northern Japan. *Fishery Bulletin* **91**, 440-454.

Gordon J., and Tyack P.L. (2002). Acoustic techniques for studying cetaceans. Pp. 293-324. In: P.G.H. Evans and J.A. Raga (Eds.) *Marine mammals: biology and conservation*, Kluwer Academic/Plenum Publishers, New York and London. 630pp.

Gregory P. R., and Rowden A.A. (2001). Behaviour patterns of bottlenose dolphins (*Tursiops truncates*) 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*. Countryside Council for Wales. 68pp.

Gunter G. (1945) *Studies of marine fishes of Texas*. Publications of the Institute for Marine Sciences, University of Texas **1**, 1-190.

Hammond, P.S., Berggren, P., Benke, H., Borchers, D.L., Collet, A., Heide-Jøorgensen, M.P., Heimlich, S., Hiby, A.R., Leopold, M.F. & Øien, N. (2002). Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent waters. *Journal of Applied Ecology*, **39**, 361-376.

Hastie G.D., Wilson B., Wilson L.J., Parsons K.M., and Thompson P.M. (2004). Functional mechanisms underlying cetacean distribution patterns: hotspots for bottlenose dolphins are linked to foraging. *Marine Biology* **144**, 397-403.

Hoyt, E. (2005). *Marine protected areas for whales, dolphins and porpoises*: a world handbook for cetacean habitat conservation. Earthscan, London. 492pp.

Ingram S.N., and Rogan E. (2002). Identifying critical areas and habitat preferences of bottlenose dolphins *Tursiops truncatus*. *Marine Ecology Progress Series* **244**, 247-255.

Irvine A.B., Scott M.D., Wells R.S., and Kaufmann J.H. (1981). Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. *Fishery Bulletin* **79**, 671-688.

Jepson P.D., and Baker J.R. (1998). Bottlenose dolphins (*Tursiops truncatus*) as a possible cause of acute traumatic injuries in porpoises (*Phocoena phocoena*). *Veterinary Record* **143**, 614-615.

Johnston D.W., Westgate A.J., and Read A.J. (2005). Effects of fine-scale oceanographic features on the distribution and movements of harbour porpoises *Phocoena phocoena* in the Bay of Fundy. *Marine Biology Progress Series* **295**, 279-293.

Lamb J. (2004). *Relationships between presence of bottlenose dolphins, environmental variables and boast traffic; visual and acoustic surveys in New Quay, Wales*. M.Sc thesis University of Wales, Bangor.

Lott R. (2004). *Group size, social associations and resident patterns of bottlenose dolphins (Tursiops truncatus) in Cardigan Bay Wales*. M.Sc thesis University of Wales, Bangor.

Morisaka T., Shinohara M., Nakahara F., and Akamatsu T. (2005). Geographic variations in the whistles among three Indo-Pacific bottlenose dolphin *Tursiops aduncus* populations in Japan. *Fisheries Science* **71**, 568-576.

Nelson D.M. (Eds.) (1992). *Distribution and abundance of the fishes and invertebrates in Gulf of Mexico estuaries*. Volume 1. Strategic Environmental Assessments Division, Rockville, MD.

Pierpoint C., and Allan L. (2004). *Bottlenose dolphins and boat traffic on the Ceredigion marine heritage coast, West Wales 2002 and 2003*. Cyngor Sir Ceredigion, 44 pp.

Pierpoint C., Baines M.E., and Earl S. (1998). *The harbour porpoise (Phocoena phocoena) in West Wales.* Report to the Wildlife Trust and WWF-UK, Nekton, Newport, Pembs. 35pp.

Read A.J. (1999). Harbour porpoise *Phocoena phocoena* (Linnaeus, 1758). In: S.H. Ridgway and Sir R. Harrison (Eds.) *Handbook of marine mammals*, Vol. 6 The second book of dolphins and porpoises. Academic Press, pp 323-355.

Read A.J., and Gaskin D.E. (1985). Radio tracking the movements and activities of harbour porpoise, *Phocoena phocoena* (L.), in the Bay of Fundy, Canada. *Fishery Bulletin* **83**, 543-552.

Read A.J., and Westgate A.J. (1997). Monitoring the movements of harbour porpoises (*Phocoena phocoena*) with satellite telemetry. *Marine Biology* **130**, 315-322.

Reichelt M. (2002). *Ecological factors determining the habitat use of bottlenose dolphins (Tursiops truncatus) in Cardigan Bay, Wales*. Diploma dissertation. University of Bremen, Germany.

Reid, J.B., Evans, P.G.H. and Northridge, S.P. (2003). *Atlas of cetacean distribution in north-west European waters.* Joint Nature Conservation Committee, Peterborough.

Reyes Zamudio M. (2005). *TPOD detection and acoustic behaviour of bottlenose dolphins in Cardigan Bay SAC: a comparison between visual and TPOD surveys*. M.Sc thesis University of Wales, Bangor.

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

Saayman G.S., Tayler C.K., and Bower D. (1973). Diurnal activity cycles in captive and free range Indian Ocean bottlenose dolphins (*Tursiops aduncus* Ehrenburg). *Behaviour* **44**, 212-233.

Santos, M.B., Pierce, G.J., Reid, R.J., Patterson, L.A.P., Ross, H.M., and Mente, E. (2001). Stomach contents of bottlenose dolphins (*Tursiops truncatus*) in Scottish waters. *Journal of the Marine Biological Association of the United Kingdom*, **81**: 873-878.

Santos M.B., Pierce G.J., Learnmonth J.A., Reid R.J, Ross H.M., Pattersson I.A.P. Reid D.G. & Beare D. (2004). Variability in the diet of harbour porpoises (*Phocoena phocoena*) in Scottish waters 1992-2003. *Marine Mammal Science* **20**: 1-27.

Shane S. (1980). Occurrence, movements, and distribution of bottlenose dolphin, *Tursiops truncatus*, in Southern Texas. *Fishery Bulletin* **78**, 593-601.

Simon M., and Evans P.G.H. (2005). *Acoustic monitoring of bottlenose dolphins in Cardigan Bay SAC.* Preliminary report to the Countryside Council for Wales. 6pp.

Simon, M., Reyes, M., Baines, M., Nuuttila, H., and Evans, P.G.H. (2006) Temporal and spatial habitat partitioning between harbour porpoises and bottlenose dolphins. Page 20. In: *Abstracts, 20th Annual Conference of the European Cetacean Society, Gdynia, Poland, 2-7 April 2006.*

Thomsen F., van Elk N., Brock V., and Piper W. (2005). On the performance of automated porpoise-click-detectors in experiments with captive harbour porpoises (*Phocoena phocoena*) (L). *Journal of the Acoustical Society of America* **118**, 37-40.

Tregenza N., and Northridge S.P. (1999). Development of an automatic porpoise detector. Presented to the Scientific Committee of the IWC, Grenada.

Tyack P.L. (2000). Functional aspects of cetacean communication. Pp. 270-307. In: J. Mann, R.C. Connor, P.L. Tyack and H. Whitehead (Eds.) *Cetacean societies – field studies of dolphins and whales*. University of Chicago Press, Chicago. 433pp.

Walker R.J. (2005). *The distribution of bottlenose dolphins within the Cardigan Bay Special Area of Conservation: the presence of core foraging areas and the implications for management*. M.Sc thesis, University of Wales, Bangor.

Wells R.S. and Scott M.D. (1999). Bottlenose dolphin *Tursiops truncatus* (Montagu, 1821). In: S.H. Ridgway and Sir R. Harrison (Eds). *Handbook of marine mammals*, Vol. 6 The second book of dolphins and porpoises. (1999). Academic Press, pp 137-182.

Wiley D.N., Wenzel F.W. and Young S.B. (1994). Extralimital residency of bottlenose dolphins in the western north Atlantic. *Marine Mammal Science* **10**, 223-226.

Williams, A.D., Williams, R., Heimlich-Boran, J.R., Evans, P.G.H., Tregenza, N.J.C., Ridoux, V., Liret, C., and Savage, S. (1997) A preliminary report on an investigation into bottlenose dolphins (*Tursiops truncatus*) of the English Channel: a collaborative approach. Pp. 217-220. In: *European Research on Cetaceans - 10.* (Editor P.G.H. Evans). European Cetacean Society, Kiel, Germany. 334pp.

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

Wolanski E. and Hamner W.M. (1988). Topographically controlled fronts in the ocean and their biological influence. *Science* **241**, 177-181.

Wood C.J. (1998). Movement of bottlenose dolphins around the south–west coast of Britain. *Journal of Zoology (London)* **246**, 155-163.

Würsig B. (1978). Occurrence and group organization of Atlantic bottlenose porpoises (*Tursiops truncatus*) in an Argentine bay. *Biological Bulletin* **154**, 348-359.

Würsig B. and Würsig M. (1979). Behaviour and ecology of the bottlenose dolphin, *Tursiops truncatus*, in the south Atlantic. *Fishery Bulletin* **77**, 399-412.