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Diurnal and Tidal Variations in Habitat Use of the Harbour Porpoise (*Phocoena phocoena*) in Southwest Britain

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Abstract

With the United Kingdom required to designate Special Areas of Conservation (SACs) under Natura 2000 by 2012, it is important to understand site-specific activity and habitat use in order to identify potential sites. Shore-based observations of harbour porpoises (*Phocoena phocoena*) were carried out from two sites in North Devon, UK. Morte Point was surveyed during August and September 2001 and Lee Bay was observed during August and September 2002. Focal group follows were conducted to monitor porpoise behaviour and movement over tidal and diurnal cycles. At Morte Point, porpoises were found to aggregate in an area of high tidal flow, where prey items are likely to be abundant. While no differences were observed in occurrence during diurnal and tidal cycles, group size and distance from shore were found to be statistically significant with time of day at Morte Point. Porpoises were observed feeding here 59.9% of the time, with 78.0% of feeding taking place in multi-species associations and larger group sizes being observed at this site. At Lee Bay, porpoises were found to utilise an area of high heterogeneity, where rocky outcrops divide an otherwise sandy bay. In contrast to Morte Point, porpoises were observed feeding at Lee Bay 27.6% of the time, spending 34.7% of the time engaged in travelling in smaller groups. Despite these differences, behaviour and group size between the two sites were not found to be significantly different. At Lee Bay, tidal variation was observed in behaviour, group size, and distance from shore. It is thought that Morte Point represents an important feeding area, while Lee Bay provides a corridor between more productive feeding sites. This study highlights the site-specific nature of diurnal and tidal trends as differences in habitat use were observed for two sites geographically close together.

Key Words: tidal, diurnal, habitat use, Special Areas of Conservation (SACs), conservation, harbour porpoise, *Phocoena phocoena*

Introduction

The harbour porpoise (*Phocoena phocoena*) is perhaps one of the most widespread and best studied of all the phocoenids. Even so, significant gaps in ecological research still remain. It is found throughout the coastal waters of the northern hemisphere and in parts of the North Atlantic, North Pacific, and Black Sea (Read, 1999). While some surveys have recorded the harbour porpoise in offshore waters, reaching a depth of 1,502 m off the coast of Scotland on the Rockall and Faroe Banks (MacLeod et al., 2003), the species is generally limited by its foraging and diving capabilities to waters less than 200 m in depth (Westgate et al., 1995; Read, 1999; Weir et al., 2001).

Around the British Isles, the harbour porpoise has been recorded throughout the east coast, northwest Scotland, on the Celtic shelf, and into the Channel, though sightings previously found to be few in the southern North Sea and eastern Channel (Reid et al., 2003) have since increased in numbers, demonstrating a north to south redistribution of individuals over the last ten years (Hammond & MacLeod, 2006). Even though some large-scale, effort-related, and opportunistic studies have been carried out, small-scale research has primarily focused on resident groups in Scotland and Wales (Borges & Evans, 1996; Weir et al., 2001; MacLeod et al., 2003). Historically, porpoises were also observed regularly along the south coast of England and further offshore into the Channel. Where 50 years ago their appearance was considered frequent (Tregenza, 1992), now they are considered a rare sight. In order to adequately conserve the harbour porpoise, it is important to accurately describe and understand the processes that determine distribution on both small and large scales (Johnston et al., 2005; Redfern et al., 2006).

Being small in size, with a high energetic demand for fitness, availability to prey is an important consideration for the harbour porpoise and so their distribution is often correlated with that of their prey (Johnston et al., 2005). Previous research has identified diurnal trends in movement, behaviour, and feeding for many cetacean species (Saaymann et al., 1973; Shane et al., 1986; Brager, 1993). In particular, the Tucuxi (*Sotalia fluviatilis*) move from open water into lakes and bays in the morning, only to return in the afternoon (Da Silva & Best, 1994). Humpback dolphins (*Sousa chinensis*), Dall's porpoises (*Phocoenoides dalli*), Hector's dolphins (*Cephalorhynchus hectori*), and bottlenose dolphins (*Tursiops truncatus*) have also been shown to demonstrate diurnal variation in both behaviour and movements (Amano et al., 1998; Karczmarski & Cockcroft, 1999; Bejder & Dawson, 2001). Dall's porpoises demonstrate diurnal feeding patterns in relation to the migrations made by their prey species (Amano et al., 1998). They have also demonstrated a degree of behavioural plasticity similar to that observed in the bottlenose dolphin (Shane et al., 1986), altering feeding times in relation to prey availability (Amano et al., 1998). A review of diurnal rhythms in Cetacea (Klinowska, 1986) indicates that for most species, where data are available, some form of diurnal pattern in feeding has been identified. What is not clear is whether such patterns are a result of internal clocks, external cues, or a result of diurnal rhythms in prey species.

Further research has concentrated on behavioural and distributional patterns linked to tidal cycles, although these are generally less common in cetacean species (Stevick et al., 2002). In the UK, Gregory & Rowden (2001) studied bottlenose dolphins at two sites in Wales. They analysed sighting information with respect to tidal state, time of day, and boat traffic. While no pattern was observed with time of day, dolphin movement was correlated with tidal state, with dolphins moving with tidal flow or during slack water. Although Shane (1990) found that bottlenose dolphin movements in Texas were also correlated with tidal movement, dolphins were found to move against the tidal flow. Humpback dolphins have also been found to move into near-shore areas, including mangroves and rivers, with the tide (Ross et al., 1994). This clearly demonstrates an increase in spatial utilisation of the area, possibly in search of prey. More recently, Mendes et al. (2002) found that bottlenose dolphins were more abundant on the flood tide than during slack water, which is thought to be due to increased foraging efficiency because of the resultant accumulation of prey.

To this point, the activity and habitat use of the harbour porpoise has not been extensively studied. Knowledge of this species is limited because of the difficulties associated with studying them at sea. They are relatively small in size, do not possess individual markings (Koopman & Gaskin, 1994), and spend only 5% of their time on the surface (Westgate et al., 1995). Previous research, which monitored porpoise movements with satellite telemetry (Read & Westgate, 1997), indicated that porpoises in the Bay of Fundy might spend periods of time ranging from days to weeks in rather restricted areas. It is believed that their movements relate to aggregations of herring (*Clupea harengus*), a primary prey item for harbour porpoises in Canada (Borjesson et al., 2003). Data published by Neave & Wright (1968) suggest that individual porpoises make discrete migrations into a wider geographic area. It is not thought that these movements are temporally coordinated, but they suggest that these may be as a result of fluctuating prey densities.

In the UK, harbour porpoises have also been found to be distributed in relation to their prey, which largely consists of pelagic and demersal species, including sandeels (*Ammodytes* sp.) and gadoids (*Gadidae*) during the summer months, with whiting (*Merlangius merlangus*) being consumed during the winter and herring, sprat (*Sprattus sprattus*), gobies (*Gobiidae*), and mackerel (*Scomber scombrus*) consumed year-round (Santos et al., 2004). Off the coast of west Wales, Pierpoint et al. (1994) described leaping behaviour in the harbour porpoise, which seemed to occur during foraging behaviour. In southeast Shetland, Scotland, porpoise distribution was also found to be correlated with prey items (Borges & Evans, 1996). In Mousa Sound, Scotland, porpoises were found to generally move in the opposite direction to tidal flow, though they were observed at all states of the tide (Evans, 1997).

The objective of this research was to provide data on the activity and habitat use of the harbour porpoise on a small scale, examining two sites, which are oceanographically quite different but are in relative close proximity along the coast. The current UK Biodiversity Action Plan for the harbour porpoise highlights the need to expand research into areas frequented by harbour porpoises. This will enable the identification of waters that may qualify for further protection as Special Areas of Conservation (SACs). While no such areas have yet been designated, despite an analysis of the UK coastline by Evans & Wang (2002), this has subsequently become of key importance because the UK Government has committed to establishing a coherent network of marine protected areas which will support Natura 2000 by 2012 (Kelleher & Phillips, 1999; Bull & Laffoley, 2003). Evans & Wang (2002) identified sites based on levels of presence throughout the year. Both sites selected in this study qualified for category one classification by Evans & Wang, which states that "porpoises have been recorded over several years, with a presence in every month of the year and concentrations in at least four months during the period April-September" (p. 25). This study tested the hypothesis that porpoises differentially use the sites through the examination of shore-based observational data. It considered diurnal and tidal variation with comparison of the activity budget between the sites.

Materials and Methods

Study Site: Morte Point, Mortehoe, North Devon

Morte Point (51° 11.290' N, 04° 13.559' W) is a large headland of National Trust land, which protrudes out between Woolacombe Bay and Rockham Bay, North Devon. From the study site, an area of approximately 3.83 km^2 can be viewed, which includes the Morte Stone channel buoy (51° 11.02' N, 04° 15.00' W) and the area just beyond it, and stretches as far east as Bull Point (51° 11.934' N, 04° 12.123' W). Although the area up to Bull Point may be observed, not all of this was included in the study site as sighting efficiency decreased with distance (Findlay & Best, 1996). A total study area of 0.80 km^2 was surveyed from a height above sea level of approximately 65 m.

The seabed surrounding Morte Point consists mainly of sand, shingle, and gravel, alternating between gravel and fine sand further out. The Morte Stone buoy not only marks the large rock formations, which protrude out into the sea, but also marks an area of tidal rapids, which form because of the prominent nature of the point. These rapids vary from 0.1 to 1.5 kts during neap tides and 0.3 to 3.2 kts during spring cycles.

The levels of boating traffic were recorded continuously throughout the study. Although small fishing boats utilise the area close inshore, their numbers are few (1 to 2 vessels per watch). The area is generally quiet in terms of marine traffic, with only one boat offering coastal tours and all large cargo ships remaining on the horizon (approximately 4.6 km offshore). Therefore, all porpoise behaviour recorded is presumed to be that of undisturbed individuals.

Study Site: Lee Bay, Lee, North Devon

Lee Bay (51° 11.918' N, 04° 10.764' W) is a relatively small inlet, situated further east from Bull Point. The cliffs on the western side of Lee provide good views over the area. Two cliff formations on either side delimited the study area, although sighting efficiency with distance was once again taken into consideration. A total area of 0.68 km^2 was studied from an elevation of approximately 30 m above sea level.

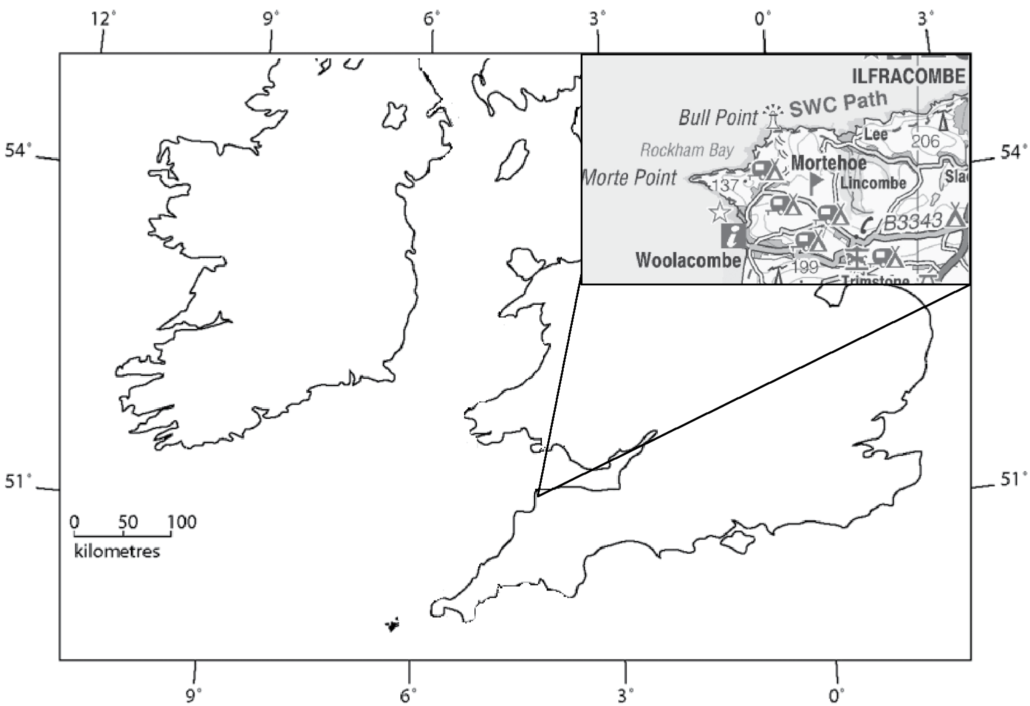

Figure 1. Study site, depicting Morte Point and Lee Bay; inset reproduced from Ordnance Survey map data by permission of Ordnance Survey, © Crown copyright.

The seabed in Lee Bay is largely homogeneous, consisting of fine sand with gravel patchily distributed. A number of submerged rock formations are present at the base of the cliffs on either side of the bay. Although no strong tidal rapids exist within the study area, those that form off Bull Point may be viewed on the far western side of the area. As with Morte Point, Lee Bay receives little marine traffic, despite its proximity to the port of Ilfracombe. Here, small fishing boats set and check lobster pots and pass through the area (1 to 2 fishing vessels per watch). All other traffic remains on the horizon.

Shore-Based Observations

At both sites, a number of shore-based observations were conducted. At Morte Point, these were carried out between August and September 2001 and consisted of watches centered on either high or low tide, with watches conducted over 4-h periods with a single observer. Similarly, Lee Bay was surveyed during August and September 2002 when once again shore-based observations were conducted over a 4-h period. After this time, it was assumed that observer effort and sighting efficiency would decrease (Findlay & Best, 1996).

During a watch, the area was scanned every 15 min using a telescope and a pair of binoculars. When a group of porpoises entered the area, they were surveyed using a focal group follow (Mann, 2000), which lasted either until the watch ended or until the porpoises left the study area. The porpoises' behaviours were monitored continuously with the aid of a dictaphone, and positional data were logged using a sighting compass and local landmarks. The area was subdivided into four concentric bands (< 125 m, 125 to 500 m, 500 to 750 m, and > 750 m from the shore for the Morte Point sector and < 125 m, 125 to 500 m, 500 to 625 m, and > 625 m from the shore for the Lee Bay sector), using headlands, cliffs, and rock formations to facilitate distance estimation and to provide a second fix on the porpoises' positions in addition to the compass bearing. Given the site, distance of the porpoises from the shore, and the size of the species involved, this was deemed to be the most appropriate method of position fixing. Minimum group size was also recorded, which was defined as the total number of animals observed at the surface at any one time. Porpoise behaviour was classified using an ethogram of six categories: (1) feeding, (2) travelling, (3) resting, (4) social interactions, (5) avoidance, and (6) other (Shane et al., 1986). In this study, they were classified as follows:

- *Feeding* was recorded when porpoises were observed chasing or in association with fish. Because of the distance and speed of the fish, it was impossible to state with any accuracy the species of fish involved. Communication with local fishermen indicated that mackerel and herring were the most frequently caught species within the area. When groups of porpoises were observed in association with feeding seabirds, usually northern gannets (*Morus bassanus*), it was assumed that the porpoises were engaged in feeding behaviour (Camphuysen & Webb, 1999).
- *Travelling* was defined as a constant movement in a particular direction.
- *Resting* was categorised as slow, repetitive surfacing and slow or unidirectional movement within a given area. Porpoises did not always remain on surface between breaths but did not generally alter position.
- *Social interactions* were classified when more than one porpoise engaged in leap, chase, or surface rushing behaviour when there was no evidence of feeding or directed travel.
- *Avoidance* was recorded when the animals were observed in association with another animal, object, or marine vessel, changing direction, staying submerged for extended duration (> 5 min), or leaving the area entirely.
- The *Other* category was established for behaviours that could not be classified into any of the above categories.

Any other interactions either with marine traffic or other wildlife (e.g., seals or birds) were also recorded in line with the sampling protocol.

During watch periods conducted over the course of 8 wks, porpoises were observed for a total of 22.25 h at Morte Point. Similarly, over 8 wks at Lee Bay, a total of 18 h were spent observing the porpoises. Although positional data were recorded continuously, preliminary analysis revealed that a time interval of 15 min was required to ensure that the data were temporally independent (Swihart & Slade, 1985). This was completed by plotting all positions for two watch periods on a chart of the area. The chart was divided into sections, dictated by 5° compass bearing sectors and concentric bands as indicated by landmarks. The mean time for the porpoises to cross a boundary line was calculated. This ensures that results are not skewed by porpoises repeatedly resurfacing in an area unless they are utilising this area for more than 15 min. It is recognised that this could represent the same group resurfacing in the same area, a new group, or the addition of new individuals to the group already recorded. The size of the areas delimited by the compass sector and the concentric bands increased with distance offshore up to a cut-off point (1 km) at which sighting individual porpoises was unreliable.

This means that sections in Band 1 (closest to the shore) at Morte Point were 0.004 km^2, Band 2 = 0.007 km^2, Band 3 = 0.03 km^2, and Band 4 = 0.01 km^2. For Lee Bay, Band 1 = 0.004 km^2, Band 2 = 0.02 km^2, Band 3 = 0.007 km^2, and Band 4 = 0.005km^2. At Lee Bay, the site was not as elevated as that of Morte Point and so a smaller study area was viewed. If the null hypothesis that porpoises show no habitat differences is correct, then counts per unit area (porpoise densities) should be proportional to area across both study sites. Dividing the total number of sightings (in any one watch) by the total area of the site resulted in an expected density of one porpoise sighting per 0.01 km^2 at Morte Point and one porpoise sighting per 0.025 km^2 at Lee Bay. A chi-squared test was used to determine whether these expected values differed from the observed distribution of porpoises.

The hypothesis that harbour porpoise sightings show variation with respect to tidal and diurnal variation was also tested using a G test, comparing number of sightings per unit effort with flood tide, high tide, ebbing tide, and low tide for both morning (1000 to 1400 h) and afternoon (1400 to 1600 h) watch periods. Harbour porpoise behaviour (feeding, travelling, resting, socialising, avoidance, other), group size (1 to 6+), and distance from shore (Bands 1 to 4) were also tested assuming the hypothesis that variation in the above-mentioned factors occurs with respect to time of day (morning, afternoon) and tidal state (flood, high, ebb, low). A three-level, nested analysis of variance (ANOVA) was conducted for each factor, time of day, and tide simultaneously at each of the study sites (Morte Point and Lee Bay). Total duration spent engaged in each behavioural category and minimum group size for each site was also calculated and plotted. Behavioural observations (activity budget) and the group sizes observed at each site were compared using a Mann-Whitney test.

Results

Morte Point

After assessment to ensure temporal independence, a total of 77 sightings were used from 8 wks of data collation. Porpoise sightings were found to be tightly clustered in one area of the bay ($\chi^2_{(6)} = 14.19$, $p < 0.01$), where 29 of the 77 sightings were observed (Figure 2).

Porpoises were observed throughout the majority of both diurnal and tidal cycles with no statistically significant difference between sightings. Equally, when behaviour was examined, no significant difference between tidal or diurnal states was observed. However, when the data were analysed for group size and distance from shore, statistically significant differences were observed with time of day (group size: $F_{47} = 8.338$, $p < 0.05$; distance from shore: $F_{31} = 14.587$, $p < 0.05$) (Figures 3 & 4).

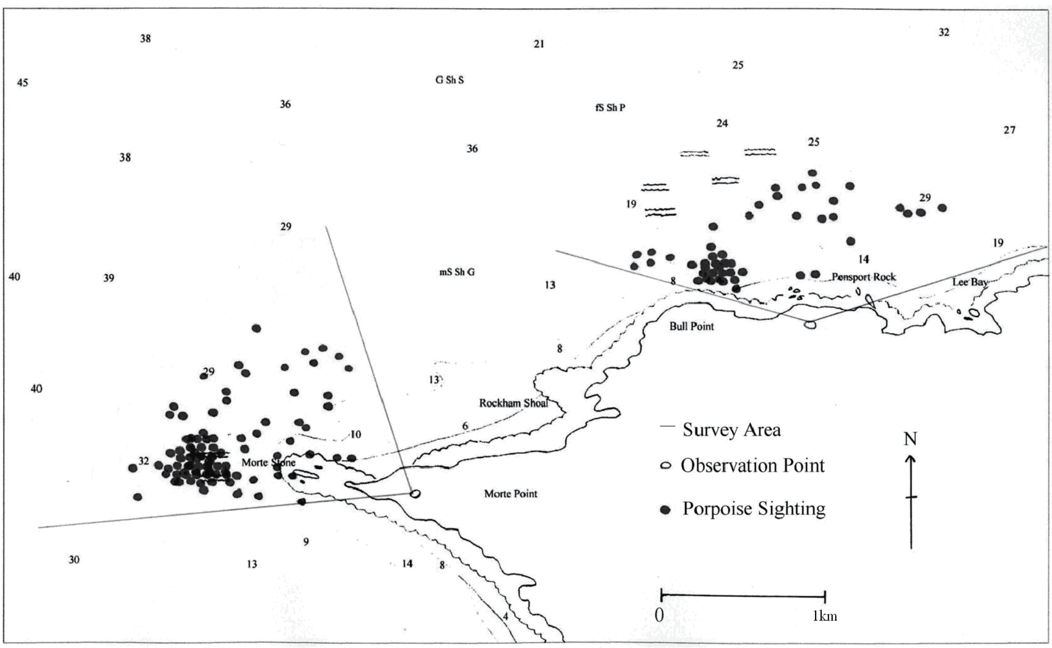

Figure 2. Map encompassing both sites: Morte Point (51° 11.290' N, 04° 13.559' W) and Lee Bay (51° 11.918' N, 04° 10.764' W), North Devon, UK, and position of all porpoise sightings

Harbour porpoises were observed feeding throughout all tidal and diurnal cycles at Morte Point and although not statistically significant, a greater proportion of feeding observations occurred during the afternoon flood tide and morning ebb tide. Group sizes were found to decrease during the afternoon, although the afternoon high tide appeared to produce equal frequencies of all group sizes. The porpoises' distance from shore was evenly distributed during the morning, with the exception of high tide when they were observed in Band 3 (500 to 750 m offshore). During the afternoon, they were found in Band 3 more frequently, in particular during afternoon flood and ebb tides.

Lee Bay

After assessment for temporal independence, a total of 39 sightings were used in the analysis. As porpoises were not observed in a large proportion of the study area (0.5 km^2), grid cells were made larger, totaling six cells within each band. Porpoise sightings seemed to aggregate in one area of the study site, however ($\chi^2_{(6)} = 33.66$, $p < 0.001$) (Figure 2).

Unfortunately, because of adverse weather conditions during some of the survey periods, no observations were made during low tide. Therefore, the tidal analysis carried out here utilises observations made during either flood, high, or ebbing tides. Porpoises were observed throughout the majority of both diurnal and tidal cycles, however, with no statistically significant differences between sightings. When behaviour, group size, and distance from shore were analysed, statistically significant differences were observed with tidal state (behaviour: $F_{35} = 21.197$, $p < 0.001$; group size: $F_{29} = 5.553$, $p < 0.05$; distance from shore: $F_{23} = 6.322$, $p < 0.05$) (Figures 5, 6 & 7).

Harbour porpoises were predominantly observed feeding on a high tide but were found to travel during both the flood and high tide; otherwise, there was no variation in behaviours observed during the ebbing tide at Lee Bay. Although not statistically significant, porpoises appeared to be more active, demonstrating an equal frequency of all behaviours during the afternoon. While porpoises' distance from shore was evenly distributed during the afternoon, with the exception of a flood tide when they

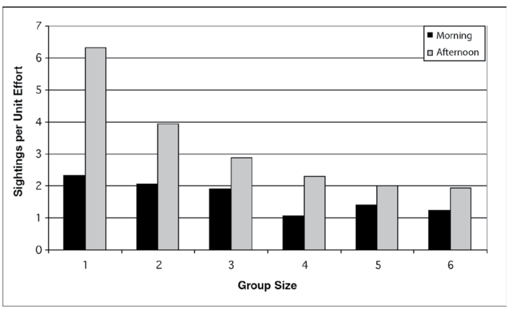

Figure 3. Sightings per unit effort for each group size recorded during morning and afternoon watch periods at Morte Point

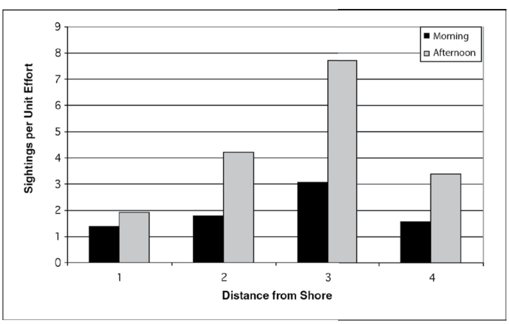

Figure 4. Sightings per unit effort observed during morning and afternoon watch periods at Morte Point; distance from shore: 1 (< 125 m), 2 (125 to 500 m), 3 (500 to 750 m), 4 (> 750 m).

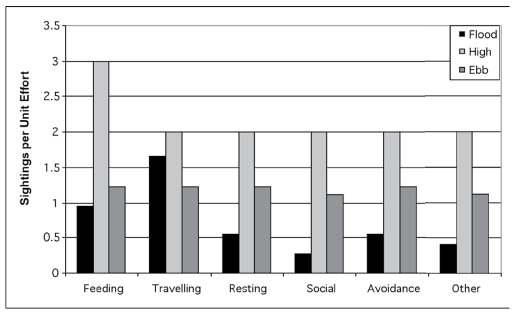

Figure 5. Sightings per unit effort for each behavioural category observed (feeding, travelling, resting, social interactions, avoidance, and other) during watch periods in each tidal state at Lee Bay

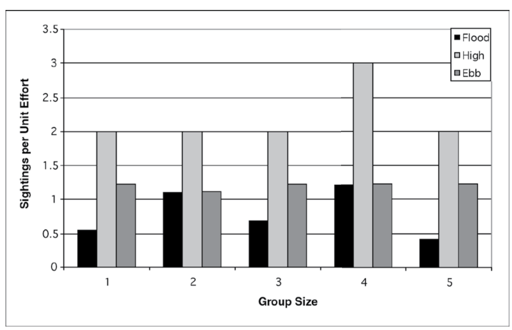

Figure 6. Sightings per unit effort for each group size recorded during watch periods in each tidal state at Lee Bay

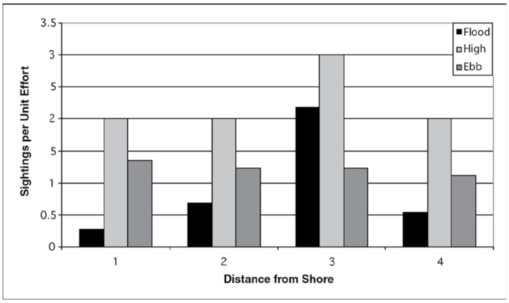

Figure 7. Sightings per unit effort observed during watch periods in each tidal state at Lee Bay; distance from shore: 1 (< 125 m), 2 (125 to 500 m), 3 (500 to 625 m), 4 (> 625 m).

were observed in Band 3 (500 to 625 m offshore), they were found in Band 3 more frequently during the morning flood and high tides.

Behaviour

The porpoises were observed for a total of 22.25 h at Morte Point during which time they spent 59.9% of the total time feeding. On 32 occasions, feeding associations were observed with northern gannets in this area. This relates to 78% of all feeding observed. At Lee Bay, porpoises were observed for a total of 18 h, of which feeding constituted 27.6% of the time. They were recorded travelling through the area 34.7% of the time; whereas at Morte Point, travelling constituted only 13.96% of the time. These differences were not statistically significant, however.

Group Size

The average group size differed little between sites: Morte Point = 2.7 individuals, ranging between 1 to 10 individuals; Lee Bay = 2.5 individuals, ranging between 1 to 6 individuals. Once again, there was no statistically significant relationship between sites. Although both study sites had on average identical group sizes, there were six occasions when 6+ (7 to 10) individuals were observed at Morte Point, whereas the largest group size at Lee Bay constituted only six individuals, and this was only seen twice.

Discussion

It is clear from the distribution of sightings, behavioural data, and physical properties of the area that an important feeding ground exists for harbour porpoises off the coast of Morte Point. In this study, harbour porpoises demonstrated a statistically significant preference for the area within the tidal race (Band 3). The tidal flow at Morte Point ranges from 0.3 to 3.2 kts on spring tides and 0.1 to 1.5 kts during neap tides. Tidal rapids are an area of high prey abundance, which may be being utilised by both the porpoises and gannets, where the majority of sightings occurred during the afternoon. It is assumed that, as such, the area would be important for prey species such as herring and mackerel (pers. comm. with local fishermen). Zamon (2003) found that where tidal rips or jets develop, piscivorous predators were also associated due to the interaction of currents, plankton, and schooling fish. Observations of porpoises feeding in tidal races have been made in other studies. Porpoises in Shetland were found in areas of strong currents, which were thought to be associated with topographical features and an increase in prey species (Evans, 1997). More recently, researchers in the Bay of Fundy, Canada, discovered that porpoises actively forage in regions of enhanced relative velocity—tidal streams or island/headland wakes—in response to an increase in prey densities (Johnston et al., 2005). The increase in feeding efficiency by utilising an area within a tidal race probably outweighs the energy required to maintain their position in the tidal currents (Shane, 1990) as observed here at Morte Point. Indeed, behavioural activity did not vary significantly in relation to tidal state, despite feeding being recorded throughout the day and subsequent tidal cycle.

Pierpoint et al. (1994) found the groups seen in connection with feeding in tidal races to only be temporary—a consequence of utilising an area of high productivity. This supports the findings of this study, which found larger group sizes during the afternoon on a high tide, possibly indicating the aggregation of groups for feeding purposes. Additionally, on average, slightly higher group sizes and increased counts of seven to ten individuals were seen at Morte Point than at Lee Bay.

For Morte Point at least, feeding occurred throughout the tidal cycle; whereas at Lee Bay, behaviour, group size, and distance from shore were found to vary with tide. Lee Bay itself lacks the tidal currents observed around Morte Point, although similar tidal streams may be observed off the promontory cliffs marking either side of the study area. Harbour porpoises did however aggregate in one area of the bay, around the rocks at the base of the cliffs. This may be a consequence of prey densities as was indicated by Hui (1979) in relation to dolphins of the genus *Delphinus*. Hui hypothesised that as seafloor relief increased, so would the frequency of occurrence of *Delphinus* species. This was based on an underlying assumption that as topographic heterogeneity increases, water movement and mixing increases and available light varies, allowing a greater diversity of microhabitats to form. Prey species may be more abundant in such areas, thus increasing the occurrence of cetacean predators.

At Lee Bay, feeding occurred on the high tide, with travel tending to occur throughout tidal states. Interestingly, if it is on the flood tide that harbour porpoises increased feeding at Morte Point, do porpoises perhaps travel around to Morte Point on the flood tide and come back around to Lee for the high tide, following prey into the region? Supporting this idea is the concurrent decrease in group size at Morte Point, with an increase in group size at Lee Bay during the afternoon, demonstrating a possible linkage between the two areas. While it is recognised that the two sites were sampled during different years, the results of this study do highlight the potential varying use of the sites by harbour porpoises in the region. Lee Bay demonstrated tidal variation in behaviour, group size, and distance from shore; while at Morte Point, only group size and distance from shore exhibited diurnal differences. Research into other cetacean species has found diurnal and tidal trends (Saaymann et al., 1973; Klinowska, 1986; Shane, 1990; Evans, 1997; Amano et al., 1998; Johnston et al., 2005). In particular, Evans (1997) found that harbour porpoises in Mousa Sound, Scotland, preferentially utilised the area on an ebb tide; and in Canada, porpoises were also found to demonstrate the same preferential use of an area during an ebb tide (Johnston et al., 2005).

While Morte Point appears to represent an important feeding area, porpoise use of Lee Bay is perhaps more complex, with travelling constituting the most frequently observed behaviour (as duration rather than sighting per unit effort) while feeding varies with tidal cycle. Previous studies have referred to the harbour porpoise as an opportunistic predator (Recchia & Read, 1989; Santos & Pierce, 2003). By definition, though, to be opportunistic would imply that the harbour porpoise is consuming prey as they are encountered, with the inference that prey availability is influencing diet selection (Santos & Pierce, 2003). Donovan & Bjørge (1995), however, note that the term *opportunistic* should not be applied to the harbour porpoise as details concerning prey selection in this species are not known. Because the porpoises were observed feeding for a proportion of the time in Lee Bay, it may be concluded that they are perhaps utilising the area as a corridor between more productive feeding sites, such as Morte Point, but are utilising the area when it presents feeding opportunities such as at high tide.

While these results do not demonstrate site differences in occurrence during tidal and diurnal cycles, they do point to site-specific differences in behaviour, group size, and distance from shore, depending on time of day and tidal cycle. While previous studies have reported both tidal and diurnal variation in cetacean species (Saaymann et al., 1973; Klinowska, 1986; Shane, 1990; Evans, 1997; Amano et al., 1998; Johnston et al., 2005), this study demonstrates that habitat use trends are site-specific. Indeed, Bannon (2006) pointed out that spatial and temporal variations in cetaceans may arise from differences in the biological, hydrographical, and topographical structure of the study area. Only by understanding the site-specific nature of cetacean occurrence, behaviour, and group size can adequate conservation measures be put in place and maintained.

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