Aquatic Mammals 2001, **27.2,** 105–113

Behaviour patterns of bottlenose dolphins (*Tursiops truncatus*) relative to tidal state, time-of-day, and boat traffic in Cardigan Bay, West Wales

Paul R. Gregory and Ashley A. Rowden

Department of Biological Sciences, University of Plymouth, Drake Circus, Plymouth, Devon PL4 8AA, UK

Abstract

Diurnal behaviour patterns of the bottlenose dolphin (*Tursiops truncatus*) were investigated at two sites in relation to tidal state, time-of-day, and boat traffic in Cardigan Bay, west Wales. The two sites chosen were New Quay and Ynys Lochtyn. Between-site variability existed in the occurrence of dolphins. However, no relationship was found between the numbers of dolphins observed in relation to the tidal cycle or time-of-day at either of the two sites. Dolphin movement patterns were correlated with tidal state at both sites, with the dolphins moving with the tidal flow or during slack water. No relationship was found between movement patterns and time-of-day. Foraging behaviour was correlated with tidal state at both sites, with dolphins foraging mainly between the flood and ebb tides of high water. Foraging in relation to group size was not significant at either site. No relationship was found between foraging behaviour and time-of-day. Statistically significant behavioural responses were noted towards boat traffic. Dolphins generally displayed a neutral response toward boats, i.e., the dolphins showed no apparent change in directional movement, prior to and after the arrival of the vessel. However, dolphins displayed a negative response toward kayaks, and a positive response toward tourist boats. Dolphin's reactions toward boats in relation to group size were not statistically significant. The study supported the findings of previous studies on bottlenose dolphins in other localities; however, the effect of kayaks requires further investigation. Recommendations are made for future avenues of research regarding this species.

Key words: bottlenose dolphin, *Tursiops truncatus*, Cardigan Bay, diurnal behaviour patterns, tidal state, time-of-day, boat traffic.

Introduction

The bottlenose dolphin (*Tursiops truncatus*, Montagu) is a cosmopolitan species, found throughout the world's tropical and temperate seas and oceans (Shane, 1990). The wide distribution of this species has allowed detailed studies at a variety of locations, such as Sarasota Bay, Florida, USA (Irvine *et al*., 1981; Wells & Scott, 1997), Kino Bay, Gulf of California, Mexico (Ballance, 1990), the Moray Firth, Scotland (Wilson *et al*., 1997), and the Shannon Estuary, southwest (SW) Ireland (Berrow *et al*., 1996). Studies showed that the bottlenose dolphin occupies a variety of marine habitats, from deep oceans to shallow coastal regions, inshore lagoons and estuaries (Leatherwood & Reeves, 1990). Populations can be either offshore-pelagic in their ranging patterns, or inshore-coastal resident populations. Little is known about the ranging patterns of pelagic bottlenose dolphins, but coastal dolphins exhibit a full spectrum of movements, including seasonal migrations, year-round home ranges, periodic residency, and a combination of occasional long-range movements and repeated residency (Wells & Scott, 1999).

Resident populations have received most attention owing to their locally dispersed geographical ranges (Bräger, 1993; Lewis & Evans, 1993; Berrow *et al*., 1996; Wilson *et al*., 1997). Most resident groups of bottlenose dolphins show systematic patterns in their behaviour, such as foraging/feeding, socializing, and moving from area to area in relation to environmental cues, such as the tides (Irvine *et al*., 1981; Leatherwood *et al*., 1983; Wilson *et al*., 1997), the time of day (Saayman *et al*., 1973; Würsig & Würsig, 1979; Bräger, 1993), and depth (Wiley *et al*., 1994).

Many potential threats exist to resident populations, often *via* contact with human activities. These anthropogenic threats include entanglement in fishing gear (Vidal, 1993), exposure to environmental

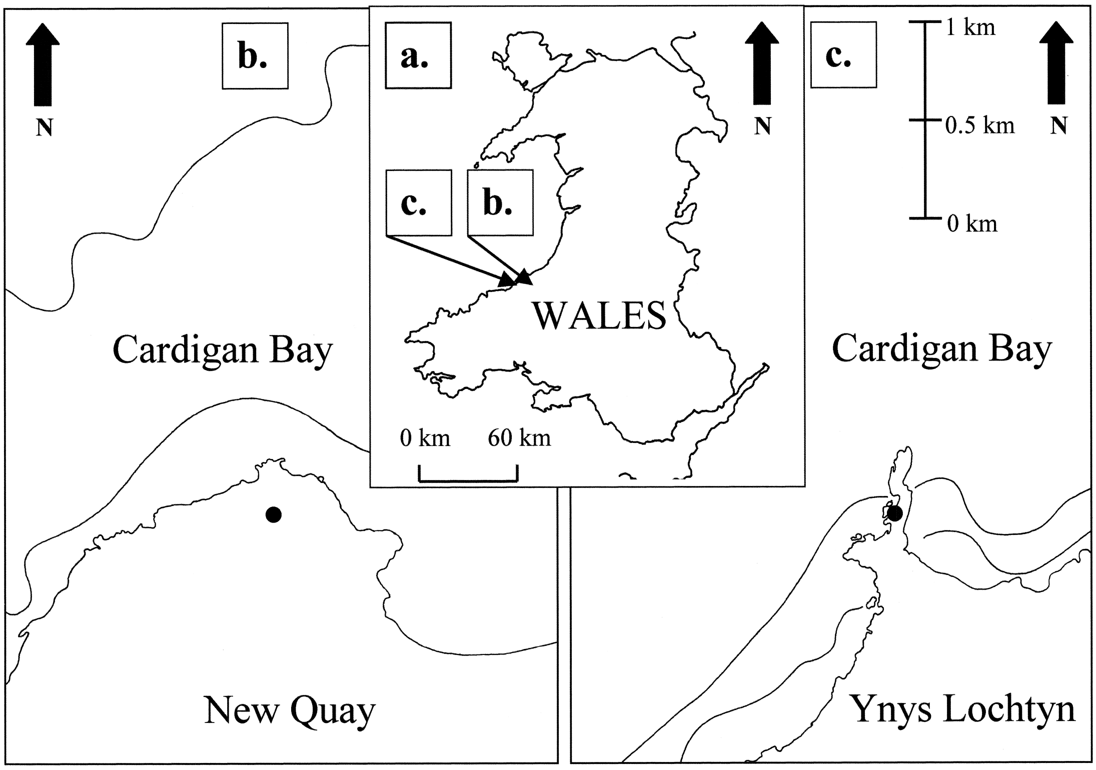

Figure 1. (a) Study sites in Cardigan Bay, West Wales, (b) New Quay, and (c) Ynys Lochtyn. (●—Observation points).

pollutants (Morris *et al*., 1989; Borrell, 1993), and disturbances from boat traffic (Sorensen *et al*., 1984; Janik & Thompson, 1996; Wells & Scott, 1997; Allen & Read, 2000). In inshore-coastal waters the bottlenose dolphin is probably the second most common cetacean in the United Kingdom (Evans *et al*., 1986; Evans, 1992). The Cardigan Bay (West Wales) population is estimated to range from 130 to 230 individual dolphins (Grellier *et al*., 1995), with only a proportion of the animals being resident throughout the year (Arnold, 1993; Lewis & Evans, 1993). Bottlenose dolphins are frequently seen within 15 km of the coast between Cardigan and Borth, from April to October. Headlands at Mwnt, Pen Peles, Aberporth, Ynys Lochtyn, and New Quay are particularly favoured feeding areas for bottlenose dolphins (Evans, 1996).

The principal aim of the present study was to determine whether the tidal cycle or the time-of-day had an affect on the diurnal movement pattern of the bottlenose dolphin population, in two pre-determined geographical locations in Cardigan Bay. In addition, because the area is frequented by boats of various kinds, the study also aimed to assess whether boat activity has a detrimental or benign effect on the movement patterns of the bottlenose dolphins.

Materials and Methods

Study area

Cardigan Bay is the largest bay in the British Isles, bound on three sides by the Welsh coast and open to the Irish Sea on its western boundary (Fig. 1a). It encompasses an area of approximately 5500 km^2. The water depth in the bay does not exceed 50 m and becomes increasingly shallower from west to east, with an average depth of approximately 40 m (Evans, 1995*a*). The nature of the seabed in the bay is extremely heterogeneous, ranging from fine sand and broken shell, to gravel, shingle, and muddy sand (Evans, 1995*a*). The tidal regime of the area, results from the tide entering the Irish Sea through St. George's Channel in the south and travelling northward to meet the southward-moving tide from the north in the vicinity of the Isle of Man. The resultant weak tidal currents run northward during the flood and southward during the ebb (Evans, 1995*b*). The tides in the area are semi-diurnal and the tidal range in Cardigan Bay is fairly uniform (*ca*. 2 m at neaps and 4 m at springs).

Boat traffic is prevalent in the area, especially around Cardigan, Aberporth, New Quay, Aberaeron, and Aberystwyth, which are frequented by tourists. During the tourist season (April to October), boats operate out of New Quay and Aberaeron, taking tourists on trips around the bay to observe the dolphins and other wildlife. Water sports and recreational boat activities increase in the summer months, with many visitors launching powerboats, sailboats, and kayaks from the above ports.

Study sites

A land-based observational study was adopted, rather than a boat-based one, to minimize the effects of observer presence on the dolphin's natural behaviour. Two study sites where chosen in Cardigan Bay, locations being New Quay Headland (52°13′05″N, 04°21′84″W) and Ynys Lochtyn, a northwesterly peninsula cliff-top (52°10′28″N, 04°27′98″W), (Fig. 1b and c). The observational areas were *ca.* 8 km^2 for both sites. New Quay and Ynys Lochtyn headlands were both chosen for their high vantage positions over looking the bay (75 m and 40 m, respectively) and because dolphins were seen on a regular basis in the past at both sites.

The New Quay site represents a shallow semi-enclosed bay with restricted tidal flow. The bottom topography is smooth, with depths ranging from 1 to 12 m in a gradual sloping direction offshore. The substrate at this site consists of coarse to fine sand. The Ynys Lochtyn site comprises of a rocky headland which experiences relatively strong tide rips and turbulence during the changes from each amplitudinal tide. The water depth is more constant and ranges from 12 to 18 m, while the substrate consists of mainly gravel to shingle and coarse sand (Evans, 1995*a*).

Field methodology

The study was conducted during the entire month of August 1999, a period when dolphin sightings are most numerous (Evans, 1996). The 12$\frac{1}{2}$ hour tidal period was divided into four observational periods: high water to $\frac{1}{2}$ ebb, $\frac{1}{2}$ ebb to low water, low water to $\frac{1}{2}$ flood, and $\frac{1}{2}$ flood to high water. One $\frac{1}{2}$ tidal cycle was covered each day, either high water—low water or low water—high water; this was dependent on the available daylight hours. Observational periods in relation to the time-of-day were divided into three time classes: 06:00–10:30, 10:30–15:00, and 15:00–19:30 hrs. The time-of-day that the study commenced each day varied, due to the variation of the tidal cycle.

Observations were alternated between the two sites every one or two days, so as not to confound the study temporally. Observations were conducted by eye continuously for a full 6 h and 15 min, covering one half tidal cycle per day. Scans of the horizon were conducted at 15-min intervals, with the aid of Opticron 8 × 24 lightweight waterproof hand-held field binoculars and Nikon field telescope. Time, position of dolphin(s) surfacing, distance offshore, direction of travel, feeding behaviour, and sea state were recorded. Data were only collected when the sea state (Beaufort Scale) was ≤ 3. With sea states >3, sightings become less reliable (Barco *et al.*, 1999). Dolphin counts were made once a dolphin(s) was sighted upon surfacing, and then observed for *ca.* 5 min or until the number of individuals counted became consistent, so as not to underestimate or overestimate dolphin numbers. Dolphin positions were recorded every 10 min once dolphin(s) were sighted, in addition to the continuous observation of the study area.

Estimated distances offshore were obtained with the aid of a 10-m motor vessel, which followed a transect offshore, stopping at distances of 500 m and 1 km. These distances were noted from shore prior to and during the study (*via* VHF radio communication with the motor vessel) and used as visual references, with the additional aid of photographs. At the New Quay site, an additional reference point (North marker buoy, 1 km offshore) was used. The position and direction of travel of the dolphin(s) were recorded with the aid of a field-sighting compass. Dolphin(s) positions and distances offshore were plotted on a 1 km^2 grid cell basis over time, using the appropriate scale on a map (New Quay; Ordnance Survey Map scale 1:10,000, SN 35 NE, SN 45 NW and SN 46 SW, and Ynys Lochtyn; Ordnance Survey Map scale 1:10,000, SN 35 SW and SN 35 NW). The reference points used for mapping were St. Ina's Church, Llanina for the New Quay site and Bird's Rock for Ynys Lochtyn (110° and 54° from the respective observation points). Each day's observations of the dolphin(s) and direction(s) were plotted individually for each determined observational period (6 hr and 15 min), to establish movement and direction in relation to tidal state at each site. A large grid cell size of 1 km^2 was chosen to overcome the problems of accurately assigning the dolphin's position to a particular location. The use of a theodolite was used initially for position fixing; however, this was found to be unsuitable when more than one dolphin group was in the area, due to the possibility of overlooking individual dolphin movements.

The direction of travel was classified as travelling inshore, offshore, or neutral (no observable direction). Offshore and inshore directional movements were recorded in association with observations of the local tidal flow (*i.e.,* changes in tideline, foamline of tidal fronts around headlands). Positive foraging behaviour was classified as repeated back and forth movements in a small discrete area, with fish occasionally chased out of the water. Behaviours, such as leaps, splashes, tail slaps, and physical contact occasionally were observed while the dolphins foraged; however, these observations were not used due to them occurring on only two occasions, and only when fish were chased out of the water. Dolphins when not engaged in positive foraging behaviour were classed as travelling (continuously moving from one area to another).

A group was defined as a collection of individuals within which no dolphin was separated by greater than 50 m. For this study, this definition pertained strictly to a spatial conformity, because individuals within such associations were observed frequently to behave independently. Group sizes were classified as: 1–2, 3–6, or >6 dolphins. Subject identification numbers were given to the dolphins or dolphin groups for each $\frac{1}{2}$ tidal cycle, if dolphin(s) merged together the subsequent subject identification numbers were collated throughout the remainder of the observation. If however, the original sighting of dolphins(s) split off into different directions, these individual observations kept the same subject identification number but with revised numbers of individuals. This was conducted to avoid counting the same individual or group twice.

Dolphin/boat interactions were recorded when a boat was no further than 250 m from any dolphin(s), with each interaction lasting no longer than *ca.* 5 min. Data were later pooled for both sites, due to low sample sizes and the fact that the majority of boats were observed at both sites. Time, boat type, boat position, distance offshore, direction of travel, dolphin(s) subject identification number, reaction of dolphin(s) towards boat, and distance of boat from dolphin(s) were recorded. Boat type was classified as: speedboat/dinghy, fishing boat/motor sailboat, tourist boat, or kayak. Boat position was plotted along with the dolphin(s) position on a grid map, to determine the dolphin(s) response towards the boat over time on a daily basis. Identification numbers were given to each dolphin/boat interaction so as to identify which boat was associated with which dolphin or dolphin group. Dolphin behaviour toward the boats was classified as negative if the dolphin(s) moved away from the vessel, positive if the dolphin(s) moved towards the vessel, or neutral if the dolphin(s) showed no apparent change in directional movement, prior to and after the arrival of the vessel. Dolphin(s) behaviour relative to group size was recorded once all dolphin(s) showed the same behavioural response towards the vessel. If behavioural variations occurred within a group (i.e., a group size of four, two dolphins moved towards the vessel, while two dolphins showed no directional movement), these observations were ignored.

Data analysis
To identify between-site variability in the number of dolphins observed in relation to the tidal state and the time-of-day, a 2-way analysis of variance (ANOVA) was performed separately for each factor (STATGRAPHICS *plus* for Windows 3.0). Dolphin movements and foraging behaviour in relation to the tidal state and the time-of-day, foraging behaviour in relation to group size, dolphin reactions to boat type and in relation to group size, were all subjected to a χ^2 (goodness-of-fit test, Microsoft Excel for Windows 97).

Results

During the study period, 142 hrs of observations were conducted. Total number of sightings observed during the course of study was 70, with 221 counted dolphins. Thirty-nine sightings were at New Quay, representing 153 counted dolphins, and 31 sightings representing 68 counted dolphins were at Ynys Lochtyn. Dolphins could only be observed effectively up to 2 km offshore at both sites, although visibility on most days was up to 5 km.

Occurrence in relation to tidal state and time-of-day
There was a significant difference in the number of dolphins between the two sites, with respect to tidal state (F=4.81, P <0.05) and time-of-day (F=13.80, P <0.001). The mean number of dolphins observed in relation to the tidal state at New Quay was highest (11.0) between low water and $\frac{1}{2}$ flood and lowest (4.2) between $\frac{1}{2}$ flood and high water. The mean number of dolphins observed at Ynys Lochtyn in relation to the tidal state was highest (5.0) between high water and $\frac{1}{2}$ ebb and also between low water and $\frac{1}{2}$ flood (4.8) and lowest (2.4) between $\frac{1}{2}$ flood and high water.

The mean number of dolphins observed in relation to the time-of-day at New Quay was highest (5.5) in the morning (06:00–10:30 hr), with numbers being relatively uniform for the rest of the day (3.3 and 3.0). The mean number of dolphins observed in relation to the time-of-day at Ynys Lochtyn was uniformly low throughout the day (2.2), means in the morning (06:00 to 10:30 hr) being 2.3 and for the rest of the day 1.8.

Movement in relation to tidal state and time-of-day
The examination of dolphin movement patterns and the tidal state at New Quay (Fig. 2a) revealed that the highest number of dolphins moved offshore between $\frac{1}{2}$ ebb and low water (32 individuals) and between low water and $\frac{1}{2}$ flood (42 individuals). The highest number moving inshore was between $\frac{1}{2}$ flood and high water (12 individuals), while 27 individuals showed neutral movements between high

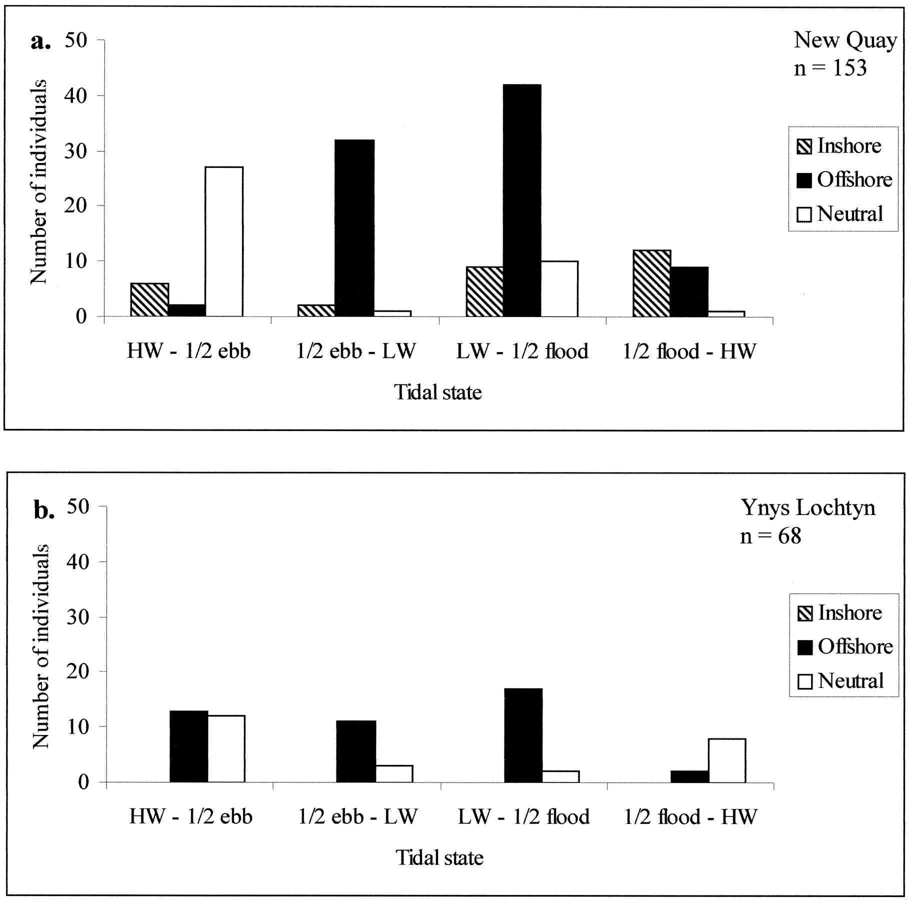

Figure 2. (a) Bottlenose dolphin directional movements relative to tidal state at New Quay (HW=high water, LW=low water), (b) directional movements relative to tidal state at Ynys Lochtyn (HW=high water, LW=low water).

water and $\frac{1}{2}$ ebb. The relationship between direction of movement and tidal state at New Quay was statistically significant (χ^2=94.55, *df*=6, *P*<0.001). Dolphins did not show statistically significant movement patterns in relation to the time-of-day at New Quay (χ^2=6.32, *df*=4, *P*>0.1).

At Ynys Lochtyn (Fig. 2b), the highest number of dolphins moved offshore between low water and $\frac{1}{2}$ flood (17 individuals), while 13 individuals moved offshore between high water and $\frac{1}{2}$ ebb and 11 individuals between $\frac{1}{2}$ ebb and low water. The highest number (12 individuals) observed showing neutral movements was between high water and $\frac{1}{2}$ ebb. There were no movements inshore at this site. The relationship between direction of movement and tidal state at Ynys Lochtyn also was statistically significant (χ^2=16.44, *df*=3, *P*<0.001). Dolphins did not show statistically significant movement patterns in relation to the time-of-day at Ynys Lochtyn (χ^2=1.97, *df*=2, *P*>0.3).

Foraging behaviour in relation to tidal state and time-of-day

Most dolphin foraging (Fig. 3a) took place between high water and $\frac{1}{2}$ ebb (27 individuals) at New Quay. Traveling behaviour (offshore or inshore) dominated the remaining tidal states, particularly between low water and $\frac{1}{2}$ flood (51 individuals). The relationship of foraging behaviour with respect to tidal state at New Quay was statistically significant (χ^2=66.35, *df*=3, *P*<0.001). At Ynys Lochtyn (Fig. 3b), dolphin foraging behaviour was concentrated between high water and $\frac{1}{2}$ ebb (12 individuals) and between $\frac{1}{2}$ flood and high water (8 individuals). Traveling behaviour was observed most often in between $\frac{1}{2}$ flood and high water, with most dolphins

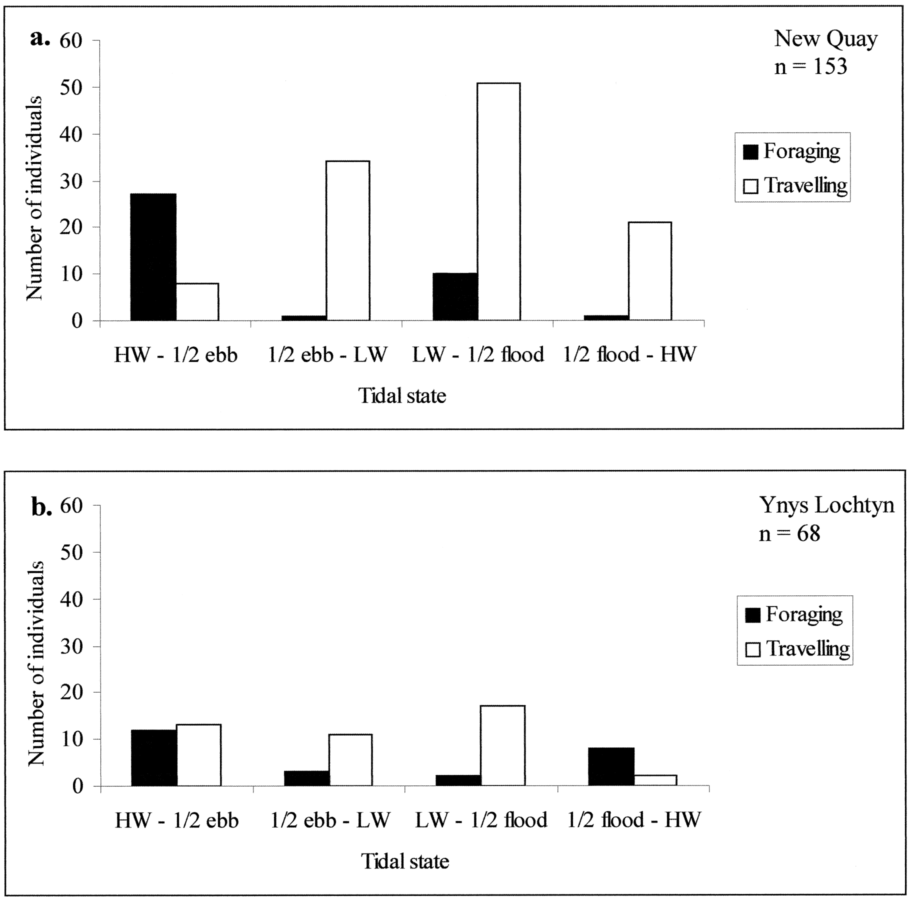

Figure 3. (a) Dolphin foraging behaviour relative to tidal state at New Quay (HW=high water, LW=low water), (b) Dolphin foraging behaviour relative to tidal state at Ynys Lochtyn (HW=high water, LW=low water).

(17 individuals) traveling (offshore direction) between low water and $\frac{1}{2}$ flood. The relationship of foraging behaviour with respect to the tidal state at Ynys Lochtyn was statistically significant ($\chi^2=23.94$, $df=3$, $P<0.001$).

No relationship was found between dolphin foraging behaviour and the time-of-day at New Quay ($\chi^2=4.35$, $df=2$, $P>0.001$). However, there was a statistically significant relationship found at Ynys Lochtyn ($\chi^2=15.52$, $df=2$, $P<0.001$), with most foraging taking place in the morning. Fourteen individuals were observed foraging between 06:00–10:30 hrs, while 24 individuals also were observed travelling offshore during this period. Relatively few dolphins were observed undertaking either activity in the evening period (Fig. 4).

No relationship between dolphin foraging behaviour in relation to group size was found at New Quay ($\chi^2=0.44$, $df=2$, $P>0.8$) and Ynys Lochtyn ($\chi^2=0.39$, $df=1$, $P>0.5$). However, at Ynys Lochtyn no group sizes above 4–6 individuals were observed.

Dolphin behaviour in relation to boat traffic

Dolphin response(s) to boats showed that 62% of observations were neutral i.e., the dolphins showed no apparent change in directional movement, prior to and after the arrival of the vessel. Twenty-two percent of observations showed a negative response (moving away from the vessel), while 16% showed a positive response (moving towards the vessel). These differences in responses in relation to boat traffic were statistically significant ($\chi^2=14.32$, $df=6$, $P<0.02$). Dolphins showed a positive response (23% of observations) towards tourist boats, while the dolphins showed a negative response (57% of observations) towards kayaks. However, the reactions towards kayaks were from the same group

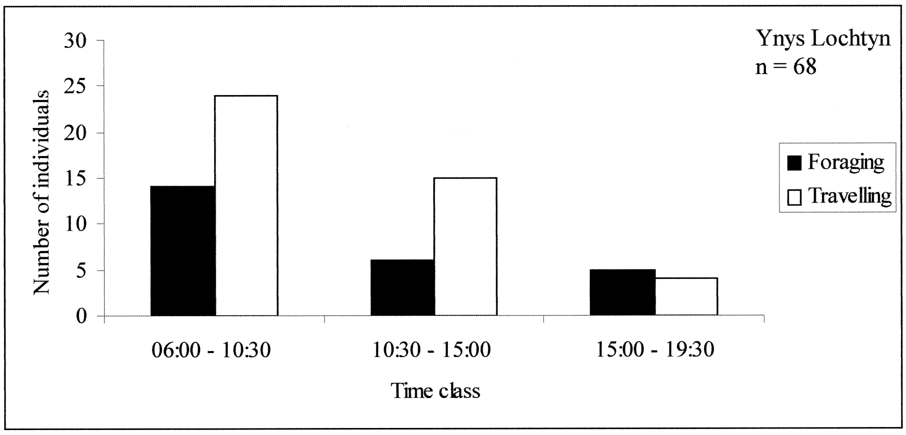

Figure 4. Number of bottlenose dolphins involved in foraging behaviour in relation to the time-of-day at Ynys Lochtyn.

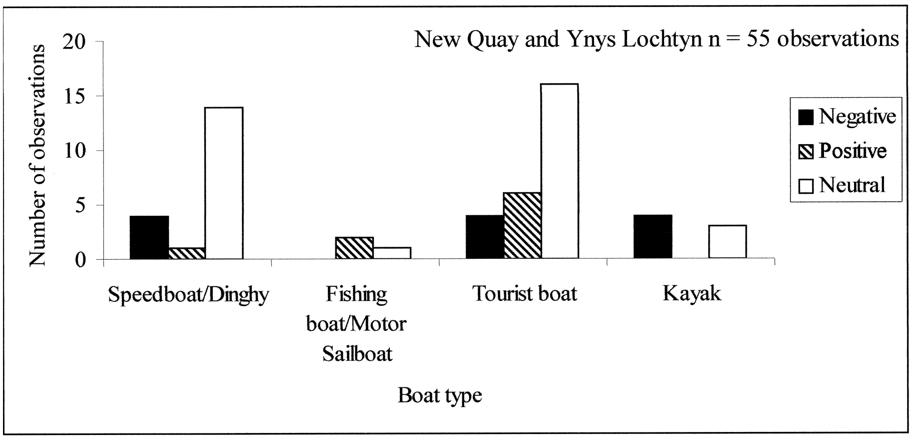

Figure 5. Bottlenose dolphin reaction(s) to boat type at New Quay and Ynys Lochtyn (Negative=move away from vessel, Positive=move towards vessel, Neutral=no apparent response to vessel).

of 4–8 dolphins. Positive response(s) were not noted towards kayaks or speedboats, while negative response(s) were not noted for fishing boat/motor sailboats (Fig. 5). The relationship between group size and the response to boat traffic was not statistically significant (χ^2=4.36, df=4, P>0.4).

Discussion

During August, the bottlenose dolphin population of Cardigan Bay showed a significant degree of site preference, with observations more frequent and consisting of larger groups at New Quay than at Ynys Lochtyn. A possible explanation could be that dolphins are feeding on different prey items. In the shallower more sheltered areas of New Quay, dolphins possibly feed on benthic fish (i.e., dab, *Limanda limanda*), which are characteristic species of soft sandy, gravely substrates. Feeding in such an environment could require more dolphins to search a given area for inconspicuous prey. In the deeper more open waters around Ynys Lochtyn dolphins could possibly feed on more conspicuous pelagic species (i.e., mackerel, *Scomber scombrus*), which bottlenose dolphins seem to show a consistent preference for (Mead & Potter, 1990). These species of fish could be detected more easily in the open water, resulting in fewer dolphins required to search an area.

Our observations suggested that the dolphins used the tides and traveling with the tidal flow, or traveling when the tidal flow is at its least strongest around slack water. By adopting such a strategy dolphins could reduce the energetic costs of moving. Dolphins appeared to be strongly influenced by the tides in the studies carried-out in the Shannon Estuary, SW Ireland, in which dolphins were frequently recorded during mid-ebb tide, when the tidal current was strongest (Berrow *et al.*, 1996). Irvine *et al.* (1981) also reported bottlenose dolphins in Sarasota Bay, Florida mainly swimming with the tidal currents.

Alternatively, dolphins could be responding to food availability due to the tidal variations by actively following their prey, since many fish species show a tendency to follow the tides in search of food (Harden Jones, 1968; Gibson, 1978; Wirjoatmodjo & Pither, 1984). Foraging behaviour was correlated with the tidal state at both study sites. Observations were greatest between high water and $\frac{1}{2}$ ebb at New Quay and Ynys Lochtyn, and also between $\frac{1}{2}$ flood and high water at Ynys Lochtyn. The foraging behaviour suggested that the dolphins could be responding to the tidal variations due to food availability, which is consistent with findings from studies conducted in the Golfo San José, Argentina (Würsig & Würsig, 1979), the coast of southern California (Hansen, 1990), and in the Shannon Estuary, S.W. Ireland (Berrow *et al.*, 1996).

Dolphin numbers generally were uniformly distributed throughout each time class, with no relationship found between dolphin movement patterns and the time-of-day at either of the two sites. There was no relationship between foraging activities and the time-of-day at New Quay, but a relationship was found at Ynys Lochtyn. This may have been because only dolphin(s) traveling offshore were recorded at this site and no inshore movements were observed. However, Saayman *et al.* (1973) found that foraging and feeding activity were strongly correlated with the time-of-day in Plettenberg Bay, South Africa, and considered that this may have been related to the availability and diurnal activity cycles of food-fish.

Foraging at New Quay and Ynys Lochtyn mainly consisted of solitary individuals. Würsig & Würsig (1979) suggested that nearshore searching for food usually involves solitary individuals, while deeper water prey searches relies on a large group that often use combined sensory and echolocation abilities to locate and capture prey. Shane (1990) reported that 'habitat structure and activity patterns' have the most influence on bottlenose dolphin group size and that 'group size tends to increase with water depth or openness of the habitat.' However, the correlation between habitat structure and activity patterns relative to group size was not tested in the present study.

Behavioural responses of bottlenose dolphins toward boats mainly were neutral, i.e., the dolphins showed no apparent change in directional movement, prior to and after the arrival of the vessel. This neutral response could be due to habituation by the dolphins toward the boats, since most boat traffic in the area consists of tourist boats, which conduct daily transects of the bay. Allen & Read (2000) found that vessel densities were not sufficient to evoke a measurable response in the bottlenose dolphins in Clearwater, Florida, and suggested that the dolphins are habituated to the level of vessel traffic encountered.

A positive response towards tourist boats was observed, with dolphins usually swimming towards these vessels to bow-ride, which has been observed in studies involving bottlenose dolphins (Lockyer, 1978; Würsig & Würsig, 1979) and other small cetacean species, such as Hector's dolphins (Stone *et al.*, 1995). Dolphins generally showed a negative response towards kayaks, with 57% of observations showing dolphins moving away from this type of vessel. The negative reactions towards kayaks were from the same group of 4–8 individuals, and were repeatedly observed actively moving away to avoid these types of vessel, often traveling up to distances of 200 m away. This reaction could be due to a 'startle response' elicited in the dolphin(s) by this type of vessel, due to their relatively silent approach compared with a motor vessel. Kayaks are able to come within a few metres of the dolphins when they are foraging before dolphins react. Negative responses of bottlenose dolphins toward boat presence have been reported in previous studies (Sorensen *et al.*, 1984; Janik and Thompson, 1996), but these were related mainly to motor-vessels (and associated noise disturbance). It has been suggested that disturbance may influence dolphin foraging activity, which has a potential affect on population structure, i.e., reduction in food consumption could result in subtle changes in growth rate, reproductive rates, or unknown physiological effects of stress from remaining in an area with high disturbance, short-term or permanent movements to less favourable areas, and ultimately survival (Grellier *et al.*, 1995).

The current study suggests that the bottlenose dolphin population of Cardigan Bay display diurnal movement patterns relative to tidal state, either moving with the tides or moving when there is least tidal resistance. It is most likely that these movement patterns are associated with distribution or movement of potential prey. Conversely, the time-of-day does not seem to be involved in the dolphin's occurrence or behaviour patterns. Local habitat preference is possibly responsible for the dolphin population's distribution between New Quay and Ynys Lochtyn. In order to better understand the ecology of the bottlenose dolphin in Cardigan Bay, detailed information on prey distribution and movement, preference for individual prey items and prey migration in relation to the tides would be most useful. In addition, insight would be further enhanced by extending future studies temporally. The present study raises interest in the effect of kayaks in Cardigan Bay, previously believed to be benign, on the behaviour of the bottlenose dolphin population. Future studies on the effects of boat disturbance would benefit from a consideration of kayaks as having a potential influence on the natural behaviour patterns of dolphins. However, in the present study certain parameters such as, change in surfacing duration, swimming speed, and changes in diving behaviour, which could indicate a reaction toward boats were unrecorded. The inclusion of such behaviours toward boats as an indication of boat disturbance would also be of benefit to future studies.

Acknowledgments

The authors thank Drs. Peter Evans and Jim Heimlich-Boran for their invaluable information and advice. Thanks must also go to Drs. Julian Stander and Peter Cotton at the University of Plymouth, Liz Allan, Alison Gill, Holly Arnold, Steve Hartley and two reviewers for comments on this manuscript. P. R. Gregory thanks Amanda Brown for her inexhaustible tolerance and assistance throughout the entirety of this work.

Literature Cited

Allen, M. C. & Read A. J. (2000) Habitat selection of foraging bottlenose dolphins in relation to boat density near Clearwater, Florida. *Marine Mammal Science* **16,** 815–824.

Arnold, H. (1993) Distribution, abundance, and habitat use of bottle-nosed dolphins in Cardigan Bay, Wales. *European Research on Cetaceans* **7,** 63–66.

Ballance, L. T. (1990) Residence patterns, group organization and surfacing associations of bottlenose dolphins in Kino Bay, Gulf of California, Mexico. Pages 267–284. In: S. Leatherwood and R. R. Reeves (eds.). *The Bottlenose Dolphin.* Academic Press, London.

Barco, S. G., Swingle, W. M., McLellan, W. A., Harris, R. N. & Pabst, D. A. (1999) Local abundance and distribution of bottlenose dolphins (*Tursiops truncatus*) in the nearshore waters of Virginia Beach, Virginia. *Marine Mammal Science* **15,** 394–408.

Berrow, S., Holmes, B. & Kiely, O. R. (1996) Distribution and abundance of bottle-nosed dolphins *Tursiops truncatus* (Montagu) in the Shannon Estuary. *Biology and Environment: Proceedings of the Royal Irish Academy* **96B,** 1–9.

Borrell, A. (1993) PCB and DDTs in blubber of cetaceans from the Northeastern North Atlantic. *Marine Pollution Bulletin* **26,** 146–151.

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

Evans, C. D. R. (1995*a*) Offshore Environment, chapter 2.2. In: J. H. Barne, 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. 239 pp.

Evans, C. D. R. (1995*b*) Wind and Water, chapter 2.3. In: J. H. Barne, 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. 239 pp.

Evans, P. G. H., S. Harding, G. Tyler & S. Hall. (1986) Analysis of Cetacean Sightings in the British Isles, 1958–1985. Nature Conservancy Council, Peterborough, 71 pp.

Evans, P. G. H. (1992) Status review of cetaceans in British and Irish waters. UK Mammal Society Cetacean Group. Report to the UK Department of Environment, London, 98 pp.

Evans, P. G. H. (1996) CCW Regional Coastal Directory—Evans, P. G. H. (1995) Whales dolphins and porpoises. Pages 137–140. In: J. H. Barne, 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. 239 pp.

Gibson, R. N. (1978) Lunar and tidal rhythms in fish. Pages 201–213. In: J. E. Thorpe (eds.). *Rhythmic Activity in Fishes*. Academic Press, London.

Grellier, K., Arnold, H., Thompson, P., Wilson, B. & Curran, S. (1995) Management recommendations for the Cardigan Bay bottlenose dolphin population. CCW Contract Science Report 134.

Hansen, L. J. (1990) California coastal bottlenose dolphins. Pages 403–420. In: S. Leatherwood and R. R. Reeves (eds.). *The Bottlenose Dolphin*. Academic Press, London.

Harden Jones, F. R. H. (1968) *Fish Migration*, Edward Arnold, London.

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

Janik, V. M. & Thompson, P. M. (1996) Changes in surfacing patterns of bottlenose dolphins in response to boat traffic. *Marine Mammal Science* **12,** 597–602.

Leatherwood, S., Foster, L. & Reeves, R. R. (1983) *The Sierra Club Handbook of Whales and Dolphins.* Sierra Club Books, San Francisco, CA.

Leatherwood, S. & Reeves, R. R. (1990) *The Bottlenose Dolphin*. Academic Press, London.

Lewis, E. J. & Evans, P. G. H. (1993) Comparative ecology of bottle-nosed dolphins *Tursiops truncatus* in Cardigan Bay and the Moray Firth. *European Research on Cetaceans* **7,** 57–62.

Lockyer, C. (1978) The history and behaviour of a solitary wild, but sociable, bottlenose dolphin (*Tursiops truncatus*) on the west coast of England and Wales. *Journal of Natural History* **12,** 513–528.

Mead, J. G. & Potter, C. W. (1990) Natural history of bottlenose dolphins along the central Atlantic coast of the United States. Pages 165–195. In: S. Leatherwood and R. R. Reeves (eds.). *The Bottlenose Dolphin*. Academic Press, London.

Morris, R. J., Law, R. J., Allchin, C. R., Kelly, C. A. & Fileman, C. F. (1989) Metals and organochlorines in dolphins and porpoises of Cardigan Bay, West Wales. *Marine Pollution Bulletin* **20,** 512–523.

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

Shane, S. H. (1990) Comparison of bottlenose dolphin behavior in Texas and Florida, with a critique of methods for studying dolphin behavior. Pages 541–558 In: S. Leatherwood and R. R. Reeves (eds.). *The Bottlenose Dolphin*. Academic Press, London.

Sorensen, P. W., Medved, R. J., Hyman, M. A. M. & Winn, H. E. (1984) Distribution and abundance of cetaceans in the vicinity of human activities along the continental shelf of the northwestern Atlantic. *Marine Environmental Research* **12,** 69–81.

Stone, G., Brown, J. & Yoshinaga, A. (1995) Diurnal patterns of Hector's Dolphin as observed from clifftops. *Marine Mammal Science* **11,** 395–402.

Vidal, O. (1993) Aquatic mammal conservation in Latin America: problems and perspectives. *Conservation Biology* **7,** 788–795.

Wells, R. S. & Scott, M. D. (1997) Seasonal incidence of boat strikes on bottlenose dolphins near Sarasota, Florida. *Marine Mammal Science* **13,** 475–480.

Wells, R. S. & Scott, M. D. (1999) Bottlenose dolphin *Tursiops truncatus* (Montagu, 1821). Pages 137–182 In: S. H. Ridgway and R. Harrison (eds.). *Handbook of Marine Mammals*. Volume 6. The second book of dolphins and the porpoises. Academic Press, London.

Wiley, D. N., Wenzel, F. W. & Young, S. B. (1994) Extralimital residency of bottlenose dolphins in the Western North Atlantic. *Marine Mammal Science* **10,** 223–226.

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

Wirjoatmodjo, S. & Pither, T. J. (1984) Flounders follow the tides to feed. *Estuarine Coastal & Shelf Science* **19,** 231–241.

Würsig, B. & Würsig, M. (1979) Behavior and ecology of the bottlenose dolphin, *Tursiops truncatus*, in the South Atlantic. *Fishery Bulletin, US* **77,** 399–412.