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RESEARCH ARTICLE

G. D. Hastie · B. Wilson · L. J. Wilson · K. M. Parsons
P. M. Thompson

Functional mechanisms underlying cetacean distribution patterns: hotspots for bottlenose dolphins are linked to foraging

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Abstract Many studies have shown that the distribution of cetaceans can be closely linked to habitat, but the underlying function of the preferred habitats often remains unclear. Only when behavioural observations are made in relation to habitat types can functional mechanisms behind the habitat use be revealed. Within the range of a bottlenose dolphin (*Tursiops truncatus*) population off NE Scotland, dolphins show clear preferences for several discrete areas. If the observed patterns of distribution are related to foraging, we predict that behaviour patterns shown by dolphins would reflect this relationship. In this study we identify behaviours of dolphins at the water surface that were related to feeding events, evaluate whether the patterns of distribution were related to foraging and whether they were related the local submarine habitat characteristics. To investigate whether visible surface evidence of foraging behaviour varied spatially, we analysed data collected from 104 regular boat-based surveys made within the Moray Firth, NE Scotland, between 1990 and 2000. To determine whether underlying bathymetry had any influence on the surface behaviour of dolphins, a land-based observation study was carried out in the populations core region of use. The results of this study show that feeding behaviour by dolphins was significantly higher in areas used intensively by dolphins. Furthermore, there were clear relationships between feeding events and the submarine habitat characteristics; certain forms of feeding occur primarily over steep seabed gradients, and in deeper waters during June and July. These results quantitatively support the hypothesis that the distinctive patterns of distribution shown by these dolphins are related to foraging behaviour or opportunities, and that submarine habitat characteristics may be a significant factor in the foraging efficiency of dolphins. Future work should focus on collecting detailed information on the distribution patterns of prey within the study area to allow direct comparisons between predator and prey distributions.

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G. D. Hastie (✉) · L. J. Wilson · K. M. Parsons
P. M. Thompson
School of Biological Sciences, University of Aberdeen,
Lighthouse Field Station, Cromarty,
Ross-Shire, IV11 8YJ, UK
E-mail: hastie@zoology.ubc.ca
Tel.: +1-604-9316204
Fax: +1-604-9316204

B. Wilson
Gatty Marine Laboratory,
Sea Mammal Research Unit,
University of St. Andrews, KY16 8LB, UK

Present address: G. D. Hastie
Marine Mammal Research Unit,
University of British Columbia,
Hut B-3, 6248 Biological Sciences Road,
Vancouver, B.C., V6T 1Z4, Canada

Introduction

Many studies have shown that the distribution of a cetacean population can be closely linked to habitat features (Watts and Gaskin 1986; Ross et al. 1987; Selzer and Payne 1988; Frankel et al. 1995; Gowans and Whitehead 1995; Baumgartner 1997; Raum-Suryan and Harvey 1998; Karczmarski et al. 2000; Davis et al. 2002), but the underlying function of the preferred habitats often remains unclear. This is because information on distribution alone does not reveal the function of these areas. Only when behavioural observations are made in relation to habitat types can a full picture of the habitat use be revealed.

Within the range of a bottlenose dolphin (*Tursiops truncatus*) population off NE Scotland, area use is heterogeneous with dolphins showing clear preferences for several discrete areas. These favoured areas share topographically distinctive characteristics in comparison to surrounding waters; they occur in unusually deep narrow entrances to coastal inlets that have steep seabed gradients (Wilson et al. 1997). It was suggested that the consistent pattern of habitat use was related to the deep narrow channels creating bottlenecks for migratory fish potentially elevating foraging opportunities (Wilson et al. 1997). Detailed investigations of one of these deep channels showed that the distribution of dolphins was closely related to bathymetry; dolphins were sighted most frequently within the deepest waters and areas of steep seabed gradients (Hastie et al. 2003a). If the observed spatial patterns of distribution are related to foraging, we predict that behaviour patterns shown by dolphins would reflect this relationship.

For many species, the behaviour that individuals exhibit within different habitats clearly indicates the ecological function that those areas provide. However, for dolphins, determining the functional value of different habitats is often less clear. This is because they are highly mobile, can range over relatively large distances, and spend the majority of their time underwater, meaning that observing the animals is challenging. Furthermore, submarine environmental characteristics are also far less obvious to the surface observer. However, as cetaceans must regularly return to the surface to breathe, their behaviour at the surface can potentially provide insights into their submarine behaviour.

Using this approach, studies have documented links between bathymetric variables including water depth and seabed gradient, and foraging behaviour (e.g. Winn et al. 1986; Heimlich-Boran 1988; Hanson and Defran 1993; Harzen 1998). However, much of the information relating dolphin foraging with bathymetry has been collected on relatively large spatial scales, covering 10s or 100s of kilometres, and it is currently unclear how foraging is influenced by fine-scale bathymetric characteristics over 10s or 100s of metres.

In this study we identify behaviours of dolphins at the water surface that were related to feeding events, evaluate whether the spatial patterns of distribution, identified in previous studies (Wilson et al. 1997), were related to foraging and whether they were correlated with local submarine habitat characteristics.

Materials and methods

Spatial variation in feeding behaviour

To investigate whether visible surface evidence of foraging behaviour varied spatially, we analysed data collected from 104 regular boat-based surveys made within the Inner Moray Firth, NE Scotland (57° 41′ N, 4° 00′ W) between 1990 and 2000 along a standard survey route (Wilson et al. 1997). At the end of each encounter with a school of dolphins, a short checklist of behaviours observed was completed. This included a note of whether dolphins were observed at the surface chasing or grasping fish. Encounters where dolphins showed an overt reaction to the vessel by bowriding were excluded from the dataset. All further analyses were restricted to the remaining 492 independent encounters with dolphin schools.

To investigate whether the distribution of dolphin schools showed a consistent pattern, the density of dolphin schools was calculated using a kernel density method (Arcview version 3.2 ESRI Inc.) and plotted (Fig. 1). Each encounter with a school was then assigned a density value based on its spatial location and the corresponding density plot.

Generalised linear models were used to investigate how the probability of observing feeding behaviours varied with the spatial density of schools. The link function was a logit suitable for binomial responses, in this case being visible surface interactions with fish. As the number of individuals in dolphin schools varied, and our observations varied in length, these factors alone could affect the probability of fish being sighted. To account for this, the number of dolphins in each school and the duration of the encounter were also tested as initial explanatory variables. Analyses were carried out using the SPLUS 2000 software package (Mathsoft Inc.).

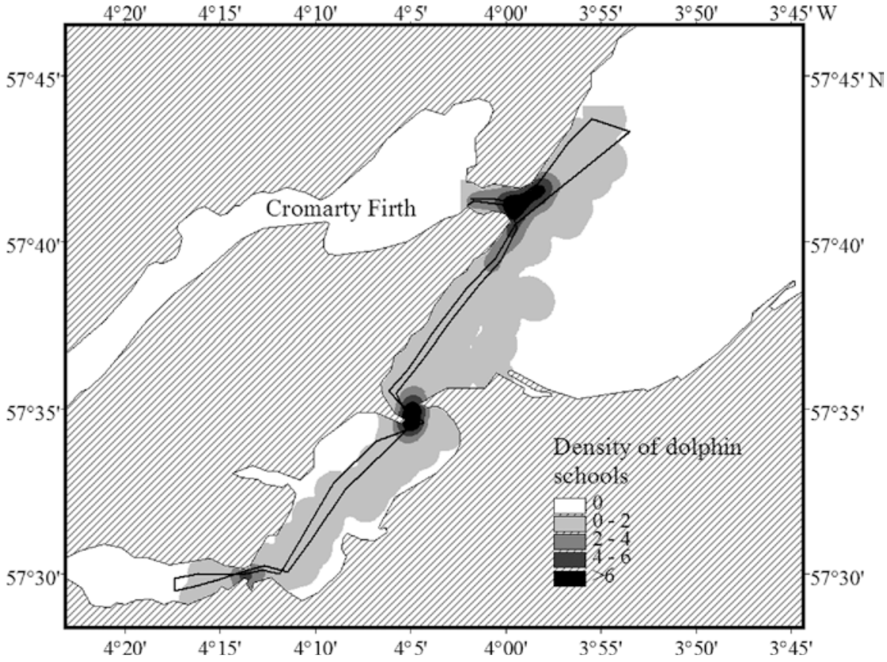

Fig. 1 The distribution of dolphin sightings in the inner Moray Firth between 1990 and 2000. One hundred and four surveys along the route shown by the *black line* were carried out during the study period. A total of 508 schools of dolphins were sighted. The *contoured shading* represents a kernel smoothing interpolation of dolphin density, estimated as the number of schools per 100 m^2

The influence of bathymetry on feeding behaviour

To determine whether bathymetry had any influence on the surface behaviour of bottlenose dolphins, a land-based observation study was carried out in the populations core region of use (Wilson et al. 1997). This was a 1.2 km^2 area spanning the narrow channel at the entrance to the Cromarty Firth (Hastie et al. 2003a).

Between 1997 and 1999, the behaviour of dolphin schools was studied using a focal-group following protocol with incident sampling of a specified list of surface behaviours (Table 1) (Altmann 1974; Mann 1999). A two-person team, using a combination of video camera and surveyors' theodolite, tracked schools from a land-based observation station approximately 90 m above sea level.

The surface behaviour of each school was video-taped using a Canon Ex2-Hi 8 video camera with an 8–120 mm zoom lens and 2× converter. This allowed detailed records of the behaviour to be collected across the whole study area. The sampling was carried out using an established protocol and data collection technique described in Hastie et al. (2003b). An auto-correlative test was carried out for the two most common behaviours "Lunge" and "Flukes up" to test for independence of samples. These were not significant ("Lunge", Spearmans Rho = 0.186, $n = 46$, $P = 0.212$; "Flukes up", Spearmans Rho = -0.192, $n = 46$, $P = 0.202$) and the samples were therefore considered independent.

An electronic theodolite was used to calculate the location of each school during sampling. Locations were measured approximately every 30 s, and were corrected for tidal height. This information was calculated using a tidal prediction software package (Admiralty Simplified Harmonic Method of Tidal Prediction, The Hydrographic Office, Taunton, UK). Predicted heights did not differ significantly from actual tidal heights measured using a paper trace tidal height recorder (Cromarty Firth Port Authority) (*t*-test, $T = 0.07$, $df = 113$, $P = 0.94$). The accuracy of the theodolite based locations was examined using a boat and Differential GPS (Garmin GPS 12 XL calibrated with an MBX-3; 2 Channel Automatic Differential Beacon Receiver). This field test showed that errors in location estimation ranged from 0.5 m to 13.3 m with an overall median error of 2.8 m (IQ range: 1.7 m–4.7 m). There was a significant increase in location error with distance from the observation station (Generalised Linear Model; Deviance (χ^2) = 52.68, $df = 1$, $P < 0.0001$).

A total of 127 dolphin behaviour samples were collected between June and September 1997, May and September 1998, and during May and September 1999. To ensure that the behaviour was unaffected by the presence of boats, samples recorded when boat traffic was present were excluded. To ensure that all behaviours were visible across the study area, samples were only collected when the Beaufort sea-state was less than 3 and in clear conditions with no precipitation. The video footage was later reviewed and the time to the nearest second of each dolphin surfacing was noted. In addition, the specific type of surfacing was noted (see Table 1).

Two multivariate methods of data reduction (hierarchical cluster analysis and non-metric multidimensional scaling analysis) were applied to identify behaviours that were associated with interactions with fish. Samples were standardised to the median sample period of 3 min. In samples longer than this, only the first 3 min of data were included leaving a total of 102 samples.

Initially, a hierarchical cluster analysis was used to search for natural behavioural groupings in the data set. Ward's clustering method was used and association values between behaviours calculated using the Pearson product-moment correlation coefficient. To determine the number of behavioural groupings present, the resultant dendrogram was examined and the largest change in distance between consecutive branches was used as the cut-off distance (Everitt 1974).

Non-metric multidimensional scaling analyses were used to confirm the groupings produced using the cluster analysis. Using the Bray-Curtis algorithm (Bray and Curtis 1957) to calculate "distances" between pairs of behaviours, a distance matrix was produced. Multidimensional scaling of this matrix was used to compute coordinates for each of the behaviours in *n*-dimensional space. Kruskal's algorithm was used to calculate stress values (Kruskal 1964). The smallest number of dimensions above which the change in stress value was minor was chosen as the number of dimensions to visualise the data (Spence 1978).

Variations in surface behaviour were examined across the study area with respect to three key bathymetric variables; water depth, seabed gradient, and distance from shore. Each surfacing was assigned to its nearest school location with respect to time. This resulted in each location having a median of 6 (IQ range = 3–13) surfacings associated with it.

The study area was divided into 50 m×50 m grid cells and the surfacings from each sample were assigned to the corresponding grid cell. If the sample spanned more than one cell, the cell with the most surfacings was used. The average depth and seabed gradient, and distance from shore were estimated for each grid cell from an interpolation of the seabed at a 1 m^2 resolution.

Generalised linear models with a logit link function were then used to investigate how the probability of sighting behaviours associated with feeding (identified using the behavioural analyses) varied with month, water depth, seabed gradient and distance from shore. Because individual samples had variable numbers of surfacings associated with them, this was also included as an explanatory variable. Analyses were carried out using the SPLUS 2000 software package (Mathsoft Inc.).

Table 1 Descriptions of 11 surface behavioural event types that were recorded during sampling from the land-based observation site. Only the first ten were used in further analyses, as the behaviour "Surface Roll" was considered as being purely for respiratory purposes

Behaviour	Description
Logging	Surfacing lasting longer than 4 s. The body does not clear the water.
Lunge	A rushing motion through the water surface creating a significant wake. The dolphins' head does not clear the water.
Fish	Any surfacing where a fish is observed being chased or manipulated by dolphins at the surface.
Flukes up	Tail flukes raised above the surface at the end of a surface roll.
Tail slap	Tail flukes raised above the surface and ventral side slapped down.
Full leap	Entire body leaves the water; the exit and entry is headfirst. NOTE: Distance made over the surface < 2 body lengths.
Half leap	As full leap, only part of the body clears the water.
Full slap	The full body clears the water and the flanks, venter or dorsum is slapped against the surface.
Half slap	Anterior half of the body clears the water and the flanks, venter or dorsum is slapped against the surface.
Porpoising	Entire body leaves the water; the exit and entry is headfirst and the venter faces down. NOTE: Distance made over the surface > 2 body lengths.
Surface Roll	The dorsal portion of the body, excluding the tail flukes, clears the water in a forward roll motion

Results

The results of this study show that feeding behaviour by bottlenose dolphins was significantly higher in areas used intensively by dolphins. Furthermore, there were clear relationships between feeding events and the submarine habitat characteristics.

Spatial variation in feeding behaviour

The results of the generalised linear modelling show that the occurrence of feeding behaviour is significantly related to spatial location and dolphin density. The resultant model predicts that when the duration of the encounter is set to its median value (27 min), the probability of sighting feeding behaviours peaks at 0.84 in regions of highest dolphin density and is only 0.56 in regions with low dolphin density (Table 2).

The influence of bathymetry on feeding behaviour

The results from the land-based part of the study showed there was a distinctive relationship between the occurrences of specific behaviours associated with feeding on large fish and bathymetry.

The hierarchical cluster analysis of behaviour types revealed that the longest distance between branches of the dendrogram (Fig. 2) was between branches 3 and 4, suggesting that there were four natural behavioural groupings. The only behaviour that was clearly associated with the presence of fish was "Porpoising". Examination of the multidimensional scaling analysis supports the results from the cluster analysis; "Porpoising" was the most closely associated behaviour to the presence of fish. Therefore, the two behaviours "Porpoising" and "Fish" were pooled and used as a single variable in the spatial analyses.

The results of the generalised linear modelling suggest that when the habitat variables, their two-way interactions and the number of surfacings were fitted, using a stepwise procedure, the number of surfacings was a significant factor in predicting the occurrence of feeding behaviours. The model predicts that as the number of surfacings increase, the probability of sighting feeding behaviours increases. In addition, both the seabed gradient and the interaction between month and water depth were significant predictors of the occurrence of feeding behaviours. The model predicts that the probability of sighting feeding behaviours peaks in areas with steep seabed gradients and deep water during June and July and is at a minimum during May, August, and September in areas with shallow waters and flat seabed gradients (Table 3, Fig. 3).

Table 2 Summary of the generalised linear models for predicting the occurrence of feeding behaviours sighted during encounters with dolphin schools from boat-based surveys, showing the coefficient (*B*) of each term, its standard error (SE) and the deviance and significance of the term. The change in deviance refers to removing the term from the final model in the case of included terms and adding the term to the final model in the case of rejected terms with *P*-values calculated using a chi-squared approximation ($n=492$)

Terms	B	SE	Deviance	df	$P(\chi^2)$
Included terms					
Constant	-3.119	0.36	–	–	–
Duration of encounter	0.014	0.01	6.687	1	0.01
Density of schools	0.114	0.05	5.708	1	0.017
Rejected terms					
School size estimate	–	–	0.083	1	0.773

Discussion and conclusions

Spatial variation in feeding behaviour

This study has shown that the functional mechanisms behind patterns of habitat use by Scottish bottlenose dolphins are linked to foraging; the probability of observing fish being chased or captured by dolphins peaks in regions that are used intensively by dolphins. Furthermore, within these regions of intensive use, there

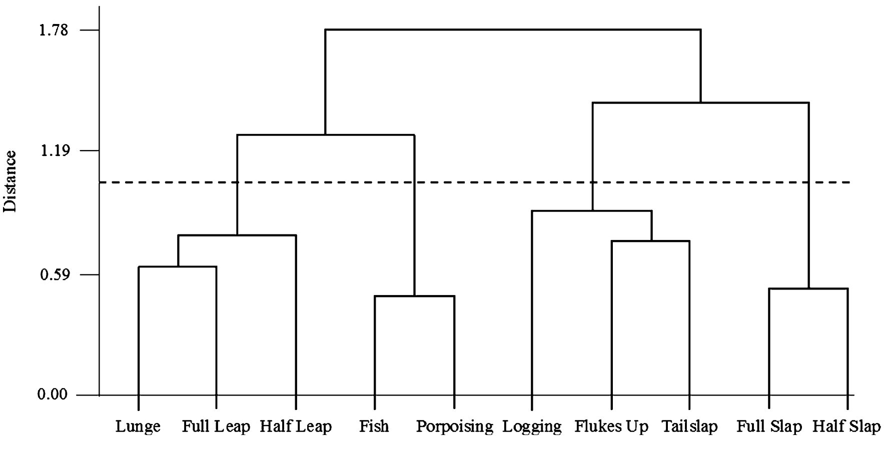

Fig. 2 Dendrogram of a hierarchical cluster analysis of ten surface behaviours (Table 1) using Ward's cluster method and a Pearson correlation measurement. Note the *dashed cut-off line* between branches 3 and 4 indicating the presence of 4 groups of behaviours

Table 3 Summary of the generalised linear models for predicting the occurrence of feeding behaviours, sighted during encounters with dolphin schools from the land-based surveys, including single variables and interactions between variables (denoted by an x). *P*-values were calculated using a chi-squared approximation ($n = 127$)

Model	Residual deviance	Deviance	Residual *df*	*df*	$P(\chi^2)$
Null model	127.14	–	136	–	–
Included terms					
Number of surfacings	121.43	5.3	135	1	0.021
Month x Water depth	99.68	21.78	126	9	0.0095
Seabed gradient	89.95	9.83	125	1	0.002
Excluded terms					
Distance from shore	88.26	1.59	124	1	0.207
Month x Seabed gradient	85.78	4.07	121	4	0.397
Month x Distance from shore	86.6	3.26	120	5	0.662

was a clear relationship between the occurrence of feeding behaviours and bathymetry. These results quantitatively support previous hypotheses that suggested that the distinctive patterns of habitat use shown by this population of dolphins are related to foraging behaviour or opportunities. Specifically, the topography of the area potentially acts as a bottleneck for migratory fish moving through the area, increasing density of prey in the area (Wilson et al. 1997; Hastie et al. 2003a).

The influence of bathymetry on feeding behaviour

Within the core region of use, dolphins showed consistent patterns in the relationships between the different surface behaviours, with four suites of behaviour covarying. Because behavioural observations were made from land, it was only possible to identify fairly large fish and these were most likely migrating salmonids (*Salmo salar* and *Salmo trutta*) (Wilson et al. 1997).

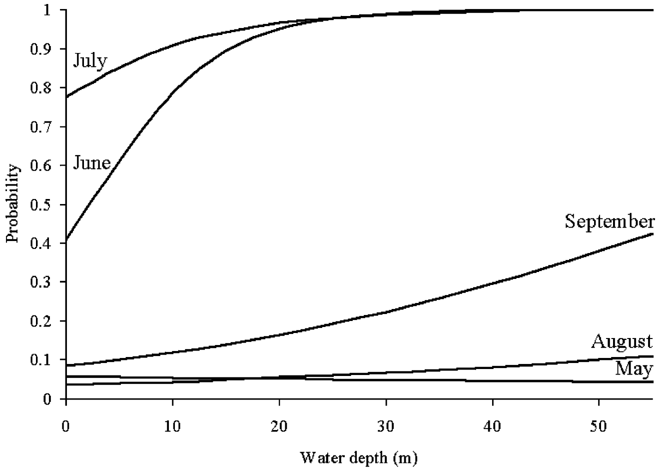

Fig. 3 Logistic curves representing the variation in the probability of sighting feeding behaviours with water depth during different months. The number of surfacings and the seabed gradient were set at standard values of 12 and 2 respectively

In a study of bottlenose dolphin acoustic behaviour within a similar coastal channel in the Moray Firth, Janik (2000) confirmed that the behaviour "Porpoising" was frequently associated with feeding on salmonids. This behaviour usually occurred immediately after a specific underwater vocalisation made by the feeding individual, and instances of this high-speed swimming associated with the feeding event were made by individuals responding to and approaching the vocalising dolphin (Janik 2000).

This study is one of the few that have quantified the spatial variation in cetacean behaviour on a scale of 10s to 100s of metres. The combination of video camera and theodolite proved to be suitable for evaluating the spatial distribution of surface behaviours within this study area. With an overall median error of less than 3 m, the theodolite was an extremely accurate tool for plotting the positions of schools of dolphins.

There was a significant relationship between foraging behaviour and water depth within the study area. This suggests that certain forms of feeding occur primarily in these deeper waters. This appears to confirm the suggestions made by Hastie et al. (2003a) that water depth may be a significant factor in the foraging efficiency by dolphins within this area. Furthermore, the model predicts that this relationship peaks during June and July; those months when numbers of fish migrating through the area are likely to be highest (Menzies 1928; Nall 1937).

However, without detailed information about the spatial distribution of fish within the study area, it is extremely difficult to make direct links between the predator and prey distributions. It may be possible that salmon migrating through the area use the deeper water as a thoroughfare and show distributions in response to this. Alternatively, it may be more profitable for a dolphin to forage in deeper water rather than in the shallower water, even if prey are distributed randomly in the study area. This is based on the potential encounter rate of prey in the deeper water; dolphins are likely to have a substantially larger potential search volume of water in which to locate prey within deeper waters (Hastie et al. 2003a). The relatively open water within deeper regions may also increase the efficiency of dolphin foraging by reducing potential refuges for fish such as the seabed.

Foraging behaviour also varied significantly with seabed gradient. The model predicted that these behaviours occur more frequently over steep seabed gradients than over shallow seabed gradients. Therefore, seabed gradient may be a significant factor in the foraging efficiency by dolphins within this area and may explain the greater use of regions within the study area characterised by steep seabed gradients.

Although other studies have suggested that seabed gradient is an important factor in cetacean foraging behaviour, quantitative data are rarely presented (Heimlich-Boran 1988; Shane 1990). It seems likely that the occurrence of feeding behaviour over steep gradients in this study will be either because prey capture is more efficient within these areas or because increased numbers of large fish occur within these areas. For example, it was suggested that killer whales use steep gradients as barriers to trap prey against (Heimlich-Boran 1988). Although this may be the case with vertical or very steep gradients, it seems unlikely that the maximum gradient within this present study area (approximately 20°) would represent a sufficient barrier for herding prey against. However, it is possible that migrating salmon rely on steep gradients as navigation cues as they travel through the area, effectively increasing their numbers over steep seabeds. Alternatively, other hydrographic features associated with steep gradients may be significant factors. For example, currents, upwellings or haloclines may result from strong tidal currents flowing over the steep gradients. These are features that have been known to delay Pacific salmon (*Oncorhynchus nerka* and *O. gorbuscha*), causing them to temporarily aggregate until they re-orientate themselves (Stasko et al. 1973; Quinn and teHart 1987). Furthermore, Atlantic salmon have been shown to use haloclines to orientate themselves during spawning migrations (Ikonen 1986). In support of this, some of the individuals within this population have been observed orientating themselves in relation to areas of current convergence in a tidal front within a similar deep, narrow channel (Mendes et al. 2002).

In conclusion therefore, this study has shown that the occurrence of foraging behaviours are greater than would be predicted in regions used intensively by dolphins. Furthermore, variation in the occurrence of specific behaviours was documented with respect to bathymetry; behaviours that were associated with feeding on large fish peaked in deep waters over steep seabed gradients during June and July. The absence of direct information on the spatial distribution of prey makes interpretation of the dolphins' spatial pattern of behaviour problematic. Therefore, future work should focus on collecting detailed information on the distribution patterns of prey within the study area to allow direct comparisons between predator and prey distributions.

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