Fine-scale habitat selection by coastal bottlenose dolphins: application of a new land-based video-montage technique

Gordon D. Hastie, Ben Wilson, and Paul M. Thompson

Abstract: Cetacean distribution and underwater topography are frequently correlated. These patterns are commonly studied on large spatial scales, over tens of kilometres, but very rarely on a fine scale. Sightings of bottlenose dolphins, *Tursiops truncatus*, within the Moray Firth, Scotland, were previously found to be concentrated within deep, narrow channels. To understand why such areas were selected, more-detailed information on the distribution of dolphins was required. This study describes the development of a video technique to study the spatial distribution and relative abundance of bottlenose dolphins. We then used the methodology to investigate whether water depth and seabed gradient influence the dolphins' distribution patterns. Furthermore, temporal patterns of use were examined with respect to seasonal, tidal, and diurnal cycles. The distribution of dolphins was significantly related to topography: dolphins were sighted most frequently in the deepest regions with the steepest seabed gradients. There was a clear temporal pattern in the use of the area, with sightings peaking during July. However, the presence of dolphins was not significantly related to tidal or diurnal cycles. The topography of the area appears to be a significant influence on its intensive use by dolphins, and patterns of use indicate that topography may facilitate foraging during seasonal migrations of fish.

Résumé : Il y a souvent une corrélation entre la répartition des cétacés et la topographie sous-marine. Ces patterns sont ordinairement étudiés à de grandes échelles spatiales de dizaines de kilomètres, mais rarement à une échelle fine. Les dauphins à gros nez, *Tursiops truncatus*, aperçus dans le golfe de Moray, en Écosse, se concentrent dans les chenaux profonds et étroits. Pour comprendre le choix de ces sites, il faut plus de détails sur la répartition des dauphins. Notre étude décrit la mise au point d'une technique vidéo pour étudier la répartition spatiale et l'abondance relative des dauphins. La technique nous a servi à déterminer si la profondeur de l'eau et le gradient du fond influencent les patterns de répartition. De plus, les patterns temporels d'utilisation de l'habitat ont été examinés pour identifier des cycles reliés à la saison, aux marées et à la journée. La répartition des dauphins est reliée de façon significative à la topographie; les dauphins sont vus le plus fréquemment dans les régions les plus profondes avec les fonds de plus forts gradients. L'utilisation de la région suit un net pattern temporel et le maximum de dauphins s'observe en juillet. La présence des dauphins n'est pas, cependant, reliée aux cycles de marée, ni aux cycles journaliers. La topographie de la région semble influer de façon significative l'usage considérable qu'en font les dauphins; les patterns d'utilisation indiquent que la topographie facilite peut-être la recherche de nourriture durant les migrations saisonnières des poissons.

[Traduit par la Rédaction]

Introduction

Studying cetacean habitat selection can be extremely challenging. The majority of cetaceans spend most of their lives under water, making observations difficult. However, as these animals must return to the surface to breathe, habitat use can be interpreted from their distribution at the surface. Distribution patterns have been frequently correlated with underwater topography, such as water depth (Watts and Gaskin 1986; Ross et al. 1987; Frankel et al. 1995; Gowans and Whitehead 1995; Baumgartner 1997; Davis et al. 1998; Raum-Suryan and Harvey 1998; Karczmarski et al. 2000) and seabed gradient (Watts and Gaskin 1986; Selzer and Payne 1988; Gowans and Whitehead 1995; Baumgartner 1997; Davis et al. 1998; Raum-Suryan and Harvey 1998; Karczmarski et al. 2000). These patterns are generally studied on large spatial scales, over tens or hundreds of kilometres. However, cetacean distribution in relation to such variables is rarely studied on a fine scale (Allen et al. 2001). The importance of understanding habitat selection by individuals over a range of spatial scales was highlighted by Pribil and Picman (1997), who showed that the relative importance of different habitat variables for birds can depend upon the spatial scale of study.

Furthermore, knowledge of temporal patterns of abundance within favoured areas can provide insights into the underlying features of their use. On a large scale, this has been observed in studies of annual migrations of large whales from temperate waters, used for feeding, to tropical waters, where calving

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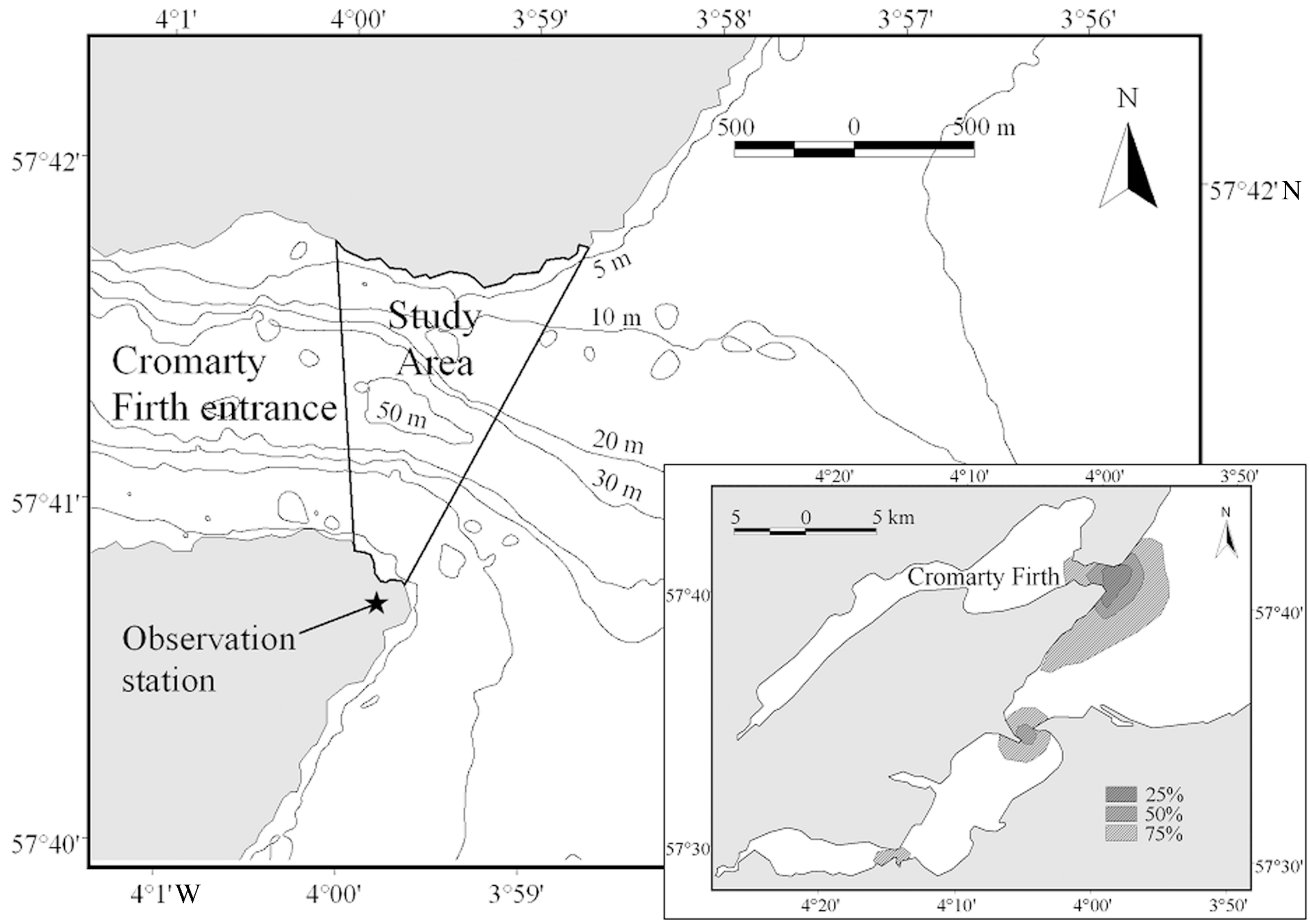
Fig. 1. Map of the inner Moray Firth (inset) showing the Cromarty Firth and the distribution of bottlenose dolphins, *Tursiops truncatus*, expressed as harmonic mean isopleths around 25, 50, and 75% of sightings (redrawn from Wilson et al. 1997). The main map shows the bathymetric contours in the region around the northernmost concentration of sightings at the entrance to the Cromarty Firth and the area used in this study.



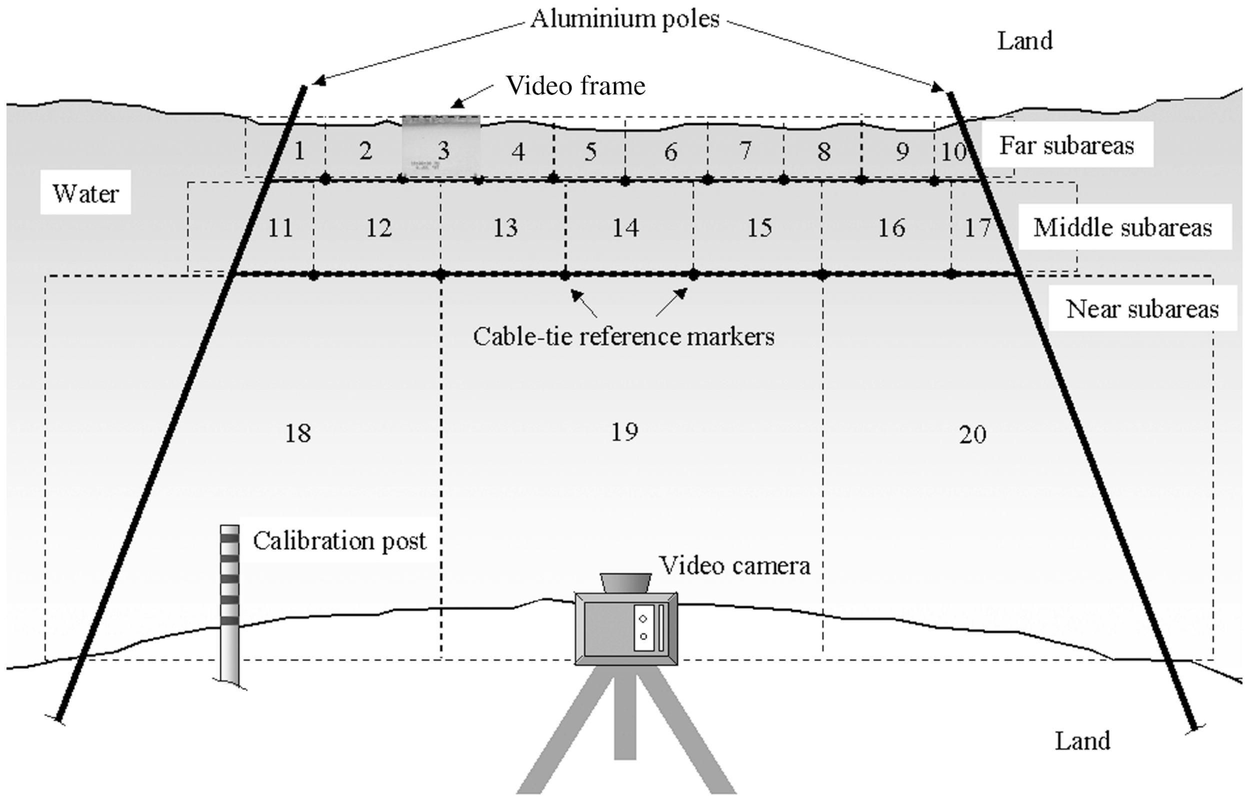
takes place (e.g., Matthews 1937), and on a small scale with local movements by individuals between habitats across a single tidal cycle (e.g., Acevedo 1991; Mendes et al. 2002).

In the inner Moray Firth, northeast Scotland (57°41′N, 4°00′W), bottlenose dolphins, *Tursiops truncatus*, exhibit a consistent spatial distribution. Dolphin sightings are concentrated within three small regions (Wilson et al. 1997) (Fig. 1). These are all deep, narrow channels subject to strong tidal currents and topographically unique compared with the flat, shallow seabed of the surrounding inner Moray Firth (Hunter and Rendall 1986). For management purposes it was recognised that because the population is small and isolated, more-detailed information on the use of these key areas was required (Wilson et al. 1997).

Previously, investigations of the fine-scale use of such areas have been constrained by the difficulty of recording cetacean positions accurately at sea. Some studies of coastal cetaceans have made use of land-based surveying instruments, such as theodolites, to locate surfacing cetaceans (Würsig and Würsig 1979; Jefferson 1987; Kruse 1991; Best et al. 1995; Harzen 1998). There are limitations in the use of theodolites, however. In particular, taking readings can often be time-consuming and this limits data collection to positions of small groups or subgroups rather than individuals. Furthermore, as groups can be distributed over tens or hundreds of metres, a single point is rarely representative of the distribution of the individuals themselves. Therefore, to examine the distribution of dolphins within these favoured areas, a method of data collection that produces accurate spatial information was required.

To overcome these problems, we adapted a survey method known as cue-counting, which has been widely used to survey populations of large whales (e.g., Larsen 1995). This is based on the idea that the "cues" within an area can be counted, and, with knowledge of the cue rate, the abundance of whales can be calculated. In most cases, the cue is defined as the moment that the whale comes to the surface to breathe. In the context of studying habitat selection, estimating the positions of individual surfacings is potentially a more accurate means of representing the position and distribution of a group of animals than a single point. DeNardo et al. (2001) used a combination of a cliff-top-mounted video and theodolite to calculate the inter-individual spacing within groups of killer whales (*Orcinus orca*) by plotting the positions of individual surfacings. The techniques employed in DeNardo et al.'s (2001) study therefore provide the potential

Fig. 2. Field equipment, including video camera, calibration post, and reference markers. The broken lines outline each of the 20 subareas in the far, middle, and near rows. A video frame of one of the subareas is indicated.



to determine the distribution of individual dolphin surfacings within an area close to land with a high degree of spatial accuracy.

The objectives of this study were (*i*) to develop a technique to accurately determine the distribution of dolphin surfacings within a small coastal study area; (*ii*) to examine the small-scale spatial patterns of dolphin surfacings (treated as cues) and test the hypothesis that their distribution was related to underwater topography; (*iii*) to examine temporal variation in the relative abundance of surfacings with respect to tidal, diurnal, and monthly cycles; and (*iv*) to use the results to investigate and identify potential factors behind the intensive use of a deep, narrow channel in the inner Moray Firth by bottlenose dolphins.

Materials and methods

We studied the relative abundance and distribution of bottlenose dolphins within a 1.2-km^2 area spanning a narrow coastal channel in the inner Moray Firth (Fig. 1). We used DeNardo et al.'s (2001) method as a basis to develop a new technique that allows land-based video recordings to be used to calculate the positions of individual dolphin surfacings. In this study, a surfacing was defined as any event where all or part of the body of the dolphin rose above the surface of the water. The numbers of surfacings were used as an index of the relative abundance and distribution of dolphins.

Field protocol

Observations were made from a cliff top, 90.5 m above sea level, immediately adjacent to and overlooking the study area. A tripod-mounted Canon Ex2-Hi 8 video camera with an 8- to 120-mm zoom lens and 2× converter (Canon, Wallington, U.K.) was used to record data. At the start of each day, the video camera and tripod were erected in the same position using permanent marks on a concrete plinth. The camera was levelled using a levelling bubble on the tripod.

The view of the study area was divided into 20 subareas as described below. Every hour during the sampling period, all 20 subareas were selected in random order and a 1-min high-resolution recording of each was made. The next hour during the sampling period the process was repeated but with the subareas recorded in a different order. Each of these samples was considered independent because the number of surfacings sighted within each sample was not correlated with the number of surfacings sighted in the subsequent sample (Pearson's correlation coefficient = 0.106, N = 199, p = 0.137).

This technique requires reference locations within the video camera's field of view that allow video samples of subareas to be combined to form a montage of the whole study area. In some situations, coastline features or moored buoys could be used to achieve this. In our study, however, this was not possible because the channel was too wide and this caused vessel-navigation issues. A wire grid was therefore erected 3 m in front of, and perpendicular to, the camera to divide the view of the study area into the 20 subareas

Table 1. The independent variables used in the general linear models.

Variable	Description
Temporal	
Year	Calendar year in which the sample was collected
Month	Calendar months between May and September inclusive
Time class	Time between sunrise and sunset divided into 10 equal periods
Tide class	Time between adjacent high tides divided into 10 equal periods
Environmental	
Cloud cover	Cloud cover in octaves (0 = clear skies; 8 = full cloud cover)
Wind direction	Direction of the wind, e.g., northeast; if there was no detectable wind, this was classed as light and variable
Sea state	Sea surface conditions measured according to the Beaufort scale

Note: All variables are categorical.

(Fig. 2). The grid was constructed using two 3 m long aluminium poles inserted into permanent sleeves in the ground. Between the poles, two lines of 1.5 mm thick wire divided the view of the study area into far, middle, and near rows of subareas. Cable ties attached along the wire were used as reference markers to further divide the study area into the 20 subareas. To ensure that the grid maintained its position, its alignment with features on the far shore was checked each day.

To ensure consistency in the probability of recording a dolphin surfacing throughout the study, samples were only collected in clear conditions with no precipitation. Environmental conditions were recorded at the start of each sample, including cloud cover, wind direction, and sea state. In total, 289 samples were collected between June and September 1997 and between May and September 1998. These were gathered during all periods between sunrise and sunset and at all tide classes (Table 1).

Video-image analysis

Samples were later reviewed to identify dolphin surfacings and determine their position. To establish the number of times a video should be viewed to identify all surfacings, 10 different 1-min sequences were each viewed five times and the surfacings were counted. It was assumed that after each of the sequences was viewed five times, all surfacings had been seen. In 9 out of 10 cases, all surfacings had been seen after the sequences was viewed twice. All samples were therefore viewed twice and video frames containing surfacings were selected and digitized using a frame grabber (Logitech Snappy Inc.) at a resolution of 1280 × 1024 pixels.

To evaluate whether the surfacings counted from the video represented the number of surfacings in the field, a second test was carried out. Three 5-min video sequences of one of the subareas in the far row were recorded. This was at a distance of between 1000 and 1500 m from the observation site. All surfacings within the subarea were simultaneously recorded in the field by two observers searching by eye and with 8 × 40 binoculars. The surfacings counted in the field were compared with those counted from the video after the footage was viewed twice. In all three sequences, more surfacings were detected in the video (9, 14, and 11) than were counted in the field (4, 7, and 9).

The positions of surfacings were then calculated using a modified version of the technique developed by DeNardo et al. (2001). The technique is based on the principle that in a video frame, the position of any object on the water surface can be calculated if three key parameters are known: (1) the focal length of the camera, (2) the height of the camera above the water surface, and (3) the location, relative to the camera, of a reference object within the video frame.

Every time an individual subarea was videotaped, a calibration pole of known size and distance from the camera was videotaped without changing the focal length. This provided the information necessary to calculate a calibration factor for the focal length of the camera (DeNardo et al. 2001). The height of the camera above sea level (Admiralty chart datum) was back-calculated from the height of an Ordinance Survey triangulation point using a Leica T460 electronic theodolite (Leica U.K. Ltd., Milton Keynes, U.K.). In addition, variations in tidal height were accounted for using tide-prediction software (Admiralty Simplified Harmonic Method of Tidal Prediction, Hydrographic Office, Taunton, U.K.).

Identifiable features on the far shore were used as reference locations in the far row of subareas; their locations were determined using the electronic theodolite at the start of the study. Up to a distance of 2 km from the observation site, the mean error in reference locations estimated using the theodolite was 2.8 m (SD = 2.6 m) (Hastie 2000). In the middle and near rows of subareas there were no land features, therefore the cable ties on the wire grid erected in front of the camera were used as line-of-sight reference locations on the water surface when viewed through the camera. If a surfacing was seen in one of the middle-row subareas, the line-of-sight location of a cable tie at the bottom of the video frame of the adjacent subarea in the far row was initially estimated using one of the land features as a reference location (Fig. 2). When the video sequence of the middle-row subarea was then viewed, the same cable tie, now positioned at the top of the video frame, could be used as a line-of-sight reference location. Using the same process, determining the locations of surfacings in a near-row subarea initially required the estimation of line-of-sight locations of appropriate cable ties in the far row, then the middle row, of subareas. The positions of all surfacings were calculated using these parameters and entered into a geographic information system (GIS) package (ArcView Version 3.1, ESRI Inc., Buckinghamshire, U.K.).

To assess the accuracy of this technique, a field experiment was undertaken. A boat was manoeuvred around each

Fig. 3. Differences (mean ± SD) between boat locations measured by theodolite and estimated using the video technique. There were significant differences between the near, middle, and far subareas ($F_{[2]} = 61.14$, $p < 0.001$).

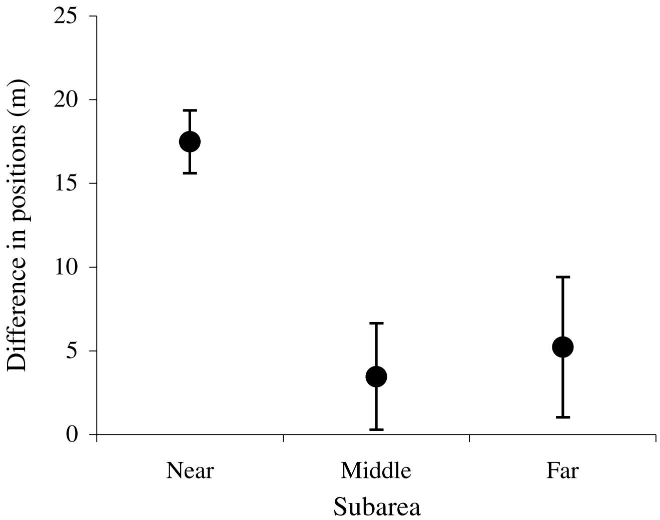
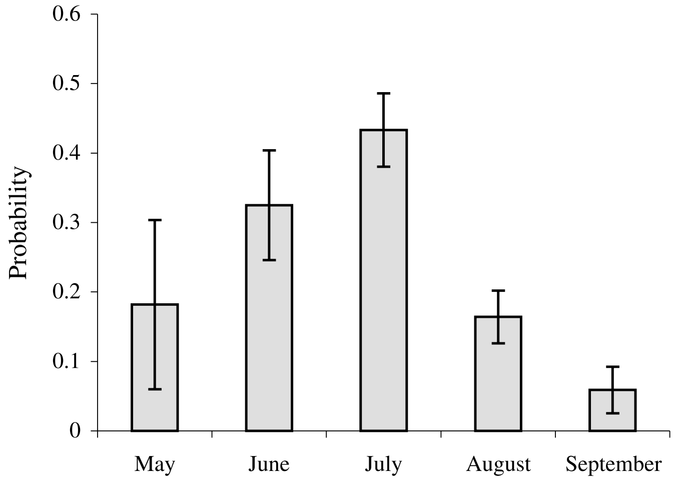


Fig. 4. Monthly variation in the predicted probability of sighting a dolphin surfacing (mean ± SD) from the general linear model.



of the 20 subareas. The corresponding subareas were videotaped and the location of the boat was recorded regularly using an electronic theodolite. The locations of the boat were then estimated using the video technique and compared with those calculated using the theodolite. To assess the variation in accuracy with distance from the observation station, errors were compared between the far, middle, and near rows of subareas using a general linear model.

Data analysis

To examine temporal changes in the rate of sighting dolphin surfacings, general linear models were used to investigate how the probability of sighting a dolphin surfacing varied with changes in both temporal and environmental variables (Table 1). The link function was a logit; this is suitable for binomial responses (e.g., Albon et al. 1986; Clutton-Brock et al. 1987), in this case the presence or absence of dolphins in a sample.

In the first round of analysis, all variables were considered singly in a model. All the variables and their two-way interaction terms were then considered simultaneously in a final model using a forward stepwise procedure in the SPSS version 8.0 statistical package (SPSS Inc., Woking, U.K.). To account for potential variation in sighting probability due to weather conditions, the environmental variables and their interactions were entered initially, followed by the temporal variables and their interactions. We tested whether explanatory variables have a predictive role using likelihood-ratio tests, with p values computed using a χ^2 approximation.

The distribution of surfacings was examined for variation across the study area with respect to water depth and seabed gradient. The study area was divided into classes according to water depth and seabed gradient; all intertidal areas were excluded from the analyses. The frequencies of sighting surfacings in water-depth and seabed-gradient classes were initially compared individually using G log likelihood ratio tests (Zar 1984). Expected values were calculated using

$$E_i = n(L_i/L_T)$$

where E_i is the expected sighting frequency in class i, n is the total sighting frequency, L_i is the surface area of class i, and L_T is the surface area of the whole study area.

A bivariate G log likelihood ratio test was then used to examine the effects of water depth and seabed gradient simultaneously. Each of the elements within the bivariate test was tested individually for significance. The proportion of the total observed sightings (and 95% confidence limits) was calculated for each class. The 95% confidence limits were calculated using a modification of the Bonferroni z statistic (Neu et al. 1974). The proportion of the surface area covered by class i was considered to be the expected proportion of sightings based on the availability of that class. If this expected proportion fell outside the 95% confidence limits of the observed proportion, the observed value was considered significantly different from the expected value.

Results

Position errors

In total, 116 locations of the boat were estimated using the video technique and compared with those estimated using the electronic theodolite. The differences in location ranged from 0.7 to 37.3 m, the overall mean difference in location being 6.4 m ($N = 116$, SD = 2.6 m). The magnitude of the differences in location varied significantly between groups of subareas with respect to distance from the observation site ($F_{[2]} = 61.14$, $p < 0.001$); the largest differences were in the near row of subareas and the smallest were in the middle row (Fig. 3). A post-hoc Tukey's HSD test reflected this pattern; there were significant differences in the mean location difference between each of the rows of subareas (near vs. middle, $p < 0.001$; near vs. far, $p < 0.001$; middle vs. far, $p < 0.05$).

Temporal variation

Dolphins were sighted within the study area in 25.3% of the samples. A total of 483 individual dolphin surfacings

Table 2. Summary of the stepwise general linear model for predicting surfacings, including single terms and interactions between terms.

Model term	Residual deviance	Deviance	df	*p*
Null model	326.67			
Included terms				
Month	300.14	26.53	4	<0.0001
Rejected terms				
Wind direction	314.86	11.81	9	0.224
Cloud cover	313.15	13.52	8	0.095
Sea state	324.245	2.425	3	0.489
Year	326.222	0.448	1	0.503
Time class	321.726	4.944	8	0.76
Tide class	321.604	5.066	9	0.829
Wind direction × cloud cover	281.13	45.54	41	0.289
Wind direction × sea state	301.35	25.32	19	0.15
Cloud cover × sea state	300.22	26.45	22	0.233
Year × month	324.14	2.53	3	0.47
Year × time	320.024	6.646	8	0.575
Year × tide	317.643	9.027	9	0.435
Time × month	296.35	30.32	26	0.254
Tide × time	283.53	43.14	61	0.96
Tide × month	299.04	27.63	32	0.688

were recorded across the whole study area (Fig. 4). The surfacings counted per sample ranged from 1 to 47, with a mean of 5.9 (SD = 2.9).

The results of the first round of modelling suggest that when each of the variables was considered singly in the model, none of the environmental variables and only one of the temporal variables, month, was significant in predicting surfacings (deviance = 32.94, df = 4, $p < 0.001$). When all the environmental variables and their two-way interactions were fitted simultaneously, none of the variables were significant factors in predicting surfacings. When all temporal variables and their two-way interactions were then added using a forward stepwise procedure, only month significantly improved the model (Table 2). The model predicts that the probability of sighting a dolphin surfacing within the study area peaks during July and is at a minimum during May and September (Fig. 5).

Spatial variation

The distribution of dolphin surfacings with respect to water depth was significantly different from that predicted by the expected distribution based on the availability of each water-depth class ($G = 45.76$, df = 5, $p < 0.0001$). The sighting frequency was highest in water depths greater than 50 m (Fig. 6). The distribution of surfacings with respect to seabed gradient was also significantly different from the expected distribution ($G = 34.9$, df = 2, $p < 0.0001$). The sighting frequency was highest within the class with a seabed gradient greater than 12° (Fig. 7).

The distribution of sightings, when examined with respect to both water depth and seabed gradient, was significantly different from the expected distribution based on the availability of each class ($G = 59.23$, df = 8, $p < 0.001$). Because there were no areas with a combined depth greater than 50 m and a seabed gradient greater than 12°, the water-depth classes between 40 and 50 m and greater than 50 m were pooled for the bivariate analysis. The highest sighting frequency was in the class with water depth greater than 40 m and a seabed gradient greater than 12°. The lowest sighting rates were within the classes with water depths less than 10 m and a seabed gradient greater than 12° and water depths between 20 and 30 m and a seabed gradient of less than 6°. Examination of each of the elements individually within the bivariate analysis showed that 10 out of 15 of the elements had observed proportions that were significantly different from the expected distribution.

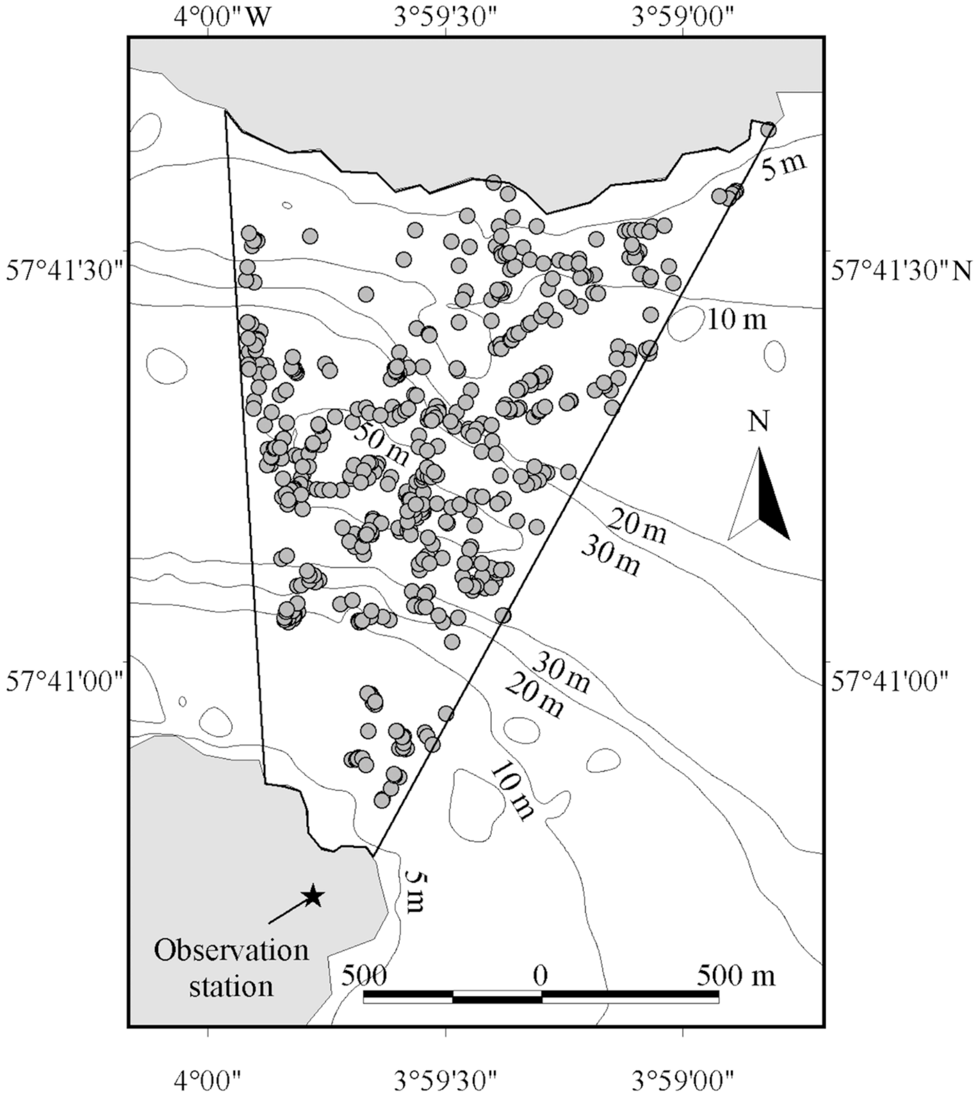
Discussion

These results show that bottlenose dolphins exhibit differential habitat use within this small, topographically variable study area and that there is a clear monthly pattern in their use of the area during the summer.

The video technique proved successful for studying the relative abundance of bottlenose dolphins over a small spatial scale. The comparison of the number of surfacings seen in the field with the number recorded on the video showed that the video quality was good enough to pick up all surfacings seen in the field and several that were missed in the field. There are several possible explanations for this outcome: (*i*) the camera's field of view remained constant throughout the test, thus cutting down the potential for missing surfacings, as the observer alternated between using the binoculars and searching by eye; (*ii*) potential distractions in the observers' peripheral field of view were reduced substantially when the video was used; (*iii*) the video allowed the data to be reviewed multiple times, which reduced the likelihood of indecision by the observers in the field.

The technique also proved successful for studying the spatial distribution of dolphin surfacings within the study area.

Fig. 5. Distribution of dolphin surfacings (shaded circles) within the study area. A total of 483 surfacings were seen in 289 samples. Data were collected between June and September 1997 and between May and September 1998. The map also shows the observation station and the bathymetric contours in the study area.



The errors in estimating the position of surfacings were very small (an overall mean error of 6.42 m at distances up to 2 km), and the technique is an extremely accurate method of determining the positions of individual dolphin surfacings. The technique is extremely versatile and relatively cheap and could easily be applied in other studies, both terrestrial and aquatic, where detailed information is required about the distribution and movements of individuals in relatively small key regions, such as the spacing behaviour of feeding birds on mud flats (Moody et al. 1997), habitat use by diving birds (Guillemette et al. 1993) and mammals (Nolet et al. 1993), and the nesting and territorial behaviour of birds in prairie habitats (Ryan et al. 1984).

As with previous studies using cue-counting, we assumed that the cue rate was constant both spatially and temporally. However, changes in surfacing rate due to changes in behaviour, both temporally and spatially, may affect the probability of sighting surfacings within the study area (e.g., Taylor and Dawson 1984). In addition, dive depth has been shown to influence both dive duration and recovery time spent at the surface (e.g., Dolphin 1987; de Leeuw 1996). Dolphins in this study area do appear to regularly dive to greater depths within the deeper waters than within the shallower waters (Hastie 2000). It is therefore possible that spatial variation in diving behaviour could influence the surfacing rate and bias the results presented here. This seems unlikely, however, as the magnitude of the change in surfacing rate would have to be four or five times to account for the observed changes in either the temporal (Fig. 5) or spatial (Figs. 6 and 7) patterns.

There was a clear monthly pattern in the occurrence of dolphins within the study area. The sighting rate rose to a peak during July and fell to a minimum during September. This temporal pattern is very similar to that reported from a boat-based study carried out in the same location between 1990 and 1993 (Wilson et al. 1997). Wilson et al. (1997) hypothesized that the overall seasonal peak in abundance may be a response to anadromous fish (primarily Atlantic

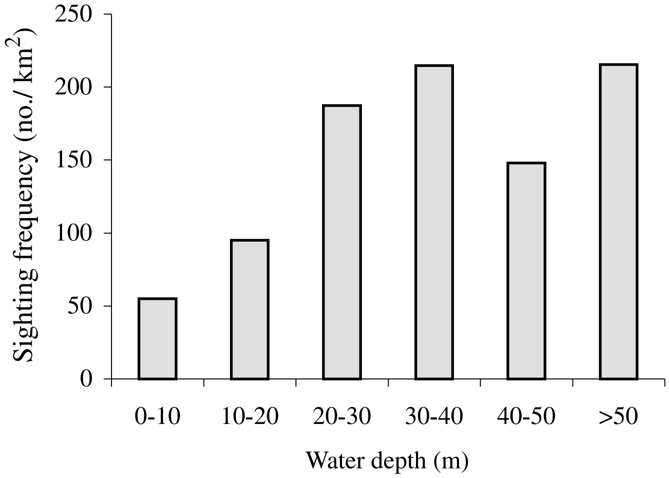


Fig. 6. Frequencies of sighting surfacings with respect to water depth. The distribution is significantly different from the expected distribution based on the availability of each water-depth category (G = 45.76, df = 5, p < 0.0001).

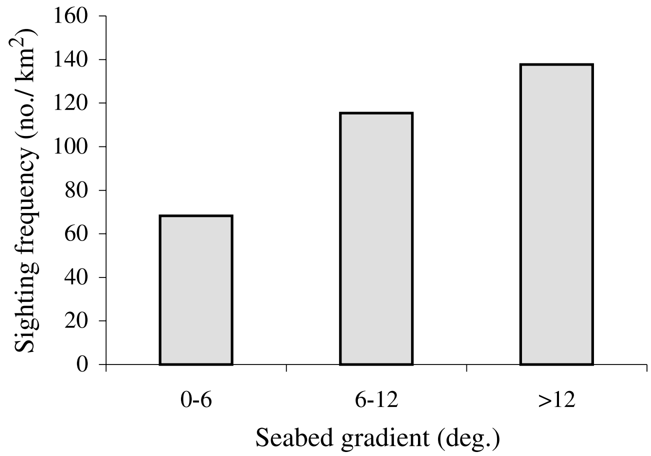


Fig. 7. Frequencies of sighting surfacings with respect to seabed gradient. The distribution is significantly different from the expected distribution based on the availability of each seabed-gradient class (G = 34.9, df = 2, p < 0.0001).

salmon, *Salmo salar*) migrating through the area during the summer months. The topography of this study area would potentially act as a bottleneck for fish moving through it (Wilson et al. 1997). It is interesting to note, however, that in contrast to the current study, Wilson et al. (1997) recorded a distinctive peak in dolphin numbers during September. The difference in that study may simply be an artefact of differences in the method of data collection. However, this seems unlikely, as a similar rise in abundance was recorded in early summer and it is therefore more likely that there was a real temporal change in the use of this area between 1993 and the present study.

Although dolphin surfacings were sighted across the study area, they were not distributed randomly. There was a positive relationship between the frequency of sighting surfacings and both water depth and seabed gradient. The sighting frequency was highest in the deepest waters with the steepest seabed gradients. In the absence of any overriding physical disturbance, a top predator is expected to be resource-limited (Hairston et al. 1960). Although the bottlenose dolphin is subject to predation across much of its range (Heithaus 2001), this population shows very few signs of predation pressure (Wilson et al. 1997) and can be considered the top predator in this system. Therefore, the observed spatial distribution in relation to water depth and seabed gradient is likely to be related to the profitability of resources within these regions. Other studies have shown that both water depth and seabed gradient are major factors determining the distribution of air-breathing marine species (e.g., Selzer and Payne 1988; Baumgartner 1997; Schneider 1997; Raum-Suryan and Harvey 1998). Although they vary in detail, all hypotheses relate water depth to the availability of prey. These studies have all been performed over relatively large spatial scales, and it is unclear whether the same biological processes are driving these patterns on smaller spatial scales. It seems likely, however, that even on this scale, such relationships are linked to the availability of prey.

With limited information on the distribution of fish species within the study area, it is difficult to make concise links between predator and prey distributions. Salmon migrating through the area could use topographical features such as seabed gradients or depth contours as navigation cues, resulting in higher densities of fish around these features. In addition, complicated currents, upwellings, or haloclines may result from a strong tidal flow over steep gradients. These features can disorient migrating Pacific salmon, *Oncorhynchus* spp., causing them to temporarily aggregate (Stasko et al. 1973; Quinn and teHart 1987), and Atlantic salmon use haloclines to orient themselves during spawning migrations (Ikonen 1986).

An alternative hypothesis states that the use of the deep areas with steep seabed gradients increases foraging efficiency. Steep seabed gradients may aid prey detection and (or) manipulation or may provide barriers against which to herd prey (e.g., Heimlich-Boran 1988). There may also be advantages to foraging in deeper water even if prey are distributed randomly. For example, it may be more profitable for a dolphin to forage in deeper water than in shallower water, based purely on the potential rate of encountering prey in the deeper water. At a distance of 60 m, the probability of bottlenose dolphins detecting a 2.54 cm radius sphere was over 90% (Murchison 1980). If we assume that fish can be detected over similar distances, for a dolphin at the surface in 50 m deep water, the potential search volume would be 450 067 m^3, substantially larger than the volume when the water is 10 m deep, 190 493 m^3.

In conclusion, this study identified clear spatial and temporal components of the fine-scale distribution of bottlenose dolphins in relation to underwater topography. It also provides a cheap and versatile technique that could easily be applied in other studies of animal distribution. In addition, the results provide an important basis for decisions concerning the management of this dolphin population and a foundation for generating meaningful hypotheses in future studies of habitat selection and behaviour.

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