

A new technique to measure spatial relationships within groups of free-ranging coastal cetaceans

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Summary

1. The development and calibration of a land-based technique to measure inter-animal spacing in free-ranging coastal cetaceans is described here. The technique was developed to study the behaviour of killer whales *Orcinus orca* in Norway.

2. A theodolite was used to measure the surfacing location of one reference individual while simultaneous video recordings of the whole group were made. Digitized video frames were then used to estimate the locations of all individuals in the video frame relative to the reference animal.

3. The technique was calibrated using a line of towed buoys with known separations. Estimated inter-buoy distances were compared with actual values to calculate errors. There was no observable bias in measurements, with a mean error of -0.014 m ($n = 304$, $SD = 0.880$). At ranges up to 2 km from the observation site, 95% of measurements were accurate to within 1.7 m.

4. The accuracy of the measurement system was characterized with a set of Monte Carlo simulations. Simulations were run at offshore ranges from 100 m to 2000 m, with random perturbations applied to all variables. Errors in inter-animal distances for $n = 16$ whales were estimated using 10 000 simulation runs for every range value. The results from the simulations agreed with experimental findings. The results showed no bias in inter-animal distance measurements, with an overall mean error of 0.0864 m.

5. The results indicate that this technique is suitable for studies on a variety of coastal cetacean populations. It provides a new tool for quantitative studies on spatial behaviour of cetaceans, and will help underpin management efforts to monitor effects of anthropogenic disturbance. With modification, the technique might also be applicable to other coastal vertebrates where inter-organism distances are required.

Key-words: cetacean behaviour, disturbance, inter-animal spacing, theodolite, video camera.

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Introduction

Group spatial structure in social animals varies depending on their behaviour (e.g. feeding, socializing, resting) and local environment (e.g. predation risks, topography, light conditions). Group-forming species probably possess mechanisms for sensing their spatial configuration. This spatial awareness of conspecifics is

particularly interesting in oceanic cetacean species that inhabit a vast three-dimensional environment.

Previous studies of group spacing in birds and terrestrial social mammals have relied on techniques for estimating inter-animal distances that cannot be applied to cetaceans. For example, distances have been estimated with the help of local topography in red deer *Cervus elaphus* (Clutton-Brock, Guinness & Albon 1982), using body lengths in hooded seals *Cystophora cristata* (Boness, Bowen & Oftedal 1988) and using photographs in oystercatchers *Haemtaopus ostralegus* (Moody, Thompson & De Bruijn 1997). Cetaceans,

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because of their entirely aquatic habitat, are far less accessible to researchers and therefore more problematic to study. They are often far ranging and are partially visible for only short periods when they surface to breathe. Not all individuals surface simultaneously, and group spacing may change continually while they are submerged. These practical constraints have severely limited quantitative studies of group spatial structure.

While reliable range measurements to cetaceans from boats can be achieved (Gordon 2001), measurements of group spacing have been generally inaccurate. For example, they have relied on distances counted in animal body lengths estimated by eye (Heimlich-Boran *et al.* 1994). Aerial stereophotogrammetry (Scott & Perryman 1991) has been used on pelagic dolphin schools to explore school structure and measure animal lengths and inter-animal distances, but this is costly and logistically difficult. Furthermore, both techniques may affect behaviour due to close approaches by either boats or aircraft.

In contrast, land-based studies can offer a cost-effective and non-intrusive alternative. Previous studies have shown that when the height and location of a land observation site are known, the surveyors' theodolite can be used to measure positions of cetaceans at sea (Kruse 1991; Wursig, Cipriano & Wursig 1991; Mayo & Goodson 1993). However, while this method can provide data on the distances to and swimming speed of individual animals (Kruse 1991; Wursig, Cipriano & Wursig 1991), data can only be recorded for one individual at a time. It has therefore not been an appropriate way of exploring group spatial structure.

Here we describe the development of a new technique for estimating inter-animal distances in cetaceans that combines the accuracy of a theodolite with the versatility of a video camera. Its value is in the ability to measure accurately the positions of more than one animal at a time. It is based on the principle that the surfacing positions of all animals in a video frame can be calculated if a theodolite is simultaneously used to measure the position of one of these animals. Once the positions for each surfacing animal are available, the inter-animal distances can be calculated and the spatial structure of the group explored. In this paper we describe and calibrate the technique, characterize its accuracy as a function of various errors, and illustrate its potential for use in both fundamental and applied studies of cetacean behaviour.

Methods

STUDY SITE

The technique was developed for studies of killer whale *Orcinus orca* behaviour. Fieldwork was conducted in Tysfjord, northern Norway (068°15'N, 016°10'E), where killer whales often overwinter (Simila, Holst & Christensen 1996). Observations were made from the summit (61.3 m above mean sea level) of a small island

with a clear view in all directions up to and beyond 2 km. The island was located within a sheltered fjord system that experienced little swell. Wave heights were generally below 0.5 m.

FIELD EQUIPMENT

Two people were needed to operate the field equipment, which consisted of a theodolite (Wild T2) and a Hi-8 video camera (Canon Ex2, Canon, Wallington, UK) with an 8–120 mm zoom lens and a 2X converter.

The theodolite tripod was set up directly over a mapped trigonometric location. A vertical pole at the water's edge and visible from the observation site was used to make hourly measurements of tidal changes in the instrument's height above sea level. The video camera was on a tripod set next to the theodolite and fixed securely to the ground. Fuji 90-min Hi-8 metal-evaporated tapes were used (Fuji Photo Film, London). The video camera's data bank was used to identify frames on playback and the stereo-audio channels recorded simultaneous commentaries from both theodolite and video operators.

FIELD PROCEDURE

The person operating the video camera focused, positioned and locked the camera frame on a group of killer whales, whilst the person using the theodolite took a reference reading of the position of an easily recognizable object (either a distinctive animal or a boat) that was also visible in the video frame. The target for the theodolite cross hairs was the waterline at the centre of the object. Each time the camera frame was repositioned, a new reference reading was taken using the theodolite.

Recordings with the video camera were made with a level horizon and at a calibrated focal length. Each time the focal length was changed it was necessary to record a frame of the calibration object. The difference in size of this object (measured in pixels from the video image) at full zoom and at selected focal lengths provided a focal length calibration factor (FLCF) (equation 1) that was used in further calculations:

$$\frac{\text{Width in pixels of the calibration object at selected focal length}}{\text{Width in pixels of the calibration object on full zoom}} = \text{FLCF} \quad \text{eqn 1}$$

Observations were made during periods of good visibility, no precipitation and a sea state at or below Beaufort 3.

MATHEMATICAL METHODS

Using the theodolite to measure the position of a reference object

The basic workings of a theodolite are depicted in Fig. 1 (for a more thorough description see Wursig, Cipriano & Wursig 1991), which also serves to establish

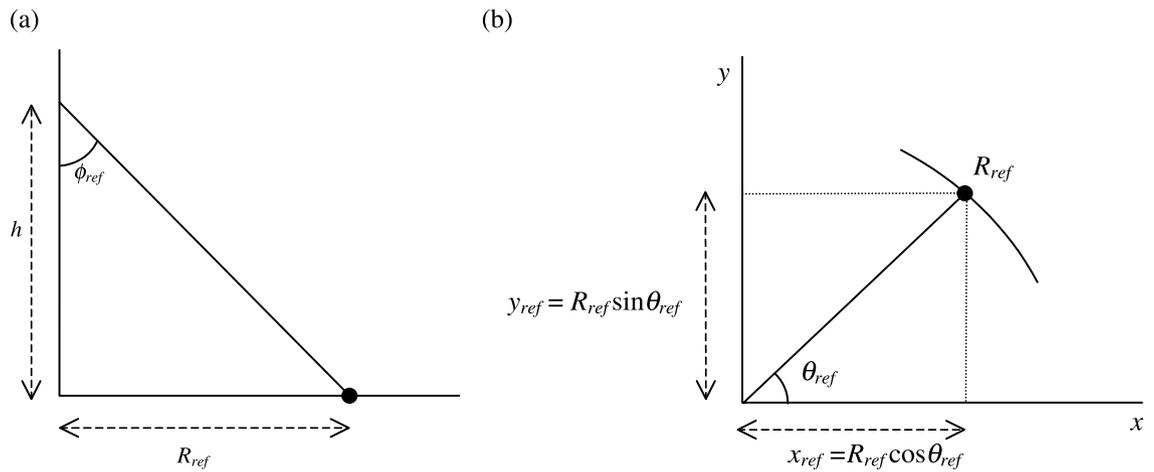


Fig. 1. (a) Side view: calculating the range R_{ref} to a reference object at sea from land when the height of the observation site h and the vertical angle ϕ_{ref} are known. (b) Overhead view: once R_{ref} has been calculated this value and the horizontal angle θ_{ref} can be used to calculate the position of the object. This position can be expressed in either polar (R_{ref}, θ_{ref}) or Cartesian (x_{ref}, y_{ref}) coordinates.

our notation. The theodolite measures the vertical angle ϕ_{ref} and the horizontal angle θ_{ref} to a reference object at sea. Vertical angles are measured with respect to a plumb line descending from the theodolite; horizontal angles are measured counter-clockwise from a line connecting the theodolite to an established geographical reference point. This line serves as the x -axis of a Cartesian (x, y) coordinate system and the polar axis of a polar (R, θ) coordinate system, a point we will address shortly.

Given the theodolite height h , the angles ϕ_{ref} and θ_{ref} completely specify the object's location on the sea surface. The range R_{ref} to the reference object can be calculated using the relationship:

$$R_{ref} = h \tan \phi_{ref} \tag{eqn 2}$$

R_{ref} and θ_{ref} then specify the object's position in polar notation. We will use polar notation for the remainder of this discussion because it matches the theodolite's native radial measurement scheme and will simplify our error analysis. We note that conversion from polar (R, θ) coordinates to the more common Cartesian (x, y) coordinates is easily achieved with the relationships:

$$x = R \cos \theta \tag{eqn 3}$$

and

$$y = R \sin \theta. \tag{eqn 4}$$

Analysing video images

On video playback, frames were selected and digitized using a video frame grabber (Snappy, Play Inc., Rancho Cordova, Canada). The video frame that was recorded simultaneously to the measurement of the reference object's position was then analysed to determine horizontal and vertical angles of separation

between the reference object and a killer whale in the frame. We describe the procedure for the vertical angle of separation ϕ_{sep} ; the horizontal angle of separation θ_{sep} was found in a similar manner (Fig. 2).

First, the distance between the killer whale and the reference object was measured in pixels along the vertical axis of the video image. This was achieved using custom-written software that allowed a user to mark both whale and reference object on a bitmap of the digitized video frame. The vertical angle of separation ϕ_{sep} was then obtained using a conversion value for the vertical angle per pixel. To estimate this conversion value, the theodolite was used to measure the angle between the top and bottom edges of a calibration object. The number of pixels between these edges was then measured from a video frame taken of the calibration object at full zoom. The vertical angle per pixel at full zoom was taken as the ratio of these two measurements; for focal lengths other than full zoom, the focal length calibration factor was used to scale the angle per pixel values appropriately.

Calculating the position of a killer whale relative to the reference object

The angles of separation ϕ_{sep} and θ_{sep} are summed with ϕ_{ref} and θ_{ref} to yield ϕ_{whale} and θ_{whale} . The whale's absolute position in polar notation could then be specified using the method described above (Fig. 2):

$$R_{whale} = h \tan (\phi_{ref} + \phi_{sep}) = h \tan (\phi_{whale}), \tag{eqn 5}$$

$$\theta_{whale} = \theta_{ref} + \theta_{sep}. \tag{eqn 6}$$

The distance between the whale and the reference object must be calculated after conversion to Cartesian coordinates. This distance is then given by:

$$d = \sqrt{(x_{ref} - x_{whale})^2 + (y_{ref} - y_{whale})^2}, \tag{eqn 7}$$

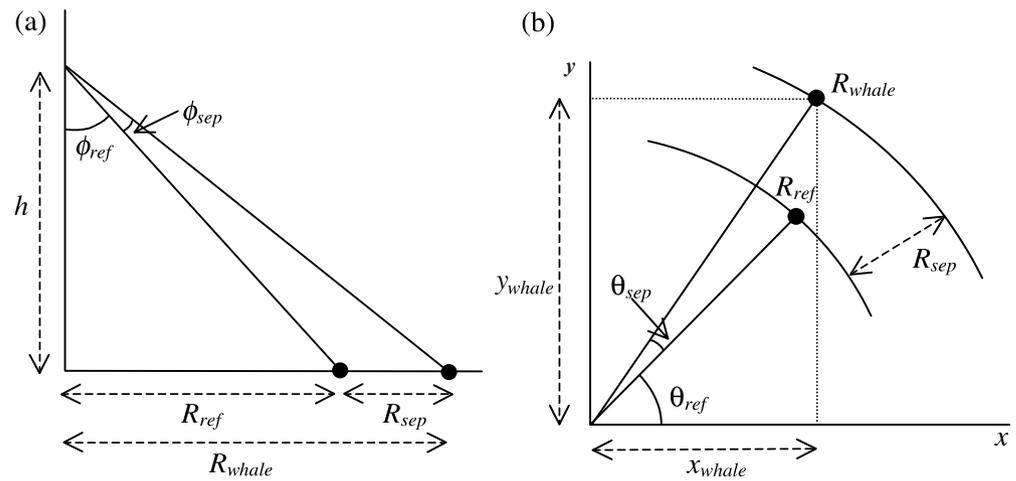


Fig. 2. (a) Side view: the station height h and the vertical angle of separation (ϕ_{sep}) between the reference object and a whale are used to calculate the range R_{whale} to the whale. (b) Overhead view: using R_{whale} , the horizontal angle of separation θ_{sep} and the reference horizontal angle θ_{ref} to calculate the position of the whale.

which can be expressed in terms of R and θ as:

$$d = \sqrt{(R_{ref} \cos \theta_{ref} - R_{whale} \cos \theta_{whale})^2 + (R_{ref} \sin \theta_{ref} - R_{whale} \sin \theta_{whale})^2} \quad \text{eqn 8}$$

In this manner the absolute and relative positions of all whales and boats of interest in the video frame can be computed. Furthermore, the original location of the reference object can be associated with a single pixel on the video screen, so that even if the reference object itself does not remain in view for multiple frames, positioning can continue until the video camera is moved.

FIELD CALIBRATION

A calibration experiment was designed to simulate a group of surfacing killer whales using a towed line of buoys with known spacing of 2 m, 3 m, 5 m and 10 m along a length of rope. They were towed behind a boat travelling through the study site at varying speeds, distances and bearings to the observation site. The vessel was used as a reference object and its position was measured using the theodolite each time the video camera was moved. The video analysis software was used to calculate buoy positions from video frames of the boat travelling through the study site. Inter-buoy distances were then estimated from these coordinates and compared with the known distances.

ERROR ANALYSIS

We now characterize the effects of various errors on inter-animal distance estimates. To simplify the analysis, we use polar notation and analyse only errors in the inter-animal range or R_{sep} . This is a reasonable approach because the native geometry of the theodolite causes the largest errors to occur in the range variable, a trait confirmed by both the underlying mathematics and our experimental data.

We first note that the inter-animal range R_{sep} is calculated using (see Fig. 2):

$$R_{sep} = R_{whale} - R_{ref}, \quad \text{eqn 9}$$

which is equivalent to (see equations 2 and 5):

$$R_{sep} = h(\tan(\phi_{ref} + \phi_{sep}) - \tan \phi). \quad \text{eqn 10}$$

To calculate the effects of errors in h , ϕ_{ref} or ϕ_{sep} , we differentiate R_{sep} with respect to the variable in question. Although we have generated the following results using differentiation, we have replaced the differential operator ∂ with the more familiar Δ , a valid approximation for small deviations.

We then calculate that an error Δh will produce the following inter-animal range error ΔR_{sep} :

$$\Delta R_{sep} = (\tan(\phi_{ref} + \phi_{sep}) - \tan \phi_{ref}) \Delta h. \quad \text{eqn 11}$$

An error $\Delta \phi_{ref}$ will have the following effect:

$$\Delta R_{sep} = h(\sec^2(\phi_{ref} + \phi_{sep}) - \sec^2 \phi_{ref}) \Delta \phi_{ref}. \quad \text{eqn 12}$$

Finally we consider an error $\Delta \phi_{sep}$ in the vertical angle of separation:

$$\Delta R_{sep} = h(\sec^2(\phi_{ref} + \phi_{sep})) \Delta \phi_{sep}. \quad \text{eqn 13}$$

Consider a typical example in which $h = 60$ m, $R = 1000$ m and $R_{sep} = +12$ m (the positive value for R_{sep} indicates that the range to the whale is 1012 m and not 988 m). From these values we calculate $\phi_{ref} = 1.5109$ radians and $\phi_{sep} = 7.089 \times 10^{-4}$ radians. We can now use the previous three formulae to determine the effects of various errors. Radians must be used in these calculations.

1. An error of 0.5 m in the height h causes an error of 0.1 m in R_{sep} . This error represents the largest average

Table 1. Monte Carlo simulation procedure

1. Height was set to 60 m. Positions for $n = 16$ whales were generated using a uniform random distribution spread across a 50×50 -m square. The square was centred at a range that was varied from 100 m to 2000 m in steps of 100 m.
2. The true inter-animal distances between all possible pairs of animals were calculated.
3. A reference whale was chosen at random, its true angles ϕ_{ref} and θ_{ref} were calculated, and from these the true separation angles ϕ_{sep} and θ_{sep} for the remaining whales were determined.
4. The separation angles ϕ_{sep} and θ_{sep} were perturbed (independently for each variable and each whale) by adding normally distributed random variables (RV) having zero mean and a standard deviation (SD) of 0.003 degrees.
5. The reference angle ϕ_{ref} was then perturbed by adding a normally distributed RV having zero mean and SD of 0.05 degrees. The reference angle θ_{ref} was not perturbed, as variations in this variable have no effect on measured inter-animal distance.
6. The perturbed separation angles ϕ_{sep} and θ_{sep} were added to the perturbed reference angles ϕ_{ref} and θ_{ref} to give perturbed angles ϕ and θ for each whale.
7. The position of each whale was recalculated using the perturbed angles. The height h for these calculations was perturbed by adding a normally distributed RV with zero mean and SD of 0.5 m.
8. The distances between all the perturbed positions were calculated and compared with the true inter-animal distances.
9. This process was repeated 10 000 times for every range value.

wave height we experienced (although there are other sources of error in h mentioned below).

2. An error of 0.00175 radians (= 0.1 degrees) in ϕ_{ref} causes an error of 0.7 m in R_{sep} . This error represents roughly twice the angular precision we observed in repeated theodolite measurements of a static target.

3. An error of 3.5×10^{-5} radians in ϕ_{sep} causes an error of 0.6 m in R_{sep} . This error represents the vertical angle encompassed by one pixel in our video camera at full zoom. (The angle per pixel increases as we zoom out, but zooming out normally occurs as the whales move closer to the observation site, and this reduction in range more than offsets the increased error associated with the angle per pixel change.)

We now consider sources of error in the variables h , ϕ_{ref} and ϕ_{sep} . Motion in the theodolite target and incorrect calibration are the primary sources of errors in ϕ_{ref} . Errors in h arise from imprecision in measuring the theodolite height above sea level (i.e. tidal estimation and station height) and from waves. Waves do not explicitly affect the measurement of h but cause variations in the observed waterline of floating objects, which is mathematically equivalent to varying h . Waves are an additional source of error for the vertical angle of separation ϕ_{sep} as they cause fluctuations in the relative heights of floating whales. Other sources of error in ϕ_{sep} include video camera shake, inaccuracies in the angle per pixel values (including the focal length calibration) and the pixel resolution of the video camera.

MONTE CARLO SIMULATION

We used MATLAB to run Monte Carlo simulations of the various error effects at different ranges (Table 1). For each simulation, $n = 16$ whale positions were generated randomly throughout a 50×50 -m square. The centre of this square was located at a range R that was varied from 100 m to 2000 m in steps of 100 m. Height was set to 60 m. We then perturbed all of the variables with random fluctuations designed to mimic realistic field conditions. The perturbed variables were used

to estimate inter-animal distances, which were then compared with the true distances. Ten thousand simulations were run at every range value.

Results

A video frame of surfacing killer whales and their positions is shown in Fig. 3.

Errors in the estimated inter-buoy lengths were calculated from measurements of 118 video frames. Of these, 59 were recorded while the boat travelled perpendicular to the line of sight. The remaining 59 were recorded while the boat travelled either along or diagonal to the line of sight. Several inter-buoy comparisons were made in each frame. There was no measurable bias in these measurements (Fig. 4). There was a mean error of -0.014 m ($n = 304$, $SD = 0.880$). There was no significant variation in error as a function of inter-buoy lengths (ANOVA; $n = 94$, d.f. = 4, $F = 0.946$, $P = 0.441$) when the vessel and buoys passed perpendicular to the line of sight. All measurement errors were under 4 m, and 95% of the errors were under 1.7 m. Error magnitude increased with range, which in this case was up to 2 km from the observation site (Fig. 5). However, there was no evidence that bias increased with increasing range (Fig. 6).

The Monte Carlo simulations produced similar results. In particular, they showed no bias in inter-animal distance measurement, and showed an increase in errors with range that agreed with experimental findings (Fig. 6). Overall mean error was 0.0864 m. Mean squared error for the simulations was also similar to experimental values (Fig. 5).

Discussion

Error analysis and experimental results indicate that our method can successfully measure distances between moving objects at sea. The results from the Monte Carlo simulation and field calibration indicate that inter-object distances can be measured to within several metres at ranges of up to 2 km (from a height of

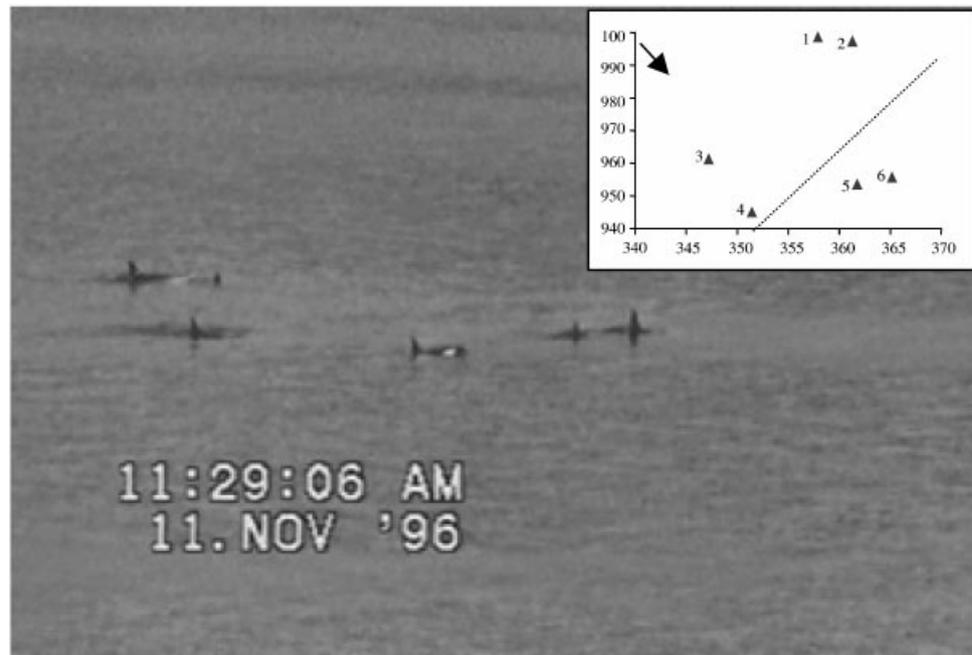


Fig. 3. A digitized video frame of six surfacing killer whales. Insert: a plan view of x, y coordinates (in metres) for the individuals in the video image. The arrow represents their direction of travel, (0, 0) is the location of the observation site, and the dotted line denotes the line of sight.

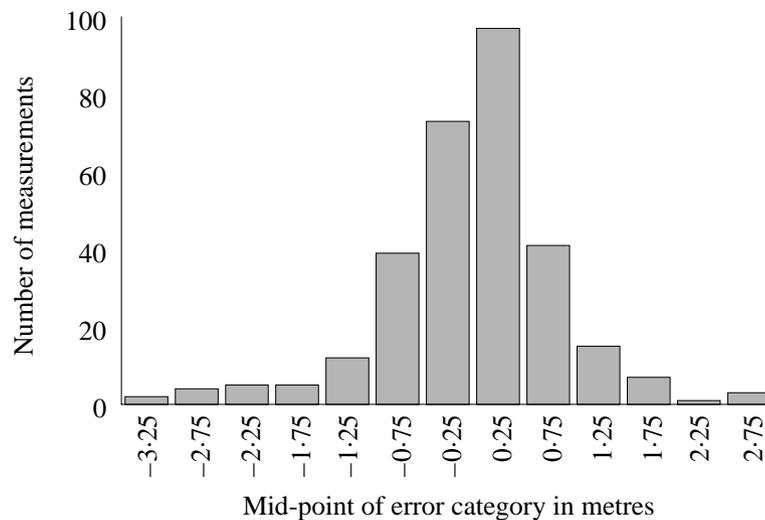


Fig. 4. The distribution of errors in measured inter-buoy distances from the field calibration experiment.

about 60 m). The accuracy of these measurements is limited primarily by theodolite positioning precision, sea state and video camera resolution, all of which induce errors that increase with range. Accuracy could be significantly improved over the results presented here by increasing the station height and/or the video resolution, which increases continually due to technological advances.

The error analysis and Monte Carlo simulation results support the data from the field calibration. More importantly, they demonstrate that this method of measuring relative inter-animal distances is more accurate than the underlying theodolite measurement of the absolute position of the reference object. For example, an error in ϕ_{ref} creates an error in the range of

the reference object, which then propagates to all other measurements. The overall effect is that the entire constellation of whales is shifted either closer to or further away from the origin (Fig. 7). Although this shift is not identical for each whale, it is similar, so that its effect on inter-animal distance estimations is much smaller than the original error in the range of the reference object. As an example, assume a range R of 1000 m, a height h of 60 m, and an inter-animal range R_{sep} of +12 m. An error of 0.00175 radians (= 0.1 degrees) in ϕ_{ref} then leads to an absolute error of 30.2 m in the range to reference animal, but an error of only 0.7 m in the inter-animal range.

Although the system we propose could be improved, even the current set-up can measure inter-animal

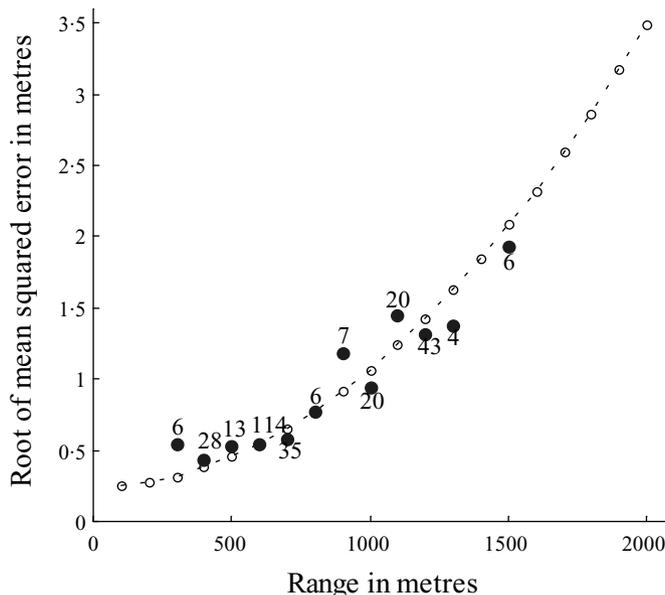


Fig. 5. Root of mean squared error in measurements of inter-object distances. The filled circles represent the results of the field calibration experiment. Sample sizes are shown. The open circles represent the results of the Monte Carlo simulations. Ten thousand simulations were run at every range value.

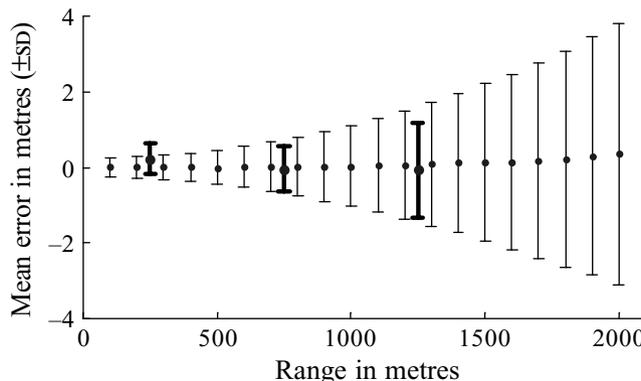


Fig. 6. Errors in inter-object distance measurements from the field calibration experiment (in bold) and the Monte Carlo simulations. Error bars represent ± 1 SD.

separations at ranges of up to 2 km, with error boundaries considerably smaller than the typical size of a killer whale. Although we welcome improvements to the technique and have suggested some here, we feel that the size and length of the study animals ultimately determines the upper limit of useful accuracy.

The methods, error analysis and simulations presented here could easily be adapted to other coastal locations, other cetacean species and possibly other vertebrate groups. A suitable field site for such work must have a land vantage point with an unobstructed view of the area used by the study species. The effective range of the method will depend on the observation site height, the video resolution and the accuracy demanded by the experiment in question. A final limitation may be posed by the study species: the distinctive black tall dorsal fin of the killer whale makes it clearly visible on video playback, while species with smaller dorsal fins may be less easily recognizable. This problem will be greatly mitigated with improved video resolution.

If the cetacean species of interest is not coastal, or a suitable land vantage point is not available, then ranges and bearings to individual animals can be measured using a boat-based technique, such as described in Gordon (2001). However, to date this method has not been used for detailed studies of inter-animal spacing, where continuous measurements of all animals in a group are measured simultaneously.

One of the most important applications of this technique is its potential to investigate anthropogenic disturbance effects from sources such as whale-watching. Previous studies have documented changes in surfacing behaviour as a response to boat approaches (Janik & Thompson 1996). Other studies that relied on visual estimates of inter-animal distances showed that pilot whales (Heimlich-Boran *et al.* 1994) and Hector's dolphins (Bejder 1997) altered their group spacing as a response to boat approaches. Using the technique described here to quantify these responses accurately should help underpin current efforts to develop suitable

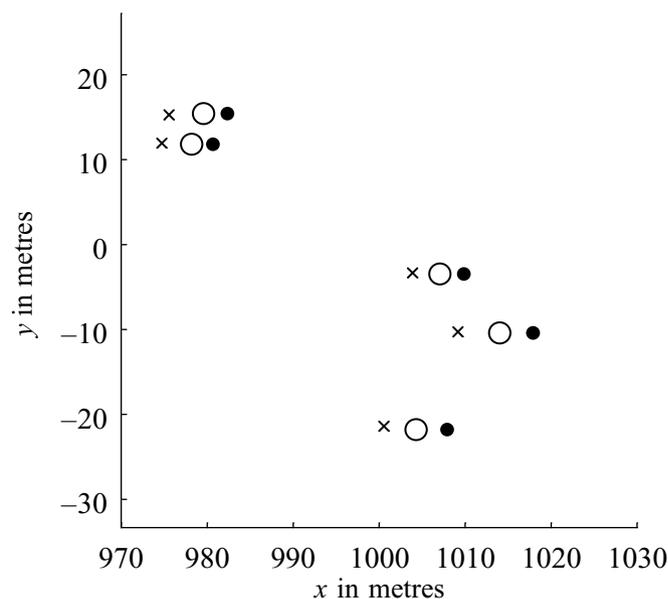


Fig. 7. Two example Monte Carlo simulation outcomes. The observation station was located at coordinates (0, 0), average range was 1000 m and five whales were used. Open circles indicate true whale positions; filled circles and crosses indicate positions estimated with perturbed variables.

management guidelines for the increasing number of commercial whale- and dolphin-watching operations around the world.

Our method of obtaining quantitative data on the spatial patterns in free-ranging cetaceans will also have considerable application to other studies of the structure and function of groups. Measuring group geometry and surfacing synchrony may help refine our definition of the term 'group' in cetacean populations and reveal the mechanisms behind group co-ordination.

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References

- Bejder, L. (1997) *Behaviour, ecology and impact of tourism on Hector's dolphins (Cephalorhynchus hector) in Porpoise Bay, New Zealand*. MSc Thesis. University of Otago, Dunedin, New Zealand.
- Boness, D.J., Bowen, W.D. & Oftedal, O.T. (1998) Evidence of polygyny from spatial patterns of hooded seals *Cystophora cristata*. *Canadian Journal of Zoology*, **66**, 703–706.
- Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. (1982) *Red Deer. Behaviour and Ecology of Two Sexes*. Edinburgh University Press, Edinburgh, UK.
- Gordon, J. (2001) Measuring the range to animals at sea from

boats using photographic and video images. *Journal of Applied Ecology*, **38**, 879–887.

- Heimlich-Boran, J.R., Heimlich-Boran, S.L., Montero, R. & Martin, V. (1994) An overview of whale-watching in the Canary Islands. *European Research on Cetaceans-8* (ed. P.G.H. Evans), pp. 37–39. Proceedings of the 8th Annual Conference ECS, 2–5 March 1994, Montpellier, France. European Cetacean Society, Cambridge, UK.
- 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.
- Kruse, S. (1991) The interaction between killer whales and boats in Johnstone Strait, BC. *Dolphin Societies* (eds K.W. Pryor & K.S. Norris), pp. 149–159. University of California Press, Berkeley, CA.
- Mayo, R.H. & Goodson, D.A. (1993) Land-based tracking of cetaceans – the practical use of surveying instruments. *European Research on Cetaceans-7* (ed. P.G.H. Evans), pp. 263–269. Proceedings of the 7th Annual Conference ECS, 18–21 February 1993, Inverness, Scotland. European Cetacean Society, Cambridge, UK.
- Moody, A.L., Thompson, W.A. & De Bruijn, B. (1997) The analysis of the spacing of animals, with an example based on oystercatchers during the tidal cycle. *Journal of Animal Ecology*, **66**, 615–628.
- Scott, M.D. & Perryman, W.L. (1991) Using aerial photogrammetry to study dolphin school structure. *Dolphin Societies* (eds K.W. Pryor & K.S. Norris), pp. 227–241. University of California Press, Berkeley, CA.
- Simila, T., Holst, J.C. & Christensen, I. (1996) Occurrence and diet of killer whales in northern Norway: seasonal patterns relative to the distribution and abundance of Norwegian spring-spawning herring. *Canadian Journal of Fisheries and Aquatic Science*, **53**, 769–779.
- Wursig, B.W., Cipriano, F. & Wursig, M. (1991) Dolphin movement patterns. Information on radio and theodolite tracking studies. *Dolphin Societies* (eds K.W. Pryor & K.S. Norris), pp. 79–111. University of California Press, Berkeley, CA.

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