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ESTIMATING SIZE AND ASSESSING TRENDS IN A COASTAL BOTTLENOSE DOLPHIN POPULATION

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Abstract. We used a case study of a coastal bottlenose dolphin population to present a framework for determining the number of individuals present and assessing the likely time scale over which trends in abundance may be determined. Such a framework is appropriate for animal species that possess natural markings sufficient for individual recognition, and may be valuable in the development and implementation of management and monitoring programs for vulnerable populations.

Population abundance was estimated using mark–recapture methods applied to photoidentification data. This experiment was designed to minimize violation of method assumptions so as to allow use of the most parsimonious model for analysis. The data were examined critically to investigate mark–recapture assumptions, while analytical methods and data were selected to minimize and, where necessary, account for violations. The estimated number of animals with long-lasting marks from left and right side estimates were 73 ± 12 and 80 ± 11 individuals, respectively (means ± 1 SE). When divided by the estimated proportion of such animals in the population (0.57 ± 0.043 and 0.61 ± 0.035, respectively) and averaged, weighted by inverse variance, a total population size of 129 ± 15 individual animals was estimated (95% CI = 110–174 animals).

Data on calves observed and carcasses recovered suggest that the population could be increasing or decreasing at an annual rate of up to 5%. A power analysis, undertaken to investigate the length of monitoring program required to detect changes in population abundance at a 90% level of certainty, showed that detection of a trend could only occur following >8 yr of research effort. Biennial sampling has power similar to that of annual sampling, but savings in resources are offset by the loss of data on the reproductive histories of individuals.

Key words: abundance; bottlenose dolphin; cetacean; management; mark–recapture; monitoring; Moray Firth, Scotland; North Sea; photoidentification; population trends; power analysis; Tursiops truncatus.

INTRODUCTION

Bottlenose dolphins (*Tursiops* sp.) are widespread in the world's temperate and tropical oceans, occupying a variety of marine habitats (Leatherwood and Reeves 1983). Many populations inhabit coastal waters where they are subject to human activities, and as with many other species of small cetacean, there is a demand for the development and implementation of conservation management and monitoring programs.

An integral part of any management strategy is the assessment of the number of individuals in a population and any trends in abundance (Taylor and Gerrodette 1993). Estimating the number of individuals in a population of cetaceans presents practical difficulties because they live in the sea, are wide-ranging, and spend much of the time underwater. However, a number of field techniques first developed for terrestrial animals have been adapted for the study of cetaceans (Hammond 1987, 1995). Line transect methods can be used to estimate cetacean population density, and therefore abundance, in a defined study area via shipboard or aerial sightings surveys (Hammond 1986*a*, Buckland et al. 1993). But for practical reasons, line transect sampling can be difficult to implement for coastal cetaceans because the behavior of the animals is often related to coastal topography (Wilson et al. 1997*a*). This coupled with highly variable school sizes (Wells et al. 1980) can lead to estimates of abundance with poor precision. Furthermore, if the exact range of a population is unknown then line transect methods cannot determine population size.

Mark–recapture methods use data on the number of animals marked and their proportion in subsequent samples to estimate population parameters including abundance (Seber 1982). These methods have begun to be applied to data derived from photographic records of naturally marked individuals (Hammond et al. 1990*a*). When the assumptions of the technique are fulfilled, mark–recapture techniques can provide unbiased estimates of population size that are more precise than those derived from line-transect sampling (Fairfield 1990, Calambokidis et al. 1990). Bottlenose

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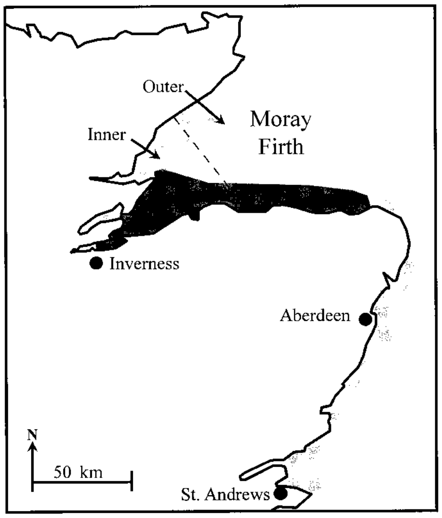

FIG. 1. Map showing the location of the Moray Firth, Scotland, study area. Known distribution of bottlenose dolphins is also shown as heavy shading (regular sightings) and lighter shading (occasional sightings).

dolphins are readily photo-identified, and the abundance of some populations has been estimated in this way (Hansen 1990, Hansen and Defran 1990, Wells and Scott 1990, Williams et al. 1993).

Bottlenose dolphins have long life spans and low reproductive rates (Wells 1991), and extensive periods of monitoring may be required to detect a trend in population size. Monitoring programs may thus represent a considerable investment of time and resources and require careful consideration at the outset. One underutilized way to investigate the ability of monitoring programs is to make use of statistical power calculations (Gerrodette 1987). These can help address practical questions related to approach, sample size, length of program, and required resources (Taylor and Gerrodette 1993, Van Strien et al. 1997).

In waters around the British Isles and northwest Europe, it is widely believed that numbers of bottlenose dolphins have declined in recent decades (Kayes 1985). Particular concern has been expressed over the well-being of the resident population in the Moray Firth, northeast Scotland (57°40′ N, 3°30′ W, Fig. 1), which is the only known population remaining in the North Sea. A high prevalence of skin lesions (Wilson et al. 1997*b*), use of waterways polluted by human sewage (Curran et al. 1996), and a growing dolphin-watching industry (Janik and Thompson 1996) have led to a demand for information on the possible impacts on the population. In addition, part of its range has been proposed as a Special Area of Conservation under the European Union's Habitats Directive (Scottish Natural Heritage 1995), requiring the establishment of management and monitoring programs.

Prior to the work reported here, the best indication of the number of dolphins in the Moray Firth was a minimum estimate of 62 individuals based on a coordinated land-based watch (Hammond and Thompson 1991). No estimate of the absolute abundance or of trends in abundance of this, or indeed of any other, population of bottlenose dolphins in the northeastern Atlantic is available.

Previous studies of cetacean abundance have been carried out as a byproduct of general purpose photo-identification studies (Hammond et al. 1990). As a consequence, they frequently suffer from violations of the assumptions of standard mark–recapture methods, including unequal capture probabilities of individuals (resulting from poor geographical spread of effort or preferential photographic effort towards particular individuals), and mark loss between sampling occasions (due to indiscriminate use of marks for identification or inappropriate sampling intervals). These lead, at best, to a necessity for more complex methods of analysis, resulting in a loss of precision. At worst, if such violations are ignored (Begon 1983), it leads to results and conclusions which may be severely biased.

In this paper, we present the results of an intensive, 3-yr photoidentification study, to estimate the absolute size of the resident population of bottlenose dolphins in the Moray Firth. Our study was designed as a mark–recapture experiment. Spatial and temporal distribution of surveys, the photographic effort at sea, the matching of photographs, and the choice of the most appropriate data sets and models were made to minimize violation of mark–recapture assumptions. These procedures avoided, as much as possible, the need for complicated analytical models. In this way, we aimed to minimize bias and maximize precision of estimated population size. The data were sufficient to investigate whether variants of standard analysis models were needed to account for assumption violations.

In this paper we examine the available data on numbers of calves born each year and numbers of dead animals of all ages to make a preliminary assessment of trends in abundance. Finally, we use power analyses to explore the investment in time and effort required to detect likely changes in the number of individuals in this population from repeated mark–recapture estimates.

MATERIALS AND METHODS

Study area

The Moray Firth is a large triangular embayment of the North Sea off northeast Scotland which can be divided into two parts (Fig. 1). The inner Moray Firth is sheltered from prevailing winds, is influenced by freshwater inputs, and features several coastal narrows with associated tidal races. The outer Moray Firth, and waters farther to the south, more closely resembles the open sea with fewer freshwater inputs and a straight rocky coastline.

Sightings of bottlenose dolphins from land-based volunteers (Evans 1980) and boat-based surveys for seabirds (G. P. Mudge et al., *unpublished report*) center around the inner Moray Firth and southern outer Moray Firth, with more occasional sightings occurring in the northern outer Moray Firth and along the coasts off Aberdeen and Saint Andrews, farther south (Fig. 1).

Data collection

Photographs of dolphins were collected during two types of boat-based survey between 1990 and 1993. In the inner Moray Firth, surveys were conducted along a predefined 42-km route. Ten surveys were carried out in 1990, and two per month were conducted between March 1991 and February 1993. To avoid problems associated with pseudoreplication these surveys were not carried out on consecutive days. In addition, 35 surveys were conducted along only part of this route. Nine surveys were conducted during September 1992, which did not follow a predefined route but ranged ≤250 km outside of the inner Moray Firth in order to determine whether different individuals were present in the outer Moray Firth. A detailed description of survey design and effort is given in Wilson et al. (1997*a*).

On surveys, dolphins encountered were counted, their location and activities noted, and photoidentification pictures of their dorsal fins and flanks taken. An autofocus 35-mm camera equipped with 75–300-mm zoom lens, databack, and ISO 200 or 400 color-transparency film was used throughout the study. Schools were defined as aggregations of dolphins within 100 m of one another engaged in similar activities and, if moving, heading in the same direction (Wells et al. 1987). The sampling protocol was to photograph as many animals as possible, from both left and right sides, in each school. Individuals with obvious marks were not preferentially recorded and back-lit shots (which give little detail of skin markings) were avoided.

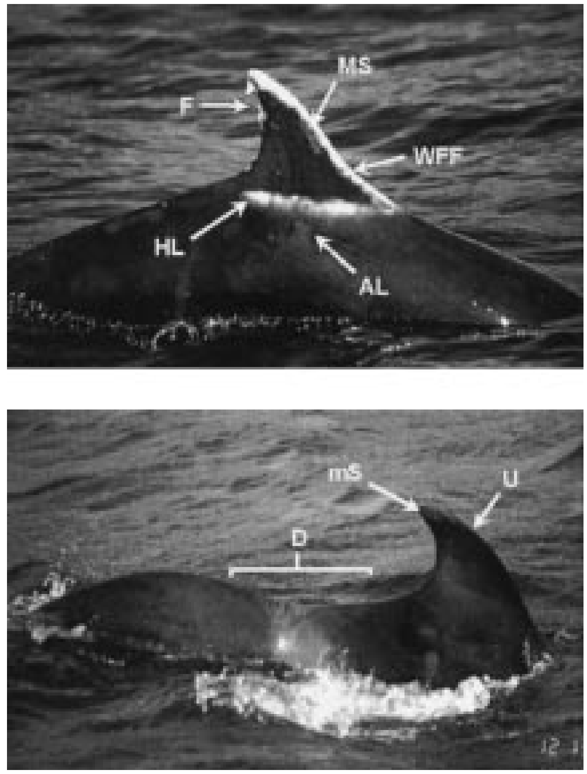

FIG. 2. Photo-identification pictures of two adult bottlenose dolphins illustrating the types of mark used for identification. F = fin nick (a piece of tissue missing from the trailing edge of the dorsal fin); MS = major scratches (as ''Deeper scratches or minor wounds'' [Lockyer and Morris 1990]); WFF = white fin-fringe (a white apigmented region around the edge of the dorsal fin); AL = active epidermal disease (as Wilson et al. 1997*b*); HL = healed epidermal disease (as Wilson et al. 1997*b*); mS = minor scratches (as ''Superficial scratches'' [Lockyer and Morris 1990]); U = unusually wide, tall, or leaning dorsal fin; D = deformity of the normal body contour.

Identifying individual dolphins from photographs

Developed films were viewed with an eyepiece over a light-table, and individuals identified from features such as nicks, rakes, deformities, and epidermal disease on both their dorsal fins and flanks (Fig. 2). Unlike several other studies of bottlenose dolphins, which used back-lit shots and were therefore limited to using only fin nicks (Defran et al. 1990, Würsig and Jefferson 1990, Williams et al. 1993), we were able to use all of the types of mark, given above, for identification.

Matches with previously identified individuals were made by comparing each new photograph, taken of the animal's left or right side, with all others in an existing archive of left- or right-side pictures (Wilson 1995). As many features as possible were used to confirm matches and reduce the possibility of false positives (Scott et al. 1990*a*, Würsig and Jefferson 1990). Animals that could not be matched were given a new identification number. The best left- and right-side picture of each individual from each trip were graded for photographic quality and filed in the archive. Grade 3 pictures were well lit, in focus, free from spray, and taken parallel with the exposed flank of the animal such that if any patches of skin with active disease were present (the most subtle marking used for identification) they would be visible. Pictures graded 1 or 2 were of lower quality and were not considered further. All dolphins encountered in the Moray Firth (except some neonates) possessed sufficient markings so that they could be identified from a grade 3 photograph.

Individuals were classified into three broad age groups based on their appearance. Large, robust animals with a dark gray or black coloration were defined as adults. Dolphins of similar length but with paler, often olive-colored skin, and a less massive body form were classed as subadults. Small dolphins with fetal folds (Kastelein et al. 1990) or substantially paler skin than subadults or adults were defined as calves.

TABLE 1. The durability of markings on bottlenose dolphins in the Moray Firth, Scotland.

	Duration of mark (days)				
Type of mark	Min.	Max.	Median	Interquartile range	Sample size
Unusual fin shapes	623†	1318†	1285	295	10
Deformities	1002†	1002†			1
Major scratches	309	1318†	696	415	15
Minor scratches	68	1318†	395.5	216	20
White fin-fringes	380	1318†	1223.5	195	6
Active disease	75	1054†	495	468	19
Healed disease	66	1318†	340	424.5	20

† Marks still present in last available photograph.

ASSESSMENT OF MARK–RECAPTURE ASSUMPTIONS

Mark recognition

Mark–recapture analyses assume that a marked animal will be recognized with certainty if recaptured. Failure to do so will bias estimates of population size upward. This assumption can be violated if poor quality photographs or ambiguous markings are used to identify individuals. In a study of North Atlantic humpback whales, Friday (1997) found, using sensitivity analyses, that mark–recapture estimates of abundance were significantly biased only if the poorest quality photographs were included. In this study, to avoid any problem, both poor *and* intermediate quality photographs were rejected. Furthermore, the high quality of the photographs used usually allowed a variety of marks to be used to confirm each identification. Therefore, we believe that violation of the mark recognition assumption was extremely unlikely.

Behavioral responses

Standard mark–recapture methods assume that marked animals have the same probability of being recaptured as unmarked animals. If the action of capture changes the future probability of recapture for an individual, this behavioral response will bias estimates of abundance. ''Trap shy'' behavior (lower probability of capture following marking) will result in overestimation of population size; ''trap happy'' behavior (higher probability of capture following marking) will result in underestimation. As photoidentification uses existing marks it involves no physical interaction between animal and researcher in relation to the marking event and so behavioral responses of this type cannot occur.

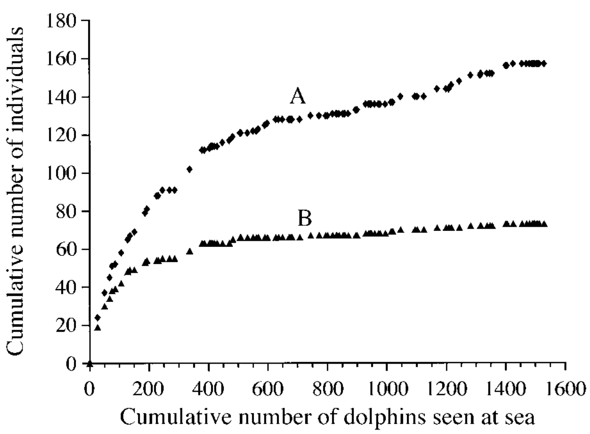

FIG. 3. Discovery curves showing the number of individuals identified against the cumulative number of dolphins encountered during the study. Line A is the curve for all animals. Line B is for animals with long-lasting markings only (nicks, deformities, and unusual fin shapes).

Mark loss

Mark–recapture methods assume that marks are not lost during the experiment; the loss of marks results in upward bias of estimates of abundance. Because the duration of different kinds of marks on small cetaceans is variable (Würsig and Jefferson 1990), we determined how long each type of mark could be expected to be visible, so that appropriately durable marks could be used for identifying individuals to include in estimates.

The types of mark used for identification were defined and their longevity measured. To do this, individuals with dorsal fin nicks (a feature believed to be permanent [Scott et al. 1990*a*]) and long photographic histories were chosen. The other marks were then followed from their first photographic documentation until the last time that they were visible and their durations calculated (Table 1). In addition to nicks, these data suggested that deformities and unusual fin shapes persisted throughout the study whilst other marks were observed to fade or completely disappear over a period of weeks to a year.

In addition, so-called ''discovery curves'' (Williams et al. 1993) were plotted for all individuals and for the subset of individuals possessing those marks determined to be long lasting (Fig. 3 [source data for the subset shown in Fig. 4]). These plots support the result that mark loss would be a problem if analyses were based on animals identified using all types of marks over the entire period of the experiment, but that this would not be a problem if identifications were made using only long-lasting marks.

Geographical closure

An estimate of abundance that purports to represent population size has limited value unless that population

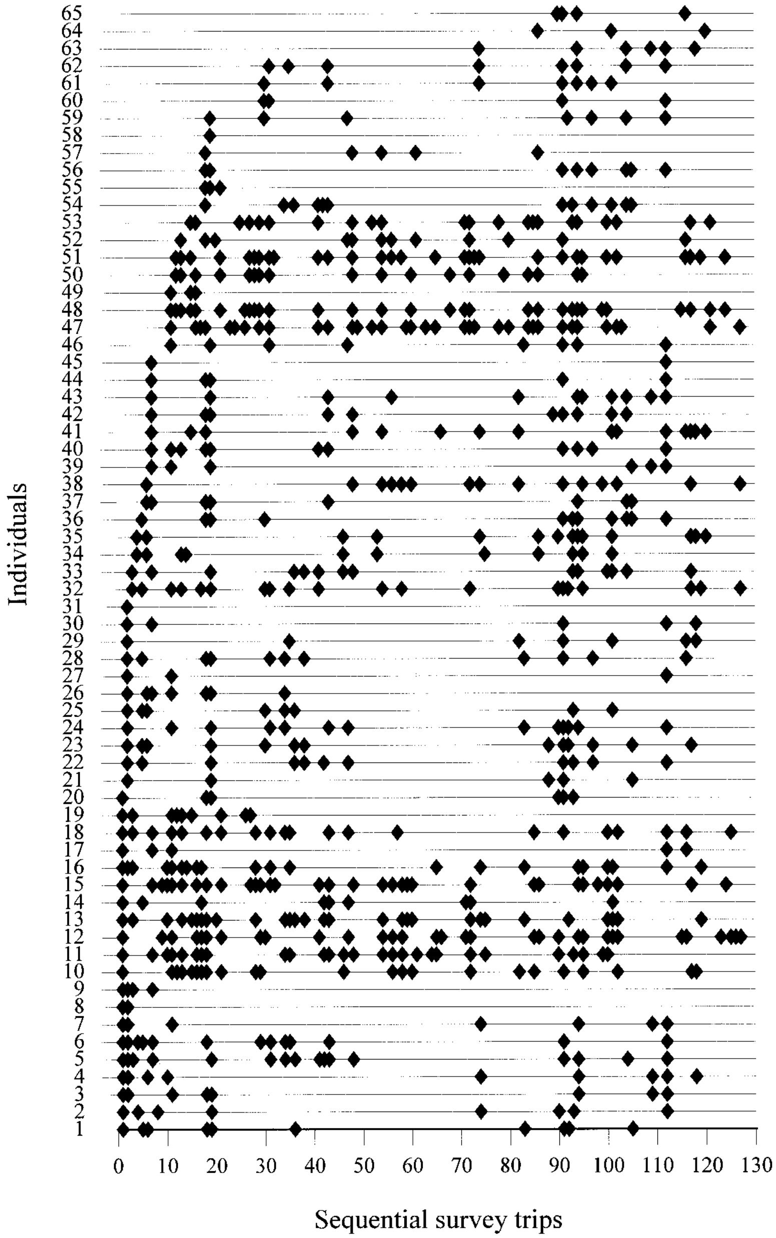

FIG. 4. Sightings of dolphins with long-lasting marks (nicks, deformities, and unusual fin shapes).

can be defined. Standard mark–recapture models are available for analyzing data collected where, first, the population is assumed closed to births, deaths, immigration, or emigration and, second, for those where these assumptions are relaxed. Population sizes estimated from these latter, open, population models are invariably less precise than those estimated from the former, closed, models.

The discovery curve for individuals with long-lasting marks (shown in Fig. 3) strongly suggests that our study population of bottlenose dolphins in the Moray Firth was closed to permanent immigration. The slight increase in curve B from 500 to 1500 animals photo-identified over time represents an addition of ~4 new individuals/yr. As on average six neonate calves were observed each year, the slight increase in the discovery curve can readily be explained by recruitment of surviving calves into the marked population.

The acquisition of dorsal fin nicks and other long-lasting marks in small cetaceans is cumulative (Würsig and Jefferson 1990) therefore animals with these marks will tend to be the older individuals, especially adults. If immature bottlenose dolphins range more widely, as is the case for many mammals (Greenwood 1980), between-population mobility of younger and therefore poorly marked individuals could be occurring. We in-

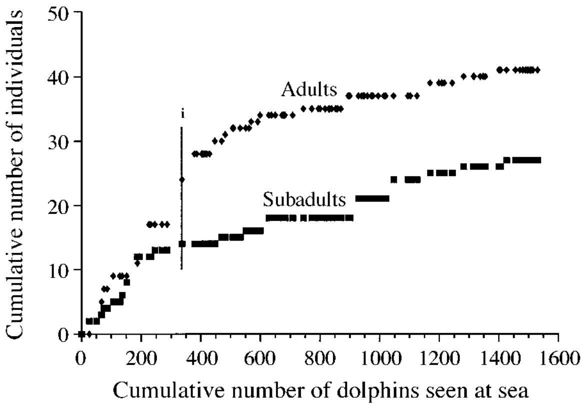

FIG. 5. Discovery curves for two age classes of animals without long-lasting markings. Each curve shows the number and point at which previously unrecognized animals joined the photo-archive.

vestigated this by comparing the discovery curves for adult and subadult animals with temporary markings. If there were a pool of mobile subadults in the population we would expect the discovery curve for subadults to be steeper than that for adults. In fact, the terminal rates of discovery for these two groups were almost identical (slope of subadult curve 0.012, adult curve 0.011, Fig. 5) providing further evidence of geographical isolation.

Male bottlenose dolphins range more widely (Scott et al. 1990*b*) and tend to have heavier body scarring than females (Tolley et al. 1995, Wilson 1995). They may, therefore, be overrepresented in the group of individuals with long-lasting marks. However, the composition of animals with long-lasting marks changed very slowly (Fig. 3, and curve B) and so suggests that interchange of males between this population and others is unlikely. Furthermore, even in populations of bottlenose dolphins with abutting ranges, as in Sarasota and Tampa Bays in western Florida, measured levels of interchange are small (3%/yr) (Wells et al. 1987). In contrast, the Moray Firth population is considerably more isolated than the populations off Florida; with the nearest other known aggregation being >450 km away (K. Grellier, *in press*). This adds support to our contention that levels of interchange between bottlenose dolphins in the Moray Firth and elsewhere are likely to be negligible.

Our data do not permit us to rule out permanent emigration as a possibility but there is no evidence that animals from the Moray Firth travel more widely than indicated in Fig 1. Overall, therefore, we are confident that the bottlenose dolphins in the Moray Firth do represent a geographically isolated and hence definable population.

Heterogeneity of capture probabilities

Standard mark–recapture methods assume that, within a sample, all individuals have the same probability of capture. This assumption is likely to be violated in cetacean mark–recapture experiments because of inherent differences in the behavior of individuals. Individual preferences for certain areas may affect the probability of encountering an animal, and individual differences in surfacing rates or boat avoidance behavior may affect the probability of obtaining a usable photograph (Hammond 1986*b*). Violation of the assumption of equal probability of capture, known as heterogeneity of capture probabilities, results in underestimation of population size.

In the Moray Firth, bottlenose dolphins most frequently use two areas: the inner Moray Firth and the southern part of the outer Moray Firth (Wilson et al. 1997*a*). Occasionally, animals extend their range to other parts of the outer Moray Firth and areas further south (Fig. 1). In addition, individuals show significant preferences for specific parts of the main areas (Wilson et al. 1997*a*). In this experiment, sampling covered as wide a geographical range as possible but was mostly within the inner Moray Firth and thus truly equal probabilities of encountering each individual could not have been achieved.

Inherent differences in surfacing rates or boat avoidance may also be expected (Payne et al. 1983, Whitehead 1996). To minimize this problem, as noted above, data collection protocol dictated that attempts be made to photograph every individual in a school and that preferentially photographing any particular individual was avoided. Furthermore, no data were derived from visual identifications made at sea.

Despite these attempts to minimize heterogeneity, it was unlikely to have been completely overcome, and thus we investigated models which allowed relaxation of this assumption.

ESTIMATING THE NUMBER OF ANIMALS WITH LONG-LASTING MARKS

Model selection

Sufficient data were available to use either open or closed population models for estimating abundance but, because of the need to allow for heterogeneity of capture probabilities, which is problematic in open population models, closed models were used. Two models were selected. One, known as M_t, allows capture probabilities to vary by time (sampling occasion) only. Darroch (1958) derived a maximum likelihood estimator for abundance for model M_t and an expression for its asymptotic variance. The second model, known as M_{th}, allows capture probabilities to vary by time and by individual. Chao et al. (1992) have derived a nonparametric estimator for abundance for model M_{th} using the idea of sample coverage (defined as the relative fraction of the total individual capture probabilities of the captured animals) and an expression for its asymptotic variance from an expanded Taylor series. We implemented both these models using program CAP-

TURE (Otis et al. 1978, Rexstad and Burnham 1991) to estimate the number of animals with long-lasting marks. Program CAPTURE derives confidence intervals under the assumption that the number of individuals not captured in the population is lognormally distributed. This has the desirable property that the lower bound of the confidence interval cannot be less than the number of captured individuals. The upper bound tends to be larger than would be the case if the abundance estimator were assumed to be normally distributed.

Data selection

Population closure is only a reasonable assumption when experiments are of relatively short duration. During our study, bottlenose dolphins showed a seasonal distribution in the Moray Firth (Wilson et al. 1997*a*) with the greatest numbers found within the inner Moray Firth in summer (May–September). Limiting analysis to data from May through September in a single year is thus a good approximation to closure. These summer data were used to estimate population size for the three years (1990, 1991, 1992) independently.

Individuals encountered during this period included almost all individuals seen in other areas of the Moray Firth and should thus also be representative of the whole population. To explore the effect of including data from a wider area than the inner Moray Firth, estimates of population size were also calculated with additional data collected between May and September of 1992 in the outer Moray Firth.

The investigation of mark duration (Table 1) showed that nicks, unusual fin shapes, deformities, major scratches and white fin-fringes were sufficiently long-lived to be considered permanent marks over these 5-mo periods. Only animals identified from these marks were used to estimate population size. Animals recorded as calves were not included because their probability of capture is not independent from that of their mothers (Wells and Scott 1990).

Results from the mark–recapture analyses give estimates of the number of animals with long-lasting marks. Separate estimates were calculated from the left and right side data sets.

Estimating Total Population Size

Total population size was estimated as

$$\hat{N}_{\text{total}} = \frac{\hat{N}}{\hat{\theta}}$$

where $\hat{N}_{\text{total}}$ = estimated total population size, $\hat{N}$ = mark–recapture estimate of the number of animals with long-lasting marks, and $\hat{\theta}$ = estimated proportion of animals with long-lasting marks in the population, with variance estimated using the delta method as

$$\text{var}(\hat{N}_{\text{total}}) = \hat{N}^2_{\text{total}}\left(\frac{\text{var}(\hat{N})}{\hat{N}^2} + \frac{1 - \hat{\theta}}{n\hat{\theta}}\right)$$

where n is the total number of animals from which θ was estimated.

Confidence intervals for total population size were calculated by assuming that the error distribution was the same as for the estimate of the number of animals with long-lasting marks, as estimated for the Darroch and Chao models, i.e., that the lower and upper confidence limits were the equivalent number of standard errors away from the estimate.

Williams et al. (1993) estimated θ from the proportion of photographs of animals with long-lasting markings. We were able to improve on this by estimating θ from the proportion of individuals encountered. This was because the variety of skin markings made it possible to distinguish all individuals in grade 3 photographs on any particular day. The number of individuals with and without long-lasting marks was determined for each survey and summed for each May–September period. If probability of capture was independent of whether or not an individual had long-lasting marks, our estimates of θ for each year should be unbiased.

Animals identified as calves were treated in the same way as those without long-lasting marks and were included in the estimates of total population size through the parameter θ.

For any set of samples, data were available to calculate estimates of abundance from left-side photographs and right-side photographs. Both the left and right sides were known for some animals but not all. We therefore calculated separate estimates for left- and right-side data and combined them as an inverse variance weighted average, assuming independence.

Analysis of Statistical Power of Monitoring Programs

To investigate the power of a series of population estimates to detect change, we used Gerrodette's (1987) general inequality model

$$r^2 n^3 \geq 12\,\text{CV}^2(z_{\alpha/2} + z_\beta)^2$$

where r is the annual rate of population change (increase or decrease), n is the number of estimates of population size, CV^2 is the squared coefficient of variation of estimated total population size, $z_{\alpha/2}$ is the one-tailed probability of making a Type I error, and z_β is the probability of making a Type II error. The probability of making a Type I or II error was set at the 0.10 level.

The effect of investing in different amounts of sampling effort was explored using a range of values for the estimated CV of population size, which encompassed the lowest and highest values from analyses conducted to estimate population size.

The seasonal distribution of bottlenose dolphins in the Moray Firth precludes estimation of population size using mark–recapture methods more than once a year. The effect of varying the frequency of population size

TABLE 2. The number of bottlenose dolphin (*Tursiops truncatus*) individuals identified from grade 3 (best quality) pictures on surveys in the Moray Firth between May and September, 1990–1992. Outer Moray Firth surveys were only conducted in 1992.

Moray Firth survey area	1990		1991		1992	
	Left	Right	Left	Right	Left	Right
Inner	67	78	66	72	80	75
Outer	0	0	0	0	11	38
Inner and outer	67	78	66	72	85	98

estimation was investigated using five different sampling regimes (annual, biennial, triennial, etc.).

RESULTS

Number of animals with long-lasting marks

Between 66 and 98 individuals were identified, from grade 3 left- or right-side photographs during each of the three years in the experiment (Table 2).

Results from the mark–recapture analyses using the M_t and M_{th} models are presented in Table 3. For each model, there are independent estimates for the three years and, within each year, independent estimates for left and right side photographs. In 1992, estimates are presented for inner Moray Firth surveys alone, and inner plus outer Moray Firth surveys combined. In all cases, the estimates from the M_{th} model were larger, in some cases much larger, than the equivalent estimates from the M_t model. This indicates that there was heterogeneity of capture probabilities within our data (Chao et al. 1992). As expected, therefore, we were unable to ensure equal probability of capture in the field. The M_{th} model is thus the most appropriate model for analysis and only these estimates are considered further.

If there were differences in the use of the inner and outer Moray Firth by individual animals, the wider coverage of the inner + outer surveys should provide a more representative sample. For this reason, and because the larger number of surveys resulted in larger sample sizes, we propose that the number of bottlenose dolphins with long-lasting marks is most appropriately estimated from inner + outer Moray Firth survey data.

Proportion of animals with long-lasting marks

The estimates of the proportion of dolphins with long-lasting marks varied from 0.56 to 0.68 depending on the sample data used (Table 4). Data were drawn from inner Moray Firth surveys (and inner + outer Moray Firth surveys in 1992), for the three years and for left- and right-side photographs.

Total population size

The estimates of the number of animals with long-lasting marks from the inner + outer Moray Firth surveys in 1992 for left- and right-side photographs are 73 and 80 individuals, respectively, and the estimates of the proportion of dolphins with long-lasting marks for these data sets are 0.57 and 0.61 of the dolphins. When combined, using the method outlined above, these give a best estimate of the total number of bottlenose dolphins in the Moray Firth in 1992 of 129 ± 15 animals (mean ± 1 SE; CV = 0.12). The 95% confidence interval is 110–174 animals.

Number of calves and dead animals

Between 1988 and 1994, 30 births of identified calves occurred within the Moray Firth dolphin population, two calves disappeared soon after birth, and 19 other carcasses, representing all age groups, were found stranded (Table 5; R. K. Reid, SAC Veterinary Services, Scottish Strandings Scheme, *personal communication*; B. Wilson, University of Aberdeen, *unpublished data*).

The mean number of known births is 6 animals/yr. When divided by the estimated population size in 1992 this gives a mean minimum annual birth (and early survival) rate of 4.6% for the population. The exact birth date of many of these calves is known and so this value is unlikely to be inflated by the presence of calves >1 yr of age. However, as not every animal in the population was photographed in each year (an estimated 8–32% were unphotographed), it is possible that

TABLE 3. Dolphin population data from mark–recapture analyses for the M_t (Darroch 1958) and M_{th} (Chao et al. 1992) models.

Year	Survey area	Side of dolphin	No. of surveys	Model M_t estimates $\hat{N}$	SE ($\hat{N}$)	CV ($\hat{N}$)	95% CI	Model M_{th} estimates $\hat{N}$	SE ($\hat{N}$)	CV ($\hat{N}$)	95% CI
1990	Inner	Left	11	58	5.8	0.100	50–75	100	26.2	0.262	67–178
		Right	11	58	3.8	0.066	53–69	76	12.2	0.161	60–112
1991	Inner	Left	21	42	1.6	0.038	40–48	45	3.7	0.082	41–58
		Right	21	46	1.5	0.033	44–51	49	3.9	0.080	45–63
1992	Inner	Left	13	68	9.2	0.135	55–93	84	19.2	0.229	60–142
		Right	14	48	3.0	0.063	44–57	59	8.9	0.151	48–86
1992	Inner and Outer	Left	16	68	7.8	0.115	57–89	73	12.4	0.170	57–110
		Right	17	64	3.8	0.059	59–75	80	11.1	0.139	66–113

Notes: Side = the side of the dolphin used to calculate the estimate. $\hat{N}$ = estimate of number of individuals in the population with long-lasting marks; SE = standard error; CV = coefficient of variation; 95% CI = 95% confidence interval derived under the assumption that the number of individuals in the population not captured is lognormally distributed.

TABLE 4. Proportion of bottlenose dolphin individuals in the Moray Firth population with long-lasting marks, as estimated from the different data sets.

Year	Side	Survey area	Long-lasting marks: Number with	Long-lasting marks: Number without	$\hat{\theta}$	SE ($\hat{\theta}$)
1990	left	Inner	75	36	0.68	0.044
	right		97	53	0.65	0.039
1991	left	Inner	107	78	0.58	0.036
	right		121	96	0.56	0.034
1992	left	Inner	68	52	0.57	0.045
	right		88	58	0.60	0.040
1992	left	Inner and Outer	77	57	0.57	0.043
	right		116	73	0.61	0.035

Notes: Side = the side of the dolphin used to calculate the estimate; $\hat{\theta}$ = estimated proportion of animals with long-lasting marks in the population; SE = standard error.

some calves were unidentified during their first year of life. Accounting for this increases the estimated annual birth rate from 4.6% to ~5–6%. This approximation encompasses the 5.5% given by Wells and Scott (1990).

The mean number of known mortalities is 3 animals/yr, representing a mean minimum annual mortality rate of 2.3% of the population. This value is a minimum because we know that not all dolphins that died were recovered; for example the two lost calves in 1991 and 1992 (Table 5) were never found. It is possible, likely even, that significant numbers of dolphin carcasses have not been recovered. If only ~one-third of carcasses were actually recovered then the annual mortality rate could be as high as 10% or more.

Thus, our most optimistic scenario is that the population is increasing at ~3%/yr but, if significant numbers of dead dolphins were not recovered, the population could be declining at a rate of ≥5%/yr.

Effectiveness of monitoring programs

When the relationship between the rate of population change and the time required to detect trends for three levels of estimate precision are plotted (Fig. 6) the following becomes clear: (i) the length of time required to detect a trend in population size decreases with increasing rate of population change; (ii) the precision of the annual estimates of population size has a considerable effect on trend detection; and (iii) as rate of change increases, the importance of precision in population estimates decreases.

As the interval between estimates increases, the number of estimates required to detect the trend decreases (Table 6). This is because the effective rate of change increases with interval. This apparent saving in resources is offset, however, by an increase in the time taken to detect the trend. Surveys conducted once every 5 yr may take up to double the time to detect a trend compared with annual surveys. This increased time until detection leads to substantial differences in the size of the population at the point of trend detection. For example, a population of 129 animals that is decreasing at a rate of 5%/yr would have decreased to 85 animals before the trend was detected using annual estimates but would have decreased to just 59 individuals using estimates every five years.

TABLE 5. Demographic data for the bottlenose dolphin population observed in Moray Firth, Scotland, during 1988–1994.

Year	Known births (observed neonates)	Known mortalities: Recovered carcasses	Known mortalities: Missing calves
1988	no data	3	no data
1989	no data	3	no data
1990	5	1	0
1991	6	0	1
1992	7	4	1
1993	2	6	0
1994	10	2	0
Annual mean	6.0	3.0	

DISCUSSION

Estimates of population size

The Moray Firth contains the only resident group of bottlenose dolphins in the North Sea and one of the best-known in European waters, but our estimate of

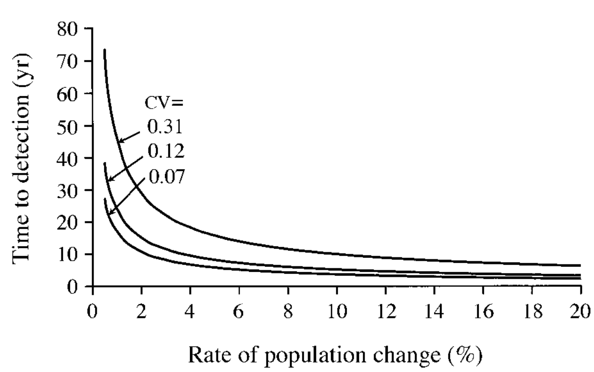

FIG. 6. Relationships between the rate of population change, time until trend detection, and estimate precision for annual population estimates. Three levels of precision are given. The highest and lowest (CV = 0.07 and 0.31) represent the range encountered in this study, and the intermediate (CV = 0.12) that of the best estimate. The probability of Type I and II errors was set at 0.10.

TABLE 6. Observation effort required to detect a statistically significant (at the 0.10 probability level) trend in population size under different directions of 5%/yr population change. Data variability is specified at CV = 0.12.

a) Increasing population

Number of years between estimates (t)	Number of survey episodes required (n)	Effective % change per interval t ($1.05^t - 1$)	Number of years to detection ($t[n-1]$)	Total % change at detection ($1.05^{t(n-1)} - 1$)
1	9	5	8	48
2	6	10.3	10	63
3	4	15.8	9	55
4	4	21.6	12	80
5	3	27.6	10	63

b) Decreasing population

Number of years between estimates (t)	Number of survey episodes required (n)	Effective % change per interval t ($0.95^t - 1$)	Number of years to detection ($t[n-1]$)	Total % change at detection ($0.95^{t(n-1)} - 1$)
1	9	−5	8	−34
2	6	−9.8	10	−40
3	5	−14.3	12	−46
4	4	−18.5	12	−46
5	4	−22.6	15	−54

absolute abundance is the first available for this population. It confirms that the minimum estimate of 62 dolphins derived by Hammond and Thompson (1991) was precisely that; only about half of the population was counted. Nevertheless, our estimate of 129 individuals (95% CI 110–174 individuals) shows that the population is very small. Many coastal populations of bottlenose dolphins elsewhere in the world appear to be of similar size (Hansen 1990, Wells and Scott 1990, Williams et al. 1993, Liret et al. 1994). However, the geographic isolation of the Moray Firth population justifies the particular concerns expressed about its vulnerability.

A key feature of this study was that the mark–recapture experiment was designed specifically to enable population size to be estimated with minimum bias and maximum precision within practical constraints. To do this, the spatial distribution of survey effort was planned so that it provided samples from the main parts of the population's known range, allowing the whole population to be included in the estimate. Survey effort was further spread over time, so that samples could be drawn to represent a variety of intervals, allowing later mark-longevity analyses (rather than sample availability) to dictate the selection of an appropriate capture history duration for the analyses. During the surveys themselves, photographs of as many individuals as possible were taken irrespective of their marks so that the proportion of marked to unmarked individuals could be estimated and so that the impact of individual heterogeneity could be reduced. Field sightings of recognizable individuals were not included in later analyses unless, like all other individuals, they were represented in the photographs. At the photo-analysis stage, all pictures were graded and middle to low standard pictures rejected to reduce the probability of marks going unrecognized at recapture. As many marks as possible were used to confirm each identification, so that false matches could be avoided, and each new picture was compared with all previous pictures so that recaptures would not be missed. Individual dolphins were stratified by their mark types so that only those with long-lasting marks were included in the mark–recapture analyses to further reduce mark loss. Finally, the choice of models was based on the assumptions of the mark–recapture technique most likely to have been broken during the sampling or photo-analysis stages.

However, it is clear that even with a substantial input of time and resources, a wide range of estimates is possible (Table 3), especially so because results were only calculated for analyses conducted after initial data and model selection. This point cannot be overemphasized. It is straightforward to calculate mark–recapture estimates from photoidentification data, but care and thought are needed before and after the data are collected to ensure that such estimates are meaningful.

In this study, 60% of photographs taken were of quality grade 3. Of the factors that reduced this quality, the most common was low light intensity. By simply choosing less cloudy days to carry out survey work, the number of rejected photographs could be reduced. However, in temperate areas such as the Moray Firth, suitable weather windows for this work are at a premium and already limit the number of surveys possible. This problem could be side-stepped by using more than one survey platform simultaneously during periods of the best weather. However, increasing sampling effort is costly and needs to be balanced against the value of increased precision of population estimates. Alternatively, improvements could be relatively easily made by choosing higher speed film or camera lenses more efficient at light gathering. The use of equivalent grain, but higher speed black and white, rather than color, film could be considered and an investment in high quality lenses has few drawbacks.

Bottlenose dolphins, like other odontocetes, are highly social and associations among individuals are not random (Wells et al. 1987). In analyses of mark–recapture experiments, ''captures'' of individuals are assumed to be independent events, but for populations that form cohesive groups this assumption will be violated. This should not bias estimates of the number of individuals in a population, but it may result in a false sense of precision (an underestimation of variance). The extent of this effect will depend on the type of social structure, on the fluidity of associations among individuals, and on the proportion of the population captured at each sampling event. The influence of social behavior on mark–recapture estimates of populations of social cetaceans is a complex issue that has yet to be addressed. However, studies of the social organization of bottlenose dolphins (Wells et al. 1987) suggest that they live in so-called ''fission–fusion'' societies in which schools often split and join, making school membership highly dynamic. Thus in this species, the impacts of social structuring on mark–recapture estimates are likely to be slight.

Similarly, if school size were to influence the detectability and subsequent photographic capture of individuals in schools then social structuring within a population could lead to biased estimates. Since a feature of bottlenose dolphins is their highly dynamic school membership, such a bias is unlikely to occur in studies of this species. However, other cetaceans in which the composition and hence size of schools is more stable (such as pilot and killer whales [Amos et al. 1991, Bigg et al. 1990]) some schools (usually the larger) may to be more visible at sea than others and so underestimation of population abundance could occur.

Trends in population size and the effectiveness of monitoring programs

Although the current trend of the Moray Firth bottlenose dolphin population is uncertain, data on the number of calves observed and the number of carcasses recovered provide an indication of the levels of population change that might be expected.

The figures given above for birth and mortality rates are crude and approximate; indeed, these vital rates are difficult to determine for cetacean populations (Wells and Scott 1990). However, the collection of individual-based data via photoidentification does allow for their estimation (Barlow 1990, Buckland 1990) and their incorporation into models to estimate population growth rates (Barlow and Clapham 1997). Data collection on Moray Firth bottlenose dolphins began in 1989 and has continued uninterrupted since then. We plan to apply the birth-interval approach of Barlow and Clapham (1997) to these data in the near future when our data set is sufficiently long to allow it.

Nevertheless, these approximate values provide a useful guide for the development of a management program for Moray Firth bottlenose dolphins. Changes in population size are likely to be slow (probably $<5\%$/yr). If mark–recapture estimates of precision similar to that presented here (CV $= 0.12$) were made annually, it would take >8 yr to detect a significant (at the 10% probability level) trend in population size (Table 6). At such small levels of annual change, the precision of estimated population size has a large effect on the length of time needed to detect this change with confidence (Fig. 6). Clearly, information on population trends cannot be produced within the space of a few years. Provision must be made to ensure the continuation of a consistent research effort, ideally as part of an overall management strategy.

Monitoring population size through biennial estimates would make little difference to the total time needed to detect the population change (Table 6) and would save survey effort and resources. However, these savings need to be balanced against the loss of information on the birth of calves to known females and on calf survival. These data are required for application of the birth-interval approach of Barlow and Clapham (1997) and to obtain a fuller understanding of the reasons for changes in population size (Taylor and Gerrodette 1993).

If mark–recapture methods continue to be used as a basis for monitoring the population of bottlenose dolphins in the Moray Firth there are some important considerations. Firstly, consistency in data collection procedures must be ensured. Hammond (1990*b*) found that the magnitude of increase in mark–recapture population estimates of humpback whales (*Megaptera novaeangliae*) in the Gulf of Maine was most likely caused in part by a combination of an expansion of the area sampled and site specificity in the distribution of individual humpbacks, resulting in a progressive reduction of the effects of heterogeneity of capture probabilities. Furthermore, Hansen and Defran 1990 found that changes in the range of bottlenose dolphins near the Californian coast lead to wide discrepancies between estimates. There is evidence of site specificity among individual dolphins in the Moray Firth (Wilson et al. 1997*a*) and minor changes in range (B. Wilson, Aberdeen University, *unpublished data*). It is important, therefore, that future survey coverage is sufficient to minimize the effects of this. This necessitates that the logistically more difficult surveys in the outer Moray Firth and fringes of the population's known range be continued. Secondly, the precision of each annual estimate should be maintained or preferably increased by increasing survey effort or through the efficiency of data collection.

However, it is also clear that a population changing in size very slowly would require considerable effort for this to be established. Furthermore, one can never be statistically confident that a population is experiencing no change. This leads to a paradox, whereby stable or healthy populations at carrying capacity may require considerable resources in monitoring when they may actually need the least conservation effort. Understanding the power of survey techniques themselves is therefore critical if limited resources for conservation are to be targeted at the populations that are actually in most need.

Many coastal cetacean species are potentially threatened by anthropogenic activities and require the development of management strategies. The proposed framework for estimating population size and assessing the likely time scale over which any trends may be determined is applicable to those species that possess natural markings sufficient for individual recognition. Similarly, as the value of photoidentification is recognized and is increasingly being applied to study other taxa, from ungulates to fish, this framework may have wider use.

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