

**Mark recapture abundance estimates and distribution of
bottlenose dolphins (*Tursiops truncatus*) using the southern
coastline of the outer Moray Firth, NE Scotland.**

Thesis submitted for the degree of
Master of Science

By

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Photo credit: Kevin Robinson / CRRU



“There is about as much educational benefit to be gained in studying dolphins in captivity as there would be studying mankind by only observing prisoners held in solitary confinement”.

- Jacques Cousteau

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Abstract

Distribution, relative abundance, group composition, and site fidelity of bottlenose dolphins (*Tursiops truncatus*) using the southern coastline of the outer Moray Firth, NE Scotland, were investigated using systematic boat surveys and photo-identification / mark-recapture techniques. Results showed that bottlenose dolphins were present in the southern outer Moray Firth throughout the summer months, with the highest number of encounters occurring in July. Further analysis of relative abundance revealed two areas that were intensively used by the dolphins. Both of these areas contained river mouths, which are used by spawning salmon (*Salmo salar*). There were a high number of neonate calves first sighted between July and September, and 81% of the total number of groups encountered had at least one calf. These results strongly imply that the outer Moray Firth is an important feeding ground and nursery/calving ground for this population.

Computer-assisted photo-identification techniques were applied to the existing bottlenose dolphin database held by the host organisation. This process revealed a total of 2 false positive and 22 false negative errors. Subsequently, 9.2% of the total number of marked individuals used in the analysis were defined as resident to the outer Moray Firth. Residency was calculated on an annual basis, with the number of residents per year varying between 3 and 9. This variability in the composition and number of residents was attributed to the social ecology of the dolphins, prey abundance, and boat traffic. Finally, using a closed population model, the abundance estimate of bottlenose dolphins using the outer Moray Firth was 108 (95% CI = 99-117).

In view of these findings, the current management scheme is discussed, with the recommendation that the current boundaries of the candidate Special Area of Conservation (cSAC) be revised in order to afford a greater level of protection to this already vulnerable population.

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1.

Introduction

In modern taxonomy, the Order Cetacea is separated into two suborders: the mysticetes (or baleen whales) and the odontocetes (or toothed whales) (Fig. 1.1). Of the 85 known species of cetacean recognised to date (after the classification by Rice, 1998 & IWC, 2001) in the world's oceans, rivers and seas, 22 have been recorded in the coastal waters to the north and north west of Scotland (see Appendix 1), making this perhaps one of the richest areas for whales, dolphins and porpoises in Western Europe.

The bottlenose dolphin (*Tursiops truncatus*, Montagu, 1821) is certainly the best known and most popular of all the cetaceans found in Scotland's coastal waters, with the Moray Firth in northeast Scotland (57°40'N, 3°30'W) being home to one of just 2 known resident populations of the species in UK waters (Hammond & Thompson, 1991); the other being in Cardigan Bay, in Wales (Bristow & Rees, 2001; Bristow *et al.*, 2001). Whilst bottlenoses are also sighted regularly in the Hebrides on the west coast of Scotland, in the Shannon estuary, in Ireland, and along the Cornish, Devon and Dorset coasts, in England (Wilson *et al.*, 1997; Grellier & Wilson, 2003; Bristow & Rees, 2001; Ingram & Rogan, 2002; Lockyer & Morris, 1986; Wood, 1998), the animals in the Moray Firth represent this very cosmopolitan delphinid at the most northern extreme of its species range (Fig. 1.2). As such, this population is regarded to be of both national *and* international importance.

Bottlenose dolphins are easily distinguished from other members of the family Delphinidae by several morphological features. These include a very robust body-form, small rostrum, falcate-shaped dorsal fin, and a lack of any intricate pattern or colouration along the body (Wells & Scott, 2002). The life history of the bottlenose is well documented from both captive and wild animals. Age studies indicate, for example, that males of the species can live for 40 years or more whilst females can typically surpass 50 years (Hohn *et al.*, 1989; Wells & Scott, 2002). The age at sexual maturity is also known to differ between males and females, with estimates between 9 to 14 years and 5 to 13 years, respectively (Wells & Scott, 2002). In temperate environments, the peak time for births appears to be in the warmer summer months (Wilson, 1995), but in tropical and sub-tropical habitats births have been reported throughout the year (Wells & Scott, 2002). The gestation period lasts approximately 1 year; this is the same throughout the species' range. However, there is variation in the suckling duration, which can differ between 1.5 to 4 years, and calving intervals, which can vary from 3 to 6 years (Mann *et al.*, 2000; Wells & Scott, 2002; Kogi *et al.*, 2004).

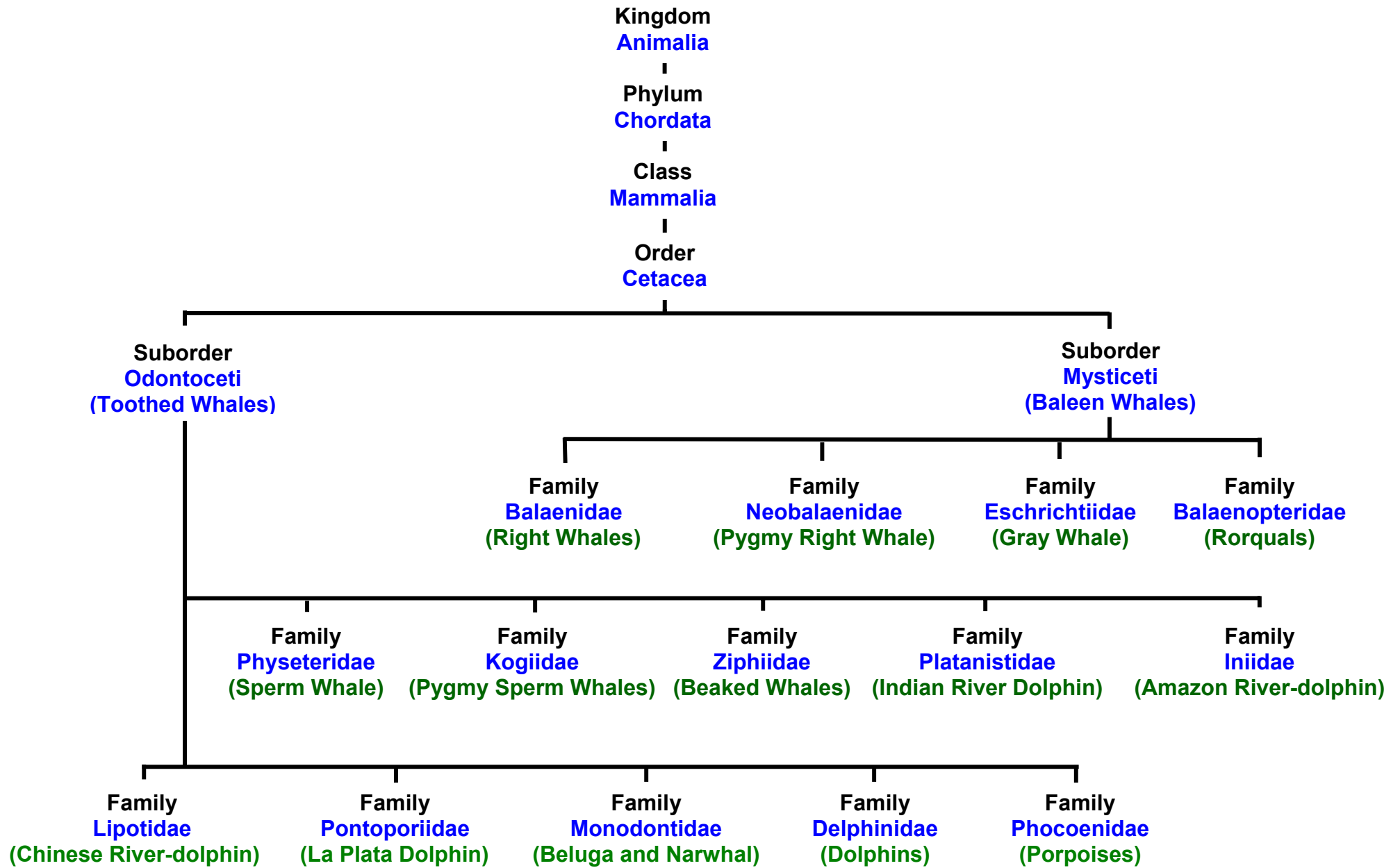


Figure 1.1. Schematic diagram showing the taxonomy of cetacean classification. In the modern nomenclature, the Order Cetacea is comprised of 14 families distributed across 2 suborders.

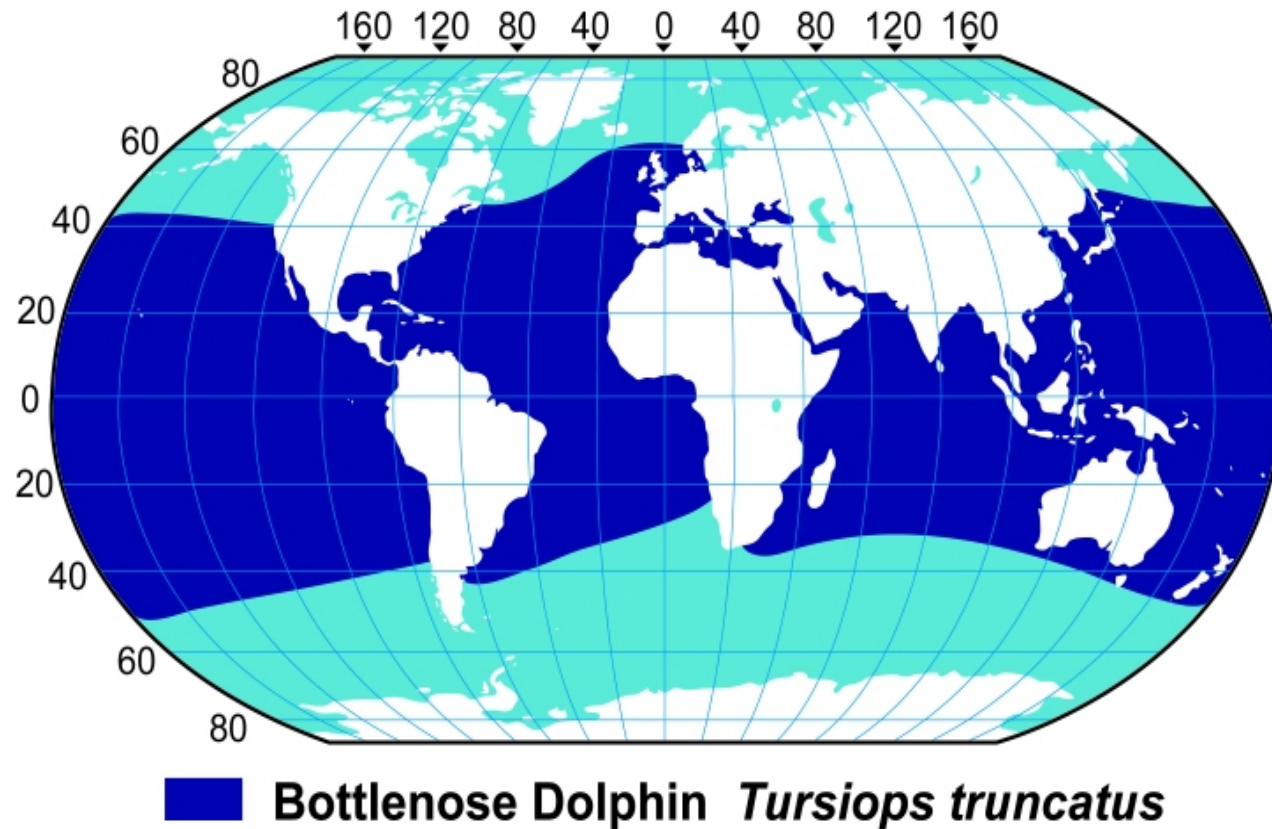


Figure 1.2. Map showing the global distribution of *Tursiops truncatus*. With the exception only of Polar Regions, the species is found throughout the world's oceans and seas. The Moray Firth in northeast Scotland (57°40'N, 3°30'W) represents the most northern extreme of the species' range. (Reproduced with kind permission from the American Cetacean Society www.ACS.online.org).

Variations in the life history and morphology of the bottlenose dolphin are primarily attributed to environmental differences from one habitat to the next. For example, the animals found at the more northerly extremes of their species' range, where water temperatures can be as low as 10°C, can attain lengths of 4 metres or more (Reid, pers. comm.), whereas adult bottlenoses in tropical and subtropical regions, where temperatures may be as high as 30°C, may only reach 2 metres in length (Ross & Cockcroft, 1990; Connor *et al.*, 2000; Wells & Scott, 2002). The bottlenoses in temperate locations are also known to possess smaller fins and flukes than those animals found in more tropical and subtropical regions. Such adaptations are indicative of the very different thermoregulatory requirements of animals in such geographically distinct locations.

Morphological and physiological variations have also been described for coastal versus pelagic-type bottlenose dolphins. The difference between the two putative types comes from features such as the general morphology, haematology and cranial morphology (Hersh & Duffield, 1990; van Waerebeek *et al.*, 1990; Kenny, 1990). Interestingly, the morphological features described for the pelagic-type bottlenose are similar to that of the northerly-located bottlenose dolphin (i.e. the animal possesses a comparatively larger body form and smaller fins and flukes than that of its coastal counterpart), which may indicate that these adaptations are necessary for survival in the comparatively colder pelagic waters (Wells & Scott, 2002). The haemoglobin concentration, packed cell volume, red blood cell counts and types of haemoglobin have all been shown to vary between the coastal and pelagic morphs as an adaptation to the dive requirements of the pelagic bottlenoses (Hersh & Duffield, 1990). In addition, skull measurements indicate that the skulls are wider in the pelagic types, which could be a further adaptation to prey species selection and foraging.

The variations in morphology, detailed above, have subsequently made the classification of *Tursiops* a controversial subject. Indeed, earlier work based on morphological differences alone suggested there were as many as 20 species of *Tursiops* (Hershkovitz, 1966). Nevertheless, *Tursiops* remained a single species genus whilst persistent classifications continued, all of which were based on morphological differences (Walker, 1981; Ross, 1977). However, when genetic studies became common practice in cetacean research, further evidence was collected suggesting that genetically isolated populations of *Tursiops* did in fact exist. This consequentially led to the classification and acknowledgement of the *T. Aduncus* type, which is found between the east coast of Africa and Taiwan, and as far south as the north of Australia (Wang *et al.*, 1999; Perrin & Brownell, 2001; Natoli *et al.*, 2004).

Whilst defining the bottlenose dolphin with reference to genetic evidence is extremely important for conservation and management of a species, it is also important, for the same reasoning, to define parameters such as distribution and density. In these types of studies, and particularly when population estimates are required, a researcher needs to be able to distinguish between individual animals; a technique often referred to as *mark capture-recapture* or *mark-recapture* for short. In early studies of coastal cetaceans, artificial tagging methods, such as freeze-branding, tattooing, flag tags, button tags, and spaghetti tags, were all used to identify individuals within a population (Evans *et al.*, 1972; White *et al.*, 1981; Irvine *et al.*, 1982; Hobbs, 1982). Whilst some of these methods are still being used today (for example, Scott *et al.*, 1990a; Silva & Martin, 2000), artificial tagging has been largely superseded by the more modern application of photo-identification.

In simple definition, photo-identification is a technique used to identify individual animals from photographs of distinctive, naturally occurring markings. This technique was first applied to bottlenose dolphins by Caldwell (1955), Irvine & Wells (1972) and Würsig & Würsig (1977), and to date, still remains one of the best and least intrusive (non-invasive) methods used for gathering information about cetacean societies in the wild. Since its introduction in the 1950's, it has been used to provide information on occurrence and intra-group affiliation patterns in a great variety of cetacean species, including: the killer whale (*Orcinus orca*) (Bain, 1990), bottlenose whale (*Hyperoodon ampullatus*) (Hooker *et al.*, 2002), humpback whale (*Megaptera novaeangliae*) (Gowans & Whitehead, 2001), blue whale (*Balaenoptera musculus*) (Calambokidis & Barlow, 2004), minke whale (*Balaenoptera acutorostrata*) (Dorsey *et al.*, 1990), fin whale (*Balaenoptera physalus*) (Agler *et al.*, 1990), gray whale (*Eschrichtius robustus*) (Jones, 1990) and sperm whale (*Physeter macrocephalus*) (Whitehead, 1990), to name but a few.

For the majority of delphinid species, pieces of tissue missing from the trailing edge of the dorsal or top fin (termed fin nicks or dorsal edge marks) provide the most unique feature for differentiating between individuals within a population. In addition, the dorsal shape (a distinctively wide or tall fin, for example), shading or colouration patterns, scratches and scars, lesions and deformities have all been used in the photo-recognition of individual bottlenose dolphins (Wilson, 1995; Eisfeld, 2003). With respect, a well-marked animal is one recognised not only by a single feature, but by a number of marks forming a distinctive individual matrix for a particular animal.

The uniqueness of photo-ID as a central tool for the recognition of individual whales and dolphins is its ability as a technique to document the life history and ecology of animals, as well as making estimations of population size within a given survey area (Whitehead *et al.*, 2000). When photographs of animals are obtained at more than one location, distribution, short-term movement patterns, and migrations can be determined (Weigle, 1990; Wells *et al.*, 1990; Würsig & Harris, 1990). Recognisable dolphins further allow for a more thorough description of inter-individual behaviours, especially if sex and reproductive conditions are known (Connor & Smolker, 1985; Wells *et al.*, 1987; Connor *et al.*, 2000). They also allow for the basic description of surfacing-respiration-dive cycles and their correlation to general behaviour patterns such as resting, socialising, travelling and feeding (Tayler & Saayman, 1972; Würsig, 1978; Shane, 1990; Balance, 1990).

Whilst fine-scale studies of distribution and habitat use may provide fundamental data for the management and conservation of a species in a given area, life history and population determinants are also crucial to our understanding of mortality, fecundity, immigration and emigration rates within a population. A greater understanding of the dynamics of a dolphin population can thus be obtained when individuals are followed for a number of years during long-term mark-recapture studies utilising photo-identification (Wilson *et al.*, 1999; Rogan *et al.*, 2000).

In order to estimate the population size in wild cetacean societies using mark capture-recapture models, the population under analysis must be defined as either *open* or *closed*. In general, closed models assume that no births, deaths, or permanent immigration or emigration occurs during the sampling period, whereas open models allow for, and even quantify, these parameters (Wilson *et al.*, 1999). The assumption that a population is demographically closed is often achieved by reducing the study period; meaning that a five-year study, for example, is divided into five annual data sets for individual analysis. However, demographic closure is only one of four specific assumptions that need to be met in order to apply a closed population model to a dataset with confidence, the full set of assumptions (after Campbell *et al.*, 2002; Shirakihara *et al.*, 2002; Chilvers & Cockeron, 2003; Irwin & Würsig, 2004) being that:

- 1) every marked animal present in the population at time (*i*) has the same probability of recapture (*pi*) (part of the demographic assumption);
- 2) every marked animal in the population after time (*i*) has the same probability of surviving to time (*i+1*);

- 3) marks are not lost or missed during the study period; and
- 4) all samples are instantaneous, relative to the interval between occasion (*i*) and (*i+1*), and each release is made immediately after the sample.

With long-lived animals such as dolphins, assumption 2 can be met with confidence. Assumption 3 can be met by using high quality photographs and experienced observers, and assumption 4 can be met if the research conducted in the field is efficient, i.e. minimal time is spent with the animals during an encounter. Assumption 1, however, can easily be broken as it assumes that all individuals within a population will react in the same manner. As this is very unlikely, it is important to counter this assumption with a model that can relax certain aspects of the supposition; as well as reducing demographic parameters.

In UK and Irish waters, estimates assuming population closure have been made for bottlenose dolphin populations in the Moray Firth and the Outer Hebrides, in Scotland (Wilson *et al.*, 1999; Grellier & Wilson, 2004), New Quay, in Cardigan Bay, in Wales (Bristow & Rees, 2001), and the Shannon estuary, in Ireland (Rogan *et al.*, 2000). Interestingly, genetic analyses of *Tursiops* from these areas, and from another area in the south of England, showed that the animals in the Moray Firth were more closely related to those in Cardigan Bay, rather than their nearest neighbouring population from the west coast of Scotland (Parsons *et al.*, 2002). This study also indicated that the within-population genetic diversity of the Moray Firth dolphins was markedly lower, and therefore more genetically isolated than the populations in the other sampling regions. This, encompassed with the most pessimistic scenario by Wilson *et al.*, (1999) suggesting a population decline of more than 5% a year, clearly indicates that the population in northeast Scotland is undoubtedly vulnerable to extinction.

The bottlenose dolphin is currently listed under Annex II of the 1992 European Community's "Habitats Directive" (Council directive 92/43/EEC) and the "inner" Moray Firth has been put forward as a candidate Special Area of Conservation (cSAC); as hosting one of just two known resident populations of bottlenose dolphins in UK waters and featuring sub-tidal sandbanks as an additional qualifying interest (MFP, 2001). Designation as an SAC requires an effective management plan for the co-operative management of anthropogenic impacts within the Firth (MFP, 2003). As such, one of the conservation objectives of this management scheme is the "establishment and maintenance of a viable population of bottlenose dolphins within the Firth". However, the physical boundaries of the cSAC only cover the "inner" area of the Moray Firth at present (shown in Fig. 2.1 in the following section), and recent studies have indicated that the home range of this population extends well

beyond the Moray Firth, even as far south as Tyneside in the north of England (Wilson *et al.*, 2004). Whilst the SAC need not cover the entire home range of the population, it should however encompass a large enough area pertinent to the “physical or biological factors essential to life and reproduction” (MFP, 2003). Indeed, Eisfeld & Robinson (in press) advise that the southern coastline of the outer Moray Firth may provide crucial habitats for a significant proportion of this North Sea population which may be particularly significant in view of the management proposals currently aimed at their protection (Curran *et al.*, 1996; MFP, 2003). Consequently, whilst earlier studies concentrated in the inner Moray Firth have been fundamental to our understanding of the biology, behaviour and ecology of this population as a whole, interpretation of some of these data would certainly benefit from studies of the animals in other focal areas within their home range.

Using original data collected in 2004 combined with earlier data collected by the host organisation from 2001 to 2003 inclusive, the principal objectives of this study aimed:

- i). to determine the distribution and site fidelity of bottlenose dolphins using the southern coastline of the outer Moray Firth;
- ii). to ascertain the composition of animals using this coastline and the relative importance of the area in terms of “physical or biological factors essential to life and reproduction”;
- iii). to estimate the number of animals utilising the study area, using mark-recapture models for evaluation;
- iv). and to discuss the significance of the outer Moray Firth in view of current boundaries of the existing cSAC.

2. The Study Area

The Moray Firth is a large triangular embayment in the north east of Scotland. Measuring approximately 5,230 km², it is generally defined as the area of sea to the west of Duncansby Head on the north coast and Fraserburgh on the south coast (Harding-Hill, 1993). It is the largest firth of its kind on the east coast of Scotland, and contains within it four smaller firths, the Dornoch, Cromarty, Beauly and the Inverness Firths. The area west of Helmsdale in the North to Lossiemouth in the South is generally referred to as the “inner” Moray Firth, whilst the area to the North and East of these landmarks is known as the “outer” Moray Firth (Fig. 2.1).

On a large scale, the bathymetry of the Moray Firth is relatively simple. From the inner Firth, the seabed slopes gently from the coast to a depth of around 50 m, approximately 15 km from the shoreline (Admiralty Chart C22, 1997). The coastline of this area consists of dune systems, cliffs and tidally exposed mudflats. In contrast, the outer Moray Firth where the present study is focused more resembles the open sea. Here the seabed slopes much more rapidly to depths greater than 200 metres within 26 km of the shoreline (Admiralty Chart C22, 1997). The characteristically rugged coastline of the outer firth is formed by a composite of headlands and small bays, which is consistent with the more irregular topography of the seabed in this area.

On a fine scale, however, the transition from the inner to the outer Moray Firth is much less distinct. Prominent submarine banks in the outer Firth create shallow areas that reduce the depth to just 33 m in some places. Conversely, the narrow mouths of the Cromarty, Beauly and Inverness Firths within the inner Firth are composed of steeply sided basins creating depths of over 50 m only 1 km offshore (Admiralty Chart C22, 1997).

The sediment in the Moray Firth is predominantly sandy, with grain size being inversely correlated to depth making the shallower areas of the Firth primarily coarse sands, whilst the deepest areas off the southern shoreline are more typically composed of mud (Reid & McManus, 1987).

A combination of coastal and mixed waters (coastal and oceanic) are found in the Moray Firth, the major part of the mixed waters being brought down from the north by the Dooley current which circulates in a clockwise direction within the embayment (Adams, 1987). There are also 12 major rivers flowing into the Moray Firth, 10 of which discharge freshwater into the inner Firth creating an estuarine-like environment that changes to the North and East (Adams & Martin, 1986). Because of this major freshwater input into the

inner Firth, the salinity is substantially reduced, particularly during the winter when salinity levels are less than 34 psu (practical salinity units). These permanent estuarine conditions gradually decrease with increasing distance from the inner Moray Firth, reaching salinity concentrations that generally exceed 34.8 psu in the outer Moray Firth (Wilson, 1995).

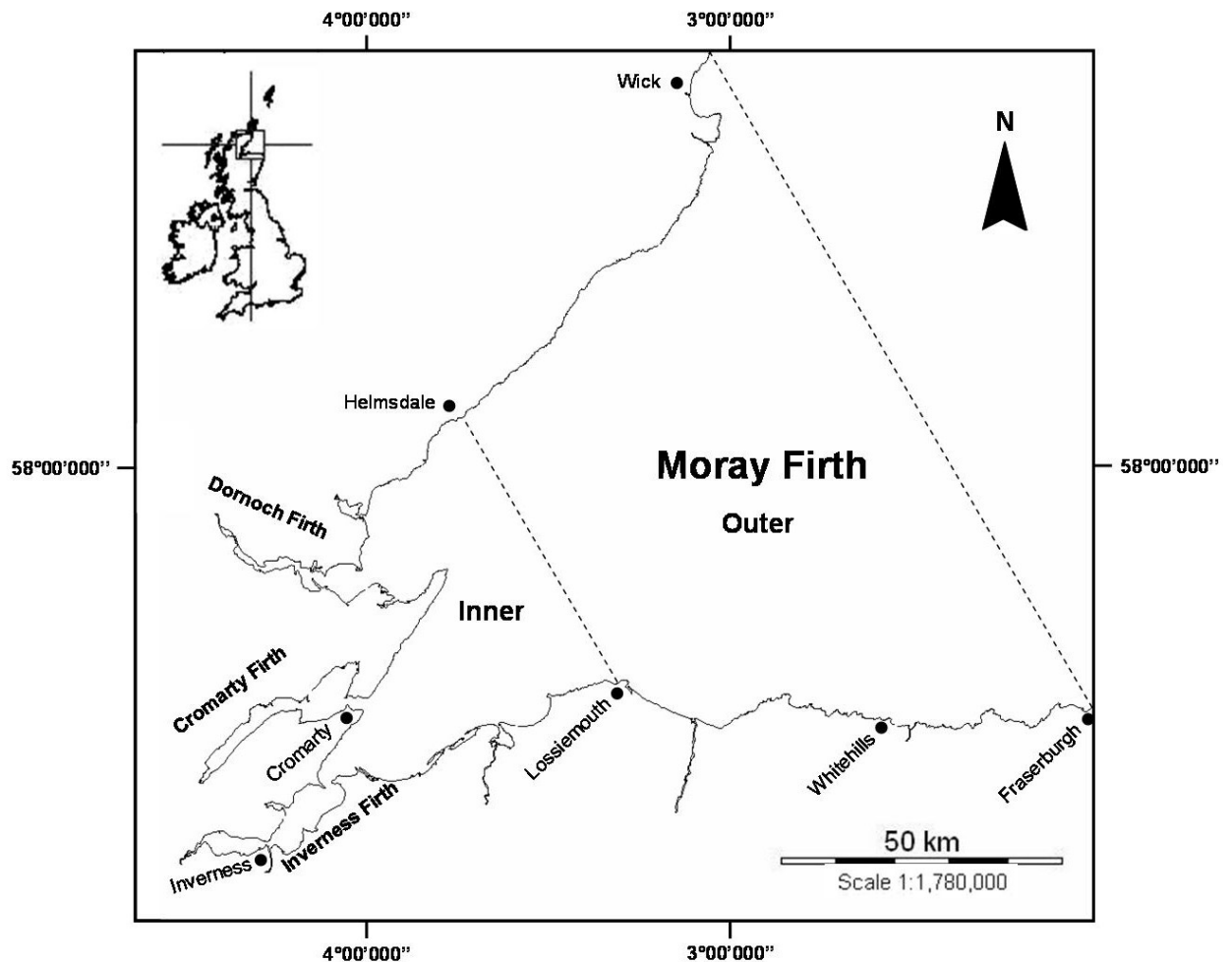


Figure 2.1. Map of north east Scotland showing the location of the Moray Firth (insert: top left). The dashed lines show the divisions between the inner and outer Moray Firth respectively. Adapted and redrawn from JNCC (1999).

3.

Methods

3.1. Data Collection

Data were collected from systematic boat surveys along the southern coastline of the outer Moray Firth between May and October from 2001 to 2004 inclusive. The survey route is illustrated in Figure 3.1 as Route 1, which covers approximately 80 km of coastline between the coastal ports of Lossiemouth and Fraserburgh. This route was divided into two part survey routes: an eastwards route to Fraserburgh and a westwards route to Lossiemouth originating from the centrally-located port of Whitehills where the survey vessel used in the present study was berthed. The surveys were conducted using a 5.4 m Avon Searider Rigid Inflatable Boat (RIB) with a 90 hp Johnston Evinrude outboard engine. A Lowrance 330C combined GPS Plotter / Sonar Unit was used for navigation during boat surveys with a crew of 4 to 7 people acting as observers. The surveys were conducted at speeds of 8-12 km h⁻¹ in sea states of Beaufort 3 or less and during good light conditions. If the sea state increased above this or if weather conditions worsened such that heavy or continuous rain occurred, then the survey was aborted.

At the beginning of each survey trip, a *Trip Log* was filled out to record the start time, GPS start position and crewmembers onboard (example shown in Appendix 2). Accordingly, on the completion of each survey, the end time and end GPS position were also recorded, along with a summary of the sea state and other environmental conditions. If bottlenose dolphins were sighted (referred to as an encounter), the boat was gradually slowed and the camera equipment and recording sheets prepared. An *Encounter Log Sheet* was used to record the start time of the encounter, the GPS position of the animals encountered, and the general landmark along the coastline (for example, see Appendix 2). Encountered dolphins were always approached cautiously at a shallow angle to their direction of travel so that the boat would eventually run parallel with the animals, approximately 20 to 50 metres from their track. Once the boat was in position, the direction and momentum of the boat were maintained as carefully as possible. If the dolphins naturally changed course, the boat was slowed accordingly and steered gently behind the animals, rather than in front, to prevent any unnecessary disturbance. If they stopped to forage or feed at any point during an encounter, the boat was slowed to idle as appropriate and maintained at a respectable distance until the group reformed and continued to transit. Hence, throughout the encounter, any alterations in speed or course were kept to the barest minimum and of utmost predictability for the animals present. Moreover, the time spent with bottlenoses was always kept to a minimum. This

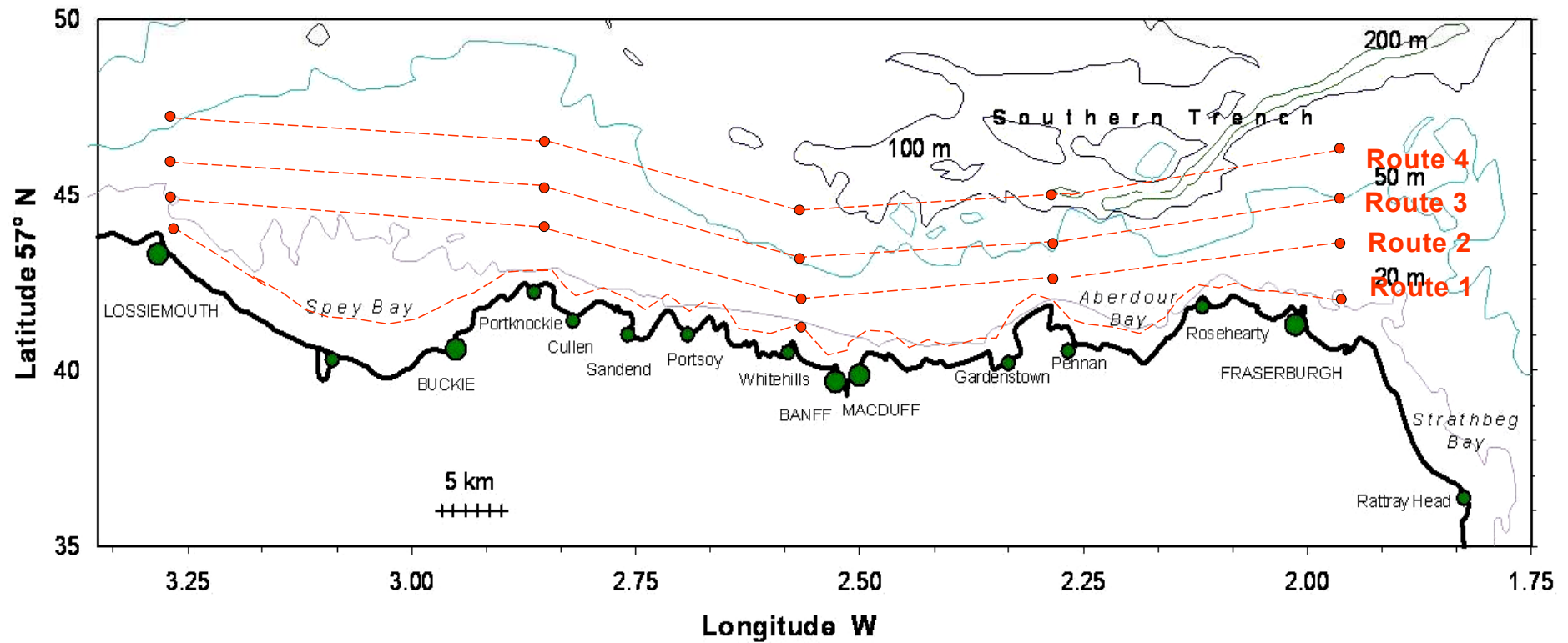


Figure 3.1. Map showing the survey routes used by the Cetacean Research & Rescue Unit during systematic boat surveys of the outer southern Moray Firth. Route 1 shows the dedicated bottlenose dolphin survey route used in the present study. Routes 2-4 comprise additional transects used by the host organisation in their studies of other cetacean species. Each of the survey routes lies approximately 45 minutes apart in latitude.

meant that the research team were only with the dolphins for as long as was necessary to collect the required data and photograph the individuals present. If this was not possible, however, or if the team felt that the animals were showing any adverse reaction to the presence of the survey vessel, the encounter was terminated immediately. All manoeuvres were conducted in accordance with the principals of the Moray Firth voluntary guidelines on handling boats around dolphins (Scottish National Heritage, 1993) and the methods laid down by the Universities of Aberdeen and St. Andrews.

3.2. Photo-Identification

During encounters, photographs were taken with a 35mm Nikon F5 auto focus camera with a F2.8 100-300 mm zoom lens. All photographs were taken using Fuji 400 or 800 ASA colour print film. Colour film was selected over black and white as the medium was considered to be more useful in recording the variety of different markings on the bodies of dolphins.

The aim during an encounter was to take sequential photographs of the dorsal fins of those individuals present. The most efficient method of doing this was to pre-focus the camera on the sea where the subject was anticipated to surface, thus minimising the time required to focus on the subject itself and allowing the photographer more time to select between desired individuals. The capture of both left and right dorsal fins of individuals was not considered necessary, so long as each individual was photographed on at least one side or the other. This was regarded as an important protocol to ensure that encounter durations, and therefore any subsequent disturbance, was minimised. In instances where group sizes were particularly large, positive identifications of known marked animals were made by eye by experienced observers. This allowed the photographer more time to photograph unknown or more subtly marked individuals, thereby reducing the time spent with groups.

If possible, the positioning of the boat adjacent to the dolphins was made in relation to the sun. Ideally, the sun would be behind the photographer so that the sunlight lit up the desired features of the dorsal fin and back of selected subjects. If the sun was behind the subject in relation to the photographer then the dorsal fin appeared as a silhouette, obscuring any markings, such as identifying scratches or lesions, on the fin and back.

Whilst the photographer was taking pictures, a note taker recorded the content of each exposure using a simple *Film Sheet* (Appendix 3). This was also used to detail mother-calf relationships, intra-group associations and sub-group compositions as observed. A separate film sheet was used for each film; the number of films required was dependent on the size of the group encountered, behaviour of the dolphins present and to some extent the

environmental conditions at the time of the encounter. A group of foraging animals, for example, would be typically dispersed with affiliates changing direction frequently, resulting in a greater number of photographs being taken. On the other hand, a travelling school of 8 to 10 closely associated dolphins surfacing in a regular, predictable manner could be photographed in a relatively short space of time using no more than two 36-exposure films.

At the end of an encounter, the number of adults, sub-adults, calves and neonates (new born calves) present were totalled (for age definitions, see section 3.3) and the information on sub-group structures recorded. This required good communication between the boat driver, photographer, note taker and other observers present to record this information accurately. A summary of the behaviour of the dolphins, the time, GPS end position and a visual landmark was then recorded accordingly. Finally, a photograph of something other than the dolphins or the sea (usually a photograph of the crew) was taken to separate any additional photos from subsequent encounters made on the same film. In the case that more than one group of dolphins was encountered during a single survey trip, each encounter was treated as a separate sample and recorded on a separate *Encounter Log*. Back on shore, the data from the *Trip* and *Encounter Logs* were transferred to a generalised *Bottlenose Dolphin Survey Form* (Appendix 4) and this information was subsequently entered into a relational database system (illustrated in Figure 3.2).

3.3. Definition of Age Classes

For the purposes of this study, bottlenose dolphins were divided into four age classes. Based on their appearance, these were: adult (A), sub-adult (SA), calf (C) and neonate (N). Sub-adults were defined as individuals of a similar size to adults, but with a slightly lighter, olive colouration and visible blood vessel rays through the dorsal fin; calves were defined as approximately two-thirds or less the length of an adult, very light in colouration, often with discernable foetal folds, and usually swimming in close association with their mothers; whereas neonates were defined by their very small size (less than one third the length of an adult), very pale colouration with bold foetal folds, often with a droopy dorsal fin and very close association with their mother (Robinson, pers. com; Shane, 1990) (Fig, 3.3).

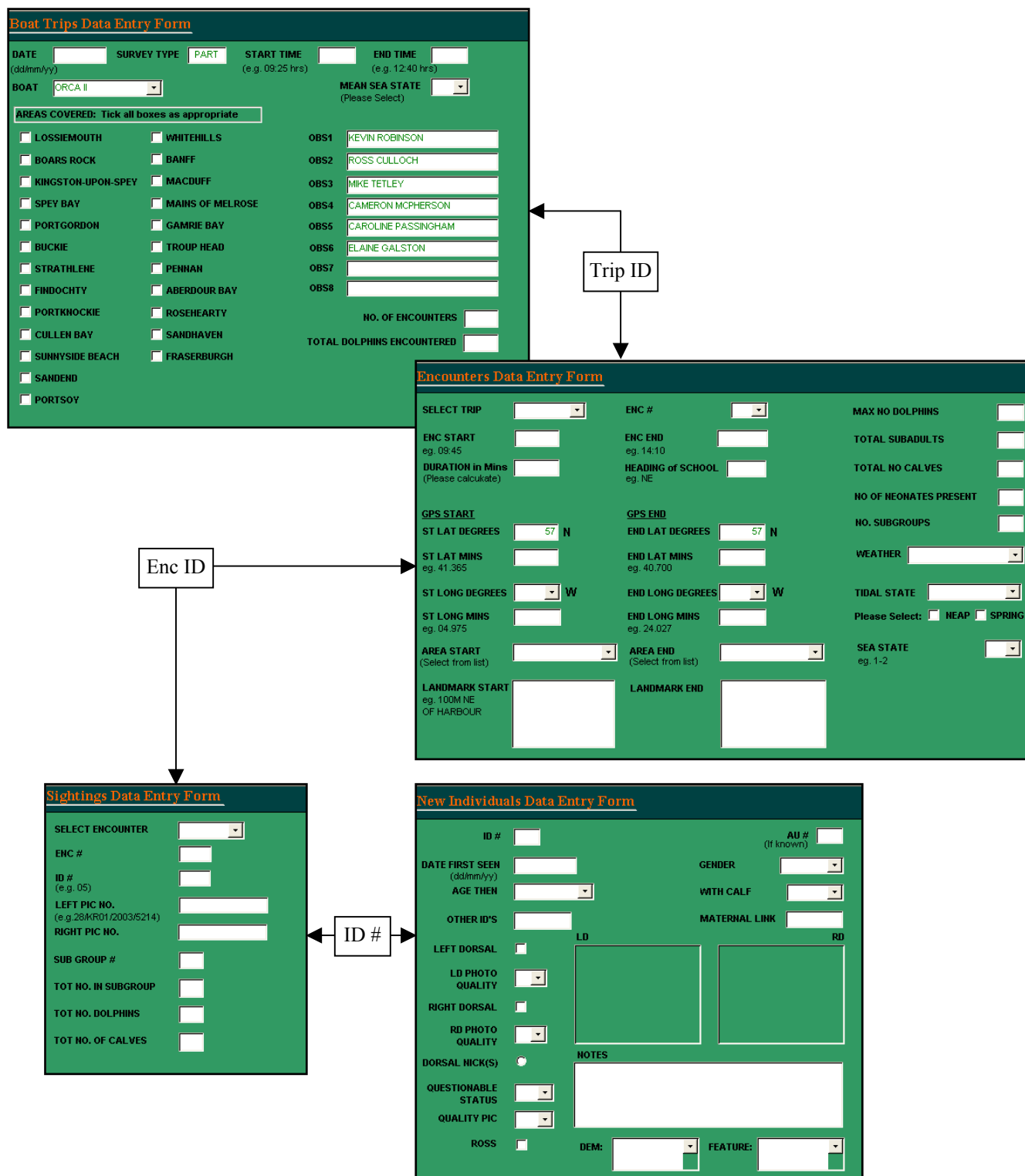


Figure 3.2. Schematic diagram showing the data entry forms constituting the CRRU's bottlenose dolphin database (designed in MS Access by Robinson & Benda). Each of the boxes depicts the fields for the "Trips", "Encounters", "Sightings" & "Individuals" tables respectively. The information entered into each table is interrelated by a number of common fields or identities (indicated by arrows) that allow the user to extract information required from simultaneous files using the database's "Queries" mode.



Figure 3.3. Photographs illustrating the features used in the present study in the categorisation of age class in bottlenose dolphins: (a) shows a sub-adult dolphin with visible blood vessel rays in the dorsal fin (seen as distinct vertical lines, shown by arrows); (b) shows a calf with visible foetal folds (light vertical banding running axially around the body); (c) shows a calf in close association with its mother (note the lighter colouration in contrast to the adult); and (d) shows a neonatal calf in tight formation with its mother. Note the very small body size of this newborn animal compared to the calves in photos (b) and (c).

3.4. Handling Photographs, Matching Animals and Record Keeping

Once the photographs from each encounter had been developed, the negatives were cut into strips and stored in transparent A4 sleeves for protection. Each sleeve was marked with a unique identification code; beginning with the initials of the photographer and the film number, and followed by the year and the film reference number as supplied by the developer i.e. KR22/04-1126. Next, the individual photographs from each processed film were labelled with the encounter date, encounter start time, the GPS position of the encounter, and the frame number and film code respectively. This allowed the photographs to be traced to source should they become mixed-up during the matching process.

An *Encounter Grid* was used to assist in the sorting procedure for photographs to the individual level. Each print was examined using a magnifying lamp over a well-lit table with a protective surface that prevented up-turned photographs getting scratched. Photographs were always handled from the corners to prevent fingerprints being left on the surface obscuring any subtle identifying marks. Photo quality was considered paramount to the subsequent method, and as such only photographs deemed to be of medium to high quality were used in the following analysis. Hence, if a subject was found to be out of focus, obscured in any way or too distant then the photograph was discarded.

The natural markings used in the subsequent recognition of individual bottlenoses are detailed in Table 3.1. The duration for which these natural-occurring marks remained useful in the process of photo-identification was variable. Dorsal edge marks (DEM's), deformities and unusual fin shapes, for example, were all considered unique and permanent markings. In contrast, minor scratches and lesions healed relatively quickly and were sometimes useful for only several weeks to months (as described by Wilson *et al.*, 1999). However, given the short duration of each field season used in the present study (May to September), animals with markings known to last longer than one field season were considered to be marked herein.

Using the encounter grid, photographs of each distinctive “marked” dolphin from an encounter was assigned a temporary unique symbol (e.g. * ♥ ☺ ● △, etc) or identification number depending on whether the animal was already known or not. The photographs for each individual were subsequently laid out and matched by left and right dorsal profile. Once complete, the *Encounter Grid* provided a summary table for all the individual dolphins recorded on a particular encounter (see Appendix 5 for a compiled example). These individuals could then be cross-matched with known individuals from the established CRRU archive; the procedure being assisted through the use of specific search queries within the purpose-designed database (utilising descriptors based on the number and position of DEM's)

Table 3.1. Naturally occurring markings used in the present study for the photo-identification of individual bottlenose dolphins (adapted and expanded from Wilson, 1995).

Dorsal fin nicks or tears	Pieces of tissue missing from the trailing, and occasionally leading, edges of the dorsal fin
Unusual dorsal shapes	Distinctively broad, narrow, tall, short or leaning dorsal fins
Major scratches or scars	Large scratches or scars on the fins and body flanks of animals
Minor scratches or scars	As with major scratches or scars, but less pronounced and superficial marks from interactions with conspecifics
White fin fringes / areas of depigmentation	Depigmented areas usually observed around the edges of the dorsal fin. Albino animals are also included in this category
Active lesions	Areas of black, cloudy, lunar or orange lesions
Healed lesions	Pale epidermal lesions / skin blemishes often used as an additional feature for differentiating individuals
Deformities (Natural & unnatural)	Distortions of the normal body contours, such as a kinked peduncle or tailstock, for example. May be congenital or otherwise, and therefore includes inflicted injuries such as those caused from boat collisions or propeller strikes, for example.

to locate animals with unique or distinctive features. Once a potential match was made from a digital image within the archive, the appropriate hanging file could be retrieved in hard copy for closer inspection of all previous photographs.

On confirmation of a positive match, the best photograph(s) of the right and/or left dorsal fin were added to the respective hanging file, along with information on the date, encounter start time, frame number and code. If no match could be found, then the unknown animal was assigned a new identification number and hanging file, and its details added to the *Individuals* file in the database accordingly. Finally, the entire encounter was recorded on a *Summary Encounter Sheet* (shown in Appendix 6), from which the information on each recognisable individual could be inputted into the *Sightings* table in the relational database for completion.

3.5. Removing False Negatives & False Positives & Data Selection

In order to estimate the number of animals using the study area in the following part of this investigation as accurately as possible, a further procedure was used to ensure the greatest confidence in the dataset being used. This involved the use of a computer-assisted identification / automated matching software package currently under development by Leiden University as part of the EC EuroPhlukes Initiative (www.europhlukes.net). As contributors to the Europhlukes Project and partners in the EC Consortium, the CRRU undertook to trial the new software on its extensive bottlenose archive with the application of a two-stage extraction/matching procedure in the form of FinEx and FinMatch™.

For each of the marked animals archived in the CRRU's bottlenose dolphin catalogue (from 2001 to 2004 inclusive), the above software was used to isolate errors resulting from misidentification. The two error types which most typically occur during the matching process are those of false positive errors, when two sightings of different individuals are classed as one and the same individual and, false negative errors, when two images of the same individual are classed as two different animals; both resulting in bias in population estimations (Gunnlaugsson & Sigurjónsson, 1990; Stevick *et al.*, 2001). With respect, the application of this computer-assisted matching software to the existing dataset, although time consuming, was considered to be an integral process for the subsequent analysis of marked individuals for predictions of the number of animals using the study area.

The process of image extraction is shown in Figure 3.4a. Depending on the fin orientation in the image selected, either the left or the right fin button in the Fin Selector

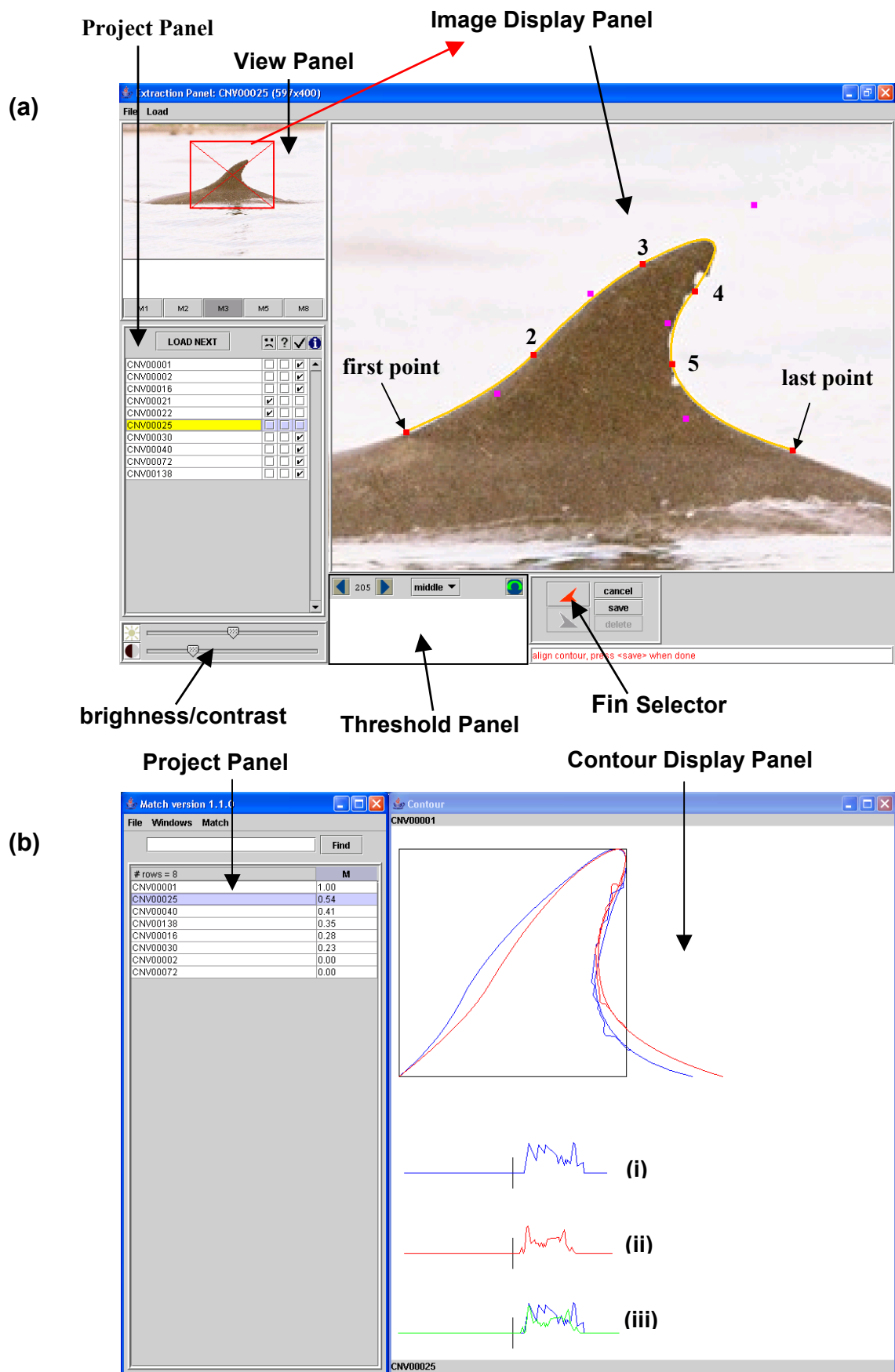


Figure 3.4. Program screen captures showing (a) the *FinEx* dorsal extraction program and (b) the *FinMatch* automated matching program used in the present study for the reanalysis of all “marked” animals (developed by the National Research Institute for Mathematics and Computer Science Department of Mathematics (CWI), Amsterdam, for the EC EuroPhlukes Project). The algorithm extractions described in the text are shown in 3.4b for: (i) the subject image, (ii) the selected match, and (iii) the overlay of the two extractions.

Panel, was nominated. Next, 6 points along the contour of the image in the Image Display were chosen (three on each side of the fin, always starting from the base at the left hand side); always ensuring that a perfect contour of the virtual (undamaged) fin was traced, and that any nicks or notches were ignored at this stage of the extraction. Once the sixth point was selected (at the base of the right hand side of the fin), five additional control points were displayed by the program (shown in pink in Fig. 3.4a). These control points could then be moved around until the orange contour line matched the perfect outline; assisted by moving the original points 2 to 5 where necessary. If, however, it was not possible align the orange curve sufficiently along the profile of the selected image, additional control points could be created by right clicking on any of the existing pink control points.

Once complete, the View Area (zoom level) was selected such that any DEM's were clearly visible in the Image Display Panel. The extraction area was then defined by dragging a rectangle (the extraction frame) around the feature. The boundary pixels were subsequently determined by the software and a threshold level redefined by the user (by moving a slider in the Threshold Panel) such that the shape of the nick or nicks was defined to the nearest contour. The definition of the nick was subsequently traced by clicking with the mouse along this path of best fit until the perfect contour was obtained. Once satisfied, the contours were saved and the extraction frame closed. This process was repeated for each encounter history for all marked individuals within the archive.

On accomplishment of the extraction process for all marked individuals within the bottlenose dolphin archive, the second stage of the procedure for the reanalysis of matched histories was carried out using FinMatch. The FinMatch program allowed the user to select a desired image for comparison against all other extracted images within a designated project file. The results of this analysis were subsequently ranked (by highest match) accordingly to a grading system ranging from 1.00 (a perfect match) to 0.00 (no match), as illustrated in Figure 3.4b.

Potential matches could be examined by selecting an extracted image file from the Project Panel. The selected image was consequently displayed as a virtual fin profile in the Contour Display Panel, overlaid for closer inspection against the subject in question. The mathematical algorithms (as determined by *FinEx*), against which the match rank was made, were also displayed for comparison at the foot of the Contour Display Panel (labelled as (i), (ii) and (iii) respectively in Fig.3.4b). Essentially, this display was used to aid the user in his or her decision.

3.6. Estimations of Population Size

Population estimates, based on the number of marked individuals in the bottlenose archive identified between 2001 and 2004, were made using the FORTRAN program MARK v.4.1 (Mark and Recapture Survival Rate Estimation) developed by the Department of Fishery and Wildlife, Colorado State University (2004). In order to analyse the data in this program, the encounter histories for the marked animals selected were first transcribed into binary: the number '1' indicating that an animal had been sighted, and '0' indicating that the animal had not been sighted. These histories were subsequently analysed using the CAPTURE application run within program MARK. This application has 11 available models that test for 3 sources of variation in sightings probabilities; that of (i) a time response, which considers that a sighting probability varies from sampling period to sampling period but that all animals within each sampling period have the same probability of being sighted (M_t), (ii) a behavioural response, where animals become either 'trap happy' or 'trap shy' after their first capture (M_b) and (iii) individual heterogeneity, where individuals vary in their capture probability (M_h). The 11 models were all based on these principles and/or combinations of the three (for example, M_{bh} , M_{th} , M_{tb}), plus one additional model where probability of capture remains constant (M_θ).

In the subsequent analyses, the models used were selected purely on biological grounds. The time model (M_t) was selected as a prerequisite for modelling this population because variations in capture between sampling periods were strongly evident in the present data set (i.e. sometimes animals were seen during surveys and sometimes they were not). In addition, the time heterogeneity model (M_{th}) was applied to test whether the capture probabilities of individuals also varied over time. Conversely, however, both the null model (M_θ) and the behavioural models (M_b) were largely ignored, the reasons being that the null model is unlikely to occur under natural circumstances, and the behavioural models were simply not applicable to the study, i.e. photo-identification is unlikely to result in a subject becoming 'trap happy' or 'trap shy.'

Using these models, the total population size could be estimated from the proportion of marked animals such that:

$$N = \frac{N - \hat{h}at}{\theta} \quad (1)$$

$$Variance\ N = \left(\frac{vN - \hat{N}}{N - \hat{N}^2} + \frac{1 - \theta}{n\theta} \right) \quad (2)$$

where:

- N = the total population estimate
- \hat{N} = the estimated of number of permanently marked individuals
- θ = the proportion of permanent marks in the sample
- V = the variance of \hat{N}
- n = the total number of animals in the sample

(The 95% confidence intervals are calculated by multiplying the square root of the variance of N by 1.96).

as described by Williams *et al.*, (1993), where the authors used the proportion of photographs that were good enough to show a “mark” if one was present. In the present study, however, after Wilson (1995) the actual ratio of marked individuals was used to give an even more accurate estimate of the size of the population by further reducing the probability of heterogeneity between recaptures. In addition, the number of calves and neonates identified during each research year were also included in the estimates made for unmarked animals.

3.7. GIS & Statistical Analysis

Density plots for distribution data were determined using the GIS software ArcView 3.3 (HCL Technologies, New Delhi, India, 2002). For statistical analyses, Anderson Darling normality tests, two-sided ANOVA Tests, and Kruscal Wallis Tests were performed using MINITAB release 13.30 (Minitab Inc., 2000). All mean results expressed throughout are given as the mean \pm one standard deviation (\pm SD) (n = number of replicates).

4.

Results

4.1. Survey Effort

Between May and October 2004, a total of 42 survey trips were carried out on 28 survey days. The survey effort for this period totalled 92 hours and 13 minutes, of which 11 hours and 43 minutes were spent observing and photographing dolphins during 9 encounters. From May to October 2001 to 2003 inclusive, an additional 151 surveys were conducted on a further 146 days producing an overall survey effort of 437 hours and 40 minutes for the entire study period. Thus, from May 2001 to Oct 2004, a total of 78 hours and 30 minutes were spent with dolphins from 62 encounters (Table 4.1).

Figure 4.1 shows that the survey effort throughout the study period from May to Oct was relatively even across the study area, between Lossiemouth to Fraserburgh (Fig.4.1a), and from one annual field season to the next (Fig.4.1b). Only two notable exceptions were observed, both of which express a bias in survey effort to the area west of Whitehills. The first of these occurred during the month of June, and the second across the 2001 field season. In both cases it seems that a greater number of surveys were carried out between Whitehills and Lossiemouth than between Whitehills and Fraserburgh, which may have influenced the observed patterns of distribution. Statistical analysis using a Kruskal-Wallis Test found a significant variation between monthly survey effort ($p = 0.00$, d.f. = 4, $H = 36.14$), this result was undoubtedly caused by the survey effort in July, which was indicated by the comparatively higher median, however, there was no significant variation in survey effort between the survey years ($p = 0.406$, d.f. = 3, $H = 2.91$). Variation in the number of encounters between months was also observed; however, further analysis showed that this was not attributed to survey effort (Fig 4.2).

4.2. Distribution & Abundance of Animals

The distribution of bottlenose dolphins between May and October 2001 to 2004 is shown in Figure 4.3 Animals were typically found throughout the study area at depths of between 5 and 25 metres. When plotted by month (as shown in Figure 4.4), their distribution was seen to be variable with no particular preferences shown for specific areas of the coastline from one month to another. Whilst the dispersal of groups appeared to be comparatively even during the months of May, July and September, however, this distribution was found to be skewed to the west in June then to the east in August respectively.

Table 4.1. Showing the survey effort for dedicated bottlenose surveys conducted between May and October 2001 to 2004.

Study Period	No. of survey days	No. of survey trips	No. of survey hours	No. of encounters	No. of encounter hours	Cumulative No. of Dolphins
2004	28	42	92.22	9	11.72	226
2003	43	53	142.82	20	27.82	230
2002	50	58	124.45	15	17.13	144
2001	39	40	78.18	18	21.83	258
Total	160	193	437.67	60	78.50	858

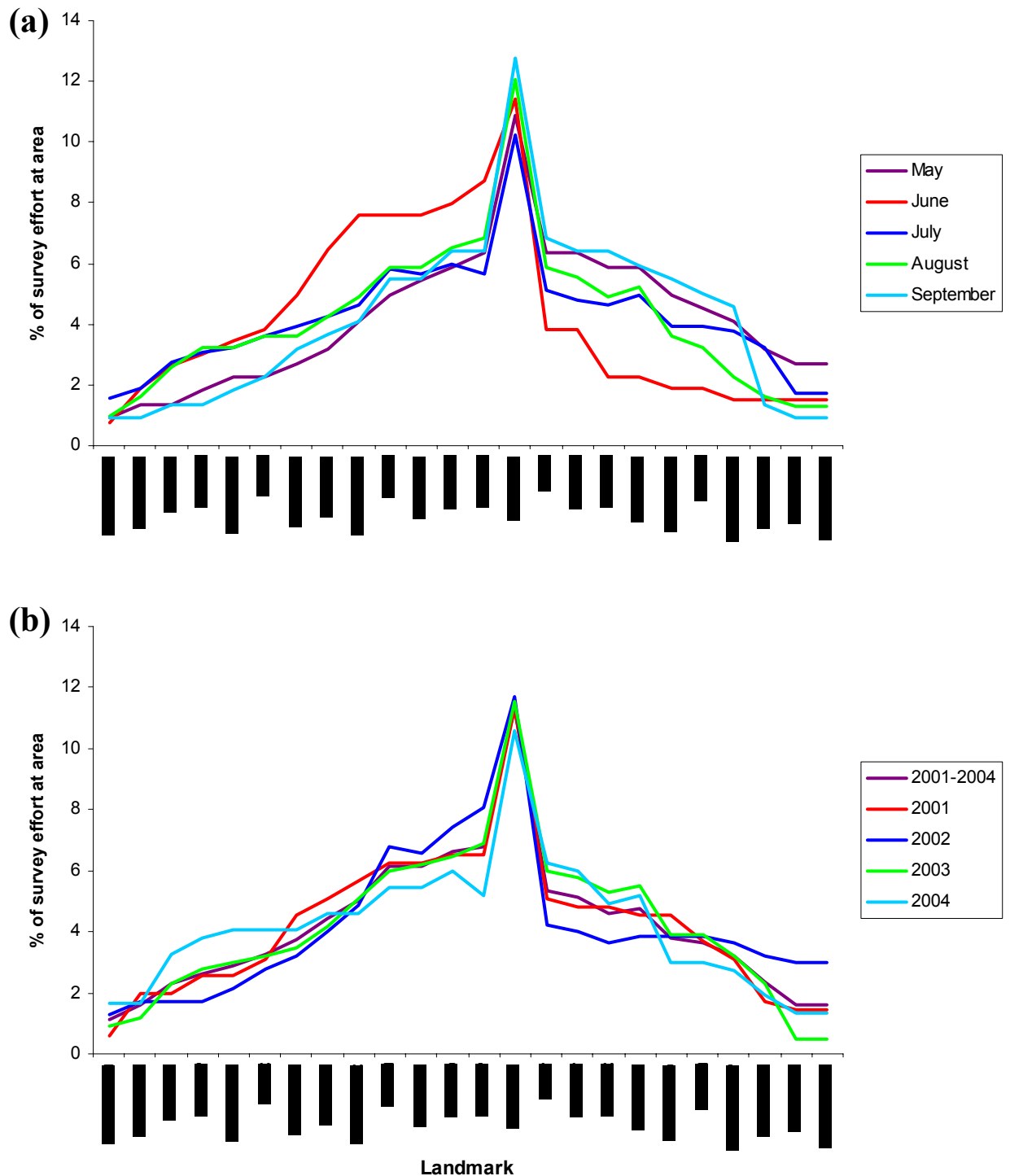


Figure 4.1. Graphs showing the distribution of survey effort across the study area as defined using visual landmarks covered during survey trips. Plot (a) shows the survey effort by month from 2001 to 2004 inclusive, whilst plot (b) shows the survey effort expressed by year. It should be noted that, for each survey, the survey vessel always departed from its berthing at Whitehills, the subsequent route being conducted in either an easterly *or* a westerly direction from this location. This accounts for the considerable peak in survey effort observed in the centre of each graph.

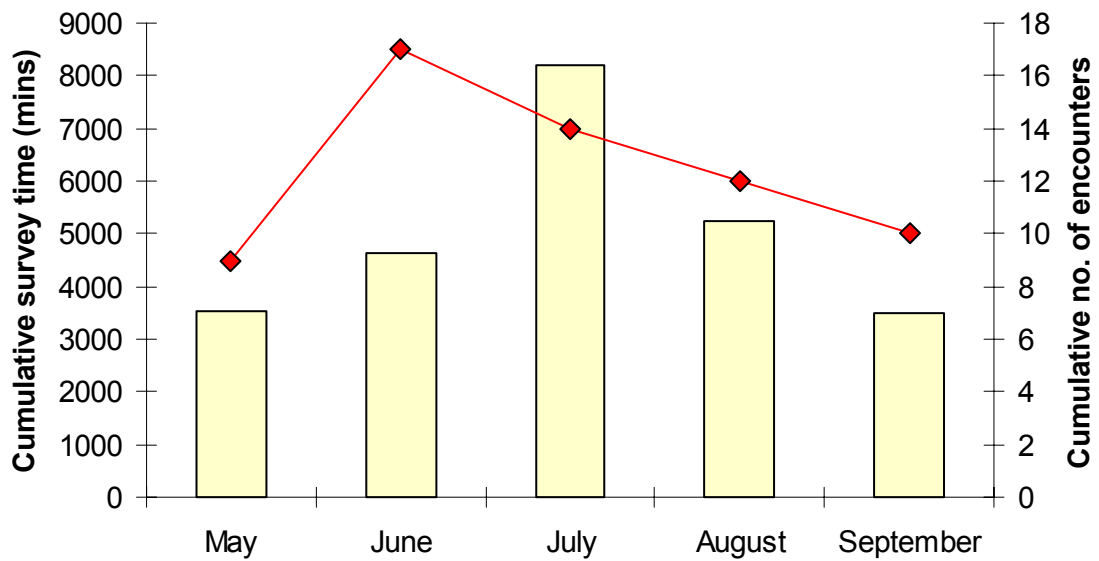


Figure 4.2. The cumulative survey effort in minutes (as depicted by the bar chart), plotted with the cumulative number of encounters (as depicted by the line chart) for the dedicated bottlenose dolphin surveys between May and October, 2001-2004.

The distribution of sightings by year is shown in Figure 4.5. With the exception of the 2004 data in which bottlenose dolphins were biased to the west of the study area (this year being an atypical year for the study area on several accounts), the animals were once again found to be regularly distributed along the entire length of the coastline between Lossiemouth and Fraserburgh.

Whilst the distribution maps simply showed the position of encountered groups, the abundance (no. of dolphins per square km) was further determined to identify any specific preferences shown by the study animals for particular areas. In the resulting GIS plot, 3 principal sites of preferential area use were identified (Figure 4.6). The first of these is seen approximately 1.5 km to the west of Whitehills, in the centre of the coastline; the second close to the river mouth in Spey Bay to the west; and the third adjacent to Banff Bay and the mouth of the River Deveron, to the east.

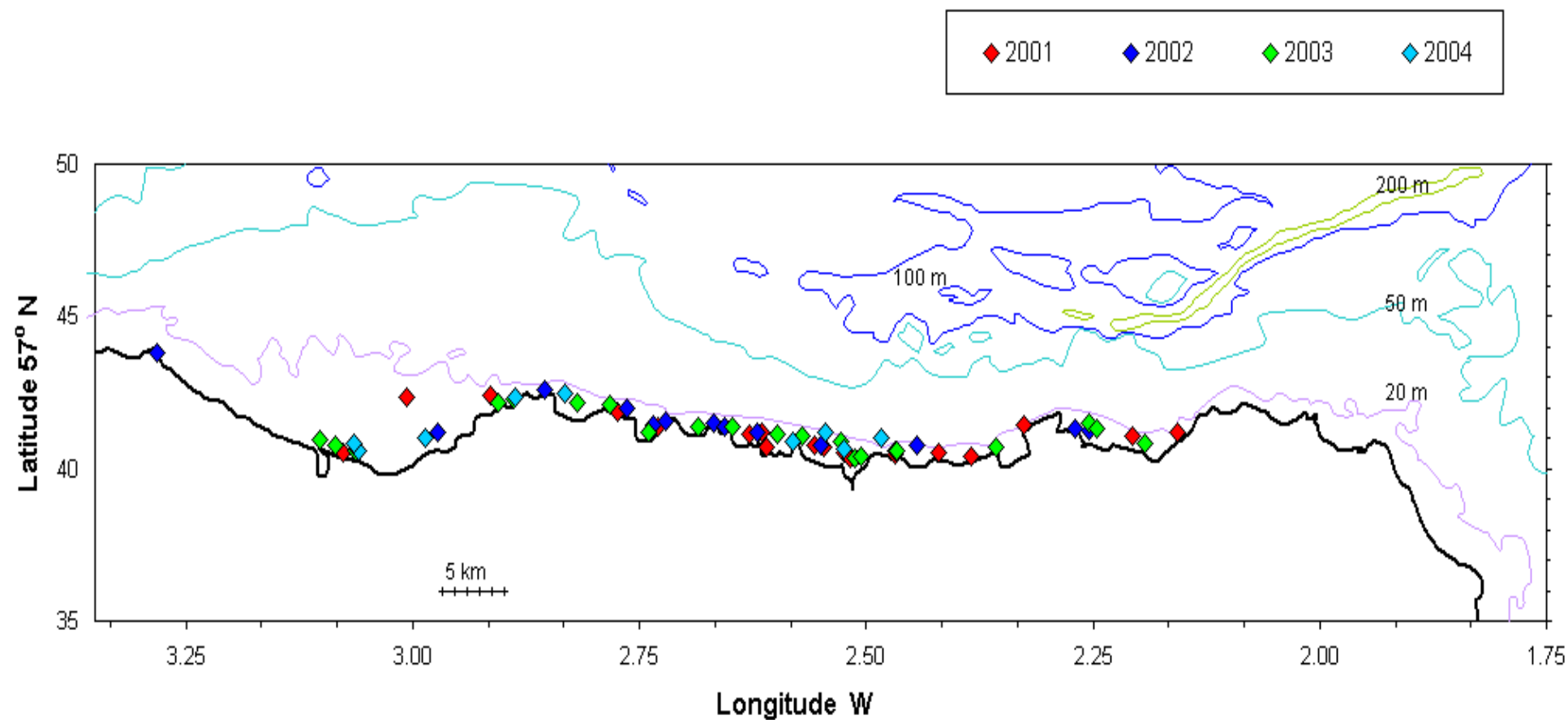


Figure 4.3. Map of the outer southern Moray Firth showing the distribution of all bottlenose dolphin sightings recorded by the CRRU between May and October of 2001 to 2004 inclusive (n = 62). The figure legend denotes the respective year for each sighting plotted. Reference landmarks for this and the following distribution maps can be found in figure 3.1 in the methods section if required.

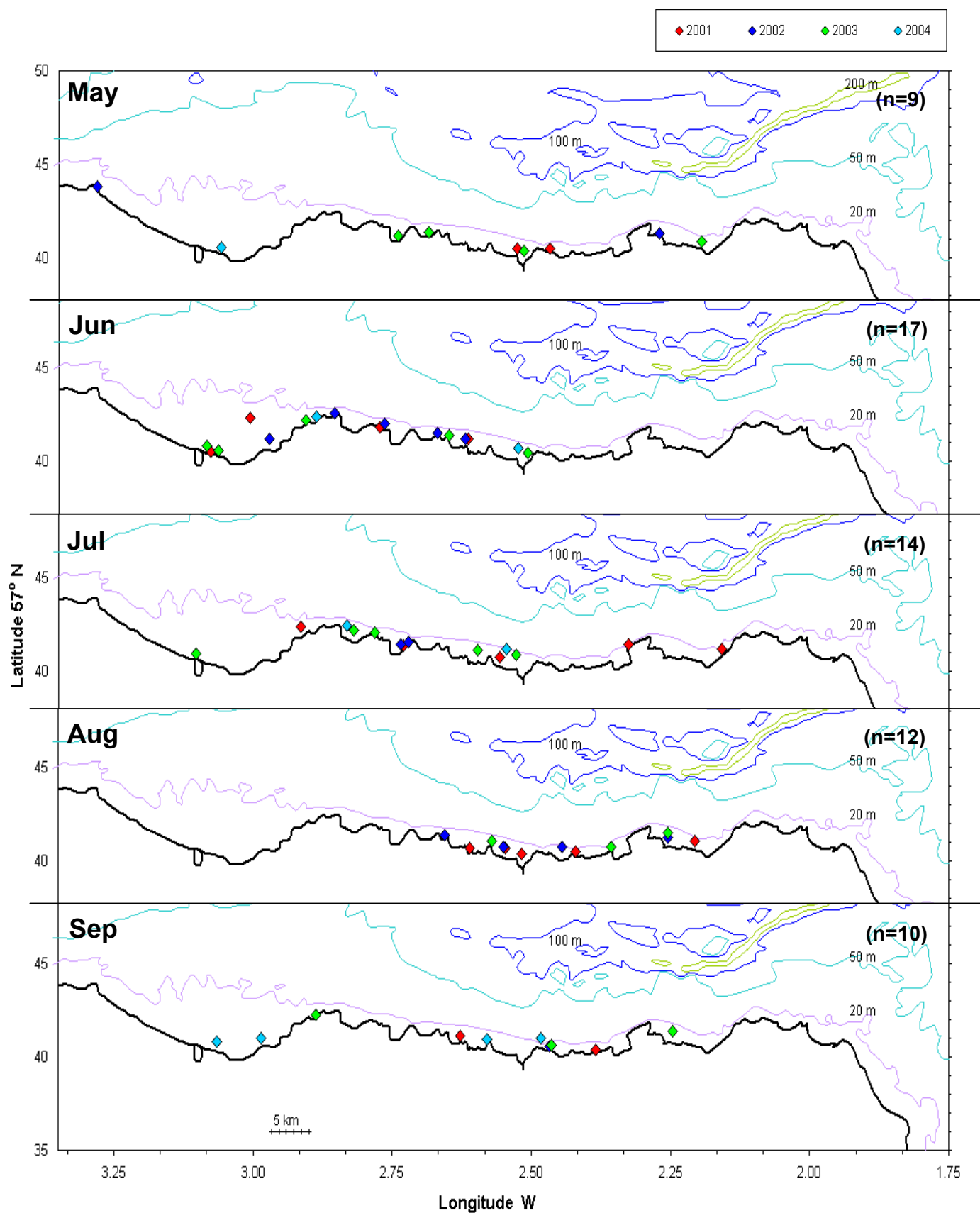


Figure 4.4. Distribution maps of the outer southern Moray Firth study site depicting the monthly changes in bottlenose dolphin occurrence/distribution between Lossiemouth and Fraserburgh from 2001 to 2004 inclusive.

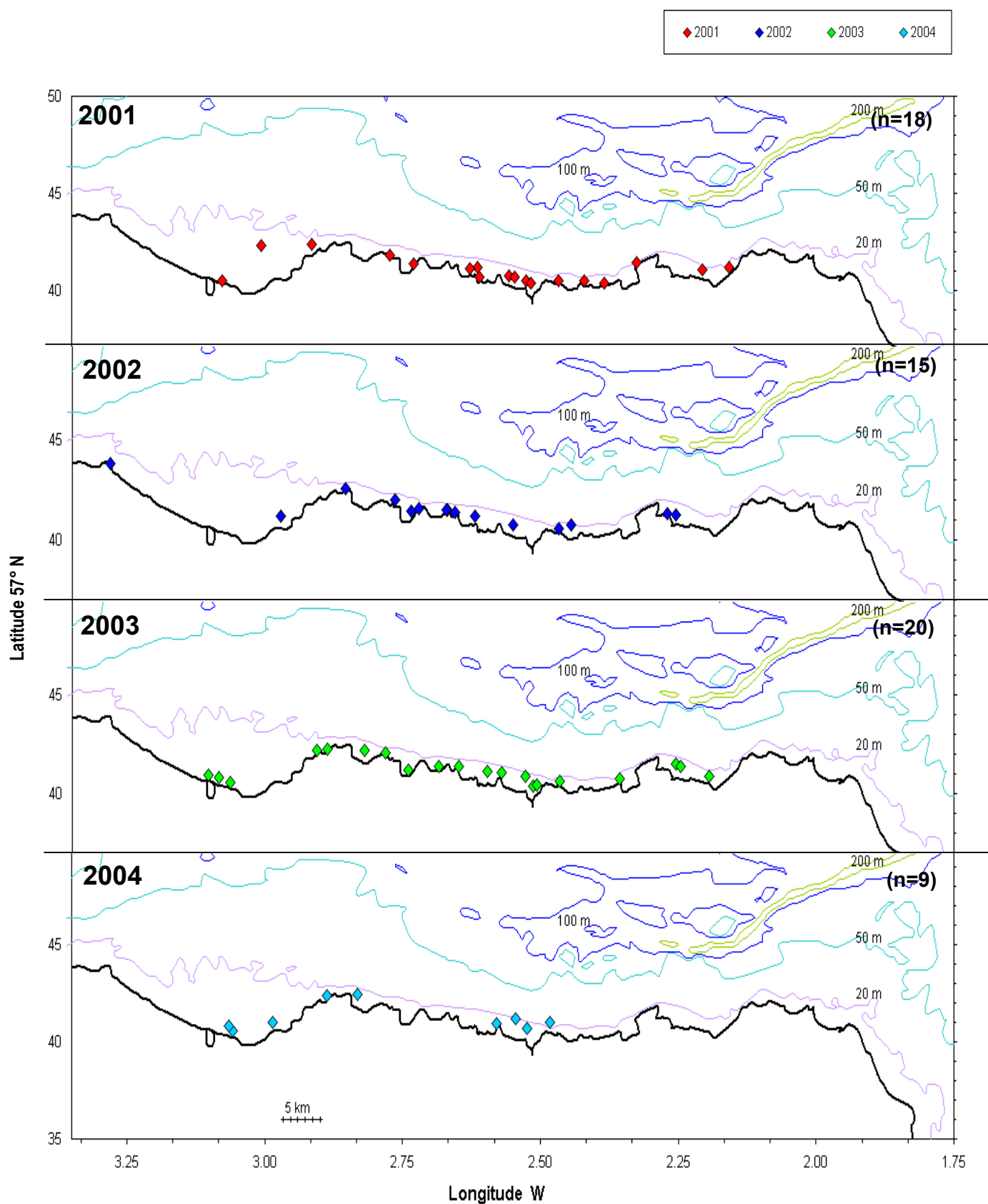


Figure 4.5. Distribution maps showing the annual changes in bottlenose dolphin occurrence/distribution between Lossiemouth and Fraserburgh for 2001 to 2004, respectively.

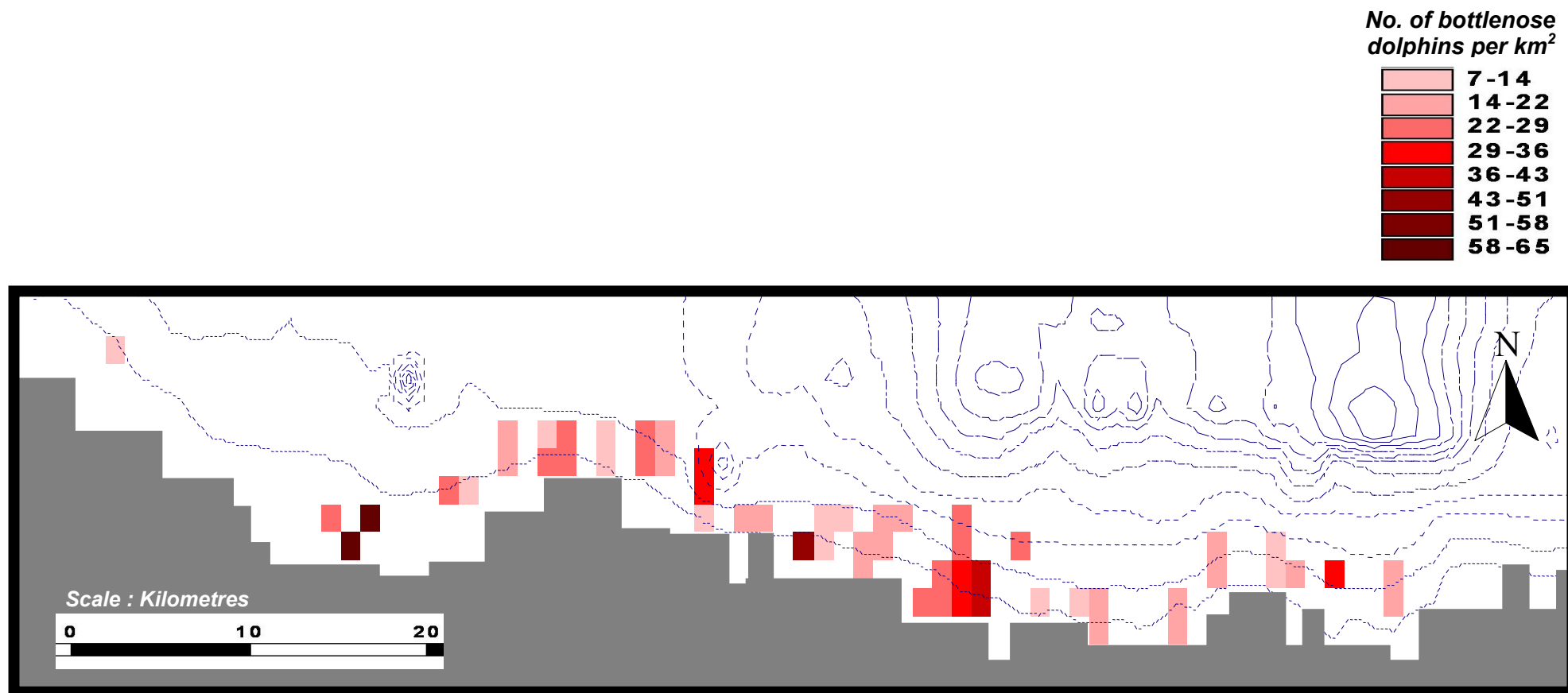
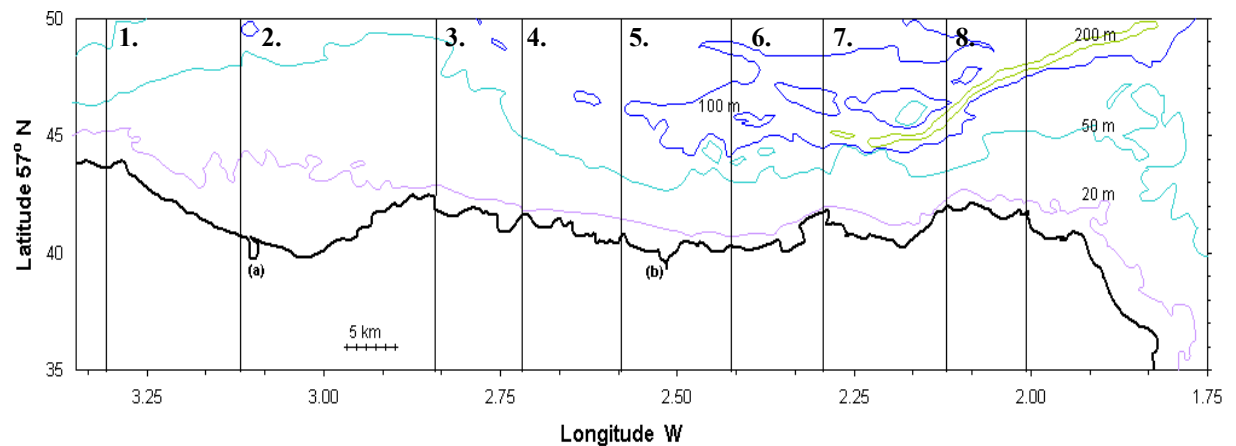


Figure 4.6. GIS plot to show the relative abundance of bottlenose dolphins recorded between May and October from 2001 to 2004 along the southern coastline of the outer Moray Firth between Lossiemouth and Fraserburgh (n = 858 animals). Each of the red blocks represents an area of one square kilometre and the cumulative frequency of animals per block is shown in the accompanying legend. This map was produced using ArcView v3.3.

The coastline was subsequently divided into 8 sub-areas (shown below, as corresponding to the GIS data) for introspection of relative abundance therein. The abundance of animals throughout the entire study area (measuring approximately 115 km²) was calculated as 0.16



animals per square kilometre. Sub-area 5 showed the highest abundance of animals per square km in this area. This was seen throughout the study period, both by month and by year (Tables 4.1 & 4.2). Moreover, this sub-area was the only area in which animals were recorded during each consecutive month of the study period across all years. The only other area in which dolphins were seen from May to September inclusive was sub-area 4, although no animals were recorded in this area during 2004. However, dolphins were further recorded during each year of the total study period in sub-areas 2 and 3. In contrast, only one sighting was recorded in sub-area 1 between 2001 and 2004, whilst sub-area 8 was the only area in which no sightings were made throughout. Statistical analysis showed that the distribution was normal for both data sets (Anderson Darling, $p = 0.00$ in both instances). Subsequently a two-way ANOVA test was used which showed that the monthly analysis was not significant across month or sub-area, respectively (d.f. = 4, $f = 1.31$, $p = <0.1$; d.f. = 7, $f = 1.93$, $p = <0.1$), and that annual analysis was not significant across year, but was significant across the sub-areas (d.f. = 3, $f = 1.05$, $p = <0.5$; d.f. = 7, $f = 3.17$, $p = >0.05$).

4.3. Group Size / Composition

Of the 62 encounters recorded between May 2001 and Oct 2004, 60 provided data that could be used in the subsequent analysis of group composition. Group sizes were found to range

Table 4.2. The relative abundance or density of bottlenose dolphins (no. animals per km²) in each of the designated sub-areas, from Halliman Skerries, in Lossiemouth, to Kinnaird Head, in Fraserburgh, expressed by month (a) and year (b), respectively.

(a)	Sub-Area	Start Landmark	End Landmark	May	Jun	Jul	Aug	Sep
	1	Halliman Skerries	Kingston-Upon-Spey	0.46	0.00	0.00	0.00	0.00
	2	Kingston-Upon-Spey	Bow-Fiddle Rock	0.37	2.84	0.16	0.00	1.39
	3	Bow-Fiddle Rock	Redhythe Point	1.00	2.14	13.43	1.14	0.00
	4	Redhythe Point	Knock Head	0.25	1.25	3.25	2.88	1.25
	5	Knock Head	Stocked Head	2.08	1.42	6.17	4.83	5.67
	6	Stocked Head	Troup Head	0.00	0.71	0.00	4.71	0.43
	7	Troup Head	White Tower	3.10	0.00	1.70	4.60	0.00
	8	White Tower	Kinnaird Head	0.00	0.00	0.00	0.00	0.00
	Total	Halliman Skerries	Kinnaird Head	0.06	0.07	0.21	0.16	0.08

(b)	Sub-Area	Start Landmark	End Landmark	2001	2002	2003	2004
	1	Halliman Skerries	Kingston-Upon-Spey	0.00	0.46	0.00	0.00
	2	Kingston-Upon-Spey	Bow-Fiddle Rock	0.74	0.47	1.53	2.03
	3	Bow-Fiddle Rock	Redhythe Point	4.43	1.86	8.71	2.71
	4	Redhythe Point	Knock Head	5.50	8.13	0.75	0.00
	5	Knock Head	Stocked Head	7.17	2.17	3.92	6.92
	6	Stocked Head	Troup Head	3.00	0.00	2.14	0.00
	7	Troup Head	White Tower	4.80	1.40	3.70	0.00
	8	White Tower	Kinnaird Head	0.00	0.00	0.00	0.00
	Total	Halliman Skerries	Kinnaird Head	0.22	0.13	0.18	0.10

between 2 and 44, with only 5 solitary animals being encountered throughout the entire study period, which accounted for just 3.3% of the total encounters. The largest school of 44 animals was recorded in September 2002.

Eighty one percent of all groups recorded contained calves. Those groups containing calves, both excluding calves from the analysis (median group size = 15) and including calves (median group size = 10), were significantly larger than those without calves (median group size = 4) (d.f. = 107, $f = 8.18$, $p = > 0.001$, one-way ANOVA). Calves were sighted across all months of the study period. Newborn or neonatal calves, however, were only recorded from July to September inclusive (Table 4.3, below).

Table 4.3. Showing the first sightings of individual neonate records from 2001 to 2004 and the percentages of groups containing calves (n=60).

	May	Jun	Jul	Aug	Sep
Number of neonates	0	0	4	4	6
% of Groups With Calves	78	75	93	58	87

4.4. Mark Recapture & Estimation of Population Size

The *FinEx* and *FinMatch* software were used to successfully locate a number of misidentifications within the existing bottlenose dolphin archive. From a catalogue previously containing 96 marked bottlenoses, 2 false positive and 22 false negative errors were identified resulting in a corrected sum of 76 marked individuals within an archive of 162 animals. All 76 of the marked animals used in the subsequent analysis are shown in Appendix 7.

The recapture rate of the resulting marked animals ranged from 1 to 21 with a median of 4 recaptures. Based on the number of recaptures, in order to examine the site fidelity of individuals using the study area, the dolphins were separated into 4 categories of occurrence (shown in Figure 4.7). Dolphins occurring 12 or more times throughout the study period were classed as *common*; those recorded 8 to 11 times *frequent*; 4 to 7 times *occasional*; and on 3 or less occasions *rare*. According to this classification, from the present dataset, 22 individuals (constituting 28.9% of the total marked individuals recorded) were graded as *frequent* to *common* in the study area, whilst 33 (43.42%) were classed as *rare*.

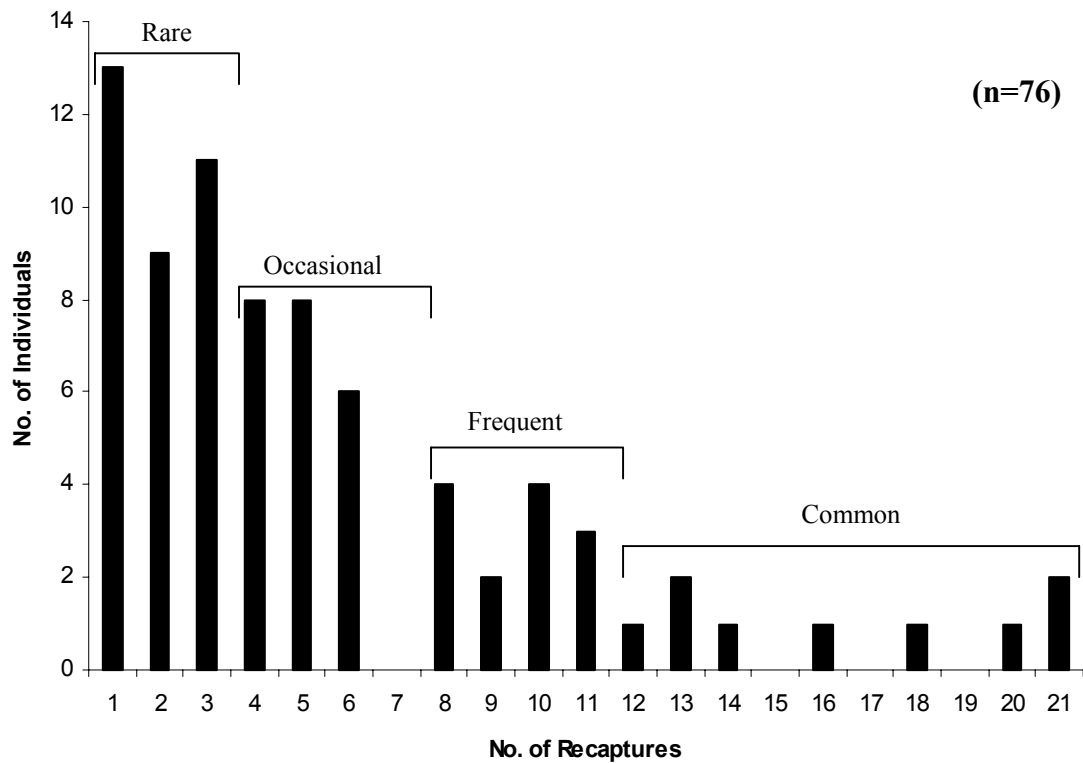


Figure 4.7. Histogram showing the distribution of recapture frequencies for all marked bottlenoses identified in the present study between May and October 2001 to 2004.

According to an adaptation of the method used to examine residence patterns in bottlenose dolphins by Zolman (2002), dolphins identified within the study area during any 3, or more, of the five months (May to September inclusive) in any single study year, were defined as seasonal “residents” for that year. Conversely, dolphins identified in only 1 of the months in any single year, were defined as “transients”. Between 2001 and 2004, the number of marked residents was accordingly found to range from 3 to 9 individuals with a median of 7.5 (Table 4.4). The highest percentage of residents was recorded in 2003 (19%) and the lowest in 2004 (9%). Conversely, the number of marked transients ranged from 19 to 30 individuals with a median of 24.5, in which the highest percentage being recorded in 2004 (66%) and the lowest in 2003 (50%). Interestingly, none of these residents were recorded across all consecutive years of the total study period, although 7 individuals (9.2% of the total marked animals) showed seasonal residence across at least two years; only one of whom was seen across three consecutive years. The encounter histories of these 7 animals are displayed in Appendix 8.

Table 4.4. Showing the annual frequencies of seasonal residence by bottlenose dolphins from 2001 to 2004.

	2001	2002	2003	2004
Total no. of marked animals recorded	49	38	48	35
No of residents animals	6	9	9	3
% of residents recorded	12%	24%	19%	9%
No. of transients	30	19	26	23
% of transients recorded	61%	50%	54%	66%

Between 2001 and 2004, a cumulative total of 19 individuals (25% of all marked animals) were found to show seasonal residence during any one year. Of these animals, 9 were females (representing 26% of all marked females; $n=35$), 9 were males (41% of all marked males; $n=22$) and 1 was of unknown sex (Table 4.5). Notably, each of these females was found to be with calf during her period of residence.

The number of marked individuals recorded in the study area between May and October 2001 to 2004 are shown as monthly and annual totals in Figures 4.8a and b, respectively. The mean totals for May and September appeared to be typically lower than those seen in Figure 4.8a for June, July and August. However, a Kruskal-Wallis-Test showed no significant difference between months ($p = 0.406$, d.f. = 4, $H = 4.00$), probably due to the considerable variability between years in numbers of individuals recorded from one month to the next (shown in Fig. 4.8b). As a result, the total number of marked individuals recorded each year across the study period showed much variation between consecutive years; ranging from a minimum of 35 to a maximum of 49 animals (Table 4.4).

For the subsequent estimation of population size from the mark-recapture data, a discovery curve was plotted to show that the population of animals using the present study area was demographically and geographically closed (Fig. 4.9). The figure shows that the population neared closure towards the end of the 4-year study period. This was acceptable for the following determination as the almost asymptotic curve accounted for expected rates of movement by animals into and out of the study area in addition to the cumulative attainment of new markings by younger animals over time.

Table 4.5. Marked bottlenoses recorded during 3 or more of the 5 survey months (May to October) in any single study year, from 2001 to 2004 inclusive (as defined as the classification for resident animals used herein). M = male, F = female, U = unknown gender, A = adult, SA = sub-adult.

ID #	Name	Sex	Age	No. of recaptures	Year of residence			
					2001	2002	2003	2004
9	Spike	M	A	10		√		
10	Sailfin	M	A	9		√	√	
20	Trekky	M	A	6				√
35	Blotchy	F	A	10				√
37	Pearly	F	A	5		√		
45	Slipper	F	A	10	√			
65	Muddy	F	A	18			√	
66	Goblin Seal	M	A	12			√	√
67	Bucks Fizz	F	A	11			√	
69	Singers	M	A	20			√	
74	Georgia	F	A	21		√	√	
77	Allegranzi	M	A	21	√	√	√	
88	Sparks	M	A	13		√		
135	Trixie	U	SA	6	√			
144	Burness	M	A	11	√			
165	Scruffy	M	SA	9	√			
197	Lower Nick	F	A	11	√	√		
216	Sax	F	A	13		√	√	
225	Dipsy	F	A	16		√	√	

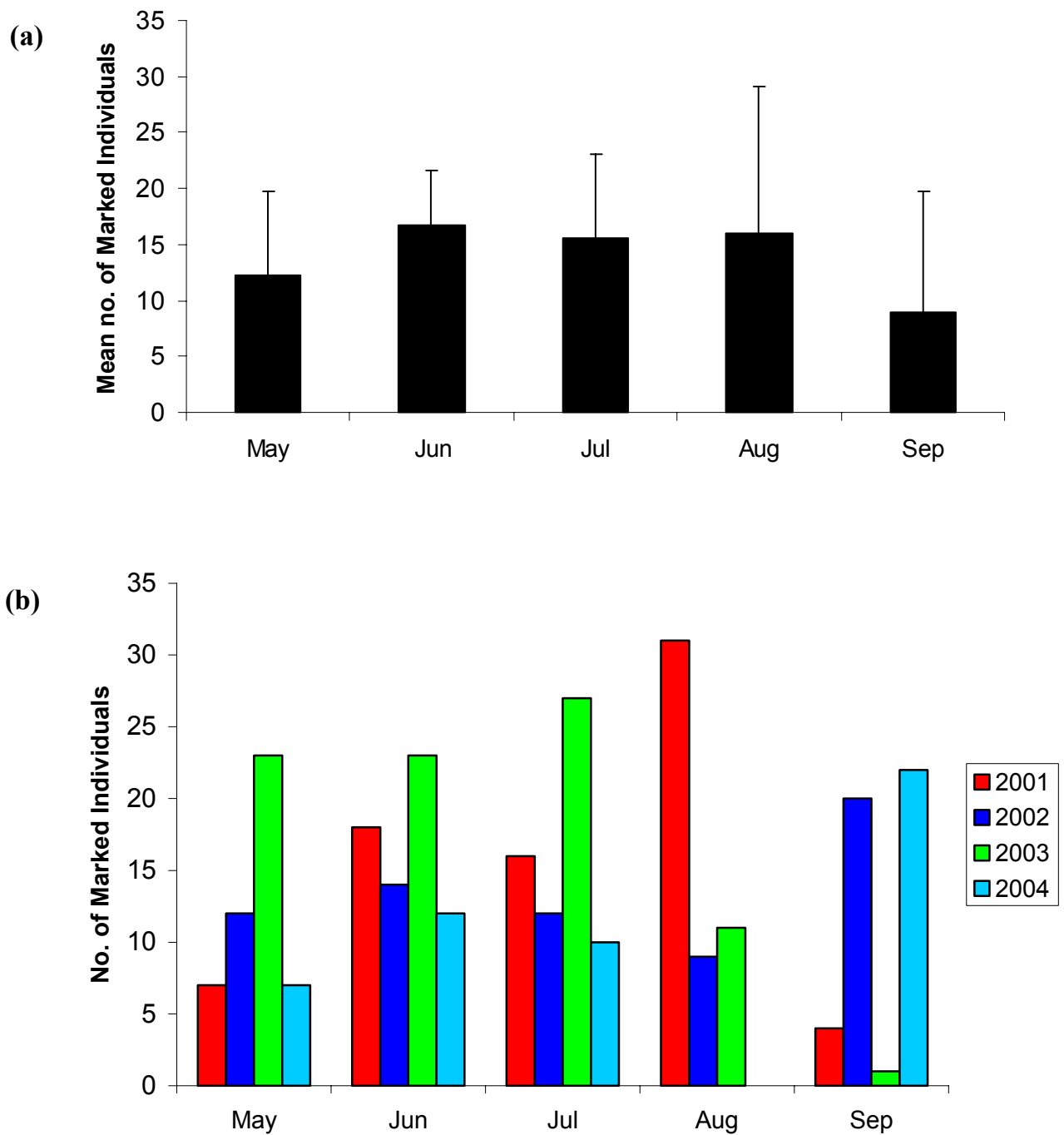


Figure 4.8. Histograms showing the occurrence and distribution of marked bottlenose dolphins using the study area: (a) shows the mean number of marked individuals by month from 2001 to 2004, and (b) shows the monthly variability of marked individuals from one year to the next. The bars in (a) show the standard deviation from the mean.

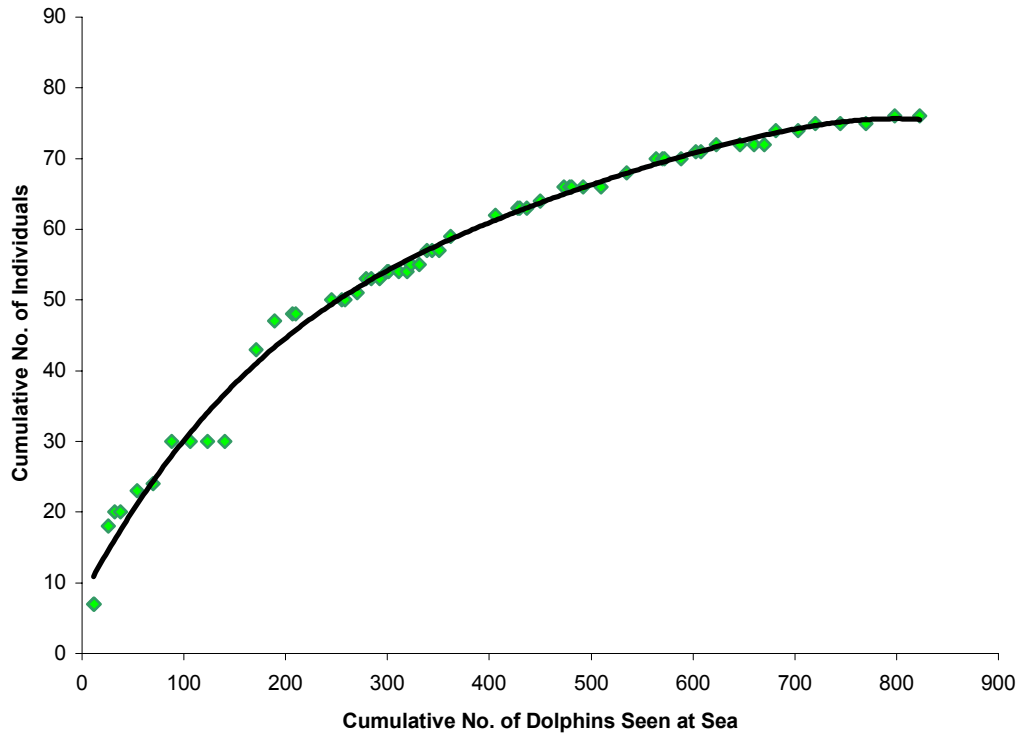


Figure 4.9. Discovery curve of the cumulative number of all individually marked bottlenoses recorded throughout the study period (n=76) plotted against the cumulative number of dolphins encountered (n=858).

The estimations of population size for the study area using the annual capture-recapture data for all marked individuals are presented in Table 4.6. In the resulting table, the Chao time-dependency model (c) (Chao *et al.*, 1992) was seen to produce the highest estimates of size, signifying the intrinsic heterogeneity of capture probabilities within the data. Consequently, the Chao (M_{th}) model was selected over all other models for the subsequent “corrections” applied to the respective annual estimates, the results of which are shown in Table 4.7.

The best estimate of population size for the study area was determined from the 2003 dataset as 108 ± 9 animals (i.e. a 95% confidence interval of between 99 and 117 individuals). Whilst the highest number of marked individuals was recorded in 2001, the derived estimation of population size (shown in Table 4.7) was significantly lower than that determined for 2003. The lowest estimation of 61 ± 11 dolphins was made in 2004, although this result can be directly attributed to the comparatively lower number of encounters recorded during this year (n=9; Table 4.3) and the lower number of individuals recorded.

Table 4.6. The results of the population estimations for each year using: (a) the Chao time-dependency model; (b) the Darroch time-dependency model; and (c) the Chao time-dependent heterogeneity model. ‘N’ = the number of individuals used in the analysis, ‘P’ = the mean probability of recapture, ‘N-hat’ = the population estimate and S.E (N-hat) = the standard error of the population estimate. The coefficient of variation and the 95% confidence intervals are also shown.

(a)	Chao (M_t)						
	Year	N	P	N-hat	S.E (N-hat)	CV (%)	95% CI
	2001	18	0.14	55	3.78	6.87	52-68
	2002	15	0.11	46	6.29	13.67	40-67
	2003	18	0.12	59	6.83	11.58	52-81
	2004	9	0.25	46	8.01	17.41	39-75
(b)	Darroch (M_t)						
	Year	N	P	N-hat	S.E (N-hat)	CV (%)	95% CI
	2001	18	0.14	53	1.77	3.34	51-58
	2002	15	0.1	43	3.15	7.33	40-52
	2003	18	0.14	51	1.83	3.59	49-56
	2004	9	0.32	36	0.59	1.64	36-39
(c)	Chao (M_{th}) ¹						
	Year	N	P	N-hat	S.E (N-hat)	CV (%)	95% CI
	2001	18	0.13	58	4.72	8.14	53-73
	2002	15	0.11	46	5.79	12.59	51-65
	2003	18	0.1	73	11.26	15.42	59-101
	2004	9	0.27	43	4.42	10.28	39-57

¹ The full results obtained from the CAPTURE application of MARK 4.1 for estimations of population size using the Chao (M_{th}) model can be seen in Appendix 9.

Table 4.7. The results of the corrected population estimate for each of the study years 2001 to 2004 using the results from the Chao time-dependence model shown in appendix 9. X = no. of marked animals and Y = no. of unmarked animals recorded.

Corrected Population Estimate – Chao (M_{th})							
Year	X	Y	Prop. X	Prop. Y	N	CV (%)	95% CI
2001	50	27	0.649	0.351	77	6.13	64-90
2002	37	16	0.698	0.302	66	8.77	54-78
2003	48	23	0.676	0.324	108	10.43	99-117
2004	36	15	0.706	0.294	61	7.25	50-72

5.

Discussion

5.1. Distribution, Density & Habitat Selection

In the present study, bottlenose dolphins were encountered along the entire coastline of the southern outer Moray Firth, at depths ranging between 5 and 25 metres. The maximum depth showed an interesting contrast with the data from studies in the inner Moray Firth where dolphins were found in their highest abundance at depths in excess of 50 metres (Hastie *et al.*, 2003a; Hastie *et al.*, 2004). Similarly, in the Shannon estuary, in Ireland, bottlenoses were typically found at depths ranging between 30 and 50 meters (Ingram & Rogan, 2002). Whilst the inner Moray Firth and the Shannon estuary are examples of an enclosed estuarine-type environment, the outer Moray Firth more resembles the open ocean. Conversely, other studies of the species in more open ocean locations such as Florida, California and Argentina have also noted preferences for shallower depths, comparable to those found in the present study (Defran & Weller, 1999; Scott *et al.*, 1990b; Würsig & Harris, 1990).

Nevertheless, variability in depth preference is not uncommon within bottlenose dolphin communities. For example, in the Gulf of Mexico, bottlenoses have been recorded in depths ranging from 65 metres to 1,316 metres (Mullin *et al.*, 2004). It is in these regions (where depth ranges vary significantly), that the community is often putatively segregated into coastal and pelagic populations. However, in the present study, and from studies in other areas of the home range of this population in the north east of Scotland, the animals have only been recorded coastally and at relatively shallow depths (Wilson *et al.*, 1999; Weir & Stockin, 2001). Therefore pelagic-type bottlenoses are not known to occur in this population.

Encounters with bottlenoses in the present study were highest in the month of June, and lowest in the month of May. Interestingly, there was a gradual decrease in the number of encounters between June and September, which suggests that the majority of animals are only using the outer Moray Firth in the summer months. In this case, it is most likely that many of these individuals do leave the survey area, particularly during the winter months, moving to other areas where important resources, such as prey, for example, may be in higher abundance. This pattern in seasonal distribution has been observed in the inner Moray Firth (Wilson *et al.*, 1997), with the converse pattern occurring along the Aberdeen coastline (Weir & Stockin, 2001). Similar trends in distribution have also been described in other regions, such as Wales, Texas, Mexico and Florida (Bristow & Rees, 2001; Maze & Würsig, 1999; Shane, 1980; Balance, 1990; Weigle, 1990). Therefore, changes in seasonal distribution are

not an uncommon observation in coastal bottlenose populations. Nevertheless, the results from the present study and from previous studies in other regions of the population's home range do indicate that the bottlenoses are most prevalent in the Moray Firth during the warmer summer months. After this point the majority of these animals appear to travel south in the winter, and return to the north in the spring.

The distribution of bottlenose groups within the southern outer Moray Firth varied spatially and temporally. These observations could be attributed to survey effort, particularly for the month of July. However, other factors may also have had a direct impact on the observed distribution, these being most commonly attributed to mating, calving, predation, prey distribution and anthropogenic impacts (Wilson, 1995; Wilson *et al.*, 2004).

Results from the present study clearly indicate that the outer Moray Firth is an area important for mother and calf pairs. The percentage of groups encountered with calves in the outer Moray Firth between 2001 and 2004 was 81%. This is comparable to Carrigaholt, in the Shannon Estuary, in Ireland (79.4%) (Berrow & O'Brien, 2003), but was far higher than any other percentages given for other areas in UK waters, such as the Aberdeen coastline, in Scotland (58%) (Weir & Stockin, 2001) and New Quay, in Cardigan Bay, in Wales (66%) (Bristow & Rees, 2001). Indeed, as the Aberdeen coastline has a far small percentage of groups with calves, it is evident that the majority of females with calves must preferentially use the outer Moray Firth. Furthermore, Bristow & Rees (2001) termed New Quay as a nursery ground based on the percentage of groups with calves. Therefore, by Bristow & Rees definition, the outer Moray Firth must be a nursery ground for this population of bottlenose dolphins.

In addition, the high numbers of neonates first sighted in July, August and September gives further support as to the importance of the outer Moray Firth as a nursery ground, and perhaps even a calving ground for pregnant females. However, in more tropical regions, births are recorded throughout the year (Wells & Scott, 2002), yet this does not appear to be the case for more temperate waters, as the same trend in first sightings of neonates was similar for the inner Moray Firth (Wilson, 1995) and for the Shannon estuary, in Ireland (Rogan *et al.*, 2000). This suggests that the time in which females are in oestrus in temperate waters is shorter than that of other populations in more tropical regions. This was reflected in the group sizes with calves, as these groups were significantly larger than those without calves, even when calves were excluded from the calculation. This indicates that males join groups of females with calves in search of females in oestrus. However, the larger group sizes when calves are present can also be attributed to allo-maternal care, which is an important factor in

shaping the group sizes within this population, as male-inflicted infanticide has been reported along the entire east coast of Scotland (Patterson *et al.*, 1998; Wilson *et al.*, 2004). Therefore, allo-maternal care can help to protect the calves of affiliates against aggressive males, meaning that females may favour larger schools in return for the added protection and care of their young (Norris & Dohl, 1980).

The diet of bottlenoses in Scottish waters is diverse, as shown by a study of the stomach contents of stranded and by-caught animals, where the remains of several species including salmon (*Salmo salar*), cod (*Gadus morhua*), saithe (*Pollachius virens*), and whiting (*Merlangius merlangus*) were found (Santos *et al.*, 2001). Indeed, bottlenose dolphins are renowned throughout their global distribution as opportunistic feeders (Gannon & Waples, 2004; Wells & Scott, 2002), although they do demonstrate a clear preference when given a choice of prey items (Cockeron *et al.*, 1990). Interestingly, the feeding behaviour of bottlenoses is just as diverse as the diet itself. For example, a common tactic for many fish or squid in an open, uniform environment is to aggregate together, resulting in a patchy distribution of prey, consequently, the dolphins take advantage of conspecifics to lessen the difficulties in locating and controlling such patches (see Norris & Dohl, 1980). This situation is likely to occur in the outer Moray Firth, particularly in the deeper range preferences of the bottlenoses. This foraging technique would also account for the larger, more dispersed groups typically encountered in the open waters of the outer Moray Firth, as larger groups of dolphins would be better able to control and feed on the prey source, and a dispersed group is more likely to find patchy aggregations of prey (e.g. Evans, 1987; Similä & Ugarte, 1993). Conversely, in more shallow waters, bottlenoses are known to trap fish against the shoreline. This behaviour has been observed to occur cooperatively and solitarily (Hoese, 1971; Hogan, 1975; Bel'kovich *et al.*, 1978). Indeed, this is also a likely method used in the outer Moray Firth by bottlenoses in the shallower depths of their range. Interestingly, the foraging methods described for the inner Firth are also based on topographic features, where the dolphins are thought to take advantage of the deep and steep areas within the inner Firth, which are heavily influenced by the effects of currents (Hastie *et al.*, 2004). The striking differences between the areas used by the dolphins in the Moray Firth may be an indication of opportunistic foraging, or it could be that specialised feeders have adapted to a specific niche, such that the dolphins found in the shallows may be exploiting different prey species to those in the comparably deeper depths, for example.

The direct anthropogenic impacts that are most abundant in the outer Moray Firth are trawlers and tourist boats, both of which can cause significant disturbance to cetacean communities (Constantine *et al.*, 2004; Lusseau & Higham, 2004; Chilvers & Cockeron,

2001; Chilvers *et al.*, 2003). In relation to the present study, trawling pressures may cause several adverse effects that could be highly detrimental to such a small, vulnerable population, these include entanglement in nets, habitat changes resulting from over-fishing, and noise pollution (Fertl & Leatherwood, 1997). Indeed, with the large group sizes commonly recorded in the outer Moray Firth, there is concern that prey items along this coastline are becoming sparse (Wilson *et al.*, 2004), and from observations during surveys, bottlenoses were rarely seen in close proximity to any trawling activities. Therefore, it could be hypothesized that the dolphins are actively avoiding trawlers. Indeed, similar observations have been made in Morton Bay, in Australia, where trawling activities have caused an adverse change in the distribution and behaviour of the coastal bottlenose population (Chilvers & Cockeron, 2001; Chilvers *et al.*, 2003).

In addition, tourist boats are also a potential threat that could inflict a negative impact on the population, causing changes in the 'normal' behaviour of the animals. These behavioural changes commonly result in a decrease in resting rate, which over time will reduce individual fitness (Constantine *et al.*, 2004; Lusseau & Higham, 2004). Indeed, research into the effects of boat traffic in the inner Moray Firth revealed that breathing synchrony of the dolphins was positively correlated with boat presence, which resulted in the animals surfacing frequently, at an energetically inefficient rate (Hastie *et al.*, 2003b). Under these circumstances, it is unlikely that the animals would be continuing their 'normal' behaviours such as foraging, for example, which could result in a negative impact on the dolphins' behaviour, health, and distribution. Since the bottlenoses in the inner Moray Firth are from the same population as those in the outer Moray Firth, it can be expected that the animals within the present study area would behave in the same manner in the presence of boat traffic. Indeed, in the present study, the use of shallow depths of 5 metres, and travelling close to the coastline, particularly in bays, may be an avoidance behaviour to unwanted disturbance caused by these boats.

In the present study, preference was noted for three specific areas along the coastline of the southern outer Moray Firth. Interestingly, the areas identified in the present study were quite different from those defined in the inner Firth, as described earlier. Two of the areas of preference in the present study were bays, both of which were characterised by the presence of a river mouth, sandy substrate, and shallow depth. The third area is also characterised by sandy substrate, but is steeper and deeper than the other two areas. The third site is also an area in which harbour porpoise (*Phocoena phocoena*) (Whaley, 2004) and minke whales (*Balaenoptera acutorostrata*) (Tetley, 2004) have been regularly sighted. Indeed, Whaley

(2004) found this area to be one of five sites intensively used by harbour porpoises, which given the violent interactions that are known to occur between harbour porpoise and bottlenoses in this area (Patterson *et al.*, 1998), it would seem unlikely that the two species would be found in such high abundance in the same vicinity. However, the largest group of bottlenoses (n=44) was sighted in this area, which is the most likely explanation for the high relative abundance, hence this site will not be discussed further.

The rivers within these bays of preference are used as spawning grounds for migrating salmon (*Salmo salar*); a known prey species of bottlenose dolphins in this region, as mentioned earlier (Harding- Hill, 1993; Janik, 2000; Santos *et al.*, 2001). Therefore, it is hypothesised that these areas are intensively used by the dolphins as feeding grounds. In the case of Spey Bay in particular, this supposition is supported further by the pilot study run in Spey Bay by the CRRU in 1997-1998, the results of which clearly show a skew in the distribution of bottlenoses towards the river mouth (Fig. 5.1). Indeed, estuarine areas, inshore bays, and river mouths have repeatedly been found to be sites of high dolphin occurrence (Balance, 1990; Scott *et al.*, 1990b), as they are often characterised by high levels of primary productivity and prey abundance (Acevedo, 1991). In addition, this finding also explains the low relative abundance for Spey Bay between 2001 and 2004, indicating, as suggested, that although the bay is an important area in itself, it is actually the river mouth, more specifically, that is highly significant to this population.

In relation to mother and calf pairs, these shallow bays would be the most suitable areas along the southern outer Moray Firth coastline as a nursery/calving ground for the species, given the hypothesis that these areas have a high abundance of prey. In addition, Spey Bay is the shallower of the two, making boat traffic in the bay almost non-existent, and thus limiting any potential disturbance. Interestingly, reproductive success has been correlated with the use of shallow areas by female bottlenoses in Shark Bay, in Australia (Mann *et al.*, 2000). The authors related this to either predator avoidance and/or prey availability. If reproductive success were related to shallow waters due to prey availability then those findings would further reinforce the hypothesis that Spey Bay, in particular is an area primarily used as a nursery/calving ground. In consideration of the predation factor, there is no evidence of shark and/or killer whale (*Orcinus orca*) attacks on bottlenoses in this area (Reid, pers. comm.). Therefore, it is unlikely that predation is a factor in shaping this population. However, protection against aggression by males in the form of harassment (Connor *et al.*, 2000), as discussed earlier, may make these areas more appealing to groups of females with calves.

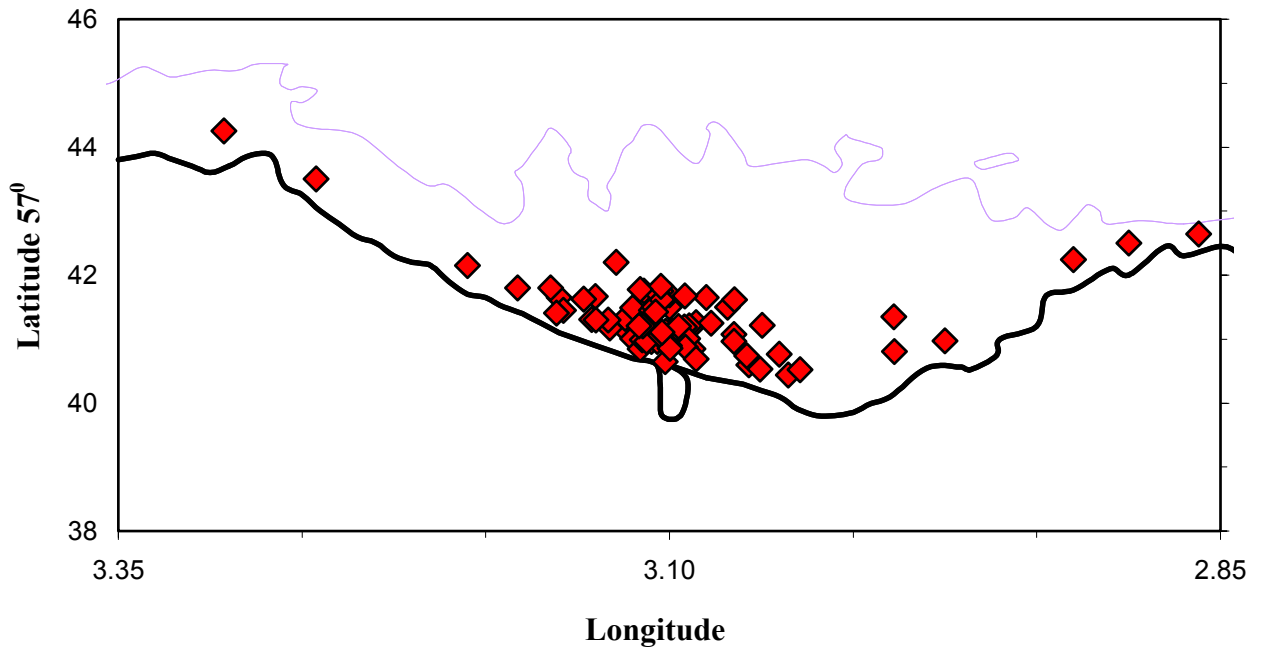


Figure 5.1. A distribution map showing the bottlenose dolphin encounters within Spey Bay between 1997 and 1998 during a pilot study carried out by the CRRU (n=80).

5.2. Site Fidelity and Abundance Estimates

The number of marked bottlenoses recorded in the study area showed considerable variation from one month to the next, with the month representative of the highest number of marked dolphins varying across every year. The number of marked dolphins also varied from year to year (varying from 35 to 49 individuals), although alternate years were very similar (i.e. 35 & 38 in 2002 & 2004, and 48 & 49 in 2001 & 2003). Analysis of individual encounter histories indicates that the composition of individuals present is more changeable in alternate years than in consecutive years (see Table 4.5). Hence the similarity in marked animals over alternative years is not attributed to the same individuals returning in alternate years. However, the inter-annual changes in the composition of individuals using the southern outer Moray Firth may be explained in terms of direct competition for resources in optimal areas. Bottlenose dolphins are known to coexist in a complex hierarchal structure in which subordinate animals may be forcefully reminded of their place (Wells *et al.*, 1987; Smolker *et al.*, 1992; Conner *et al.*, 1992). Interestingly, stratified movements of individuals between three key foraging grounds have been recorded in the inner Moray Firth (Wilson *et al.*, 1997; Hastie *et al.*, 2004). These movements were attributed to either area defence by individuals, or to social grouping of associates. Indeed, the patterns observed by Wilson *et al.*, implied that

not all individuals within the population had equal access to all parts of the inner Moray Firth. Therefore, it is highly likely that the same social factors will occur along the southern coastline of the outer Moray Firth, where the most probable key areas with these optimum resources are the two areas of highest relative abundance, Spey Bay and Banff Bay.

The number of captures of marked individuals ranged from 1 to 22. Further analysis of individual capture histories revealed that 9.2% of these marked individuals demonstrated a seasonal residence in the summer months over at least two consecutive years. These findings indicate that a significant number of particular individuals may use the outer Moray Firth almost exclusively across the summer months. Of these resident animals, approximately 50% were found to be of female gender. Interestingly, every one of these females was found to be with calf during her period of residency. In other words, 100% of resident females were identified with a calf, which strongly supports the earlier supposition that areas along the southern outer Moray Firth coastline must be important as nursery/calving grounds for the species. Furthermore, the 50:50 ratio of males and females also supports the other previous hypothesis that males will remain with groups of females, waiting for their opportunity to mate with females entering oestrus.

As not all animals considered residents are resident over the full study period, it seems highly likely that the aforementioned social factors play a prominent role in which individuals use the area. In the present study the changes in composition of individuals and residents inter annually can be termed as a 'substitution effect', whereby an individual that uses the area almost exclusively in one year may be 'substituted', or displaced by another individual in the subsequent year. As a result, the number of resident animals in any one year varied from 3 to 9. This may be an indication as to the quality and quantity of resources available to the animals, i.e. if the resources in one year can support 9 resident dolphins, the area would be expected to support 9 resident dolphins in the following year. However, the number of residents was not constant, and given the hierarchal structure of bottlenoses it is unlikely that animals would not use these areas if resources were plentiful. Therefore, resources such as prey, for example, may be significantly variable between years, and hence unstable and undependable to the dolphins. Alternatively, it may be disturbance factors such as trawlers or tourist boats, causing the animals to move to other, more desirable areas where these disturbance factors are reduced. Indeed, it could be a combination of these factors, and perhaps other underlying environmental factors such as temperature and salinity, for example; both of which have been related to changes in distribution and social structure of bottlenose dolphin populations (Lusseau *et al.*, 2004; Wilson, 1995).

In contrast, there are a high percentage of transient dolphins in the outer Moray Firth. These animals are presumed to enter the outer Firth occasionally, but are thought to primarily reside in the inner Firth, or along the Aberdeen coastline. However, it is possible that the number of residents calculated for each year is an underestimate, and that the number of transients could in-turn, be an overestimate. This thinking is based on the irregular intervals between dedicated surveys, which is a common problem in temperate areas such as the outer Moray Firth, where suitable weather windows for this work are at a premium, and already limit the number of surveys possible. However, it can be said with confidence that surveys were conducted during all possible windows during the study period; therefore, the results presented are the best possible representation of the data.

The application of mark-recapture models is relatively straightforward in regards to calculation of abundance estimates from photo-identification data. However, care should be taken to ensure that these estimates are indeed meaningful (Wilson, 1995). Therefore, false positive and false negative errors have to be minimised. Hence the importance of grading photographs and the application of computer-assisted photo-identification during the present study, giving the utmost confidence in the subsequent estimates calculated.

As a result, the best estimate of the number of animals using the southern outer Moray Firth was calculated from the 2003 dataset as 108 (95% CI = 99-117). This was the highest estimate of the four years. Interestingly, the estimates obtained are a reflection of the survey effort for each year, where the higher the survey effort, the higher the abundance estimate. This trend was not true of the 2004 dataset; however, the 2004 dataset is considered atypical. In addition, the coefficient of variation (CV) for the 2003 estimate may have been the higher of the four years (CV = 15.42), but it is comparable to the CV accepted by other population studies (Wilson, 1995 (CV = 15.1); Chilvers & Cockeron, 2003 (CV = 15); Read *et al.*, 2003 (CV = 13 & 15)), meaning that there is confidence in the precision of the estimate given in the present study. In contrast, however, the CV has been calculated to be significantly lower in other studies too (Williams *et al.*, 1993 (CV = 2.8-6.9); Scott *et al.*, 1990b (CV = 2); Shirakihara *et al.*, 2002 (CV = 5.41-8.2)). This variation in CV is most probably related to the low average capture probabilities in the present study (0.1-0.32 – see Tables 4.6 a-c). However, the comparison of the CV between different studies is likely to be problematic, as bottlenose dolphins, like most odontocetes, are highly sociable, making the associations among individuals non-random (Wells & Scott, 1990; Eisfeld, 2003). Therefore, as individuals are encountered on sampling occasions the probability of seeing other particular individuals may be increased or reduced. This non-independent probability of sighting

individuals should not affect the abundance estimates, but is likely to result in an underestimate of their variance (Wilson *et al.*, 1999). The extent of this effect will vary depending on the type of social structure and fluidity of associations within a population, as well as the proportion of animals in the population that are captured at each sampling event. This presents a complex problem, which has yet to be adequately addressed for capture-recapture estimates of populations of social cetaceans (Wilson *et al.*, 1999).

Regardless, the estimate of 108 (95% CI = 99-117) animals is undoubtedly a significant percentage of the estimated 129 (95% CI = 110-174) animals in the entire population as estimated by Wilson *et al.*, (1999). Note that the estimate in the present study is an estimate of the abundance of bottlenoses using the southern outer Moray Firth, and is by no means an absolute estimate of the population size of bottlenoses in the north east of Scotland. Interestingly, these findings support the previous supposition that not all individuals may have equal access to all areas within the population's home range. Indeed, if this were not the case, one may expect the estimates to be extremely similar. Therefore, the access the animals have to areas within their home range may be limited, such that individuals may, for example, be seen almost exclusively in the outer Moray Firth. Indeed, two recent studies of this population have shown this to be the case (Wilson *et al.*, 2004; Durban *et al.*, in press). Firstly, Wilson *et al.*, (2004) described a gradual movement of individuals out of the inner Moray Firth over an 11 year study period, however, these individuals were not necessarily leaving altogether, but the distance in which they travelled into the inner Firth notably decreased over time. Essentially, the home range of these animals appears to have extended over the study period, which would go on to give good reason as to why the community using the outer Moray Firth is changeable inter-annually, and also give further support to the 'substitution effect'. Furthermore, Durban *et al.*, (in press) conducted photo-identification studies from three areas within the home range of the bottlenoses; these were the inner Moray Firth, Spey Bay in the outer Firth, and just off St. Andrews. In all of these areas several identifiable individuals were only seen at that particular site. Hence, individual bottlenoses displayed sole site fidelity to all three of these areas.

5.3. Conservation & the candidate Special Area of Conservation

Although recent evidence suggests that, over the last decade, the home range of the bottlenoses has stretched further south (Wilson *et al.*, 2004), it appears, however, that the importance of the different areas within the outer Moray Firth (present study) and inner Moray Firth have remained relatively stable (Hastie *et al.*, 2003c). Nevertheless, the home range has extended, and this has to be the result of one, or perhaps several underlying factors.

The most apparent of these would be an influx of individuals from other populations, an increase in population growth, changes in predation pressures or changes in prey abundance. Since there is no evidence of individuals entering the population (Wilson *et al.*, 1999; Parsons *et al.*, 2002), or any increase in population growth (Wilson *et al.*, 1999; Sanders-Reed *et al.*, 1999), or any changes in predation pressures (Wilson, 1995), it seems most likely, therefore, that changes in prey resources is the major contributing factor. If this hypothesis is correct, then the importance of Spey Bay and Banff Bay to this population is highly significant. In addition, the use and importance of the entire outer Moray Firth as a foraging ground is also apparent from observations of foraging and feeding activities during encounters with bottlenoses travelling. Although this may suggest that the area is a ‘corridor,’ whereby the dolphins are travelling between areas thought to be more desirable, such as the inner Moray Firth and St. Andrews bay, the present study has shown that this is not the case.

The management initiatives that are in place to protect this population were based on information collected in the 1980s and early 1990’s which, at the time, the inner Moray Firth was considered to be a large proportion of the population’s home range. More than 10 years on, as the management scheme is actually being implemented; the cSAC now covers a relatively small section of the population’s known range. Arguably, when protecting a specific population, the optimal protected area should cover that population’s year-round distribution (Hooker & Gerber, 2004). However, where this is not possible (as so often is the case), it can be further argued that an individual is at worst, protected for a proportion of its life span, even if only a relative section of its home range were protected (Hooker & Gerber, 2004). However, this argument is not feasible for this population of bottlenoses, given the heterogeneity of individual ranging behaviour (present study; Wilson *et al.*, 2004; Durban *et al.*, in press). Therefore, the results from the present study, and from previous studies, have shown that the cSAC will give a differing level of protection to individuals. This is a considerable cause for concern, as giving protection to only a limited part of such a small population may have serious repercussions; as such management measures are unlikely to allow the population to increase at the same rate as might be expected of a more fecund species. Therefore, the current management proposals are deemed inadequate to the point unto which they are not fulfilling the key conservation objective of the cSAC, which is the “establishment and maintenance of a viable population of bottlenose dolphins within the Firth”. In order to give adequate protection to the population, the cSAC would have to be extended, and from the present study it is clear that the outer Moray Firth is an area which encompasses both physical and biological factors essential to life and reproduction, indeed, if

the majority of the animals do travel further south during the winter then surely those areas must also encompass physical or biological factors essential to life and reproduction. Therefore, a different approach to the conservation and management initiatives in place should be considered in order to afford much needed additional protection to this vulnerable population of bottlenose dolphins.

6. Summary & Conclusions

The present study has shown that the outer Moray Firth, in general, is an area of significant importance to this population of bottlenoses dolphins. The bottlenoses were shown to use the entire coastline, and were always encountered in waters no deeper than 25 metres. There were two similar areas (Spey Bay and Banff Bay) where a high relative abundance of dolphins occurred throughout the study period. The abundance estimate of animals using the outer Moray Firth was 108 (95% CI = 99-117), which is a considerable proportion of the 129 animals estimated for the entire population (Wilson *et al.*, 1999). There is variability in the composition and number of animals defined as residents between years, nevertheless, individuals do display high levels of site fidelity, as 9.2% of the total number of marked animals were regarded as resident in at least one year.

More specifically, the high percentage of groups with calves, the high number of neonates first sighted between July and September, and 100% of the female residents having calves, all indicates the importance of the outer Moray Firth as a nursery/calving ground. The preferential use of Spey Bay as a nursery/calving ground is most likely, given the lower levels of boat traffic that occur in the bay due to its shallower depth. Furthermore, both Spey Bay and Banff Bay are used by spawning salmon, making these areas in particular, prime feeding grounds.

Notably, the management scheme in place at present does not have to cover the entire home range of the population, however, it does have to encompass the “physical or biological factors essential to life and reproduction” (MFP, 2001). The present study has shown that the outer Moray Firth is, without a doubt, an area in which the bottlenoses use as feeding grounds and nursery/calving grounds. Furthermore, the present study found that there is heterogeneity of individuals ranging behaviour, hence the cSAC will give individuals a varying level of protection. Consequently, the protection of a limited part of this already small population’s home range may have serious repercussions; as such management measures are unlikely to allow the population to increase at the same rate as might be expected of a more fecund species. Therefore, it is suggested that a different approach to conservation initiatives should be considered, and as the home range appears to be expanding, it is becoming apparent that the area covered by the cSAC must expand with it in order to adequately protect this already vulnerable population.

There is much known about cetacean species in the inner Moray Firth, with the initial studies on bottlenoses now over a decade old (Hammond & Thompson, 1991), and with the number of cetacean studies in the outer Moray Firth growing (Eisfeld, 2003; Whaley, 2004; Tetley, 2004), so is our understanding of these complex communities. However, it is evident that greater collaboration between researchers, both in the Moray Firth and elsewhere, is required in order to maximise the outcome of fieldwork addressing fundamental questions about the Moray Firth population. The most beneficial collaboration would come from the merging of photo-identification catalogues. Arguably, this is a lengthy process, with several questions raised about possible false negative and false positive errors that may already be present in the existing catalogues. However, the use of computer-assisted photo-identification has been shown in the present study to reduce these error types. Therefore, the application of such programs to existing catalogues previous to merging, and during merging would greatly reduce the potential for errors. As mentioned earlier, this would be a lengthy process, but the information gained on an individual's presence or absence from an area, which potentially encompasses the majority of its home range, would be invaluable in further understanding the use of these areas by individuals. Indeed, the information gained would not only be on distribution of individuals, but it would also encompass behavioural observations and associations with other animals, thus giving researchers the potential to understand further, the complex social ecology of these animals across their entire home range.

This study has broadened the range of environmental conditions in which the bottlenose has been studied; therefore, the findings presented here serve to further our understanding of the factors influencing distribution patterns and habitat use of this and other small, coastal cetacean populations in temperate, open ocean environments. Furthermore, monitoring the use of particular habitats that are of known importance to bottlenose dolphins, and other cetacean communities, is essential for the successful management and conservation of a species. It is clear that marine protected areas (MPAs) are important to small, coastal cetacean communities, but their successful implementation requires careful consideration regarding the underlying uses of the habitat by these communities. In conclusion, the findings of the present study can be applied to improve the current management scheme for this, and other small, coastal cetacean communities in other regions.

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Appendix 1. A systematic list of the cetacean species recorded in northeast Scottish waters and their occurrence (adapted from Evans, 1996).

Common Name	Scientific Name	Status
Harbour porpoise	<i>Phocoena phocoena</i>	Common
White-beaked dolphin	<i>Lagenorhynchus albirostris</i>	Common
Risso's dolphin	<i>Grampus griseus</i>	Common
Common dolphin	<i>Delphinus delphis</i>	Common
Bottlenose dolphin	<i>Tursiops truncatus</i>	Common
Killer whale	<i>Orcinus orca</i>	Common
Long-finned pilot whale	<i>Globicephala melas</i>	Common
Atlantic white-sided dolphin	<i>Lagenorhynchus acutus</i>	Common
Striped dolphin	<i>Stenella coeruleoalba</i>	Uncommon
Northern bottlenose whale	<i>Hyperoodon ampullatus</i>	Uncommon
Sperm whale	<i>Physeter macrocephalus</i>	Uncommon
Cuvier's beaked whale	<i>Ziphius cavirostris</i>	Uncommon
Soweby's beaked whale	<i>Mesoplodon bidens</i>	Rare
False killer whale	<i>Pseudorca crassidens</i>	Rare
Narwhal	<i>Monodon monoceros</i>	Rare
Beluga	<i>Delphiapterus lecuas</i>	Rare
Minke whale	<i>Balaenoptera acutorostrata</i>	Common
Sei whale	<i>Balaenoptera borealis</i>	Uncommon
Fin whale	<i>Balaenoptera physalus</i>	Uncommon
Blue whale	<i>Balaenoptera musculus</i>	Rare
Humpback whale	<i>Megaptera novaeangliae</i>	Rare
Northern right whale	<i>Eubalaena glacialis</i>	Very Rare

a) Appendix 2. Showing examples of the *Trip* and *Encounter* log sheets (a & b respectively) used in the present study during boat surveys. The tables were laminated as A4 sheets for use at sea, with information being recorded using waterproof china graph pens.

a)

CETACEAN RESEARCH AND RESCUE UNIT




DATE: (DD/MM/YY)	16/10/04	OBSERVERS: (PLEASE CIRCLE)	(KR) ND (ADD OTHERS):	RC, MT, CM, CP, EG
START TIME: (HH:MM 24 hrs)	15:30	END TIME: (HH:MM 24 hrs)	17:50	SURVEY: (PART) / FULL
DEPART FROM:	WHITEHILLS	SEA STATE:	0 ① 2 3 4	(CIRCLE AS APPROPRIATE: 0-Calm, 1-Ripples, 2-Slight wavelets, 3-Larger waves, 4-Choppy, many white caps)
GPS - DEPARTURE: (N 00° 00' 00" W 00° 00' 00")	N 57 41 230 W 2 34 527			

ACTUAL ROUTE COVERED:
(WHITEHILLS-CROVIE-PENNAN ETC.) WHITEHILLS → GARDENSTOWN → WHITEHILLS

ADDITIONAL INFORMATION / REMINDER:

b)

CETACEAN RESEARCH AND RESCUE UNIT - Encounter Form v4.0



ENCOUNTER NO. (e.g. #1, #2 etc.)	1	DATE: (DD/MM/YY)	16/10/04	OBSERVERS:	(KR) ND KD RC MT CM CP EG
TIME START: (HH:MM 24 hrs)	GPS START: (N 00° 00' 00" W 000° 00' 00")	TIME END: (HH:MM 24 hrs)	GPS END: (N 00° 00' 00" W 000° 00' 00")		
15:45	N 57 40 673 W 2 31 420	17:10	N 57 40 825 W 2 20 471		
GENERAL AREA at START: (e.g. Buckie harbour)		BANFF		G. AREA at END: GARDENSTOWN	
LANDMARK (e.g. 100m NW of harbour entrance)		LEVEL WITH ESSO GARAGE 2 500M		L.MARK at END: GAMRIE BAY, BY CROVIE	
INDIVIDUALS PRESENT			PHOTO I.D.		
Structure of subgroups: (e.g. 3A (1C) + 6A + 2A)	N/A		Film Nos. (e.g. KR61 & ND3 etc)	KR07 / KR08 KR09	
Total:	12				
Activity (PLEASE TICK)					
<input checked="" type="checkbox"/> FORAGING <input checked="" type="checkbox"/> TRANSITING <input type="checkbox"/> AGGRESSION <input type="checkbox"/> MILLING <input checked="" type="checkbox"/> HALF BREACHING <input checked="" type="checkbox"/> SYNCHRONISED BREACHING <input checked="" type="checkbox"/> FEEDING <input type="checkbox"/> TAIL SLAPS <input type="checkbox"/> SPY HOPS <input checked="" type="checkbox"/> BOW RIDING <input checked="" type="checkbox"/> FULL BREACHING <input type="checkbox"/> PORPOISING <input checked="" type="checkbox"/> OTHER (PLEASE SPECIFY) OR COMMENTS					
FISH THROWING					

Appendix 3. An example of a *Film Sheet* used during an encounter to assist in the subsequent organisation and identification of photographs taken. A = Adult, SA = Subadult, C = Calf, RD = Right Dorsal, etc.

FILM SHEET FOR BOAT TRIPS



Film type : (eg ISO 800, 400)	400	Exposure No: 24	36
Code: (eg KR ??/03)	KR07/04	16/10/04	

Insert date and time of trip at appropriate frame number

Frame No.	Frame No.
1. Miss	19. Miss
2. Miss	20. # 66 LD
3. # 67 RD & C	21. Jump
4. "	22. # 35 RD
5. C	23. # 35 RD
6. Jump	24. " & C
7. C	25. Miss
8. Miss	26. SA (2) RD
9. "	27. A (2) ? LD
10. A (1) RD	28. "
11. Miss	29. Miss
12. "	30. "
13. # 69 ? RD	31. "
14. Jump	32. "
15. # 69 RD	33. A (3) RD
16. SA (1) RD	34. Jump
17. # 66 LD	35. A (3) RD
18. # 66 LD	36. A (4) LD

Appendix 4. An example of a *Bottlenose Dolphin Survey Sheet* onto which the general data from each trip and encounter (where applicable) was recorded from the respective *Trip & Encounter* logs (shown in Appendix 2) at the end of each survey day.

Cetacean Research & Rescue Unit Bottlenose Dolphin Survey Form



Trip info	DATE: 16/10/04	OBS 1: LEVIN ROBINSON
	VESSEL: KETOO	OBS 2: ROSS CULLOCH
	START TIME: 15:30	OBS 3: MIKE TETLEY
	END TIME: 17:50	OBS 4: CAMERON MCPHERSON
	AREAS COVERED: W/HILLS →	OBS 5: CAROLINE PASSINGHAM
	G/TOWN → W/HILLS	OBS 6: ELAINE GALSTON

ENC # 1. ENCOUNTER START 15:45 (24 hrs) ENCOUNTER END: 17:10 (24 hrs)

GPS START: N 57 40 673 GPS END: N 57 40 825
W 2 31 420 W 2 20 471

AREA START: BANFF AREA END: GARDENSTOWN
e.g. Cullen Bay

LANDMARK START: LEVEL WITH THE ESKO CAIRN (2500m) e.g. 100m East of Bow Fiddle Rock

LANDMARK END: CAMBIE BAY, BOW CAIRN

MAX NO DOLPHINS: 12 [NO. SUBADULTS: 2 TOTAL CALVES: 2 NO. NEONATES: 0]

NO. SUBGROUPS: N/A SUB-GROUP STRUCTURE (e.g. 3 + 2 + 3 + 5): N/A

ACTIVITY:

☒ FORAGING ☒ FEEDING ☒ TRANSITING ☐ MILLING
☒ FULL BREACHING ☐ SPY HOPS ☐ TAIL SLAPS ☐ PORPOISING
☒ HALF BREACHING ☒ BOW RIDING ☐ AGGRESSIVE BEHAVIOUR
☒ SYNCHRONISED BREACHING ☒ OTHER FISH THROWING

NOTES / SUMMARY:

THE GROUP WAS V. DISPERSED, MAKING JUDGEMENT OF SUB-GROUPS V. HARD. THE CALVES SPENT MOST OF THE ENCOUNTER ON THE BOW OF THE BOAT. THE 2 SA'S WERE SEEN THROWING FISH AT ONE POINT.

ENVIRONMENTAL INFORMATION:


WEATHER: ☒ SUNNY ☐ CLOUDY BUT BRIGHT ☐ OVERCAST ☐ RAIN ☐ FOG
☐ OTHER

SEA STATE (Beaufort scale e.g. 1-2): 1 TIDAL STATE (e.g. HWS, LWN):


PHOTO ID: YES NO FILM Nos: K207/08/09 FRAMES: 1-36/1-36/1-8

KNOWN INDIVIDUALS PRESENT: 67, 328, 69, 35, 345, 66

Appendix 5. Showing the *Encounter Grid* used in the present analysis. The grid is simply used to separate individual dolphins photographed during each encounter. This process is assisted using the respective *Film Sheet(s)*, as detailed in Appendix 3, and the summary information recorded on the *Bottlenose Dolphin Survey Sheet* shown in Appendix 4.

		<u>Encounter Grid</u>					
		Enc #: 1.....		Date: 16/10/04			
		No. dolphins: 12... Calves: 2.....		Time: 15:45			
R D		67	328	☺	69	*	66
		<u>KR07</u> 3, 4 <u>KR08</u> 8, 9	<u>KR08</u> 32, 34	<u>KR07</u> 10	<u>KR07</u> 13, 15 <u>KR08</u> 21	<u>KR07</u> 16	<u>KR08</u> 35, 36
L D			<u>KR07</u> 5, 7 <u>KR09</u> 4	<u>KR08</u> 3, 6, 24		<u>KR08</u> 11, 12 <u>KR09</u> 1, 2	<u>KR07</u> 17, 18, 20 <u>KR08</u> 20, 22 29
R D		35	344	△	□	+	▽
		<u>KR07</u> 22, 23 <u>KR09</u> 8	<u>KR07</u> 24	<u>KR07</u> 26 <u>KR08</u> 17	<u>KR09</u> 6, 7	<u>KR07</u> 33, 35	<u>KR08</u> 15, 16, 30
L D			<u>KR08</u> 27, 28		<u>KR07</u> 27, 28 <u>KR08</u> 7, 26		<u>KR07</u> 36

Appendix 6. A completed *Summary Encounter Sheet* for a group of 12 bottlenose dolphins. Note the mother-calf pairs identified, depicted by brackets.



Summary Encounter Sheet

DATE: 16/10/04 ENC #: 1

START TIME: 15:45 END TIME: 17:10

GROUP STRUCTURE:

NUMBERS:

AGE: (AD, SUB-A, CALF)					
	(A C)	(A C)	A	A	A
ID:	(67 328)	(35 344)	66	69	89

NUMBERS:

AGE: (AD, SUB-A, CALF)				
	SA	SA	A	103
ID:	290	322	48	85

NUMBERS:

AGE: (AD, SUB-A, CALF)	
ID:	

SUBBROUPS: ✓

SUBGROUP STRUCTURE:
e.g. {3 + 5 + 2} N/A

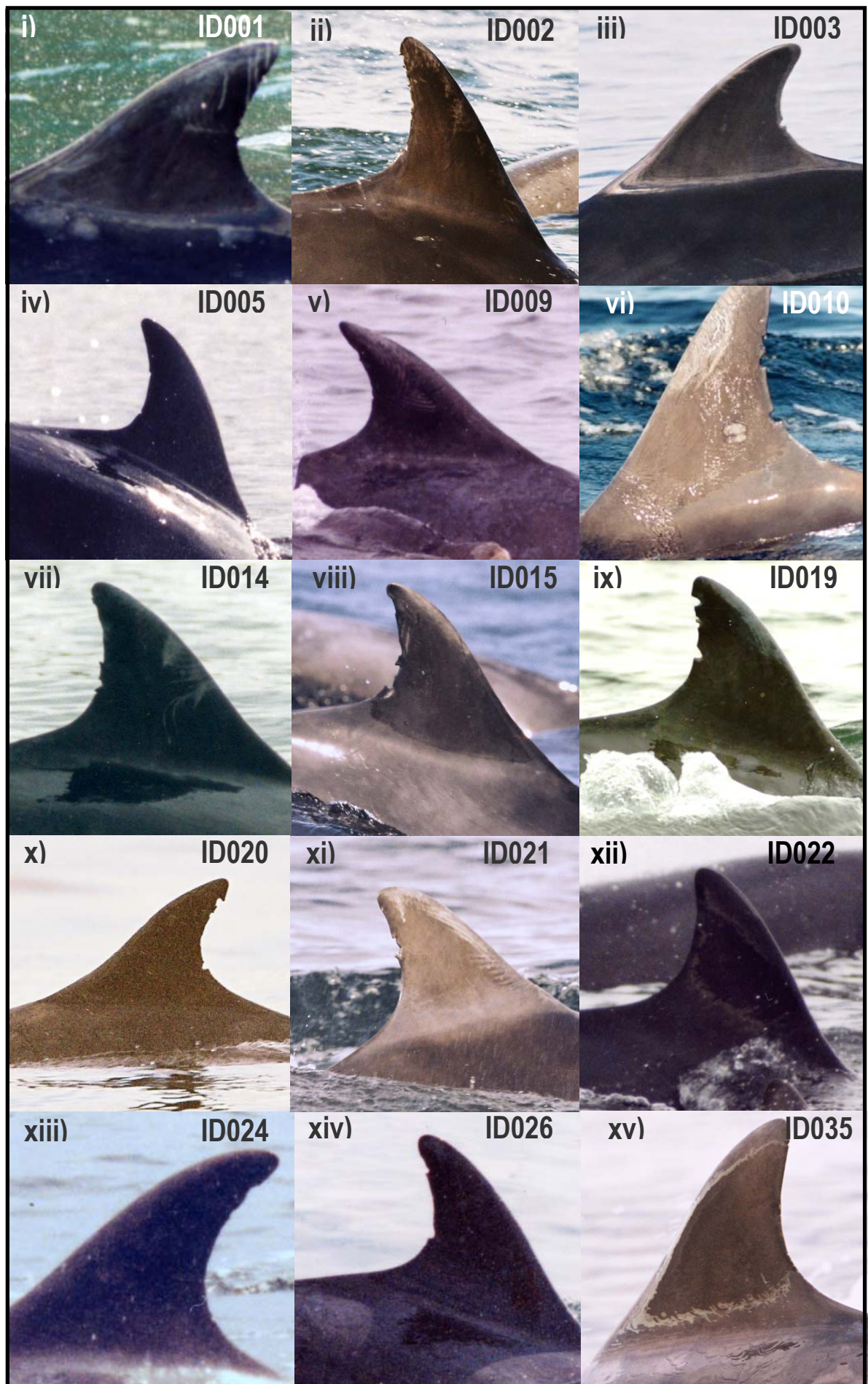
WHOLE GROUP (Y/N): Y

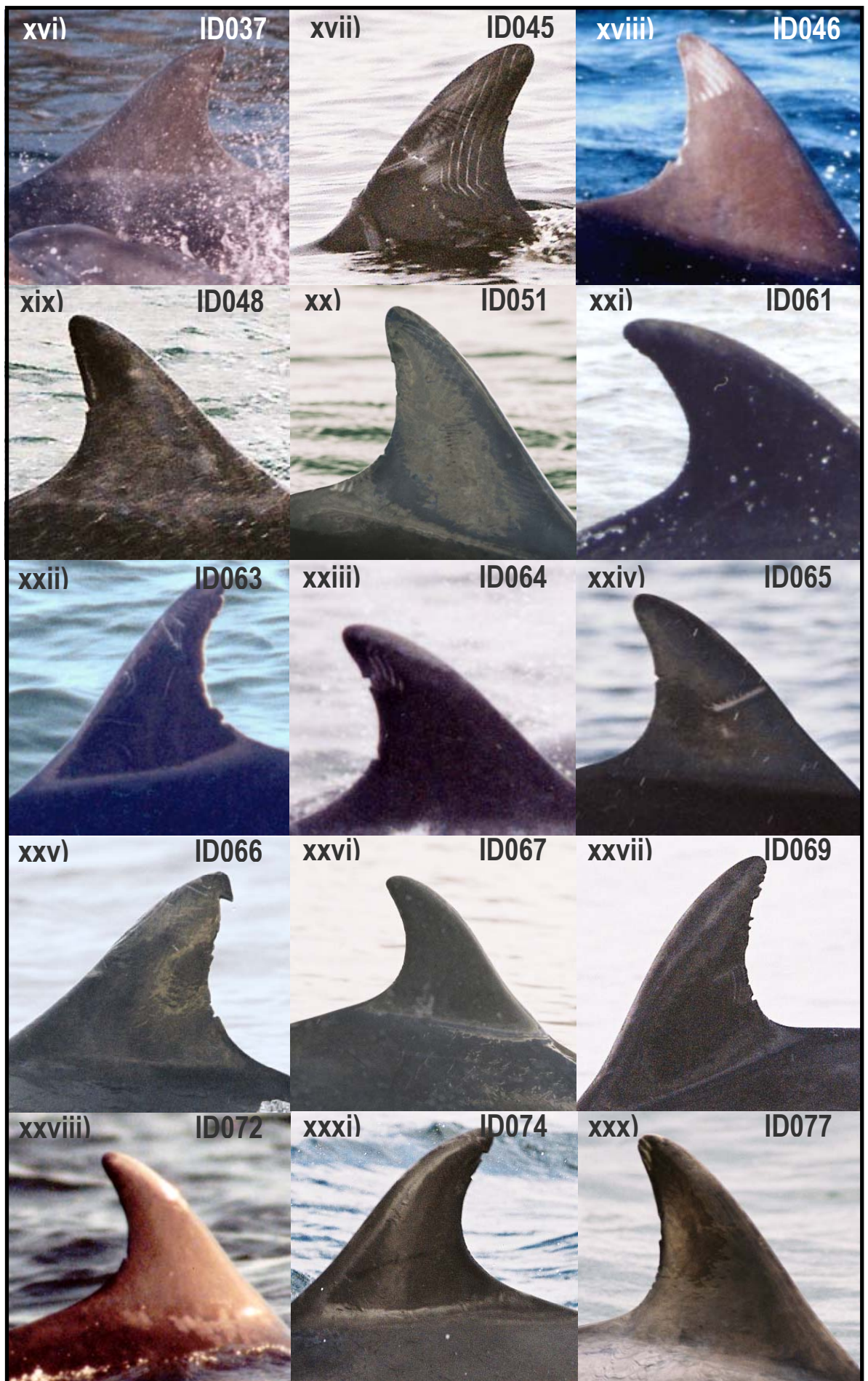
TOTAL NO. WITH DEM'S: 9

GENERAL: 12 animals, including 2 older calves.

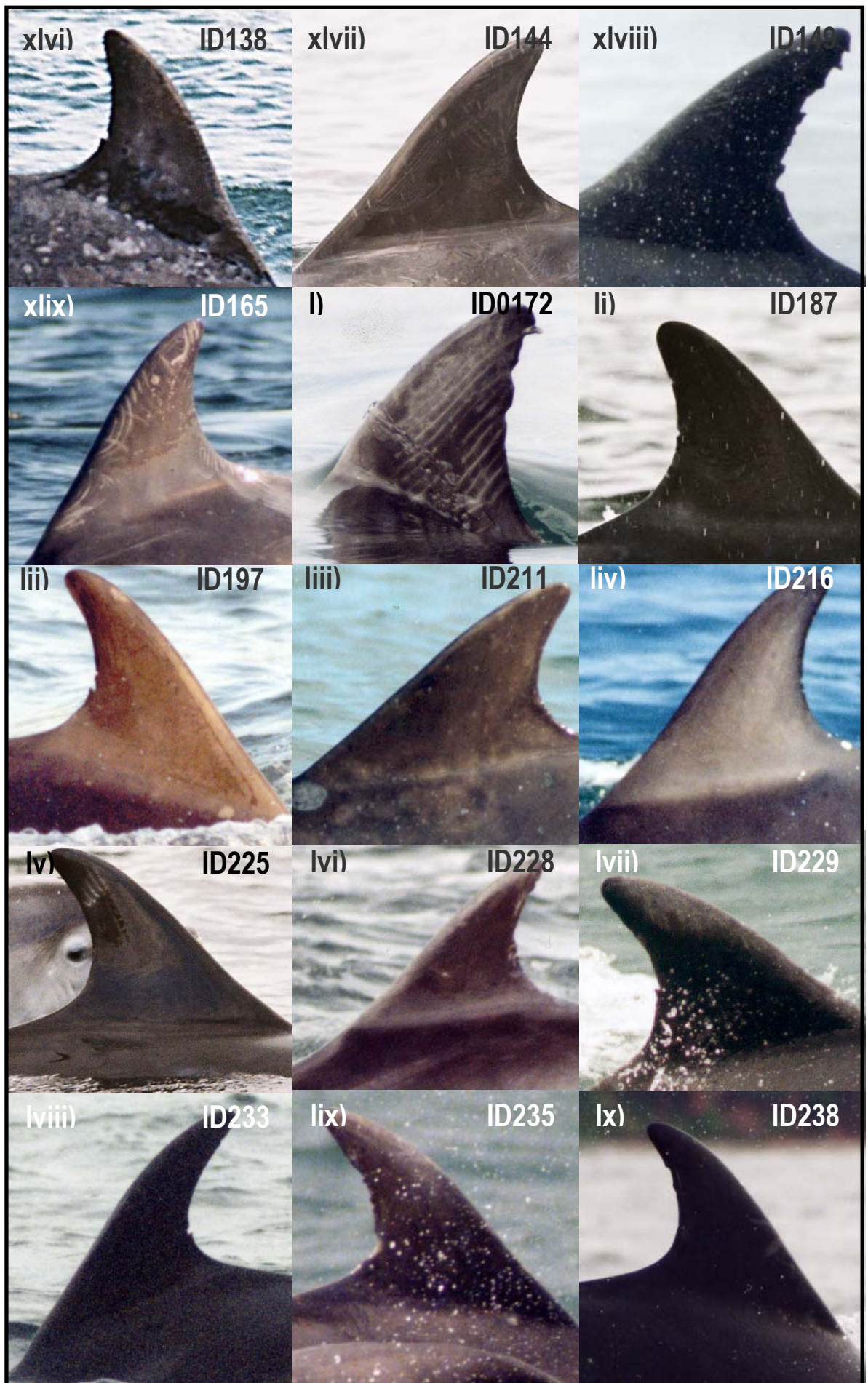
☒ Info entered into "Sightings" database?

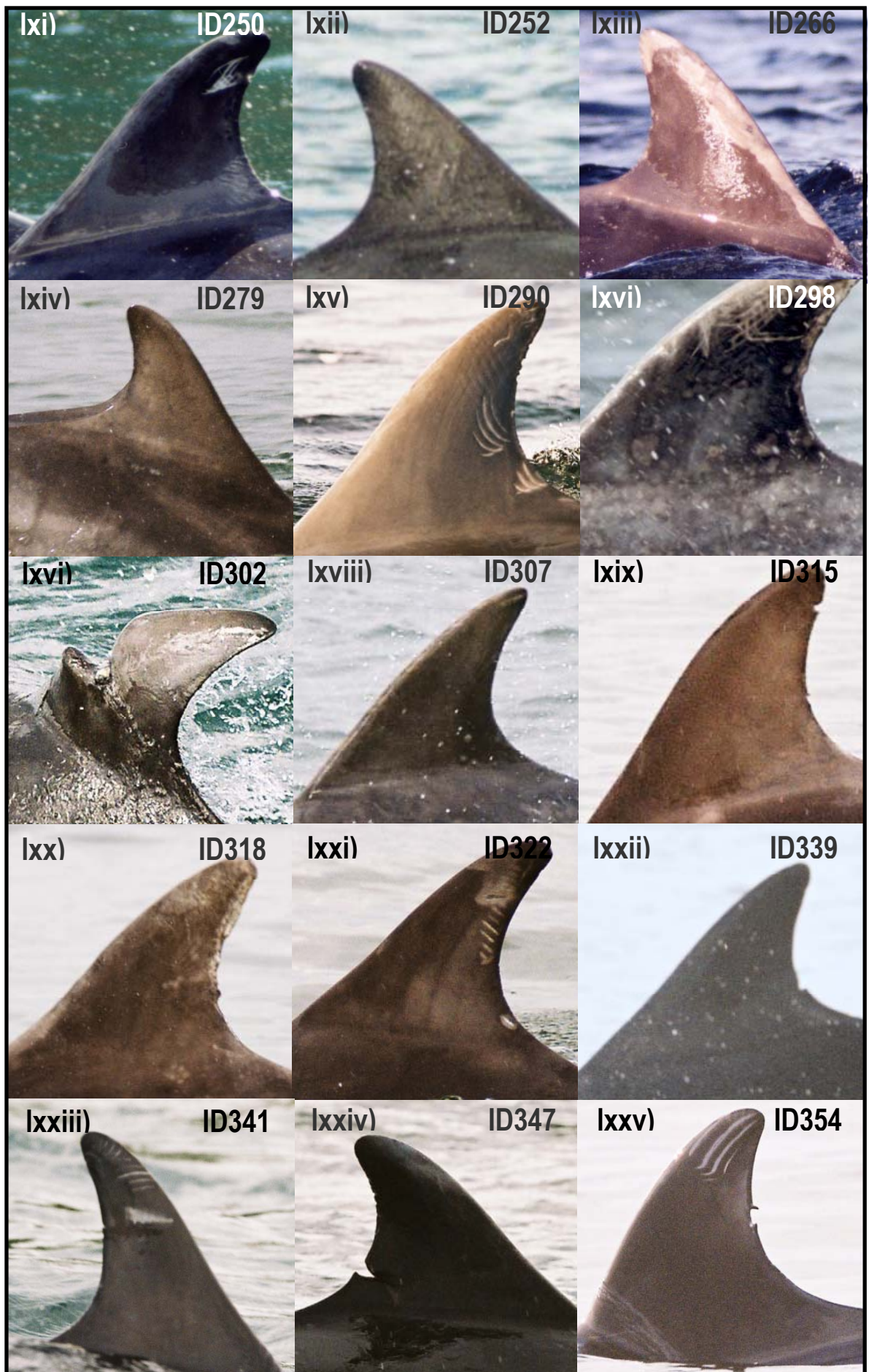
Appendix 7. The following pages show the “marked” individual dolphins used in the present study for the estimation of population size (n=76).











lxxvi)

ID362



Appendix 8. Table showing encounter histories for the 7 resident dolphins encountered during 3 or more of the 5 months (May to September inclusive) for at least two consecutive years of the study period, 2001 to 2004 inclusive.

	10	66	74	77	197	216	225
21/05/2001							
25/05/2001							
06/06/2001							
10/06/2001							
12/06/2001							
23/06/2001							
02/07/2001							
10/07/2001							
14/07/2001							
17/07/2001							
23/07/2001							
01/08/2001							
07/08/2001							
10/08/2001							
17/08/2001							
29/08/2001							
12/09/2001							
22/09/2001							
21/05/2002							
31/05/2002							
04/06/2002							
07/06/2002							
22/06/2002							
24/06/2002							
24/06/2002							
01/07/2002							
17/07/2002							
09/08/2002							
13/08/2002							
13/08/2002							
26/08/2002							
27/09/2002							
03/10/2002							
22/05/2003							
26/05/2003							
27/05/2003							
30/05/2003							
04/06/2003							
06/06/2003							
06/06/2003							
21/06/2003							
26/06/2003							
08/07/2003							
15/07/2003							
22/07/2003							
25/07/2003							
25/07/2003							
04/08/2003							
04/08/2003							
18/08/2003							
24/09/2003							
26/05/2004							
12/06/2004							
29/06/2004							
01/07/2004							
07/07/2004							
01/09/2004							
02/09/2004							
05/09/2004							
07/09/2004							

Appendix 9. The results obtained from the Chao (M_{th}) models for population sizes, using CAPTURE run through MARK v4.1, for the years 2001 to 2004, respectively.

(a) 2001

Input---title='BND'
 Input---task read captures x matrix occasions=18 captures=18
 Input---data='Group 1'
 Input---format='(a6,18f1.0)'
 Input---read input data

Summary of captures read
 Number of trapping occasions 18
 Number of animals captured 50
 Maximum x grid coordinate 1.0
 Maximum y grid coordinate 1.0

Input---task population estimate mth-chao
 Population estimate under time variation and individual heterogeneity in capture probabilities.
 See model M(th) of Chao et al. (1992).

Group 1
 Number of trapping occasions was 18
 Number of animals captured, M(t+1), was 50
 Total number of captures, n., was 134

Frequencies of capture, f(i)
 i=1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
 f(i)= 14 14 6 12 0 2 2 0 0 0 0 0 0 0 0 0 0 0

Estimator	Gamma	N-hat	se(N-hat)
1	0.1898	58.80	4.95
2	0.1737	57.76	4.70
3	0.1750	57.84	4.72

p-hat(j) = 0.12 0.00 0.22 0.12 0.02 0.21 0.16 0.12 0.10 0.10 0.10 0.33 0.26 0.19 0.03 0.14 0.03 0.05
 Bias-corrected population estimate is 58 with standard error 4.7184
 Approximate 95 percent confidence interval 53 to 73

(b) 2002

Input---title='BND'
 Input---task read captures x matrix occasions=15 captures=15
 Input---data='Group 1'
 Input---format='(a6,15f1.0)'
 Input---read input data

Summary of captures read
 Number of trapping occasions 15
 Number of animals captured 37
 Maximum x grid coordinate 1.0
 Maximum y grid coordinate 1.0

Population estimate under time variation and individual heterogeneity in capture probabilities.
 See model M(th) of Chao et al. (1992).

Group 1

Number of trapping occasions was 15

Number of animals captured, $M(t+1)$, was 37

Total number of captures, n ., was 76

Frequencies of capture, $f(i)$

$i = 1 \ 2 \ 3 \ 4 \ 5 \ 6 \ 7 \ 8 \ 9 \ 10 \ 11 \ 12 \ 13 \ 14 \ 15$

$f(i) = 15 \ 9 \ 10 \ 2 \ 1 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0$

Estimator	Gamma	N-hat	se(N-hat)

1	0.0647	47.31	6.05
2	0.0428	45.93	5.70
3	0.0483	46.28	5.79

$p\text{-hat}(j) = 0.13 \ 0.11 \ 0.07 \ 0.17 \ 0.13 \ 0.02 \ 0.09 \ 0.13 \ 0.07 \ 0.04 \ 0.13 \ 0.02 \ 0.13 \ 0.17 \ 0.24$

Bias-corrected population estimate is 46 with standard error 5.7909

Approximate 95 percent confidence interval 41 to 65

(c) 2003

Input---title='BND'

Input---task read captures x matrix occasions=18 captures=18

Input---data='Group 1'

Input---format='(a6,18f1.0)'

Input---read input data

Summary of captures read

Number of trapping occasions 18

Number of animals captured 48

Maximum x grid coordinate 1.0

Maximum y grid coordinate 1.0

Input---task population estimate mth-chao

Population estimate under time variation and individual heterogeneity in capture probabilities.

See model $M(th)$ of Chao et al. (1992).

Group 1

Number of trapping occasions was 18

Number of animals captured, $M(t+1)$, was 48

Total number of captures, n ., was 125

Frequencies of capture, $f(i)$

$i = 1 \ 2 \ 3 \ 4 \ 5 \ 6 \ 7 \ 8 \ 9 \ 10 \ 11 \ 12 \ 13 \ 14 \ 15 \ 16 \ 17 \ 18$

$f(i) = 20 \ 14 \ 4 \ 2 \ 1 \ 1 \ 2 \ 4 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0$

Estimator	Gamma	N-hat	se(N-hat)

1	0.7379	74.71	11.70
2	0.7111	72.93	11.24
3	0.7125	73.02	11.26

$p\text{-hat}(j) = 0.19 \ 0.01 \ 0.04 \ 0.14 \ 0.15 \ 0.03 \ 0.03 \ 0.08 \ 0.16 \ 0.25 \ 0.22 \ 0.07 \ 0.03 \ 0.10 \ 0.10 \ 0.05 \ 0.05 \ 0.01$

Bias-corrected population estimate is 73 with standard error 1.2590

Approximate 95 percent confidence interval 59 to 106

(d) 2004

Program version of 16 May 1995 11-Oct-2004
Input and Errors Listing
Input---title='BND'
Input---task read captures x matrix occasions=9 captures=9
Input---data='Group 1'
Input---format='(a6,9f1.0)'
Input---read input data

Summary of captures read
Number of trapping occasions 9
Number of animals captured 36
Maximum x grid coordinate 1.0
Maximum y grid coordinate 1.0

Input---task population estimate mth-chao
Population estimate under time variation and
individual heterogeneity in capture probabilities.
See model M(th) of Chao et al. (1992).

Group 1
Number of trapping occasions was 9
Number of animals captured, M(t+1), was 36
Total number of captures, n., was 105

Frequencies of capture, f(i)
i= 1 2 3 4 5 6 7 8 9
f(i)= 11 4 6 9 4 2 0 0 0

Estimator	Gamma	N-hat	se(N-hat)
1	0.2337	43.08	4.48
2	0.2207	42.47	4.32
3	0.2290	42.86	4.42

p-hat(j) = 0.16 0.14 0.16 0.16 0.16 0.40 0.40 0.49 0.37
Bias-corrected population estimate is 43 with standard error 4.4207
Approximate 95 percent confidence interval 39 to 57

Appendix 10. Statistical Analysis

i) Analysis of Survey Effort

Kruskal-Wallis Test: Survey Effort versus Month

Month	N	Median	Ave Rank	Z
May	24	9.000	46.9	-2.14
Jun	24	8.500	51.6	-1.40
Jul	24	23.000	96.8	5.71
Aug	24	11.000	62.1	0.25
Sep	24	9.500	45.1	-2.42
Overall	120		60.5	

H = 36.05 DF = 4 P = 0.000

H = 36.14 DF = 4 P = 0.000 (adjusted for ties)

Kruskal-Wallis Test: Survey Effort versus Year

Year	N	Median	Ave Rank	Z
2001	24	16.00	42.6	-1.20
2002	24	17.50	54.3	1.18
2003	24	17.00	52.1	0.73
2004	24	15.00	45.0	-0.71
Overall	96		48.5	

H = 2.90 DF = 3 P = 0.407

H = 2.91 DF = 3 P = 0.406 (adjusted for ties)

ii) Relative Abundance Estimates

One-way ANOVA: Relative Abundance versus Month

Analysis of Variance for Response

Source	DF	SS	MS	F	P
Month	4	29.42	7.36	1.10	0.371
Error	35	233.66	6.68		
Total	39	263.09			

				Individual 95% CIs For Mean Based on Pooled StDev	
Level	N	Mean	StDev	-----+-----+-----+-----+	
1	8	0.907	1.119	(-----*-----)	
2	8	1.045	1.069	(-----*-----)	
3	8	3.089	4.715	(-----*-----)	
4	8	2.270	2.237	(-----*-----)	
5	8	1.092	1.938	(-----*-----)	
Pooled StDev = 2.584				-----+-----+-----+-----+	
				0.0	1.6 3.2 4.8

One-way ANOVA: Relative Abundance versus Sub-Area

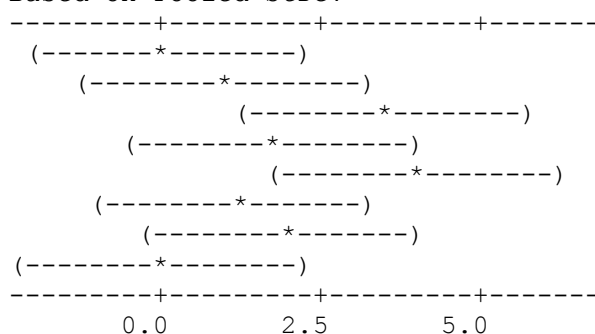
Analysis of Variance for Response				
Source	DF	SS	MS	F
Sub- Area	7	75.96	10.85	1.86
Error	32	187.13	5.85	
Total	39	263.09		

P 0.110

Sub-Area	N	Mean	StDev
1	5	0.092	0.206
2	5	0.952	1.186
3	5	3.542	5.579
4	5	1.776	1.252
5	5	4.034	2.152
6	5	1.170	2.002
7	5	1.880	1.999
8	5	0.000	0.000

Pooled StDev = 2.418

Individual 95% CIs For Mean
Based on Pooled StDev



One-way ANOVA: Relative Abundance versus Year

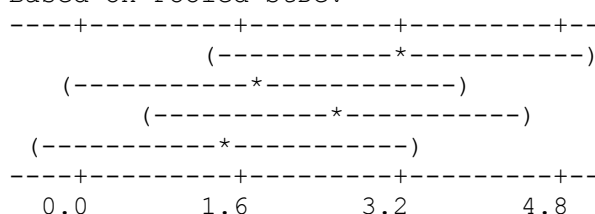
Analysis of Variance for Relative				
Source	DF	SS	MS	F
Year	3	14.80	4.93	0.68
Error	28	203.05	7.25	
Total	31	217.85		

P 0.572

Year	N	Mean	StDev
1	8	3.205	2.718
2	8	1.811	2.684
3	8	2.594	2.893
4	8	1.458	2.460

Pooled StDev = 2.693

Individual 95% CIs For Mean
Based on Pooled StDev



One-way ANOVA: Relative Abundance versus Sub-Area

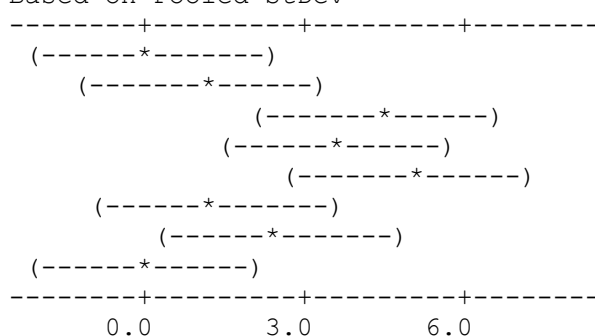
Analysis of Variance for Relative				
Source	DF	SS	MS	F
Sub-Area	7	104.32	14.90	3.15
Error	24	113.52	4.73	
Total	31	217.85		

P 0.017

Sub-Area	N	Mean	StDev
1	4	0.115	0.230
2	4	1.193	0.717
3	4	4.428	3.049
4	4	3.595	3.882
5	4	5.045	2.420
6	4	1.285	1.525
7	4	2.475	2.175
8	4	0.000	0.000

Pooled StDev = 2.175

Individual 95% CIs For Mean
Based on Pooled StDev



iii) Analysis of Group Sizes

One-way ANOVA: With Calves (Inc. Calves), With Calves (Ex. Calves), No Calves

Analysis of Variance

Source	DF	SS	MS	F	P
Factor	2	1384.9	692.4	12.53	0.000
Error	105	5801.3	55.3		
Total	107	7186.2			

				Individual 95% CIs For Mean Based on Pooled StDev			
Level	N	Mean	StDev	-+-----+-----+-----+-----			
With Cal	48	15.813	8.634	(-----*-----)			
With Cal	48	12.146	6.907	(---*---)			
No Calve	12	4.000	2.256	(-----*-----)			
				-+-----+-----+-----+-----			
Pooled StDev =		7.433		0.0	5.0	10.0	15.0

iv) Analysis of Distribution of Marked Individuals

Kruskal-Wallis Test: Month versus Marked Individuals

Kruskal-Wallis Test on Month

Marked I	N	Median	Ave Rank	Z
47	1	38231	5.0	1.41
49	1	38108	1.0	-1.41
62	1	38169	3.0	0.00
64	1	38200	4.0	0.71
67	1	38139	2.0	-0.71
Overall	5		3.0	

H = 4.00 DF = 4 P = 0.406

* NOTE * One or more small samples