

The social affiliation and group composition of bottlenose dolphins (*Tursiops truncatus*) in the outer southern Moray Firth, NE Scotland

Thesis submitted for the degree of
Master of Science

By

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In association with the
Cetacean Research & Rescue Unit



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In memory of my beloved grandma
Zum Andenken an meine kleine Oma

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

Declaration

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

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Statement 1

This dissertation is being submitted in partial fulfilment of the requirements for the degree of M.Sc.

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This dissertation is the result of my own independent work/investigation, except where otherwise stated. Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

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Abstract

Group sizes, composition, and association patterns of bottlenose dolphins (*Tursiops truncatus*) using the southern coastline of the outer Moray Firth, NE Scotland, were investigated between May and August 2003 using systematic boat surveys and photo-identification / capture-recapture techniques. In the subsequent analysis, additional archived data for the period October 1997 to 2002 (provided by the host organisation) was used.

Group sizes ($n = 132$) ranged from 1 to 44 with a mean of 11.07 ± 7.93 animals (median = 9.0). Schools containing calves (both excluding calves from the analysis and including calves respectively) were significantly larger than groups in which calves were absent. Over the period 1997 to 2003, 182 individual dolphins were photographically identified (including 22 known males and 53 females), 94 of which displayed dorsal edge marks (DEMs). From these records, 40 representative individuals (19 females, 17 males and 4 of unknown sex) which had been identified 5 or more times, were used to calculate coefficients of association (CoAs) ranging from 0.00 to 0.73 (mean = 0.11 ± 0.04).

Associations between and within sex classes were not significantly different from one another. Further, the results of permutation tests for non-random associations indicated that dolphins did not associate preferentially with some individuals or avoid others. Analyses of lagged association rates, however, suggested short-term association of individuals over periods of days with rapid disassociations, except for a smaller number of constant companions by the end of a few weeks.

The size and structure of dolphin groups frequenting the study area is primarily attributed to the reproductive state of the female. Notwithstanding, however, other implications such as the social ecology, relatedness, dispersal and anthropogenic impacts on this population are discussed. Whilst contributing to our understanding of the factors influencing distribution patterns and sociality of the coastal dolphins in UK waters, the present findings may be particularly significant in view of management proposals currently aimed at this internationally important, North Sea population.

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1.

Introduction

Whales, dolphins and porpoises belong to the order Cetacea, comprising 85 species to date (Rice, 1998; Hoesel, 2001; IWC, 2001) and traditionally divided into two suborders¹: the mysticetes (or baleen whales) and the odontocetes (or toothed whales). The mysticetes are made up of four families, totalling 14 species, whilst the odontocetes include ten families: the *Physeteridae* (sperm whales), *Kogiidae* (pygmy and dwarf sperm whales), *Monodontidae* (narwhal and beluga), *Ziphiidae* (beaked whales), *Delphinidae* (dolphins), *Phocoenidae* (porpoises) and four families of river dolphins (see Appendix A for full classification). With 37 species, the family *Delphinidae* is the largest of all the odontocete families. Members of this family are generally characterised by the presence of a distinct beak, two or more fused cervical vertebrae, and 20 or more pairs of teeth in the upper jaw (Martin, 1990).

The bottlenose dolphin (*Tursiops truncatus*) is one of the larger members of the *Delphinidae*. Measuring up to 4.1 metres in length and 350 kg in weight (Bob Reid, personnel communication), it has a robust, chunky body, a distinct sickle-shaped dorsal fin, and a well-defined, sharply demarcated beak. Unlike other members of the same family, however, the bottlenose does not show intricate patterns of colouration. Rather, the skin is pigmented in a counter-shaded fashion: the back, flukes and flippers are generally dark grey charcoal or brown in colour, and the flanks pale gradually to a pale cream or grey on the belly. Lacépède (1804) first described the bottlenose dolphin as *Delphinus nesarnack*. Montagu (1821) called a dolphin from the River Dart in England *Delphinus truncatus*, because he thought that its flattened tooth tips were a characteristic of the species, rather than being due to wear. The species was subsequently placed in a new genus by Gray in 1843, which was later named *Tursiops* by Gervais (1855). The current scientific name, *Tursiops truncatus*, derives from the Latin *Tursio*, meaning dolphin, the Greek suffix *-ops* (appearance) and the Latin *trunco* (truncated).

A variety of common or vernacular names have been used for the bottlenose dolphin in both the US and the UK – from grey dolphin, black dolphin and cowfish to bottlenose porpoise, (Wilson, 1995) – and the spelling of its most generic name has been known to vary widely from bottlenosed, bottle-nose to bottle-nosed. In the northeast of Scotland, the species is still often referred to as the Louper dug (leaping dog), and sometimes no distinction is made between them and the locally abundant harbour porpoise (*Phocoena phocoena*), as they are simply just called porpoise.

¹ Molecular findings that place the sperm whale closer to the mysticetes than the odontocetes may change the aspect of this classification (Milinkovitch *et al.* 1994).

The bottlenose dolphin is a truly cosmopolitan species. Found throughout the world's oceans and seas – from temperate to tropical waters of the Atlantic, Pacific and Indian Oceans, as well as the Mediterranean, Black and Red Seas – it is widely distributed throughout a range of mainly near shore, coastal habitats (Shane, 1990b), in sheltered and exposed areas of estuaries, lagoons and continental coasts, to pelagic offshore waters and around oceanic islands (Scott & Chivers, 1990; Rudolph & Smeenk, 2002; Wells & Scott, 2002). In Britain, bottlenoses are predominantly recorded in Scotland's Moray Firth and in Cardigan Bay in Wales (Evans, 1980; Hammond & Thompson, 1991). They have also been regularly seen along the Cornish, Devon and Dorset coasts, around the Hebrides, and in the Shannon Estuary, Ireland. This species is able to tolerate a wide variety of water temperature regimes and is able to withstand prolonged periods in hypo-saline (Caldwell & Caldwell, 1972) and hyper-saline waters (Smolker *et al.*, 1992). Because of this adaptability, the bottlenose is capable of surviving in extreme conditions; including some of the world's most industrialised and polluted waters, such as Galveston Bay in Texas (Maze-Foley & Würsig, 2002). It has also been kept most successfully in captivity (Schroeder, 1990; Wells & Scott, 1994).

The appearance of different bottlenose dolphin populations varies considerably throughout its range. Populations inhabiting shallow, tropical waters are typically smaller, pale greyer and have proportionally larger fins and flukes than those in pelagic or temperate waters (Hersh & Duffield, 1990). Ross & Cockcroft (1990) linked variation in body size to water temperature along both coasts of Australia, concluding that larger forms were found in colder water. Whilst small and large bottlenoses were seen to occur in close proximity, the smaller dolphins appeared to be primarily coastal, whilst the larger ones were attributed to deeper (and indeed colder) offshore waters. Due to the relatively cold waters around the UK, only one morph occurs. The resident bottlenose dolphins in the Moray Firth represent the species at the northern extreme of their species range (Hammond & Thompson, 1991). As such, they are perhaps the largest bottlenoses described so far.

Free-ranging bottlenose dolphins can live to considerable ages. Males can live up to 40 years whilst females can live to over 50 years (Hohn *et al.*, 1989; Cockcroft & Ross, 1990). Reproductive senescence is not thought to occur in the species, as even the oldest females continue to give birth and raise young (Wells & Scott, 1994). But the reproductive rate of the bottlenose dolphins is low, females producing a single calf just once every 3 to 4 years following a gestation period of approximately one year (Cockcroft & Ross, 1990).

As calving (and therefore conception) does not appear to take place at a specific time in the species, births of young bottlenoses may occur at almost any time of the year (Urian *et al.*,

1996). Indeed, studies on captive adult dolphins have shown that female bottlenoses ovulate repeatedly during a breeding season, and that males have prolonged periods of elevated testosterone levels and, therefore, a long period of sexual activity each year (Schroeder, 1990). That saying, it is generally thought that calving is timed to take best advantage of seasons when the water temperature represents a physiological advantage to the newly-born calf (Würsig, 1978; Mann *et al.*, 2000), and reduces the energy demand on the pregnant female (Wells *et al.*, 1987; Wells, 1991a).

Studies in the western North Atlantic and northern Gulf of Mexico have suggested that bottlenose dolphins are not sexually dimorphic (Hersh *et al.*, 1990, Mead & Potter, 1990), but in the Moray Firth, sexual dimorphism in the species may be apparent from the size and shape of dorsal fins, as in killer whales; the broadest and tallest dorsals typically belonging to mature adult males (Robinson, personal communication). In addition, investigations on growth rates carried out in western Florida have demonstrated that females grow initially faster and reach asymptotic sizes at an earlier age than males (12 years in females, 20 years in males) (Read *et al.*, 1993), leading to a subtle sexual dimorphism in adult body length, girth and mass. Indeed, similar observations have been made by Cockcroft & Ross (1990) for dolphins in South Africa.

Bottlenose dolphins are generalist feeders (Barros & Odell, 1990) but, as suggested in findings by Corkeron *et al.* (1990), they seem to be selective when given the opportunity. They consume a wide variety of fish, cephalopods and shrimps (Gunter, 1951), including some small rays and sharks (Mead & Potter, 1990), but the feeding techniques employed by the bottlenose are diverse. Both schooling and solitary prey may be pursued throughout the water column (as well as into the air above), into the sand below and even onto the shore. These dolphins are often reported to circle around fish shoals, with one or more cooperating animals darting into the shoal to feed (Leatherwood, 1975; Hamilton & Nishimoto, 1977; Bel'kovich *et al.*, 1991). Rossbach & Herzing (1997) observed bottlenose dolphins in the Bahamas diving into the sand up to their eyes after prey. Although intense echolocation is typically heard during these feeding episodes, it is unclear whether buried prey is detected with echolocation, or visually by some surface disturbance in the sand. In salt marshes in Georgia and South Carolina, dolphins pursue fish onto mud banks and slide back into the water (Hoese, 1971). Shane (1990a) observed bottlenose dolphins that stunned or killed fish by throwing them up to 9 metres into the air with their flukes. Lewis & Schroeder (2003) described a unique foraging technique in bottlenose dolphins in the Florida Keys where the dolphins created a mud plume in shallow water and then lunged through it in order to prey on the fish that aggregated in the plume. Furthermore, Pryor *et al.* (1990) reported co-operative fishing between dolphins and fishermen in Brazil, the dolphins driving

shoals of mullet towards lines of fishermen who then cast their nets while the dolphins feed on the fleeing fish.

Whether feeding, reproducing or travelling, the bottlenose dolphin is clearly a highly social mammal. It spends most of its life in schools of varying size and composition. Bottlenose dolphin communities around the world have been described as fission-fusion societies (Würsig & Würsig, 1977; Smolker *et al.*, 1992, Connor *et al.*, 2000). Individuals associate in small groups in which the composition changes very dynamically, even several times per day (White, 1992); as opposed to stable family groups observed in more gregarious delphinids, such as pilot whales (*Globicephala melas*) (Ottensmeyer & Whitehead, 2003) or killer whales (Ford *et al.*, 2000). Bottlenose dolphins tend to swim together with other animals of a similar age or reproductive stage, often forming long-term associations within groups that change in composition. Although calves are weaned after about 18 months, they associate with the mother for 3 to 5 years (Connor *et al.*, 2000, and references therein) until they leave to join mixed groups of other juveniles, where they may stay until they reach sexual maturity at 5 – 12 years for females and 10 – 13 years for males (Odell, 1975).

Particularly in pelagic waters, bottlenose dolphins also mix with other odontocetes (Scott & Chivers, 1990; Herzing & Johnson, 1997). The reason for this is still not known, but may comprise the use of the other species' more specialised prey detection or capturing abilities, or perhaps provide protection from predators by increasing the number of animals in a school (Scott & Chivers, 1990).

Ascertaining group composition and the affiliation of individual animals within a dolphin population are certainly prerequisites fundamental to our understanding of the social structure and behaviour of these long-lived mammals. Indeed, early researchers recognised that aspects of their studies were greatly enhanced by the recognition of individuals (Würsig & Jefferson, 1990). Although artificial marking and tagging were considered almost rudimentary for behavioural work in the 1950s and 1960s, increasing numbers of long-term studies of wild animals have shown that especially large and long-lived vertebrates can usually be identified from natural marks. Individual killer whales, *Orcinus orca* (Balcomb *et al.*, 1982; Bigg, 1982), Indo-Pacific humpbacked dolphins, *Sousa chinensis* (Saayman & Tayler, 1973; 1979) and Hawaiian spinner dolphins, *Stenella longirostris* (Norris & Dohl, 1980a), for example, have all been recognised and catalogued in this way in order to provide information on occurrence and intra-group affiliation patterns. Caldwell (1955), Irvine & Wells (1972) and Würsig & Würsig (1977) were amongst the first researchers, however, to use naturally occurring markings from the dorsal fins of bottlenose dolphins to identify individual animals.

For the majority of dolphin species, pieces of tissue missing from the trailing edge of the easily tattered dorsal fin (termed fin nicks or dorsal edge marks (DEM's)) provide the most unique feature for differentiating between individuals within a population. In addition, the shape of the dorsal fin (particularly unusual fin shapes such as distinctively wide or tall dorsals), shading or colouring of the fin and body, scratches and scars, pigmentation patterns, lesioning and deformities, have all been used in the photo-identification of individual bottlenoses (Table 1.1), As such, a well-marked dolphin is one that is recognised not only by a single feature, but by

Table 1.1. External features used in the recognition of individual bottlenose dolphins in the Moray Firth. Adapted by Robinson from Wilson (1995).

Fin nicks or Dorsal Edge Marks (DEM's)	Pieces of tissue missing from the trailing edge of the dorsal fin
Unusual fin shapes	Such as distinctively wide, tall or leaning dorsal fins
Major scratches	Large scratches on the dorsal fin or flanks
Minor scratches	Like major scratches, but superficial or smaller
White fin fringes	A white, depigmented region around the edge of the dorsal fin (also seen on flippers and tail flukes)
Active lesions	Areas of black, cloudy, lunar or orange lesions
Healed lesions	Pale coloured epidermal lesions
Deformities (Natural or man-made)	Distortions of normal body contours, such as a kinked peduncle or tailstock. Also individuals with propeller injuries or boat strikes. Albino animals would also fall into this category.

a number of marks that form a distinctive matrix for that individual. Estimations of population size might be obtained through mark and recapture techniques (Hansen, 1990; Wells & Scott, 1990). However, natural marks need to be recognizable over time, as well as being unique to the animal and having approximately equal probability of being sighted and re-sighted in order for such estimates to be realistic (Würsig & Jefferson, 1990).

Thus, the photo recognition of individual whales and dolphins can be used as a central tool for a rather large variety of focal studies on the distribution, ecology and natural history of cetacean species. 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 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, 1990a; Balance, 1990).

A greater understanding of the life history and the dynamics of whale and dolphin populations can be obtained when individuals are followed for many years through photo-identification studies. Long-term behavioural studies, for example, can provide information about reproductive and total life span, age at sexual maturity, calving intervals, lactation periods and disease and mortality rates, without the need to sacrifice animals (Balance, 1990). If identifying photographs are collected with sufficient data for associations and/or groups to be defined, however, they also have the potential to provide a sound model for social structure (Whitehead, 1995; Whitehead *et al.*, 2000).

The general procedure to convert long-term photographic identification databases into models of social structure, is to define and calculate association indices between all pairs of identified animals that together make up an association matrix (e.g. Cairns & Schwager, 1987; Ginsberg & Young, 1992). Using methodologies such as cluster analyses or sociograms (see Wells *et al.*, 1987; Bigg *et al.*, 1990), the association matrices for a particular dataset can be displayed. To test for preferred companionships, permutations of association measures can further be used (Slooten *et al.*, 1993; Bejder *et al.*, 1998; Whitehead, 1999b).

The Cetacean Research and Rescue Unit (CRRU) has compiled a database of individually identifiable bottlenose dolphins using the southern coastline of the outer Moray Firth between Lossiemouth and Banff since 1997. The significance of this dataset is particularly relevant in view of the status of this bottlenose population. One of just two known populations of

bottlenoses in British waters (the other being in Cardigan Bay, Wales), and the only population in the North Sea, this population has both national and international importance. Currently estimated at 130 individuals (Wilson *et al.*, 1999), the small size and isolated position of this population makes it undoubtedly vulnerable to extinction. The study area for which the data examined in this investigation was collated, is an area that has received little research attention to date, but current studies suggest the southern outer Moray Firth may provide important calving and feeding areas for a significant proportion of this North Sea population (Robinson, personal communication). This is particularly significant in terms of management proposals presently aimed at these animals (Curran *et al.*, 1996; Moray Firth Partnership, 2001).

A greater understanding of the social formation and ecology of the dolphins seen to use the coastline of the present study area is considered to be particularly relevant to the development of conservation policies required to extend the current Special Area of Conservation designation applied to the inner Moray Firth. Also from this consideration, stems the extreme interest in comparing the social ecology and behaviour of this population with other bottlenose dolphin communities around the world; to understand how the interplay of different factors, such as environmental conditions and food availability, for example, may combine to shape the social structure of this coastal dolphin species. In this regard, the present study was identified.

Using original data collection and the established bottlenose identification database, the principle objectives of this study aimed:

- to determine the group size and composition of bottlenose dolphins frequenting the coastline of the southern outer Moray Firth;
- to calculate and define association indices between pairs of identified animals, through the creation of an association matrix;
- to evaluate and interpret patterns of affiliation between individual dolphins with the use of cluster analyses and permutation tests for preferred associations;
- to estimate the probabilities of association between individuals over time.

2.

Study area: The Moray Firth

Measuring approximately 5230 km², the Moray Firth (57°40'N, 3°30'W) is the largest embayment in the northeast of Scotland (Tilbrook, 1986). Bounded on two sides by land - from Duncansby Head in the north, to Inverness in the southwest, and to Fraserburgh in the east - it contains within it three smaller Firths and a number of smaller bays and inlets. Following Harding-Hill (1993), 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 (Figure 2.1).

The bathymetry of the Moray Firth is relatively simple on a large scale. From the inner Firth, the seabed slopes gently from the coast to a depth of about 50 m, approximately 15 km offshore (Admiralty Chart C22, 1997). The coastline of this area consists of dune systems, cliffs and tidally exposed mudflats. Of 12 major rivers flowing into the Moray Firth, 10 discharge freshwater into the inner Firth creating an estuarine-like environment that changes to the North and East (Adams & Martin, 1986). In contrast, the outer Moray Firth where the present study is focused resembles more the open sea. Here, the seabed slopes more rapidly to depths of up to 200 m within 26 km of the shoreline (Admiralty Chart C22, 1997), and the typically rugged coastline forms a composite of headlands and small bays consistent with the more irregular topography of the seabed in this area.

On a fine scale, the transition between the inner Moray Firth and the outer Firth is less distinct. A number of prominent submarine banks in the outer Firth create shallow areas that reduce the depth to just 33 m in places. Conversely, the narrow mouths of the Cromarty, Inverness and Beaulieu Firths, in the inner Moray Firth, are composed of steeply sided basins creating depths of over 50 m only 1 km offshore. Whilst sediments in the Moray Firth are predominantly sandy, grain size is inversely correlated to depth (Reid & McManus, 1987). The shallower areas of the Firth are made up of coarse sands, whilst the deepest areas off the southern shoreline are typically composed of mud.

A combination of coastal and mixed waters (coastal and oceanic) is found in the Moray Firth. The main part of the mixed waters is brought down from the North by the Dooley current, which then circulates in a clockwise direction within the Firth (Adams, 1987). Because of the major freshwater input into the inner Moray Firth, the water salinity is substantially reduced. Since “permanent” estuarine conditions decrease gradually with increasing distance from the inner Moray Firth, the salinity in the outer Moray Firth typically exceeds 34.8 psu (practical salinity units).

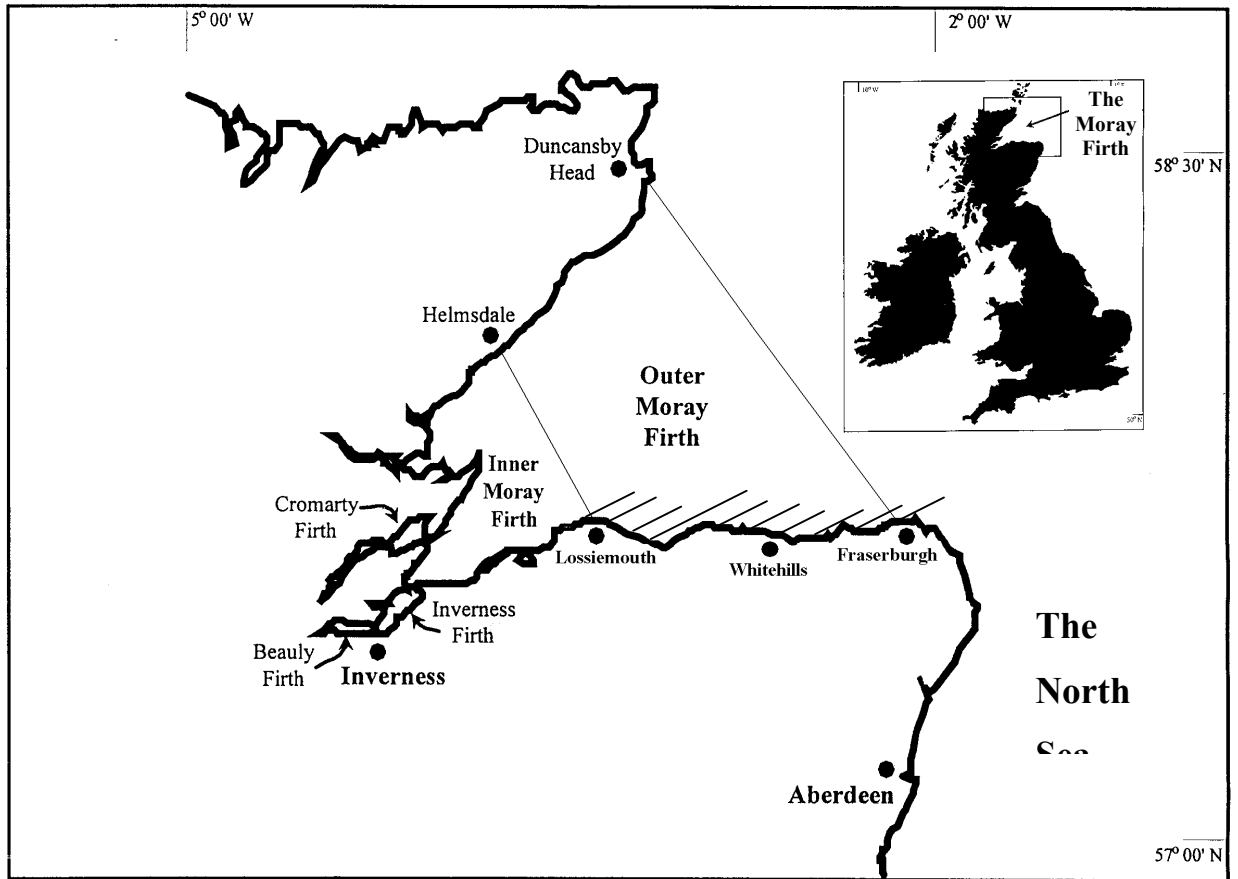


Figure 2.1. Map of Northeast Scotland showing the location of the Moray Firth and the area in which the present study was carried out (shaded area). Redrawn and adapted from Wilson (1995).

3.

Methods

3.1. Data collection

Data were collected during boat-based surveys conducted from mid May to August 2003 along an 82 km stretch of coastline of the southern outer Moray Firth, between Lossiemouth and Fraserburgh (Figure 2.2). The survey area was divided into two part surveys, using an east and a west route from Whitehills harbour; where the survey vessel was berthed. All surveys were made using a 5.4 metre Avon Searider Rigid Inflatable Boat (RIB) fitted with a 90 hp Johnston Evinrude outboard engine. A crew of between five to seven people were onboard the boat during surveys acting as observers.

Survey trips were conducted at sea states of Beaufort three or less during good light conditions. If the sea state increased above this, or heavy or continuous rain occurred during the course of a trip, the survey was aborted. Surveys were conducted at speeds between 8 to 12 km h⁻¹.

A detailed *Trip Log* of the route covered, survey start and finish time, sea state / environmental conditions and GPS positions were recorded for each survey trip undertaken (see Figure 3.1 a). When dolphins were sighted (referred to as an encounter), the boat was gradually slowed, camera and equipment prepared, and the animals were slowly approached as the encounter began. At the start and end of each encounter, the time, GPS positions, general landmarks and observations about the activities of the dolphins were noted on the dolphin *Encounter Log* (Figure 3.2 b).

During each encounter, the dolphins were approached at a shallow angle until the boat could be positioned parallel to the track or activity of the dolphins, at a distance of approximately 20 to 50 metres. Alterations in the speed and direction of the survey vessel were kept to an absolute minimum throughout the encounter. The course of the boat was only altered whenever the dolphins naturally changed course or when it was necessary for the vessel to be positioned on either the left or the right hand side of the group as required by the photographer. In such a situation, the boat was slowly steered behind the track of the dolphins, rather than in front, ensuring that minimum disturbance to the animals was caused. When the animals stopped to forage or feed, the boat was slowed to idle as appropriate. All manoeuvres were conducted in accordance with the principles of the Moray Firth voluntary guidelines on handling boats around dolphins (Scottish Natural Heritage, 1993) and the methods laid down by the University of Aberdeen (personal communication).

a)

CETACEAN RESEARCH AND RESCUE UNIT			
DATE: (DD/MM/YY)	22/07/03	OBSERVERS: (PLEASE CIRCLE)	(KR) ND CC, PE, CH, HS
START TIME: (HH:MM 24 hrs)	14:40	END TIME: (HH:MM 24 hrs)	17:10
DEPART FROM:	WH	SEA STATE: (CIRCLE AS APPROPRIATE)	0 - 1 2 3 4
GPS - DEPARTURE: (N 00° 00' 00" W 00° 00' 00")	N W		
ACTUAL ROUTE COVERED: (WHITEHILLS-CROVIE-PENNAN ETC.) <i>Whitehills → Boars Rock</i> ADDITIONAL INFORMATION / REMINDER: <i>outer minke whale survey on way back to Whitehills</i>			

b)

CETACEAN RESEARCH AND RESCUE UNIT - Encounter Form v4.0															
ENCOUNTER NO. (e.g. #1, #2 etc.)	1	DATE: (DD/MM/YY)	22/7/03												
		OBSERVERS:	(KR) ND KD CC, PE, CH, HS												
TIME START: (HH:MM 24 hrs)	GPS START: (N 00° 00' 00" W 00° 00' 00")	TIME END: (HH:MM 24 hrs)	GPS END: (N 00° 00' 00" W 00° 00' 00")												
16:07	N 57° 40.957 W 003° 06.158	17:07	N 57° 41.544 W 003° 10.381												
GENERAL AREA at START: (e.g. Buckie harbour)	Kingston upon Spey	G. AREA at END:	Spey Bay												
LANDMARK (e.g. 100m NW of harbour entrance)	1 km off river mouth	L. MARK at END:	Boars Rock												
INDIVIDUALS PRESENT		PHOTO I.D. Film Nos. (e.g. KR51 & ND3 etc)	KR31: 4-36 KR32: 1-12												
Structure of subgroups: (e.g. 3A (1C) + 6A + 2A)	2A (13A) + 2A (1C)														
Total:	6														
Activity (PLEASE TICK) <table border="0"> <tr> <td><input checked="" type="checkbox"/> FORAGING</td> <td><input type="checkbox"/> TRANSITING</td> <td><input type="checkbox"/> AGGRESSION</td> <td><input checked="" type="checkbox"/> MILLING</td> <td><input type="checkbox"/> HALF BREACHING</td> <td><input type="checkbox"/> SYNCHRONISED BREACHING</td> </tr> <tr> <td><input checked="" type="checkbox"/> FEEDING</td> <td><input checked="" type="checkbox"/> TAIL SLAPS</td> <td><input type="checkbox"/> SPY HOPS</td> <td><input checked="" type="checkbox"/> BOW RIDING</td> <td><input type="checkbox"/> FULL BREACHING</td> <td><input checked="" type="checkbox"/> PORPOISING</td> </tr> </table> OTHER (PLEASE SPECIFY) OR COMMENTS <i>sexual behaviour, fish throwing</i>				<input checked="" type="checkbox"/> FORAGING	<input type="checkbox"/> TRANSITING	<input type="checkbox"/> AGGRESSION	<input checked="" type="checkbox"/> MILLING	<input type="checkbox"/> HALF BREACHING	<input type="checkbox"/> SYNCHRONISED BREACHING	<input checked="" type="checkbox"/> FEEDING	<input checked="" type="checkbox"/> TAIL SLAPS	<input type="checkbox"/> SPY HOPS	<input checked="" type="checkbox"/> BOW RIDING	<input type="checkbox"/> FULL BREACHING	<input checked="" type="checkbox"/> PORPOISING
<input checked="" type="checkbox"/> FORAGING	<input type="checkbox"/> TRANSITING	<input type="checkbox"/> AGGRESSION	<input checked="" type="checkbox"/> MILLING	<input type="checkbox"/> HALF BREACHING	<input type="checkbox"/> SYNCHRONISED BREACHING										
<input checked="" type="checkbox"/> FEEDING	<input checked="" type="checkbox"/> TAIL SLAPS	<input type="checkbox"/> SPY HOPS	<input checked="" type="checkbox"/> BOW RIDING	<input type="checkbox"/> FULL BREACHING	<input checked="" type="checkbox"/> PORPOISING										

Figure 3.1. Showing (a) the boat survey log used in the present study and the fields recorded during each boat trip; and (b) the encounter log sheet used to record information relating to each encounter made per trip. These A4 sheets were laminated for use at sea, and information was recorded on each sheet using a chinagraph pen.

During encounters, photographs were taken with a Nikon F5 auto focus camera with a F2.8 100-300 mm zoom lens. By pre-focusing the camera on the sea where the subjects were anticipated to surface, the focusing time was minimised so that the photographer could use valuable time to select subject animals to photograph, thus reducing the encounter time to a minimum. All photographs were taken using Fuji 400 or 800 ASA colour print film. Colour film was selected as oppose to black and white, as this medium was considered to be more useful in recording a variety of different patterns on the skin of dolphins which are useful in the identification of individuals, in addition to dorsal edge marks (DEMs) (see Appendix B for features used in the identification of individual bottlenoses in the present study).

The aim during each encounter was to photograph the dorsal fin of each dolphin from at least one side, preferably both. It was further important to obtain a clear idea of the total number of individuals present during the encounter and the positions of any sub-groups relative to one another. To this end, the driver of the boat, the photographer, note taker and other observers present, needed to work closely together to record this information accurately. Whilst the driver carefully manoeuvred the boat into the correct position, the note taker would record the number and composition of sub-groups encountered, the presence of known individuals, and details of the activities of the school. A *Film Sheet* was also used to record the content of the photographs taken: the age and sex of the subject (where possible), any observed maternal link, and any associated affiliates, for example (see Figure 3.2).

The number of photographs taken during a particular encounter was variable depending upon the size of the group and behaviour of the animals. A foraging group, for example, would typically be dispersed and the members might often change directions quickly, resulting in a greater number of films being used. On the other hand, a travelling group of only eight dolphins surfacing in a regular manner could be adequately photographed in a short space of time using just one or two 36-exposure films.

When more than one group of dolphins was encountered during a single survey trip, each was treated as a separate sample and was separated in the notes and photographs accordingly. Each was then respectively assigned a unique encounter number and recorded on its own encounter sheet (Figure 3.1 b). A summary on the number of animals counted, any recognisable individuals present, the location and time of the encounter, and the behaviour of the dolphins, was taken by the note taker at the termination of the encounter. Finally, a picture of something other than dolphins or the sea, such as a crewmember for example, was taken at the end of each encounter to separate the photographs taken from any subsequent encounters on the same film. Data from both trip and encounter sheets were transferred to a summary *Boat Form* on return from the day at sea. This is shown in Figure 3.3.

PHOTO-IDENTIFICATION FILM SHEET FOR BOAT TRIPS



Film type: (eg ISO 800) Fuji 800	Exposure No: 24 (36)
Code: (eg KR65) KR31 / 03	22/7/03

Insert date and time of trip at appropriate frame number

Frame No.	Frame No.
1. Birds	19. RD ♂
2. "	20. RD ?
3. "	21. RD ♂ (pluto?)
4. #69 RD 2217	22. RD ♂
5. no features RD	23. RD ♂
6. out of focus #69 + RD other	24. mother
7. #69 + other	25. 4 individuals
8. calf RD	26. towards us
9. miss	27. LD #69
10. miss	28. LD ?
11. mother RD *calf on frame 8	29. LD pluto?
12. LD #2090 ♂ following	30. miss
13. LD ♂ mother + calf	31. calf + jellyfish
14. LD ♂	32. calf + "
15. LD ♂	33. calf LD
16. mother RD	34. LD
17. RD ♂	35. LD lesioned
18. RD mother	36. to lower nick

CRRUForms\2002\Film Sheet.doc

Figure 3.2. Showing an example of a completed photo-identification film sheet detailing the content and relationship of photographs taken during a particular encounter.



**Cetacean Research & Rescue Unit
Boat Survey Form**

DATE: 22/7/03
 VESSEL: Orca II
 ROUTE: Whitehills → Boars Rock
 OBS 1: KR
 OBS 2: Cammy Carter
 OBS 3: PE
 OBS 4: Cathy Harshaw
 Mark Schulten
 SURVEY START TIME: 14:40
 SURVEY FINISH TIME: 17:10
 Boat survey info entered into database?
 Encounter info entered into database?
 ENC # 1 SPECIES: bottlenose dolphin
 START TIME: 16:07 OF ENC. (hrs) END TIME: 17:07 OF ENC. (hrs)
 GPS START: N 57°40.957 W 003°06.158
 GPS STOP: N 57°41.644 W 003°10.381
 AREA START: Kingston upon Spey e.g. Tarlair AREA STOP: Spey Bay
 LANDMARK START: 1 km off rivermouth e.g. 100m NW from swimming pool
 LANDMARK STOP: Boars Rock
 NO. OF INDIVIDUALS: 6 ADULTS: 4 SUBADULTS: 1 CALVES: 1 NEONATES:
 SUB-GROUPS (Y/N): Y SUB-GROUP STRUCTURE (e.g. 3 + 2 + 3): 3 + 3

ACTIVITY:

FORAGING FEEDING TRANSITING MILLING
 FULL BREACHING SPY HOPS TAIL SLAPS PORPOISING
 HALF BREACHING BOW RIDING AGGRESSIVE BEHAVIOUR
 SYNCHRONISED BREACHING OTHER: sexual behaviour, fish throwing

NOTES / SUMMARY:

headed west to meet dolphins milling slowly in Spey Bay. Easy to photograph since they moved really slowly.
 The calf came close to the boat and entertained us with jelly fish throwing.

ENVIRONMENTAL INFORMATION:

WEATHER: SUNNY CLOUDY BUT BRIGHT OVERCAST RAIN FOG
 OTHER

SEA STATE (Beaufort scale e.g. 0 - 4): 0-1 SEA HEIGHT (m):

PHOTO ID: YES NO YES NO FILM Nos: KR31, KR32 FRAMES: 4-36, 1-12
 ANY KNOWN INDIVIDUALS PRESENT: #69, #51?, 67 + C, 329? 197?

C:\CRRUF\Forms\2003\Boat Survey Form.doc

Figure 3.3. Summary trip and encounter sheet onto which the data from each encounter was transferred from the respective boat sheets (depicted in figures 3.1 a & b) on return from the day at sea.

All group size estimates were made to include adults (A), sub-adults (SA), calves (C) and neonates (or newborn calves) (N) present. Sub-adults were defined as individuals of a similar size to adults, but with a slightly lighter colour and with visible blood vessel rays on the side of the dorsal fins (Plate 3.1 a). According to the definition of Shane (1990a), calves were defined as individuals of a light colouration (sometimes with visible foetal folds) (Plate 3.1 b), judged by eye to be two-thirds or less the length of an adult and swimming beside or slightly behind an adult (Plate 3.1 c). In addition, a dolphin “group” was defined as any collective comprising at least two or more individuals seen together at any time during a single encounter. The 10-m chain rule proposed by Smolker *et al.* (1992), where each member of a group is within 10 m of any other member, was not applicable in this study in view of the known fluidity and dispersion of animals and relationships in the particular study area (Robinson, personal communication). The dolphins tended to spread out while foraging where the water was most shallow, and regroup when travelling. Instead, schools were defined, using an extended definition to that proposed by Wells *et al.* (1987), as aggregations of individuals within 500 m of each other, engaged in similar activities and, if moving, heading in the same direction. With respect, sub-groups could therefore be defined in the present study as smaller units of one or more individuals seen together within a larger school. In view of this latter definition, the 10-m chain rule can be applied here in terms of the subgroups themselves.

3.2. Matching photographs

Once the photographs from each encounter were developed, the negatives were cut into strips and stored in transparent plastic A4 sheets. Each film sleeve was individually marked with a unique code starting with the initials of the photographer and the film number, the year, and the negative number, for example KR01/2003-6112. The photographs were individually labelled with the encounter date, encounter start time, GPS positions, frame number and the code; allowing photos to be retraced to their original film should they become mixed during the matching process.

An encounter sheet (Figure 3.4) was used to assist in the sorting procedure for photographs to the individual level. The photographs were examined one by one with a magnifying glass. The first animal with a distinguishing feature, such as a dorsal edge mark or characteristic fin shape for example, was assigned a temporary unique symbol (e.g. * □ ☺ ○ ♥ ☼ ◇ etc.) or an identification number, depending upon whether the animal was well known or not. The next animal with an identifiable feature was then noted down and assigned a symbol or

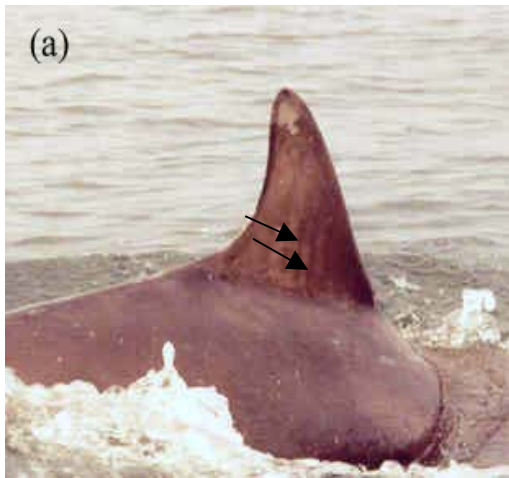


Plate 3.1. Bottlenose age categories based on their appearance in photographs. (a) Shows a sub-adult dolphin with visible blood vessel rays (seen as vertical lines, see arrows) in the dorsal fin, (b) shows a calf with visible foetal folds (light banding seen running axially around the body), and (c) calf in close association with its mother, showing lighter coloration and small body size. Photos courtesy of Dr. Kevin Robinson / CRRU.

Encounter Grid

Enc #: 1.....

Date: 22/06/03

No. dolphins: 6 Calves: 1.....

Time: 16:07



	#69	★	□ calf	○	△ 122?	☺
R D	<u>KRB1</u> 5,8 <u>KRB2</u> 9	<u>KRB1</u> 6,7, 10,12,17, 25	<u>KRB1</u> 9	<u>KRB1</u> 19,20, 21,22,23,24	<u>KRB1</u> 26	
L D	<u>KRB1</u> 28 <u>KRB2</u> 1,4	<u>KRB1</u> 29,36	<u>KRB1</u> 34,35	<u>KRB1</u> 13,14, 15,16,30	<u>KRB2</u> 2,3, 5,7	<u>KRB2</u> 6,8,10

Figure 3.4. Showing an example of an encounter grid in use. This table is used to segregate the individual dolphins photographed during an encounter, assisted by notes taken pertaining to the photographs at the time of the encounter, and additional information recorded on the encounter log sheet.

ID number accordingly and so on. Photographs with insufficient data (out of focus, obscured, distant, etc.) were disregarded in this process. The encounter grid thus represented a summary table identifying each individual dolphin recorded during a particular encounter from all photographs taken. Animals with nicks, scars or distinctive fin shapes (which could be identified from either side) had frame numbers in both the left and right dorsal boxes (see figure 3.4). For those animals lacking such features, it was sometimes very hard, if not impossible, to match the right with the left hand side of the animal. However, this may have been possible with further encounters.

Once this stage of the analysis had been completed, the cross matching of individuals identified from an encounter with those known individuals from a larger, established archive (composing seven years worth of data) could begin. This process was assisted by the use of a purpose-designed, relational database (section 3.3), into which the details for each encounter and sighting were entered, along with respective photographs and details for each animal recorded. Using the queries facility of this Access database, specific searches could be made to locate animals with unique or distinctive dorsal features (such as lower, mid or upper nicks, multiple serrations, unique fin shapes, lesions, scars, or deformities, for example) thereby aiding the matching / identification process for individual bottlenoses. Once a potential match was made, the appropriate hanging file could then be retrieved in hard copy for closer inspection.

On confirmation of the match, the best photographs of the right and left dorsal fin from the new encounter were added to the respective hanging file, along with information on the date, encounter start time, frame number and film code. If no match could be found, then the unknown animal was assigned a new identification number and hanging file, and its details were added into the *Individuals* file of the database accordingly. Subsequently, the entire encounter was entered onto a *Summary Encounter Sheet* (Figure 3.5), which was used to detail the resolved group structures and corresponding associations. Sub-groups and relationships, such as mother-calf associations, were depicted with the use of brackets. If the group had been precisely counted at sea and the same numbers of individuals were identified from the photographs, it was assumed that all the animals present had been correctly identified.

In conclusion, this information was finally entered into the *Sightings* file of the database (see following section).



Summary Encounter Sheet

DATE: 22/07/03 ENC #: 1

START TIME: 16:07 END TIME: 17:07

GROUP STRUCTURE:

NUMBERS: 3 3

AGE: (AD, SUB-A, CALF) A A C A A SA

ID: 51 67 328 69 122 340

NUMBERS:

AGE:
(AD, SUB-A, CALF)

ID:

NUMBERS:

AGE:
(AD, SUB-A, CALF)

ID:

SUBGROUPS: 4 (2)

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

WHOLE GROUP (Y/N): Y

TOTAL NO. WITH DEM'S: 3

GENERAL: 6 animals including 1 older calf
♀ 122 without a calf

Info entered into "Sightings" database?

Figure 3.5. Showing a completed example of a summary encounter sheet for a group of 6 bottlenoses. Note the identified sub-groups, depicted in the above example by brackets.

3.3. The relational database for the bottlenose archive – data entry and retrieval

All information and data collected during survey trips were entered into a relational database. Designed and written for Microsoft Access by Dr. Kevin Robinson and Jeroen Benda of the Cetacean Research & Rescue Unit (CRRU) and based on a model proposed by Wilson (1995), the database was principally compartmentalised into the four following files or tables:

1) Trips - This first file included entry fields for information pertaining to the boat trips made. Fields used included the date of the trip, name of the vessel used, names of the observers on board, start and end times of the trip, the route covered, sea state, the number of encounters recorded and the total number of animals encountered per trip.

2) Encounters – The encounters file was used to relate the data recorded during an encounter to the respective trip information. In this file, entry fields included details such as the start and end times of the encounter, its location (using landmarks and GPS positions), the maximum number of dolphins counted, number of calves present and the number of sub-groups identified.

3) Sightings - This table was used to relate the individuals identified to the encounter. Fields recorded included the identification number of the individual photo-identified during each encounter, the code for the best photograph confirming the identification and the date and encounter in which that identification was made.

4) Individuals - This file contained information about the individual dolphins themselves; for example the unique ID number, date when first seen, the age (adult, sub-adult, calf, neonate), gender and maternal links where appropriate. In addition, the best pictures of the left and right dorsal fin were entered along with any comments or notes on the animal. Individuals marked with a questionable status (Q) were dolphins identified from a poor quality photograph might already be represented elsewhere in the database.

The structure and entry fields for these four files are shown (in form entry view) in Figure 3.6. These files were linked by common fields (relationships) that allowed the user to interrogate the system using the “queries mode” of the Access database program.

Boat Trips Data Entry Form

DATE SURVEY TYPE PART START TIME END TIME
(dd/mm/yy) (e.g. 09:25 hrs) (e.g. 12:40 hrs)

BOAT MEAN SEA STATE
(Please Select) (Please Select)

AREAS COVERED: Please tick boxes as appropriate

<input type="checkbox"/> LOSSIEMOUTH	<input type="checkbox"/> WHITEHILLS	OBS1	<input type="text"/>
<input type="checkbox"/> BOARS ROCK	<input type="checkbox"/> BANFF	OBS2	<input type="text"/>
<input type="checkbox"/> KINGSTON-UPON-SPEY	<input type="checkbox"/> MACDUFF	OBS3	<input type="text"/>
<input type="checkbox"/> SPEY BAY	<input type="checkbox"/> MAINS OF MELROSE	OBS4	<input type="text"/>
<input type="checkbox"/> PORTGORDON	<input type="checkbox"/> GAMRIE BAY	OBS5	<input type="text"/>
<input type="checkbox"/> BUCKIE	<input type="checkbox"/> TROUP HEAD	OBS6	<input type="text"/>
<input type="checkbox"/> STRATHLENE	<input type="checkbox"/> PENNAN	OBS7	<input type="text"/>
<input type="checkbox"/> FINDOCHTY	<input type="checkbox"/> ABERDOUR BAY	OBS8	<input type="text"/>
<input type="checkbox"/> PORTKNOCKIE	<input type="checkbox"/> ROSEHEARTY		
<input type="checkbox"/> CULLEN BAY	<input type="checkbox"/> SANDHAVEN		
<input type="checkbox"/> SUNNYSIDE BEACH	<input type="checkbox"/> FRASERBURGH		
<input type="checkbox"/> SANDEND			
<input type="checkbox"/> PORTSOY			

NO. OF ENCOUNTERS

TOTAL DOLPHINS ENCOUNTERED

Encounters Data Entry Form

Select Trip ENC #

ENC START ENC END
eg. 09:45 eg. 14:10

DURATION (mins)

HEADING
eg. NE

AREA START
(Select + or - from list)

MAX COUNT

LOCATION START
eg. 100M NE OF HARBOUR

NO. SUBGROUPS

NO. CALVES

TOTAL NO. DEM'S

GPS START

ST LAT DEGREES N

END LAT DEGREES N

ST LAT MINS W

END LAT MINS W

ST LONG DEGREES N

END LONG DEGREES N

ST LONG MINS W

END LONG MINS W

CONDITIONS
Add + or - for rising or falling tides eg. 3.82+

TIDE (in metres)

SEA STATE
eg. 1-2

GPS END
eg. 24.027

Sightings Data Entry Form

SELECT ENCOUNTER

ENC #

ID #
(e.g. 05)

LEFT PIC NO.
(e.g. 28/R01/2003/5214)

RIGHT PIC NO.

SUB GROUP #

TOT NO. IN SUBGROUP

TOT NO. DOLPHINS

TOT NO. OF CALVES

New Individuals Data Entry Form

ID # AU #
(if known)

DATE FIRST SEEN GENDER

AGE THEN WITH CALF

OTHER ID'S MATERNAL LINK

LEFT DORSAL LD

LD PHOTO QUALITY

RIGHT DORSAL RD

RD PHOTO QUALITY

DORSAL NICK(S)

NOTES

QUESTIONABLE STATUS

QUALITY PIC

DEM: FEATURE:

Figure 3.6. Schematic diagram depicting the user-friendly, data entry forms of the CRRU bottlenose dolphin database. Each of the above boxes shows the entry fields for each of the “Trips”, “Encounters”, “Sightings” & “Individuals” files. These files are related to one another by a number of common fields or identities, which allow the user to extract information required from one or more of the files with the use of “Queries”.

3.4. Data analysis

In addition to data collected between the months of May to August 2003 in the present study, additional data previously collated from May to October 1997 to 2002 were also utilised in the following section of this thesis.

Association indices, originally applied to ecological studies of plant community assemblages, were used to calculate the coefficients of association (CoA) between individual dolphins from the study area. This was carried out using the SOCPROG program (version 1.3), developed by Whitehead (1999a, 1999b) for MATLAB (version 5.1). This software was used to test observed association patterns of individual bottlenoses against those expected from random associations.

According to Maze-Foley & Würsig (2002), the term affiliate is used for an individual that is sighted within the same group as a specified individual. For the present analysis, only affiliates of dolphins with distinctive DEM's that had been recorded five or more times between 1997 and 2003 were used in the calculation of coefficients of association (CoAs). Although different cut-off levels have been used for including individuals in the analyses of association coefficients, ranging from 2 sightings per individual (e.g. Slooten *et al.*, 1993; Bräger, 1999) to 10 sightings (e.g. Smolker *et al.*, 1992; Quintana-Rizzo & Wells, 2001), with various intermediates, a cut-off level of five was selected as an appropriate number for the size of the existing dataset. A decision was further made to exclude calves from this analysis, because it was expected that range and association patterns were dependent upon those of the mother, as described by Rossbach & Herzing (1999).

The index most commonly used in the analysis of social structure in cetacean populations is the Half Weight Index (HWI) (see Wells *et al.*, 1987; Smolker *et al.*, 1992; Slooten *et al.*, 1993; Herzing & Brunnick, 1997; Bejder *et al.*, 1998; Bräger, 1999; Möller *et al.*, 2001; and Maze-Foley & Würsig, 2002), also known as the Dice or Sorensen Index. Since with photo-identification data it may have been difficult to photograph and identify all individuals within a group, scoring animals apart (adding to the denominator), as oppose to scoring both individuals together (adding to the numerator), only requires that one individual is identified. In this respect, the HWI is least biased when pairs are more likely to be seen when separate than when together (Cairns & Schwager, 1987). Notwithstanding, however, Ginsberg & Young (1992) argued that although the HWI may be biased in the correct direction for a particular study, the weighting itself is arbitrary and cannot alleviate the bias and, as such, the use of the Simple Ratio (SR) is recommended. Therefore, in the present analysis, all CoA's were calculated using both the HWI (Equation 1, Cairns & Schwager, 1987), and the SR (Equation 2, Ginsberg & Young, 1992):

$$\text{HWI} = \frac{X}{X + \frac{1}{2}(Y_a + Y_b)} \quad (1)$$

$$\text{SR} = \frac{X}{X + Y_a + Y_b} \quad (2)$$

where:

X = the number of times both individual a and b were seen together in the same group,

Y_a = the number of times individual a was seen, and

Y_b = the number of times individual b was seen.

The social organisation of the population was graphically represented for the entire study period using a hierarchical cluster analysis (average linkage method) of the HWI and SR matrices. This technique clusters individuals not only by preferred partnerships, but also using least preferred partners (Whitehead, 1999a). The significance of the association indices of all possible pairs (or dyads) of animals in the sample used, and, therefore, the significance of the groups discriminated by the cluster analyses, was assessed using a Monte Carlo randomisation approach (Manly, 1995; Bejder *et al.*, 1998; Whitehead, 1999b). In this test, individuals within groups were randomly permuted, keeping group size, and the number of times each individual was seen, the same as in the original dataset.

The permutation test “permute groups within samples”, within the SOCPROG program, was further utilised to test the null hypothesis that the distribution of association indices from the empirical data was not different from that of the permuted data sets. In other words, that there are no preferred or avoided companions (individuals who preferentially grouped together or avoid one another), given the total number of groups each animal was seen in during the present study. Whilst this test takes into account that individuals sighted in many groups are likely to group together at random, it also accounts for situations in which not all individuals are present for each sampling interval (because of birth, death or migration, for example). Following the methods of Bejder *et al.* (1998) and Whitehead (1999a), the number of permutations performed in this test was increased until the P value obtained from the Monte Carlo simulation became stabilised and the confidence intervals decreased. If more than 95% of the expected HWI or SR were found to be smaller than the observed HWI or SR, a pair of dolphins was defined as a preferred companionship, i.e. the pair of dolphins was more likely to be seen together than by chance.

A Mantel test, using 1000 permutations, was utilised to examine the dataset for differences in association depending on sex. To determine the stability of associations among individuals, variations in lagged association rates (i.e. the average rates of association over time) were further calculated for all associations. The proportion of companions that any one individual had at time t , that remained companions at time $t + d$, where d is the time lag, was calculated and averaged over all individuals selected. Precision was estimated by jack-knifing this data over a typical sampling trip (1 day), and lagged association rates were then compared to the null association rate (representing the lagged association rate of the dataset if individuals were associating at random) to determine whether or not preferred associations were present in the dolphins selected.

The temporal pattern of association of the dataset used in the present analysis was then compared to models of social organisation, as developed by Whitehead (1995). These models consider three types of associates: constant companions that stay associated until death, casual acquaintances that disassociate over time, and rapid disassociations (associates that disappear quickly). The best model was subsequently selected for using maximum likelihood and binomial loss techniques (see Whitehead, 1995; 1999a).

In the analysis of group size, descriptive statistics, Komolgorov-Smirnov normality tests, Levene Median tests for equal variance, Kruskal-Wallis tests and Mann-Whitney-U tests were performed using MINITAB version 13 (Minitab Inc., 1999). If the data passed the tests of normality and equal variance, parametric tests were used. If the data failed a test of normality, but passed an equal variance test, nonparametric tests were used accordingly. Throughout this thesis, mean values are expressed as the mean \pm one standard deviation (\pm SD).

4.

Results

4.1. Survey effort and sightings

Thirty-two boat surveys were conducted on 25 days during the 9-week study period in 2003 (Table 4.1). The survey effort totalled 94.58 hours, of which 24.51 hours were spent observing and photographing dolphin groups on 14 separate encounters.

For the period 1997 – 2002, a total of 206 surveys were conducted on 178 survey days, producing a total survey effort of 429.29 hours, of which 128.97 hours were spent with dolphins on 119 encounters.

Table 4.1. Showing the survey effort and encounter information for all boat trips recorded in the present study and by the CRRU for the period 1997 to 2003.

Study period	No. of survey trips	Total no. of survey days	Total survey hours	Total encounter hours	Total no. of encounters made
2003 (present study)	32	25	94.58	24.51	14
1997 - 2002	206	178	429.29	128.97	118
Total period	238	203	523.87	153.48	132

4.2. Group size and composition

For 2003, the group sizes of bottlenose dolphins ranged from 2 to 29, with a mean size of 13.0 ± 9.27 , median = 12.0 (Figure 4.1 a). The most frequently encountered group sizes contained between 6 to 10 or 21 – 25 animals.

For the period 1997 – 2003 the group size data were pooled (Table 4.2), since a Kruskal-Wallis-Test showed that group sizes for each year were not significantly different from one another ($p = 0.336$, d.f. = 6, $H = 6.84$). The mean school size for all seven years was thus calculated as 11.07 ± 7.93 , with a median value of 9.0. Single animals were not commonly observed and the largest group recorded for the period totalled 44 animals.

The frequency distribution of group sizes was skewed towards smaller groups (Figure 4.1 b), yet more than 45% of the groups encountered were larger than 10 individuals. The larger schools seemed to increase in frequency with the progression of the field season (Figure 4.2), but

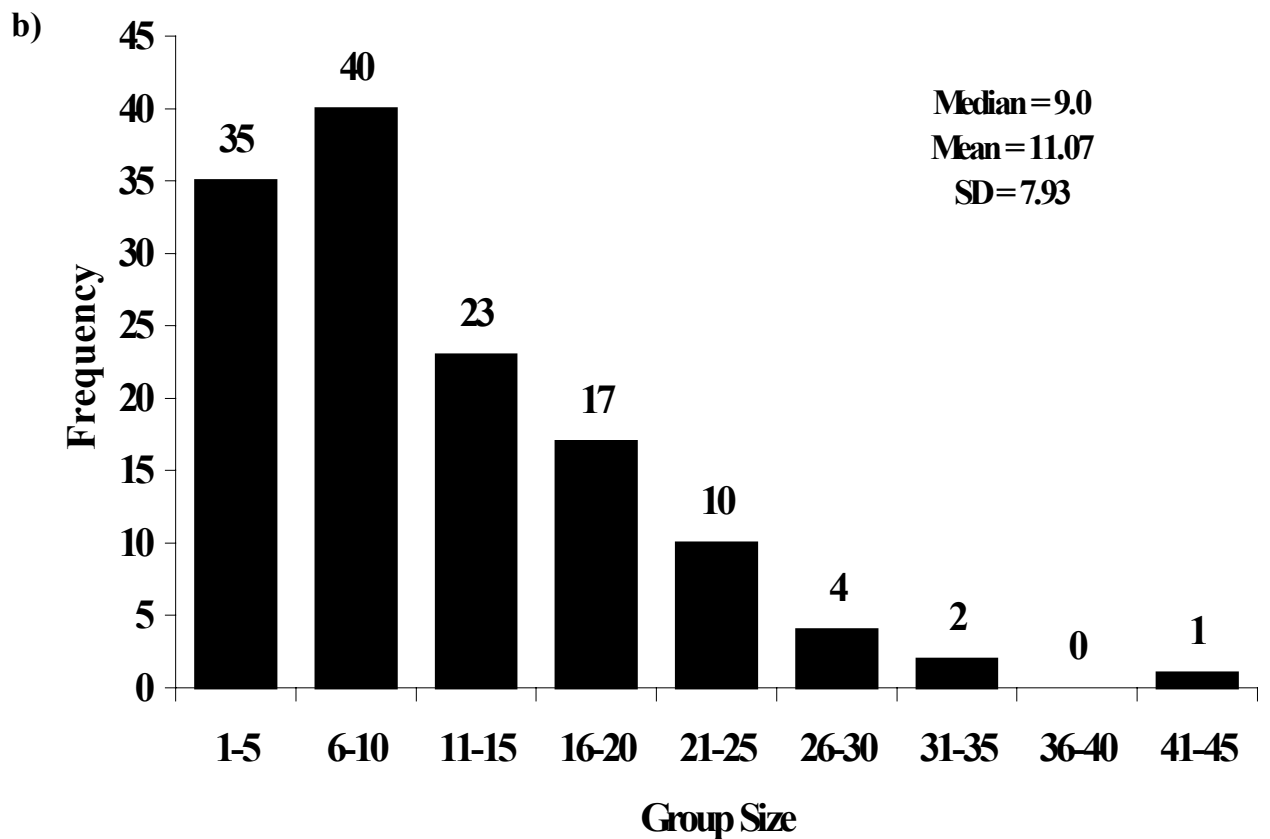
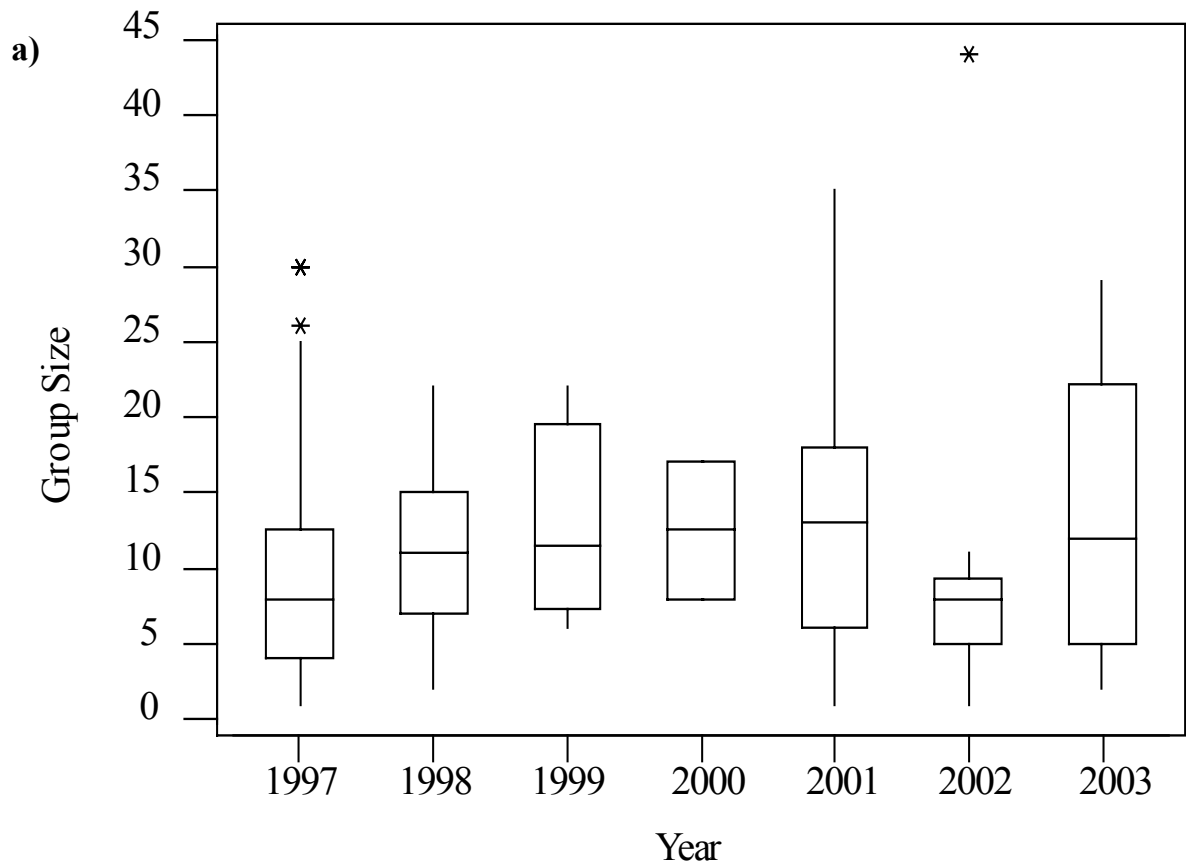


Figure 4.1. (a) Showing the variations in school size of bottlenose dolphins in the southern outer Moray Firth from one year to the next. The horizontal lines inside the boxes represent the median, the whiskers above and below the boxes show the interquartile ranges, and the asterisks denote outliers. (b) Frequency distribution graph of the group sizes for the total period 1997 to 2003 (n = 132).

Table 4.2. Showing the group size statistics for encountered bottlenose dolphin groups recorded from 1997 – 2003.

Year	Cumulative no. of dolphins	Mean group size	Standard deviation	Median	Min. count	Max. count
2003 (present study)	182	13.00	9.27	12.0	2	29
1997 – 2002	1300	10.92	7.77	9.0	1	44

a Kruskal-Wallis-Test showed no significant differences in group sizes between months ($p = 0.285$, d.f. = 4, $H = 5.02$). The data for October were not included in this analysis, because only one group was encountered in this month between 1997 and 2003.

During this study, it was extremely difficult to record sub-groups in any detail during an encounter, due to the extremely fluid structure and changeability of the dolphin associates within the study area, particularly in the larger, dispersed groups. Calves, for example, took every opportunity to leave their mothers to take a free ride on the bow of the boat, meeting with other youngsters and sub-adults and thereby resulting in an immediate change in the composition of the group in our presence. Even, when viewed from some distance, the sub-groups were seen to alter almost continuously.

Of 132 encounters recorded between 1997 and 2003, 124 provided data that could be used in an analysis of group composition. Of these, 96 (77%) of the groups analysed had one or more calves present. Calves were sighted in all survey months, but neonate calves (newborns) were only observed from July to October (see table 4.3). Groups containing calves, both excluding calves from the analysis (median group size = 8.5) and including calves (median group size = 11), were significantly larger than groups without calves (median group size = 4) ($P < 0.001$, Mann-Whitney-U-test). 11% of the groups recorded had one or more neonates present and all groups with one or more neonates also contained one or more calves. 63% of the groups had one or more sub-adults present. 72% of those groups with sub-adults also contained one or more calves. 6% of the groups were comprised only of sub-adults. Group sizes for those purely sub-adult groups (median = 3) were, however, significantly smaller than group sizes containing both adults and sub-adults (median = 10) ($P < 0.001$, Mann-Whitney-U-test), ranging from one to five dolphins.

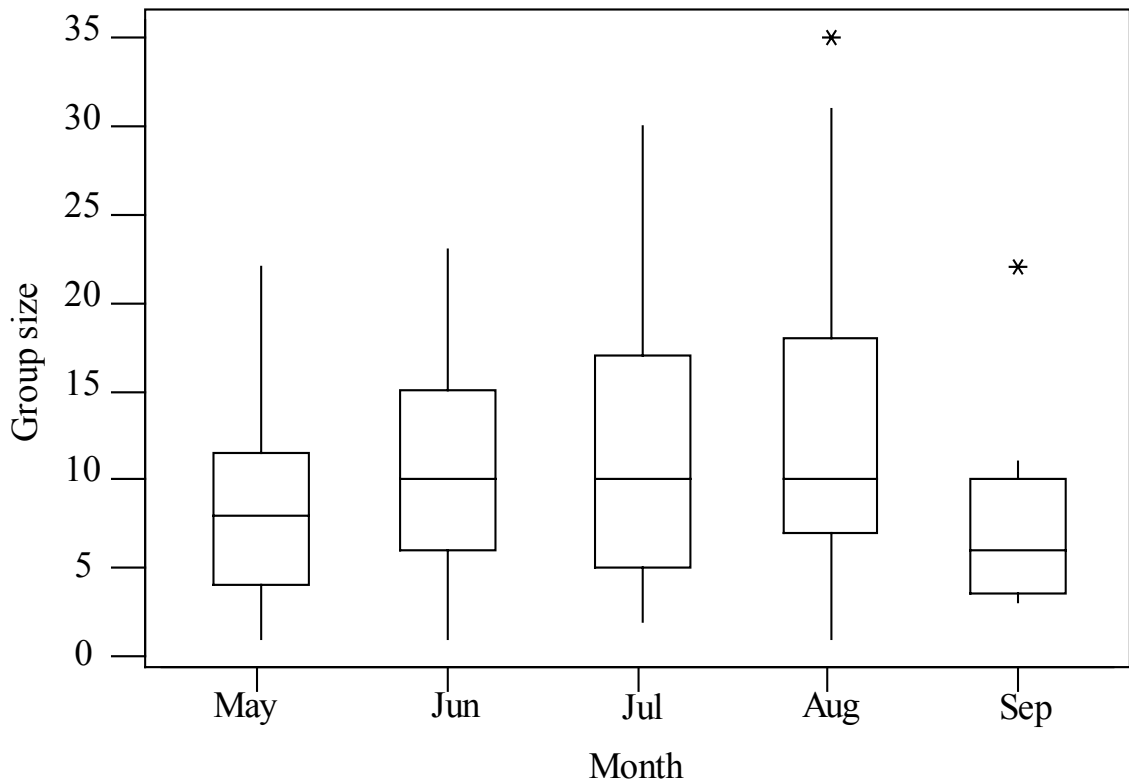


Figure 4.2. Showing monthly variations in school sizes of bottlenose dolphins in the southern outer southern Moray Firth, combining data from 1997 to 2003. Horizontal lines inside the boxes represent the median, the whiskers above and below show the interquartile ranges, and the asterisks denote outliers.

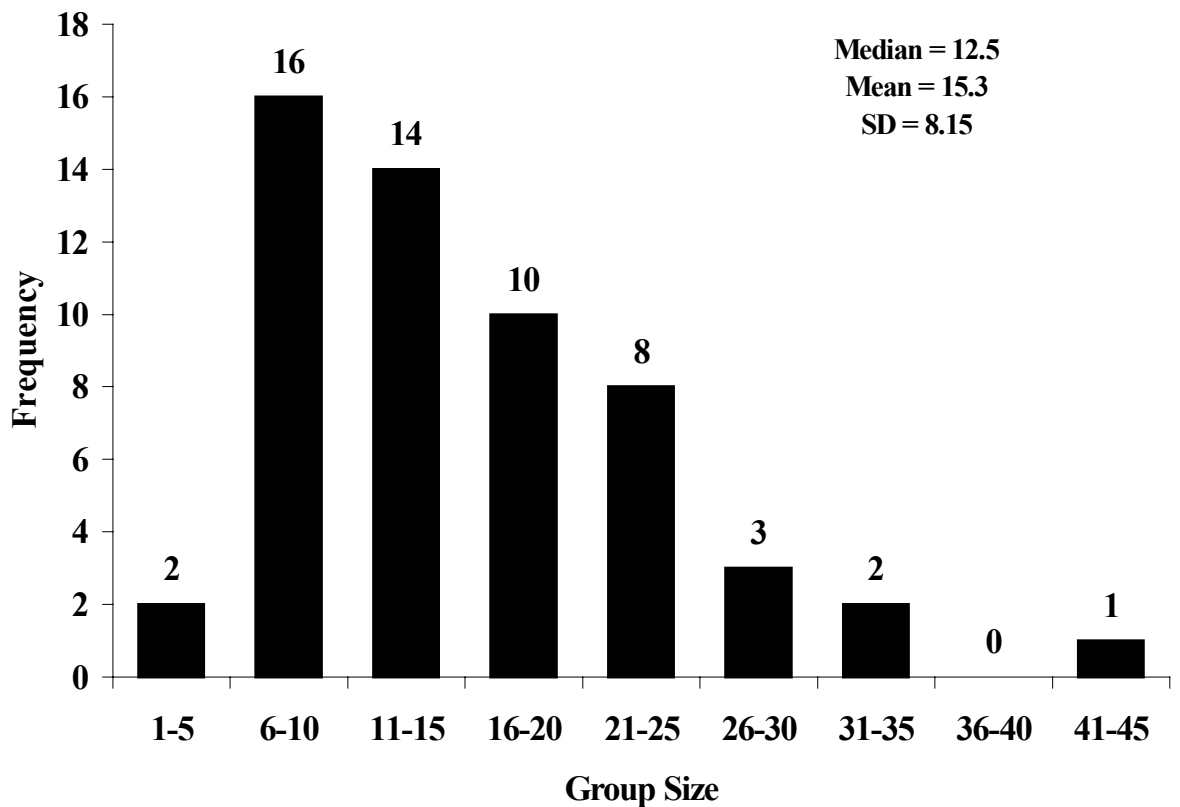


Figure 4.3. Shows a frequency distribution graph of the bottlenose group sizes for known mixed-sex groups recorded between 1997 and 2003 (n = 56).

Table 4.3. Individual neonates recorded between 1997 and 2002 (none were recorded in 2003)

Month	No. of neonates
May	0
June	0
July	3
August	4
September	3
October	5

Of the 132 groups recorded in the CRRU bottlenose archive, 56 (42%) were found to be of mixed sex, as indicated by the presence of at least one known adult male and one known adult female. Forty-nine of the mixed-sex groups also contained calves, further indicating groups of mixed composition since calves typically accompany their mothers for several years (Wells *et al.*, 1987; Smolker *et al.*, 1992). The sexual composition of the remaining 77 groups could not be determined. For the 56 confirmed mixed-sex groups (median = 12.5), group sizes were significantly larger than those reported for all 132 groups (median = 9) ($P < 0.001$, Mann-Whitney-U-test). The range of mixed-sex groups, from 4 to 44 dolphins, was slightly narrower than the total range and shifted towards larger group sizes (Figure 4.3).

4.3. Individuals identified

One hundred and eighty two bottlenose dolphins including adults, sub-adults and calves were photographically identified between the months of July 1997 and August 2003. Each of these was seen at varying frequencies up to a maximum of 22 times. Twenty-two dolphins (12%) were positively identified as males by lack of association with a calf or observation of their genital slits. Fifty-three dolphins (29%) were identified as females based on consistent association and synchronized surfacings with a calf or observation of genital and mammary slits. Ninety-four individuals (52%) of the animals archived exhibited dorsal edge marks (or DEMs).

From this pool of individuals with DEM's, forty distinctive individuals recorded 5 or more times (capture-recapture) were selected for the analysis of association (Table 4.4, see also appendix B for photographs). Of all individuals selected, 19 were known adult females, 17 were

Table 4.4. Individual bottlenose dolphins used in the analysis of association. M = male, F = female, A = adult, SA = sub-adult

ID #	Name	Sex	Age	No. of recaptures
1	Sharky	M	A	7
2	Jagged Edge	M	A	9
3	Thatcher	F	A	8
4	Spearhead	M	A	5
5	Sunrise	F	A	19
9	Spike	M	A	11
10	Sailfin	M	A	11
14	Ziggy	M	A	5
15	Sooty	F	A	9
19	Carter	M	A	10
20	Trekky	M	A	6
21	Paper clip	M	A	11
26	Punch	F	A	7
37	Pearly	F	A	10
46	Double U	F	A	5
55	Runny Paint	M	A	10
61	Scratchy	M	A	15
63	Chunks	M	A	7
64	Hubbs	F	A	6
65	Muddy	F	A	19
66	Goblin Seal	M	A	12
67	Bucks Fizz	F	A	17
69	Singers	M	A	20
71	Chanonry	M	A	9
72	Yorkie	F	A	11
74	Georgia	F	A	18
77	Allegranzi	M	A	18
78	Guinness	F	A	5
81	Shadow	F	A	10
89	Happy Dragon	F	A	6
102	Salami	?	SA	7
115	Voodoo Head	M	A	8
118		F	A	5
119	Spot	?	SA	7
122		F	A	8
134	Julia	F	A	5
145	Craig	?	SA	6
197	Lower Nick	F	A	14
216	Sax	F	A	10
274	Sparks	?	A	7

known adult males and 4 were of unknown sex. The number of recaptures ranged from 5 to 22 times with a mean of 9.90 ± 4.62 (Figure 4.4).

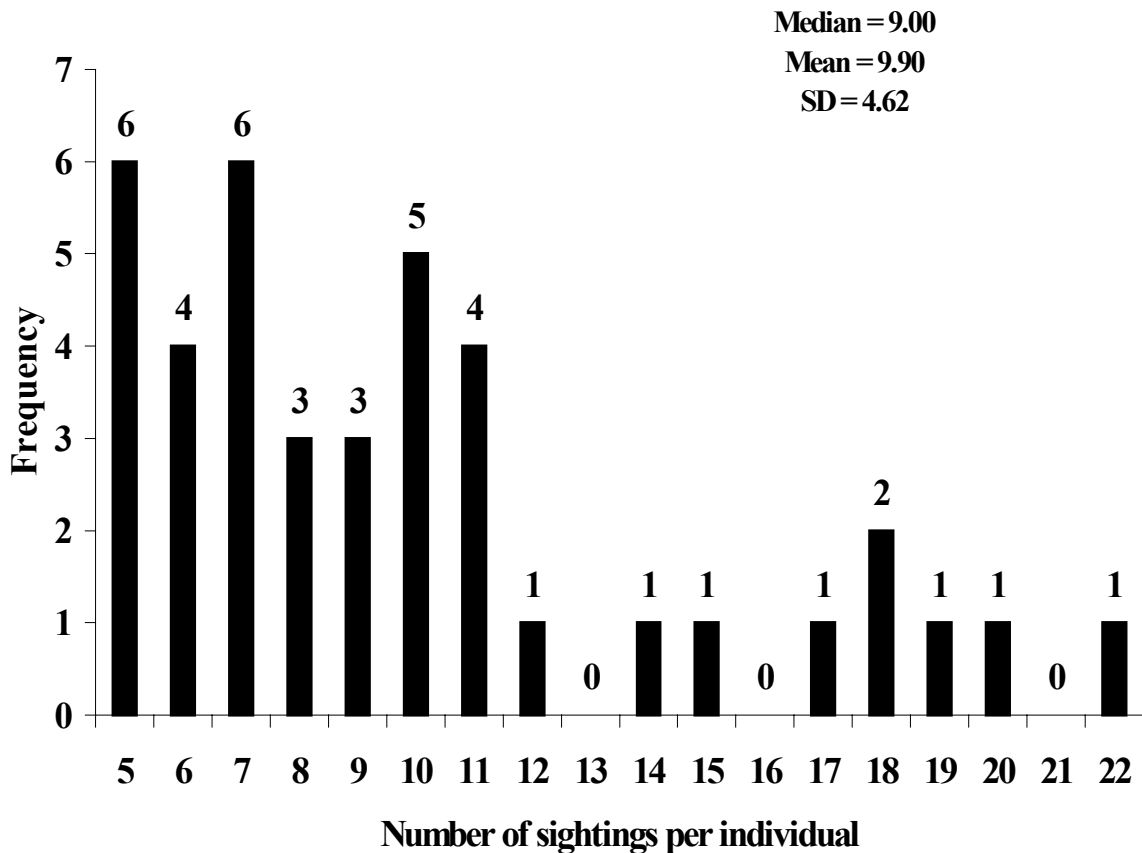


Figure 4.4. Sightings frequency for all photographically identified individuals used in the analyses of association seen ≥ 5 times ($n = 40$).

4.4. Association Patterns for the individuals selected

The number of affiliates was found to range from 2 to 32, with a median of 24. Since, the half-weight index (HWI) and the simple ratio (SR) analyses used in the present study produced very similar results, only the HWI is presented in the forthcoming results.

The distribution of CoAs for all individuals ($n = 1600$) was clearly skewed towards lower values with many of the sample animals showing no association at all with some others (Figure 4.5 a). Coefficients of association for individuals ranged from 0.00 to 0.73, with a mean of 0.11 ± 0.04 . The most frequently occurring levels were 0.00 (no association) and 0.30. The distributions of the mean CoA and the maximum CoA for each dolphin are shown in figure 4.5 b, c, and table 4.5 respectively. The mean CoAs were found to range from 0.02 to 0.18 (Figure 4.5b), with the most frequently CoAs occurring between 0.06 and 0.15. The maximum CoAs ranged from 0.30 to 0.73 (Figure 4.5c).

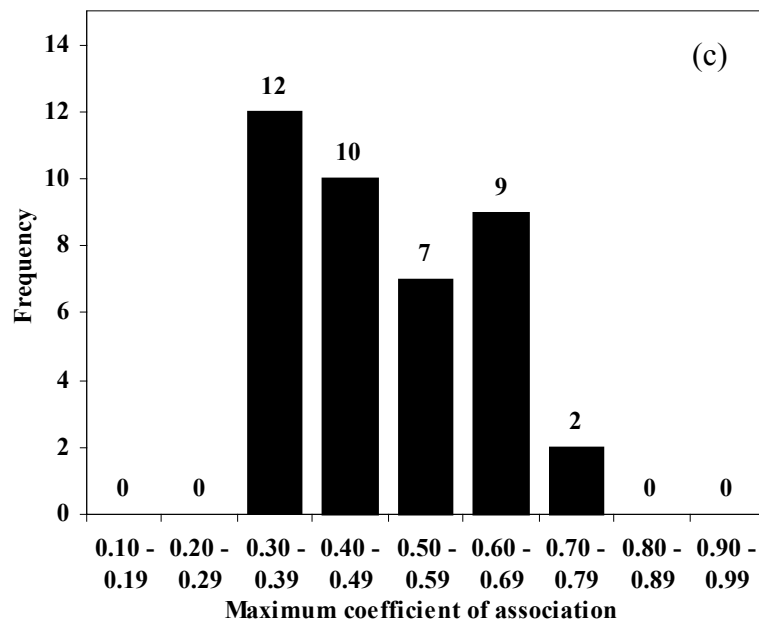
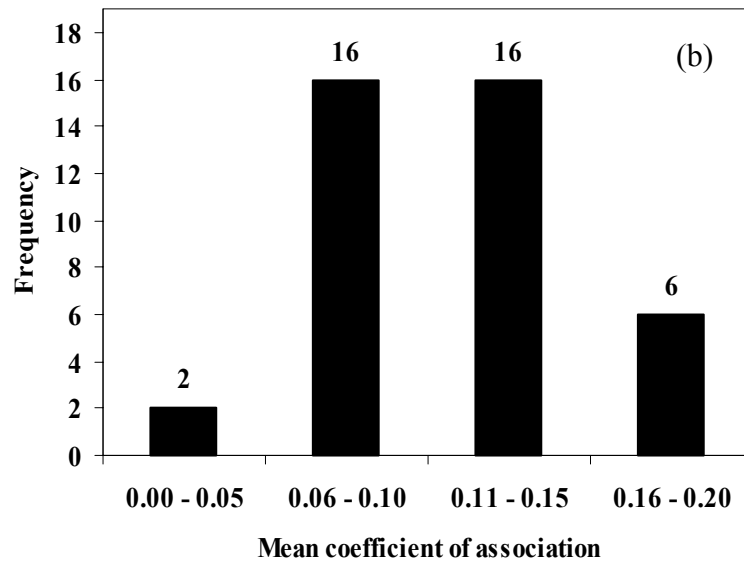
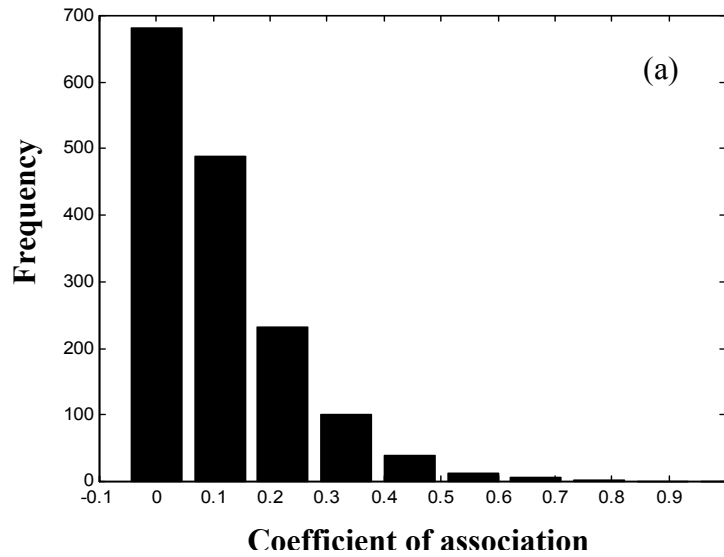


Figure 4.5. The frequency distribution of CoAs of the selected 40 individual dolphins identified ≥ 5 times: (a) shows the distribution for all pairwise comparisons ($n = 1600$), (b) shows the mean CoA for each individual, and (c) shows the distribution of maximum CoAs for each individual.

Interestingly, associations between and within sex classes were not found to be significantly different (Mantel test, $t = 0.024$, $p = 0.51$). Inter-sexual associations were seen to be as strong as intra-sexual associations (Table 4.6). Whilst there was no tendency for either male – male, female-female or female-male associations to be stronger than one another, the maximum and mean HWI within the different sex groups were seen to follow a slightly different trend (table 4.6). However, the variation observed between sex classes indicates inconsistency of the HWI from the mean to the maximum amongst individuals within the sample.

Figure 4.6 illustrates the male (a) and female (b) associations using sociograms. In the outer, southern Moray Firth, both sex classes were found to show a tight network of associations with 24% of the males and 21% of the females displaying a HWI of ≥ 0.50 . All males and females in the sample were found to have a considerable number of associations of variable strength, with ID numbers # 21 and # 1 (both males) and ID # 15 (female) displaying the highest.

It was apparent from the sociograms that a number of dolphins of both sexes spent more time with certain other individuals of the same sex. Number 9 (Spike) and # 10 (Sailfin), both males, for example showed the highest HWI of all. Furthermore, the male dolphins # 69 (Singers), 66 (Goblin Seal) and 61 (Scratchy) showed multiple associations with other males, but all formed a strong triad between themselves with the strongest association existing between # 69 and # 66.

Similarly, in the female network, the highest HWI occurred between # 3 (Thatcher) and # 134 (Julia). Three triads (#'s 3, 5, 15; #'s 26, 78, 47 and #'s 74, 197, 216) were also apparent, but once again all of the members of each triad were however seen to maintain additional associations within the network with other female dolphins. The only exception to this was the female # 134 (Julia), who was not seen to form such multiple relationships, but had only one, but very strong association.

The association dataset was randomly permuted 20,000 times and the resulting permuted mean coefficient of association was not found to be significantly higher than the observed mean (random, permuted, mean = 0.10819, observed mean = 0.10836, $p = 0.87520$) suggesting that observed individuals did not show preferred or avoided preference/tendency for associations, but instead tended towards random associations over the 7 years of the study. In addition, the observed standard deviation was found to be slightly lower than the random one (observed SD = 0.12735, random SD = 0.12790), further suggesting a random association between individuals as described by Whitehead (1999a). The permutation test supported these findings as no dyads were seen to be significantly different from the permuted data, even though 37 dyads were expected to be different (as derived from SOCPROG 1.3).

Table 4.5. The mean and maximum coefficients of association (half-weight index, HWI) for the bottlenose dolphin sample used in the present study, as derived from SOCPROG version 1.3 (standard deviations not available).

ID #	Name	Mean HWI	Maximum HWI
1	Sharky	0.12	0.40
2	Jagged Edge	0.07	0.30
3	Thatcher	0.07	0.67
4	Spearhead	0.08	0.44
5	Sunrise	0.11	0.38
9	Spike	0.13	0.73
10	Sailfin	0.13	0.73
14	Ziggy	0.08	0.40
15	Sooty	0.15	0.32
19	Carter	0.08	0.32
20	Trekky	0.08	0.60
21	Paper clip	0.11	0.32
26	Punch	0.08	0.36
37	Pearly	0.12	0.36
46	Double U	0.11	0.44
55	Runny Paint	0.13	0.35
61	Scratchy	0.17	0.53
63	Chunks	0.08	0.31
64	Hubbs	0.09	0.37
65	Muddy	0.16	0.53
66	Goblin Seal	0.16	0.62
67	Bucks Fizz	0.17	0.62
69	Singers	0.18	0.61
71	Chanonry	0.11	0.44
72	Yorkie	0.09	0.44
74	Georgia	0.13	0.56
77	Allegranzi	0.16	0.56
78	Guinness	0.09	0.67
81	Shadow	0.12	0.40
89	Happy Dragon	0.07	0.38
102	Salami	0.09	0.67
115	Voodoo Head	0.09	0.32
118		0.11	0.60
119	Spot	0.13	0.50
122		0.12	0.40
134	Julia	0.02	0.67
145	Craig	0.05	0.42
197	Lower Nick	0.10	0.50
216	Sax	0.12	0.50
274	Sparks	0.07	0.48

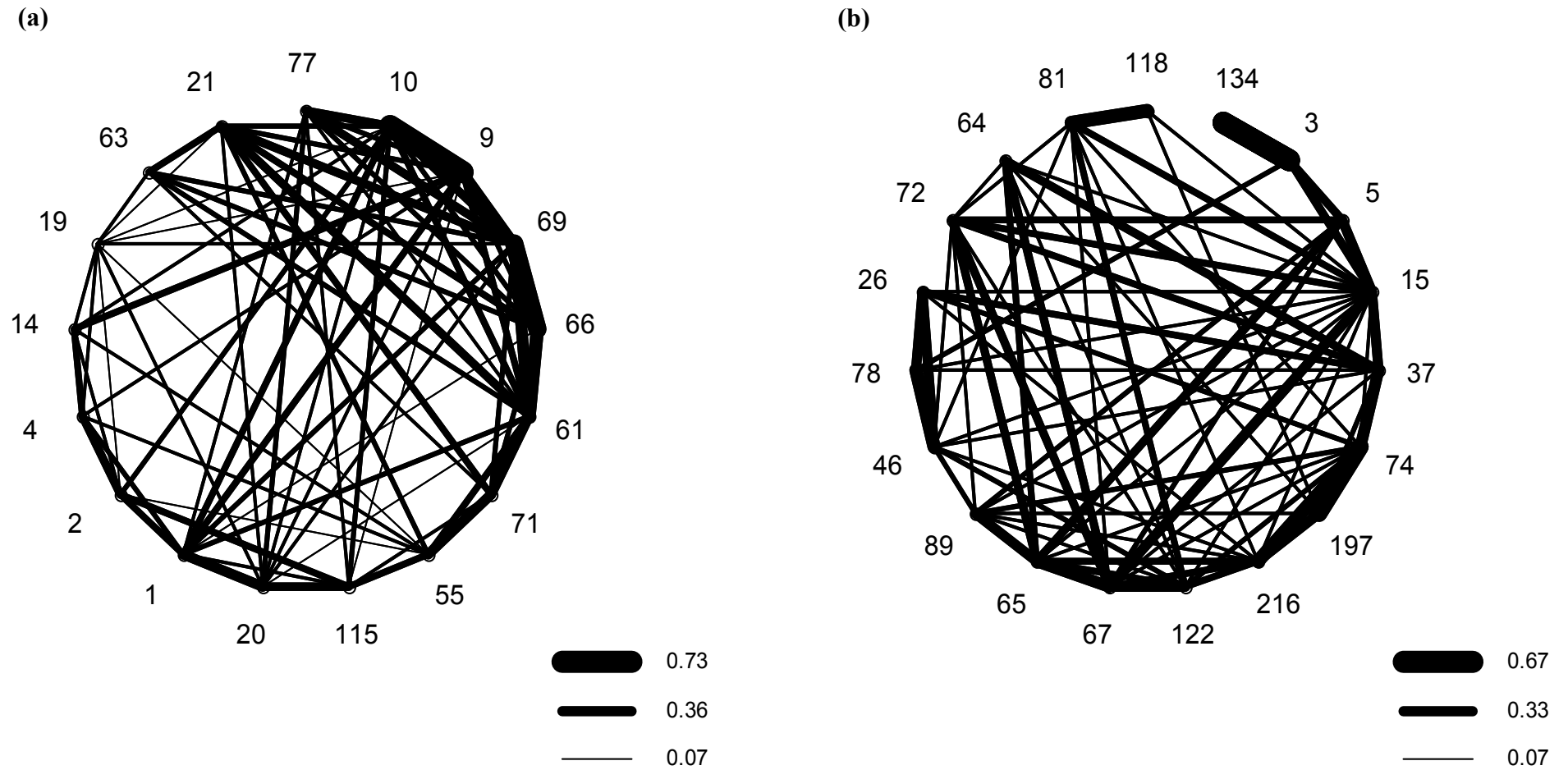


Figure 4.6. Sociogram representations of (a) male-male and (b) female-female half-weight coefficients of association. Dolphin identities are indicated by their ID-number. As indicated in the legend, lines of increasing thicknesses correspond to the increasing strength of pairwise associations.

Table 4.6. Mean and maximum half-weight index (HWI) between and within sex classes.

	Mean HWI (SD)	Maximum HWI (SD)
All individuals	0.11 (0.04)	0.48 (0.13)
Female – Female	0.10 (0.03)	0.40 (0.11)
Male – Male	0.12 (0.05)	0.39 (0.17)
Female – Male	0.12 (0.05)	0.40 (0.13)

Figure 4.7 shows a cluster analysis for all sex classes. No clear divisions were found in the community, the echelon pattern of the resulting dendrogram expressing no clear architecture, as defined by Lusseau *et al.* (2003), except for dyads, triads and their multiple networks. All individuals were found to form mixed-sex groups and were associated at a HWI of < 0.1 . As suggested by the earlier analyses, there were more mixed-sex pairs ($n = 10$) depicted than male-male ($n = 1$) or female-female pairs ($n = 2$). In mixed sex dyads, association indices ranged from 0.31 – 0.62, whilst a range of 0.32 – 0.66 was seen in female dyads. The highest association index, however, was found to occur between two known males, # 9 (Spike) and # 10 (Sailfin), with a HWI of 0.73 (Table 4.7). There were two male-female-male triads (#'s 66, 67, 69, and #'s 71, 72, 55), with a higher HWI between one of the males with the female, but with the possibility of the two males sharing the female.

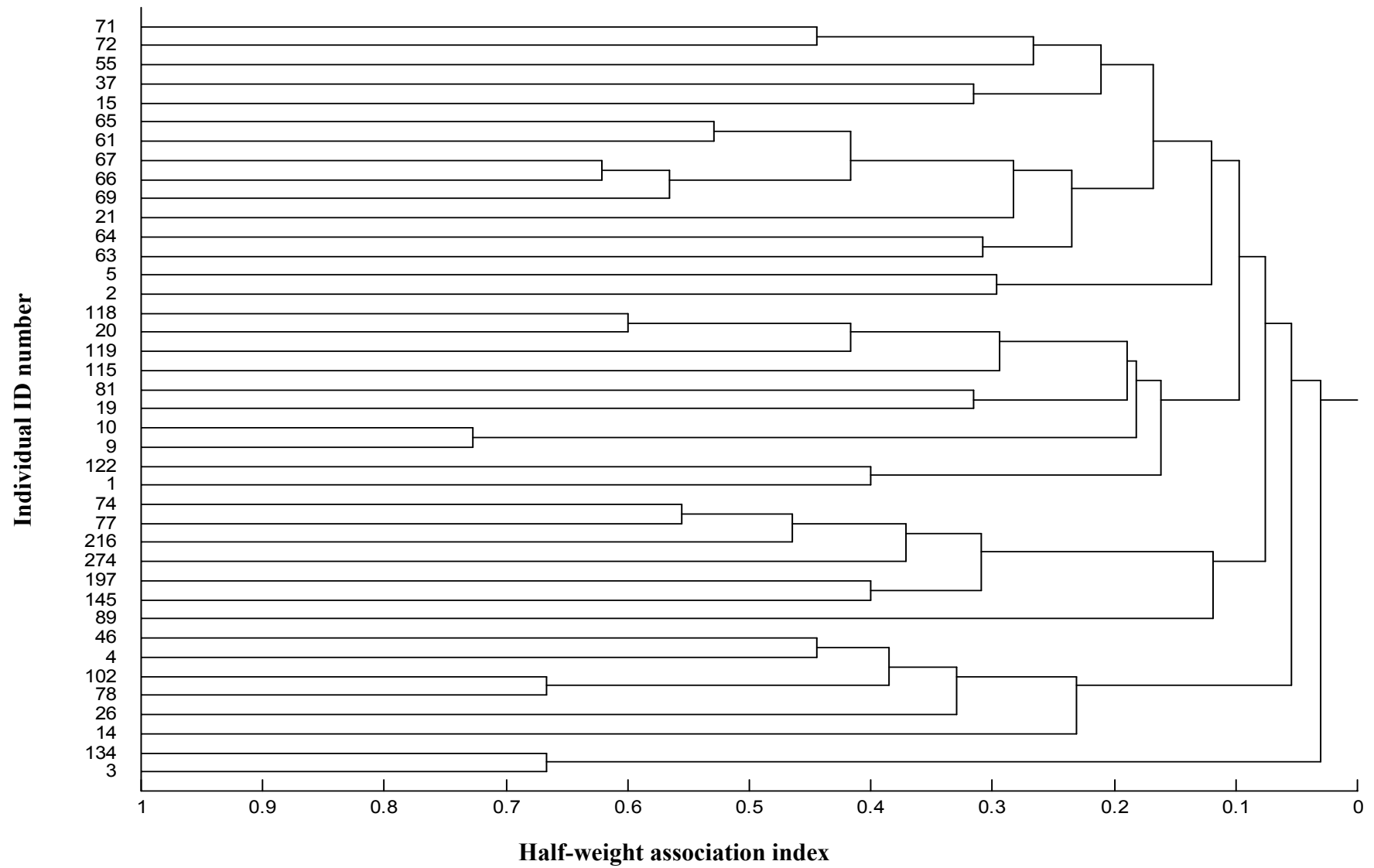


Figure 4.7. Dendrogram showing the average-linkage cluster analysis of associations between well-marked individual bottlenose dolphins seen ≥ 5 times in the outer southern Moray Firth, from 1997 - 2003.

Table 4.7. Association matrix showing the HWI for the 40 individual bottlenose dolphins sampled. Resulting coefficients for pairs of individuals range from 0.00 (= never sighted together) to 1.00 (always sighted together). Only the lower triangle is shown, since the matrix is symmetrical.

9	1.00
10	0.73 1.00
1	0.22 0.22 1.00
2	0.10 0.19 0.24 1.00
4	0.13 0.00 0.18 0.29 1.00
5	0.07 0.07 0.08 0.30 0.10 1.00
122	0.11 0.11 0.40 0.11 0.17 0.08 1.00
3	0.00 0.00 0.00 0.12 0.00 0.25 0.00 1.00
14	0.25 0.13 0.00 0.13 0.22 0.09 0.00 0.17 1.00
15	0.10 0.20 0.13 0.21 0.00 0.31 0.12 0.25 0.29 1.00
19	0.10 0.10 0.00 0.11 0.15 0.15 0.12 0.13 0.14 0.11 1.00
20	0.13 0.13 0.33 0.00 0.00 0.09 0.00 0.17 0.00 0.00 0.14 1.00
21	0.19 0.19 0.00 0.00 0.00 0.15 0.22 0.24 0.00 0.11 0.11 0.13 1.00
26	0.11 0.00 0.00 0.12 0.36 0.08 0.00 0.00 0.17 0.13 0.13 0.00 0.00 1.00
37	0.10 0.10 0.00 0.20 0.29 0.07 0.00 0.00 0.13 0.32 0.00 0.00 0.00 0.24 1.00
55	0.10 0.00 0.00 0.10 0.14 0.15 0.22 0.12 0.13 0.21 0.11 0.00 0.20 0.24 0.30 1.00
46	0.13 0.00 0.17 0.00 0.44 0.00 0.15 0.00 0.40 0.14 0.00 0.00 0.00 0.33 0.13 0.13 1.00
72	0.00 0.10 0.00 0.10 0.00 0.22 0.11 0.00 0.00 0.21 0.00 0.00 0.00 0.00 0.20 0.20 0.13 1.00
61	0.23 0.23 0.18 0.00 0.00 0.38 0.17 0.09 0.00 0.25 0.00 0.10 0.32 0.00 0.08 0.24 0.10 0.16 1.00
63	0.00 0.00 0.00 0.00 0.00 0.08 0.00 0.00 0.00 0.25 0.13 0.00 0.24 0.14 0.24 0.00 0.00 0.00 0.18 1.00
64	0.00 0.00 0.00 0.00 0.00 0.09 0.14 0.00 0.00 0.13 0.00 0.00 0.25 0.00 0.25 0.13 0.00 0.13 0.19 0.31 1.00
65	0.27 0.27 0.15 0.00 0.00 0.28 0.22 0.00 0.00 0.14 0.07 0.08 0.28 0.00 0.07 0.21 0.08 0.28 0.53 0.08 0.24 1.00
66	0.17 0.17 0.11 0.00 0.00 0.14 0.20 0.11 0.00 0.19 0.10 0.00 0.27 0.00 0.09 0.09 0.12 0.09 0.44 0.21 0.33 0.52 1.00
67	0.07 0.14 0.08 0.07 0.00 0.18 0.32 0.08 0.00 0.31 0.08 0.09 0.22 0.00 0.15 0.30 0.09 0.30 0.31 0.25 0.26 0.39 0.62 1.00
69	0.38 0.31 0.21 0.00 0.00 0.16 0.21 0.07 0.08 0.20 0.13 0.15 0.32 0.00 0.13 0.06 0.15 0.13 0.39 0.21 0.37 0.45 0.61 0.53 1.00
71	0.00 0.00 0.00 0.00 0.00 0.24 0.00 0.13 0.00 0.24 0.00 0.00 0.22 0.00 0.11 0.33 0.15 0.44 0.35 0.13 0.29 0.22 0.20 0.24 0.21 1.00
77	0.21 0.28 0.16 0.00 0.00 0.06 0.23 0.08 0.09 0.15 0.07 0.17 0.07 0.08 0.21 0.07 0.09 0.07 0.12 0.08 0.08 0.16 0.20 0.23 0.31 0.00 1.00
78	0.13 0.00 0.00 0.00 0.44 0.09 0.00 0.17 0.20 0.14 0.00 0.00 0.13 0.33 0.13 0.27 0.40 0.00 0.10 0.00 0.00 0.00 0.00 0.00 0.15 0.00 1.00
81	0.19 0.29 0.12 0.00 0.00 0.07 0.22 0.00 0.13 0.21 0.32 0.13 0.10 0.00 0.00 0.20 0.13 0.10 0.16 0.12 0.00 0.07 0.09 0.15 0.19 0.22 0.21 0.00 1.00
89	0.00 0.00 0.15 0.00 0.00 0.17 0.14 0.00 0.00 0.13 0.00 0.00 0.00 0.00 0.00 0.18 0.13 0.38 0.00 0.00 0.32 0.22 0.09 0.07 0.00 0.17 0.00 0.00 1.00
102	0.11 0.00 0.29 0.00 0.36 0.00 0.13 0.00 0.17 0.00 0.00 0.00 0.00 0.29 0.12 0.12 0.33 0.00 0.00 0.00 0.15 0.08 0.11 0.08 0.07 0.00 0.00 0.67 0.12 0.00 1.00
74	0.00 0.07 0.24 0.00 0.00 0.00 0.15 0.00 0.00 0.15 0.00 0.00 0.00 0.16 0.36 0.00 0.09 0.00 0.06 0.16 0.08 0.11 0.13 0.11 0.15 0.00 0.56 0.00 0.14 0.17 0.16 1.00
115	0.11 0.21 0.13 0.22 0.00 0.00 0.13 0.00 0.00 0.12 0.00 0.31 0.00 0.00 0.11 0.22 0.00 0.22 0.09 0.00 0.00 0.00 0.00 0.32 0.00 0.13 0.15 0.15 0.22 0.00 0.13 0.00 1.00
118	0.25 0.25 0.33 0.00 0.00 0.00 0.00 0.00 0.20 0.14 0.14 0.60 0.00 0.00 0.00 0.13 0.00 0.00 0.20 0.00 0.00 0.08 0.00 0.09 0.23 0.15 0.26 0.00 0.40 0.00 0.00 0.00 0.31 1.00
119	0.22 0.22 0.29 0.00 0.00 0.00 0.27 0.00 0.00 0.00 0.13 0.33 0.12 0.00 0.00 0.35 0.00 0.12 0.27 0.00 0.00 0.15 0.11 0.17 0.21 0.13 0.24 0.00 0.35 0.15 0.00 0.08 0.27 0.50 1.00
134	0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.12 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 1.00
145	0.12 0.12 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.15 0.13 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 1.00
216	0.10 0.19 0.12 0.00 0.00 0.00 0.22 0.00 0.00 0.11 0.11 0.00 0.20 0.12 0.00 0.00 0.13 0.00 0.16 0.12 0.00 0.21 0.27 0.22 0.26 0.00 0.50 0.00 0.10 0.13 0.00 0.43 0.00 0.00 0.00 0.00 0.38 1.00
197	0.16 0.16 0.29 0.08 0.00 0.00 0.00 0.00 0.00 0.00 0.11 0.00 0.10 0.17 0.00 0.00 0.00 0.07 0.10 0.10 0.00 0.00 0.00 0.11 0.00 0.31 0.00 0.00 0.10 0.10 0.50 0.09 0.11 0.19 0.00 0.40 0.33 1.00
274	0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.13 0.00 0.00 0.00 0.24 0.00 0.00 0.00 0.00 0.14 0.00 0.08 0.11 0.08 0.07 0.00 0.40 0.00 0.00 0.15 0.00 0.48 0.00 0.00 0.14 0.00 0.00 0.24 0.29 1.00
	9 10 1 2 4 5 122 3 14 15 19 20 21 26 37 55 46 72 61 63 64 65 66 67 69 71 77 78 81 89 102 74 115 118 119 134 145 216 197 274

4.5. Temporal pattern

An analysis of the rates of associations between individuals over time showed that the association rate fell, over approximately 200 days, but then appeared to stabilise above the null association rate from 200 days to 27 years (see figure 4.8). Since this estimated lagged association rate (LAR) showed stabilisation above the null rate (the rate expected if individuals were associating at random) at longer time lags, long-term relationships are predicted to exist in this Moray Firth population. However, the error bars estimated at time lags of approximately 700, 5,000 (~ 14 years) and 50,000 days (~137 years) crossed the null association rate, showing high variation in such associations between the individuals used in this analysis.

The social-system model that was found to best fit the LAR curve describes three levels of associates: casual (short-term) acquaintances, constant (long-term) companions and rapid disassociations (associates that leave very quickly). The model curve fell until lags lasted approximately 80 days. This suggests that typically, individuals remained with a set of associates over periods of days (a mix of casual acquaintances and constant companions), but by the end of a few weeks, they had largely disassociated from all individuals except a smaller number of constant companions. The error bars on the LAR are quite large. Hence, it should be noted these are general trends, which therefore cannot predict the association pattern of all groups at all times. The level at which the lagged association rate stabilised relative to its maximum may be interpreted as the proportion of the total number of dolphins present in the short term that actually remained with a given individual.

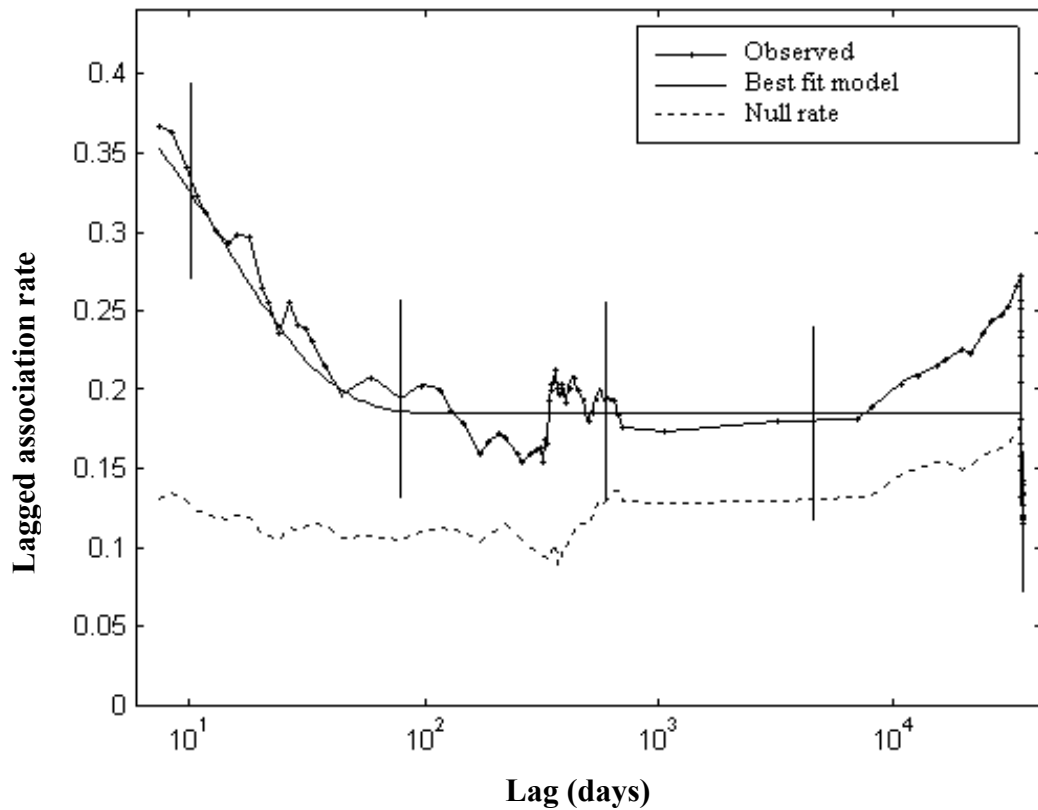


Figure 4.8. A graph to show the lagged association rate for the individuals selected for analyses in the present study. The moving average over 1200 associations is shown. Approximate error bars were generated by jack-knife technique (± 1 standard error). The maximum likelihood best fit model represents associations with rapid disassociation, casual acquaintances and constant companions. The null association rate represents the theoretical lagged association rate if individuals associated randomly.

5.

Discussion

5.1. Sociality and group size in bottlenose dolphins

Bottlenose dolphins are highly social mammals and the population of animals in the outer Moray Firth is certainly no exception. Indeed, in the present analyses, over 99% of schools were found to comprise two or more individuals. Mean group sizes recorded for this area (11.07 ± 7.93) were well within the range reported for the species from other parts of the world (Table 5.1). Unfortunately, however, the definition of groups (*vis-à-vis* school, herd, pod) varies considerably between authors, making it impossible to compare school size data between different studies and geographic areas in any detail. For example, Wells *et al.* (1987) and Smolker *et al.* (1992) give clear and repeatable definitions (see section 3.1) of school size that are not compatible with one another. Conversely, Saayman & Tayler (1973) use a very loose definition of dolphin groups that states: “The mean size of schools [...] are based upon individual sightings, which in many cases incorporated several groups of animals widely dispersed”.

In general, delphinid species that inhabit more open, pelagic habitats are known to form larger groups (Norris & Dohl, 1980b), and this seems to hold true for bottlenose dolphins too (see review by Shane *et al.*, 1986). In temperate waters no less, the group size of bottlenose dolphins inhabiting coastal inlets and estuaries, such as the inner Moray Firth or the Shannon Estuary in Ireland, are found to be significantly smaller than in waters that resemble more the open sea, as in the present study area and in the coastal waters off of Aberdeen (Weir & Stockin, 2001) (Table 5.1).

Behavioural ecologists commonly attribute variation in group size to either food availability or predation pressure. As a habitat becomes more uniform, there are fewer refuges for prey. A common tactic for many fish or squid in such an environment is to aggregate together, which results in a patchy distribution of prey for dolphins. The dolphins subsequently take advantage of conspecifics, to lessen the difficulties in locating and controlling such patches (see Norris & Dohl, 1980b). Such an explanation might account for larger group sizes in the open waters of the Moray Firth, since larger dolphin schools would be better able to control and feed on the prey source (for examples see Evans, 1987; Similä & Ugarte, 1993). Cooperative feeding was very much a behavioural feature of the animals in this area. Members of a group were often observed to be widely dispersed during encounters, spread out in search of prey. Once located, aerial displays were used to call other members for assistance.

Conversely, the smaller group sizes recorded in the inner Moray Firth are thought to be related to the contrasting topography of this area. Wilson *et al.* (1997) found that dolphins showed a preference for feeding in deep, narrow channels subject to strong tidal flows. In this

more complex habitat, there are perhaps greater refuges for prey and, therefore, a tendency for fish to form smaller shoals. In conclusion, group size in the Moray Firth appears to be indirectly linked to the distribution and abundance of available prey.

Predation pressure might also contribute to school size in dolphin communities. Numerous studies on a variety of animal species have demonstrated that safety from predators often comes with increase in group size. Long-tailed macaques (*Macaca fascicularis*), for example, are seen to form larger groups in North Sumatra, where tigers (*Panthera tigris*), golden cats (*Felis temminckii*) and clouded leopards (*Neofelis nebulosa*) feed on primates, than on the island of Semeulue off the coast of Sumatra, where no feline predators are present (van Schaik & van Noordwijk, 1986). Similarly, in the open ocean, dolphins may seek protection from shark or killer whale attacks by aggregating in large groups (Wells *et al.*, 1980). In this respect, the size of bottlenose schools (Table 6.1) may be proportional to the pressures of predation from one geographic area to the next.

In the Moray Firth, the risk of predation is thought to be minimal. Of the shark species most commonly attributed to bottlenose dolphin predation worldwide, including the tiger shark (*Galeocerdo cuvier*), dusky (*Carcharhinus obscurus*), bull (*Carcharhinus leucas*) and great white (*Carcharodon carcharias*) (Wood *et al.*, 1970; Corkeron *et al.*, 1987; Connor & Heithaus, 1996; Mann & Barnett, 1999), no records exist for these species in the coastal waters of the Moray Firth (Biological Records Office, Marine Biological Association UK, Plymouth). That saying, predation upon marine mammals by killer whales, (*Orcinus orca*) (documented by Würsig & Würsig, 1979; Dawson *et al.*, 1998), has been recorded in Scottish waters, typically upon seals at Sumburgh Head in Shetland (Loates, 1997). Whilst examinations by the Scottish Agricultural College and the Royal Zoological Society of the stomach contents of stranded killer whales have found no evidence of dolphin predation by this species in UK waters (Bob Reid and Paul Jepson, personal communication), the infrequent presence of killer whales along the coastline of the present study area has been clearly defined (Robinson, personal communication). Thus, whilst predation pressure may be far less influential on group size and more immediate influences, such as the distribution and abundance of prey might be, it may still present a consideration.

Interference competition from conspecifics might further be influential on group formation. Wrangham (1980), for example, suggested that cooperative defence of food patches in primates might select for group living. Where food occurs in patches that can support a limited number of individuals, groups of relatives may defend those patches against conspecifics, or even other species (see Buss, 1981). In view of the latter, the very large numbers of harbour

Table 5.1 (a - c). The size of bottlenose dolphin schools recorded from studies carried out around the world. NG denotes where data were not given.

a)

Area	Location	Environment	Range	Mean (SD or SE)	Median	Reference
North Sea	Outer Moray Firth, Scotland	Coastal	1 - 44	11.07 (7.93, SD)	9.0	Present study
	Inner Moray Firth, Scotland	Exposed estuary	1 – 46	6.45 (0.31, SD)	4.5	Wilson, 1995
	Coastal waters of Aberdeenshire, Scotland	Coastal	1 – 60	8.0 (NG)	6.0	Weir & Stockin, 2001
Irish Sea	Cardigan Bay	Shallow, sandy bay	< 6 – 26	3.39 (0.20, SD) summer	NG	Bristow & Rees, 2001
				4.59 (0.47, SD) winter		
NE Atlantic	Shannon Estuary, Ireland	Narrow and steep sided estuary	2 - 20	6.54 (3.03, SD)	6.0	Duguid, in prep.
	Sado Estuary, Portugal	Enclosed estuary (<40m deep)	1 – 40	13.7 (9.2, SD)	NG	dos Santos & Lacerda, 1987
NW Atlantic	Cape Hatteras to Nova Scotia	Coastal	1 – 350	15.4 (0.7, SE)	NG	Kenney, 1990
SW Atlantic	Golfo San José, Argentine	Coastal	8 – 22	15.0 (3.28, SD)	NG	Würsig & Würsig, 1977
South Africa	SE Cape coast	Open coast	3 – 1000	140.3 (± 21.4)	NG	Saayman & Tayler, 1973
Western Australia	Shark Bay	Enclosed shallow bay	2 – 20	4.8 (2.7, SD)	4.0	Smolker <i>et al.</i> , 1992
New Zealand	Doubtful Sound	Deep coastal	NG	17.2 (NG)	14.0	Lusseau <i>et al.</i> , 2003

(b)

Area	Location	Environment	Range	Mean (SD or SE)	Median	Reference
Pacific	Southern California Bight	Open coast	2 – 20	19.8 (18.4, SD)	NG	Weller, 1991
	Californian coast	Open coast	1 – 139	19.5 (NG)	NG	Hansen, 1990
	Kino Bay, Gulf of California, Mexico	Shallow, sandy bay	1 – 125	15 (23.6, SD)	NG	Balance, 1990
	Gulf of California, Northern Gulf	Shallow, turbid and estuarine	1 – 60	10.1 (11.04, SD)	NG	Silber <i>et al.</i> , 1994
Eastern tropical Pacific	All	All five	1 – 10000	57.0 (NG)	10	Scott & Chivers, 1990
	Coastal	Coastal	NG	94 (NG)	12	
	Around islands	Around islands	NG	93 (NG)	20	
	Near-coastal	Near-coastal	NG	72 (NG)	12	
	Far-western	Far-western	NG	44 (NG)	9	
	Offshore	Offshore	NG	40 (NG)	10	
Gulf of Mexico	Sarasota Bay, Florida	Enclosed shallow bays and inlets	NG	7.0 (NG)	NG	Scott <i>et al.</i> , 1990
	Lower Tampa Bay, Florida	Enclosed bay with channels and passes	1 – 40	5.0 (4.9, SD)	NG	Weigle, 1990
	Port Aransas, Texas	Dredged channels	NG	3.8 (\pm 2.85) travel feed 6.9 (\pm 5.84) socializing	NG	Shane, 1990b
	Sanibel Island, Florida	Open bays, with seagrass beds	NG	2.4 (\pm 1.51) travel feed 7.4 (\pm 3.96) socializing	NG	Shane, 1990a

(c)

Area	Location	Environment	Range	Mean (SD or SE)	Median	Reference
Gulf of Mexico	San Luis Pass, Texas	Flat bays	1 – 29	10.6 (± 8.23)	10	Maze-Foley & Würsig, 2002
	Sarasota Bay, Florida	Enclosed shallow bays	1 – 39	7.04 (6.0, SD)	NG	Wells <i>et al.</i> , 1987
Bahamas	East and south coasts of Great Abaco Island	Shallow inshore waters	NG	107 (36.2, SD)	NG	Parsons <i>et al.</i> , 2003

porpoise (*Phocoena phocoena*) in the existing study area (Whaley, in prep.) might actively compete for food resources or interfere with the feeding activities of the bottlenose dolphins utilising the same area. In 1996, observations by Ross & Wilson (1996) exposed the violent interactions occurring between dolphins and harbour porpoises from post-mortem examinations of stranded porpoises and considered these reasons for such interspecific aggression. A similar phenomenon has been described by Kruuk (1972) between lions and hyenas; the two species competing for food which sometimes results in violence and the ultimate death or injury of either party.

Whilst predators, food availability and competition for resources may all serve to shape the size of groups in bottlenose dolphin populations, both the constraints and benefits of sociality may also play an important role. Bottlenose dolphins co-exist in a complex hierarchal structure in which subordinates are often forcefully reminded of their place. In this respect, the sociality of individual animals may be extremely influential upon group formation, producing school sizes proportionally larger or smaller than the optimum required for co-operative foraging or predation avoidance. Reproductive and the raising of young is a central biological requirement for the success of a population. In parts of the outer Moray Firth, such as Spey Bay for example, specific areas are believed to form important calving or nursery areas for the species (Robinson, personal communication), and the composition of groups at these locations is undoubtedly determined by such activity.

The mother-calf relationship in bottlenose societies is known to be the strongest of all bonds (e.g. Wells *et al.*, 1987; Smolker *et al.*, 1992; Wilson, 1995). In a social unit, however, it may be the responsibility of several individuals to protect, assist and interact with the young (e.g. Shane 1990a). It is generally believed that the majority of large, long-lived mammals share the

responsibility of successfully raising their young with related associates as well as non-related affiliates.

In the Moray Firth bottlenose population, individuals other than the mother may often help to protect the calves of affiliates against aggression by males. In 1998, Patterson *et al.* described the phenomenon of infanticide by male dolphins in the Moray Firth population. Since bottlenose females produce a single calf once every two to four years, male-inflicted infanticide may serve to increase the reproductive fitness of individual male suitors, similar to that reported in other mammalian species (Hrdy, 1979; Pusey & Packer, 1994). Females, therefore, may favour schools larger than those optimal for foraging to permit alloparental care and protection for their young (Norris & Dohl, 1980b). Protection against aggression by males, in the form of harassment (Connor *et al.*, 2000) may also promote grouping among females. Such behaviour might account for the significantly larger sizes of schools with calves than those without calves observed in the present study. Since females are arguably the most important resource for males (who may cooperate extensively to defend their interests against other males), the presence of so many males within schools in the present study, might be directly related to this interest. Males may join schools of already optimal size in search of oestrus females, for example, thus occupying larger groups and feasibly accounting for the predominance of mixed-sex groups observed in this study.

5.2. Group membership and organisation

The organisation of the bottlenose dolphin community in the outer Moray Firth is dissimilar to that seen in other bottlenose dolphin populations in that the animals appear to live in large mixed-sex groups where strong associations occur within and between both sexes. Perhaps unusually, no clear sub-units were found to exist in the society, yet some males and females tended to spend more time together than with others.

Many animal species live in stable social groups which are often of permanent membership. Killer whale pods (Balcomb *et al.*, 1982; Bigg, 1982; Bigg *et al.*, 1990; Baird, 2000) and naked mole rats (*Heterocephalus glaber*, Jarvis *et al.*, 1994), for example, live in the most stable groups known amongst mammals, with high levels of association recorded between the members of each group. In contrast, a wide variety of animal species also occur in groups with highly dynamic group memberships. Chimpanzees (*Pan troglodytes*, Goodall, 1986; Wrangham, 1986), spider monkeys (*Ateles* sp., Struhsaker & Leland, 1979), lions (*Panthera leo*, Schaller, 1972; Packer, 1986), humpback whales (*Megaptera novaeangliae*, Clapham, 1993) and Przewalski horses (*Equus przewalskii*, Rubenstein, 1986), for example, are all thought to live

within a social network of subunits which change frequently in composition; termed fission-fusion societies by Struhsaker & Leland (1979).

According to the definitions of Struhsaker & Leland, the Moray Firth bottlenose population seems to form such a society. In the present findings, the individuals examined were found to associate with a variable number of other individuals and were linked, at least indirectly, with all other members of the population to form a larger social network. The whole of the network was never observed together at any one time, but rather as smaller units and subunits of the network group. Schools photographed on one day often remained intact until the following day, when photographed again, or two groups that were seen separately on consecutive days were later seen together on the following day. The rates of change of the composition of these subunits (groups) were too difficult to quantify within the constraints of this study, since they were found to change in composition very quickly. Dispersion, however, must have lasted longer than a day since the dispersion of individuals into subgroups took place over a considerable range covering the coastline of the southern Moray Firth and beyond.

Rubenstein (1986) and Clapham (1993) suggested such fission-fusion societies arose when social species feed on food patches of variable size and quality. In the present study area, changes in the availability of prey species, for example, could cause the dolphins to leave one area or alternatively to occupy an area until a patch is depleted. The animals then move to other patches and fissioning occurs again. In the inner Moray Firth, changes in the distribution of fish have been linked to changes in the distribution of harbour seals, *Phoca vitulina* (Thompson *et al.*, 1996). Since the dolphins in the study area probably have a similar opportunistic diet to the seals, such an influence might conceivably affect the formation of long-term associations observed in the present analyses of association and even the dominance hierarchies no less.

A further consideration for the fluidity of social formation in this study might also be attributed to the differences in occurrence patterns and home ranges of the bottlenose dolphin population discussed. In many study areas, populations of bottlenose dolphins are known to be resident, staying within a limited area, year round and over several years (Corkeron, 1989; Wells, 1991a; Smolker *et al.*, 1992). At other locations, seemingly resident animals suddenly extend their usual range by hundreds of kilometres (Wells *et al.*, 1990; Würsig & Harris, 1990), whilst some populations make considerable annual migrations (Shane *et al.*, 1986; Kenney, 1990). Home ranges of individual dolphins within the same population can differ considerably as well. For example, Scott *et al.* (1990) found that adult female bottlenoses had very limited ranges which centred around productive sea grass meadows, whilst males moved over much wider ranges, visiting different female groups one after another. Some individuals in the present study were observed intermittently over several months from one year to the next, while others were

sighted during all months of the field season in one year, but not in the next (Figure 5.1). Interestingly, eight females (ID #'s 3, 5, 26, 64, 72, 78, 118 and 134) and five males (ID #'s 4, 14, 20, 55 and 71) selected for the analyses of association were not encountered in the study area since 2001 or longer, although several of these animals have been reported off the coast of Aberdeen (Sarah Canning², personal communication). It is interesting to note, that most of these individuals are positioned next to each other in the dendrogram (Figure 4.7; result section), i.e. many of these individuals may be affiliated at some level. It is apparent that the Moray Firth population has a considerable home range, with some individuals travelling several hundred kilometres. Recognisable animals from the Moray Firth population are reported with increasing regularity off the Aberdeen coastline and further south throughout the summer months (Weir & Stockin, 2001), and intimations have been made as to a possible southwardly shift in this northeast population (Paul Thompson, Aberdeen University, personal communication). The home range of this population is known to extend at least from Duncansby Head, the northern tip of the outer Moray Firth (Wilson, 1995), to Tyne-on-Wear in England, and it is apparent that dispersion, migration and substitution may all contribute to the fluidity of the present sample population.

Shane *et al.* (1986) observed a trend along the NE coast of the United States for increased migratory behaviour of bottlenose dolphins at greater latitudes. Based on these findings, the occurrence patterns of bottlenose dolphins in the Moray Firth (the world's highest latitude population of *Tursiops* yet studied) would be expected to be highly migratory in nature and concentrated in the summer months when the water in the Firth is warmest. Indeed, Wilson (1995) has shown for the inner Moray Firth that, although dolphins are observed in all months of the year (thereby indicating a resident population), the number of individuals shows an increase with rising sea temperature during the summer months. Similar seasonal fluctuations have been reported in several other studies (Shane, 1980; Balance, 1990; Weigle, 1990) and these have been attributed to the additive effect of incomers (migrants or offshore animals) joining an already resident population. Migratory movements throughout the present study area might conceivably be made to take best advantage of local conditions, making one area more preferable over another for foraging (Irvine *et al.*, 1981), raising of calves (Scott *et al.*, 1990), mating (Wells *et al.*, 1980) and/or predator avoidance (Wells *et al.*, 1980).

Human activities can also affect the social behaviour of mammals through the modification of habitats, changes in predation pressure or by alterations in food distribution and availability. In terms of anthropogenic food sources, delphinids exhibit great flexibility in their

² Regional South-Grampian co-ordinator for the Sea Watch Foundation

foraging strategies (Baird, 2000; Connor *et al.*, 2000) and feeding co-operatives exist which may discretely modify social structure.

Trawling, for example, is known to affect both the behaviour of bottlenose dolphins and their community membership (Chilvers & Corkeron, 2001). Whilst cooperative feeding associations with fisheries exist in which the dolphins derive a tangible benefit, the adverse effects of fishing, such as entanglement in nets or habitat changes resulting from overfishing, might be highly detrimental to populations (Fertl & Leatherwood, 1997). Recreational activities, such as boating, jet skiing and even whale watching activities may also cause further disruptions to dolphin communities. Mothers with calves might tend to stay away from areas of heavy boat traffic, whilst other adults might move into a specific area in order to exploit a particular resource, such as bow riding to save energy, for example. Whilst such effects are not discussed in further detail here, these examples clearly indicate, that animals in the present analyses may respond to such impacts in a manner resulting in either social separation and/or changes in group membership.

5.3. Associations, affiliations and group membership

In most mammals, the majority of all parental investment is performed by the females of the species (Clutton-Brock, 1989). Resources that can be translated into offspring therefore limit reproduction in females, whereas access to females limits reproduction in non-investing males. In bottlenose dolphins, the female invests heavily in each offspring and probably discriminates between males where some trait that may benefit their offspring is apparent. Male bottlenose dolphins, on the other hand, as in other mammals that do not participate in parental care, prefer to channel their reproductive efforts towards obtaining females (Connor *et al.*, 2000). To this end, different strategies are utilised by males: from that of individual animals roving between female groups, to the formation of alliances by several animals to herd females (Wells *et al.*, 1983; Connor *et al.*, 1992a; Möller *et al.*, 2001).

Whilst statistical analyses of association tests in the present study were not in favour of alliance formation in males, there was, however, some evidence for associations between several mature males; with four of the males forming dyads with CoAs of 0.61 and 0.73 respectively. Moreover, personal observations between May and August 2003 indicated short term alliance formation of male bottlenose dolphins in the study area. One such observation was made on 8th July, when a group of 25 bottlenose dolphins including five calves was encountered. Two male dolphins who had the highest CoAs in the analyses (# 9, Spike and # 10, Sailfin) were observed trying to herd # 81 (Shadow) and her calf. They repeatedly tried to isolate this female and her calf from each other and from the rest of the group, and were observed trying to jump on the calf

and hold it beneath the water, similar to an account described by Patterson *et al.* (1998) of pre-infanticidal behaviour.

In Shark Bay, Australia, male bottlenoses are also known to cooperate in triads (or triplets), usually comprised of a closely associated pair with a third member seen less consistently with both of the other members. Whilst such all-male relationships were not observed in the present study, a number of mixed-sex triads were evident. The clear majority of these associates consisted of two males to one female, whereas only one male-female-female triad was determined. The implication of these results might therefore imply that male bottlenose dolphins in the present study area do actually form coercively maintained consortships with individual females after all.

Three reasons for alliance formation have been proposed to date. Firstly, alliances permit males to better compete against rival males for access to females (Corkeron, 1989; Smolker *et al.*, 1992; Conner *et al.*, 1992a). Sharing copulatory access to a female with another individual is probably better than no copulatory success at all. Conversely, if the two members of an alliance are kin, sharing copulations with a relative would reduce any compromise by increasing the inclusive fitness of both members of the alliance. In addition, alliances may permit males to control movements of females and possibly force copulation (Wells *et al.*, 1987; Connor *et al.*, 1992a). Such herding might be a “war of attrition” (Connor *et al.* 1992a, 1996) in which females mate with their male consorts because they are prevented from mating with preferred males. Finally, alliance formation might further function to reduce the threat of predation or attacks from sharks, with one member guarding the other during periods of rest or illness, (Wells, 1991a, b).

This then begs the question, why, if association by alliance strongly benefits both reproductive success and survivability, would the males observed in the present study choose to act independently at all? One explanation considered by Wilson (1995), is that competition between males for females is low in the Moray Firth, as the sex ratio is biased towards females, i.e. there would be less need for males to form alliances to obtain copulations. Another reason, however, might be explained in terms of the topography of the Moray Firth. Here, the water depth, whilst variable (≈ 20 m), is generally far greater than that in Shark Bay, Australia, and Sarasota, Florida, where the phenomenon of alliance formation is most predominantly observed; the added depth possibly providing greater opportunity for females to escape the advances of cooperating males. If females could exercise choice, or if males were not capable of controlling access to females as a result of their environment, would not such alliance formation be defunct? On the other hand, perhaps the topography of the particular study area might suggest an even greater need for alliance formation in mature males? As further information on the gender of

more adult dolphins in the Moray Firth becomes available, however, perhaps it will be possible to re-examine this hypothesis in greater detail.

Connor *et al.* (2000) have suggested that herding and alliance formation in male bottlenoses is age related, and primarily the domain of mature, adult, males. It is certainly interesting that the two male pairs that yielded the highest CoAs in the present analyses were formed by older males. But this trend is difficult to prove in view of the lack of information on the maturity/age of most individuals.

In female bottlenose dolphins, association patterns determined in the present study were similar to those described for females in other populations (Wells *et al.*, 1987; Wells, 1991a; Smolker *et al.*, 1992). Primarily, females were seen to network with a large number of associates, and were linked to most other females either through mutual associates or by occasional occurrence in the same sub-groups. Also, within this social network, the majority of females were found to associate most strongly with a subset of other females in “bands” or “cliques” such as those described by Wells *et al.* (1987) and Smolker *et al.* (1992). A minority of females seemed to belong to no particular band at all.

In the present study, females with calves of similar ages tended to associate with one another within bands, as found by Wells *et al.* (1987), but never in entirely female groups. Observations in Sarasota over a 25 year period suggest that bands of females may maintain their basic structure for many years, but can change over time with the change in composition of the female community (Wells, unpublished data, as cited in Connor *et al.*, 2000). The reproductive status is known largely to influence group formation in bottlenose dolphin social structure and in the present study, this could account for the large variability in group composition observed.

According to Wells (1991b), females raising their offspring within bands have a significantly higher probability of successfully rearing their calves than do non-band members. Day-to-day tasks such as finding and catching food, spotting and avoiding potential predators and babysitting new calves are all very much easier within a group. In addition, female bands also cooperate to repel the unwanted advances of harassing males (Connor *et al.*, 1992b). In this respect, it can be hypothesised that the survivorship of calves in the Moray Firth is indirectly related to the stability and composition of bands or schools.

Kin selection is often used to explain the social interaction and cooperative behaviour of mammals. Recent work, however, suggests that the influence of genetic relatedness on patterns of affiliation and cooperation is not constant across taxa, nor within the genus *Tursiops*. For example, in south-eastern Australia, Möller *et al.* (2001) have shown a distinct lack of kinship within male bottlenose dolphin alliances, yet studies in the Bahamas have revealed highly significant correlations between patterns of association and patterns of genetic relatedness

(Parsons *et al.*, 2003). In addition, Wells (1991b) found from long-term observations and preliminary genetic analyses that a proportion of young females who join bands are in fact returning to their natal band. Whilst, this is difficult to comment on in the present study, future studies of genetic relatedness in the Moray Firth would be very interesting. It may in fact be that dispersal, rather than kinship, is the prime factor influencing association patterns of females in the outer southern Moray Firth. If the dispersal of females from natal groups was high, for example, opportunities to form relationships with siblings and/or other relatives would be decreased. In addition to genetic analyses, focal follows could be used to further clarify this subject.

In interpretation of the present findings, it is important to assume, that the estimates of association coefficients reported herein are negatively biased, due to the inherent difficulties of the methodology used as discussed by Stevick *et al.* (2001), most notably, the inability to photograph each individual present during each and every encounter. In addition, the cut-off level chosen for association analyses would undoubtedly bias the results obtained. Choice of selection criteria is presumed to require a balance between the maximum number of individuals, ensuring representative data, and the maximum sighting frequencies for reliability of data (Chilvers & Corkeron, 2002). That saying, most authors did not, however, include their rationale for choosing selection criteria in their methodologies and different cut-off levels or number of individuals would certainly result in a quite unique set of findings. The trade-off between representative and reliable data often depends on the research questions asked. Studies involving surveys to provide descriptive investigations of a community's overall social organisation may be based on a large number of individuals with lower sighting frequencies. Studies using focal follows to identify long-term or certain interactions between individuals, however, may be based on fewer individuals with higher sighting frequencies (Mann, 1999). The size and distribution of the society sampled and the sampling period are other factors which may need to be considered. If, as in the present study, the sampling period is split or seasonal, then selection criteria may be restricted to sighting animals across all sampling periods. The chance of introducing a bias in either direction is thereby increased with a decreasing number of sightings per dolphin due to the smaller sample size used. The weight of two dolphins reported as found together when they are actually usually found apart, and vice versa, is lessened by a larger sample size. Less weight is given to such errors like sightings that may include an individual thought to be absent. Therefore, the choice of data to be included in the analyses might also have biased the present results, since a lower threshold could possibly have yielded a quite different result.

6.

Conclusions

Findings from the present study indicate that group sizes of bottlenose dolphins in the outer southern Moray Firth are significantly larger than those occupying the more estuarine-like conditions of the inner Moray Firth. Whilst this might be attributed to environmental differences between the two areas, moreover, group size and formation in this dolphin community could further be explained by the feeding ecology, availability of prey items and the potential risk of predation in this species. In addition, the social ecology and dynamics of the population are thought to further shape the formation and size of dolphin groups in the Moray Firth.

The social structure of bottlenose dolphins in the coastal study area was revealed to be fluid in the short term, continually coalescing and fragmenting, but a number of adults exhibited stronger relationships with preferred companions which showed consistency over the longer term. This changeability of units and sub-units was directly related to the differences in occurrence patterns observed, and is considered to reflect the extensive home range and migratory/seasonal movements identified in this “resident” population.

The composition of preferred associations shown was typically mixed, and this is considered in view of the direct advantages of cooperation and the implications of sexual interactions within this bottlenose society. Since groups with calves were found to be typically larger than those without, the benefits of alloparental care and implications for the survivorship of calves are further discussed.

In the outer Moray Firth, females of the same reproductive status are thought to group together, as in other bottlenose dolphin populations, whilst evidence for relationships between adult males were not conclusive in the present analyses; further study in this area is recommended. Associations between males and females were primarily attributed to the reproductive state of the female, but other factors such as relatedness, ecological constraints, dispersal and anthropogenic impacts may all combine to shape sociality in this Moray Firth population.

The majority of associations of individuals were established to be short-term, lasting only several days. Consequently, most were seen to disassociate from all other individuals within just a few weeks. However, a small number of individuals showing constant companions in the analyses of association *were* predicted to form long-term associations.

The bottlenose dolphin is certainly one of the most adaptable of all marine mammals. Even so, changes to its habitat, as a result of overfishing for example, could lead to significant changes in the distribution and social ecology of the species in the study area, which need to be taken into account in view of the management proposals currently aimed at this population. The

Moray Firth bottlenose dolphin population is both small and isolated and, living in the fragile coastal areas where almost all human related activities causing general deterioration of the ecosystem are concentrated, is undoubtedly vulnerable to extinction. In this respect, the results of the present studies will be extremely important in the development and implementation of effective management policies for the protection of this and other bottlenose dolphin populations and their habitats in the UK.

Whilst it can be difficult to detect subtle changes in dolphin populations of individually recognisable animals, other sources of evidence must also be explored in the assessment of population structure over different temporal and spatial scales. Direct evaluation of relatedness patterns of the bottlenose dolphins of the outer Moray Firth utilising genetic sampling methods for example, would add greatly to our understanding of the social structure and dynamics of this population. The degree of genetic variability characteristic of the mitochondrial DNA (mtDNA) control region has been widely used in studies of population structure (Awise, 1994) and can be useful in identifying meaningful population subdivisions (Moritz, 1994). Since genetic sampling of live animals is an invasive procedure, however, focal behaviour follows might be a more appropriate method to assess the dynamics of this population, particularly in view of the conservation concerns highlighted above.

Any analysis of social structure inherently requires detailed information on the interactions between individual members of the population collected over a considerable period of time. Obtaining accurate information on the ecology and behaviour of a dolphin population can, however, present many problems. Cetaceans generally live in an environment that is inhospitable to observers for the majority of the time. In the temperate environment of the Moray Firth, data collection from boats has to be carried out during periods of calm conditions between bouts of often unpredictable weather. Such unfavourable weather conditions may limit the chances to locate animals at sea, as the ability to sight surfacing dolphins decreases with increasing sea state (Hammond, 1986) masking the presence of animals in different areas and the size and composition of groups.

Our current understanding of the outer Moray Firth social system is by no means complete. Individual variation in dolphin behaviour continues to challenge our abilities to identify general patterns. Whilst, with time, it may become apparent that parts of the analyses presented here are not entirely correct, the discussion herein offers the most useful interpretation to date. Many questions, though, remain. Of particular importance to our understanding of the social structure of the Moray Firth population, is a better knowledge of the mating system(s) of this particular population. It would be interesting to know, for example, which males are siring

calves during the breeding season. Are breeding males closely associated with the females they mate with? Furthermore, do females have a choice of mating partners?

Greater collaboration between researchers, both in the Moray Firth and elsewhere, to maximise the outcome of field work addressing fundamental questions about the Moray Firth population, would be desirable. Standardisation of data collection techniques from one long-term study to another, for example, would enhance the value of data collected by facilitating comparisons. Such comparisons, especially between differences in sociality from a variety of different environments, might provide important insights into the evolution of bottlenose dolphin social systems.

The conservation of ecologically important sites for species such as the bottlenose dolphin makes the monitoring of coastal dolphin populations which exclusively use particular habitats a necessity. By broadening the range of environmental conditions in which the species has been studied, the findings presented here serve to further our understanding of the factors influencing distribution patterns and sociality of this and other small, coastal cetacean populations in UK waters. The northerly location of the Moray Firth bottlenose population, in itself, presents unique opportunities for understanding the mechanisms of adaptation of these top marine predators to cold temperate environments, such as the North Sea. From this consideration stems the extreme interest in comparing the social ecology and behaviour of this population with other bottlenose dolphin communities around the world; to further understand how the interplay of different factors combine to shape social structure in this species. Thus, the present study provides a broad foundation for future studies of social and behavioural ecology of bottlenose dolphins in this unique, northern habitat.

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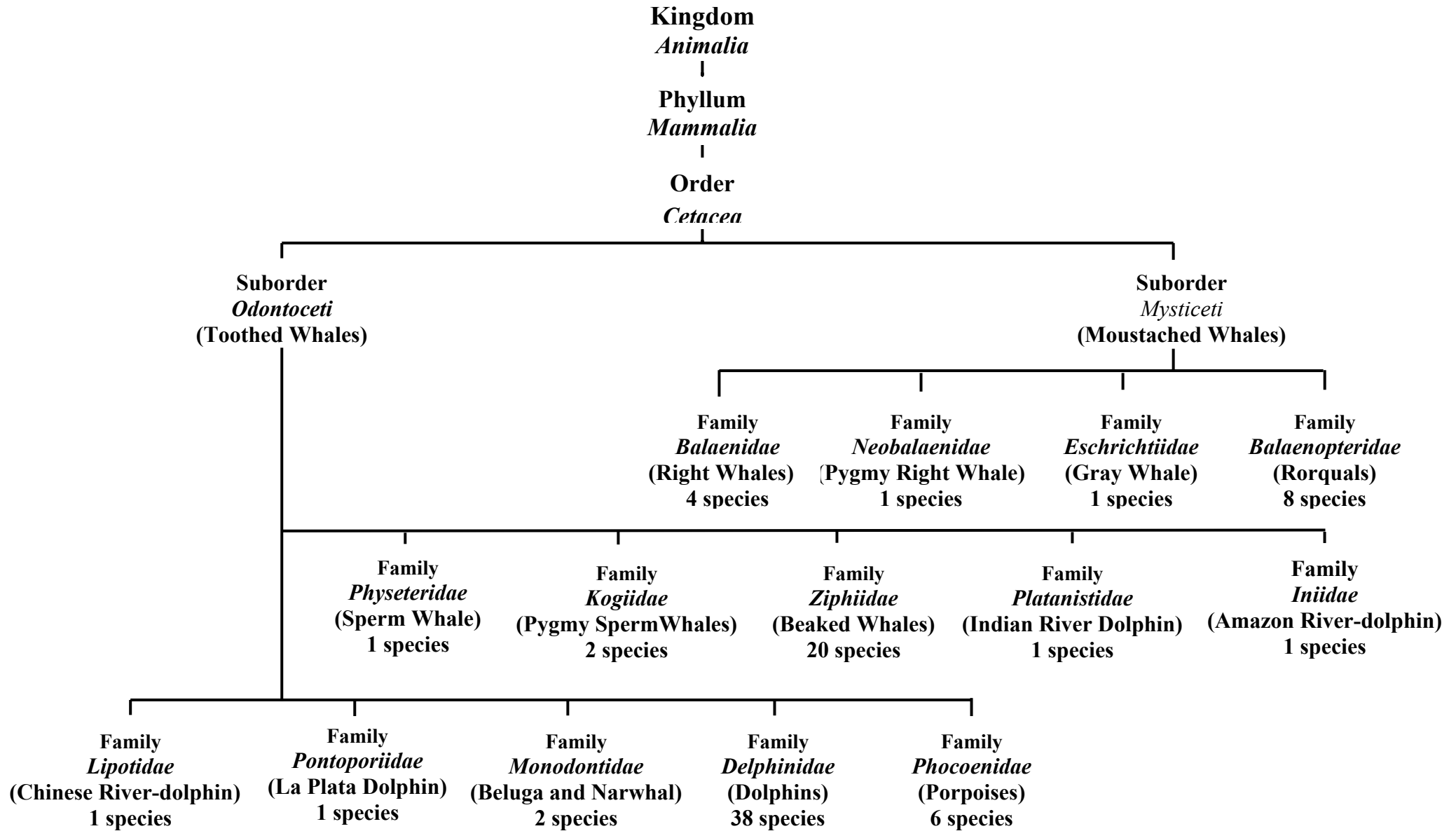
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Appendices

Appendix A: Cetacean Taxonomy - flow diagram showing the main cetacean families



Appendix B: i-xl. Individual bottlenose dolphins identified between 1997 and 2003 used in the present study for the association analysis

i) ID # 1 Sharky (RD)



ii) ID # 2 Jagged Edge (RD)



iii) ID # 3 Thatcher (LD)



iv) ID # 4 Spearhead (RD)



v) ID # 5 Sunrise (RD)



vi) ID # 9 Spike (LD)



vii) ID # 10 Sailfin (RD)



viii) ID # 14 Ziggy (RD)



ix) ID # 15 Sooty (RD)



x) ID # 19 Carter (RD)



xi) ID # 20 Trekkly (RD)



xii) ID # 21 Paperclip (LD)



xiii) ID # 26 Punch (RD)



xiv) ID # 37 Pearly (LD)



xv) ID # 46 Double U (RD)



xvi) ID # 55 Runny Paint (RD)



xvii) ID # 61 Scratchy (LD)



xviii) ID # 63 Chunks (RD)



xix) ID # 64 Hubbs (RD)



xx) ID # 65 Muddy (RD)



xxi) ID # 66 Goblin Seal (RD)



xxii) ID # 67 Bucks Fizz (LD)



xxiii) ID # 69 Singers (RD)



xxiv) ID # 71 Chanonry (LD)



xxv) ID # 72 Yorkie (RD)



xxvi) ID # 74 Georgia (LD)



xxvii) ID # 77 Allegranzi (RD)



xxviii) ID # 78 Guinness (RD)



xxix) ID # 81 Shadow (RD)



xxx) ID # 89 Happy Dragon (LD)



xxxi) ID # 102 Salami (LD)



xxxii) ID # 115 Voodoo Head (RD)



xxxiii) ID # 118 (RD)



xxxiv) ID # 119 Spot (RD)



xxxv) ID # 122 (LD)



xxxvi) ID # 134 Julia (LD)



xxxvii) ID # 145 Craig (LD)



xxxviii) ID # 197 Lower Nick (LD)



xxxix) ID # 216 Sax (RD)



xl) ID # 274 Sparks (RD)



Appendix C: Statistical analyses

Group size

Kruskal-Wallis Test: Group Size versus Year

Year	N	Median	Ave Rank	Z
1997	61	8.000	60.5	-1.68
1998	19	11.000	71.7	0.64
1999	4	11.500	81.3	0.78
2000	2	12.500	81.3	0.55
2001	18	13.000	80.4	1.66
2002	14	8.000	54.9	-1.20
2003	14	12.000	73.1	0.69
Overall	132		66.5	

H = 6.84 DF = 6 P = 0.336

H = 6.86 DF = 6 P = 0.334 (adjusted for ties)

NOTE * One or more small samples

Test for Equal Variances

Response Group Size
Factors Year
ConfLvl 95.0000

Bonferroni confidence intervals for standard deviations

Lower	Sigma	Upper	N	Factor Levels
5.95417	7.4375	9.78	61	1997
3.86627	5.6372	9.81	19	1998
3.15248	6.7020	48.5	4	1999
2.18413	6.3640	1421.75	2	2000
6.12692	9.0156	16.01	18	2001
6.63508	10.2177	20.17	14	2002
6.01664	9.2653	18.29	14	2003

Bartlett's Test (normal distribution)

Test Statistic: 6.784

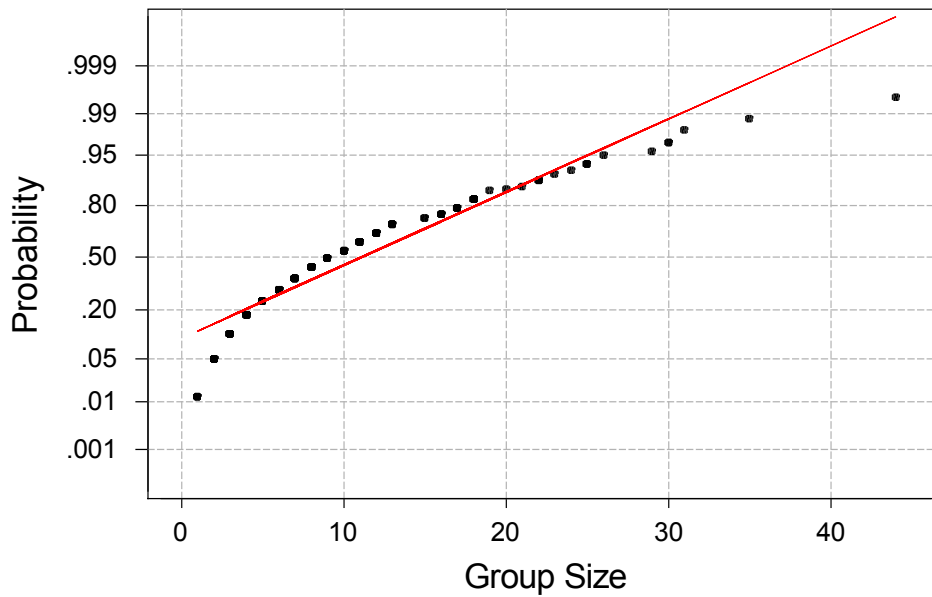
P-Value : 0.341

Levene's Test (any continuous distribution)

Test Statistic: 0.819

P-Value : 0.557

Normal Probability Plot



Average: 11.0682
StDev: 7.92734
N: 132

Kolmogorov-Smirnov Normality Test
D+: 0.112 D-: 0.094 D: 0.112
Approximate P-Value < 0.01

Group size per month

Kruskal-Wallis Test: Group size versus Month

Month	N	Median	Ave Rank	Z
August	44	10.000	71.2	1.23
July	43	10.000	68.5	0.65
June	17	10.000	64.5	-0.12
May	13	8.000	54.3	-1.13
September	13	6.000	48.7	

H = 5.02 DF = 4 P = 0.285

H = 5.03 DF = 4 P = 0.284 (adjusted for ties)

Group composition SA

Mann-Whitney Test and CI: Group size of groups with A & SA; Group size of SA-only groups

Group si N = 71 Median = 10.000

Group si N = 7 Median = 3.000

Point estimate for ETA1-ETA2 is 7.000

95.2 Percent CI for ETA1-ETA2 is (4.001; 11.999)

W = 3029.0

Test of ETA1 = ETA2 vs ETA1 not = ETA2 is significant at 0.0001

The test is significant at 0.0001 (adjusted for ties)

Group composition sex

Mann-Whitney Test and CI: group size mixed sex; group size all

gr.size N = 56 Median = 12.500

gr.size N = 133 Median = 9.000

Point estimate for ETA1-ETA2 is 4.000

95.0 Percent CI for ETA1-ETA2 is (2.000;5.999)

W = 6590.0

Test of ETA1 = ETA2 vs ETA1 not = ETA2 is significant at 0.0002

The test is significant at 0.0002 (adjusted for ties)

Group size calves

Mann-Whitney Test and CI: Max count of groups with calves; Max count of groups without calves

Max coun N = 96 Median = 11.000

Max coun N = 28 Median = 4.000

Point estimate for ETA1-ETA2 is 6.000

95.0 Percent CI for ETA1-ETA2 is (3.999; 8.001)

W = 6846.5

Test of ETA1 = ETA2 vs ETA1 not = ETA2 is significant at 0.0000

The test is significant at 0.0000 (adjusted for ties)

Mann-Whitney Test and CI: Max count excluding calves; Max count of groups without calves

Max coun N = 96 Median = 8.500

Max coun N = 28 Median = 4.000

Point estimate for ETA1-ETA2 is 4.000

95.0 Percent CI for ETA1-ETA2 is (2.001; 6.001)

W = 6651.5

Test of ETA1 = ETA2 vs ETA1 not = ETA2 is significant at 0.0001

The test is significant at 0.0001 (adjusted for ties)

Appendix D: HWI analyses (SOCPROG 1.3)

» social

» Number of individuals = 40

Number of groups = 106

No group data for

ID	No. groups	Sex
10	11	M
1	7	M
122	8	F
14	5	M
15	9	F
19	10	M
102	7	
115	8	M
118	5	F
119	7	
134	5	F
145	6	
197	14	F
2	10	M
20	6	M
21	11	M
26	7	F
216	10	F
274	8	
3	8	F
37	10	F
4	5	M
46	5	F
5	19	F
55	10	M
61	15	M
63	7	M
64	6	F
65	19	F
66	12	M
67	17	F
69	21	M
72	11	F
71	9	M
77	8	M
78	5	F
74	8	F
81	10	F
89	6	F
9	11	M

Permuting groups within samples

Number of individuals = 40

Number of random permutations = 20000

Real association indices:

all: mean = 0.10836; s.d. =0.12735

non-zero elements: proportion = 0.56282; mean = 0.19253; s.d. =0.11227

Random association indices (mean over permutations):

all: mean = 0.10819; s.d. =0.12790

non-zero elements: proportion = 0.56014; mean = 0.19315; s.d. =0.11309

p-values(large p indicates large real value compared to random values):

all: mean = 0.87520; s.d. =0.12570

non-zero elements: proportion = 0.87720; mean = 0.21410; s.d. =0.11565

Two-sided significance level for diads = 0.05

Expected number of significant diads = 37

Number of significant diads = 0

Time for permutations = 39.537s

prr = 0.8620

Test matrix:

M	1.00		
F	0.00	0.00	
*	0.00	0.00	0.00
	M	F	*

Mantel test, $t= 1.0706$ ($p=0.85782$)

Significance using 1000 random permutations: $p=0.862$

Matrix correlation = 0.05643

	Mean Assoc. (sd)	Typical Gp. Size (sd)	Max. Assoc. (sd)
9	0.13	6.25	0.73
10	0.13	6.16	0.73
1	0.12	5.82	0.40
2	0.07	3.68	0.30
4	0.08	4.28	0.44
5	0.11	5.20	0.38
122	0.12	5.68	0.40
3	0.07	3.83	0.67
14	0.08	4.11	0.40
15	0.15	6.68	0.32
19	0.08	3.98	0.32
20	0.08	4.20	0.60
21	0.11	5.27	0.32
26	0.08	4.26	0.36
37	0.12	5.64	0.36
55	0.13	6.07	0.35
46	0.11	5.22	0.44
72	0.09	0.43	0.44

61	0.17	7.54	0.53
63	0.08	4.16	0.31
64	0.09	4.52	0.37
65	0.16	7.08	0.53
66	0.16	7.13	0.62
67	0.17	7.62	0.62
69	0.18	8.15	0.61
71	0.11	5.30	0.44
77	0.16	7.33	0.56
78	0.09	4.51	0.67
81	0.12	5.77	0.40
89	0.07	3.86	0.38
102	0.09	4.58	0.67
74	0.13	5.96	0.56
115	0.09	4.64	0.32
118	0.11	5.39	0.60
119	0.13	6.02	0.50
134	0.02	1.78	0.67
145	0.05	2.96	0.42
216	0.12	5.62	0.50
197	0.10	4.85	0.50
274	0.07	3.54	0.48

Classed by Sex:

M	0.12 (0.04)	5.53 (1.41)	0.47 (0.15)
F	0.11 (0.03)	5.15 (1.31)	0.48 (0.12)
*	0.08 (0.03)	4.27 (1.34)	0.52 (0.11)
M-M	0.12 (0.05)	2.98 (0.72)	0.39 (0.17)
M-F	0.12 (0.04)	2.22 (0.77)	0.41 (0.12)
M-*	0.08 (0.05)	0.33 (0.21)	0.22 (0.11)
F-M	0.12 (0.05)	1.99 (0.85)	0.40 (0.13)
F-F	0.10 (0.03)	2.78 (0.60)	0.40 (0.11)
F-*	0.10 (0.08)	0.38 (0.32)	0.24 (0.19)
*-M	0.08 (0.06)	1.39 (1.06)	0.34 (0.06)
*-F	0.10 (0.02)	1.81 (0.36)	0.52 (0.11)
-	0.02 (0.03)	1.07 (0.08)	0.07 (0.08)
Overall	0.11 (0.04)	5.23 (1.37)	0.48 (0.13)

Test for differences in association between/within classes:

Mantel test, $t = 0.024363$ ($p = 0.50972$)

Matrix correlation = 0.0009234

Temporal analysis of ' All-All '

Moving ave of 1200 assocs; Median time interval = 324 units

Function type: $a_2 + a_3 \cdot \exp(-a_1 \cdot td)$

Explanation: Rapid dis. + const. comps + casual acqs

Log likelihood = -4777.431 Number of parameters = 3

$a_1 = 0.066024$ (s.e. 0.04609)

$a_2 = 0.18418$ (s.e. 0.024607)

$a_3 = 0.2757$ (s.e. 0.077257)

Fitted function: rate = $0.18418 + 0.2757 \cdot \exp(-0.066024 \cdot td)$

Appendix E: SR analyses (SOCPROG 1.3)

» social

» Number of individuals = 40

Number of groups = 106

No group data for

ID	No. groups	Sex
10	11	M
1	7	M
122	8	F
14	5	M
15	9	F
19	10	M
102	7	
115	8	M
118	5	F
119	7	
134	5	F
145	6	
197	14	F
2	10	M
20	6	M
21	11	M
26	7	F
216	10	F
274	8	
3	8	F
37	10	F
4	5	M
46	5	F
5	19	F
55	10	M
61	15	M
63	7	M
64	6	F
65	19	F
66	12	M
67	17	F
69	21	M
72	11	F
71	9	M
77	18	M
78	5	F
74	18	F
81	10	F
89	6	F

Permuting groups within samples

Number of individuals = 40

Number of random permutations = 20000

Real association indices:

all: mean = 0.06298; s.d. =0.08099

non-zero elements: proportion = 0.56282; mean = 0.11190; s.d. =0.07862

Random association indices (mean over permutations):

all: mean = 0.06291; s.d. =0.08129

non-zero elements: proportion = 0.56014; mean = 0.11230; s.d. =0.07905

p-values(large p indicates large real value compared to random values):

all: mean = 0.76910; s.d. =0.18385

non-zero elements: proportion = 0.87720; mean = 0.20015; s.d. =0.18295

Two-sided significance level for diads = 0.05

Expected number of significant diads = 37

Number of significant diads = 0

Time for permutations = 39.227s

pr = 0.8590

Test matrix:

M	1.00		
F	0.00	0.00	
*	0.00	0.00	0.00
	M	F	*

Mantel test, t= 1.0792 (p=0.85976)

Significance using 1000 random permutations: p=0.859

Matrix correlation = 0.05411

	Mean Assoc. (sd)	Typical Gp. Size (sd)	Max. Assoc. (sd)
9	0.08	4.07	0.57
10	0.08	4.04	0.57
1	0.07	3.74	0.25
2	0.04	2.50	0.18
4	0.05	2.96	0.29
5	0.06	3.36	0.23
122	0.07	3.62	0.25
3	0.04	2.68	0.50
14	0.05	2.79	0.25
15	0.08	4.21	0.19
19	0.04	2.62	0.19
20	0.05	2.88	0.43
21	0.06	3.43	0.20
26	0.05	2.85	0.22
37	0.07	3.61	0.22
55	0.07	3.87	0.21
46	0.06	3.44	0.29
72	0.05	2.94	0.29

61	0.10	4.87	0.36
63	0.05	2.76	0.18
64	0.05	3.00	0.23
65	0.09	4.58	0.36
66	0.10	4.73	0.45
67	0.10	4.96	0.45
69	0.11	5.28	0.43
71	0.06	3.51	0.29
77	0.09	4.70	0.40
78	0.05	3.14	0.50
81	0.07	3.69	0.25
89	0.04	2.60	0.24
102	0.05	3.13	0.50
74	0.08	4.00	0.40
115	0.05	3.04	0.19
118	0.07	3.64	0.43
119	0.07	3.90	0.33
134	0.01	1.56	0.50
145	0.03	2.16	0.26
216	0.07	3.68	0.33
197	0.06	3.23	0.33
274	0.04	2.48	0.32

Classed by Sex:

M	0.07 (0.02)	3.63 (0.87)	0.32 (0.13)
F	0.06 (0.02)	3.41 (0.76)	0.33 (0.11)
*	0.05 (0.02)	2.92 (0.77)	0.35 (0.10)
M-M	0.07 (0.03)	2.16 (0.47)	0.26 (0.15)
M-F	0.07 (0.03)	1.29 (0.48)	0.26 (0.10)
M-*	0.05 (0.03)	0.19 (0.12)	0.13 (0.07)
F-M	0.07 (0.03)	1.15 (0.52)	0.26 (0.10)
F-F	0.06 (0.02)	2.03 (0.33)	0.26 (0.10)
F-*	0.06 (0.05)	0.23 (0.20)	0.15 (0.13)
*-M	0.05 (0.04)	0.79 (0.61)	0.21 (0.05)
*-F	0.06 (0.01)	1.09 (0.22)	0.35 (0.10)
-	0.01 (0.01)	1.04 (0.04)	0.04 (0.04)
Overall	0.06 (0.02)	3.46 (0.82)	0.33 (0.12)

Test for differences in associations between/within classes:

Mantel test, $t = -0.0012732$ ($p = 0.49949$)

Matrix correlation = $-4.7801e-005$

Temporal analysis of ' All-All '

Moving avge of 1000 assocs; Median time interval = 281 units

Function type: $a_2 + a_3 \cdot \exp(-a_1 \cdot td)$

Explanation: Rapid dis. + const. comps + casual acqs

Log likelihood = -4777.431 Number of parameters = 3

$a_1 = 0.066024$

$a_2 = 0.18418$

$a_3 = 0.2757$

Fitted function: rate = $0.18418 + 0.2757 \cdot \exp(-0.066024 \cdot td)$