

**GROUP SIZE, SOCIAL ASSOCIATIONS AND RESIDENT PATTERNS
OF BOTTLENOSE DOLPHINS (*Tursiops truncatus*)
IN CARDIGAN BAY, WALES.**

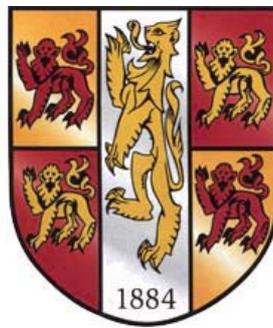
By

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2003 – 2004

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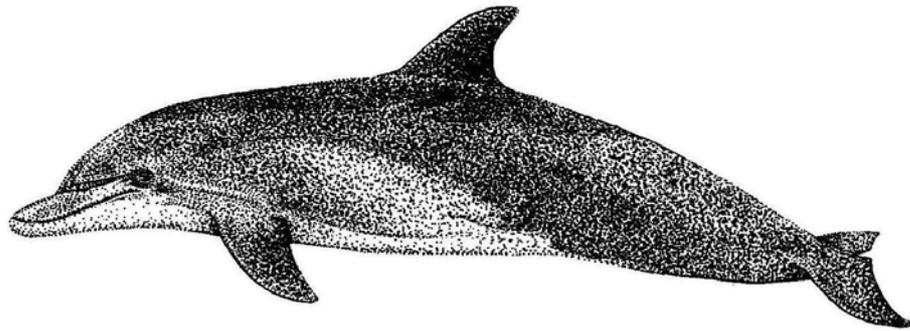
**In association with the Sea Watch Foundation
and Cardigan Bay Marine Wildlife Centre.**



November 2004

Thesis submitted in partial fulfilment for the degree of Master of Science.

*Dedicated to my parents,
Vivian and Barbara Lott.*



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To quote researcher David Bain (1990) in his paper on inferences drawn from photo-identification.

“The inferences are like threads. If correct, they may be woven together to produce an elegant portrait of a species socioecology; or, if there are errant conclusions, they may produce a hopeless tangle of contradictions.”

DECLARATION

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

Signed (candidate)

Date

STATEMENT 1

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

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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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STATEMENT 3

I hereby give consent for my dissertation, if accepted, to be available for photocopying and for inter-library loan, and for the title and summary to be made available to outside organisations.

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Abstract

This work sought to investigate group sizes, social associations and the resident patterns of bottlenose dolphins (*Tursiops truncatus*) in the Cardigan Bay candidate Special Area of Conservation using boat-based photo-identification surveys. The present study is the first in which an analysis of the social associations of bottlenose dolphins in Cardigan Bay has been undertaken. A total of 222 surveys were made from 2001-2004 which resulted in 537 encounters. 83% of all encounters were with animals in groups rather than alone. Group size varied significantly between years and ranged from singletons to 42 animals. The mean group size over all years was 5.85 ± 5.89 (median = 4).

Some individually identified dolphins were photographed in the study area in successive seasons and years and appear to be seasonally resident in Cardigan Bay. Moreover, certain individuals exhibited a preference for core areas *within* the cSAC. However, these areas are not considered to be 'home ranges' of the dolphins as it is thought all animals leave the cSAC on occasion.

Associations were studied using half-weight association indices and cluster analysis. In addition, temporal analyses of association patterns were made plotting changes in the standardised reassociation rate over time. Selection criteria were based on the number of times an individual was sighted during the 2003 study period. The social organisation was characterised by relatively fluid association patterns, with little stability over periods longer than a few days though some longer-term companions were evident. Permutation tests revealed non-random associations and the presence of preferred and/or avoided companions. Both males and females interacted with a large number of other individuals and there were significantly stronger associations between certain male pairs.

The long-term site fidelity demonstrated by certain animals in this study highlights the fact that photo-identification monitoring needs a good geographical spread and greater effort will provide significant value in assessing the bottlenose dolphins' future management needs.

1.

Introduction

Whales, dolphins and porpoises belong to the order Cetacea and occur throughout the world's oceans and seas, from the polar Antarctic waters through the Tropics to the far reaches of the Arctic polar seas (Leatherwood *et al.*, 1983). The order currently comprises 85 species to date (IWC, 2001) and can be divided into two suborders: the mysticetes (or baleen whales) and the odontocetes (or toothed whales).

Many cetaceans show a migratory lifestyle; baleen whales, such as the northern right whale (*Eubalaena glacialis*), humpback (*Megaptera novaeangliae*) and fin whale (*Balaenoptera physalus*), tend to feed in the colder waters of the Arctic/Antarctic in the summer months, but travel to the warmer sub-tropical waters to breed (Leatherwood *et al.*, 1983). The toothed whales, such as the dolphins and porpoises, generally do not show such extensive breeding related migratory patterns, but tend to follow short fish migrations to ensure ample food supply (Ridgway and Harrison, 1999). The smaller cetaceans, such as the bottlenose dolphins (*Tursiops truncatus*), harbour porpoise (*Phocoena phocoena*) and Hector's dolphin (*Cephalorhynchus hectori*), tend to show a certain degree of residency in specific geographical regions (e.g. Arnold, 1997; Evans, 1995; Slooten *et al.*, 1993).

The bottlenose dolphin was described by Montagu (1812) from a specimen caught in the River Dart in Devon, UK, basing the key characteristics of the species on the appearance of the specimen's flattened teeth. These characteristics were later to be identified as a precursor to age and diet and not as to aid identification of the species (Wells and Scott, 1999). Gray subsequently placed the species in a new genus 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).

The bottlenose dolphin is probably the most characteristic of all dolphin species. It is easily recognisable as it is the most common cetacean on display in aquaria (Defran and Pryor, 1980) and has a long history of association with humans in coastal waters (Lockyer, 1990). It has a robust, chunky body, a distinct sickle-shaped dorsal fin, and a well-defined, sharply demarcated beak. The main body colour may vary from slate grey to charcoal grey or brown, with off-white or pink undersides. Calves are often a much lighter shade than adults and darken with age. Individual sex discrimination is notoriously difficult, due to lack of obvious sexual dimorphism in

the adults and because the ventral genitalia and mammary slits are usually hidden from view when the animals are submersed (Connor *et al.*, 2000).

The bottlenose dolphin is a truly cosmopolitan species, occurring throughout the world's tropical and temperate seas and oceans (Shane, 1990b). It has been documented as far north as the southern Okhotsk Sea and Kuril Islands (60°N) in the Western North Pacific, to the coastal waters of the Lofoten Islands (60°N) in the eastern North Atlantic. In the southern hemisphere they are found as far south as Concepción, Chile (36°S), eastern South Pacific, while in the western South Atlantic they have been observed as far south as 300km (45°S) off the Peninsula Valdez, Argentina (Wells and Scott, 1999). The species is highly adaptable, can tolerate a range of water temperatures and can withstand prolonged periods in hypo-saline (Caldwell and Caldwell, 1972) and hyper-saline waters (Smolker *et al.*, 1992). Furthermore, they are capable of surviving in some of the world's most industrialised and polluted waters, such as Galveston Bay, Texas, USA (Maze-Foley and Wursig, 2002).

In many regions around the globe there are considered to be two forms of bottlenose dolphins, namely 'inshore' and 'offshore'. These two forms are recognised on the basis of gross morphology, haematology, cranial morphology, and parasite faunas (Hersh and Duffield, 1990; Van Waerbeek *et al.*, 1990). The inshore form is considered the smaller body form and is restricted to warmer, lower latitudes (Gowans and Whitehead 1995). The striking regional variation in body size between these two forms is clearly illustrated in comparing the population found in Shark Bay, South Australia, where adults range from 2.2 – 2.3 metres (Ross and Cockcroft, 1990) with those found in the UK coastal waters of the northeastern Atlantic where adult sizes range from 3.5 – 4.1m (Lockyer, 1985). Adults vary in weight depending on body form, but they range from 150kg – 650kg .

Studies in Sarasota Bay, Florida, USA have revealed that the average adult life expectancy of the bottlenose dolphin is between forty and fifty years, based on dentinal and cemental growth layer groups in the teeth (Hohn *et al.*, 1989). Age at sexual maturity of free-ranging bottlenose dolphins varies by sex and region. In the warm waters of northeast Florida, USA, sexual maturation within females occurs between five and twelve years of age and with males between ten and thirteen years of age. Off southern Africa, females reach sexual maturity between nine and eleven years of age (Wells and Scott, 1999). The reproductive rate of bottlenose dolphins is

low, with females producing a single offspring every 3 to 4 years after a gestation period of 12 months (Shroeder, 1990). The calves may be born any time throughout the year. Generally, however, seasonal calving has been reported from most studies to date, with peaks in calving during the warmer months (Wells and Scott, 1999).

Coastal populations normally inhabit shallow environments with water depths commonly less than 50m (Ballance, 1990; Corkeron, 1990, Smolker *et al.*, 1992) but this is not always the case, especially in fjord systems (Williams *et al.*, 1993, Lusseau *et al.*, 2003). These coastal areas have a wide variation in habitat types, from exposed open coasts to enclosed sheltered estuaries or bays, and complex bathymetry to flat muddy seabeds (Martin *et al.*, 1990). The broad distribution of the species has allowed studies to be conducted in a wide variety of locations, although research in the tropics predominates.

Bottlenose dolphins are generalist feeders and prey on a wide variety of fish, as well as squid, octopus, occasionally shrimp and small rays and sharks (Gunter, 1951, Mead and Potter, 1990). However, their diet varies with local prey availability (Wells and Scott, 1999).

Feeding and foraging strategies are extremely diverse. They may consist of individual and co-operative group foraging behaviours, pursuing schooling and solitary prey through the water column and hunting prey residing on the seabed (Connor *et al.*, 2000). Individual feeding is probably most prevalent, with prey captures involving behaviours such as herding, high-speed chasing and partially beaching, to capture the prey (Shane, 1990a,b).

Dolphin foraging and feeding behaviours may rely on co-operative group feeding strategies, such as co-operative driving and trapping of fish between dolphin groups (Saayman *et al.*, 1973) and co-operative encircling of fish with individual dolphins charging through the fish school to feed (Caldwell and Caldwell, 1972a). The bottlenose dolphin utilises echolocation to locate prey items hidden from view residing within the substrate (Wells and Scott, 1999). It has been suggested by Wursig and Wursig (1979), that nearshore searching for food usually involves individuals, while deeper water prey searches rely on groups (greater than fifteen individuals) that often utilise the combined sensory echolocation abilities to locate and capture prey.

Bottlenose dolphins show daily patterns in their behaviour, such as foraging and feeding, socialising or moving from area to area in relation to environmental cues,

such as the tides (Irvine *et al.*, 1981), the time of day (Saayman *et al.*, 1973), and depth (Wiley *et al.*, 1994). Bottlenose dolphin movement patterns in Cardigan Bay were correlated with the tides (Gregory and Rowden, 2001) with the animals moving with the tidal flow or travelling when the tidal flow was at its least strongest, around slack water.

Wells *et al.*, (1987) suggests that habitats protected from open oceans may attract small populations with site fidelity and limited movement patterns. This does not necessarily mean that all members of the community are present at all times (Wursig and Harris, 1990). Dolphins may roam, most commonly subadults (Wilson *et al.*, 1999) and males (Wells *et al.*, 1987), and there can be varying degrees of site fidelity, resulting in resident and transient animals (Weller and Wursig, 2004).

Within the coastal areas of the Great Britain and Ireland, there exists at present three distinct seasonally 'resident' populations; one in the Moray Firth, northeast Scotland; one in the Shannon Estuary in Ireland and one in Cardigan Bay, west Wales (Lewis and Evans, 1993, Ingram, 2000). The Moray Firth population is considered to be an isolated or 'closed population' (Wilson *et al.*, 1997,1999); that is, births, deaths, immigration and emigration are negligible. In the Shannon estuary and Cardigan Bay the situation is less clear. In Cardigan Bay Grellier *et al.*, (1995) and Evans *et al.*, (2000) believe the population to be 'open' i.e. one that changes in size and composition from births, deaths, immigration and emigration over time. It is thought that only a proportion of the bottlenose dolphins are resident throughout the year (Arnold *et al.*, 1997; Lewis and Evans, 1993), and that the population is comprised of both resident and transient individuals (Grellier *et al.*, 1995). It has been estimated that between 173 -240 dolphins use the Moray Firth, 113 use the Shannon estuary and in Cardigan Bay the dolphin population contains around 130 – 350 animals (Wilson, 1999; Ingram, 2000; Evans *et al.*, 2000). Recently, Ugarte (personal communication) estimated 138 dolphins utilised a core area within Cardigan Bay.

The function of animal groups is attributable to four main evolutionary benefits namely; increased foraging efficiency, reproduction and access to mates, defence against predation and social learning. A description of the social structure of a species is a first step toward understanding its social organisation and, ultimately, the evolutionary processes that shaped its social system (Wells *et al.*, 1987). Important principal factors, such as the units of a population, group size, group composition and the associations between individuals and groups, need to be identified in order to

analyse social data. Furthermore, it is necessary to identify the parameters that affect the dynamics and structure of a society, such as mobility, home-range overlap and resource exploitation.

Detailed studies on the patterns of interactions between mammals in aquatic environments can be logistically difficult because of observational limitations. The development of photo-identification techniques in the 1970's, therefore, revolutionised the study of many cetacean populations. In wild dolphin studies, individual animals were able to be identified by recognition of scars, nicks and scratches and the shape of the dorsal fin, which is conveniently projected above the water surface each time the dolphin breathes. In addition, the utilisation of natural markings for photo-ID allows for observations of natural behaviour with minimal disturbance. The long-term maintenance of photographic catalogues of identifiable individual bottlenose dolphins has generated studies on life history and population dynamics (Hohn *et al.*, 1989), ranging patterns and habitat use (Irvine and Wells, 1972) as well as research into social associations and social development (Wells *et al.*, 1980).

Wursig and Jefferson (1990) suggested that in order to obtain accurate data collection from photo-ID studies, the natural markings should be recognisable over time, be unique to a specific individual, and not be biased towards re-sightings and repeat identifications. If an individual cannot be recognised from one sampling period to the next, then the identifications are useless, as resightings cannot be linked. Lockyer and Morris (1990) found that the permanency of scars and scratches depended on the severity of the injury, with superficial scratches disappearing after a few weeks, while deeper wounds were visible for the entirety of the animal's life. Furthermore, not all individuals possess identifiable markings, e.g., calves, juveniles or adult females that do not play or fight with conspecifics may be less prone to acquire markings. However, some 70-80% of bottlenose dolphins are thought to contain identifiable markings (Bearzi *et al.*, 1997, Karczmarski and Cockcroft; 1998), and most of these are adult animals which are most important for the majority of studies.

The use of techniques pioneered for the analysis of plant communities has enabled researchers to quantify many mammalian social structures (Cairns and Schwager, 1987, Ginsberg and Young, 1992). The increasing sophistication and refinement of these available statistical techniques has led to an increasing number of

studies examining the social structure of many vertebrate species, including marine mammals.

In the study of marine mammals, the general procedure is to use long-term photographic identification databases to create models of social structure in order to define and calculate association indices between all pairs of identified animals. This is achieved by making an association matrix (e.g Cairns and Schwager 1987; Ginsberg and Young, 1992). Often, data relate to photographic records of recognisable individuals within groups and, as a consequence, animals observed within a predefined unit or animals observed within a predefined time are considered as associated. Using methodologies, such as cluster analysis and sociograms (see Wells *et al.*, 1987; Bigg *et al.*, 1990), the association for a particular subset 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 analysis of associations between identifiable individuals has revealed the variation and structure of odontocete societies. For example, ephemeral fission-fusion societies have been described in many bottlenose dolphin communities (Wursig & Wursig, 1977; Wells *et al.* 1987; Smolker *et al.*, 1992, Connor *et al.*, 2000) where individuals associate in small groups of rapid and complex flux in which the composition changes often on a daily or hourly basis. In contrast, long-term stable matriarchal societies have been found in pilot whales (*Globicephala melas*) (Heimlich-Boran and Heimlich-Boran, 1990) and killer whales (*Orcinus orca*) (Bigg *et al.*, 1990).

As a relatively accessible coastal species, bottlenose dolphins have been studied in detail in various locations around the world. A common finding in previous studies of bottlenose dolphin populations has shown the species to have a fluid and dynamic social structure (Wursig and Wursig, 1979; Ballance, 1990, Smolker *et al.*, 1992, Williams *et al.*, 1993, Wilson, 1995).

Long-term studies of bottlenose dolphins resident in Sarasota Bay, Florida (Wells *et al.*, 1987) and Shark Bay (Smolker *et al.*, 1992) have shown that the strongest associations exist between females and their dependent calves, and in alliances between pairs of sexually reproductive males (Scott *et al.*, 1990, Wells, 1991, Connor *et al.*, 1992). The close mother-calf associations remained together for about four years while the long-term alliances between pairs of males remained stable for up to ten years. In Sarasota, males and females associated most frequently during

the breeding season and male pairs ‘roved’ through the home ranges of female cohorts. Observations in Shark Bay show male pairs isolating and herding single non-pregnant females. It is thought these females may be in oestrus and are forcibly isolated by the alliance for hours, or even weeks, at a time (Connor *et al.*, 1992; Smolker *et al.*, 1992). Outside of these stronger bonds, members of bottlenose dolphin populations form temporary associations within groups with no apparent long-term pattern of allegiance. In contrast to the highly complex and stable structure of bottlenose dolphin populations in Sarasota and Shark Bay, work in the Moray Firth and the Shannon estuary in Ireland, Scotland has shown the only strong bonds to occur are between mother and calf, with little evidence for male alliances between resident dolphins (Wilson, 1999; Ingram, 2000).

This study provided an opportunity to examine the strength of associations and determine the social structure of a population of animals living in a northern, Atlantic habitat (see also, Ingram, 2000 and Wilson, 1995).

The study has the following aims;

- (i) to investigate the group size of the bottlenose dolphin population of Cardigan Bay;
- (ii) to determine whether these dolphins are resident, by showing long-term site fidelity and regular resightings.
- (iii) to calculate the association indices between pairs of identified individuals and test for non-random associations by the presence of preferred and/or avoided companions;
- (iv) to investigate the temporal stability of associations between individuals over time;
- (v) to examine the spatial distribution of frequently sighted individuals.

2.

Study Area: The Cardigan Bay cSAC

Cardigan Bay is the largest bay in the British Isles, bound on three sides by the Welsh coast and open to the Irish Sea on its western boundary (Fig 2.1). It measures 100 km from St David's Head, at its southernmost point, to the Lleyn Peninsula and Bardsey Island, at its northernmost point (Roberts *et al.*, 1998) and encompasses an area of approximately 5,500 Km². The water depth in the Bay does not exceed 50m and becomes increasingly shallower from west to east, with an average depth of approximately 40m (Evans, 1995a). The nature of the seabed in the bay is extremely heterogeneous, ranging from fine sand and broken shell, to large stones and pebbles. (Evans, 1995b; Evans *et al.*, 2000). The tide enters the Irish Sea through St. George's Channel in the south and then proceeds north and meets the southward-moving tide that originates in the north around the Isle of Man; this results in weak tidal currents that run north during flood tide and south during ebb tide (Evans, 1995b). The tides in the area are semi-diurnal and the tidal range in Cardigan Bay is fairly uniform (ca. 2m at neaps and 4m at springs). Tidal streams or currents in Cardigan Bay are relatively weak compared to the Irish Sea. The seabed in the bay north of New Quay is generally higher, and this may be caused in part by the occurrence of the major estuary outlets in this northern area, and/or may be the result of tidal residual movements (Roberts, *et al.*, 1998)

Bottlenose dolphins are frequently seen within 15 km of the coast between Cardigan and Borth, from April to October. Areas such as Cardigan Island, Mwnt, Aberporth, Ynys Lochlyn and New Quay are of particular importance to the bottlenose dolphin population (Evans, 1995). For this reason efforts have been made to protect these animals by managing parts of the Bay. These efforts began in 1992 when the site was established as a voluntary Ceredigion Marine Heritage Coast, and was then followed more recently by the establishment of the Cardigan Bay candidate Special Area of Conservation (cSAC); identified under the European Habitats and Species Directive of 1992. Subsequently, Ceredigion County Council has drawn up a management plan (Ceredigion County Council, 2001). The Cardigan Bay cSAC is situated off the south coast of Ceredigion and north Pembrokeshire in the southern part of Cardigan Bay.

Recreational boat traffic is prevalent in the coastal areas, especially around Cardigan, Aberporth, New Quay, Aberaeron and Aberystwyth, which are frequented by tourists. During the tourist season (April – October), boats operate out of New Quay and Aberaeron, taking tourists on trips around the Bay to observe the dolphins and other wildlife. Water sports and recreational boat activities increase in the summer months, with many visitors launching powerboats, sailboats, jet skis and kayaks from these popular coastal areas.

The study site comprised of the area within the arbitrary boundaries of the Cardigan Bay cSAC. The two seaward corners of the boundaries being $52^{\circ} 13' 7''$ N, $5^{\circ} 0' 15''$ W and $52^{\circ} 25' 6''$ N, $4^{\circ} 23' 48''$ W, with the two landward corners of the boundaries being $52^{\circ} 04' 5''$ N, $4^{\circ} 46' 10''$ W, and $52^{\circ} 15' 4''$ N, $4^{\circ} 13' 50''$ W. The cSAC covers an area of approximately 968 Km² with the seaward boundaries of the ‘box ‘ extending approximately 23 Km offshore.

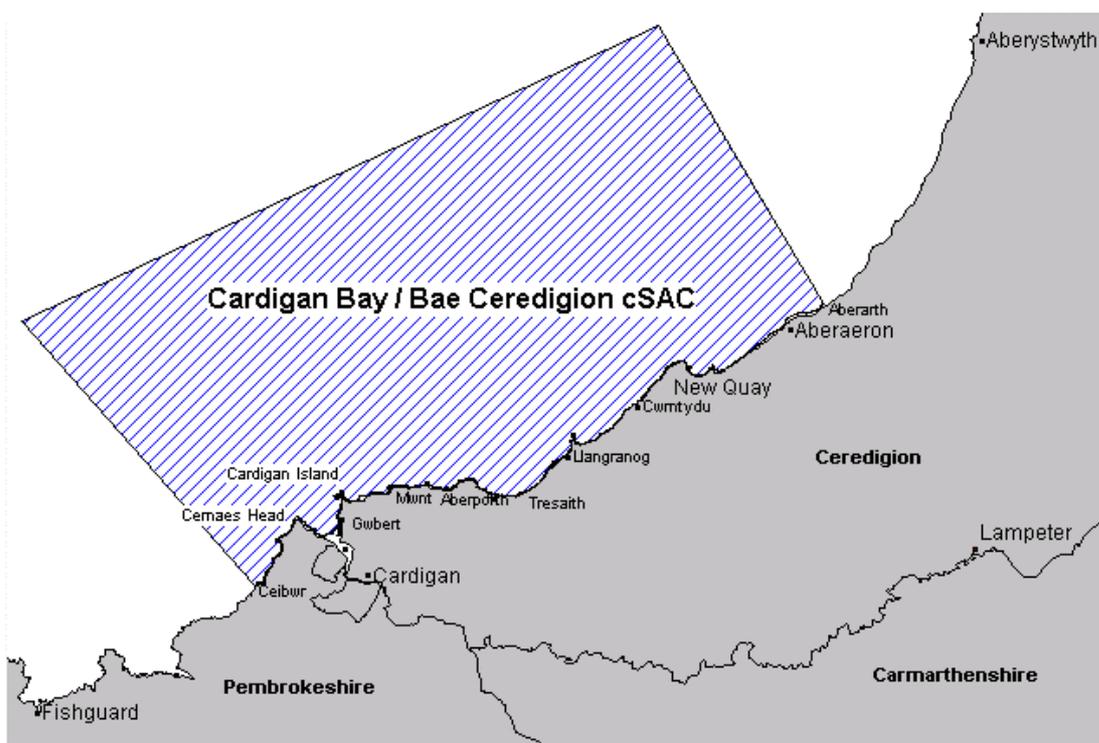


Figure 2.1 The Cardigan Bay cSAC. (courtesy of Ceredigion County Council, Cardigan Bay cSAC Management Plan).

3.

Methods

3.1. Data collection.

Data for 2003 and 2004 were collected during boat-based, photo-identification surveys within the coastline of the candidate Special Area of Conservation. All surveys were conducted aboard the MV *Sulaire*, a 10m charter vessel with a semi-displacement hull and 380hp turbo diesel engine. The vessel was equipped with a Global Positioning System (GPS) shipmate RS 5700. Observational height from the vessel was 3m above sea level; angle of view was 360° but observers concentrated mainly on the 180° to the side and ahead of the boat.

The vessel was based and operated out of New Quay harbour on a daily basis. Whenever possible, boat surveys followed a predefined transect route to uniformly cover the area of the cSAC. The average distance of each transect was approximately 11km. Each transect was conducted at a speed of 14km per hour (8 knots).

Data was collected during a combination of dedicated 8-hour research trips in addition to utilising the vessel as a ‘platform of opportunity’ to gather information during scheduled dolphin-watching trips funded by the public.

Sea state was recorded as: 0 = mirror calm; 1 = slight ripples, no foam crests; 2 = small wavelets, glassy crests, but no white caps; 3 = large wavelets, crest begin to break, few whitecaps (Reeds Nautical Almanac, 2003).

Survey trips were conducted at sea states of Beaufort three or less during good light conditions. If the sea state increases above 3, then sightings become less reliable (Barco *et al.*, 1999). When the sighting conditions were good, i.e. sea state 2 or less, low swell and no precipitation or fog, the photo-identification surveys were combined with distance-sampling surveys for bottlenose dolphins, harbour porpoise (*Phocoena phocoena*) and Atlantic grey seals (*Halichoerus grypus*).

On the majority of surveys, voluntary observers were present and varied in numbers from 2 to 14 individuals, including crew.

For each trip a detailed **Effort Form** was filled out which included information on survey start and finish time, the effort type i.e. casual watch (CW), dedicated search (DS), line transect (LT) or photo-id (ID); GPS positions, boat speed and course, visibility and sea state/environmental conditions. (Fig 3.1)

Effort form

Boat: Sulaire other _____ Person responsible of data: F.V.
 Date: 24/5/04 Time start: 13.14 Time end: 20.49 Type of trip: 2hr TR NTR Crew: IK, SR Page 1 of 1

Leg	Time	Lat.	Long.	Speed	Course	Effort type	Precipitation			Visibl lity (km)	Sea state	Sightings ref.	Stratum & comments
							Type	Intensity	Direction				
1	13.14	NS2°	W004°	6.5	314°	(CW) LT	DS	(N) F	I	0-1	2	1,	
1	13.43	NS2°	W004°	8	229°	CW	DS	(N) F	I	0-1	1		
2	14.09	NS2°	W004°	8.3	169°	LT	DS	(N) F	I	0-1	0		
3	14.15	NS2°	W004°	6.0	292°	(ID) LT	DS	(N) F	I	0-1	0	3,2,3	
3	14.43	NS2°	W004°	7.3	353°	CW	DS	(N) F	I	0-1	0	4,	
3	15.00	NS2°	W004°	5.8	260°	LT	DS	(N) F	I	0-1	1	5,	
3	15.06	NS2°	W004°	10.7	080°	CW	DS	(N) F	I	0-1	1	6,	
3	15.10	NS2°	W004°	4.9	074°	LT	DS	(N) F	I	0-1	1	7,	
3	15.15	NS2°	W004°	6.7	067°	LT	DS	(N) F	I	0-1	1		
3	15.17	NS2°	W004°	7.9	288°	(ID) LT	DS	(N) F	I	0-1	1		

Comments:

Entered into computer

Fig 3.1. Effort Form showing data collected during photo-identification surveys.

A *Sightings Form* (Fig 3.2) was also completed to log the presence of bottlenose dolphins. This recorded GPS positions, estimated distance, behaviour, and reaction to the boat.

Once dolphins were sighted, the time and their location was recorded, the vessel then left the transect and approached the dolphins to enable each individual to be photographed. The time spent photographing a dolphin group was termed an *encounter*. During an encounter, photographs were taken with a Canon EOS 5 analogue camera and a Canon D60 digital camera with 75-300mm zoom lens (f 4.0 – 5.6) and Fujichrome Sensia II, 200 ASA transparency film.

The aim of each encounter was to obtain as many photographic images of both sides of each individual as possible. This information was then entered on to a bottlenose dolphin *Encounter Sheet*. (Fig 3.3) Information on the composition of each group encountered included a breakdown of the number of Adults (A), Juveniles (J), and Calves (C).

Group size was defined as the total number of dolphins, including calves, counted in spatial proximity to one another, moving in the same direction and usually engaged in the same behaviour (Shane, 1990a).

Other details recorded included the encounter number, encounter length, GPS position, behaviour and a log of the photographic frames taken.

During an encounter with a dolphin group, attempts were made to photograph all group members. Encounters continued until i) all dolphins in the group had been photographed or, ii) contact with the group had been lost (after approximately ten minutes without a sighting); iii) the dolphins showed signs of avoidance such as swimming away from the boat or diving as the boat approached, or iv) the survey leader decided to go back to the tracking and continue the distance-sampling survey. Ideally, during combined distance-sampling/ photo-ID surveys, each encounter lasted less than ½ hour.

Frequently, more than one group of dolphins were encountered on a survey trip and so each group sighting was recorded as a separate encounter. In these situations it was important to separate the photographic record and so a spacer picture of the encounter form (showing date, time, and film information) was taken at the start of the encounter to distinguish any subsequent encounters on the same film. A spacer picture was also taken at the start of each film.

Sightings form

Date: 24/05/04

Type of trip: 2hr TR NT

Page: 1 of 1

* Lat	* Long	* Dir	Distance		* Species	* Total no.	A	J	C	N	B	* Time	Effort type		Sea state	Beh Dir / Orient.		Reac. to Boat	Seen by	
			Est.	Ruler									D	LT		DS	HT			HT
-1	12.486	W004°	(D)S	90°	50m	3	3					13.21	(CW) LT	DS	2		Hauled out	A	N	AM
-2	09.666	W004°	P-(S)	50°	300	3						14.40	(CW) LT	DS	1			A	N	FU _{SP}
-3	0.385	W004°	(D)S	60°	300	1						14.52	(CW) LT	DS	1			A	N	F.U.
-4	0.290	W004°	(D)S	50°	1000	1						15.04	(CW) LT	DS	1		Leaping	A	N	SP
-5	0.386	W004°	P-(S)	90°	300	1						15.08	(CW) LT	DS	1			A	N	AM
-6	0.291	W004°	(D)S	90°	200							15.10	(CW) LT	DS	1			A	N	S.H
-7	0.840	W004°	P-(S)	90°	600	3						15.25	(CW) LT	DS	1			A	N	F.U.
-8	10.155	W004°	P-S	30°	120	5						15.25	(CW) LT	DS	1			A	N	F.U.
-9	0.839	W004°	P-S	90°	230	2	1					18.10	(CW) LT	DS	0			A	N	F.U.
-0	NS2°	W004°	P-S											(CW) LT	DS			A	N	

Effort: Casual Watch, Dedicated Search, Line Transect or ID work
 Behaviours: BND & HP- T: travel, SF: suspected feeding, FF: feeding (fish seen), O: other, N: unknown.
 GRS- H: hauled out, S: swim
 Direction (only BND & GRS): Either degrees from compass or variable (VAR)
 Boat reaction (only BND & GRS): swimming Away from us, Towards us or Neither

Fig 3.2. Sightings Form showing data collected during photo-identification surveys.

BND Encounter Sheet

Record No.: 04.022

Date 05/06/04 Boat SULAIRE Sighting ref 16 Enc. # Page 1 of 1
Person responsible of data F.U. Notes by S.P. Crew SH, SP, TE, KL, RL, JL, FU.
Start: Time 13:10 N 52° 07.825 W 4° 47.075 End: time 13:42 N 52° 07.567 W 4° 45.565

No. of animals (best guess) 14 Adults 12 Juveniles 2 Calves 0 NBs 0
Animals photographed ≈ 14 Adults 12 Juveniles 2 Calves 0 NBs 0

Subgroups: [14] Well marked: W0303?

Travel Probably feed Feed Other Bowride Leap Splash Contact
Swimming direction Comments Same group as earlier, plus more
Until time 13:42, @ N 52° 07.567 W 4° 45.565

Subgroups: Well marked:

Travel Probably feed Feed Other Bowride Leap Splash Contact
Swimming direction Comments
Until time , @ N 52° W 4°

Subgroups: Well marked:

Travel Probably feed Feed Other Bowride Leap Splash Contact
Swimming direction Comments
Until time , @ N 52° W 4°

Film no. 1 Start time Spacer frame 20 of SERGI End frame 36 by SH
DIGITAL Film no. D Start time Spacer frame of End frame by FU
Film no. 2 Start time 13:10 Spacer frame 1 of SERGI End frame 36 by FU
Film no. 3 Start time Spacer frame 1 of FORM End frame 7 by SH

Fig 3.3. Bottlenose Dolphin Encounter Sheet.

Additional data from further sources were used for the purpose of this study. Mick Baines, Dr Peter Evans and Maren Reichelt (unpublished) made available photographs, positions and group size data from boat-based surveys in 2001. Janet Baxter submitted land-based photographic data for 2003. The Cardigan Bay Marine Wildlife Centre (CBMWC) provided group size information for 2002. Finally, a Countryside Council for Wales Report (Arnold *et al.*, 1997) provided data for four seasons from 1990-1993.

3.2 Individual recognition from identification pictures.

Individual dolphins were identified from photographs showing their dorsal fin morphologies, naturally occurring markings, such as skin pigmentation, naturally occurring fin notches and tears, natural deformities, tooth rakes and skin lesions on both their dorsal fins and flanks. Using as many features as possible to confirm matches reduces the possibility of false positives (Scott *et al.*, 1990b; Wursig and Jefferson, 1990).

Estimation of group size was supported with the aid of photo-identification data. All group estimates recorded details on group composition, where ‘calves’ included young animals with pale skin and visible foetal folds on their flank and included neonatal calves in their first days or weeks of life. ‘Juveniles’ had pale skin and were judged by eye to be at least two-thirds the length of adults, and ‘adults’ were full grown animals with darker skin colour. (Ingram, 2000).

The consistent and close escort of a calf with an adult was used to define the adult as a ‘probable female’. Although bottlenose dolphins show only a slight degree of morphometric sexual dimorphism (Hersh *et al.*, 1990), males have been shown to acquire a higher degree of scarring on their dorsal fins through intraspecific interactions (Tolley *et al.*, 1995). As the degree of marking of an individual cannot be used as a definite identifier of gender, during this study animals with heavy scarring and multiple fin nicks were therefore assigned ‘probable males’ (Fig 3.4). Once the film for each encounter was processed, the slides were marked with the encounter date, film number, frame number, photographer’s initials and encounter number. The photographic transparencies were analysed over a light box using a 8X magnifier lupe or a dissecting microscope. Digital pictures were downloaded and analysed on screen using Fax Viewer and Adobe Photoshop software.



Fig 3.4. Heavily scarred ‘probable male’ W0329 and ‘probable female’ W0325 (with calf W0326).

A *Film Sheet* (Fig 3.5) was completed for slides and an Excel spreadsheet for any digital pictures taken. Each picture was assigned a quality grade (scored 1-4) based on image size, focus, lighting, angle of fin and exposure. For example, a photograph that has the subject full frame, in sharp focus and at a good angle is recorded as 1, whereas, a photograph where only part of the fin is visible will be recorded as 4. Photographs with insufficient data or of poor quality were discarded. Other features of the dolphin’s natural markings were noted. If an individual was distinctively marked and those marks were an identifying feature from both right and left sides of the animal then it was categorised as well marked (WM). Animals with no obvious distinguishing features were termed challenging (CH). Other categories included pigmented individuals (PI) and those displaying small nicks (SN).

Once matches were identified, each match was then subjected to independent analysis by a second observer to avoid bias and reduce the possibility of identifying false positives or false negatives.

The best images of each animal were selected for both right and left profiles to be catalogued. Any ‘new’ study animal was then given a unique number and added to one of three catalogues: left-side, right-side or well-marked/small nicks.

Finally, the data on all identified individuals, together with encounter number, group size and date was entered on to an Excel spreadsheet.

ID Film Sheet

Date 7 / 8 / 04 Records no. 90, 91 Film no. 67 By S.H.

IDs ENCOUNTER 90 - ID's W0306, W0307, W0376
W0393.

Enc	Fr	Time	Quality	Marking	ID	Comments
90	1	11:39	X			FORT
	2	11:48	3	WM		
	3	"	2	WM		W0307
	4	"	2	WM		W0306
	5	"	4	WM		
	6	"	2	WM		
	7	"	4	WM		W0393
	8	11:49	X	-		
	9	"	2	WM		W0393
	10	"	3	WM		
	11	11:50	3	WM		W0306
	12	"	3	WM		W0376
	13	"	X	-		
	14	11:51	3	WM		W0306
	15	11:54	4	WM		W0393
	16	"	4	WM		W0376
	17	"	4	WM		
	18	"	4	WM		W0393
	19	12:00	3	WM		W0306, W0307
	20	"	4	WM		W0306
	21	"	3	WM		W0393
	22	"	3	WM		W0393
	23	"	3	WM		W0307, W0306
	24	"	4	WM		W0306
	25	"	3	WM		W0306
	26	"	X	-		
	27	"	2	WM		W0307
	28	"	2	WM		W0393
	29	12:03	4	WM		W0376
	30	"	4	WM		
	31	"	4	WM		W0306
	32	"	3	WM		
✓	33	"	3	WM		W0393
91	34	12:54	X	-		FORT
↓	35	12:55	4	WM		
↓	36	"	3	WM		W0303

Fig 3.5. Film Sheet recording photographic information and identifications.

3.3 Data Analysis.

3.3.1 Long-term residency.

An analysis of well-marked individuals identified during this present study was made by comparing all available photographic archives to examine aspects of site fidelity and long-term residency.

3.3.2 Group Size.

Group size analysis was conducted on data representing 2001 – 2003. Statistical analysis on this dataset was conducted using SPSS (v.12.01). Standard deviations are reported with means. Seasonal changes over the winter were unable to be determined due to limited resources and unfavourable weather. However, two trips, one in November 2003 and one in February 2004, were made although no dolphins were seen.

3.3.3 Social Organisation.

3.3.3.1 Choice of selection criteria and association index.

Data from the 2003 season was used to calculate the coefficients of association (CoA's). Association indices are most accurate when all members of all groups have been identified and each individual has been seen several times. Only adult individuals that had been recorded three or more times in a group where at least 50% of the animals were identified OR at least five animals were identified were selected for analysis. This figure was considered appropriate for our dataset and facilitates comparison with other studies (e.g. Chilvers and Corkeron, 2002). With a minimum of three sightings for each animal there was a minimum of four possible association values per dyad depending on the frequency of sightings together and apart. Calves were excluded from all analyses because it was expected that range and association patterns were dependent on those of the mother (Rossbach and Herzog, 1999).

For the purpose of this study all individuals identified within a group were considered to be associated with each other, a definition of association commonly used in studies of dolphin structure (Whitehead and Dufault, 1999). Thus the more frequently a pair (dyad) of dolphins were sighted together in the same group rather than in a separate group, the closer they were associated.

The degree of association in cetacean populations has typically been measured using the Half Weight Index (HWI) (Cairns and Schwager, 1987) (e.g. Smolker *et al.*, 1992; Brager *et al.*, 1994). This index is often chosen as the most appropriate as it introduces a bias to correct for missed identifications of one member of a dyad. Ginsberg and Young (1992), however, contended that the HWI overestimates associations with its bias and they advocated the use of Simple Ratio index (SR) as the least biased. The SR is least biased when the sample is random (Cairns and Schwager, 1987) and this method has been used in cetacean association studies (Slooten, 1993, Ingram, 2000, Shane, 2004) where researchers had achieved complete identification of individuals of most groups sighted. The HWI is least biased when one member of a pair is more likely to be sighted when separate than when together, which I believe is the case for the dolphins examined in this study.

Sampling methods in this current study may fail to photographically identify both members of a co-occurring pair because of incomplete coverage of the group or poor quality photographs, thus underestimating their association. The HWI bias in the correct direction will therefore alleviate this bias.

On balance, the HWI was selected in the present analysis, as the identification of all group individuals could not be ascertained. Moreover, as it is the most commonly used index on bottlenose dolphin populations it will facilitate comparison with other studies.

$$\text{Half Weight Index} = \frac{x}{x + \frac{1}{2}(Ya + Yb)}$$

where:

- x = the number of encounters that included both dolphins a and b ,
- Ya = the number of encounters that included dolphin a but not dolphin b ,
- Yb = the number of encounters that included dolphin b but not dolphin a .

The association indices range from 0.00 for two dolphins that are never seen together, to 1.00 for two dolphins that are always seen together.

To test whether the resulting association matrix differed significantly from a random distribution of association, coefficients of association were calculated for identified individuals in the study area.

3.3.3.2 Association analysis.

The dataset was analysed using SOCPROG 1.3, a program developed for MATLAB (version 5.1) to analyse the social organisation of animal communities (Whitehead, 1999a).

The HWI matrices for the study period were graphically represented by a hierarchical cluster analysis (average-linkage). This method clusters individuals not only by preferred partnerships but by also using the least preferred partnerships (Lusseau *et al.*, 2003). Furthermore, the HWI association matrix was subjected to principal coordinate analysis (PCoA) in order to identify patterns of association between assemblages of individuals within the population. This enhances the results of cluster analysis by graphically quantifying association levels between individuals on a number of multidimensional axes. The amount of data explained by PCoA can be assessed by calculating the proportion of the total eigenvalues of all dimensions expressed by these plotted axes. An arbitrary threshold of separation will produce a number of assemblages resulting from cluster analysis. In order to identify a suitable association index for defining assemblages the rate of agglomeration of groups within the hierarchical clustering can be examined (Ingram, 2000).

The Monte Carlo randomisation technique (Manly 1995, Bejder *et al.* 1998) was employed to assess the significance of all the possible dyads of animals within the known study sample by comparing any association patterns in the real data with a distribution of random data. Individuals within sampled groups are randomly permuted, keeping group size and the number of times each individual was seen the same as in the original dataset.

The permutation tests performed will test the hypothesis that the distribution of association indices from the empirical data was not different from that of the permuted data sets. After a certain number of permutations, the P value should stabilize indicating the point where the randomly generated P number best represented the P value of the actual data and confidence intervals decreased.

As the association analysis is based on a relatively short sampling period i.e. May – October, it is assumed that all individuals are present during the sampling

period with no loss due to birth, death or migration and consider the ‘permuting all groups’ test in the SOCPROG program to be most appropriate. This will allow the null hypothesis to be tested in that there are no preferred or avoided companions (individuals who preferentially group together or avoid one another) given the number of groups each animal was seen in during each sampling period. If preferred or avoided companionships are present then a significantly high SD of the real association indices will indicate this.

After the permutations, the HWI’s were calculated for each dyad, and the random (expected) HWI was compared with the real (observed) HWI (Lusseau *et al.* 2003). If more than 95% of the expected HWI were found to be smaller than the observed HWI, then a pair of animals could be considered to be preferred companions rather than a random association.

In order to assess differences in association depending on sex, a Mantel test was used with 1,000 permutations.

3.3.3.3 Spatial distribution

The core areas used by dolphins agglomerated in the cluster analysis were examined using the MapInfo program. Sighting locations were plotted for all groups whose composition contained a *majority* (i.e. >50%) of animals belonging to a single cluster. This allowed core areas for these assemblages to be visualised.

Dolphins seen more than 20 times and in more than one season were chosen to highlight individual preferred core areas.

3.3.3.4 Temporal Analysis.

The sightings data contributing to association analyses are typically collected over extended periods of time. In order to examine the permanency of these associations the time between dyad sightings should be considered. Using SOCPROG, the temporal stability of associations between individuals sighted in Cardigan Bay was examined. The model used allows for the probability of two animals remaining associated after various time lags to be calculated where for each individual SOCPROG calculates the proportion of companions the individual had at time t that remained companions at time $t + d$ where d is the time lag. This proportion is then averaged over all individuals in the study. The rate of decay of these

associations can be then be compared with a number of mathematical models describing different rates of exponential decay.

4.

Results

4.1 Survey effort.

In 2003, from May to October, a total of 72 surveys were made resulting in 134 encounters and in 2004, from May to September, a total of 58 boat surveys were conducted in the Bay, resulting in 119 encounters with dolphin groups. Table 4.1 shows the effort for the four year period analysed in this study.

Table 4.1. Survey Effort 2001-2004.

	Boat Surveys	Survey Effort(hrs)	Encounter Hours	Encounters Made
2001	26	246.5	Unknown	44
2002	66	366	Unknown	240
2003	72	328	17.05	134
2004	58	263	26.3	119
TOTAL	222	1203.5	43.35 (2003/4)	537

4.2 Group Size.

From 2001-2004 the group sizes ranged from singletons to 42 animals, with a mean group size of 5.85 (\pm 5.89). An analysis of the group sizes over the four years showed that average group size in each year were significantly different (Kruskal-Wallis test, $x^2 = 105.865$, d.f. =3, $p < 0.001$, Fig 4.1). 83% of all encounters with dolphins in this study were with groups rather than alone.

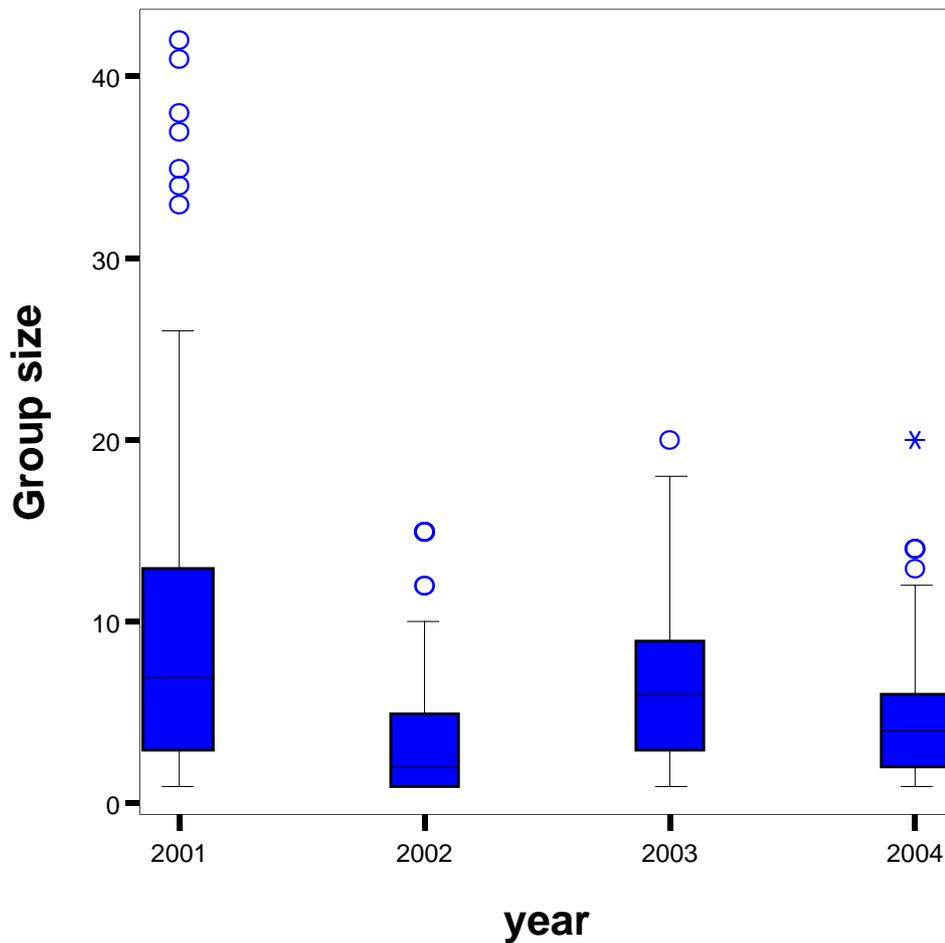
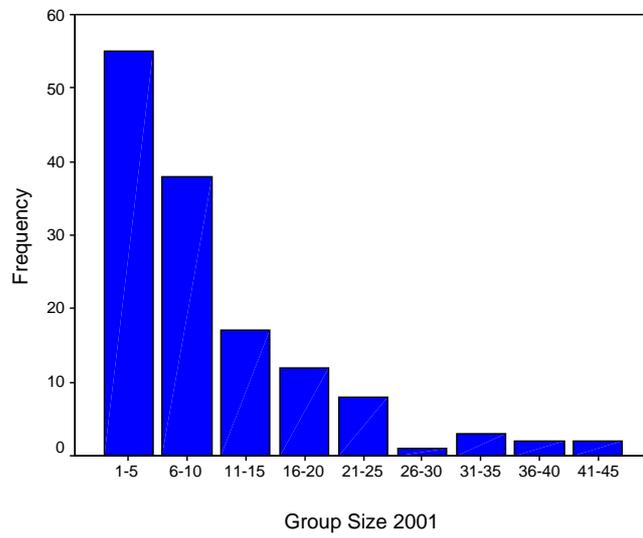


Fig 4.1. Box plot of group size for each year of the study. Horizontal lines inside boxes represent the median; whiskers above and below show interquartile ranges and \circ symbols denote outliers and * extremes.

The frequency distribution of group sizes was skewed towards smaller groups for each year with the majority of groups involving 1-5 animals (Fig 4.2 a-d, Table, 4.2). Maximum group size in 2002 was 15 animals and in 2003 and 2004 a maximum group size of 20 dolphins was observed. In 2001, however, 18 (13%) of the encounters contained groups with > 20 animals. Analysis of group size by month showed no significant difference between months (Kruskal-Wallis test, $\chi^2 = 5.284$, d.f. = 4, $p = 0.259$) (Fig 4.3). The highest mean group size was recorded in August (6.50 ± 7.11) and the lowest in May (4.36 ± 3.85) (Appendix 2).

a)



b)

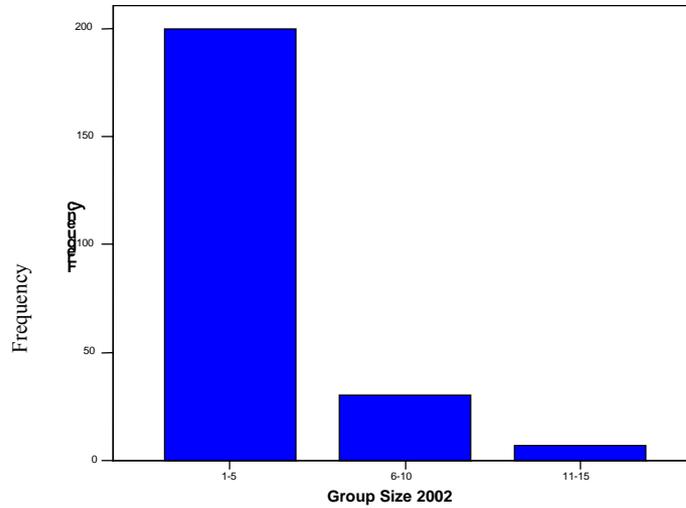
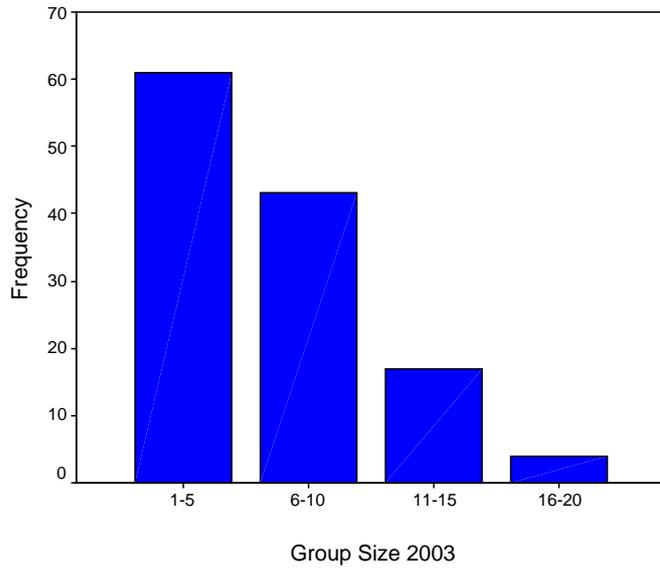


Fig 4.2. Frequency distribution of group size of bottlenose dolphins in Cardigan Bay during: a) 2001, b) 2002, c) 2003 and d) 2004.

c)



d)

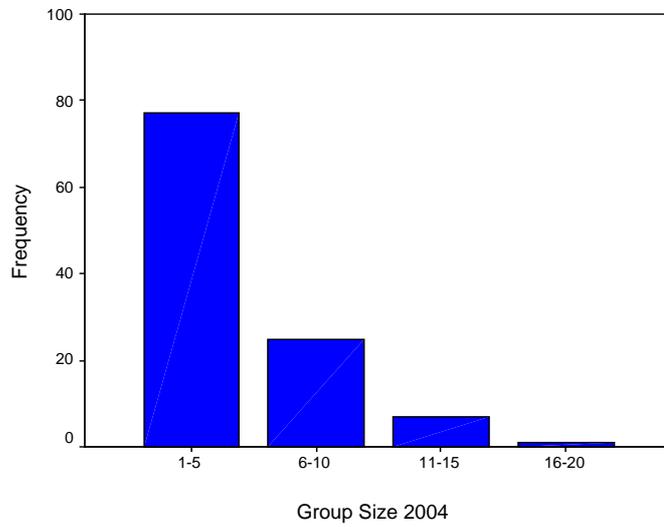


Fig 4.2. (cont.) Frequency distribution of group size of bottlenose dolphins in Cardigan Bay during: a) 2001, b) 2002, c) 2003 and d) 2004.

Table 4.2. Showing the mean, median, max. and min. group size for all years.

	2001	2002	2003	2004
Mean	9.56(±8.96)	3.43(±2.96)	6.41(±4.19)	4.76(±3.61)
Median	7	2	6	4
Max	42	15	20	20
Min	1	1	1	1

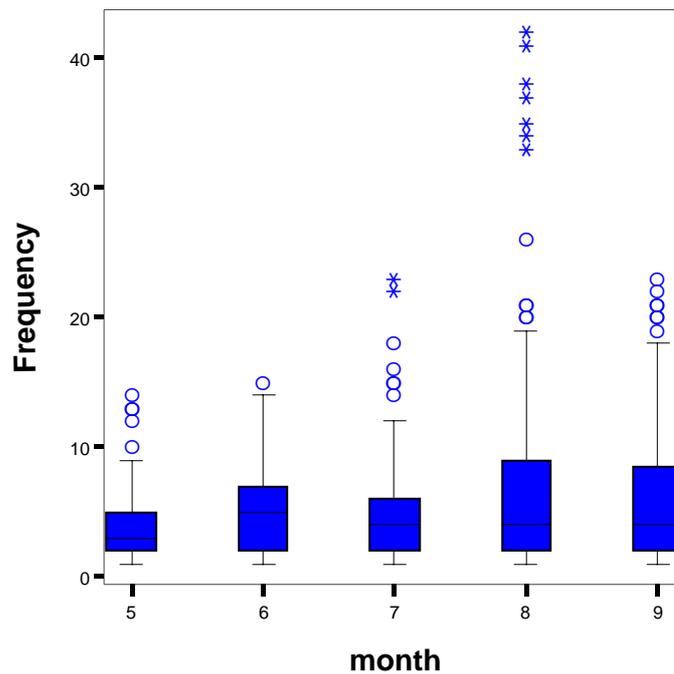


Fig 4.3. Box plot of monthly variations (May-September) in group size from 2001-2004 in Cardigan Bay. Horizontal lines inside boxes represent the median; whiskers above and below show interquartile ranges and \circ symbols denote outliers and $*$ extremes.

4.3 Individuals identified and sex ratio.

To date, ninety-eight well-marked bottlenose dolphins have been identified in the study area. Of this population, eighty-seven are adults, nine juveniles and two calves. In addition, twenty animals have been identified from their left sides only and a further twenty from their right indicating that a minimum of 118 recognisable individuals are present in Cardigan Bay.

A plot of the number of identifications made against the size of the catalogue indicates that a significant proportion of well-marked animals in the study area have now been identified (Fig 4.4).

From the photo- identification pictures of 2003, 17 animals were classed as 'probable females' and 29 as 'probable males'. The maximum number of resightings for any animal was for dolphin #317 sighted in 14 groups. In contrast, 28 dolphins were sighted only once throughout the study.

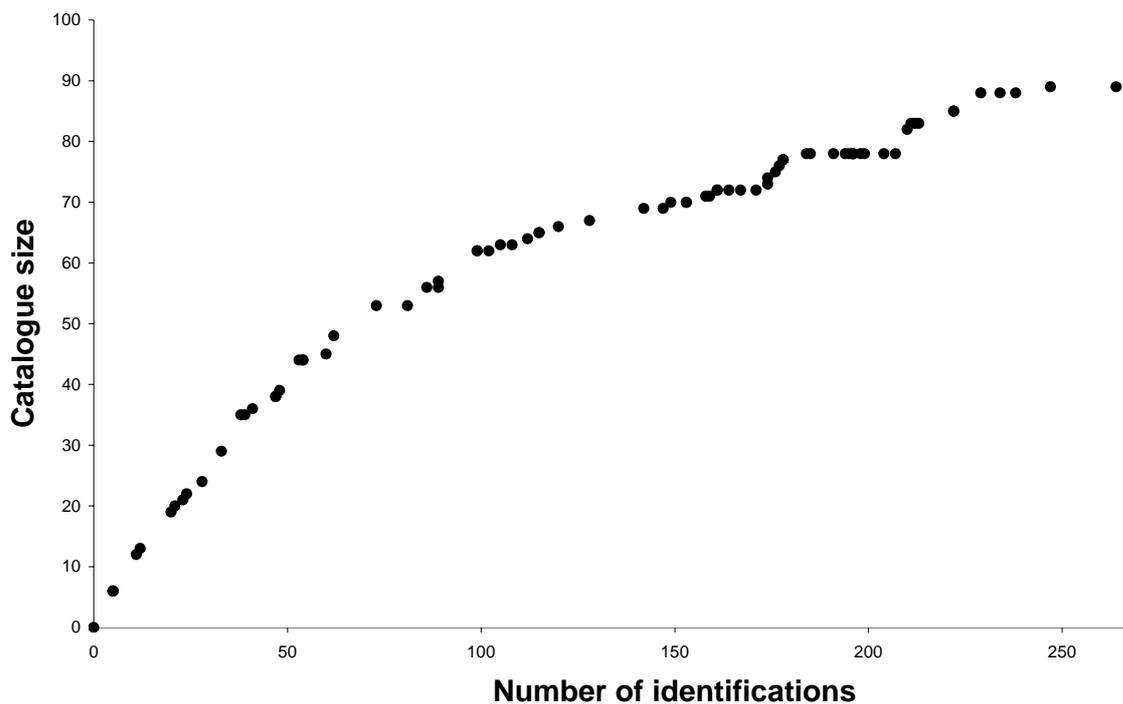


Figure 4.4 Discovery Curve illustrating the number of identifications against catalogue size for 2003.

4.4 Long-term residency.

Some dolphins have shown site fidelity for up to 15 years and 32 individuals were seen at least 3 times and in more than one season (Table 4.3). One individual, a female #377, has been seen in every field season since 1990 (Steve Hartley, personal communication). Female #304 was first sighted as an adult in 1990 and has been seen 25 times during the years of this current study (1990-1993, 2001, 2003 and 2004).

Table 4.3 Sightings frequency of long-term 'resident' bottlenose dolphins in Cardigan Bay.

ID(CBMWC)	AGE	SEX	1990	1991	1992	1993	2001	2003	2004	Total Times seen in 7 years
W0304	A	F	X	X	X	X	X	X	X	25
W0305	A	M	X		X	X	X	X	X	17
W0306	A	M					X	X	X	14
W0307	A	F					X	X	X	11
W0310	A	F					X	X	X	14
W0312	A	M	X	X	X	X	X	X		11
W0313	A	?					X	X		10
W0314	A	?					X	X		9
W0316	A	F					X	X	X	8
W0317	A	F					X	X	X	25
W0322	A	M	X	X	X	X	X	X		15
W0325	A	F					X	X	X	9
W0328	A	M			X	X	X	X		15
W0331	A	?					X	X	X	12
W0336	A	?					X	X		12
W0338	A	F	X	X	X	X	X	X	X	24
W0345	A	?					X	X	X	10
W0347	A	M					X	X	X	15
W0348	A	?					X	X	X	15
S0349	A	?					X	X		6
W0351	A	F		X	X	X	X	X	X	23
W0354	A	M					X	X		9
W0356	A	M					X	X		6
W0358	A	?					X	X	X	27
W0364	A	M					X	X		10
W0367	A	F					X	X	X	11
W0368	A	F		X	X	X	X	X	X	22
W0376	A	M					X	X	X	11
W0377	A	F	X	X	X	X	X	X	X	13
W0381	A	F					X	X	X	17
W0393	A	M					X	X	X	3
W0395	A	?	X	X	X	X	X	X	X	14

4.5 Associations of Individuals

During 2003, 66 encounters were selected where more than 50% of the group and/or ≥ 5 individuals were identified. From these encounters, 52 animals that were sighted ≥ 3 times were selected for the social association analysis (Table 4.4, and Appendix 1.). Within this subset, 16 (30%) were ‘probable females’, 18 (35%) ‘probable males’ and 18 (35%) of unknown gender. The median number of resightings per dolphin was 5 (mean 5.85 ± 2.06) and the maximum number of resightings was for dolphin #317, photographed in 12 groups (Fig 4.5).

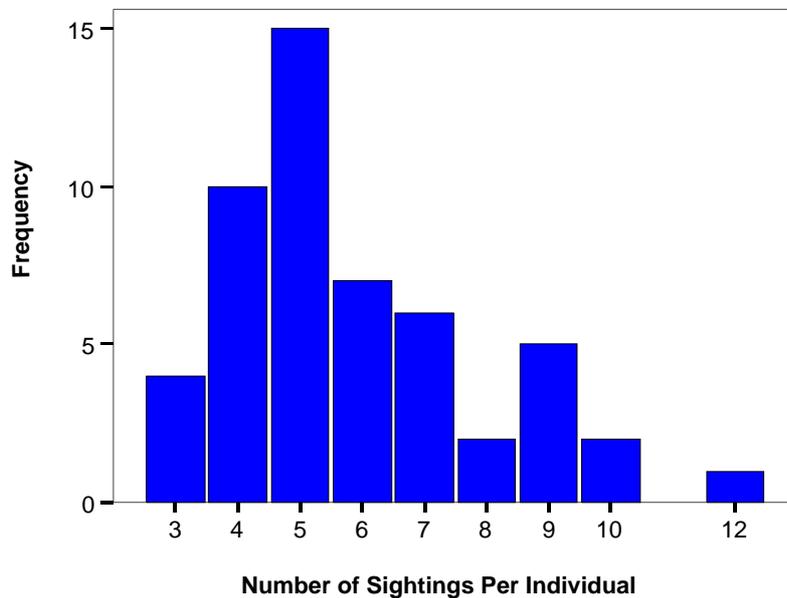


Fig 4.5. Sightings frequency of study animals seen ≥ 3 times ($n = 52$) in encounters with satisfactory identification coverage (mean = 5.85, S.D.= 2.06)

The distribution of Coefficient of Associations (CoA's) for all individuals ($n=2704$) was clearly skewed towards low values (Fig 4.6 (a)) with all dolphins showing low or no associations at all with most others and only a few dolphin pairs with high CoA's. The CoA's ranged from 0.00 (never seen together) to 1.00 (always seen together) with a mean of 0.10 ± 0.03 . (Appendix 3)

Table 4.4. Individual bottlenose dolphins used in the analysis of association.
M = male, F = female, A = adult, W= well-marked, S= small nicks and L= left-side.

ID	Sex	Age	No. of recaptures. 2003
W0301	?	A	3
W0302	F	A	3
W0305	M	A	7
W0306	M	A	9
W0307	F	A	9
W0308	F	A	4
W0309	?	A	4
W0310	F	A	5
W0312	M	A	5
W0313	?	A	9
W0314	?	A	5
W0315	?	A	6
W0316	F	A	6
W0317	F	A	12
W0321	F	A	5
W0325	F	A	4
W0329	M	A	4
W0331	?	A	5
W0335	M	A	10
W0336	?	A	10
W0338	F	A	7
W0340	M	A	6
S0343	M	A	6
W0345	?	A	7
W0347	M	A	8
W0348	?	A	7
S0349	?	A	5
W0352	F	A	4
W0353	M	A	5
W0354	M	A	5
W0355	M	A	4
W0356	M	A	4
W0358	?	A	9
S0359	M	A	5
W0364	M	A	5
W0367	F	A	8
W0371	?	A	5
W0372	F	A	5
W0373	M	A	7
W0374	M	A	5
W0376	M	A	6
W0377	F	A	7
W0381	F	A	6
W0387	?	A	3
W0390	M	A	3
W0396	F	A	5
W03100	?	A	4
W03101	F	A	9
S03103	?	A	6
S03110	?	A	4
S03111	?	A	4
L312	?	A	5

The associations witnessed most frequently were at levels between 0.00 – 0.20. The distribution of the mean and maximum CoA's are shown in Fig 4.6 (b) and 4.6 (c). The mean CoA's ranged from 0.03 to 0.18, while the maximum CoA's ranged from 0.30 to 1.00.

a)

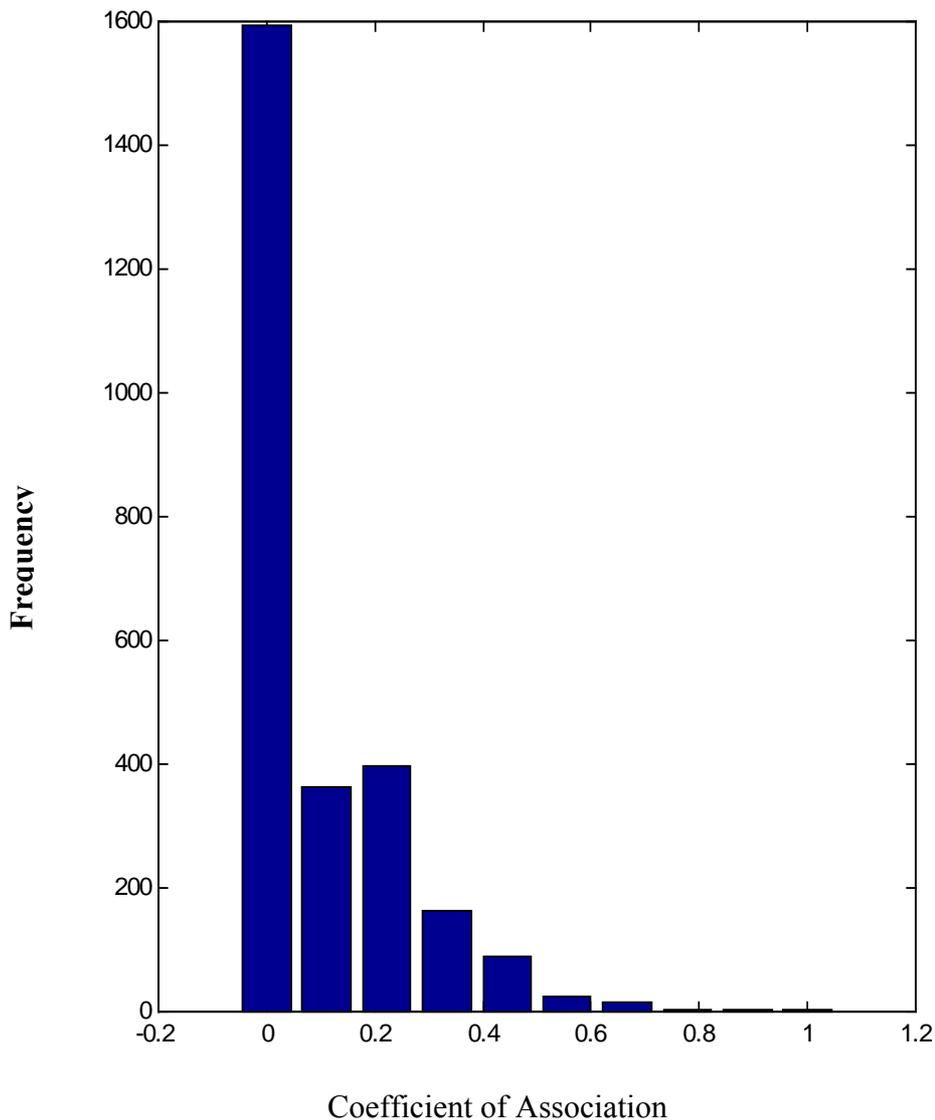
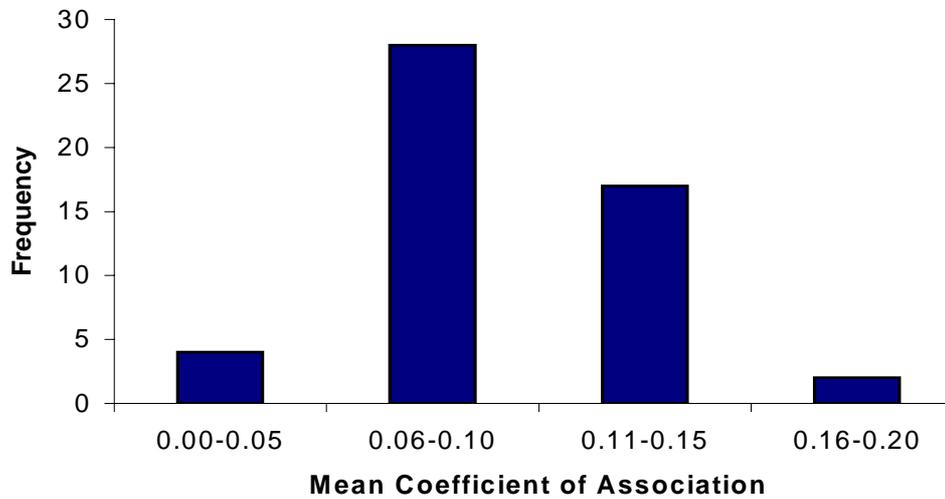


Fig 4. 6 Distribution of: a) Coefficient of Associations for all pairwise comparisons of 52 individuals identified three or more times (n=2704), b) mean CoA's for 52 individuals identified ≥ 3 times and c) maximum CoA's for 52 individuals sighted ≥ 3 times.

b)



c)

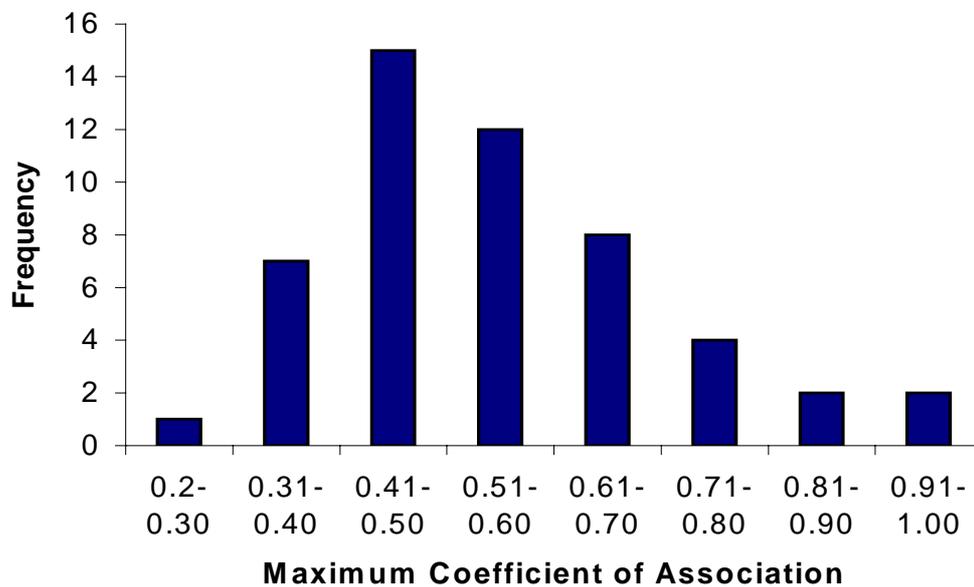


Fig 4.6.(cont.) Distribution of: a) Coefficient of Associations for all pairwise comparisons of 52 individuals identified three or more times (n=2704), b) mean CoA's for 52 individuals identified ≥ 3 times and c) maximum CoA's for 52 individuals sighted ≥ 3 times.

Associations between and within the sexes were found to be significantly different (Mantel test, $t = 2.6891$, $p = 0.99642$, matrix correlation 0.071565). There was a tendency for male-male associations to be stronger (0.14, c.f.0.10 for all individuals), while female-female associations were weaker than intersexual associations (Table 4.5).

Table 4.5 Average and maximum CoA's between and within sex classes.

	Av. CoA (SD)	Max. CoA (SD)
All individuals	0.10 (0.03)	0.56 (0.16)
Female-Female	0.10 (0.04)	0.42 (0.12)
Male-Male	0.14 (0.06)	0.50 (0.17)
Male-Female	0.11 (0.03)	0.45 (0.16)

The number of associates for each individual in the association matrix (Fig 4.8) was found to range from 4 to 33 with a mean of 20.31 (SD=6.77, n=52). Amongst individuals of known sex, females associated with between 4 and 31 other animals (mean=20.62, SD=7.75, n=16) while males had a range from 9 to 30 associates (mean=21.56, SD=5.64, n=18). Within this set, females # 307 and 338 both had the highest number of associates at 31, whereas amongst males #335 had the highest number with 30 associates.

31 dyads associated at a level of 0.50 or higher, which indicates they spent at least as much time together as apart. Of those dyads where sex was determined, 3 were female-female pairs, 7 male-male and 9 male-female.

The highest CoA of all study animals (1.00) was observed between #301(an adult of unknown sex) and #302 (an adult female) who were consistently seen together in May, June and July.

301 1.00
 302 1.00 1.00
 3103 0.22 0.22 1.00
 305 0.00 0.00 0.15 1.00
 306 0.00 0.00 0.13 0.13 1.00
 307 0.00 0.00 0.00 0.25 0.33 1.00
 308 0.00 0.00 0.00 0.36 0.31 0.31 1.00
 309 0.00 0.00 0.00 0.36 0.15 0.46 0.50 1.00
 310 0.00 0.00 0.00 0.17 0.29 0.29 0.22 0.22 1.00
 312 0.00 0.00 0.31 0.00 0.25 0.38 0.00 0.00 0.33 1.00
 313 0.00 0.00 0.13 0.00 0.22 0.22 0.00 0.00 0.14 0.38 1.00
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Fig 4.8 Association matrix showing the HWI for the 52 study animals. CoA's ranged from 1.00 (always seen together) to 0.00 (never seen together)

Sociograms illustrate the strength of the relationship between individuals of known gender. Within mixed sex individuals, a male-female dyad between #321 and #329 had the highest association at 0.67 (Fig 4.9)

A number of animals of both sexes spent more time with certain other individuals of the same sex. Three male-male pairs associated at a level greater than 0.5, of those the males #373 and #374 had the highest association index of all known sex individuals at 0.83 (Fig 10a). Amongst the females, #367 and #307 had the highest CoA at 0.59. The sociograms for intrasexual associations depict a higher level of associations (i.e. stronger) for male- male dyads (ranging from 0.08 - 0.83) than for female-female pairs (0.06 - 0.59) (Fig 4.10b)

Strong networks were evident where certain individuals had a central position. Female #338 had associations greater than 0.62 with the three males, #340, 354 and 356. Furthermore, male #335 had associations of 0.5 or higher with three other animals - females #338 and 396 and the male #340.

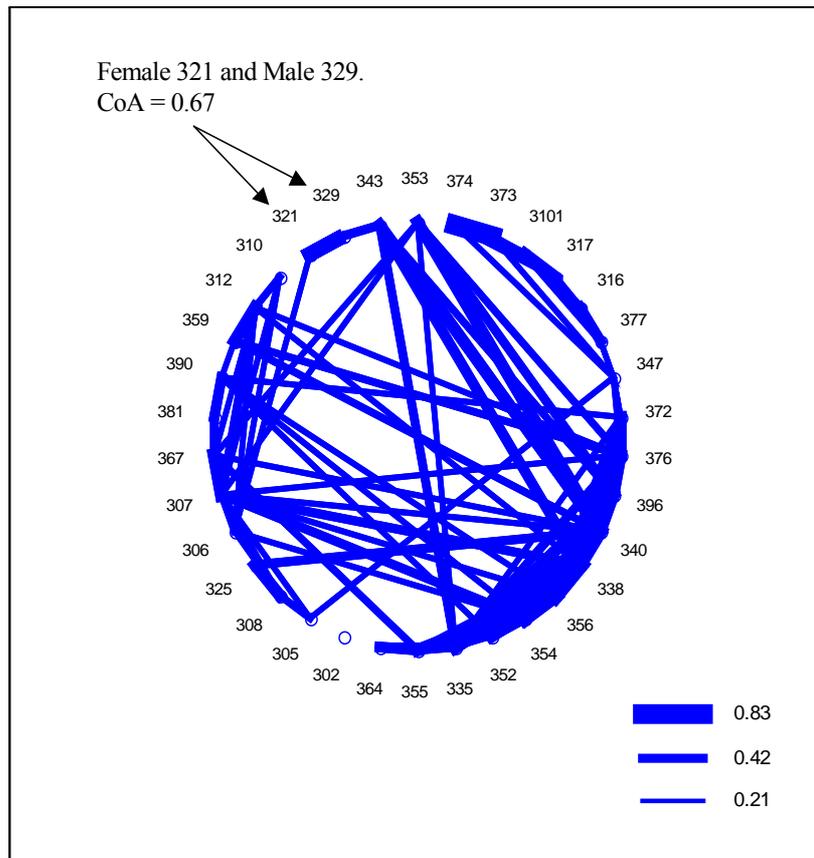
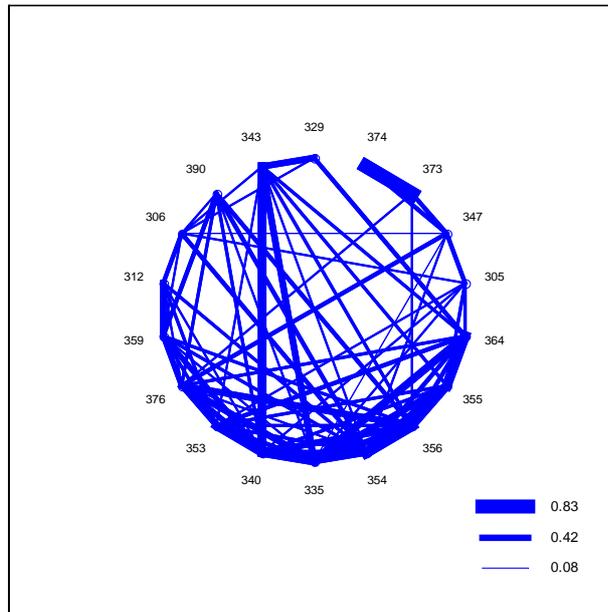


Fig 4.9 Sociogram showing the associations between all known sex individuals. The strongest associations between mixed sex adult study animals was between the female #321 and the male #329.

a)



b)

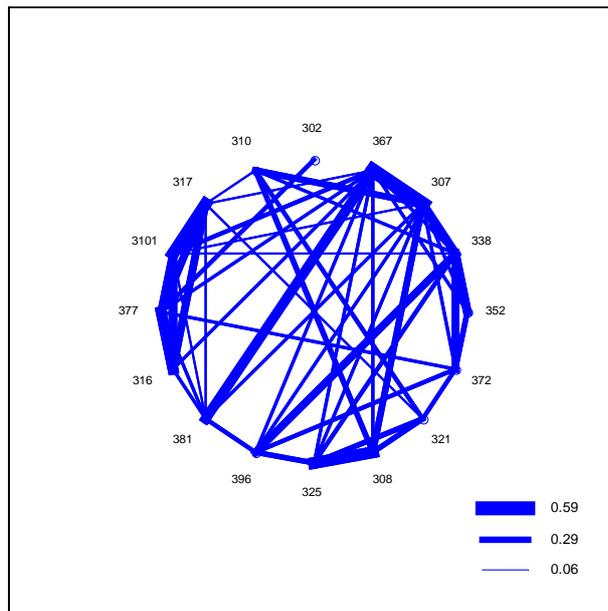


Fig 4.10 Sociogram showing the associations between: a) Male-Male and b) Female-Female HW Coefficients of Associations. Lines of increasing thickness correspond to increasing pairwise associations. Study animals are represented by their ID numbers.

4.5.1 Permutation tests.

The association dataset was randomly permuted 20,000 times and the resulting permuted coefficient of association was not found to significantly differ from the observed mean (real mean = 0.10922, random mean 0.10731, $p = 0.82970$). However, the observed SD was significantly higher than the random one (real SD=0.15867, random SD = 0.13303, $p > 0.9999$), which would indicate a wider range of associations than expected if dolphins associated at random. The permutation test supported these findings (with a two-sided significance level for dyads = 0.05) where 70 significant dyads were present compared to the 64 expected by SOCPROG if the dolphins associated randomly (Appendix 3).

4.5.2 Identification of dolphin assemblages.

Hierarchical cluster analysis (using average group linkage) (Fig 4.11) and PCoA (Fig 4.12) of the 52 study animals indicated loosely associated assemblages. The agglomeration plot of hierarchical clustering showed a linear increase in the number of clusters with decreasing association values with a slight increase in the rate of agglomeration occurring at an association index of 0.13 (Fig 4.13), supporting the choice of this value for defining assemblages (Ingram, 2000). There were six clusters of dolphins defined at the 0.13 association value (Fig 4.11 and 4.12). All clusters were determined to be of mixed sex, however, cluster 6 was composed of just two members #301 (unknown gender) and #302 (adult female).

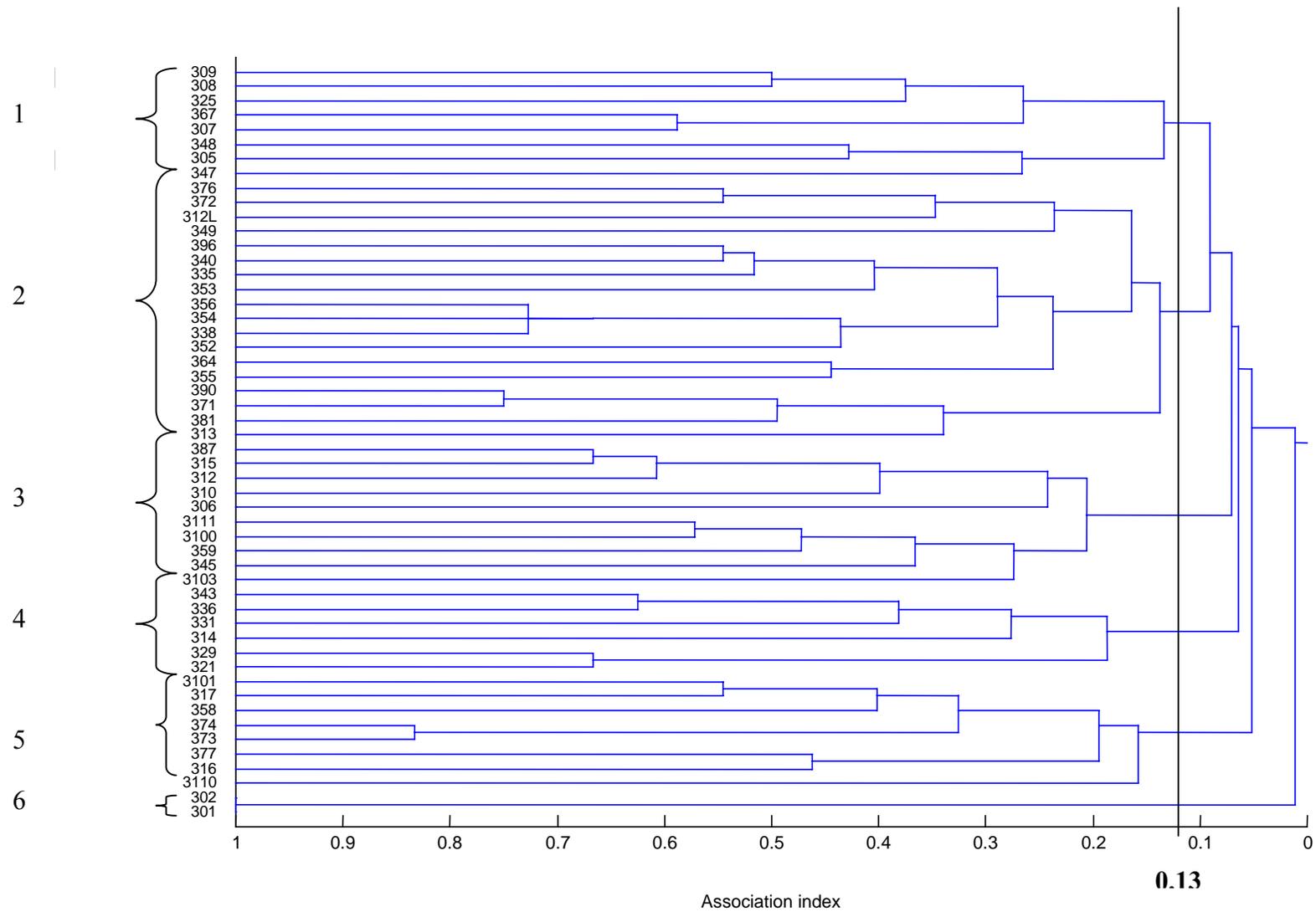


Fig 4.11. Cluster analysis of study animals (n=52) seen \pm 3times in 2003. 6 clusters are defined at the 0.13 association value.

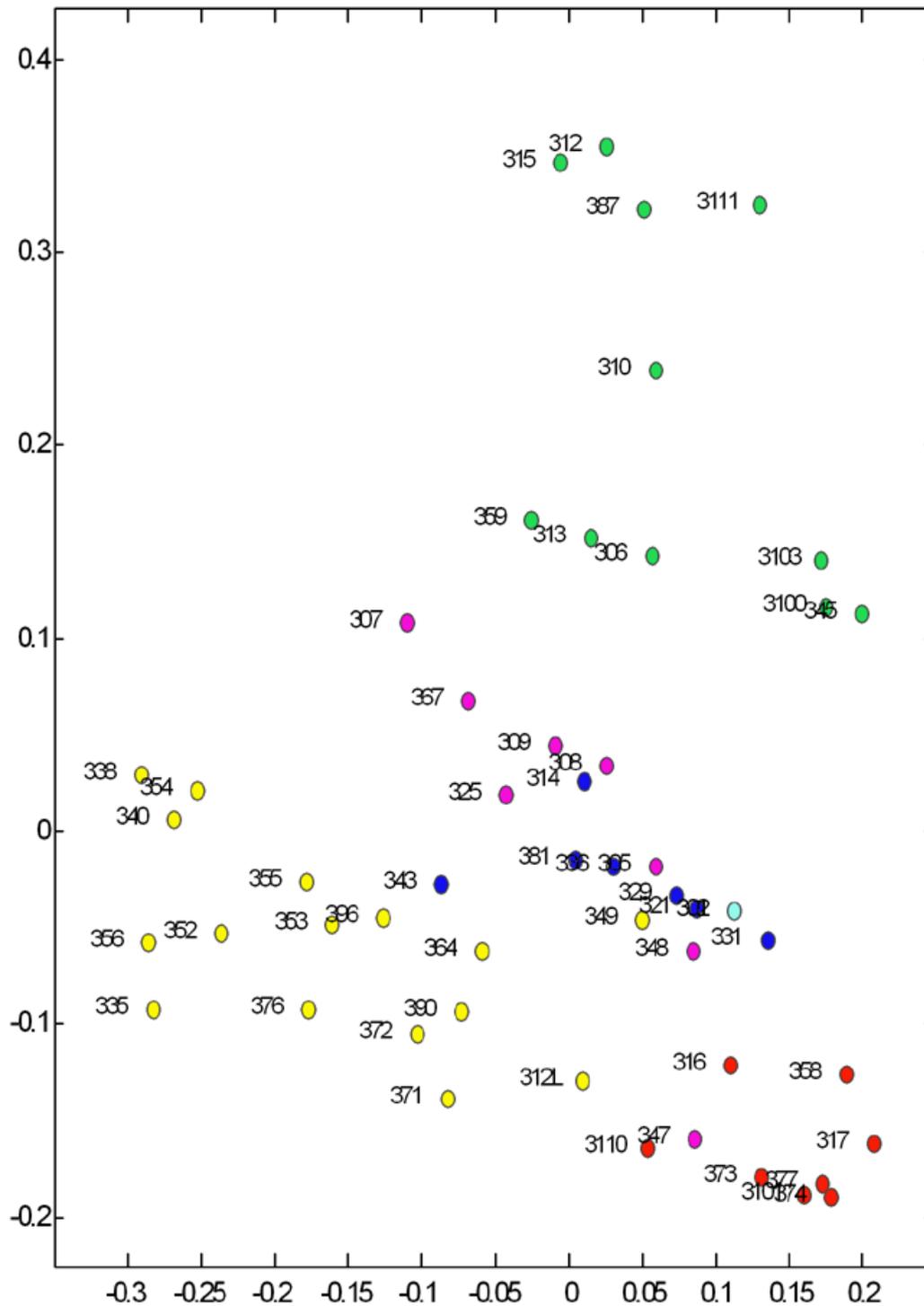


Fig 4.12. Results of principal coordinate analysis of associations between 52 animals seen ≥ 3 times. Coloured areas show clusters defined at the 0.13 association value. Cluster 1 (pink), Cluster 2 (yellow), Cluster 3 (green), Cluster 4 (light blue), Cluster 5 (red) and Cluster 6 (dark blue).

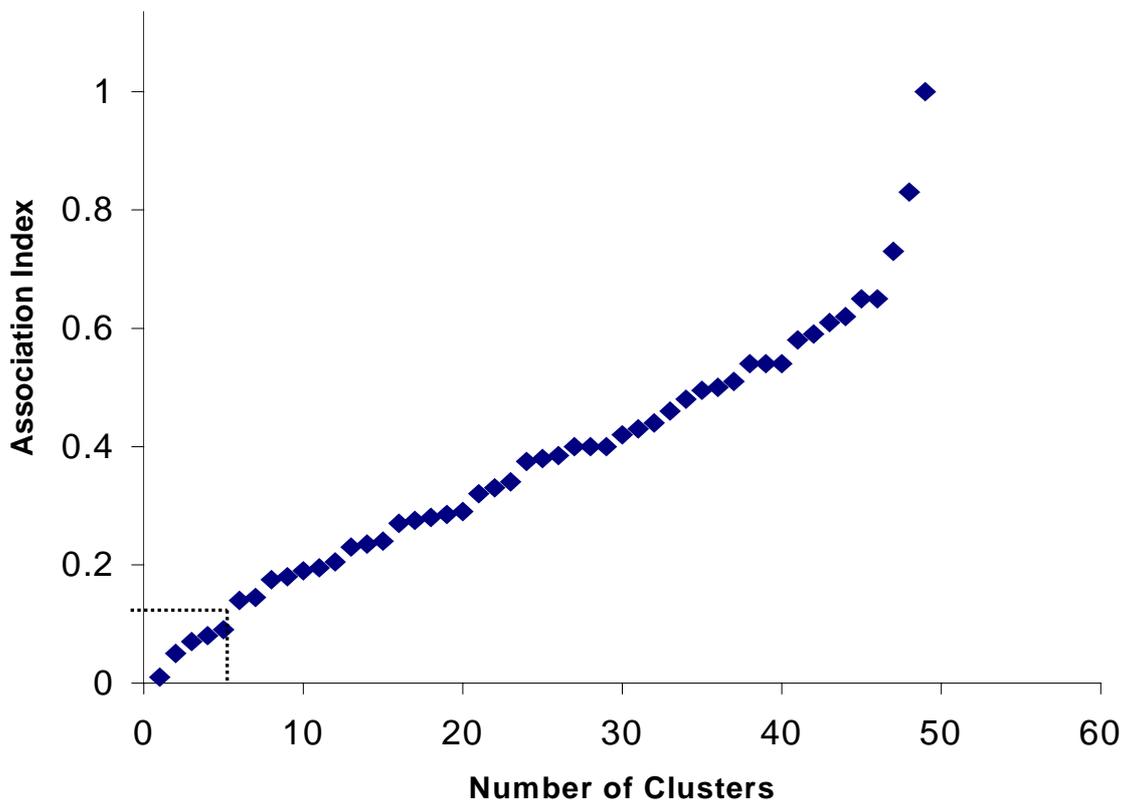


Fig 4. 13 Agglomeration of clusters produced by hierarchical clustering of dolphins sighted at least three times. (The dashed line indicates the clustering at an association index of 0.13 used to define dolphin assemblages.)

4.5.3 Spatial distribution.

Most dolphin groups encountered contained a majority of individuals (>50%) belonging to one of the six clusters of dolphins defined at 0.13 association value (Fig 4.14). An analysis of sightings locations of these six clusters suggests a degree of partitioning of habitat and range. For example, dolphins belonging to Cluster 2 were mainly encountered in Aberporth Bay, while cluster 3 animals were found predominately in the south of the cSAC between Aberporth and Mwnt. Cluster 5 animals were found to have a range concentrated around New Quay and Ynys Lochlyn (Fig 4.15 a-f). However, there were also overlapping ranges present, which highlighted a more complex picture; for example, dolphins belonging to cluster 4, seemed to utilise the whole of the cSAC.

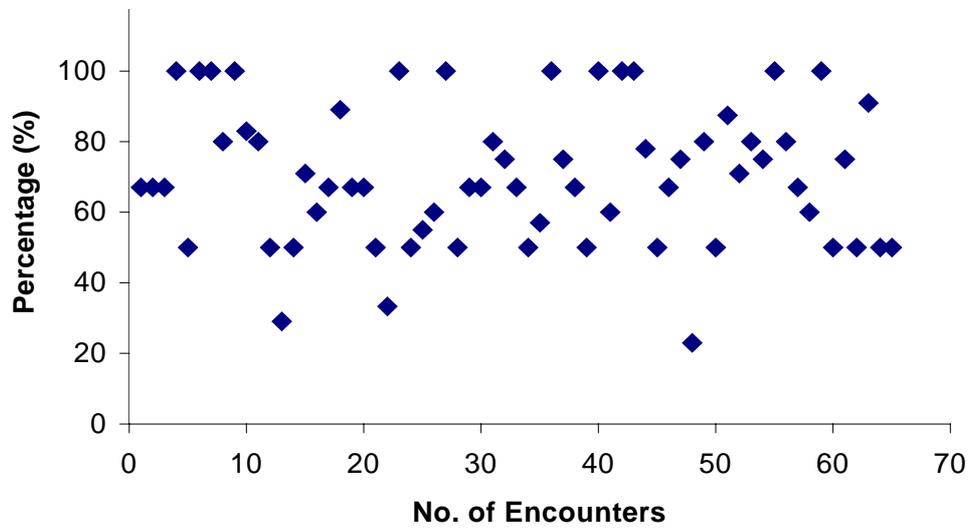


Fig 4.14 Percentage of animals in each encounter where the majority of individuals belonged to one of the six clusters defined at the 0.13 association value.

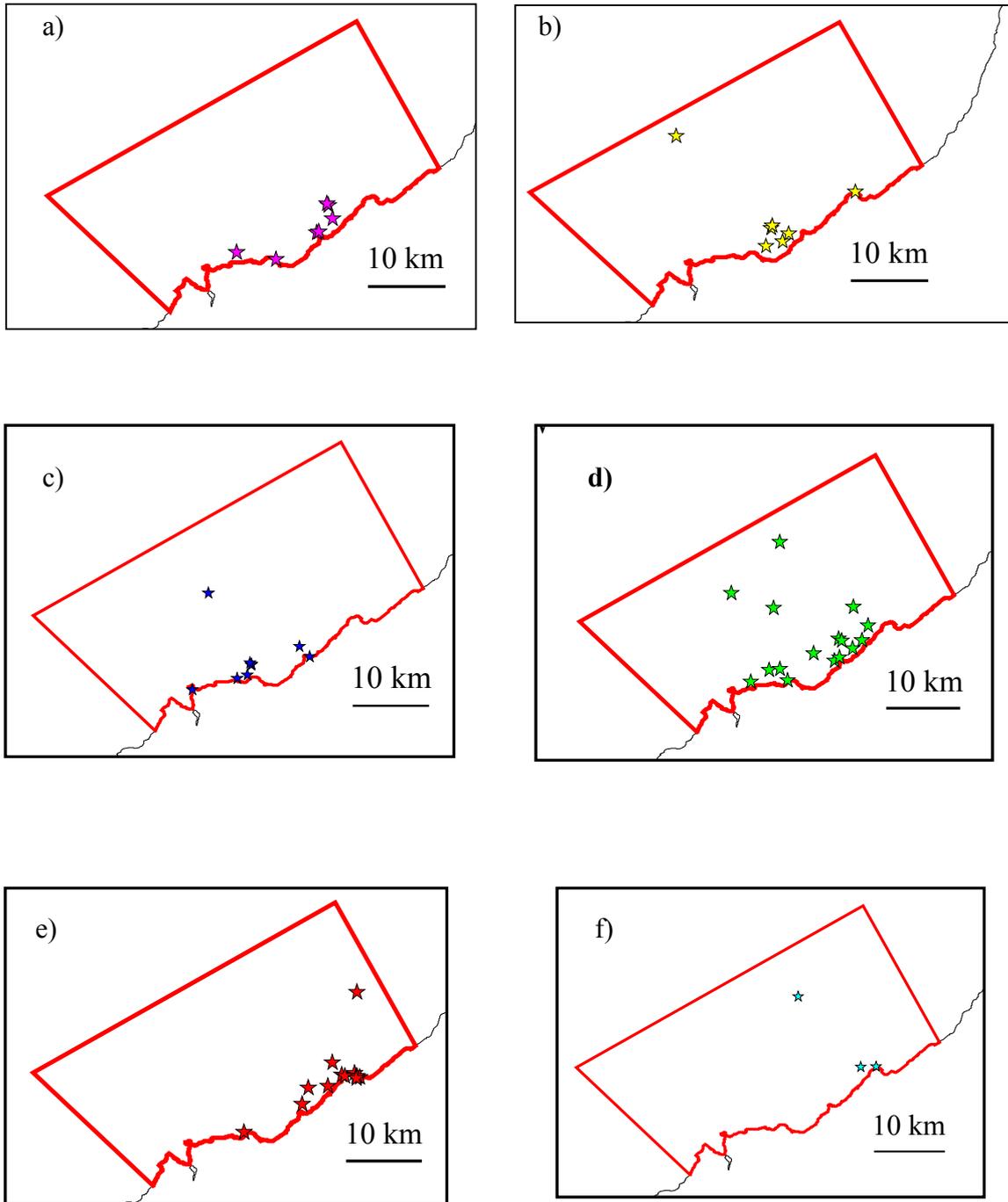


Fig 4.15. Plots of the locations of encounters with the clusters of dolphins in defined at 0.13 association value: a) cluster 1; b) cluster 2; c) cluster 3; d) cluster 4; e) cluster 5 and f) cluster 6.

4.5.4 Spatial distribution of long-term ‘residents’.

Six dolphins were seen more than 20 times and in more than one season (Table 4.3). For example, during 2003, individuals #317 and #358 were both found in the Cluster 5 assemblage and appeared to prefer the coastline between Ynys Lochtyn and New Quay headland in the northern cSAC. These individuals are well known to researchers and analysis of data shows these areas were favoured in 2001 and 2004. In 2001, 2003 and 2004 these individuals were seen 25 and 27 times respectively (Fig 4.16 a and b). Conversely, individual #351 has shown site fidelity for over 15 years in an area between Aberporth and Mwnt and has only once been seen in the northern part of the cSAC. (Fig 4.16 c and d).

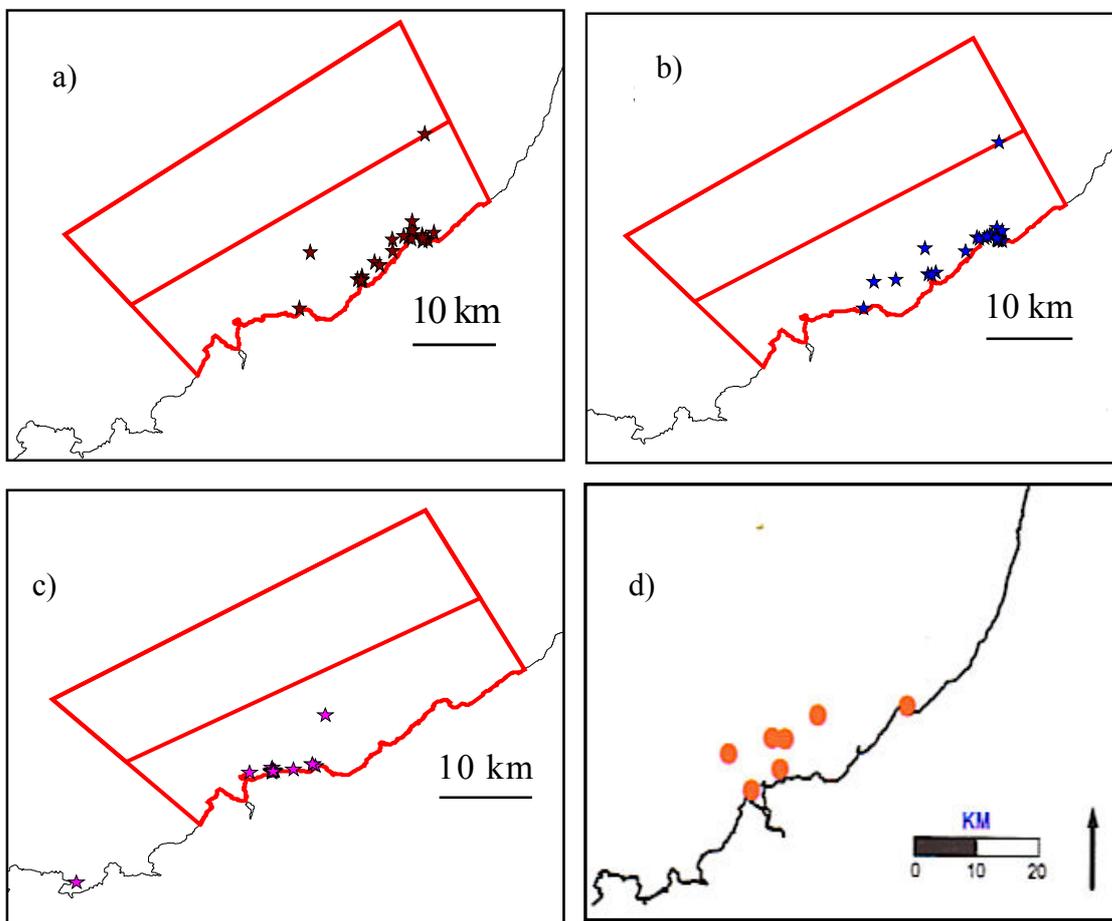


Fig 4.16. Map showing preferred ranges within the cSAC of individuals: a) 317; b) 358; c) 351 in 2001-2004; d) 351 between 1990 –1993 (d taken from Arnold *et al* 1997).

4.5.5. Temporal Analysis

Lagged association rates showed a decrease in dyads being sighted together again after more than a few days (Fig 4.18). However, the estimated lagged association rate stabilises above the null rate (i.e. the rate if animals associating randomly) as time increases indicating that the Cardigan Bay population contains longer term stable relationships.

The best-fit model curve indicates three levels of associates found in this population. i) rapid dissociations (i.e. some associates leave very quickly); ii) casual acquaintances (who associate for a certain length of time and then disassociate); and iii) constant companions (Whitehead, 1999).

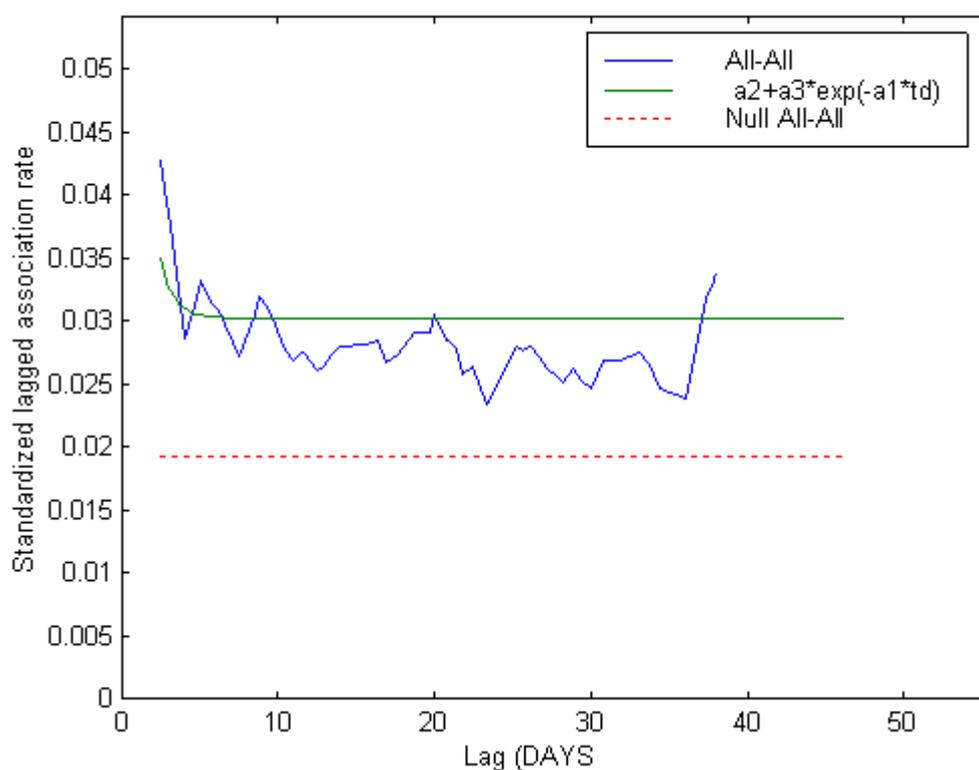


Fig 4.18. Lagged association rates for dyads associated within groups. The plot shows the probability of associations persisting after increasing time lags. The best fit curve (represented by $a_2+a_3 \cdot \exp(-a_1 \cdot t_d)$) represents a population of rapid disassociations, casual acquaintances and constant companions.

5.

Discussion

5.1 Function and Size of Dolphin Groups.

5.1.1. Group size

Observed group size of bottlenose dolphins from 2001 to 2004 changed significantly between years with a lowest yearly mean of 3.43 (± 2.96) in 2002 ranging up to 9.56 (± 8.96) in 2001, though a distribution over the four years ranged from single animals to 42 individuals.

Group size is highly variable for bottlenose dolphins due, in part, to differing perceptions of the definition of a dolphin ‘group’ (e.g. pod, herd, school, subgroup, sighting) and the different criteria used to determine membership in such a unit. The fluctuations in group size over the years observed in this study may well be an artefact of different researchers in Cardigan Bay using different criteria to assess actual numbers. Indeed, in other studies around the world the definition of ‘group’ is a problematic issue that makes it difficult to make detailed comparisons across locations. Two of the best-described bottlenose dolphin populations, Shark Bay in Australia and Sarasota Bay in the U.S., highlight this inconsistency by adopting group size definitions that are not compatible across study sites.

Though significantly different from year to year, the group sizes observed in Cardigan Bay, are similar to those found in other coastal populations of bottlenose dolphins (e.g. Shane *et al.*, 1986; Wells *et al.*, 1987). The mean group size over all four years was 5.85 (± 5.89), which was particularly comparable with mean group sizes of bottlenose dolphins in other temperate North Atlantic populations that inhabit coastal areas and estuaries, namely the inner Moray Firth in Scotland and the Shannon estuary in Ireland, where mean group size was found to be 6.3 and 6.6 respectively (Wilson *et al.*, 1995; Ingram, 2000).

Group size in dolphins varies enormously with habitat type, though generally group size tends to increase with increased water depth or openness of habitat (Shane *et al.*; 1986) (Table 5.1). In order to understand the social structure of an animal population, the selective pressures forming the society must be considered so, in

Table 5.1 Group sizes on *Tursiops* studies in 17 locations (adapted from Connor *et al.*, 2000.)

Country	Location	Av. Group Size	Environment	Source
Argentina	Golfo San Jose	14.9	Coastal	Wursig 1978.
Australia	Shark Bay	4.8	Shallow Bay	Smolker <i>et al.</i> , 1992.
Australia	Moreton Bay	10.4	Shallow bay and inlets	Corkeron, 1990.
Croatia	Cres and Losinj Is.	7.4	Coastal	Bearzi <i>et al.</i> 1997.
Ireland	Shannon estuary	6.6	Estuary	Ingram, 2000.
Mexico	Kino Bay	15.0	Shallow bay	Ballance, 1990
New Zealand	Doubtful Sound	17.2	Fjord	Lusseau, 2003.
Pacific Ocean (offshore)	Off North and South America	57	Offshore	Scott and Chivers, 1990
Portugal	Sado estuary	13.7	Estuary	dos Santos & Lacerda, 1987.
Scotland	Moray Firth	6.3	Coastal	Wilson <i>et al.</i> , 1993
South Africa	Eastern Cape	140.3	Open coast	Saayman and Taylor, 1973.
United States	California	19.8	Open coast	Defran and Weller, 1999.
United States	Florida, Sanibel Is.	2.4-7.4	Open bay	Shane, 1990.
United States	Florida, Sarasota Bay	7.0	Shallow bay	Wells <i>et al.</i> , 1987
United States	Texas, Aransas Pass	3.8-6.9	Dredged channels	Shane, 1990.
United States	Texas, Galveston Bay	4.4	Shallow bay	Brager <i>et al.</i> 1994
Wales	Cardigan Bay	5.85	Shallow bay	Present study

addition to habitat, the size and composition of the group may be determined by their activity. Shane (1977) reported that groups engaged in travelling, feeding and resting were the same size and were smaller than socialising groups. Dolphin groups may be travelling or resting in small numbers as they do not need the company of others and would be less likely to be detected by predators. It may well be the case that the years where smaller group size was observed in this study relates to food availability and so groups spent more time foraging than socialising. Though there are tendencies for groups of particular sizes to be engaged in particular activities, these are not necessarily consistent from location to location.

5.1.2 Cooperation and group size.

Cooperation is often a prime motivation for animals to form groups (Rodman, 1981). The functions of cooperation within dolphin groups are considered to include the following benefits: 1) predator avoidance, 2) foraging, 3) social integration and 4) reproduction (Norris and Dohl, 1980b).

1) *Predator avoidance*: Predation pressure is known to be an influence on the social behaviour of bottlenose dolphin populations (Wells *et al.*, 1980). In the Bahamas, observations of shark bites and missing pieces of fluke or pectoral fin indicate a significant predation pressure from these animals (Herzing and Johnson, 1997). The risk of predation though, in Cardigan Bay is thought to be minimal. All of the shark species most commonly linked to bottlenose dolphin predation i.e. tiger (*Galeocerdo cuvier*), dusky (*Carcharinus obscurus*), bull (*Carcharinus leucas*) and great white shark (*Carcharodon carcharias*) (Wood, Caldwell and Caldwell, 1970; Corkeron, Morris and Bryden, 1987) are infrequent visitors to British waters and not a single individual in all recent surveys has shown any sign of a shark encounter. Killer whales are considered the other potential dolphin predator (Wursig and Wursig, 1979) and have very occasionally been sighted within the cSAC but again; no documented attack has ever been recorded (Ceredigion County Council Report, 2001).

Smaller group size would be predicted where predation risks are relaxed and this is reflected in mean group size in Cardigan Bay if compared, for example, with the Cape coast population in South Africa (mean group size 140.3 ± 21.4) where predation is recognised as a potential threat to dolphin groups (Saayman and Tayler, 1973). Conversely, other study sites such as Sarasota Bay, show group size to be

surprisingly small (mean = 4.8, Irvine *et al.*, 1981) in an area where sharks are known to occur and so further considerations to this debate may be that factors such as the relatively large body size of bottlenose dolphins and relative water depth or openness of habitat also play a role in influencing predation risk (Scott and Chivers, 1990).

2) *Foraging*: If predation pressure is indeed negligible, then group size may reflect an adaptation evolved to increase foraging efficiency, rather than protection from predation. Coastal communities of bottlenose dolphins feed primarily on shoaling fish species (Wells *et al.*, 1980) and cooperative feeding may improve their individual fitness. The feeding preferences of bottlenose dolphins in the Cardigan Bay area are not entirely known but stranding records indicate that their diet includes a range of benthic and pelagic fish species (Natural History Museum, 1995). During this study, observations of fish tosses suggest they eat a number of different species in the Bay, including garfish (*Belone belone*), sewin (*Salmo trutta*), sea bass (*Dicentrarchus labrax*), mackerel (*Scomber scombrus*) and salmon (*Salmo salar*). Indeed, Mead and Potter (1990) suggest that bottlenose dolphins show a consistent preference for pelagic prey items such as mackerel. Anecdotal evidence from local fishermen has suggested that the frequency and number of dolphin sightings increase in relation to the arrival of mackerel. Grellier *et al.*, (1995) suggest the seasonal migration of mackerel moving from the shallow waters of Cardigan Bay, to areas offshore and further south in the colder months may partly explain the seasonal distribution of dolphins in the Bay. Other species that are available year round include plaice (*Pleuronectes platessa*), mullet (*Liza ramanda*), brill (*Scophthalmus rhombus*), small turbot (*Psetta maxima*), dogfish (*Scyliorhinus canicula*), skate (*Raja clavata*), and dabs (*Limanda limanda*) (Bristow, 1999).

Most encounters in Cardigan Bay were close to shore in shallow waters where dolphins were found foraging in the tidal races off reefs and headlands such as Cerreg Ina and Ynys Lochtyn. Greater refuge is available to prey inshore and smaller dolphin groups or even solitary animals in these areas would probably be more efficient at capturing small single prey items. This may explain the fact that over the four-year study, 17% of encounters were with solitary animals rather than groups and is a much higher figure than the 9% reported by Ingram (2000) in the Shannon estuary and <1% reported in the outer southern Moray Firth (Eisfeld, 2003).

Some encounters, however, occurred offshore and usually involved larger groups of animals. In these more open waters, the habitat is more uniform and

provides less refuge for prey and so larger groups, integrating their sensory capabilities, may increase the probability of locating these patchy but rich food resources. Large groups may be better than small ones at cooperatively herding schooling fish. Interestingly, the largest group in this study occurred in the autumn of 2001 when 42 animals were encountered in Fishguard Bay. Their appearance in this area coincided with the concentration of spawning herring (Baines *et al.*, 2002).

The large range in observed group sizes in this study illustrates the fact that the foraging behaviour of dolphin schools in the Cardigan Bay population falls under the definition of a fission-fusion society as proposed by Clapham (1983). This occurs when a social species feeding on food patches of variable size and quality live within a social network of subunits frequently changing in size, composition and distribution.

On a larger scale, the influence of ocean climate variation on grouping behaviour has been recently investigated. Lusseau *et al.*, (2004) examined group sizes of bottlenose dolphins in the Moray Firth and killer whales on the west coast of Canada and found they varied from year to year in relation to large-scale ocean climate variation. Both populations tended to live in smaller groups when there was less salmon available in both areas which seem to occur two years after the low phase of the North Atlantic and Pacific Decadal Oscillations. They concluded that even in these highly social mammals, climate variation may influence social organisation through changes in prey availability.

Interspecific competition may be influential on group formation in Cardigan Bay and the bottlenose dolphin population may aggressively defend limited food resources from the sizeable harbour porpoise population in the area. Violent interactions with bottlenose dolphins are a major cause of harbour porpoise mortality in Cardigan Bay (Penrose, 2004). Jepson *et al.*, (1998) suggests that such lethal aggression may be a common behavioural feature of bottlenose dolphins whenever their ranges overlap with those of harbour porpoises. Based on the fact that in Wales, the stomach contents of virtually all porpoises killed by dolphins analysed so far contain fresh food remains, Penrose (2004), suggests that competition for food is an important factor in these violent interactions. An interesting feature of this current study is that the mean dolphin group size was smaller in 2004 than 2003, which may be related to food availability. Interestingly, the number of harbour porpoise exposed by post mortem examination to have been killed by violent bottlenose dolphin interactions in Welsh waters has steadily risen over the past few years with 25

fatalities having occurred so far in 2004 (Rod Penrose, personal communication). Thus availability of prey could account for an increase in lethal encounters between dolphins and harbour porpoise and a reduction in group size among bottlenose dolphins.

3) *Social integration*: Acoustic communication between group members may serve to share information regarding habitat resources or information relating to individuals. The high capacity for social learning amongst odontocetes may be related to relatively large brain size (Connor *et al.*, 1998) and, with constantly changing school composition, information could be shared rapidly throughout the community. Furthermore, bottlenose dolphin populations have been shown to evolve foraging methods based on social learning and local tradition or culture. For example, isolated populations of dolphins in the tidal creeks of Georgia and South Carolina, USA have been observed preying on mullet by chasing them out of the water onto mudbanks (Rigley, 1983). In addition, bottlenose dolphin populations in Brazil cooperate with local fishermen by shoaling mullet in shore and then sharing the catch (Pryor and Lindbergh, 1990).

4) *Reproduction*: Cardigan Bay may provide an opportunity for members of the community to mix and mate during the summer months during a period of abundant food resources. Connor *et al.*, (2000) states that associations between males and females are related to the reproductive state of the females and seem to be mainly linked to a reproductive goal. Cardigan Bay appears to provide favourable conditions in which to give birth and raise calves. Lack of predators, a shallow water habitat and abundant resources all correlate with calf survivorship (J. Mann, unpublished data; in Connor, 2000). Grellier *et al.*, (1995) observed newborn calves in the area from May to September and estimated that five calves a year are born to this population.

During boat survey work, the larger groups encountered in the cSAC almost always contained calves (personal observation) and these larger aggregations may be females favouring such numbers to permit alloparental care and provide protection for their calves (Norris and Dohl, 1980b). The sociality of individual animals in such a complex society may well influence the size and composition of groups, making them larger or smaller than the optimum required for cooperative foraging and predator avoidance. Group composition during the summer months, therefore, will undoubtedly be determined by such important activities as calving and raising young.

5.2 Resighting patterns and site fidelity.

Long-term site fidelity is a characteristic of many bottlenose dolphin populations (Wells *et al.* 1987; Smolker *et al.* 1992; Maze-Foley and Wursig, 2002) and Cardigan Bay appears to be no exception. In the Sarasota population, 75% of the animals first seen in 1970-71 were still under observation over 20 years later in 1995. Six individuals in this study (#'s 305,312,336,338,377 and 381) were first sighted in 1990 (Arnold *et al.*, 1997) and demonstrates, through regular resightings, that some individuals exhibit long-term site fidelity of up to 15 years.

Several individuals were resighted on repeated occasions, both within one year and over a span of 15 years, suggesting that the studied dolphins were members of at least one resident population. It is not known whether these dolphins are seasonally resident or remain in Cardigan Bay year round. However, a decrease in the number of sightings off New Quay Bay from November to March suggests that the dolphins are seasonally resident (Bristow, 1999).

During summer, specific areas within the cSAC appear to be more favourable in sighting dolphins. Hastie *et al.*, (2004) working in the Moray Firth, showed that areas used intensively by the animals had a significantly higher degree of feeding behaviour. Furthermore, there were clear relationships between feeding events and the submarine habitat characteristics and that these features were a significant factor in the foraging efficiency of dolphins.

The discovery rate of new individuals in the area levels off after only a few months, suggesting that this community contains a relatively closed resident population, and that the majority of the well-marked individuals have been identified. Ballance (1987, 1990) reported similar findings for bottlenose dolphins in the Gulf of California where a large percentage of identified dolphins were photographed over a short period of time at the onset of the study and most individuals were identified within approximately one month of the study. Shane (1987) reported that the rate of discovery for bottlenose dolphins in Sanibel Island, Florida began to reach asymptote by the end of a one-year study. However, both authors express caution over the over-interpretation of this levelling trend and suggest only more time in the field would allow the existence of these trends to be confirmed.

It was interesting to note that 28 animals were only sighted once, which may indicate that some dolphins are non-resident, or that the Cardigan Bay cSAC

represents only part of the home range of many members of this population, or that more effort is needed in order to repeatedly photograph all the animals in the study area. In fact, several of the animals have been matched to photographs from areas outside of the cSAC (Arnold *et al.*, 1997, Baines, personal communication) though none to date have been matched outside of Cardigan Bay. The presence of both resident and non-resident animals in this area would be a similar feature to that found in other populations of coastal bottlenose dolphins (Wursig and Wursig; 1997, Wells *et al.*, 1987, Quintanna-Rizzo and Wells, 2001).

The inshore area of the cSAC covers an area of 450km² and is not considered to be the entire home range of these animals (Ceredigion County Council, 2001). The Sarasota Bay population, similar in many respects to Cardigan Bay (i.e. a long-term, 'resident', coastal community), have a smaller home range, estimated to be 125 km² (Wells *et al.*, 1980). During the summer months the Sarasota dolphins concentrate in the inshore waters but for the remainder of the year they move in to deeper waters of the Gulf of Mexico. Shane *et al.*, (1986) suggests such seasonal habitat shifts are common in nearshore populations and are related to water temperature changes, either through the thermal requirements of the dolphins themselves or changes in the distribution of their prey.

Based on the fact that the 98 dolphins with irregularities in their dorsal fins that have been identified seem to be a large proportion of the well marked animals in the study area, and that an average of 72% of the dolphins encountered are well marked, it has been estimated that the study area was used by a total of approximately 138 dolphins during 2003 (F.Ugarte, personal communication). Because these dolphins exhibit long-term site fidelity and their numbers are relatively small, it is reasonable to assume that each individual will have the opportunity to interact with, and be aware of, the existence of most other animals in the study area. Thus, dolphins within the Cardigan Bay cSAC should have ample opportunity to establish bonds and present preferred and/or avoided associates.

5.3 Social Associations.

5.3.1 Association indices.

In this current study, individual dolphins were sighted with a variety of associates over the study period and were linked, at least indirectly, with all other members of the population to form a large social network. The dolphins associated regularly, with each individual associating with up to 33 other animals, a finding that was similarly reported for the Sarasota Bay bottlenose population who show associations with a large number of community members (Wells *et al.*, 1987). The average number of associates did not significantly vary by gender with males having only slightly more associates than females. The mean association index between pairs which had been observed in groups together throughout this study was low (0.10, SD = 0.03). These values are similar to the ones estimated in both the Shannon estuary and Moray Firth and appear to be consistent with other bottlenose dolphin societies where mean association indices between dyads are found to be less than 0.4 (Smolker *et al.*, 1992; Brager *et al.*; 1994; Wilson, 1995; Rossbach and Herzing, 1999, Ingram, 2000).

Permutation tests revealed evidence that the dolphins were associating with preferred partners. Evidence of avoidance was also provided by the permutation tests, as the proportion of non-zero association indices is lower in the real data (0.39894), than in the random data (0.45574) (Whitehead, 1999). An example of this could be female #302; although seen consistently with #301 (of unknown sex), had low association values with all other individuals and so may actively be avoiding contact with other members of the community.

The existence of preferred associations in this population was indicated by higher standard deviation of the real association index compared with random data (0.15867 and 0.13303, respectively). This was further revealed by the fact that the number of observed significant dyads was larger than the number expected from the permutation tests, indicating these dyads were significant and could be considered and described separately.

The associations between pairs of dolphins were found to be temporarily unstable with a rapid decrease in probability of pairs remaining associated after only a few days. The best-fit model predicted a general decline in the number of dyads

remaining associated with time but also showed existence of some constant companions. The general decline after a few days for most dyads is comparable to the temporal associations reported by Ingram (2000) on the bottlenose dolphin population of the Shannon estuary.

Although the temporal analysis in this current study was conducted over one season, Owen *et al.*, (2002) analysed temporal stability in the Sarasota population over an eight-year period. It was found that predicted association rates were not adversely affected by longer time periods spanning several years. Therefore, the declining number of dyads remaining with preferred companions over time that brought them closed to randomly associating individuals was not affected by the time period over which associations were modelled.

5.3.2 Gender-related associations.

Coefficients of association have been well studied in the Sarasota Bay population but comparisons with this present study are difficult, as both age and sex is known for most animals in the Florida community.

Of the 52 study animals, sex was tentatively determined for only 34 of the individuals (65%), so a cautionary approach is required in interpreting if the preferred or avoided associations revealed by the permutation test resulted from preferences to associate with the same or opposite sex. Despite a paucity of information on age and sex in Cardigan Bay, certain features are evident. Comparing association strengths of known male-female affiliates highlighted the presence of strong networks within the community, for example, the female (#338) had a high association with three males (#'s 340, 354, 356) and so these individuals were probably preferred companions for this particular female. During 2003, this female was seen in association with one or more of these males on six occasions between June 15th and August 3rd. The female was mother of a large calf and it is not impossible that she was ready to mate again in 2003. If so, the association of female #338 with the three males could have been related to reproduction. Associations between particular females and males in both Sarasota and Shark Bay were much higher when a female was cycling than during years when she was pregnant.

Male individuals #373 and #374 had the highest CoA of all known-sex animals at 0.83 and relatively weak associations (< 0.40) with all other males. This is

comparable with the association coefficients of male alliances in Shark Bay that range from 0.7 to 1.00 (Connor *et al.* 1992b, 1999). Other strong male associations occurred between #'s 354 and 356 and between #'s 340 and 353, with CoA's of 0.67 and 0.54 respectively. The reason for these alliances is usually attributed to increased reproductive access to females; i.e., herding/coercing females (Wells, 1991, Connor *et al.* 1992a) or to better chances of success in aggressive interactions with other males (Wells, 1991; Connor *et al.*; 1992; Felix, 1997). The strongest associated male-male pair (373 and 374) during this present study were encountered in groups with at least one 'probable female' of reproductive age present. Owen *et al.*, (2002) contend that the male pair bond is the dominant male reproductive strategy for bottlenose dolphins.

Bottlenose dolphins have a 12-month gestation (Schroeder, 1990) and, in Cardigan Bay, newborn calves have been observed mainly during July and August, a time that coincides with the presence of dolphins with fresh wounds (F.Ugarte, personal communication). Fresh battle wounds during mating time in Cardigan Bay are a strong indication that aggressive interactions among possible males are likely to occur, suggesting that male alliances may indeed be an advantage while competing with other males for mating opportunities.

Interestingly, a four-year study on the bottlenose population of the Moray Firth in Scotland failed to reveal any high-level associations between dolphins of adult size that were anywhere near the range of associations found in Shark Bay and Sarasota. All the CoA's above 0.5 were between calves and adults, and thus likely mother-calf pairs (Wilson *et al.*, 1992). However, in a more recent Scottish study, there was some evidence of tighter associations between adult males forming two dyads with CoA's of 0.61 and 0.73 respectively (S. Eisfeld, personal communication). One possible explanation for the apparent lack of male alliances in the Moray Firth may well relate to the topography of the area. Shallow water depth is a topographical feature of the Cardigan Bay study site and one that is shared with both the Shark Bay and Sarasota sites where the phenomenon of male alliances is predominantly observed. Deeper water in the Moray Firth may allow females greater opportunity to escape the advances of cooperating males, rendering male alliances less profitable. This view is supported by the fact that bottlenose dolphins in the Shannon estuary, which is deep, do not seem to form male alliances (Ingram, 2000). However, it could also be argued that just such a feature would create a greater need for males to act cooperatively.

Besides increased success during competition with other males and coercion of reproductive females, another suggested reason for the formation of male alliances is the defence against predating sharks (Wells, 1991). Wilson (1993) argued that the low number of predators in the Moray Firth could account for the lack of stable alliances in the area. If so, the fact that predation does not seem to be an important risk in Cardigan Bay, where male alliances may exist, suggest that defence against a predators is not a crucial reason for the formation of such alliances.

If alliances are present in Cardigan Bay then kin selection may play an important part in the formation of these male alliances as it will markedly affect the benefits accrued by cooperating males in a reproductive context (Parsons *et al.*, 2003). Males are thought to occupy larger home ranges than females (Scott *et al.*, 1990) and closely related males would forge strong associations simply because of frequent chance encounters. Moreover, related males may be able to distinguish one another as kin on the basis of a selection criterion, such as phenotypic similarity or acoustic identification of conspecifics. The unique signature whistles of male calves are remarkably similar to that of their mother (Sayigh *et al.*, 1990) and this acoustic signature may function as a method of evaluating the matrilineal origin of potential allies. Because male alliances function as a mating strategy through agonistic interactions with other alliances, and consortships with receptive females (Connor *et al.*, 1992), kin-based evaluation of long-term allies would enhance the inclusive fitness of allied dolphins. Males in some alliances are more strongly bonded than males in others and this may be correlated to their genetic relatedness. Other theories suggest male alliance formation is actually based on age (Connor *et al.*, 2000) and are more prevalent in mature adult males. At present, these theories are difficult to prove in the Cardigan Bay population in view of the lack of information on the age and genetic relationship of individuals. A closer examination of the temporal stability of the potential male alliances identified in this study, Developing a data base spanning several years, coupled with DNA analysis and /or long-term photo identification of males of known age, will allow a closer examination of the temporal stability of the potential male alliances identified in this study. This may reveal the existence and nature of male alliances among the dolphins in Cardigan Bay and illuminate the role of kinship in male-male relationships.

The associations amongst females were generally of a low level between a variety of individual female associates, and no individual was seen with every other

female in the community. The strongest associated female dyad was between #307 and 367 at 0.59, though not as strong as some of the male-male associations observed.

No evidence was found in this community of the all female ‘bands’ that are a feature of the Sarasota Bay population where up to four generations of kin associate in same sex groups (Wells, *et al.*, 1987). As with the present study, observations on the social associations of known sex dolphins in the Shannon estuary and in the Moray Firth demonstrated no evidence of female cohorts (Wilson *et al.*, 1995, Ingram, 2000). Interestingly, this is in contrast with studies from lower latitudes, where the existence of female cohorts has been well documented (Wells, *et al.*, 1987, Smolker *et al.*, 1992). The low risk of predation on dolphin calves in Scotland, Ireland and Wales may influence the lack of obvious female cohorts in the populations studied in these areas.

The female associations can be related to the reproductive status of the individuals (Connor *et al.*, 2000). Rogers *et al.*, (2004) working in the Bahamas, found that females of similar reproductive condition associated with each other and when their reproductive status changed, their highest association values were then with other similar status females. Other delphinids species have also shown this type of segregation (Wells *et al.*, 1987).

It is likely that the females in Cardigan Bay, similar to Shark Bay and Sarasota, have a large network of associates and are linked to most other females in the area either through mutual associates or occasional occurrence in the same subgroup. A striking feature of both Shark Bay and Sarasota is the variation among females ‘sociability’ with some rather solitary individuals while others are found in groups (Smolker *et al.*, 1992, Wells *et al.*, 1987). The relatively high number of solitary animals encountered in this region may well account for this being a feature in Cardigan Bay. Smolker *et al.*, 1992 thought this difference in sociability may be related to feeding strategies.

5.3.3 Spatial distribution.

Within this loosely associated community, cluster analysis and principal coordinates of association, indicated the presence of six assemblages of dolphins defined at a threshold association index of 0.13. This threshold index is comparable with the 0.14 value used by Ingram (2000) studying the Shannon estuary bottlenose

population in which he defined three assemblages. Ballance (1990), also using 52 study animals, described nine separate assemblages in a Gulf of California population. Geographic analysis of the clusters found in Cardigan Bay showed that some groups were spread throughout the cSAC, while other groups appeared to prefer certain areas along the coastline which could be interpreted as a possible core area for these animals.

Five of the six clusters were of mixed sex, containing both ‘probable males’ and ‘probable females’, reinforcing the lack of evidence for all female ‘bands’. The assemblages in Cardigan Bay may, therefore, be a result of shared use of habitat areas rather than purely due to social cohesion. Such a scenario, where social cohesion is influenced by preferred home range, has been suggested for the bottlenose dolphins of the Shannon estuary (Ingram, 2000).

5.3.4 Cautionary remarks.

While this current project set out to avoid the pitfalls encountered by previous studies surrounding sampling methodologies and protocols, it is important to bear in mind that the association data presented here is negatively biased. In any social study, the number of occasions each animal included in an analysis of social structure is sighted, affects the result, and so the more frequently an animal is sighted the more accurately its social behaviour will be described. Furthermore, complete identification of a group will help determine social dynamics e.g., Chilvers and Corkeron (2002) found that when all individuals in a group had been identified, the mean association indices increased, as did the probability of association patterns being different from random. Wursig and Jefferson (1990) suggest that if four identifiable photographs of each individual are taken then there is a 95% probability that all members of a group have been photographed. In practice, however, attempts to take multiple photographs of each member of a group during this study were often thwarted by weather conditions or changes of group composition due to animals leaving or joining the group. The negative bias in the present study, therefore, is due to the fact that not all individuals present in all encounters were identified and that there was a large proportion of individuals of unknown gender. Thus, actual levels of association may be higher than the ones revealed in this report.

The selection criteria for data used in this current analysis (i.e. individuals sighted ≥ 3 times or encounters in which more than 50% of group members were identified) were chosen to enable a balance between the maximum number of individuals, thus ensuring representative data, and maximum sighting frequencies for reliability of data. The trade-off between representative and reliable data depends on the research questions being asked. For example, studies using intensive behavioural surveys, such as individual focal follows to identify long-term or important interactions between individuals, are based on fewer individuals with higher sighting frequencies. In comparison, broad-scale studies to provide descriptive investigations of a community's overall social organisation are based on large numbers of individuals with lower sighting frequencies (Mann, 1999) and was the case in this present study.

To continue the work started in this study, the sightings data contributing to association analyses should be collected over as long a time period as possible in order to examine the permanency of these associations. Further issues to consider relate to the differences in permanency of marks between age and sex classes. Through time, this will lead to a difference in the ability to recognise individuals. Slightly marked animals may rapidly become unrecognisable due to healing of identifying marks or the subsequent acquisition of new obscuring marks.

To summarise, therefore, most of the observed patterns of association can be characterised as weak and are casual or transitory in nature. However, some evidence indicated that relatively stable associations occur between certain individuals over longer periods of time. The fact that the majority of the association values are low indicates a high level of fluidity of grouping within the population rather than a highly structured society. The Cardigan Bay population may therefore be best described as an assemblage of individuals that reside in the same area and periodically associate with one another (from Bigg *et al.*, 1990).

As with other mammal species in general and bottlenose dolphins, in particular, the Cardigan Bay population may exhibit social behaviour that differs from other locations due to unique environmental pressures, resource availability, predation pressure or the phenotypes of the individual members of a population.

Conclusion

The bottlenose dolphin has been described as a highly social, group-living species, characterised by a fluid and dynamic social structure (Shane *et al.*, 1986). Research reported in this thesis on the social ecology of bottlenose dolphins in Cardigan Bay, is consistent with this generality.

The study set out to compare group size in Cardigan Bay and the results presented here indicate that group size varies significantly between years. Possible explanations for this variation included predation risk, prey availability, reproduction and sociality.

This study has highlighted regions of particular hydrological and topographical significance in the Bay that appear to produce favourable conditions for either the dolphins' prey or for the dolphins to forage efficiently, resulting in a degree of site fidelity. Regions within the study area such as Aberporth Bay, Ynys Lochtyn and New Quay are all important habitats as suggested by the concentration of sightings. Moreover, evidence is presented here, through regular resightings, that some individuals show long-term site fidelity of up to 15 years.

Social association analysis suggested that the study animals have preferred and/or avoided associations. While most associations were relatively weak, there appear to be a few stronger associations in the population, most noticeably between male-male pairs. These male-male associations had potential impacts on the mating strategies of bottlenose dolphins. The study also highlighted the existence of six loosely defined assemblages of animals and examined their spatial distribution within the study site.

The bottlenose dolphins of Cardigan Bay are a relatively small, seasonally resident population, similar in size to the populations found in the Moray Firth and the Shannon estuary. The Cardigan Bay candidate Special Area of Conservation was established under the EU Habitats and Species Directive in 1992 in recognition of the importance of this area to the bottlenose dolphins. A management plan subsequently addressed the potential vulnerability of dolphins living in close proximity to human activity. Factors relating to the human use of the Bay include oil and gas exploration, sea fisheries, waste disposal and recreational activity all need to be considered in light of the management proposals aimed at this population. Cardigan Bay is a popular tourist destination and the seasonal boat traffic is a highly visible presence within the

cSAC. An example of the potential adverse effect of human activity in the area was provided by Lamb (in prep.), who surveyed boat activity and dolphin presence around New Quay Bay and showed a distinct diurnal pattern with a greater tendency for dolphin activity at night rather than during the busier hours of the day when most boat charters were operational.

Recommendations for future work in Cardigan Bay includes a greater geographical spread of survey effort to determine the dolphins' wider movements which could ultimately establish their entire home range and may illuminate any possible interchange with adjacent communities such as Ireland or the South of England. Further research on prey abundance and distribution within Cardigan Bay will assist in this goal.

Increasing the frequency of survey trips, extending the fieldwork throughout the whole year and identifying all individuals in an encounter, will greatly improve the analysis of associations through time. Continuing the photo-identification survey work over many seasons will allow important life history information, such as age and possibly gender, to be collected. This would provide a much larger data set and allow for more robust statistical analysis – an element that is essential in any conservation monitoring programme.

The 2003 and 2004 monitoring work has focussed on the cSAC and on the New Quay area in particular. The study highlighted potential core areas for clusters of dolphins though it is important to realise that such a relatively small area may not be representative of Cardigan Bay as a whole.

Advances in molecular genetic techniques have demonstrated an ability to answer questions that simply cannot be addressed by any other means and may, for example, provide an insight into the paternity of this population and show to what extent the dolphins' social behaviour is determined by kinship. Similar molecular techniques could also address the general health of the animals and determine, for example, how significant a threat pollution is to their well being. However, for the most part, these procedures are considered invasive and may only be appropriate for the Cardigan Bay population if the potential gains to other animals are *very* large and no alternative method is available.

As highlighted in this current study, there may be a subjective element in gathering data and this may partially explain, for example, the variation in group size

over the years. Therefore, standardisation of data collecting techniques and agreements on definitions of social ecology (e.g. group size) would allow for accurate comparisons across study sites.

This present study is the first in which an assessment of the social associations of bottlenose dolphins in Cardigan Bay has been undertaken and the results emphasise the importance of long-term studies of dolphin communities. During the study a relatively small data set was used and this provided good baseline information. It does not, however, give a complete description and may be missing important information about the dolphins' social lives. It is essential, therefore, to look at changes and trends over many years in order to accurately describe the social structure of these highly social, long-lived marine mammals.

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Appendix 1: - Study animals.



W0301



W0302



W0305



W0306



W0307



W0308



W0309



W0310



W0312



W0313



W0314



W0315



W0316



W0317



W0321



W0325



W0329



W0331



W0335



S0336



W0338



W0340



S0343



W0345



W0347



W0348



S0349



W0352



W0353



W0354



W0355



W0356



S0358



S0359



W0364



W0367



W0371



W0372



W0373



W0374



W0376



S0377



W0381



W0387



S0390



W0396



W03100



W03101



S03103



S03110



S03111



L312

Appendix 2: Statistical analyses

Group size.

Ranks

	year	N	Mean Rank
groupsiz	2001	138	394.59
	2002	237	241.01
	2003	125	348.92
	2004	110	283.34
	Total	610	

Test Statistics^{a,b}

	groupsiz
Chi-Square	105.865
df	3
Asymp. Sig.	.000

a. Kruskal Wallis Test

b. Grouping Variable: year

Frequencies

2001

Statistics

NUMBER

N	Valid	138
	Missing	0
Mean		9.56
Median		7.00
Mode		1
Std. Deviation		8.958

2002

Statistics

number

N	Valid	237
	Missing	0
Mean		3.43
Median		2.00
Mode		1
Std. Deviation		2.963
Skewness		1.866
Std. Error of Skewness		.158
Percentiles	25	1.00
	50	2.00
	75	5.00

2003

Statistics

NUMBER

N	Valid	125
	Missing	0
Mean		6.41
Median		6.00
Mode		2(a)
Std. Deviation		4.195

a. Multiple modes exist. The smallest value is shown

2004

Statistics

NUMBER

N	Valid	110
	Missing	0
Mean		4.76
Median		4.00
Mode		2
Std. Deviation		3.614

Monthly Analysis

Ranks

	month	N	Mean Rank
number	May	33	270.38
	June	86	301.91
	July	146	285.50
	August	242	320.89
	September	103	311.94
	Total	610	

Test Statistics^{a,b}

	number
Chi-Square	5.284
df	4
Asymp. Sig.	.259

a. Kruskal Wallis Test

b. Grouping Variable: month

Report

number

month	Mean	N	Std. Deviation	Minimum	Maximum	Variance
May	4.36	33	3.855	1	14	14.864
June	4.91	86	3.500	1	15	12.250
July	4.70	146	4.069	1	23	16.557
August	6.50	242	7.108	1	42	50.525
September	6.15	103	5.918	1	23	35.028

Appendix 3 : HWI analyses (SOCPROG 1.3)

Permuting all groups

Number of individuals = 52

Number of random permutations = 20000

Real association indices:

all: mean = 0.10922; s.d. =0.15867

non-zero elements: proportion = 0.39894; mean = 0.27377; s.d. =0.13435

Random association indices (mean over permutations):

all: mean = 0.10731; s.d. =0.13303

non-zero elements: proportion = 0.45574; mean = 0.23551; s.d. =0.09296

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

all: mean = 0.82970; s.d. =0.99990

non-zero elements: proportion = 0.00015; mean = 0.99995; s.d. =0.99960

Two-sided significance level for dyads = 0.05

Expected number of significant dyads = 64

Number of significant dyads = 70

302	301	0.99940
315	3103	0.97545
348	305	0.98605
309	307	0.99390
310	307	0.97615
367	307	0.99410
354	307	0.97580
309	308	0.97935
315	310	0.97800
387	310	0.99885
315	312	0.99805
359	312	0.99045
3111	312	0.99880
387	312	0.99585
315	313	0.98575
3111	313	0.97780
381	313	0.98920
390	313	0.98245
315	314	0.98040
396	314	0.97770
3111	315	0.98055
387	315	0.99885
3111	359	0.99520
340	359	0.98450
3111	3100	0.99895
345	3100	0.97670
345	3111	0.98815
3101	317	0.99765

377	316	0.99085
374	3101	0.99710
355	367	0.97930
381	367	0.99290
348	377	0.99270
329	321	0.99885
374	373	0.99905
336	331	0.98865
343	336	0.99730
329	336	0.99060
338	335	0.99960
340	335	0.99495
396	335	0.99675
352	335	0.98020
354	335	0.99920
356	335	0.99290
371	335	0.98430
376	335	0.99340
340	338	0.99980
352	338	0.99495
354	338	0.99880
355	338	0.98975
356	338	0.99955
396	340	0.99040
352	340	0.98415
353	340	0.99555
354	340	0.98245
356	340	0.98675
376	396	0.98875
348	345	0.99155
312L	349	0.98400
354	352	0.99125
356	352	0.99745
355	354	0.98680
356	354	0.99640
356	355	0.98860
312L	364	0.98595
371	381	0.99765
390	381	0.99450
390	371	0.99950
376	372	0.99280
312L	376	0.99260

Time for permutations = 45.064s

Mean and Maximum HWI for the study animals as derived from SOCPROG.

	Mean Assoc.(sd)	Typical Gp. Size (sd)	Max. Assoc. (sd)
301	0.03	2.59	1.00
302	0.03	2.59	1.00
3103	0.09	5.49	0.36
305	0.09	5.41	0.43
306	0.10	6.12	0.33
307	0.14	8.25	0.59
308	0.06	4.18	0.50
309	0.06	3.96	0.50
310	0.08	5.18	0.50
312	0.14	8.31	0.62
313	0.14	7.94	0.40
314	0.12	6.95	0.40
315	0.15	8.48	0.67
359	0.12	7.19	0.50
3100	0.09	5.56	0.57
3111	0.08	5.07	0.60
317	0.10	5.94	0.55
3110	0.07	4.63	0.33
358	0.06	4.16	0.42
316	0.07	4.37	0.46
3101	0.11	6.86	0.55
367	0.11	6.81	0.59
377	0.09	5.64	0.46
321	0.05	3.73	0.67
325	0.08	5.08	0.50
373	0.09	5.44	0.83
374	0.06	4.18	0.83
331	0.07	4.79	0.40
336	0.09	5.36	0.63
343	0.11	6.66	0.63
329	0.05	3.66	0.67
335	0.16	8.91	0.59
338	0.18	10.12	0.73
340	0.15	8.88	0.62
396	0.12	7.18	0.55
345	0.09	5.77	0.43
347	0.08	4.88	0.31
348	0.10	6.27	0.43
349	0.06	4.07	0.29
352	0.09	5.39	0.50
353	0.12	7.05	0.55
354	0.14	7.90	0.67
355	0.09	5.63	0.50
356	0.15	8.49	0.73
364	0.10	6.28	0.44

387	0.08	4.88	0.67
381	0.10	6.01	0.55
371	0.11	6.81	0.75
390	0.09	5.52	0.75
372	0.11	6.50	0.55
376	0.14	8.09	0.55
312L	0.11	6.80	0.44

Classed by sex:

	Mean	Av. Group size.	Max
F	0.10 (0.04)	5.86 (1.82)	0.58 (0.13)
M	0.11 (0.03)	6.59 (1.61)	0.58 (0.15)
*	0.09 (0.03)	5.53 (1.49)	0.52 (0.18)
F-F	0.10 (0.04)	2.45 (0.57)	0.42 (0.12)
F-M	0.11 (0.07)	1.99 (1.25)	0.41 (0.17)
F-*	0.08 (0.03)	1.42 (0.62)	0.42 (0.19)
M-F	0.11 (0.03)	1.77 (0.53)	0.45 (0.16)
M-M	0.14 (0.06)	3.30 (1.01)	0.50 (0.17)
M-*	0.08 (0.04)	1.52 (0.76)	0.39 (0.15)
*-F	0.08 (0.04)	1.26 (0.57)	0.38 (0.19)
*-M	0.08 (0.04)	1.52 (0.74)	0.41 (0.18)
-	0.10 (0.05)	2.75 (0.89)	0.39 (0.16)
Overall	0.10 (0.03)	6.00 (1.67)	0.56 (0.16)

* = unknown gender.

Test for differences in associations between/within classes:

Mantel test, $t = 2.6891$ ($p = 0.99642$)

Matrix correlation = 0.071565