Social networks of bottlenose dolphins *Tursiops truncatus* in Cardigan Bay, Wales

Thesis submitted for the degree of
Master of Science

By

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DECLARATION

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

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In memory of the Black sea bottlenose dolphins
Nana and Nika


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"Knowing that we may never fully understand
what we study, inspires our wonder and strengthens
our respect for what we are privileged to observe "
-C.Saylan

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Abstract

The social structure of a population is a fundamental component of its biology and ecology. Mating strategies, foraging techniques and the ability to explore surrounding environment are closely related to the network of relationships between individuals

In the present study network analytical techniques, developed for the analysis of human sociality, were employed to construct and investigate bottlenose dolphins' social networks in Cardigan Bay. Pooled data social network for the 5-yr period (2001-2006) was moderately dense ($\rho = 0.60$) with a high number of direct ties among individuals ($k = 27.48$). The variability of properties in annual networks indicated the dynamics of relationships. Divisions within networks were detected, and could have been influenced by the degree homophily of the preferred companionships, while sex of individuals did not seem to play a significant role in association pattern. However, these findings were considered with caution due to the low number of individuals with known sex, age and kin relatedness in this population. Highly central individuals positioned on the boundaries of network components were identified. Their importance was discussed in relation to the transfer of information and spread of disease.

Analysis of spatial distribution of bottlenose dolphins revealed areas of Mwnt, Ynys Lochtyn and New Quay as being centers of activity for the majority of sampled population in this his study. Known ranges calculated for the network components showed overlap in the area usage, and extended travel further north from the Cardigan Bay SAC. Increased effort in the north of Cardigan Bay resulted in the identification of new individuals.

Epidermal skin abnormalities (lesions) were categorized, and their prevalence examined in regards to the topology of individuals in the network. Non random frequencies of lesion distribution found in network components prompted strong recommendations towards more detailed future investigation on the severity of these markings in different age/sex groups and their link to the environmental variables.

Network approach was found to be useful in exploring social structure of this population. The potential to combine such characteristics as individual position in the network, spatial distribution and skin anomalies by incorporating them into the analysis highlighted the efficiency of this technique to further our knowledge in understanding the processes and consequences of a social organization. Furthermore, it pointed to the importance of network of relationships be considered in defining management and conservation guidelines for this, and other cetacean populations.

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1. Introduction

1.1 General biology and sociality of the species

The bottlenose dolphin is a member of the order *Cetacea*, the suborder *Odontoceti*, family *Delphinidae*. Despite the variation in size, coloration, and cranial characteristics, two species of genus *Tursiops*, *T. truncatus*, the "common bottlenose dolphin", and *T. aduncus*, the "Indian Ocean bottlenose dolphin", are currently recognized (Wells and Scott, 2002). Bottlenose dolphins are a cosmopolitan species, widely distributed in a range of mainly nearshore coastal habitats from tropical to temperate seas, in sheltered and exposed areas of estuaries, lagoons, continental coasts, and also in pelagic waters offshore and around oceanic island coasts (Connor et al., 1998).

The bottlenose dolphin is a medium size delphinid ranging from 220-230 cm in Shark Bay, Australia to 350-410 cm in the Northeastern Atlantic. Larger body size is generally related to colder water temperatures (Ross and Cockcroft, 1990), but whether this relation is due to a direct adaptation to thermal requirements or is more related to the differences in diet is unclear. A large variety of fish and squid forms most of the diet, although generally bottlenose dolphins show preference for sciaenids, scombrids, and mugilids (Wells and Scott, 2002). The dolphin body coloration ranges from slate grey to charcoal, with a noticeably lighter ventral pigmentation (Wells et al., 1987).

Analyses of dentinal and cemental growth layer groups in teeth have shown that female common bottlenose dolphins can live up to more than 50 years, and males reach up to 45 years of age (Wells and Scott, 1999). Age of sexual and physical maturity varies by region, with females generally reaching sexual maturity at 5-13 years, and males at 9-14 years. The reproductive life span for females is prolonged up to 48 years of age. Calving intervals of 3 to 6 years are common for *T. truncatus*. Calves are born after a gestation period of about 12 months, and range in length from 80 to 140 cm in different geographic regions. Maternal investment for calves extends for about 3-6 years, and separation often coincides with the birth of the next calf (Connor et al., 1999). Vulnerability of newborn marine mammals in the aquatic habitat may have been one of the major factors in shaping the complex social lives that is found in some toothed whales (Connor et al., 1998). Predation risk may be another common reason animals join in groups. Two kinds of predators are most often implicated in predation on bottlenose dolphins: sharks and killer whales (Shane et al., 1986). The vigilance of other group members may allow individuals to reduce their own vigilance in favour of foraging. The benefits of cooperative feeding may also favour the formation of the groups. Bottlenose dolphins may cooperate to trap fish between groups, or on shore. The size of prey schools or individual prey may restrict the size of cooperative groups (Wursig, 1986). On the other hand, group living has its costs. The price of mingling with conspecifics includes the risk of socially transmitted parasites and competition for limiting resources. The benefits of group formation must exceed these costs for animals to seek each others company (Connor, 2000).

Social relationships emerge from the pattern of social interactions between individuals within a group over time (Hinde, 1976). Individuals have relationships with a number of others in a population forming a network of relationships or social structure. Social bonds are social relationships that include a consistent affiliative component. Connor (2000) favours the term “bonding strategy” because it promotes an understanding of bonds as social tools by which individuals attempt to increase their reproductive success, and which should vary with ecological conditions, age, sex, social position, and the strategies employed by others. Patterns of bond formation give rise to description of social structure.

Bottlenose dolphins live in classic fission-fusion societies in which individuals associate in small groups that often change in size and composition (Wursig and Wursig, 1977; Wells et al., 1987). Strong male-male bonds that may last up to two decades have been described from two sites: Shark Bay, Western Australia (*T. aduncus*) and Sarasota Bay, Florida (*T. truncatus*). In Sarasota stable male pairs are common but trios are unknown possibly because males are larger, and exhibit more sexual dimorphism than in Shark Bay where maneuverability is though to be the optimal strategy during the male conflict over oestrous females (Wells et al., 1987; Wells, 1991). Bottlenose dolphins are larger in the Moray Firth, Scotland, where strong bonds have not been found among any adults .At the same time, as was suggested by Wilson et al. (1993) low predation risk, food distribution or the lower rate of interactions between rival males due to greater day ranges might explain the lack of male alliances among bottlenose dolphins in this area.

Female-female bonds are weaker but variable. Females appear to maintain a large network of weak or moderate bonds, and their associates at a given time may depend on their reproductive state (Mann et al., 2000). Bonds with their maternal kin are valuable to females when they confer protection from predators or allow cooperative defends of resources. If those resources are distributed in small patches that cannot feed more than one individual, then females cannot afford to travel together. If foraging occurs in distinct boots, however, individuals may form groups between bouts if the benefits outweigh the cost of traveling (Connor, 2000). Another kind of resources that might potentially bond females is alloparental care which has been reported in several odontocetes species (Whitehead and Mann, 1999). Resource abundance and distribution may also impact dolphin bonds indirectly, by changing the rate at which conspesifics encounter each other.

An association and the frequency of interactions between males and females usually depend on female reproductive state, and are much higher when female is cycling (Wells et al., 1987). Several patterns can be recognized: for example solitary males in Sarasota may range in a smaller area used by particular female while pairs of males range within larger area, and do not stay long with a particular female (Wells et al., 1987). In contrast, in Shark Bay, males in pairs and trios form consortships with single females up to a month (Connor et al., 1999). Although males do not usually strongly associate with females, mixed sex groups are not uncommon, especially if they use part of their natal range (Connor et al., 2000).

Not surprisingly, calf's association with its mother is the strongest bond for the first few years. Paradoxically, bottlenose dolphin calves exhibit precocious locomotion, but prolonged dependence on their mothers. One of the possible explanations comes from the fact that foraging skills develop slowly. While the social behaviour develops rapidly during the first six months, it appears to take several months to practice before a calf actually catches fish, and years before it can forage independently (Mann and Seargent, 2003). A sharp decline in the strength of associations may be observed when the mother becomes pregnant again, but not necessarily. Juvenile males and females associate with male and female peers after they leave their mothers (Wells et al., 1987). In some cases male-male bonding develops even before males are weaned. Immature dolphins spend considerable time in large groups possibly practicing social skills through different kinds of social play such as continuous chasing, sexual behaviour, displays (Connor et al., 2000). Even though both males and females spend up to ten years in postweaning/ prereproductive stage this period remains poorly explored. The delayed maturation and extended learning for social and foraging skills may provide a selective advantage, and further reinforce this life history strategy (Pagel and Harvey, 1993)

1.2 Home range and short-term movements

The literature clearly shows that at least some coastal bottlenose dolphins maintain home ranges. A home range, according to Burt (1943), is an area regularly used by an individual performing its normal daily activities. The most detailed and informative study of *T. truncatus* home ranges has been conducted on the west coast of Florida (Irvine and Wells, 1972; Irvine et al., 1981; Wells et al., 1980).

In general, bottlenose dolphins inhabit ranges that are common to entire groups, and exclusive of other groups (these may be considered population ranges); in other areas there may be seasonal overlap in the ranges of individuals; and in still other areas dolphins may make extensive migrations (Defran et al., 1999). Each location of interest must be examined individually to determine the nature of the ranges of the individuals inhabiting the region.

Seasonal habitat shifts are common in nearshore populations (Shane et al., 1986), and might be related to the thermal requirements due to the water temperature changes or fluctuations in the distribution of prey or predators. On the other end of a spectrum, larger seasonal range shifts are described as migratory. For example, the mid-Atlantic bottlenose dolphin population in USA extends their home range over 400 km due to seasonal migrations (Wells et al., 2002). Lockyer (1978) described the movements of an adult bottlenose dolphin off Great Britain as covering over 500 km in 18 months.

Individual variations within populations are also observed, and much of this variation can be explained by sex differences. Females preferentially use smaller core areas which they share with other females. Males more frequently have extended ranges, and more often interact with dolphins in adjacent waters (Bearzi et al., 1997). Hastie et al. (2004) and Mellink et al (2006) linked bottlenose dolphin distribution and habitat preference to foraging activity. Lear and Bryden (1980) believed that bottlenose dolphins in eastern Australia seek shelter near shore to avoid rough water offshore during storms. They also reported that there is evidence of tidally-related movements. The links between habitat use and foraging specializations, as well as suggested maternal transmission (Mann and Sargeant, 2003) of such behaviours, indicates the need to incorporate knowledge of sociality into the management structure for bottlenose dolphin communities (Weiss, 2006).

1.3 Field studies

Its accessibility in nearshore waters has made the bottlenose dolphin one of the best-studied cetaceans. Longitudinal studies of individual wild bottlenose dolphins began in early 1970s in a number of countries ranging from Argentina, to Scotland and Australia, representing a variety of inshore habitats (Irvine and Wells 1972; Wursig and Wursig, 1977). Two longest running studies of bottlenose dolphins were initiated in 1970 in Sarasota Bay, Florida (Irvine and Wells, 1972) and in 1984 Shark Bay, Australia (Connor and Smolker 1985), and covered topics from population social structure, life history to vocal communication.

The development of photo-identification techniques (Wursig and Wursig 1977; Wells et al., 1980) opened a new era in bottlenose dolphin research. Recognition of individual bottlenose dolphins is based on scars, nicks and the overall shape of the dorsal fin which is projected above the water surface each time a dolphin breathes. In addition to identity, if the photographs are collected together with sufficient data for associations, then they also have the potential to provide a model of social structure. The general procedure is to define and calculate association indices between all pairs of identified individuals which together make up an association matrix. The matrix can then be displayed using such methods as sociograms or social network analysis techniques. (Whitehead and Dufault, 1999; Whitehead et al., 2000; Lusseau et al., 2006).

1.4 Social network approach

Multiple origins of network concept to social structure date back to 1930s when german scientists Jacob Moreno and Kurt Lewin, influenced by developments in field theory in physics, transferred the network idea to the examination of human social interactions (Scott, 2000). The influence of a mathematical approach in 1950s helped to transform the study of social networks from description to analysis. One of the first applications of network theory in animal social systems comes from 1970s primate research (Sade et al., 1994). With the advent of powerful computers over the last decades analytical packages such as Ucinet and NetDraw have been developed to construct and analyze complex social networks. They can help to describe the architecture of networks of animal social relationships, and also to find the features driving them (Lusseau and Newman, 2004). A traditional way of looking at animal sociality was from dyadic interactions perspective. These associations, however, are tightly integrated in the social network. Although animal social networks are much harder to study than networks in human societies because animals do not fill out questionnaires and data must be collected by direct observations. Nevertheless, number of studies managed to determine meaningful measures of associations in a number of species, and revealed similarities to human networks (Connor et al., 1999; Lusseau et al., 2003a; Lusseau et al., 2006)

Looking from a population level network structure could allow to follow the speed of information or spread of disease within the population (Newman, 2002b; Corner et al., 2003), and the way that the population exploits its environment (Connor et al., 1998). Centrality measures on network graph can identify the location of individuals in relation with others (Wasserman and Faust, 1994; Newman, 2003b; Lusseau and Newman, 2004; Croft et al., 2005). Concentrating on individual and its degree of connectivity to others may reveal key animals important in the cohesion of all community. Such approach may be particularly useful in a fission–fusion societies characteristic to bottlenose dolphins (Lusseau and Newman, 2004). Thus, understanding network structure from global (as one entity) and local (subdivisions) scale can reveal new processes, and enhance our knowledge on the way population functions. Consequently, bottlenose dolphins' community structure at many coastal sites may provide identification of population units that can form the basis for the management. Many threats to coastal bottlenose dolphins are geographically localized (e.g., fisheries, point-source pollution, coastal development), thus, the definition of management units makes it possible to relate specific threats to particular population unit, allowing evaluation of potential impacts, and providing the focus for mitigation efforts (Grellier et al., 1995; Hoyt, 2005). With the help of long-term studies of individually recognized dolphins, and combination of approaches, it may become possible to monitor trends in population dynamics and health (Wells and Scott, 1991).

So far the subtle effects from disturbance or pollution through increasing levels of stress that result in not immediately fatal diseases or immunosuppresion remain poorly known (Wilson et al., 2000). More recent studies suggest that the social network structure and topology, i.e. the pattern of connectedness in the network, could be an important factor in determining the probability of disease invasion, the number of animals infected or the speed of disease spread (Keeling, 1999; Moore and Newman, 2000). Even though assessing the health status of cetaceans is challenging certain features such as skin abnormalities might be an important tool to monitor some aspects of the health of free-ranging cetaceans The potential to document their appearance, prevalence and severity from the distance (Thompson et al., 1992; Harzen and Brunnick, 1997) using photo-identification techniques proved to be promising tool in studying the development of epidermal diseases in bottlenose dolphin populations worldwide (Wilson et al., 1999) but those have not been combined with the association data analyzed in the present study.

Thus, network analysis may expand our knowledge of the forces driving the social organization of the Cardigan Bay bottlenose dolphin population, and this species in general. It may also improve our understanding of the effects of anthropogenic activities on animal populations.

1.5 Aim and objectives:

This study aimed to construct and quantitatively explore social network of the bottlenose dolphins of Cardigan Bay. To achieve this aim, five objectives were to be met:

- perform association analyses to assess the relationships among individuals and derive preferred companionships
- calculate the following connectivity measures of individuals in the network: density, average path length, clustering, degree, and betweenness
- investigate the assortativity of individuals according to sex, vertex degree, and geographic distribution
- analyze the prevalence and appearance of epidermal markings (lesions) within the components of the network

2. Study area: Cardigan Bay and the Cardigan Bay Special Area of Conservation (SAC)

Cardigan Bay is one the largest bays in the British Isles extending over 100 km from its southernmost point at St. David's head to the Llyn Peninsula in the north (Roberts et al., 1998). It has a mainly open coastline, and is exposed to prevailing south-westerly, westerly winds. The Bay is relatively shallow with an average depth not exceeding 60 m. The mean annual temperature is just over 11^{o} C with larger fluctuations in shallow coastal areas. Local water temperatures, salinity, and water quality are also affected by the fresh water input from Aeron, Ina and Teifi rivers. Semidiurnal tides predominate in this area entering the Bay from St. Georges Channel. Tidal current speed affects the distribution of seabed sediments which range from gravel in a strong current zone to mud where the water energy is low (Evans, 1995a).

In Cardigan Bay year-round sightings of bottlenose dolphins are recorded since the early 1920s. More regularly they are seen in inshore waters from Aberystwyth to the Teifi estuary, especially in the small embayments close to New Quay, Ynys Lochtyn, Aberporth, and Mwnt (Grellier, 1995; Evans et al., 2000). The number of individuals increases during summer months. In late September large aggregations up to 50 dolphins can be recorded. Information to date suggests they use the area for all essential activities such as breeding, socializing and feeding (Evans, 1995b). Having one of the two resident populations of bottlenose dolphins in the UK waters Cardigan Bay is of local, national and international importance. Moreover, bottlenose dolphins were listed as a species whose conservation requires the designation of Special Areas of Conservation in the European Union Habitats Directive 1992. For this reason in 1996, the southern part of Cardigan Bay was submitted by the UK Government to the European Commission as a candidate Special Area of Conservation (cSAC) for its bottlenose dolphins (*Tursiops truncatus*) population (Ceredigion County Council, Cardigan Bay cSAC Management Plan, 2001). The full status of SAC was given in November, 2004. Furthermore, the Pen Llyn a'r Sarnau cSAC in the north of Cardigan Bay has added the bottlenose dolphin to its list of features. The involvement of local community was encouraged from the early stages of the conservation activities because dolphins are affected by a wide range of human induced factors from general disturbance, noise and harassment to pollution, prey depletion, and habitat change. The importance of research activities together with increasing public awareness, and education is recognized as a vital part of management scheme in understanding dolphins requirements in the Cardigan Bay SAC and surrounding area.

The main study site was the Cardigan Bay SAC (Fig. 2.1). It covers area of approximately 1039 km2 (Baines et al., 2002), and is bounded by the coordinates presented in Table 2.1.

Table 2.1. The boundaries of the Cardigan Bay SAC expressed as decimal degrees.

Corner	Latitude	Longitude
South	52.0783	4.7650
West	52.2186	5.0042
North	52.4300	4.3967
East	52.2500	4.2333

Taking into consideration the mobility of the Cardigan Bay dolphins, and their variable individual residence (Wood, 1998) as well as potential impacts outside the Cardigan Bay SAC, in 2006 study effort was increased outside the SAC reaching Pwllhelli Harbour (52.8869^{o} N, 004.3917^{o} W) in the Pen Llyn a'r Sarnau cSAC in the north of Cardigan Bay.

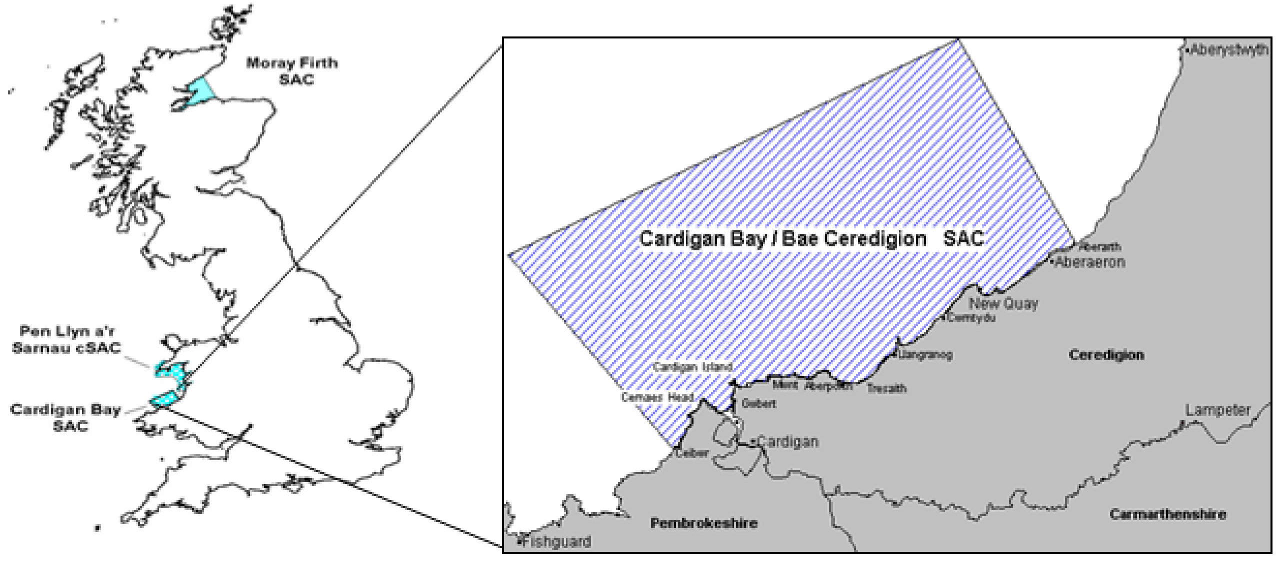


Fig 2.1. Location of the Cardigan Bay SAC, the main study area. (adapted from Ceredigion County Council, Cardigan Bay cSAC Management Plan, 2001)

3. Methods

3.1 Field data collection

Data for 2006 were collected during boat-based surveys within the Cardigan Bay SAC as well as in the northern part of the Bay reaching the Pwhelli Harbour. The surveys were conducted aboard the following vessels:

- 32 ft motor vessel "**Dunbar Castle 2**" (Fig. 3.1 (b)) powered by a 100 hp inboard diesel engine. The boat has a bench on the roof on which two observers could sit giving eyesight high of approximately 3.5 m above the sea level. This research vessel was mainly utilized for distance sampling surveys in conjunction with photo-identification surveys within the Cardigan Bay SAC. The area was divided into inshore and offshore zones along the median line of the SAC approximately 11km (6nm) from the coast. Transects followed a zigzag pattern between the coast and the median parallel or the outer boundary of the SAC, and at any given day was selected at random. A minimum of 5 observers took part in every survey, although on most occasions 6-10 observers were present.
- 33 ft sailing boat "**Celine**" (Fig. 3.1 (a)) powered by a 30 hp inboard diesel engine was used for the photo-identification surveying of the Pen Llyn a'r Sarnau cSAC. The boat survey followed predetermined routes designed to investigate the area of the sarns, where animals were known to concentrate for feeding purposes. Three to five observers took part in every survey. Fieldwork started and ended in the Aberystwyth harbour.
- 36 ft commercial passenger boat "**Ermol V**"(Fig. 3.1 (c)) powered by two 100 hp inboard diesel engines was utilized as a "platform of opportunity" during dolphin-watching trips with 1-3 observers on board. The vessel was based and operated from New Quay harbour on a daily basis (weather permitting).

Fig. 3.1. Research vessels employed to collect data in the present study. (a) – sailing boat “Celine”, (b) – motor boat “Dunbar Castle 2”, (c) – motor boat “Ermol V”. (photographs by courtesy of E.Magileviciute)

All surveys were conducted at sea state Beaufort three or less during good light conditions. If the sea state increased above three or/and the visibility was reduced by heavy rain or fog the survey trip was aborted because of unreliable sightings probabilities, and reduced chances of taking photographs suitable for photo-identification (Agler, 1992).

Effort was recorded on a form designed for this survey (Fig. 3.3). An entry on the form was completed at any change in effort status, at every sighting event, at every change of course in the boat’s track, and otherwise at 15 minute intervals. The data recorded on the form were: time, position (latitude and longitude in degrees and decimal minutes), effort status (casual watch, dedicated search, photo-id, line transect), sea state and swell height, visibility conditions, precipitation presence and type, and then on the line transect- the angle subtended by any glare in the observer’s field of view. When an entry was following a sighting, a unique reference number for the sighting was recorded in association with the effort data. The same reference number was recorded on the sightings form completed by the observer on the roof.

The sightings form (Fig. 3.4) recordings included: sightings reference number, time, species, group size and number of adults, juveniles, calves, newborns, and behavioural characteristics. Behaviour was recorded as one or more of the following categories: slow or normal swim, fast swim, feeding, leaping/splashing, tail-slaps, bow-riding, resting/milling, socializing, and reaction to boat.

When sighted, dolphins were slowly approached in order to perform photo-identification following Wursig and Jefferson (1990). A time spent photographing dolphin was termed as an encounter. Photographs were taken of the dorsal fins and backs of the animals at a perpendicular angle. Photography was attempted if the animals appeared to be approachable, irrespective of a group size. Attempts were made to photograph every dolphin present in an encounter irrespective of how well marked individual dolphins were.

All bottlenose dolphins photographed during the same encounter were considered members of the same group. Group size was defined as the total number of individuals encountered, moving in the same direction or engaged in the same activity within spatial proximity less than 100m (Wells et al., 1987). Arbitrary age categories included: adult, juvenile, calf, newborn, and were defined based on the size to an adult, skin colorations, behavioural pattern of swimming, and proximity to an adult (Bearzi et al., 1997). Dolphins seen repeatedly with a small calf were assumed to be mothers, and therefore adult females (Fig. 3.2a). Large, heavily scarred dolphins were considered probable males (Fig.3.2b). In some cases the gender was determined from photographs of the genital area during aerial behaviour or bow-riding (Smolker et al., 1992)

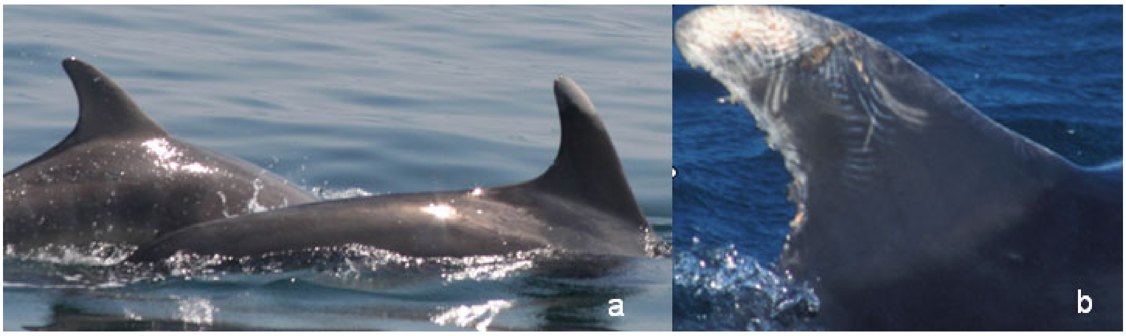
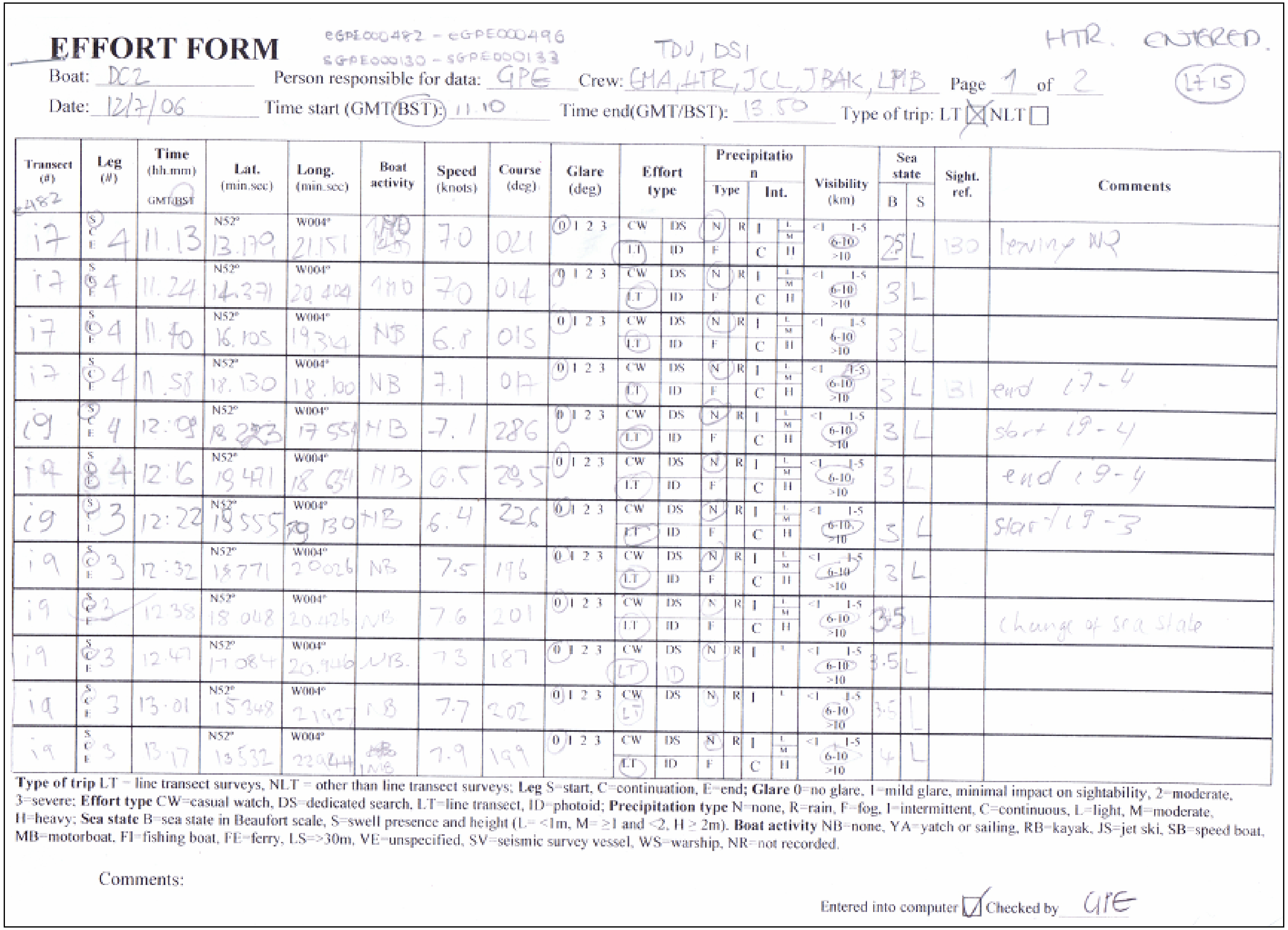


Fig. 3.2. Photographs of (a)- female #033-06S (on the right) with a calf; (b)- a scarred dorsal fin of a male #060-01W (photographs by courtesy of E.Magileviciute)



EFFORT FORM

eGPE000482 – eGPE000496
sGPE000130 – sGPE000133
TDU, DSI
HTR. ENTERED.
(17:15)

Boat: DC2 Person responsible for data: GPE Crew: GMA, HTR, JCL, JBAK, LPMB Page 1 of 2

Date: 12/7/06 Time start (GMT/[✓ BST]): 11.10 Time end(GMT/BST): 13.50 Type of trip: LT ☒ NLT ☐

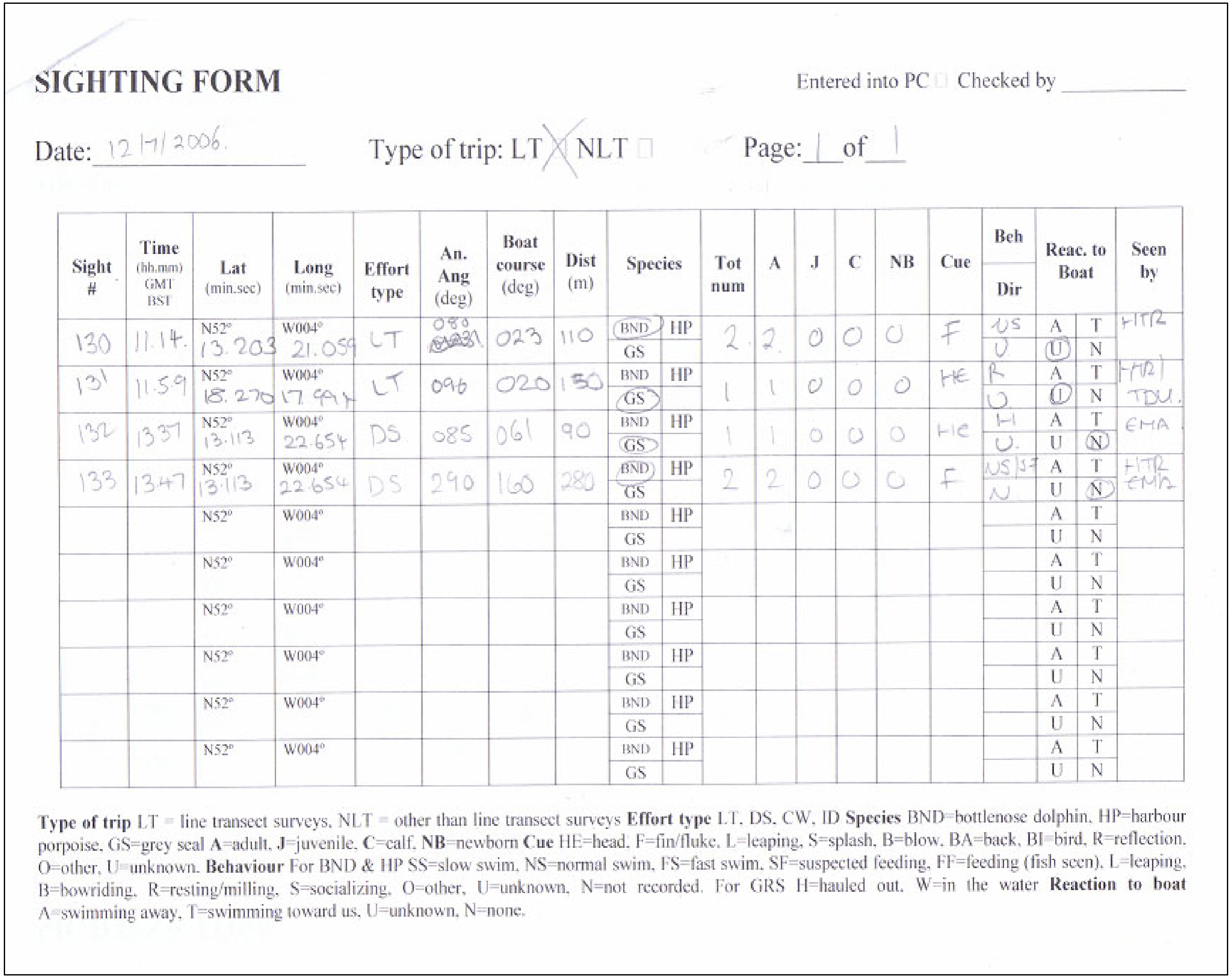
Transect (#) 482	Leg (#)	Time (hh.mm) GMT/[✓ BST]	Lat. (min.sec)	Long. (min.sec)	Boat activity	Speed (knots)	Course (deg)	Glare (deg)	Effort type	Precipitation Type	Precipitation Int.	Visibility (km)	Sea state B	Sea state S	Sight. ref.	Comments
i7	[✓ S] C E 4	11.13	N52° 13.179	W004° 21.151	NB	7.0	021	[✓ 0] 1 2 3	CW DS [✓ LT] ID	[✓ N] R F	I C L M H	<1 1-5 [✓ 6-10] >10	2.5	L	130	leaving NQ
i7	S [✓ C] E 4	11.24	N52° 14.371	W004° 20.404	NB	7.0	014	[✓ 0] 1 2 3	CW DS [✓ LT] ID	[✓ N] R F	I C L M H	<1 1-5 [✓ 6-10] >10	3	L		
i7	S [✓ C] E 4	11.40	N52° 16.105	W004° 19.314	NB	6.8	015	[✓ 0] 1 2 3	CW DS [✓ LT] ID	[✓ N] R F	I C L M H	<1 1-5 [✓ 6-10] >10	3	L		
i7	S [✓ C] E 4	11.58	N52° 18.130	W004° 18.100	NB	7.1	017	[✓ 0] 1 2 3	CW DS [✓ LT] ID	[✓ N] R F	I C L M H	<1 [✓ 1-5] [✓ 6-10] >10	3	L	131	end i7-4
i9	[✓ S] C E 4	12:09	N52° 18.283	W004° 17.559	NB	7.1	286	[✓ 0] 1 2 3	CW DS [✓ LT] ID	[✓ N] R F	I C L M H	<1 1-5 [✓ 6-10] >10	3	L		start i9-4
i9	S C [✓ E] 4	12:16	N52° 19.471	W004° 18.634	NB	6.5	295	[✓ 0] 1 2 3	CW DS [✓ LT] ID	[✓ N] R F	I C L M H	<1 1-5 [✓ 6-10] >10	3	L		end i9-4
i9	[✓ S] C E 3	12:22	N52° 19.555	W004° 19.130	NB	6.4	226	[✓ 0] 1 2 3	CW DS [✓ LT] ID	[✓ N] R F	I C L M H	<1 1-5 [✓ 6-10] >10	3	L		start i9-3
i9	S [✓ C] E 3	12:32	N52° 18.771	W004° 20.026	NB	7.5	196	[✓ 0] 1 2 3	CW DS [✓ LT] ID	[✓ N] R F	I C L M H	<1 1-5 [✓ 6-10] >10	3	L		
i9	S [✓ C] E 3	12.38	N52° 18.048	W004° 20.426	NB	7.6	201	[✓ 0] 1 2 3	CW DS [✓ LT] ID	[✓ N] R F	I C L M H	<1 1-5 [✓ 6-10] >10	3.5	L		change of sea state
i9	S [✓ C] E 3	12.47	N52° 17.084	W004° 20.946	NB.	7.3	187	[✓ 0] 1 2 3	CW DS [✓ LT] ID	[✓ N] R	I L	<1 1-5 [✓ 6-10] >10	3.5	L		
i9	S [✓ C] E 3	13.01	N52° 15.348	W004° 21.927	NB	7.7	202	[✓ 0] 1 2 3	CW DS [✓ LT]	[✓ N] R	I L	<1 1-5 [✓ 6-10] >10	3.5	L		
i9	S [✓ C] E 3	13.17	N52° 13.532	W004° 22.944	~~NB~~ NB	7.9	199	[✓ 0] 1 2 3	CW DS [✓ LT] ID	[✓ N] R F	I C L M H	<1 1-5 [✓ 6-10] >10	4	L		

Type of trip LT = line transect surveys, NLT = other than line transect surveys; **Leg** S=start, C=continuation, E=end; **Glare** 0=no glare, 1=mild glare, minimal impact on sightability, 2=moderate, 3=severe; **Effort type** CW=casual watch, DS=dedicated search, LT=line transect, ID=photoid; **Precipitation type** N=none, R=rain, F=fog, I=intermittent, C=continuous, L=light, M=moderate, H=heavy; **Sea state** B=sea state in Beaufort scale, S=swell presence and height (L= <1m, M= ≥1 and <2, H ≥ 2m). **Boat activity** NB=none, YA=yatch or sailing, RB=kayak, JS=jet ski, SB=speed boat, MB=motorboat, FI=fishing boat, FE=ferry, LS=>30m, VE=unspecified, SV=seismic survey vessel, WS=warship, NR=not recorded.

Comments:

Entered into computer ☑ Checked by GPE

Fig. 3.3. Effort form showing data collected during line-transect and photo-identification surveys



SIGHTING FORM

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Date: 12/7/2006.

Type of trip: LT ☒ NLT ☐

Page: 1 of 1

Sight #	Time (hh.mm) GMT BST	Lat (min.sec)	Long (min.sec)	Effort type	An. Ang (deg)	Boat course (deg)	Dist (m)	Species	Tot num	A	J	C	NB	Cue	Beh Dir	Reac. to Boat	Seen by
130	11.14.	N52° 13.203	W004° 21.059	LT	080	023	110	[✓ BND] HP GS	2.	2.	0	0	0	F	NS U	A T [✓ U] N	HTR
131	11.59	N52° 18.270	W004° 17.994	LT	096	020	150	BND HP [✓ GS]	1	1	0	0	0	HE	R U	A T [✓ U] N	HTR TDU.
132	1337	N52° 13.113	W004° 22.654	DS	085	061	90	BND HP [✓ GS]	1	1	0	0	0	HE	H U.	A T U [✓ N]	EMA
133	1347	N52° 13.113	W004° 22.654	DS	290	160	280	[✓ BND] HP GS	2	2	0	0	0	F	NS SF N	A T U [✓ N]	HTR EMA
		N52°	W004°					BND HP GS								A T U N	
		N52°	W004°					BND HP GS								A T U N	
		N52°	W004°					BND HP GS								A T U N	
		N52°	W004°					BND HP GS								A T U N	
		N52°	W004°					BND HP GS								A T U N	
		N52°	W004°					BND HP GS								A T U N	

Type of trip LT = line transect surveys, NLT = other than line transect surveys **Effort type** LT, DS, CW, ID **Species** BND=bottlenose dolphin, HP=harbour porpoise, GS=grey seal **A**=adult, **J**=juvenile, **C**=calf, **NB**=newborn **Cue** HE=head, F=fin/fluke, L=leaping, S=splash, B=blow, BA=back, BI=bird, R=reflection, O=other, U=unknown. **Behaviour** For BND & HP SS=slow swim, NS=normal swim, FS=fast swim, SF=suspected feeding, FF=feeding (fish seen), L=leaping, B=bowriding, R=resting/milling, S=socializing, O=other, U=unknown, N=not recorded. For GRS H=hauled out, W=in the water **Reaction to boat** A=swimming away, T=swimming toward us, U=unknown, N=none.

Fig. 3.4. Sighting form showing data collected during line-transect and photo-identification surveys

An encounter was terminated when all dolphins in the group were photographed; dolphins showed signs of avoidance such as prolonged dives or change of direction in the proximity of the boat; dolphins were lost from the view; time specified in the license given by Countryside County for Wales to conduct cetacean photo-identification studies expired (Pesante.G., pers. comm., 2006)

If more than one group was encountered during a survey trip each sighting was recorded as a separate encounter, and a spacer picture (e.g. face of the observer) was taken in order to separate the photographic records of different groups. A spacer picture was also taken if the sex of a particular individual was seen by the photographer or observer. All photo-identification notes were recorded on an audio tape and later transcribed.

During most of the encounters two photographers were present in order to increase the probability that all animals during the encounter were photographed. Photographs were taken with a Cannon D20 digital camera with a 28-300 mm zoom lens, and Cannon EOS 350D digital camera with a 75-300 mm zoom lens. Pictures were exposed using the maximum diaphragm aperture at shutter speeds of 1/1000 sec.

Data previously collected by Sea Watch Foundation were used for the years 2003, 2004 and 2005. Janet Baxter made available land, and boat based photographs from Mwnt, Ynys Lochtyn and Aberystwyth for the years 2003 and 2004. In addition Mick Baine's catalogue from the year 2001 was utilized in constructing pooled data network for the five year period 2001-2006, excluding year 2002 due to the insufficient data for the analysis.

3.2 Data analysis

3.2.1 Photograph matching

Digital pictures from each survey were downloaded into the computer, and analyzed on the screen using ACDSee 5.0.1 digital imaging software following the matching protocol developed by the Sea Watch Foundation.

In order to avoid false positive or false negative errors (Scott et al., 1990; Stevick et al., 2001) only high-quality photographs were used to identify individual dolphins in the encounter based on the pattern of nicks, lesions, scars and variation of the dorsal fin shape (Wilson et al., 1999). Photographs with distinctive body features alone were also used for the matching analysis if they could be linked to the individual, which was already identified based on its dorsal fin. The number of dolphins in the group, and the major age categories that were assessed visually *in situ*, were verified through the analysis of the photographs. After the matching with the main photo-ID catalogue each dolphin was assigned a unique alpha numerical code. The code consisted of the three-digit number followed by the year when dolphin was first identified, and a letter signifying the level of markings (e.g. W-well marked, S-slightly marked) was given to each dolphin(e.g. 051-91W). Photographs were classified into one of three catalogues:

- Marked- pictures of dolphins with irregularities on the dorsal fin that allow identification from either side of the animal
- Right- pictures taken from the right side of a dolphin without irregularities in their dorsal fins
- Left- pictures taken form the left side of a dolphin without irregularities in their dorsal fins

Photographs of reliably marked individuals were further utilized in the social network and spatial distribution analysis.

3.2.2 Social organization

3.2.2.1 Defining associations and preferred companionships

Dolphins sighted in the same group were considered to be associated (Smolker et al., 1992). Dolphins sighted in five or more encounters were included in the association analyses. New identified dolphins in 2006 that were seen two or more times were also included in the analysis.

Half weight index (HWI) was utilized as a measure of associations because it accounts best for the observer bias during photo-identification surveys where identifications of entire group may be difficult to attain (Cairns and Schvager, 1987). It also allows comparison to other bottlenose dolphin studies (Wells et al., 1987; Lusseau et al., 2003b; Lusseau et al., 2006). Associations were calculated as follows:

$$\mathbf{HWI = X / (X + 0.5(Ya + Yb))} \qquad \textbf{(Eqn.1)}$$

Where: X - the number of times dolphins a and b were sighted in the same group

Ya – the number of groups where dolphin a was encountered but not dolphin b

Yb – the number of groups where dolphin b was sighted but not dolphin a

HWI quantifies associations on a scale from 0 (two individuals never seen together) to 1 (two individual always seen together).

HWI cut-off technique was used to define preferred companionships in order to filter associations that might happen by chance during aggregations (Lusseau et al., 2006). All pairs with HWI greater than $HWI_{null,}$ i.e. the average association index if individual associates at random in the population (Whitehead, 1995), were included in the social network. HWI_{null} was calculated using the following equation:

$$\mathbf{HWI_{null} = n / (N\text{-}1)} \qquad \textbf{(Eqn.2)}$$

Where: n – average group size in which an individual is found

N – population size

The calculations of the HWI were performed using SOCPROG version 2.3 (for MATLAB 7.1) (Whitehead, 2006)

3.2.2.2 Network properties

Social networks of bottlenose dolphins in Cardigan Bay, Wales were constructed for the years 2003 to 2006. Data from 2001 were added to build up the pooled data social network for the 5-yr period.

In order to explore the structure of the social networks the following network properties were investigated. Density, average shortest path, and clustering coefficient of these networks were calculated as the representation of an average structure of a network. Density, ρ, is the proportion of all possible ties (edges) in the network Average shortest path length, l, between two vertices (vertex- an individual in a network graph) shows how quickly information can be transferred, and how many individuals we have to go through on the way. For example in human population these values range from l of 6. It means that any two humans could be connected using five intermediates (Milgram, 1967, Newman and Girvan, 2004a). Clustering coefficient, C, measures the social relatedness of individuals within a network as a number of triads, i.e. that the two associates of a dolphin *a* are associates themselves. These measures provide an opportunity to classify the network as being random, ordered or small world (Newman et al., 2001). Small world networks have high clustering coefficient as in ordered networks, and short average path length as in random networks.

Degree, k, i.e. the number of edges that are connected to a vertex, together with betweenness, i.e. the proportion of times an individual lies on the shortest path between other individuals, are commonly used to determine the centrality of an individual, and the influence over the flow of information in the network. In the dolphin networks, the vertices with the highest betweenness are found on the boundaries of the communities (clusters), and may play a key role in maintaining the social cohesion of the population (Lusseau and Newman, 2004). Therefore the Girvan-Newman algorithm which employs the “betweenness” measure was used to detect natural divisions within the networks (Girvan and Newman, 2002). Modularity index, Q, (Newman, 2004b) was used to select the best division, i.e. groups with the higher number of edges within the group than between the groups. The first local peak in Q values indicates the divisions between the groups.

Furthermore, several studies have suggested that association processes may be influenced by certain level of assortative mixing. This study investigated assortativity of individuals by sex, and vertex degree, i.e. by the number of edges connected to the vertex. For example in human networks gregarious individuals more often form ties with other gregarious individuals than with hermits (Barabassi and Abert, 1999).The level of assortative mixing was measured using assortativity coefficient r, which is defined as:

$$r = \sum_i e_{ii} - \sum_{ijk} e_{ik}\, e_{jk} / 1 - \sum_{ijk} e_{ik}\, e_{jk} \qquad \textbf{(Eqn.3)}$$

Where: e_{ij} – the fraction of edges in the network that connects individuals of type i to individuals of type j.

This quantity ranges from 1 when we have perfect assortative mixing, i.e. individuals associate only with others of the same type, and 0 when mixing is random. Values between 1 and 0 define partial mixing. Mixing can also be disassortative: individuals may associate preferentially with others of different types. In that case, r will take a negative value (Newman, 2002a). The standard deviation of r was calculated as described in Newman (2003a).

Pooled data social network properties were also compared to random networks with the same number of vertices but randomly distributed edges among vertices.

The networks were constructed, and network properties were calculated using Ucinet (Borgatti et al., 2002), the networks were drawn using NetDraw (Borgati, 2002), and random networks were designed using Pajek (Batagelj and Mrvar, 2002). Statistical analyses were conducted using Minitab (v.14.20).

3.2.2.3 Ranges of individual dolphins and network components.

Data related to the encounters of dolphins in this study were restricted to the selected study area within Cardigan Bay. Thus, the calculated ranges of individual dolphins, and groups were treated as the area the dolphin has been sighted within, rather than the complete “home-range”. The study area was subdivided into seven subareas (Fig.3.5). The outer part of Cardigan Bay SAC was defined as the “Outer” subarea, the inner part of the SAC was subdivided into the following subareas: Cemaes Head (CH), Mwnt (M), Ynys Lochtyn (YL) and New Quay (NQ). The surveyed area in the north of Cardigan Bay was subdivided into “Aberystwyth” (A) and “North” subareas.

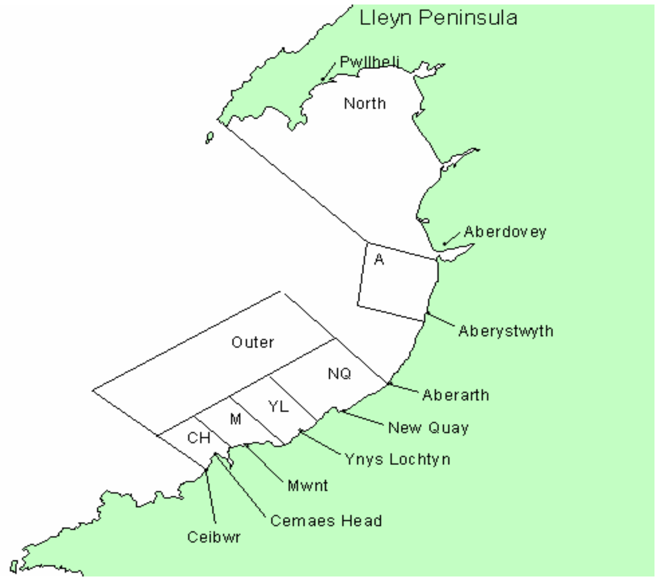


Fig. 3.5. Division of the study area within Cardigan Bay, Wales into seven subareas: Cemaes Head (CH), Mwnt (M), Ynys Lochtyn (YL) and New Quay (NQ), Outer (outer part of the Cardigan Bay SAC), Aberystwyth (A), North (northern part of the Cardigan Bay)

Two home range analysis models from Home Range Extension (HRE) for ArcView GIS 3.3 were utilized. The kernel method was employed in order to determine centers of activity from the density of utilization distribution (Seamann and Powell, 1996). Minimum convex polygon (MCP) areas were calculated to define the range of the components within the network. MCP is simply the polygon that connects the outermost points recorded for an animal, and gives a minimum area that the animal traveled within. MCP's are easy to calculate and allows for comparisons between the studies. The number of subareas covered by the range of individual dolphin was further included in calculating the correlation with the degree of each vertex in the network.

3.2.2.4 Epidermal skin markings (lesions)

The actual reason for the occurrence of abnormal epidermal markings remains unclear- whether they are direct consequence of a disease or just naturally occurring on the skin of an animal. For that reason the assignation of the name" lesion" to different markings should be treated with caution. However, based on previous publications

(Wilson et al.,1997a; Harzen et al.,1997; Wilson et al.,1999) different type of markings were treated as skin lesions in the present study.

High quality photographs from the Sea Watch Foundation database as well as pictures taken in April-September 2006 were selected for the analysis of epidermal markings (lesions) of the individuals from the network 2006. Presence or absence of skin lesions was determined by examining photographs of a back and dorsal fins of individuals. The categorization of different skin lesion types was adapted from Wilson et al. (1997a) based on similar visible characteristics (Table 3.1). The majority of abraded dorsal fin tips seemed to be tooth rake marks, resulting from physical injuries rather than consequence of pathology. This category was not included in the statistical analysis as suggested by Wilson et al. (1997a).

Table. 3.1 Classification of skin lesions of bottlenose dolphins in the network 2006 (adapted from Wilson et al., 1997a)

Lesion type	Description
Black patches	Uniformly black, circular or amorphous patches with rounded edges
White patches	Circular or amorphous white patches with rounded edges. Sometimes they have matt, chalky appearance
White fin-fringe lesions	Smooth, white, elongated patches on the leading edge of a dorsal fin.
Abraded fin tips	White areas of the top of the leading edge of the dorsal fin with jagged or diffuse edges
Cloudy lesions	Complex mixture of white, black, grey skin extending over large areas especially on the dorsal part of the tail trunk.
White-fringe spots	cream or white halos surrounding small circles of normally coloured or black skin
Black-fringe spots	Pale areas of skin surrounded by dark halos. Usually circular.

The prevalence of skin lesions in the network 2006 as well as in each component of this network was estimated as the proportion of dolphins in that sample with those features. Statistical analyses were performed using Minitab (v.14.20).

4. Results

4.1 Survey effort and identified individuals

Between 2001 and 2006, April to October, there were 518 encounters with bottlenose dolphins during which group composition was collected. Of those 381 groups were used for the analysis based on the selection criteria. Table 4.1 summarizes the effort for the five year period analyzed in the present study.

Table 4.1 Survey effort for the 5-yr period 2001-2006

Year	No. of survey trips	No. of survey hours	No. of encounters
2001	27	239	108
2003	84	514	139
2004	54	231	121
2005	114	409	80
2006	198	461	70
Total	477	1854	518

To date 156 reliably marked bottlenose dolphins are contained in the photo-id catalogue. Eighty four dolphins identified in 2001-2005, and 25 dolphins identified in 2006 were included in the analysis. Out of 109 individuals, 25 were classed as “probable females” and 28 as “probable males”.

Frequency of sightings per individual is presented in Fig. 4.1. Dolphin #17 was encountered the most often, 37 times, during the study period. One third of new identified dolphins were sighted twice during present study period.

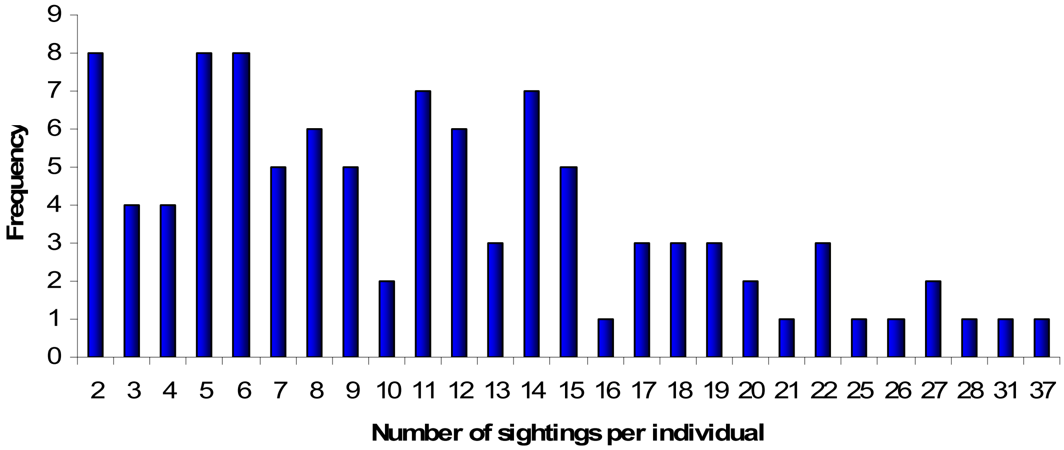


Fig. 4.1. Frequency of dolphins sightings during study period 2001-2006 (mean = 15.77, SD = 9.23)

4.2 Associations of individuals and preferred companionships

Eighty nine bottlenose dolphins were used for the 5-yr pooled data analysis. The majority of Coefficients of Association (CoA's) values ranged between 0 and 0.2 (Fig. 4.2 (a)). The distribution of mean and maximum CoA's is presented in Fig. 4.2(b), with a mean CoA ranging from 0.01 to 0.07 (mean=0.04, SD=0.02), and maximum CoA ranging from 0.1 to 0.67 (mean=0.32, SD=0.11). The highest association was observed between dolphins #184 and #185 (0.67).

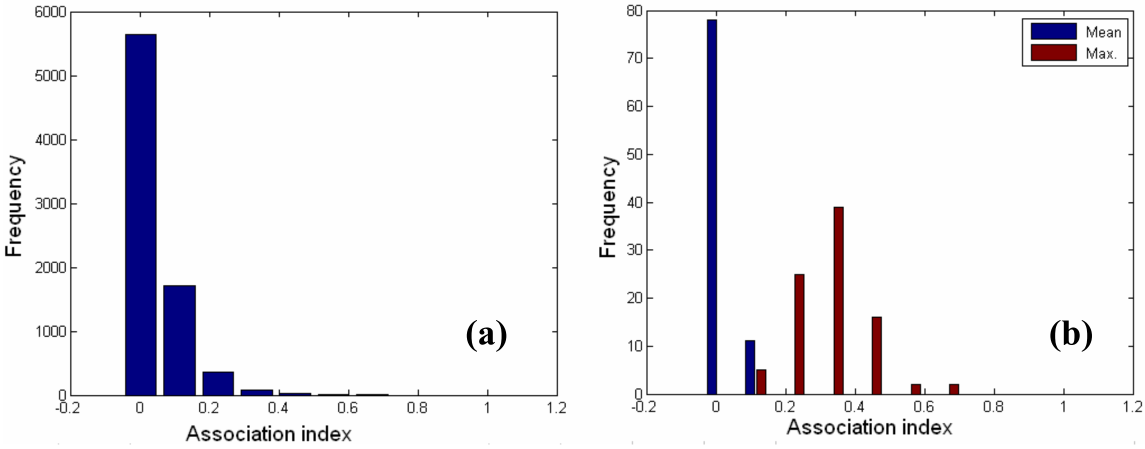


Fig. 4.2. (a) - Distribution of Coefficient of Association (CoA) values for all pairwise comparisons of 89 individuals (n = 5774); (b)- distribution of mean and maximum CoA's of 89 individuals in the pooled data analysis.

Annual results produced higher values (Table 4.2). For example in 2006 maximum CoA ranged from 0.33 to 1.However the results might be biased because of the lower number of encounters during one season comparing to the pooled data analysis for the five year period.

Table 4.2 Mean and maximum CoA values for the annual and pooled data; n- number of individuals

Year	Mean CoA (SD)	Maximum CoA (SD)
2003 (n=71)	0.04 (0.02)	0.48 (0.17)
2004 (n=71)	0.04 (0.02)	0.55 (0.19)
2005 (n=52)	0.07 (0.02)	0.69 (0.30)
2006 (n=85)	0.04 (0.02)	0.73 (0.26)
Pooled data 2001-2006 (n=89)	0.04 (0.02)	0.32 (0.11)

$HWI_{null,}$ i.e. the average association index if individual associates at random in the population (Whitehead 1995), was calculated (Eqn. 3) for each year, and pooled data. An average group size of n = 5.89 was considered based on the previous studies in the Cardigan Bay SAC (Lott, 2004). All dyads with HWI_{null} higher that 0.084 (SD = 0.019) were defined as preferred companionships, and were included in a social network construction.

4.3 Social networks

All dolphins were connected in one social network (Fig. 4.3). The 89 individuals in the pooled data network were linked by 2362 preferred companionships (edges). and therefore the average connectivity, k, of the network was 27.48 (SD = 13.35), with 60 % of all possible ties present ($\rho = 0.60$). However, different annual variations were observed (Table 4.3).

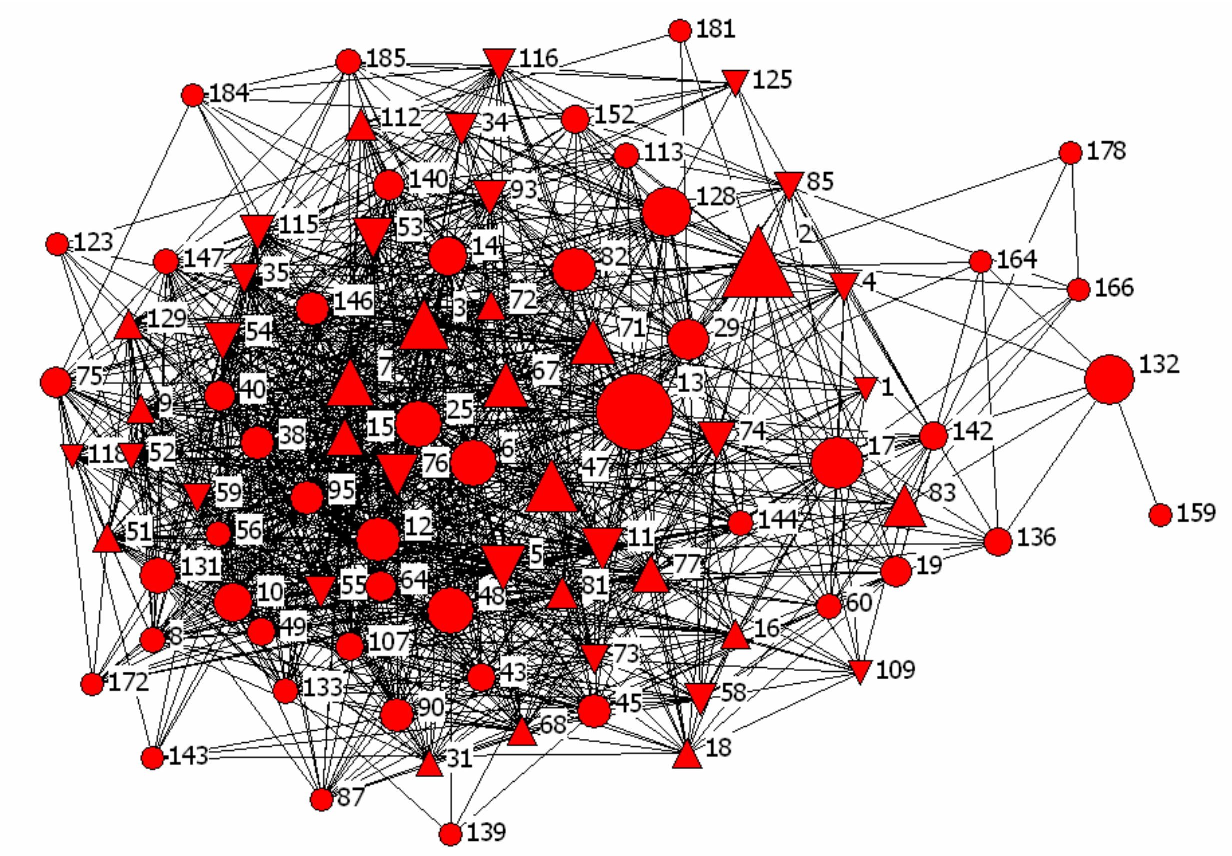


Fig. 4.3. The pooled data social network of bottlenose dolphins in Cardigan Bay, Wales; each vertex represents an individual and each edge represents the pair of individuals that are preferred companionships. Vertex number indicates dolphin ID in the catalogue. Females are presented as up-triangles, males as down-triangles, and individuals of unknown sex as circles. The size of each symbol shows the level of betweenness.

The network 2003 had 30% more edges than the network 2004, both having the same number of vertices. Only 15% of all possible ties were found in the network 2006. It had similar amount of individuals as the pooled data network, but its density value was four times lower.

Table 4.3 Network statistics for the Cardigan Bay bottlenose dolphin annual social networks, and 5-yr pooled data social network 2001-2006; n- is the number of vertices, m- the number of edges, ρ – density of a network, C – the clustering coefficient, l – the average shortest path between the vertices in the network, k – the degree (connectivity) of the vertex, r_s – the assortativity coefficient by sex, r_d - the assortativity coefficient by degree.

Year	n	m	ρ	C	l	k	r_s (SD)	r_d (SD)
2003	71	1226	0.49	0.559	1.89	16.93	0.041 (0.016	0.103 (0.008)
2004	71	836	0.34	0.591	2.13	14.96	0.041 (0.003)	-0.079 (0.011)
2005	52	458	0.34	0.785	2.38	8.81	-0.04 (0.0057)	0.305 (0.021)
2006	85	562	0.15	0.753	3.36	6.91	0.037 (0.008)	0.111 (0.002)
2001-2006	89	2362	0.60	0.555	1.77	27.48	-0.042 (0.01)	0.138 (0.009)

The social network of bottlenose dolphins was compared to a random network (10 networks were designed) with the same number of vertices and edges. Both random and dolphin network had similar diameter (expressed as the shortest path length); $l_{dolphin}$= 1.77 vs l_{random} = 3.03, SD = 0.08 but dolphin social network was highly clustered $c_{dolphin}$ = 0.555 vs c_{random} = 0.055, SD = 0.014. Pooled data network displayed certain level of homophily (Table 4.3), i.e. individuals tended to associate with others that had similar number of associates. The strongest assortativity by degree was found in the social network 2005. In contrast, the network 2004 presented low but significantly negative assortativity by degree meaning that individuals were more likely to associate with the ones of different type. Dolphin #13 had the highest overall number of associates (n = 57) while dolphin #159 had only one (Appendix 2). The proportion of different levels of degree is displayed in Fig. 4.4.

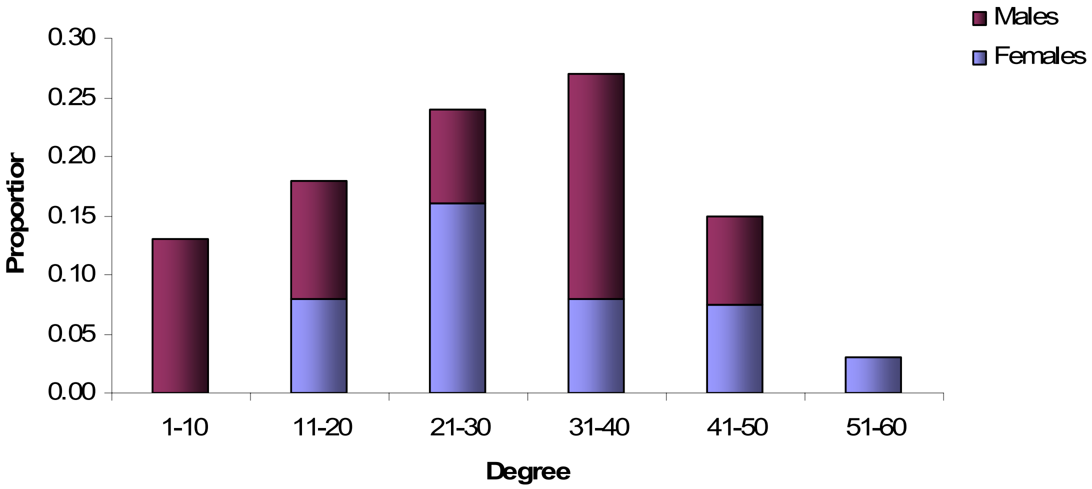


Fig. 4.4. The proportion of individuals having different levels of degree in the pooled data network 2001-2006.

For the annual networks, Mann-Whitney U test showed no significant difference between the degree of individuals in 2005 and 2006 (W=4067.0, p=0.109), while the degree in 2003 and 2004 was found to be significantly different (W=5931.0, p<0.001). Assortativity coefficient by sex indicated that sex of individuals did not seem to play any significant role in the association pattern of individuals in this population (Table 4.3). However the results could be biased because the sex was known only for 55 dolphins included in this analysis.

4.3.1 Network divisions and centrality of individuals

Natural divisions within each network were identified using Girvan-Newman algorithm (Girvan and Newman, 2002). Pooled data network was broken into five components (Fig. 4.6). The first maxima of modularity index Q = 0.324 was achieved after removing 57 individuals (64%) with the highest betweenness (nbetweenness > 0.425) which represents the centrality of an individual within the network (Fig. 4.5). nBetweenness is the betweenness divided by the maximum possible betweenness expressed as a percentage.

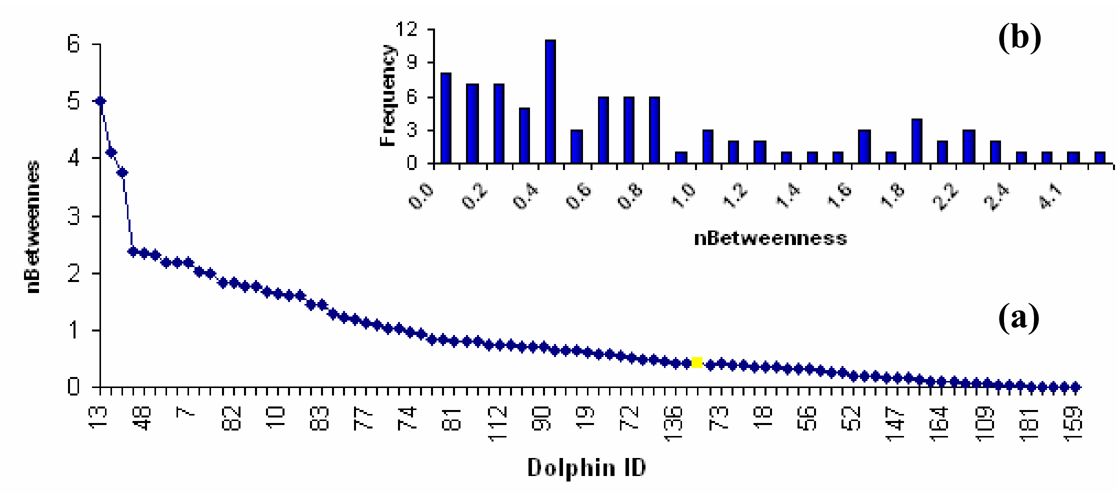


Fig. 4.5. (a)- the proportion of individual with the highest nbetweenness removed from the network; yellow symbol marks cut-off point. (b)- frequency of the nbetweenness scores.

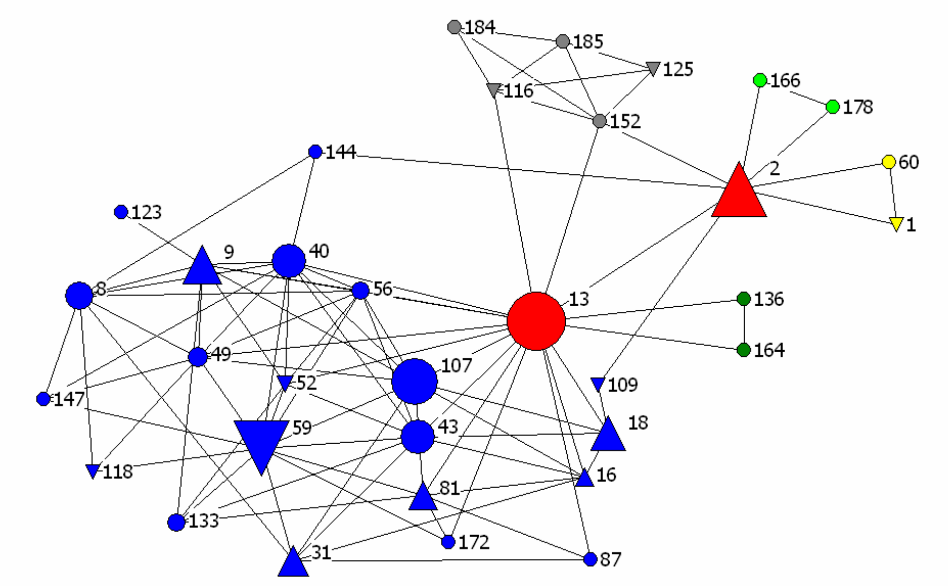


Fig. 4.6. The division of the pooled data network into five components. Females are presented as up-triangles, males as down-triangles, and individuals of unknown sex as circles. Vertex number indicates dolphin ID, vertex colour- group membership. The size of each symbol shows the level of betweenness. Individuals #13 and #2 had the highest betweenness scores within the network and connected all five groups.

The division in the social network 2003 (Fig. 4.7(a)) was achieved by removing 40% (n = 29) of individuals with the highest betweenness leading to the Q value of 0.396, and resulting in six interconnected groups and one isolated component of the size two (Fig. 4.8). The network 2004 (Fig. 4.7(b)) was divided into six components, and one isolated component was also present (Fig. 4.8). The first local peak of Q = 0.447 was achieved by removing 21% (n = 15) of individuals with the highest betweenness.

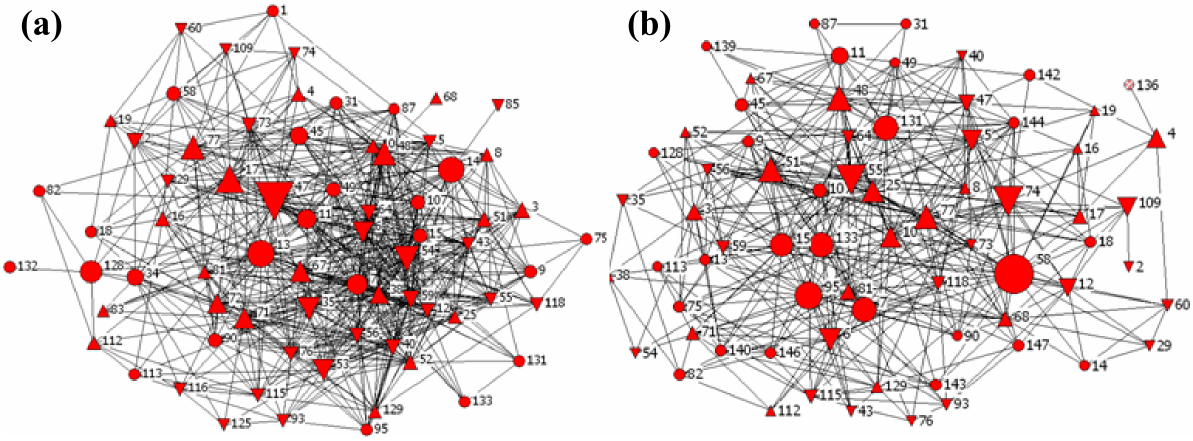
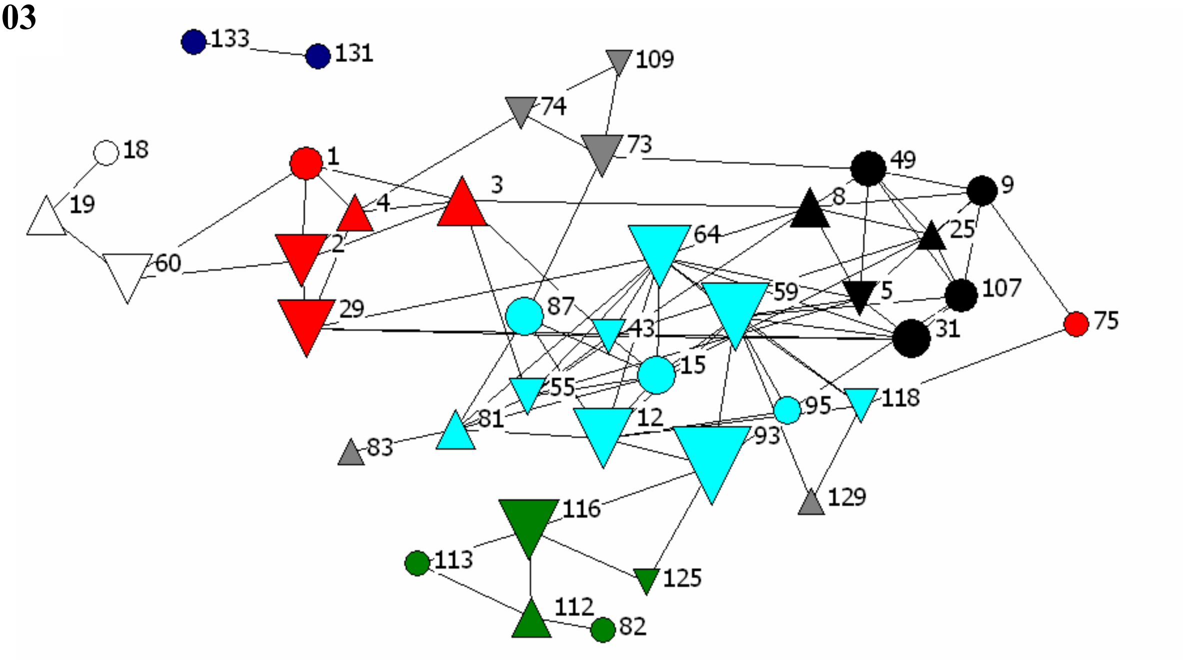


Fig. 4.7 Networks 2003 (a) and 2004 (b) before the Girvan-Newman algorithm defined natural subdivisions. Each vertex represents an individual and each edge represents the pair of individuals that are preferred companionships. Vertex number indicates dolphin ID in the catalogue. Females are presented as up-triangles, males as down-triangles, and individuals of unknown sex as circles. The size of each symbol shows the level of betweenness.

Network 2005 was divided in three major and one isolated component consisting of two individuals. All vertices were present when the first maxima of Q = 0.324 was achieved (Fig. 4.9). Similar pattern was observed in the network 2006 with a high value of Q = 0.607 achieved with all vertices present. The algorithm produced four interconnected components within the network (Fig. 4.9)

2003



2004

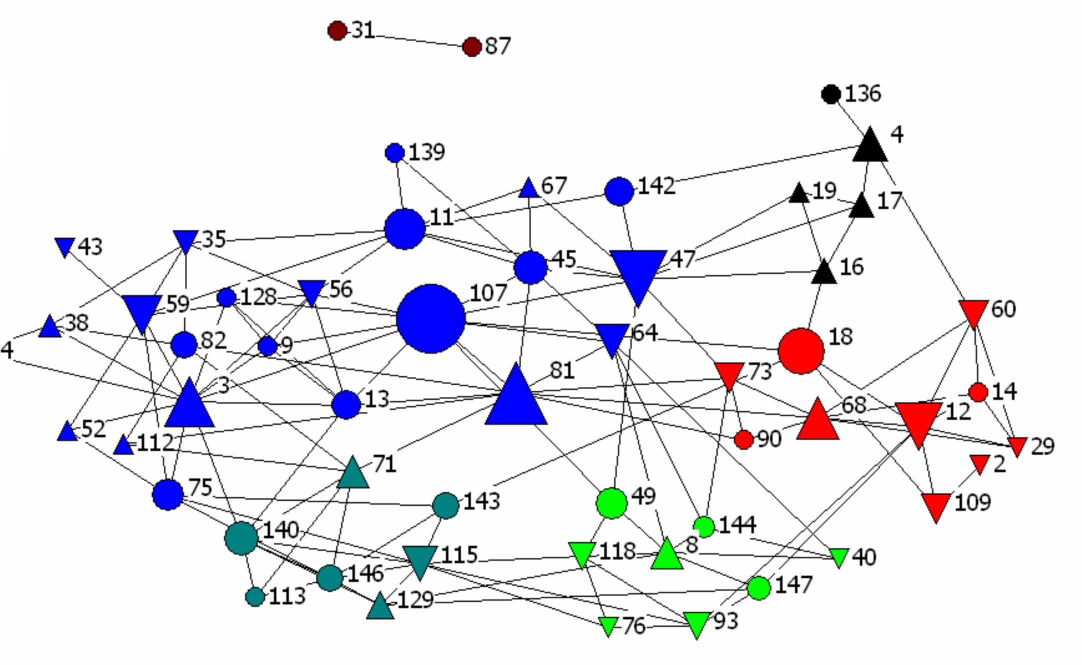


Fig. 4.8 Divisions in the dolphin social networks 2003 and 2004 using Girvan-Newman (2002) algorithm based on betweenness. Vertex number indicates dolphin ID, vertex colour indicates group membership. Females are presented as up-triangles, males as down-triangles, and individuals of unknown sex as circles. The size of each symbol shows the level of betweenness of each vertex.

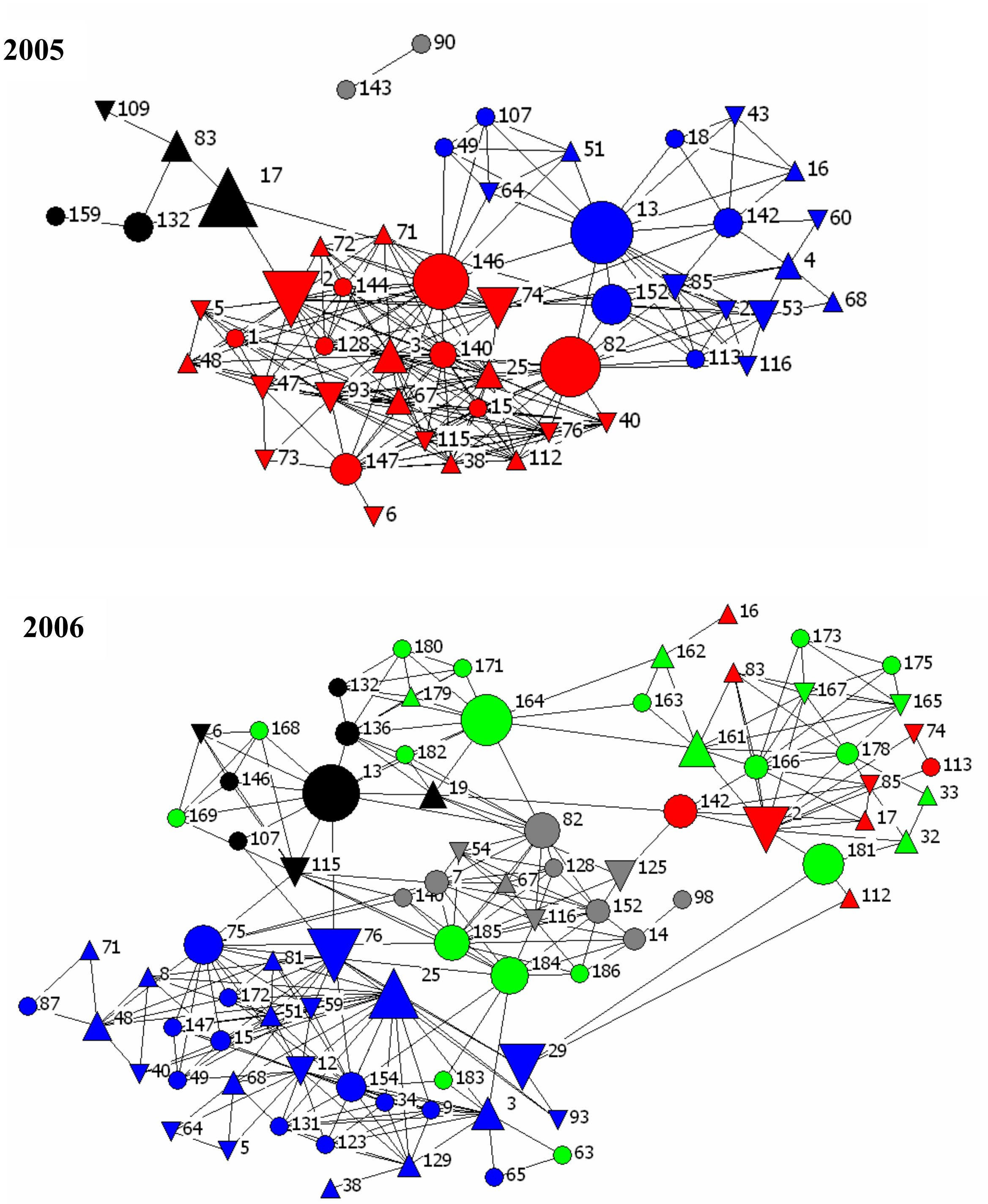


Fig. 4.9 Divisions in the dolphin social networks 2005 and 2006 using Girvan-Newman (2002) algorithm based on betweenness. Vertex number indicates dolphin ID, vertex colour indicates group membership. In network 2006 vertices in green are all new identified dolphins in 2006. Females are presented as up-triangles, males as down-triangles, and individuals of unknown sex as circles. The size of each symbol shows the level of betweenness of each vertex

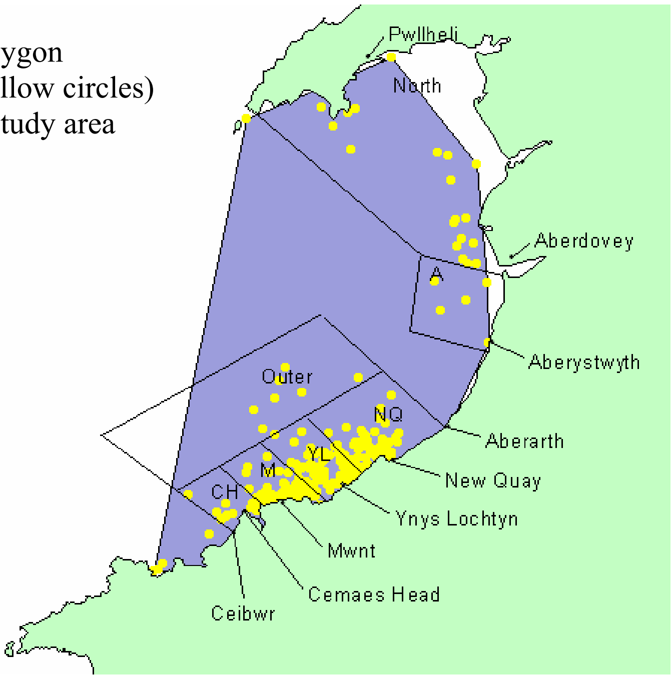
Two components in the network 2006 contained high number of new identified individuals. “Red” component consisted of 47% (n = 7) of the dolphins identified in 2006, and 57% (n = 15) of all members in the “Black” component were new animals.

The tendency of division similarities in 2003, 2004 and pooled data networks in regards to the removal of individuals with high betweenness, and contrasted results from the networks 2005 and 2006 (no removal of vertices) led to the comparison of clustering values of these networks. Subsequently, there was no significant difference found in clustering coefficients between networks 2003, 2004 and pooled data network (Mann-Whitney test W = 14755.0, p = 0.439). Networks 2005 and 2006 did not show significant difference in clustering as well (W = 3112.0, p = 0.550). However, a significant difference was found by analyzing clustering coefficients between networks 2003/ 2004/ pooled data network and networks 2005/ 2006 (W = 16533.5, p < 0.001). Thus, the network formation pattern in different years might be the outcome of difference or similarity in clustering.

4.3.2 Known ranges of the social network components and individual dolphins.

The known range of all individuals included in the analysis extended form the southern part of the Cardigan Bay SAC to the most northern point of Cardigan Bay (Fig. 4.10), and spread over all subareas in the study area.

Fig. 4.10 The minimum convex polygon area that included all encounters (yellow circles) selected for the analysis within the study area for the period 2001-2006



The kernel method was employed to analyze centers of activity of each dolphin included in the analysis. The summary of the frequency of utilization of each subarea is presented in Fig. 4.11. Mwnt, Ynys Lochtyn and New Quay were the subareas with the most bottlenose dolphin sightings. North and Aberystwyth subareas had the lowest number of individuals who were sighted more regularly in that area. However, this difference could be explained by the lower number of effort in that area.

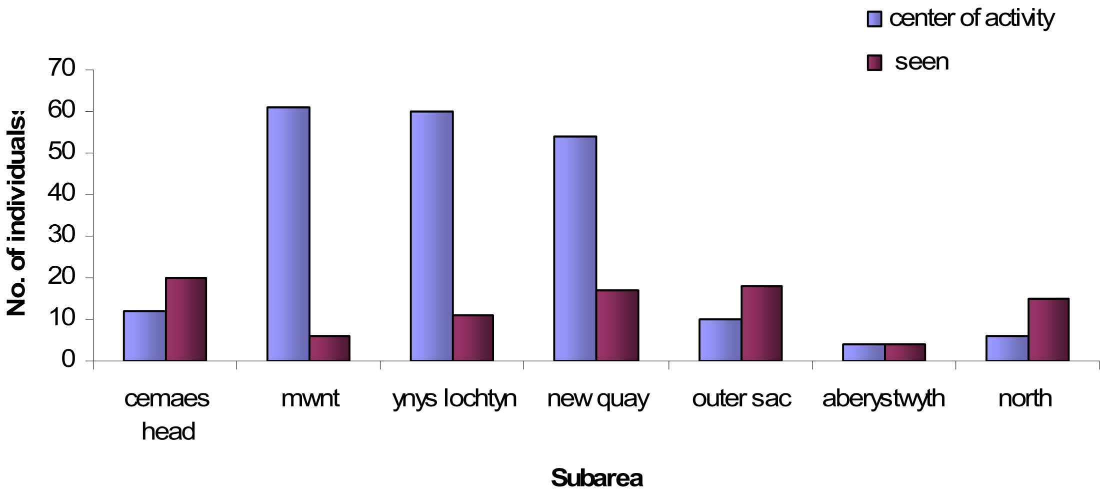


Fig. 4.11. Frequency of utilization of each subarea as center of activity or visit by all dolphins (n=89) included in the pooled data analysis.

Dolphins #14, #38 and #53 had five centers of activity, and were most often sighted within the whole Cardigan Bay SAC but never in the Aberystwyth or North subareas whereas dolphins #164, #166, #178, and #181 have been encountered only in the North of Cardigan Bay. Dolphin #55 was sighted in the highest number of subareas (6) from Cemaes Head to North, with the center of activity in Mwnt.

There was found significant positive correlation (Pearson's correlation coefficient $r = 0.590$, $p < 0.001$) between the number of subareas the known range extends, and the degree of an individual in the social network (Fig. 4.12). Dolphins, sighted in three to six subareas were more likely to associate with higher number of preferred companionships.

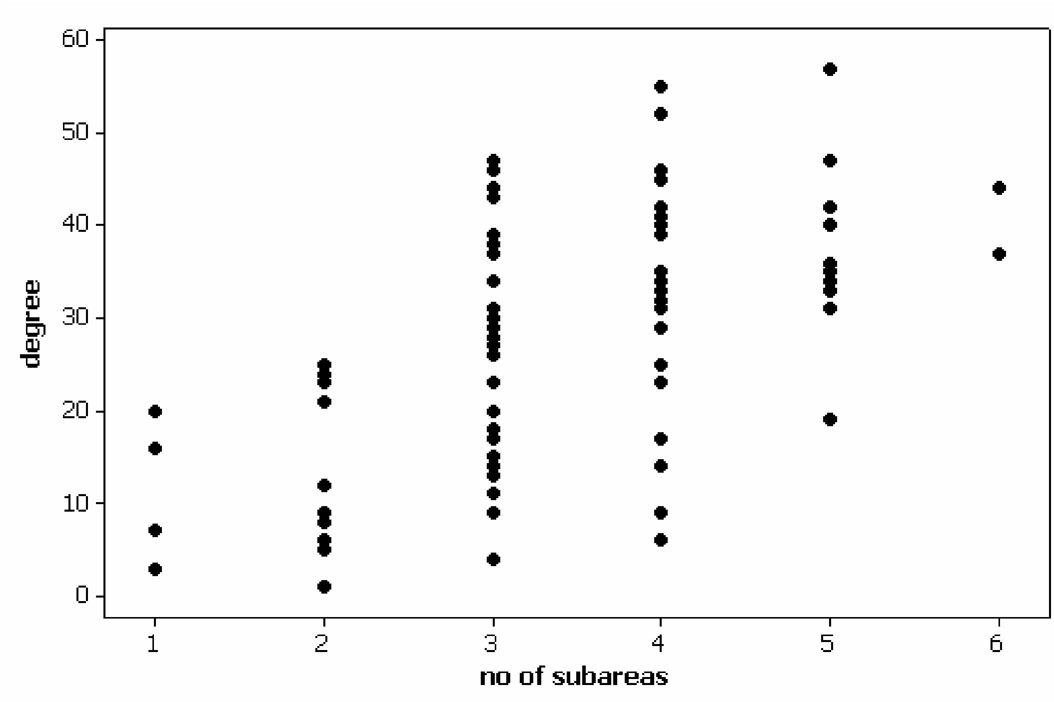


Fig. 4.12 Correlation between the number of subareas that a dolphin visits and the degree of an individual in the social network

MCP's were calculated for the five components in the pooled data network (Fig. 4.13). Not surprisingly, the most numerous component C5 had the largest range within study area, however, components C2 and C3 also ranged from Mwnt to the north of Cardigan Bay. Component C1 was mostly localized in Ynys Lochtyn and New Quay subareas, whereas C4 in the North. The kernel method produced centers of activity for each component. More than 50% of C1 sightings were recorded in Ynys Lochtyn, and C4 was mostly encountered in the North. The activity of these two components had tendency to be concentrated in the smallest area comparing to the other ones. C2, C3, and C5 all shared New Quay subarea as the center of activity. However, C2 had the same probability to be encountered in the North.

The known range of two dolphins #13 and #2 with the highest betweenness in the social network covered all subareas within the study area, the main activity centers being in Ynys Lochtyn and New Quay.

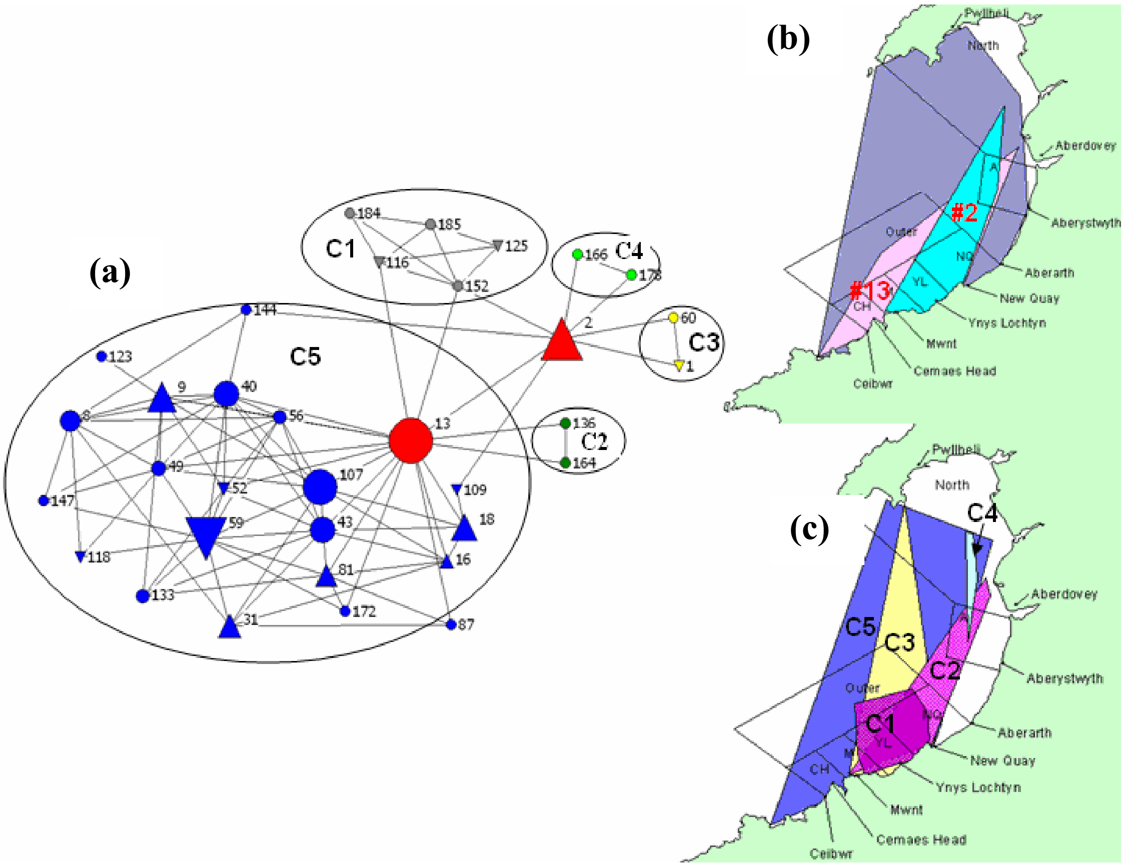


Fig. 4.13. (a) – the division of the pooled data network into five components (C1,C2,C3,C4,C5) after removing individuals with the highest betweenness; (b) – known ranges of dolphins with the highest betweenness in the social network; (c) – known ranges of all five components of the pooled data social network

Two components "Red" and "Black" in the social network 2006 (Fig. 4.9) had high number of individuals identified in 2006. Therefore the known ranges of these two components were calculated in order to look at the distribution within the study area as well as the area of encounters of new identified dolphins (Fig. 4.14). In both cases the known ranges extended from Mwnt to the North subarea. However, all new identified dolphins in the "Red" component were seen only in the northern subareas, while the range of the new dolphins in the "Black" component reached Mwnt in the south of the study area.

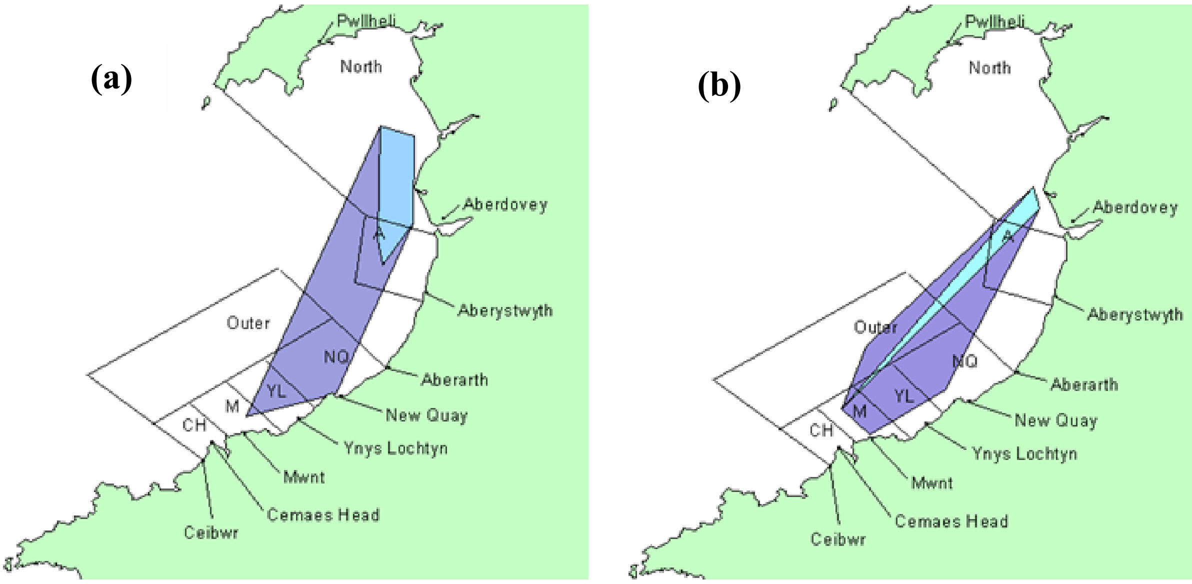


Fig. 4.14. (a) – known range of the "Red" component in the social network 2006 (Fig. 4.9), with lighter blue showing the range of sightings of dolphins identified in 2006; (b) – know range of the "Black" component in the social network 2006 (Fig. 4.9) with lighter blue range showing the distribution of new identified dolphins in 2006.

Thus, the results indicate that dolphins traveled over the large area from the south of the Cardigan Bay SAC to the most northern part of Cardigan Bay reaching the Pen Llyn a'r Sarnau cSAC. Moreover, increased studies in the north of Cardigan Bay resulted in a high number of new identified bottlenose dolphins.

4.3.3 Epidermal lesions in the social network 2006

Categories of epidermal skin markings were defined according to their visual characteristics (Wilson et al., 1997a). Eighty-two dolphins from the network 2006 were included in the analysis. One or more lesions have been observed on the skin of 61% individuals. The most prevalent ones were found to be black-fringe spots (BFS). Summarized results are shown in Table 4.4. Examples of each skin lesion types found in the present study are displayed in Fig. 4.15.

Table 4.4 Percentage prevalence of epidermal markings (lesions) in the network 2006, and its components. Sample size is given in parentheses.

	Network components				
Lesion type	Blue	Grey	Black	Red	Total per network 2006
Cloudy lesions (CL)	48 (10)	38 (3)	11 (1)	8 (1)	30 (15)
White patches (WP)	38 (8)	25 (2)	11 (1)	31 (4)	30 (15)
Black patches (BP)	24 (5)	0	22 (2)	8 (1)	18 (9)
Black-fringe spots (BFS)	19 (4)	38 (3)	67 (6)	69 (9)	44 (22)
White-fringe spots (WFS)	0	0	11 (1)	15 (2)	6 (3)
White fringe-fin (WFF)	0	13 (1)	0	0	2 (1)
Total	66 (21)	57 (8)	60 (9)	62 (13)	61 (50)

All components in the network 2006 had more than 50% of the individuals with epidermal markings. The "Blue" group had the most animals with one or more types of markings (66%), while the "Grey" group had the least (57%). The "Blue" group also contained the highest concentration of animals with cloudy lesions (CL). 66% of total CL type lesions were present in that group. Similarly, 69% of total BFS were present in group "Red".

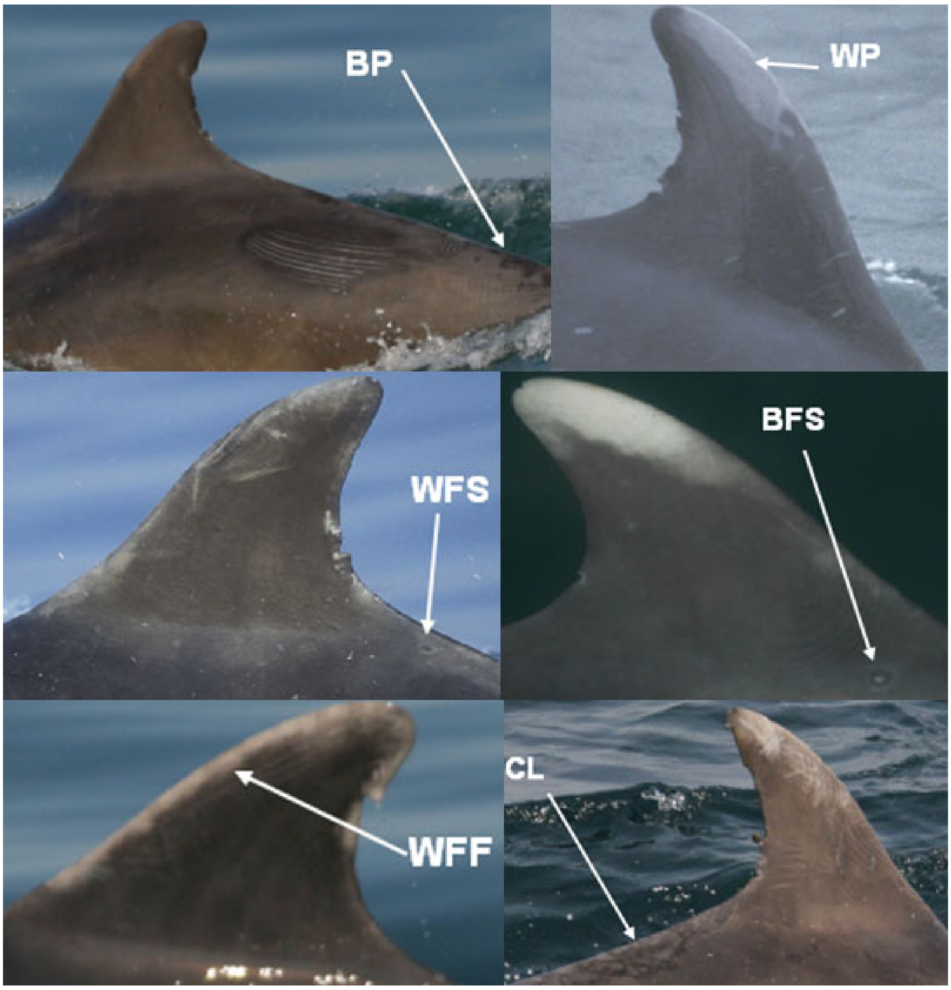


Fig. 4.15. Epidermal markings (lesions) in bottlenose dolphins in Cardigan Bay, Wales. Categorized as in Wilson et al. (1997a), with local adjustments of cloudy lesion category (see Materials and Methods). BP- black patches (dolphin #006), WP- White patches (dolphin # 017) WFS- white-fringe spots (dolphin #074), BFS- black-fringe spots (dolphin #032) CL- cloudy lesions (dolphin #40), WFF- white fin-fringe (dolphin # 014) Photographs by courtesy of the Sea Watch Foundation.

Chi-squared test was employed in order to assess whether observed frequencies conform to a standard distribution. The results were found to be significant for all components ($p < 0.01$) except the “Grey” ($\chi^2 = 12.533$, df = 6, $p = 0.051$) meaning that the distribution of epidermal lesions was not occurring at random. Prevalence of epidermal lesions in the groups “Blue” and “Red” are displayed in Fig. 4.16.

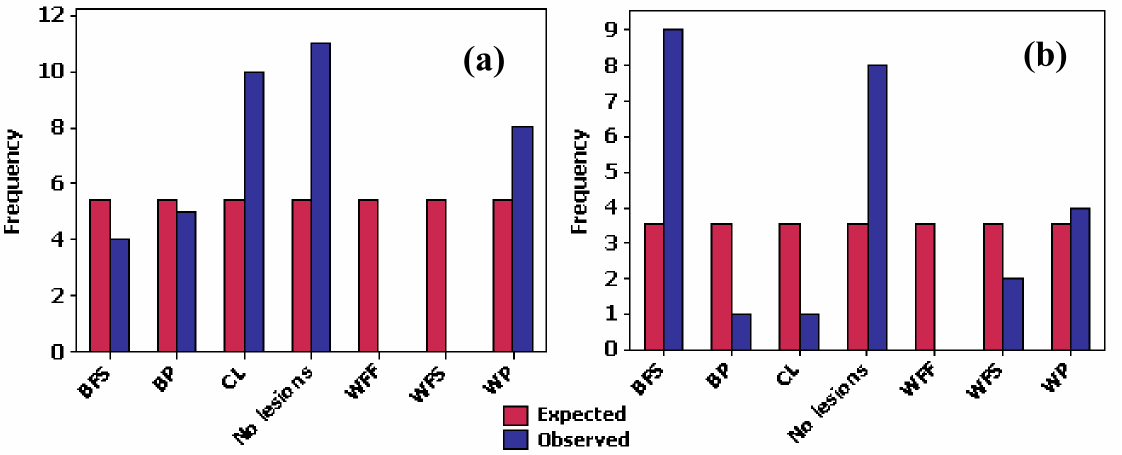
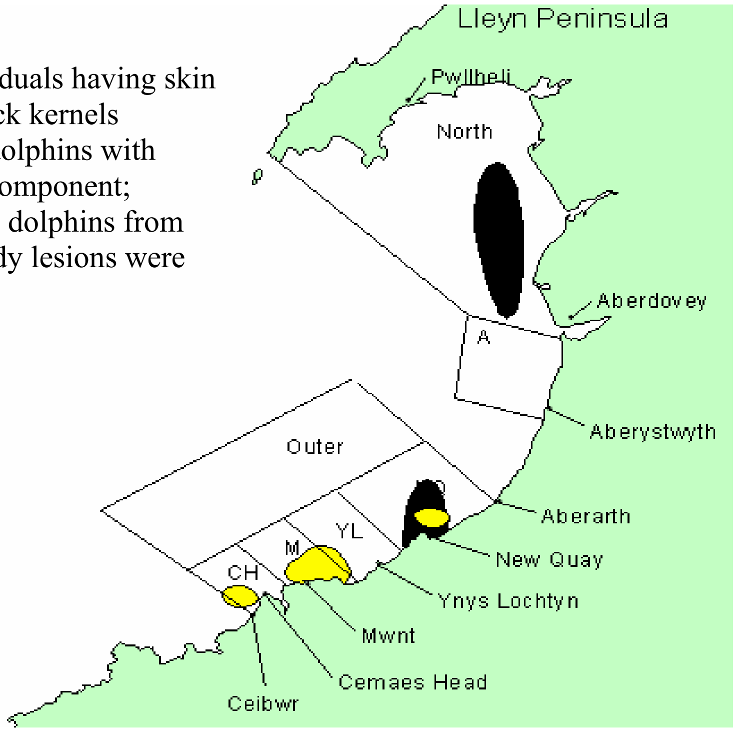


Fig. 4.16 Frequencies of prevalence of different lesion categories plotted against expected frequencies in the components "Blue" (a), and "Red" (b) in the network 2006. BFS-black-fringe spots, BP-black patches, CL- cloudy lesions, WFF – white fin-fringe, WFS- white-fringe spots, WP- white patches.

High prevalence of cloudy lesions and black-fringe spots in the two components led us to examine the distribution of dolphins affected by these lesions. The results are illustrated in Fig. 4.17. Dolphins having BFS were mostly encountered in the North subarea, while dolphins from the "Blue" component with the prevalence of CL had centers of activities in Cemaes Head and Mwnt. In the New Quay subarea there was observed an overlap in area utilization.

Fig. 4.17. Distribution of individuals having skin lesions in the network 2006. Black kernels represent centers of activity for dolphins with black-fringe spots in the "Red" component; yellow kernels show areas where dolphins from the "Blue" component with cloudy lesions were most often encountered.



5. Discussion

5.1 Social networks

The social structure of the bottlenose dolphins in the study area in Cardigan Bay was explored using network analytical techniques. It was found that the pooled data network 2001-2006 is composed of a single component with all the individuals connected to all others in the population. The general linkage among all individuals expressed as network density showed that this network was “moderately knit”, having 60% of all possible ties present. A mean degree, k = 27.48, indicated that individuals are directly connected to 31% of the network. Furthermore, standard properties, such as the shortest path length and clustering coefficient of dolphin social network were in substantial agreement with a “small world” network features (Watts and Strogatz, 1998). The average path length was similarly short as in random networks, whereas the clustering coefficient was much higher, likewise in the bottlenose dolphin networks constructed for the communities in the Moray Firth, Scotland and Doubtful Sound, New Zealand (Lusseau, 2003a, 2003b; Lusseau et al., 2006). It is hypothesized by some researchers such as Barabasi and Bonabeau (2003) that the prevalence of small world networks in biological systems may reflect an evolutionary advantage of such pattern. One possibility is that small-world networks are more robust to perturbations than other network structures. At the same time the information may travel very quickly in the network.

In addition to the pooled data network, annual networks were constructed in order to investigate the variations, and dynamics of associations in this community. After reviewing cautionary remarks about the potential problems in comparing social networks (Faust and Skvoratcz, 2002; Scott, 2000), there was decided that the comparison among the annual networks in the present study was possible because the networks did not significantly differ in size, were composed of individuals from the same population, and exhibited similar structural tendencies.

Thus, the annual density calculations showed that the network 2006 was sparsely knit having only 15% of all possible ties which is more than two times less than in previous years. Wellman (1979) discovered that in human societies the densest networks with ρ ranging from 0.76 to 1.0 tended to be those mainly composed of kin. A fission-fusion grouping pattern which predominates in this species as well as changing ecological factors might partially explain lower densities. On the other hand, the following analysis of the other network properties might further elucidate this feature.

The variability of the average shortest path length showed the difference of efficient connectivity between any two members in this community. It is an important element in network analysis because it gives an indication of how quickly, for example, ideas or resources can be diffused through the network (Scott, 2000). In addition, the multiplicity of short paths from one individual to another, as in the pooled data network which is dominated by the 1 to 2 path lengths, may suggest that the information flow is not likely to break down because many dolphins have alternative ways to communicate. In networks 2003-2005 any two individuals could be connected through approximately two others which would be similar to the Moray Firth bottlenose dolphin community (Lusseau et al., 2006), but network 2006 differs in this context showing higher average path length value of 3.36 (Table 4.3) which coincides with the Doubtful Sound community in New Zealand (Lusseau, 2003a). However, it is necessary to mention that some interstudy comparisons should be taken with caution because Lusseau (2003a) used permutation technique in a network construction, while Moray Firth dolphin associations were analyzed using HWI cut-off techniques as in the present study.

Progressing further we investigated the clustering measure of the networks. In assessing the degree of clustering the suggestion by Hanneman and Riddle (2005) was considered, and the clustering coefficient was compared to the overall density of a network. Thus, in the pooled data network the density of the local neighborhood, i.e. clustering, C, was very close in value to the overall network density indicating more or less evenly interconnected individuals, unlike in the network 2005, and especially in the network 2006. High difference in between clustering coefficient ($C = 0.753$) and overall density ($\rho = 0.15$) in 2006, according to Hanneman and Riddle (2005), shows strong subdivisions within the network. The advantage of highly clustered networks is that, for example, it may prevent the disease spreading through so much of the population due to the breakage into several components, but at the same time it lowers the threshold of spreading within that subdivision (Newman, 2002b).

Proceeding from the density of local neighbourhood to the size of individual's neigbourhood, the degree of each vertex in the network has shown how well it is connected to the local environment. The average degree in the pooled data network (k = 27.48) was considerably higher comparing to annual variations. Dolphin #13 was encountered in the company of 57 other individuals over the 5-yr period, and dolphin #7 was observed to have 36 different companions within one season. Study by Lott (2004) on bottlenose dolphin associations in the Cardigan Bay SAC found 33 as the maximum number of associates in this population. Some results from the other sites might be more striking. In the study of Weller (1991) from San Diego, California the most sighted bottlenose dolphin was seen with 259 different affiliates over the 6-yr period while range of associates in Sarasota Bay, Florida varied from 21 to 91 (Wells et al., 1987). The lowest number of average associates in our study was found in 2006 with 6.91 per individual. As pointed out by Brager et al. (1994) such variations could be explained by the difference in population size, availability of potential associates or the extent of population range. In comparing annual differences of the degree of individuals in the present study the hypothesis by Tyack (1986) could be considered as an appropriate explanation. It says that dolphins do not regularly associate with the same individuals because they recognize and remember each other as affiliates over long periods of time. Consequently, he related individual recognition as a prerequisite for reciprocal altruism which, according to Brager et al., (1994), facilitates relations in social groups especially the ones with high association fluidity. It follows thence that this feature allows efficiently aggregate the appropriate number of dolphins for different activities such as travel, feeding, and socializing (Whitehead and Mann, 1999).

Looking from the individual-centered position the degree could be an important factor in spreading novelties in the community. If one individual produces a new foraging technique, for example Shark Bay sponge carrying dolphin (Smolker et al., 1997; Weiss, 2006), thus, a high degree and therefore more central position may facilitate the introduction of this feature into the entire population. However, there is another side. If the network is highly clustered, as in the present study network 2006, the spread of the innovation might be restricted within the component of the network where it has originated. The same thoughts were expressed in the works by Byrne (2000) and Krause et al. (2002). They related individuals with a high degree to the archetypical symbolic representations of leaders. These members of the community would have a good knowledge of individuals within their component but would be poorly acquainted with the ones outside it, and might be unreliable source in making decisions on how to avoid resource competition between the groups.

The network perspective suggests that the influence of individual vertex depends on its relations with others (Hanneman and Riddle, 2005). Even though the distribution of power of structural positions remains the most complex and difficult to interpret aspect even in human societies, herewith it is interesting to further an investigation into two basic sources of advantageous position in the network - high degree and high betweenness. Sometimes these two measures correlate, i.e. an individual having high degree of connections might be an important player in the overall network connection. However there are possibilities of disjuncture between these two characteristics. Individuals with a high betweenness usually are found on the boundaries between the subdivisions (components) in the network, and might be influential over the flow of information between the others (Freeman, 1979). Thus, our pooled data network showed that dolphins #13 and #2 had the highest betweenness values. Interestingly, dolphin #13 was the one with the most connections, while dolphin #2 with 33 companions over the 5-yr period was close to an average degree in the network.

Apart from this, annual variations were also present. In the networks 2005/2006 dolphin with the highest betweenness was #13, and dolphin #2 was in the top five with the highest betweenness but their degree values did not show the same tendency. Lusseau (2006) suggested that individuals with high betweenness should have more diverse affiliations within the social network, and could be more knowledgeable about the circumstances and potential competitors because they were more exposed to them. Thus, it would be more advantageous for the entire group to follow such individuals to the contrary of the ones with the highest degree within the local component.

Betweenness being a reflection of a level of centrality of an individual in the network can also be utilized in detecting natural divisions in that network (Girvan and

Newman, 2002). If the network contains components that are loosely connected by a few edges; removing these edges that are the most "between" the components may reveal underlying community structure (Newman and Girvan, 2004).

As a result Fig. 4.6 illustrates the 5-yr pooled data network division into five components ranging in size from 2 to 21. The two dolphins # 13 and #2 having highest betweenness connected all components into one. The satisfactory division quality of the structure was achieved after removing 64% of the individuals with the highest bewteenness from the initial network (Fig. 4.3). These results supported the suggestion expressed by analyzing density and clustering. These measures did not indicate strong divisions within this network, and little likelihood of finding powerful "brokers" in this structure. On the other hand, continues position of dolphin #13 with a high centrality through years deserves more attention, and could be suggested to investigate this dolphin's ego-network dynamics in future studies.

Annual networks were more diverse. Comparatively high value of Q = 0.607 was produced by the algorithm for the network 2006 with all the vertices present, and revealed several dolphins with high betweenness. The removal of these individuals would break up the network into isolated components. For example, removal of dolphin # 164 would result in the disruption of direct contacts between components "Red" and "Black"; dolphin # 142 appeared to be important in connecting "Red" and "Grey", while dolphin #29 operated as a link between components "Red" and "Blue" (Fig. 4.9). Only long term studies or experiments in the natural conditions could provide prove that these models work in the real world. The following example from the Doubtful Sound bottlenose dolphin community (Lusseau and Newman, 2004), however, may provide some practical evidence. The temporal disappearance of individual with the highest betweenness during their study restricted interactions between the two communities in that population, and became more common after that dolphin reappeared. These findings suggested that these "brokers" or key individuals may play a significant role in maintaining the cohesion of that dolphin community. Furthermore, in the present study the difference in the size of components within annual networks or pooled data network could be related to the subtle social strategies that individuals employ in maintaining the cohesion of the group as was observed in bonnet macaques. The extended social networks of these primates were explained by difference in social time distributed among the members of group (Kudo and Dunbar, 2001). On the other hand, varying ecological factors together with social costs and benefits may play an influential role in determining social unit size in a fission-fusion society. Dunbar (1992) suggested that such societies minimize the size of the main component by splitting during periods of higher competition, and they resume the cohesion when the costs of aggregating are low or benefits of sociality are high (van Schaik, 1999). As was documented by Moss and Poole (1983), elephants may find greater social benefits from larger aggregations during breeding season in attracting mates. Alternatively, intragroup information exchange, hypothesized by Foley et al. (2001) as a function to form larger components, may also serve as a factor influencing the size of social units. Wittermyer et al. (2005) considered possibility that social formations could be an epiphenomenon, occurring as a result of a need to socially interact rather than based on socially derived benefits.

In the present study the ecological conditions in different years were not included in the analysis. However it would be interesting to investigate the potential link between the environmental factors and the level of clustering and cohesion in the networks of the bottlenose dolphin society in Cardigan Bay.

Newman (2002a) pointed out that one of the mechanisms for the formation of communities within a society is homophily, or assortative mixing, i.e. individuals associate with others who are like them in some way. For example, study by Lusseau and Newman (2004) have found significant assortative mixing by sex among the dolphin population in the Doubtful Sound, New Zealand while mixing based on age was considerably lower. The present study also looked at the potential assortativity by sex; however, the coefficient values were very low, and in two cases (pooled data network and network 2005) negative (Table 4.3). These results partially could be explained by the lack of information on the sex of majority of dolphins in this population. On the other hand Lusseau et al. (2003b) proposed the hypothesis of food acquisition and not mating strategies as a driving force for the social organization. This theory could explain mixed sex associations as a facilitating factor in information exchange in maximizing overall fitness of population.

Our findings seem to accord with the study results on the same population by Lott (2004), and Moray Firth bottlenose dolphin population (Wilson et al., 1993) with no evidence of strong female or male bonds that are the feature of Sarasota Bay population, where up to four generations of kin associate in the same sex groups (Wells et al., 1987). Nevertheless, Lott (2004) found a strong bond between the two males #73 and # 74. These two dolphins together with #109 formed one of the components in the network 2003 in the present study. Even though in general the results did not show significant assortativity by sex certain tendencies towards that could be observed. For example, largest component in the network 2003 (n = 11) consisted of seven males, one female and three dolphins of unknown sex. Male alliances are known to be a feature of Shark Bay, Western Australia bottlenose dolphin population, and on a major part related to the mating strategies in that community. According to Connor et al. (2001) bottlenose dolphins comprise the only species outside humans where males form two levels of nested alliances within a social group to obtain access to females. First order alliance, comprised of males in pairs and trios cooperate to form consortships with individual females. Teams of trios or pairs form second order alliances (up to 14 individuals), and attack other alliances in contests over females or defend against such attacks (Connor, 2000).

However, the opposite tactics was also observed. Single adult males in Sarasota Bay, Florida, Moray Firth, Scotland and juvenile males in Shark Bay, Australia without alliance partners obtained paternity (Krutzen et al., 2004). This tactics was found to be in parallel with so called “friendship” in savanna bonobos (*Papio anubis*) (Smuts and Smuts, 1993) Single male dolphins were observed spending much more time with females than male pairs. It is possible that mixed sex associations, which are likely to be a feature of the networks in the present study, represent more equal involvement in reproductive strategies by both sexes. Thus, it is not clear which tactics is more successful. As Connor et al. (2000) points out, long term studies in different habitats should provide an opportunity to look at mating strategies variability in relation to ecological influences.

The strength and stability of the female group is likely to be centered on socio-ecological benefits in areas such as calf protection from predators or conspecifics, food acquisition and social support. The opinion, that a calf protection may be the key function for the stable groups of females, and the fact that the timing of associations could be critical, was pointed out by Whitehead and Mann (1999). The study by Gero et al. (2005) suggested that mature females and their depended calves tended to group together with other mother/calf pairs forming a network of relationships. According to Connor et al. (2001) the associations of animals with similar requirements for food and defense are beneficial. At the same time it may lead to the synchrony of estrus as was observed in humpback and sperm whales (Best and Butterwork, 1980), but this process is not well understood. However if the reproductive status changes (e.g. female looses her calf) it might be more efficient to join non-calf groups in order to avoid competitive costs in food accessibility. As was observed by Mann and Sargeant (2003) females often associated with individuals who do not share their foraging tactics.

In the present study the network 2004 contained one component (n = 5) composed of four females and one dolphin of unknown sex. Individual details of these dolphins revealed that female #4 was first identified in 1991, while the rest of the group in 2001-2004. Female #17 was observed with a calf in 2003 and female #19 in 2006. Due to the fact that this study is limited to examining surface social structure of this population one could only speculate about the social roles within that group of females. Knowing genetic relatedness of individuals together with detailed investigation of calving history would provide more discussable information. Thus, certain findings in this study may suggest a broader research into the grouping pattern in this population.

Assorative mixing by degree, i.e. the number of associates individuals have was also investigated in the present study. This type of mixing is often observed in human societies where gregarious individuals tend to associate among themselves than with more solitary individuals (Newman, 2002a). Dolphin networks in this study also showed such bias. The mechanisms that initiate such mixing are thought to come from the triadic interactions where individuals are more likely to interact with friends of the friends (Davidsen et al., 2002), and from preferential attachment among more gregarious or more solitary individuals (Barabasi and Albert, 1999).

Overall assortativity calculated for the 5-yr pooled data network showed some degree of homophily (r_d = 0.138, Table 4.3). The result is similar to the Moray Firth bottlenose dolphin community (Lusseau et al., 2006). The strongest assortativity was observed in the network 2005 (r_d = 0.305), however, other annual variations produced even negative values similar to the Doubtful Sound, New Zealand bottlenose dolphin community. Thus, it appears that even though mechanisms that drive homophily might be the same as in human societies (Newman, 2003b), bottlenose dolphins can remarkably vary in the degree of assortative mixing.

Directing our attention to the function of assortativity, Brede and Sinha (2005) argued that assortative mixing by degree reduces the stability of a network, especially if a network is sparse. Similar view was expressed by Newman (2002a) saying that the core group of assortatively mixed network could sustain an epidemic even if the network is not sufficiently dense as was pointed out by the before-mentioned author. However, it is also recognized that the disease would probably be restricted to a smaller component of the population than in the case of neutral or disassortative network. Another feature of assortativity refers to the resilience of a network to removal of individuals with the highest degree which could lead to the destruction of the overall connectivity (Pastor-Satorras et al., 2002). If vertices with a high degree tend to cluster together they produce the redundancy of paths for the spread of information or disease. Thus, in the latter case, the network properties should be considered before applying any management actions.

Social network approach applied in analyzing social structure of bottlenose dolphins in the study area in Cardigan Bay gave an indication of how socially fragmented the population is. Differences found in annual networks could be a starting point in analyzing dynamic processes underlying observed association patterns for future studies.

5.2 Known ranges

Knowledge of the habitat use and population range is essential for the successful conservation actions of bottlenose dolphin population in the Cardigan Bay. An increased effort in the north of Cardigan Bay indicated that the SAC does not represent the whole of this population’s range. Bottlenose dolphins were encountered through study area but there not equally distributed within the Bay. Specific patterns of terrestrial mammal distribution have been linked to the heterogeneity of their habitat (Samuel et al., 1985). Habitat quality also affects animal home range (Balance, 1992). Some patches may support larger concentrations of food others may be barren. According to Wursig (1978) and Wilson et al. (1997b) coastal bottlenose dolphins tend to aggregate around entrances to estuaries, lagoons and bays, often concentrating on areas with fast tidal currents. It appears that the major centers of activity in this study were Mwnt, Ynys Lochtyn and New Quay subareas, and in this respect represented typical bottlenose dolphin habitats, especially the Mwnt subarea which could be described as a small embayment close to the Teifi estuary. Some studies relate habitat preferences to the foraging specializations (Smolker et al., 1992; Mellink et al., 2006); others say that high abundance of potential prey that certain systems support rather than specializations condition dolphin distribution (Watson 2005). Defran et al. (1999) found evidence that supported their hypothesis on the range characteristics and fluctuations in prey variability.

However, bottlenose dolphins live in an extended network of associates with the rate of change in group composition up to several times a day (Smolker et al., 1992; Connor et al., 2000). Based on the maps showing all the calculated known ranges in the present study, the results indicate that all components in the pooled data network shared their ranges (Fig. 4.13). It coincides with the observation by Ingram et al., (2002) that extensive overlap could be expected in a fission-fusion social system. The size and amount of an overlap may determine the level of interactions among the groups. The examination of MCPs showed that subareas where known ranges of four groups overlap were Ynys Lochtyn and New Quay. Perhaps some embayments in these areas were more productive compared to the others, which allowed several groups to coinhabit that area for a certain period (Lusseau et al., 2006), and at the same time served as the "socializing grounds" by facilitating the aggregations of individuals, especially during mating season.

The density of animals in the area may also affect the size of an individual or group home range, particularly if there is competition over resources. Thus, as could be seen from Fig. 4.13 the known range of the three components in the pooled data network extended from the Cardigan Bay SAC to the northern subareas. Generally in bottlenose dolphins, males have larger home ranges than females indicating male-mediated gene flow, and increased mating opportunities by dispersal over the larger area (Smolker et al., 1992; Wells et al., 1987). In addition, some researches suggest that females with calves have more extended ranges than females without calves in order to fulfill their energetic requirements during lactation (Wells et al., 1980; Gubbins, 2002). On the other hand the presence of a calf may restrict the distance mother can travel (Cheal et al., 1991). In the present study female #51 had one of the smallest known ranges in the network, and was mostly seen in the Mwnt subarea. Through years 2003 to 2006 she was accompanied by at least two different calves. The matrilineal transition of foraging strategies was recorded among sponge carrying Indian Ocean bottlenose dolphins in Shark Bay, Australia (Krutzen et al., 2005). Male #55 was traveling from the south of the SAC to the north of the Bay covering range of about 83 km. Male #53 had five centers of activity, and an equal probability to be encountered in all the Cardigan Bay SAC. Sexual differences in range of movements were suggested by Bearzi et al. (1997) with females covering smaller areas than males. Limiting factor of our study was high percentage of individuals with unknown sex which restricted the extent to which findings could be generalized. For example, component C3 in the pooled data network consisting of one male and one individual of unknown sex covered extensive range from Mwnt to the North subarea, but at the same time members of the component C1 (2 males and 3 unknown sex) their activities concentrated in the inner SAC (Ynys Lochtyn and New Quay) (Fig. 4.13). On the other hand male #2 – one of two individuals with the highest betweenness - was encountered from Mwnt to the North of Cardigan Bay (Fig. 4.13). He had an overlap with and extensive range of dolphin #13 with the highest bewteenness and the highest degree in the pooled data network. These findings led to us to the hypothesis of the potential link between the degree, i.e. number of associates each dolphin had, and the number of subareas the range covered. Positive correlation between these two variables illustrated in the Fig. 4.12 indicates that there was a tendency for more gregarious individuals to explore larger areas, or vice versa the gregariousness could have been the outcome of a more extensive dispersal.

In the network 2006 out of 24 new identified dolphins included in the analysis 19 (79%) were found in two components. Thus, considering more effort in the north of the Bay this year, it was anticipated that the majority of these dolphins would be distributed in the Aberystwyth - North subareas. The result seemed to be consistent with our initial hypothesis. As can be seen from Fig. 4.14 all new individuals (57% of the component) in the “Red” component were found only in the northern subareas. Several new dolphins from the “Black” group were encountered in Mwnt, however the majority of sightings were also recorded in the north.

These findings may be of considerable importance since they suggest that the Cardigan Bay SAC being an important habitat for bottlenose dolphins does not include full geographic range of this population. Defran et al. (1999) pointed out to the problem when the range of individuals exceeds the limits of the respective study area. These limitations may mask real movement patterns of dolphins in particular area. By continuing studies in the north as well as extending the range of future surveys to the south of Cardigan Bay may improve our knowledge about dolphin movements in this area, and contribute to the conservation needs of this population. In addition, detailed survey of prey distribution and habitat analysis would be important in correlating ecology and sociality (Rogers, 2004).

5.3 Epidermal lesions

The occurrence of natural, non-lethal diseases that may happen during the lives of wild bottlenose dolphins, and their link to the behaviour and ecology of these animals remains poorly known (Wilson et al., 2000). Epidermal disease in cetaceans is well documented but most of the findings come from studies in captivity or from dead individuals (Geraci, 1989; Baker, 1992). The population of bottlenose dolphins in Cardigan Bay is small, thus it is important to investigate all potential threats, and to establish whether or not there is a cause for concern. This study took the preliminary step towards understanding of the skin lesion prevalence in this population as well as the potentials causes of their occurrence.

Social network analysis has already been applied to the transmission of HIV and syphilis in human populations (Rothemberg et al., 1995; Bell et al., 1999), and *Mycobacterium bovis* in captive possums (Corner et al., 2003). Network centrality measures were examined to identify individuals pivotal in the spread of disease. Cross et al. (2004) in the study on the disease dynamics in African buffalos suggested that increased susceptibility to disease is one of the costs of sociality. Recent studies indicate that network structure, dynamics and topology of individuals plays an important role in determining the probability of disease invasion, number of infected individuals, and the speed of disease spread, especially if the infectious period is short (Keeling, 1999; Newman, 2002b). Associations data similar to those presented here are often collected by researchers (Smolker et al., 1992; Whitehead, 1999) but have not been combined with the disease models.

This study categorized the most evident epidermal markings (lesions), and examined their prevalence in the network 2006. In this case dynamic network models (e.g. annual networks) may more accurately reflect connections within and between groups than associations based on data from a longer time frame that can be biased in favour of too many connections as in our pooled data network. One or more lesion types have been found on the skin of the 61% of individuals in the network 2006. In comparison, study on ten populations of bottlenose dolphins around the world found 63% to 100% of animals being affected (Wilson et al., 1999). More than 50% of each component in the network 2006 consisted of individuals possessing different lesion types, and non random frequencies of occurrence were observed. Among all four components two, “Blue” and “Red”, had significantly higher prevalence of cloudy lesions (CL) and black-fringe spots (BFS) (Table 4.4). Circular marks such as BFS have been attributed to parasites and infections e.g. pox virus (Greenwood et al., 1974), or temperature variations and immunosuppressive pollutants (Haebler et al., 1993).

Interestingly, there was also found different distribution of individuals having these two types of cutaneous abnormalities in the study area. Dolphins with CL from the “Blue” component concentrated their activities near the southern borders of the Cardigan Bay SAC close to the Teifi estuary while majority of dolphins with BFS were encountered in the North subarea (Fig. 4.17) Thus, examining these patterns from the network perspective it could be hypothesized that relations of individuals within the group, and potentially limited movements between the components, as well as the difference in local distribution, and exposure to the same environmental conditions may have influenced prevalence of particular lesion type. In addition, more central individuals in the network are likely to be at a greater risk of a disease (Christley et al., 2005). At the same time they might be responsible for the faster spread of the disease within the component or whole network, if they are positioned at the boundaries between the network divisions. For example, in the “Blue” component network 2006 (Fig. 4.9), individuals # 65 and #63 with CL are found at the periphery, and should be experiencing lower chance of infection, however they are directly connected to dolphin #3 with CL and a high degree, who is connected to dolphin #25 one of the most central individuals in this component. The latter individual may facilitate the spread of disease within the component due to the high inside centrality but this individual does not have direct connections outside the group. Exploring further there could also be noticed that dolphins #75, #76, and #29 who may serve as the "brokers" with other components did not possess these lesions types, thus it could be expected that the occurrence of this feature might be restricted within this component.

White patches were another of more prevalent lesion types in the network. Thompson et al. (1992) described them as depigmentation marks; however the direct cause is unclear. Case worth attention is related to the two members of the "Red" component in the network 2006. Dolphins #32 and # 33 with white depigmentation marks on the tip of the dorsal fin were sighted in the group with the other two adults (#011-06R and #085-05R) with the similar white patches (Fig. 5.1). The latter ones were not included in the network analysis due to the restrictions of the present study. Dolphin #33 was accompanied by a calf whose skin disruptions on the tip of the dorsal fin also showed tendency towards the white patchiness. Lack of data on kin relatedness of individuals allows only to hypothesize that such a similarity could have had genetic roots or exposure to similar environmental conditions resulted in similar susceptibility to certain agents.

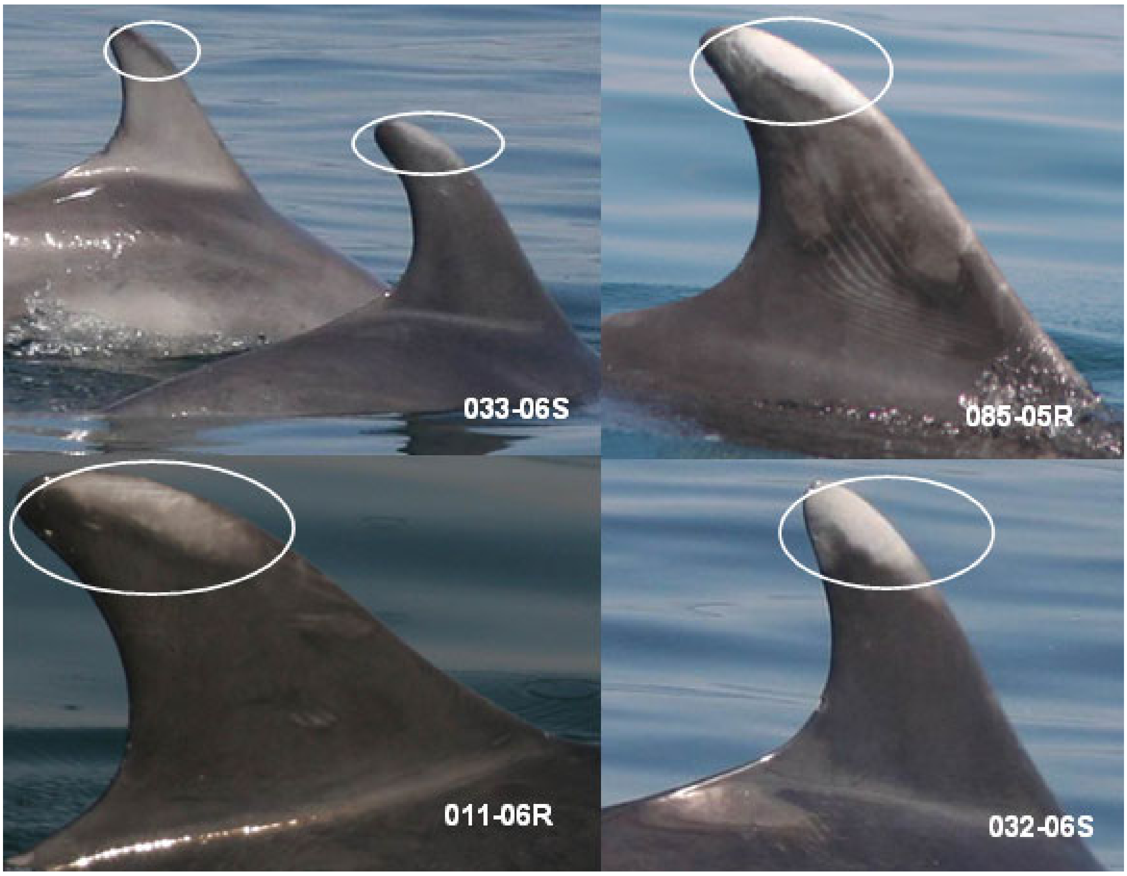


Fig. 5.1 Group encountered in July 2006 with a similar pattern of depigmentation markings. Dolphin 033-06S was accompanied by a calf (on the left) showing tendency towards development of similar depigmentation pattern on the tip of the dorsal fin. Photographs by courtesy of E. Magileviciute.

Dark lesions (black patches in the present study) were observed on many animals in the Moray Firth bottlenose dolphin community (Wilson et al., 1997a). Thompson et al. (1992) found their appearance to be similar to the skin disorders as result of subcutaneous candidiasis, described for captive cetaceans (Dunn et al., 1977). The correlation between the prevalence of pale lesions (cloudy lesions and white patches in the present study) and dark lesions (black patches in this study) was reported by Wilson et al. (1999). Studies on the development of dark and pale lesions (Wilson et al., 2000) suggested that dark lesions could be precursors of pale lesions. However, several cases observed in the bottlenose dolphins in Cardigan Bay seemed to contradict to these indications. For example, dolphin

#82 was observed with the white patches on the tailstock in 2003, but three years later this area was covered by the black patches (Fig. 5.2). Similar transition in lesion appearance has been observed in dolphin #115.

The lack of yearly photographs of an equal exposure of the same body parts for each individual induced limitation with regard to the generalization of the results. On the other hand it pointed to the need of more detailed investigation on the skin lesion evolution in this population, and in general.

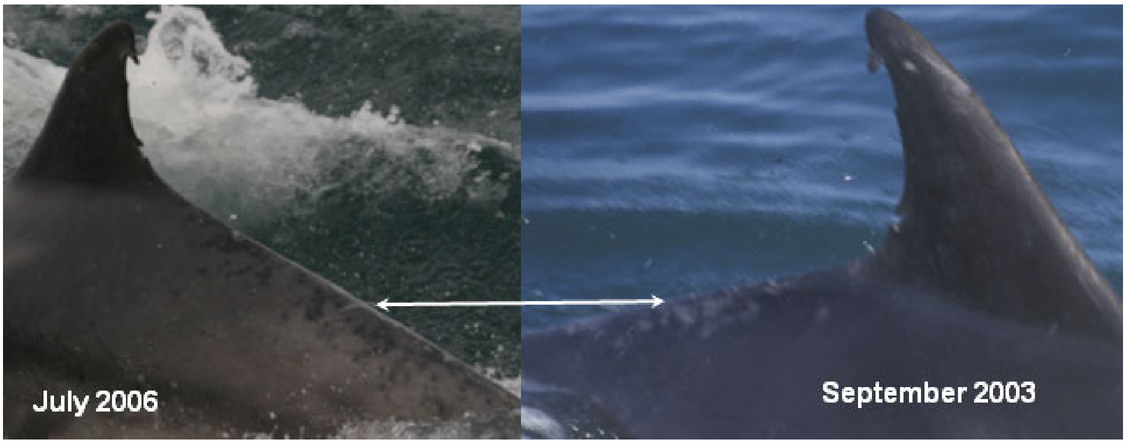


Fig. 5.2 Photographs of a dolphin #82 showing the transition in skin lesion appearance from white patches in 2003 to black patches in 2006. Photographs by courtesy of the Sea Watch Foundation.

This study did not calculate statistics in relation to the age or sex of individuals with skin disorders but the work of van Bressen et al. (2003) drew attention to the fact that the more extensive presence of skin lesions in young dolphins could be related to the loss of their passive immunity against the infectious agents together with a higher risk of close contacts with infected members of a group. Calves were found to be one of the most affected groups in the study of Wilson et al. (1997a) in the Moray Firth bottlenose dolphin population. Quite a few calves and juveniles encountered during our data collection in 2006 showed high severity of different types of abnormal epidermal discolorations (Fig. 5.3). A lower prevalence in adult dolphins may be due to the development of immune response to the infective agents (van Bressen et al., 2003).

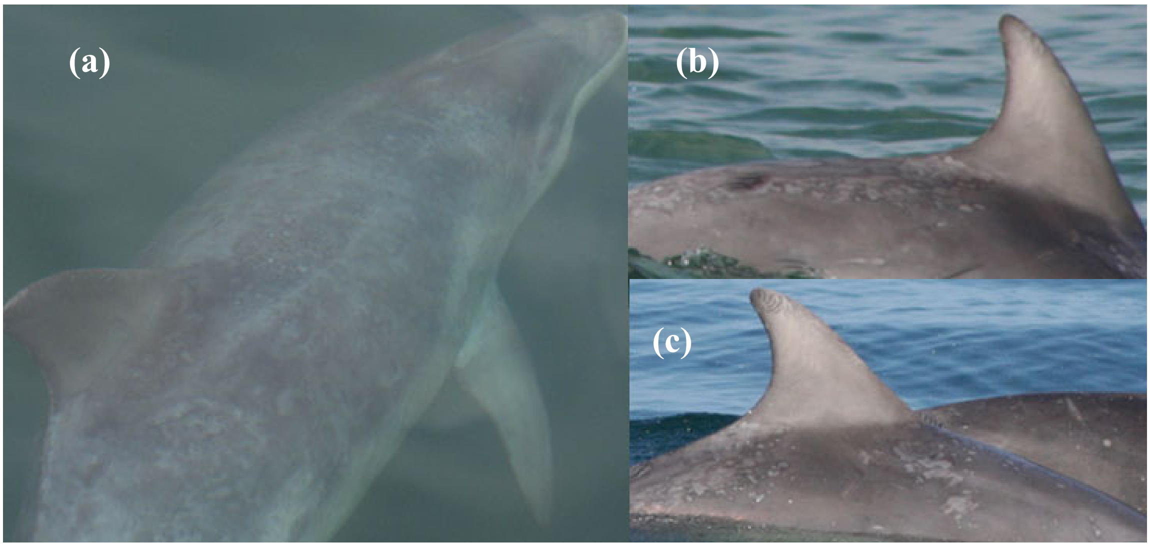


Fig. 5.3 Photographs demonstrating an extensive epidermal discolorations on the body of two unknown calves (a), (b) and a calf encountered in the company of a female #68 (c). Photographs by courtesy of E. Magileviciute

Furthermore, Wilson et al. (1997a) found that lesions on adult females and calves in the Moray Firth covered significantly greater areas of skin than on adult males. They related the difference in lesion severity to the fact that the females and calves accompany each other, and share same geographic range and social associates. In addition, higher level of philopatry reported for bottlenose dolphin females (Natoli et al., 2005) may result in prolonged exposure to the same conditions, and contribute to the higher severity of skin disorders. At the same time, if males have wider dispersal, and cover more diverse environments the effects of particular agents in certain areas might not be so serious.

Variety of factors have been identified as causing epidermal lesions in cetaceans: fungal and bacterial infections (Dierauf, 1990), vitamin deficiency (Wells, 1991), reaction to parasites, anthropogenic pollutants or electrolyte imbalance from the fresh water (Fraser and Mays, 1986). The fact that lesions are mostly observed on the dorsal surface of a dolphin body led Rowntree et al. (1994) to infer the possibility of sunlight effect on the viral infection. They suggested the possible immunosuppression due to the UVB radiation could be responsible. On the other hand, a study by Wilson et al. (1999) examined correlation of environmental and anthropogenic factors with a lesion prevalence and severity in ten bottlenose dolphin populations ranging from Sarasota bay in Florida to Doubtful Sound, New Zealand. They found linear relationship between the occurrence of lesions and low water temperature and low salinity in contrast to the initial hypothesis of the contaminants being the major cause.

In the Cardigan Bay any of these factors might be potential candidates. Both human and agricultural sewage enter the Bay as well as industrial effluent, and contribute to the chemical pollution (Grellier et al., 1995). Highly persistent toxic organochlorines and heavy metals can remain for decades in the environment after the release. Fresh water inputs from Teifi, Ina and Aeron riverine systems may reduce water salinity. Moreover, Harzen and Brunnick (1997) pointed out to the problematic nutrient enrichment, or eutrophication in many estuaries which may result in harmful algal blooms, and gradual deterioration of the habitat suitable for cetaceans.

To establish the contribution of human activities in the prevalence of skin diseases requires long term studies with the examination of contaminant levels especially in the areas most frequently visited by bottlenose dolphins.

It should be noted however, that combination of all the factors from disturbance induced stress to climatic changes may play a part in reducing immune system response which is probably of a greater threat in facilitating spread of disease and increased mortality. An example to illustrate comes from the spread and impact of Morbillivirus in striped dolphin population of the Mediterranean (Aquilar et al., 1994) and seals of the Dutch Waden Sea (Brouwer et al., 1989), which was possibly related to the immunosuppresion induced by polychlorinated biphenyl (PCB).

Whatever is the cause, these epidermal anomalies do not seem to be immediately fatal (Wilson et al., 2000). However, their impacts still remain unclear.

Results of this study may represent minimized estimates of the prevalence because not all individuals had equal body coverage examined. More research of the severity and prevalence in different age/sex groups, and the relation to environmental factors is needed in order to look at the long-term epidermal condition, lesion development, and individual survival in this population.

6. Conclusion

The bottlenose dolphin population in Cardigan Bay is relatively small and in size is similar to the Moray Firth and Shannon estuary populations. Based on the association evidence, and comparing our findings to the patterns observed in other bottlenose dolphin communities it is likely that this population could be regarded as a fission-fusion social system with a large number of bonds, and many redundant paths for the transfer of information.

Significantly frequent associations between individuals were used a basis for the social network construction. The bottlenose dolphin social network displayed features of a "small world" network. Recent developments in computer algorithms for the network analysis allowed to identify a number of divisions within the population. Pooled data social network (2001-2006) was characterized as a moderately dense with a high degree of connections. Variations in annual networks indicated dynamic organization within this population. Assortative mixing by degree was conjectured as one of the factors underlying the network divisions. Although this conclusion should be considered with caution as the sex, age and kin relatedness was still unknown for the majority of individuals in the Cardigan Bay bottlenose dolphin population. On the other hand, certain tendencies towards same sex groupings could have been observed in one of the annual networks. Different reproductive strategies between females and males, genetic relatedness, ecological constraints, dispersal or anthropogenic impacts as well as the interaction among all these factors have been described as having considerable influence on the different levels of sociality in cetacean species (Connor et al., 2000).

In the present study there was also observed the existence of potential "brokers" or key players with high centrality. These individuals were located on the boundaries between the components of the networks. In particular, the ego-network of the dolphin #13 with its high centrality in regards to the degree and betweenness over the years would be suggested for more detailed investigation in future studies. Reference to Lusseau and Newman (2004) highlighted the importance of such individuals in the society.

High frequency of sightings in several areas gave an indication of regions with particular significance to bottlenose dolphins in Cardigan Bay. Mwnt, Ynys Lochtyn and New Quay were defined as centers of activity for the majority of sampled population in the present study. Even though the Cardigan Bay SAC is an important habitat for this population some dolphins had much wider ranges reaching Llyn Peninsula in the north of the Bay. In 2006 the extended effort into the north from the Cardigan Bay SAC resulted in the identification of a relatively high number of new individuals. The majority of them were found in the two components within the network 2006, and encountered only in the northern subareas. These findings suggested that the Cardigan Bay SAC does not include a full geographic range of this population.

Epidermal skin abnormalities (lesions) in bottlenose dolphins were identified and categorized in the present study. The purpose was to collect baseline information on the prevalence of these markings in the Cardigan Bay population. Despite the relatively small quantity of photographs for more extent examination of the dolphin body surface the records were satisfactory. Skin lesions were investigated from the social network perspective. Non random distribution of different types of these skin disorders within the components of the network, and possible interpretations in regards of the topology of individuals in the network pointed to the need of further research with more detailed investigation into the observed tendencies in this study. In addition, data collected during photo-identification surveys were found to be suitable in recording, and remotely monitoring the limited range of epidermal condition.

Our current understanding of the Cardigan Bay bottlenose dolphin social system is far from completion. Although there are few limitations, such as classical significance testing that need to be solved to contribute to the robustness of the results before the social network approach could be widely applied, the results derived from the methods presented here provided a flexible framework for combining the association data with animal distribution or even disease dynamics. This study may complement to the observation by Lusseau et al. (2003b) on this species social plasticity as an important factor in ability to explore and inhabit a remarkable variety of habitats.

Limitations of the study and future research

It is readily acknowledged that the present study had a number of limitations which could have biased the results and the subsequent interpretations.

The size and the distribution of the population sampled, and the sampling period are the factors that need to be considered. In this study sampling period was seasonal (April to October) due to the environmental factors such as a rough sea state in winter months making unsuitable conditions for surveys.

The largest survey area was covered in 2006, while in previous years main effort was concentrated in the Cardigan Bay SAC. Data from the land based sightings were also included in the analysis, and could have biased certain areas towards higher utilization.

Not all individuals present in all the encounters were identified due to the lack of reliable markings. Thus, actual level and structurization of the network could be higher than it was revealed in this study.

Preferred companionships for the social network constructions were derived using HWI cut-off technique which was chosen because it relies directly on the association indices, however, being a proportion, they provide only an indication of the association strength, and are based on the number of times two individuals were seen together (Lusseau et al., 2006). Due to this fact the data were restricted to individuals sighted at least five times.

The approach outlined in this study may suggest more detailed research activities as listed bellow.

- Increased survey effort in the north of Cardigan Bay, extended study area to the south from the Cardigan Bay SAC, and even exploration of all study area would reduce bias from efforts focused in particular areas.
- The most frequent encounter locations of bottlenose dolphins could be compared to the surrounding environment conditions such as bathymetry, water temperature, salinity and productivity. In addition identification of prey species and their movements would be important on correlating dolphin movements and centers of activities.

- Important data that should be collected include more accurate age, and verified sex as well as genetic relatedness for any member of this population.
- Focal follow observations would increase knowledge on interactions occurring among dolphins in this population. At the same time examinations of a network surface structure in the present study should further into the exploration of ego-networks, in particular concentrating on more "central" individuals. On the other hand, it would be interesting to look into the position of the structurally peripheral members in the network, and investigate their distribution and residency patterns.
- A close examination of mother- calf sighting history could reveal different trends in social network dynamics. It would help to establish age at the first birth, calving rates and interbirth intervals for all females, and would determine reproductive success of this population.
- The monitoring of the prevalence and severity of epidermal markings (lesions) in different age and sex groups, correlation with environmental variables, documentation of lesions dynamics by recording their transition from one type to another could elucidate the potential effects, and provide useful clues in exploration of this important question.
- In addition, the investigation of the pollutant levels in the water, especially in the areas of higher utilization – defined as centers of activity in the present study- are recommended. Bottlenose dolphins are top predators, and therefore bioaccumulate contaminants in their tissue and blubber which may result in low immune response to the disease or reproductive impairment. (Aquilar et al., 2002).

To summarize, some findings highlighted in the present study may suggest that techniques that allow combination of parameters to be incorporated into the analysis may advance our understanding towards a more complete picture on social interactions of this species, and its variable environment. Furthermore, this approach may provide practical benefits in devising management protocols, and contribute to the conservation of this, and other cetacean species.

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Appendix 1. Attribute data of the bottlenose dolphins selected for the analysis in the present study

F-female,M-male, U-unknown sex

0- never seeen in that subarea, 1- seen in that subarea, M,YL,NQ,O,A,N- define centers of activity

* no data available

				Subareas						
ID	Sex	No. of sightings	No. of subareas	Cemaes Head	Mwnt	Ynys Lochtyn	New Quay	Outer SAC	Aberystwyth	North
001-03	U	6	5	0	1	0	NQ	0	0	0
002-03	M	15	4	0	M	YL	NQ	0	1	1
003-01	F	17	4	1	M	1	NQ	1	0	0
004-91	F	20	5	0	M	YL	NQ	0	0	0
005-92	M	21	3	0	M	YL	1	0	0	0
006-01	M	25	3	0	M	1	1	1	0	0
007-01	U	20	4	1	M	YL	1	0	0	0
008-03	F	19	4	CH	M	YL	0	0	0	0
009-03	U	7	4	1	M	0	1	0	0	0
010-01	F	26	3	1	M	YL	1	1	0	0
011-03	U	22	6	0	M	YL	1	1	0	0
012-91	M	15	3	CH	1	YL	NQ	1	0	0
013-01	U	28	5	0	1	YL	NQ	1	0	1
014-01	U	17	4	CH	M	YL	NQ	0	0	0
015-03	U	18	5	1	M	YL	0	O	0	0
016-01	F	15	4	0	0	0	NQ	0	0	1
017-01	F	37	5	0	M	YL	NQ	0	1	1
018-03	U	11	4	0	0	YL	NQ	0	0	1
019-03	F	7	4	0	0	0	NQ	0	0	1
020-03	U	6	3	0	0	YL	NQ	0	0	0
025-01	F	19	3	1	M	YL	1	0	0	0
029-03	M	11	6	0	M	YL	NQ	1	0	1
031-01	U	14	3	1	M	YL	NQ	0	0	0
032-06	F	2	*	*	*	*	*	*	*	*
034-01	U	5	5	0	M	YL	0	0	0	0
035-03	M	16	5	0	M	YL	NQ	O	0	0

038-91	F	14	4	CH	M	YL	NQ	O	0	0
040-03	M	12	5	0	M	YL	NQ	O	0	0
043-03	M	8	4	0	0	YL	NQ	O	0	0
045-01	U	14	5	0	M	YL	NQ	0	0	0
047-01	M	27	3	0	M	YL	1	0	0	0
048-01	F	27	3	0	M	YL	NQ	0	0	0
049-01	U	12	4	1	M	YL	NQ	0	0	0
051-91	F	31	5	1	M	1	0	0	0	0
052-03	F	12	4	0	M	0	1	1	0	0
053-01	M	10	4	CH	M	YL	NQ	O	0	0
054-01	M	12	3	CH	M	1	1	1	0	0
055-01	M	17	5	1	M	1	1	1	0	1
056-01	M	12	4	1	M	YL	NQ	1	0	0
058-01	U	13	5	0	1	1	NQ	0	0	1
059-03	M	18	4	1	M	YL	0	1	0	0
060-01	M	10	3	0	M	1	NQ	0	0	0
064-01	M	19	3	1	M	YL	NQ	0	0	0
067-01	F	15	3	0	M	YL	1	0	0	0
068-91	F	12	4	0	M	YL	NQ	0	0	0
071-03	F	14	4	1	1	YL	NQ	0	0	0
072-03	F	8	3	1	0	YL	1	0	0	0
073-03	M	14	3	0	M	YL	NQ	0	0	0
074-03	M	22	3	0	1	1	NQ	0	0	1
075-03	U	9	3	CH	M	1	1	0	0	0
076-01	M	18	3	1	M	YL	NQ	0	0	0
077-91	F	22	3	0	1	YL	NQ	0	0	0
081-91	F	14	3	0	M	YL	NQ	0	0	0
082-01	U	13	3	0	M	YL	NQ	1	0	1
083-03	F	11	4	0	0	0	NQ	0	A	0
085-03	M	5	2	0	0	YL	NQ	O	A	0
087-03	U	9	2	0	M	YL	1	0	0	0
090-03	U	9	3	0	M	YL	NQ	0	0	0
093-01	M	9	2	CH	M	YL	NQ	0	0	0
095-91	U	14	4	CH	M	YL	NQ	0	0	0
107-03	U	11	4	1	M	YL	NQ	0	0	0

109-01	M	9	2	0	1	0	NQ	0	0	1
112-01	F	6	1	0	M	0	NQ	0	0	1
113-01	U	8	3	CH	M	0	NQ	1	0	1
115-03	M	13	5	0	1	YL	NQ	1	0	0
116-03	M	8	3	0	M	YL	NQ	1	0	0
118-03	M	5	3	1	M	1	0	0	0	0
123-04	U	5	3	0	M	0	0	0	0	0
125-03	M	5	4	0	0	YL	NQ	0	0	0
128-03	U	7	1	0	M	YL	NQ	0	0	0
129-03	F	11	3	0	M	YL	1	0	0	0
131-03	U	15	3	0	M	1	1	0	0	0
132-03	U	5	3	0	0	YL	NQ	0	A	0
133-03	U	5	4	1	M	0	0	0	0	0
136-04	U	8	3	0	1	0	NQ	0	0	N
139-04	U	6	3	0	M	YL	NQ	0	0	0
140-04	U	11	2	1	M	YL	0	1	0	0
142-04	U	8	3	0	0	YL	NQ	0	1	0
143-04	U	6	4	0	0	YL	NQ	0	0	0
144-04	U	11	3	0	0	YL	0	0	0	0
146-04	U	7	2	CH	M	YL	0	0	0	0
147-04	U	6	2	CH	M	0	0	0	0	0
152-05	U	6	1	0	0	YL	NQ	O	0	0
159-05	U	5	4	0	0	0	NQ	0	0	1
161-06	F	2	*	*	*	*	*	*	*	*
162-06	F	2	*	*	*	*	*	*	*	*
164-06	U	4	2	0	0	0	0	0	A	N
165-06	M	2	*	*	*	*	*	*	*	*
166-06	U	3	2	0	0	0	0	0	1	N
167-06	M	2	*	*	*	*	*	*	*	*
171-06	U	2	*	*	*	*	*	*	*	*
172-06	U	7	3	0	M	YL	NQ	0	0	0
178-06	U	3	1	0	0	0	0	0	0	N
181-06	U	3	1	0	0	0	0	0	0	N
184-06	U	4	2	0	M	YL	NQ	O	0	0
185-06	U	6	2	0	M	YL	0	O	0	0

Appendix 2. Network statistics for the pooled data (2001-2006) and annual networks

FREEMAN'S DEGREE CENTRALITY MEASURES:

Network 2003

ID	1 Degree	2 NrmDegree	3 Share
7	35.67	50.957	0.03
54	33.67	48.1	0.028
47	33	47.143	0.027
38	32.67	46.671	0.027
35	31.67	45.243	0.026
67	29.67	42.386	0.025
6	29.67	42.386	0.025
40	28.67	40.957	0.024
53	28	40	0.023
71	27.67	39.529	0.023
17	27.67	39.529	0.023
64	27	38.571	0.022
59	26.67	38.1	0.022
56	25.67	36.671	0.021
11	24.67	35.243	0.021
15	24.67	35.243	0.021
76	24.67	35.243	0.021
52	24.67	35.243	0.021
72	24.67	35.243	0.021
13	24.12	34.457	0.02
48	24	34.286	0.02
77	23.67	33.814	0.02
12	22.67	32.386	0.019
14	21.67	30.957	0.018
49	20.67	29.529	0.017
90	20.67	29.529	0.017
10	20.67	29.529	0.017
45	20.67	29.529	0.017
51	19	27.143	0.016
43	18.67	26.671	0.016
81	17.67	25.243	0.015
25	17.67	25.243	0.015
55	17	24.286	0.014
107	17	24.286	0.014
5	17	24.286	0.014
16	16.67	23.814	0.014
73	15.67	22.386	0.013
115	15.67	22.386	0.013

Network 2004

ID	1 Degree	2 NrmDegree	3 Share
58	29	14.478	0.032
95	28	13.07	0.029
25	27	12.772	0.029
77	26	12.367	0.028
55	24	11.002	0.025
133	24	10.917	0.024
15	23	10.917	0.024
7	23	10.896	0.024
48	22	10.832	0.024
131	22	10.661	0.024
74	21	10.384	0.023
10	21	9.893	0.022
51	20	9.467	0.021
5	19	9.403	0.021
6	19	9.254	0.021
81	18	9.19	0.021
3	18	8.635	0.019
10	17	8.443	0.019
47	15	8.337	0.019
9	14	8.316	0.019
64	14	7.91	0.018
8	14	7.74	0.017
68	14	7.591	0.017
11	13	7.591	0.017
56	13	7.505	0.017
59	13	7.484	0.017
73	13	7.186	0.016
12	13	7.122	0.016
13	12	7.058	0.016
115	12	7.036	0.016
144	12	6.503	0.015
45	11	6.354	0.014
118	11	6.333	0.014
140	11	6.205	0.014
146	11	6.162	0.014
75	10	5.501	0.012
71	10	5.458	0.012
90	10	5.437	0.012

8	15	21.429	0.012	49	9	5.33	0.012
129	14.67	20.957	0.012	17	9	5.309	0.012
3	14	20	0.012	18	9	5.203	0.012
9	14	20	0.012	40	8	5.053	0.011
31	14	20	0.012	67	8	5.032	0.011
34	13.67	19.529	0.011	52	8	4.819	0.011
58	13	18.571	0.011	129	8	4.797	0.011
29	12.67	18.1	0.011	93	8	4.712	0.011
87	12.67	18.1	0.011	128	7	4.691	0.01
93	12	17.143	0.01	82	7	4.584	0.01
4	12	17.143	0.01	143	7	4.35	0.01
2	11.67	16.671	0.01	147	7	4.328	0.01
95	11	15.714	0.009	16	7	4.307	0.01
116	10	14.286	0.008	109	7	4.264	0.01
118	10	14.286	0.008	35	6	4.179	0.009
128	8.67	12.386	0.007	38	6	4.072	0.009
19	8	11.429	0.007	60	6	3.987	0.009
131	8	11.429	0.007	113	5	3.966	0.009
18	8	11.429	0.007	112	5	3.838	0.009
74	8	11.429	0.007	43	5	3.561	0.008
112	7	10	0.006	76	5	3.156	0.007
113	7	10	0.006	29	5	3.092	0.007
60	6	8.571	0.005	14	5	2.708	0.006
133	6	8.571	0.005	4	5	2.495	0.006
109	6	8.571	0.005	19	5	2.431	0.005
1	6	8.571	0.005	142	4	2.239	0.005
83	5.67	8.1	0.005	139	4	2.175	0.005
125	5	7.143	0.004	54	4	2.154	0.005
75	4	5.714	0.003	87	3	1.962	0.004
82	4	5.714	0.003	31	3	1.343	0.003
68	1	1.429	0.001	136	1	1.066	0.002
132	1	1.429	0.001	2	1	0.618	0.001
85	1	1.429	0.001	116	1	0.362	0.001

DESCRIPTIVE STATISTICS

		1 Degree	2 NrmDegree	3 Share
1	Mean	16.933	24.190	0.014
2	Std Dev	8.995	12.850	0.007
3	Sum	1202.240	1717.486	1.000
4	Variance	80.904	165.111	0.000
5	SSQ	26101.674	53268.727	0.018
6	MCSSQ	5744.195	11722.849	0.004
7	Euc Norm	161.560	230.800	0.134
8	Minimum	1.000	1.429	0.001
9	Maximum	35.670	50.957	0.030

		1 Degree	2 NrmDegree	3 Share
1	Mean	15.236	6.304	0.014
2	Std Dev	1.511	3.222	0.007
3	Sum	835.000	447.591	1
4	Variance	2.283	10.38	0
5	SSQ	782.758	3558.624	0.018
6	MCSSQ	162.105	736.971	0.004
7	Euc Norm	27.978	59.654	0.133
8	Minimum	29.000	0.362	0.001
9	Maximum	1.000	14.478	0.032

Network Centralization = 27.54%

Network centralization=8.41%

```
Heterogeneity = 1.81%.  Normalized = 0.40%          Heterogeneity = 1.78% Normalized = 0.37%
----------------------------------------            ----------------------------------------
Running time:  00:00:01                             Running time:  00:00:01
Output generated:  23 Oct 06 11:32:26               Output generated:  24 Oct 06 11:15:26
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      FREEMAN'S DEGREE CENTRALITY MEASURES:
      ------------------------------------------------------------------------------
Network 2005                                  Network 2006
              1              2            3                1             2             3
ID    Degree     NrmDegree     Share          ID    Degree     NrmDegree     Share
      -----------
      -          ------------  ------------         ------------ ------------  ------------
  3     23         45.098        0.05         25      22           25          0.036
146     20         39.216        0.044        12      18         20.455        0.029
 82     19         37.255        0.041       154      16         18.182        0.026
140     19         37.255        0.041       185      15         17.045        0.024
 93     19         37.255        0.041        76      14         15.909        0.023
 25     19         37.255        0.041        75      14         15.909        0.023
 67     18         35.294        0.039         3      13         14.773        0.021
  2     17         33.333        0.037         2      13         14.773        0.021
 13     16         31.373        0.035        13      13         14.773        0.021
147     15         29.412        0.033       184      13         14.773        0.021
 38     12         23.529        0.026       166      12         13.636         0.02
 76     12         23.529        0.026        82      12         13.636         0.02
 15     12         23.529        0.026        51      12         13.636         0.02
112     12         23.529        0.026       164      12         13.636         0.02
115     12         23.529        0.026       152      12         13.636         0.02
 74     12         23.529        0.026       131      11          12.5         0.018
 40     12         23.529        0.026       116      11          12.5         0.018
 47     11         21.569        0.024         7      11          12.5         0.018
144     10         19.608        0.022        59      11          12.5         0.018
 85     10         19.608        0.022        15      10         11.364        0.016
 53      9         17.647         0.02       129      10         11.364        0.016
 71      9         17.647         0.02       115      10         11.364        0.016
128      9         17.647         0.02        34       9         10.227        0.015
 72      9         17.647         0.02         9       9         10.227        0.015
152      9         17.647         0.02       165       9         10.227        0.015
  5      8         15.686        0.017       124       9         10.227        0.015
 48      8         15.686        0.017       123       9         10.227        0.015
  1      8         15.686        0.017       167       9         10.227        0.015
142      8         15.686        0.017       161       9         10.227        0.015
 29      7         13.725        0.015       136       9         10.227        0.015
116      7         13.725        0.015       172       8          9.091        0.013
113      7         13.725        0.015        48       8          9.091        0.013
  4      6         11.765        0.013        81       8          9.091        0.013
107      5          9.804        0.011       178       8          9.091        0.013
 49      5          9.804        0.011        14       7          7.955        0.011
 51      5          9.804        0.011        19       7          7.955        0.011
 64      5          9.804        0.011        67       7          7.955        0.011
 16      4          7.843        0.009       128       7          7.955        0.011
```

18	4	7.843	0.009
43	4	7.843	0.009
17	4	7.843	0.009
83	3	5.882	0.007
73	3	5.882	0.007
132	3	5.882	0.007
68	2	3.922	0.004
60	2	3.922	0.004
109	1	1.961	0.002
143	1	1.961	0.002
90	1	1.961	0.002
6	1	1.961	0.002
159	1	1.961	0.002
136	0	0	0

54	7	7.955	0.011
68	7	7.955	0.011
147	6	6.818	0.01
83	6	6.818	0.01
114	6	6.818	0.01
186	6	6.818	0.01
49	6	6.818	0.01
153	6	6.818	0.01
142	6	6.818	0.01
8	6	6.818	0.01
169	5	5.682	0.008
132	5	5.682	0.008
146	5	5.682	0.008
175	5	5.682	0.008
182	5	5.682	0.008
29	5	5.682	0.008
174	5	5.682	0.008
173	5	5.682	0.008
168	5	5.682	0.008
140	5	5.682	0.008
171	5	5.682	0.008
179	5	5.682	0.008
180	5	5.682	0.008
6	5	5.682	0.008
17	4	4.545	0.007
85	4	4.545	0.007
181	4	4.545	0.007
40	4	4.545	0.007
162	4	4.545	0.007
32	4	4.545	0.007
125	4	4.545	0.007
5	3	3.409	0.005
163	3	3.409	0.005
183	3	3.409	0.005
64	3	3.409	0.005
93	3	3.409	0.005
107	3	3.409	0.005
74	2	2.273	0.003
63	2	2.273	0.003
87	2	2.273	0.003
33	2	2.273	0.003
71	2	2.273	0.003
113	2	2.273	0.003
65	2	2.273	0.003
112	2	2.273	0.003
16	1	1.136	0.002
98	1	1.136	0.002
38	1	1.136	0.002
61	0	0	0
62	0	0	0

```
                                        109        0              0              0

                              DESCRIPTIVE STATISTICS

          1          2          3                                1          2          3
                Degree    NrmDegree       Share                        Degree    NrmDegree       Share
          ------------ ------------ ------------                  ------------ ------------ ------------
 1     Mean        8.808       17.270       0.019            1     Mean        6.899        7.840       0.011
 2  Std Dev        5.900       11.568       0.013            2  Std Dev        4.321        4.911       0.007
 3      Sum      458.000      898.039       1.000            3      Sum      614.000      697.727       1.000
 4 Variance       34.809      133.830       0.000            4 Variance       18.675       24.116       0.000
 5      SSQ     5844.000    22468.281       0.028            5      SSQ     5898.000     7616.219       0.016
 6    MCSSQ     1810.077     6959.158       0.009            6    MCSSQ     1662.090     2146.294       0.004
 7 Euc Norm       76.446      149.894       0.167            7 Euc Norm       76.798       87.271       0.125
 8  Minimum        0.000        0.000       0.000            8  Minimum        0.000        0.000       0.000
 9  Maximum       23.000       45.098       0.050            9  Maximum       22.000       25.000       0.036

Network Centralization = 28.94%                          Network Centralization = 17.55%
Heterogeneity = 2.79%.  Normalized = 0.88%               Heterogeneity = 1.56%.  Normalized = 0.45%
----------------------------------------                 ----------------------------------------
Running time:  00:00:01                                  Running time:  00:00:01
Output generated:  23 Oct 06 15:09:43                    Output generated:  23 Oct 06 14:28:46
                              Copyright (c) 1999-2005 Analytic Technologies
```

FREEMAN'S DEGREE CENTRALITY MEASURES:

```
--------------------------------------------------------------------------------
Network 2001-2006
            1              2             3
ID     Degree    NrmDegree     Share
       -----------
       -         ------------  ------------
 13       57        64.773        0.023          116       23          26.136          0.009
 25       55         62.5         0.022           34       21          23.864          0.009
  7       52        59.091        0.021          144       20          22.727          0.008
  3       47        53.409        0.019          118       20          22.727          0.008
 67       47        53.409        0.019          113       19          21.591          0.008
 47       46        52.273        0.019           18       18          20.455          0.007
 15       46        52.273        0.019            4       18          20.455          0.007
 76       46        52.273        0.019           87       17          19.318          0.007
  6       45        51.136        0.018          152       17          19.318          0.007
 48       44          50          0.018           19       16          18.182          0.007
 10       44          50          0.018           60       15          17.045          0.006
  5       43        48.864        0.018          142       15          17.045          0.006
 38       42        47.727        0.017           85       14          15.909          0.006
 71       42        47.727        0.017           83       14          15.909          0.006
 12       42        47.727        0.017          185       13          14.773          0.005
 64       41        46.591        0.017          172       13          14.773          0.005
 54       40        45.455        0.016            1       12          13.636          0.005
 40       40        45.455        0.016          109       11            12.5          0.004
 95       39        44.318        0.016          184        9          10.227          0.004
 59       39        44.318        0.016          136        9          10.227          0.004
```

51	38	43.182	0.016
55	37	42.045	0.015
77	37	42.045	0.015
82	36	40.909	0.015
53	36	40.909	0.015
11	35	39.773	0.014
17	35	39.773	0.014
35	35	39.773	0.014
56	34	38.636	0.014
81	34	38.636	0.014
131	34	38.636	0.014
115	34	38.636	0.014
2	33	37.5	0.013
58	33	37.5	0.013
49	32	36.364	0.013
72	31	35.227	0.013
14	31	35.227	0.013
74	31	35.227	0.013
29	31	35.227	0.013
93	31	35.227	0.013
146	30	34.091	0.012
52	29	32.955	0.012
90	29	32.955	0.012
140	29	32.955	0.012
107	29	32.955	0.012
9	29	32.955	0.012
45	28	31.818	0.011
129	28	31.818	0.011
68	27	30.682	0.011
128	26	29.545	0.011
8	26	29.545	0.011
43	26	29.545	0.011
73	26	29.545	0.011
75	25	28.409	0.01
133	25	28.409	0.01
147	24	27.273	0.01
112	23	26.136	0.009
16	23	26.136	0.009
31	23	26.136	0.009
125	9	10.227	0.004
143	8	9.091	0.003
123	7	7.955	0.003
132	6	6.818	0.002
166	6	6.818	0.002
164	5	5.682	0.002
139	4	4.545	0.002
181	3	3.409	0.001
178	3	3.409	0.001
159	1	1.136	0

```
                DESCRIPTIVE STATISTICS
                   1          2          3
                Degree   NrmDegree     Share
          ------------ ------------ ------------
 1     Mean     27.483     31.231      0.011
 2  Std Dev     13.250     15.057      0.005
 3      Sum   2446.000   2779.545      1.000
 4 Variance    175.576    226.725      0.000
 5      SSQ  82850.000 106986.055      0.014
 6    MCSSQ  15626.225  20178.492      0.003
 7 Euc Norm    287.837    327.087      0.118
 8  Minimum      1.000      1.136      0.000
 9  Maximum     57.000     64.773      0.023

Network Centralization = 34.31%
Heterogeneity = 1.38%.  Normalized = 0.26%
----------------------------------------
Running time:  00:00:01
Output generated:  23 Oct 06 14:22:45
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```

FREEMAN BETWEENNESS CENTRALITY

Network 2004			Network 2003		
	1	2		1	2
ID	Betweenness	nBetweenness	ID	Betweenness	nBetweenness
	------------	------------		------------	------------
58	246.445	10.205	47	197.076	8.16
74	165.059	6.835	17	121.352	5.025
55	162.321	6.721	13	115.393	4.778

95	153.348	6.35	14	106.141	4.395
51	126.387	5.233	54	96.759	4.007
133	126.05	5.219	48	91.185	3.776
131	125.842	5.211	77	89.844	3.72
7	124.039	5.136	35	81.276	3.365
48	119.926	4.966	128	79.339	3.285
15	112.518	4.659	7	71.245	2.95
77	108.884	4.509	67	70.059	2.901
25	100.94	4.18	71	69.721	2.887
6	97.872	4.053	6	68.768	2.848
10	91.376	3.784	53	68.618	2.841
5	88.376	3.659	72	60.625	2.51
4	71.876	2.976	11	56.247	2.329
109	69	2.857	38	52.63	2.179
12	56.289	2.331	45	46.878	1.941
11	55.748	2.308	59	39.204	1.623
81	52.595	2.178	34	35.417	1.467
3	48.242	1.998	40	32.783	1.357
47	46.671	1.933	64	32.6	1.35
68	38.7	1.602	3	30.978	1.283
107	36.677	1.519	2	29.898	1.238
17	35.643	1.476	16	24.623	1.02
59	30.61	1.267	51	23.648	0.979
118	27.678	1.146	73	23.303	0.965
64	22.519	0.932	49	23.171	0.959
115	21.88	0.906	10	22.898	0.948
45	19.195	0.795	12	22.542	0.933
71	18.554	0.768	4	22.481	0.931
56	18.413	0.762	56	21.503	0.89
146	17.056	0.706	52	20.087	0.832
8	15.69	0.65	90	19.793	0.82
140	12.949	0.536	58	19.022	0.788
93	11.98	0.496	76	17.077	0.707
144	11.319	0.469	15	16.142	0.668
9	10.817	0.448	107	14.931	0.618
82	10.752	0.445	115	13.696	0.567
60	9.498	0.393	9	13.617	0.564
35	9.11	0.377	81	13.027	0.539
75	8.763	0.363	43	12.775	0.529
147	8.322	0.345	29	12.51	0.518
18	8.306	0.344	116	11.147	0.462
143	7.866	0.326	5	10.142	0.42
142	7.64	0.316	25	9.453	0.391
13	7.482	0.31	31	9.28	0.384
129	7.258	0.301	112	8.85	0.366
38	7.091	0.294	93	8.833	0.366

```
  73      5.688           0.236          8       7.564        0.313
                                        11
  49      4.897           0.203          8       6.891        0.285
  67      3.278           0.136         55       6.052        0.251
                                        12
  52      3.04            0.126          9       5.231        0.217
  16      2.223           0.092         74       4.344        0.18
 139      0.304           0.013         19       3.553        0.147
  43      0               0              1       3.342        0.138
  31      0               0             82       3.266        0.135
  90      0               0             87       3.231        0.134
  29      0               0             18       2.639        0.109
                                        11
 116      0               0              3       2.297        0.095
 113      0               0             60       2.237        0.093
  76      0               0             95       1.004        0.042
  40      0               0             75       0.97         0.04
                                        13
 136      0               0              1       0.793        0.033
 112      0               0             85       0            0
                                        12
  87      0               0              5       0            0
  54      0               0             68       0            0
                                        10
 128      0               0              9       0            0
  14      0               0             83       0            0
                                        13
  19      0               0              2       0            0
                                        13
   2      0               0              3       0            0
```

```
                  DESCRIPTIVE STATISTICS FOR EACH MEASURE

              1          2                          1          2
        Betweenness nBetweenness              Betweenness nBetweenness
        ------------ ------------             ------------ ------------
 1     Mean      39.592      1.639      1     Mean      31.155      1.290
 2  Std Dev      52.775      2.185      2  Std Dev      37.267      1.543
 3      Sum    2811.000    116.398      3      Sum    2212.000     91.594
 4 Variance    2785.186      4.776      4 Variance    1388.795      2.381
 5      SSQ  309040.031    529.884      5      SSQ  167519.156    287.230
 6    MCSSQ  197748.188    339.061      6    MCSSQ   98604.445    169.068
 7 Euc Norm     555.914     23.019      7 Euc Norm     409.291     16.948
 8  Minimum       0.000      0.000      8  Minimum       0.000      0.000
 9  Maximum     246.445     10.205      9  Maximum     197.076      8.160

Network Centralization Index = 8.69%      Network Centralization Index = 6.97%
Running time:  00:00:01                   Running time:  00:00:01
Output generated:  23 Oct 06 13:06:44     Output generated:  23 Oct 06 11:35:26
              Copyright (c) 1999-2005 Analytic Technologies
```

FREEMAN BETWEENNESS CENTRALITY

Network 2005			Network 2006		
	1	2		1	2
ID	Betweenness	nBetweenness	ID	Betweenness	nBetweenness
		------------		------------	------------
13	192.811	15.122	13	762.862	19.928
82	178.615	14.009	164	630.952	16.483
17	176	13.804	25	600.418	15.685
146	164.043	12.866	76	503.636	13.157
2	162.381	12.736	2	496.669	12.975
152	94.683	7.426	29	486.548	12.71
74	92.404	7.247	181	422.475	11.036
3	67.091	5.262	75	374.292	9.778
147	61.203	4.8	184	362.543	9.471
93	51.38	4.03	161	333.062	8.701
142	47.199	3.702	185	324.65	8.481
132	47	3.686	82	318.723	8.326
83	47	3.686	142	311.576	8.139
53	43.561	3.417	3	251.997	6.583
140	40.849	3.204	125	228.734	5.975
25	40.849	3.204	154	183.279	4.788
4	32.897	2.58	48	181.525	4.742
67	30.724	2.41	12	174.593	4.561
85	27.278	2.139	166	165.217	4.316
47	18.364	1.44	115	162.675	4.25
144	2.668	0.209	153	146.409	3.825
1	0	0	19	134.464	3.513
38	0	0	136	121.333	3.17
40	0	0	152	121.294	3.169
29	0	0	7	93.679	2.447
71	0	0	162	84	2.194
15	0	0	14	84	2.194
73	0	0	129	84	2.194
43	0	0	68	76.845	2.007
48	0	0	32	55.759	1.457
5	0	0	178	53.565	1.399
6	0	0	16	53.379	1.394

			5		
72	0	0	167	53.379	1.394
90	0	0	116	46.616	1.218
16	0	0	131	43.608	1.139
107	0	0	15	41.34	1.08
18	0	0	51	30.761	0.804
112	0	0	59	22.947	0.599
113	0	0	81	13.389	0.35
115	0	0	172	13.389	0.35
116	0	0	8	12.668	0.331
128	0	0	40	0.75	0.02
76	0	0	65	0	0
136	0	0	5	0	0
49	0	0	64	0	0
51	0	0	87	0	0
143	0	0	112	0	0
60	0	0	54	0	0
64	0	0	34	0	0
109	0	0	33	0	0
68	0	0	85	0	0
159	0	0	123	0	0
			124	0	0
			71	0	0
			107	0	0
			74	0	0
			17	0	0
			132	0	0
			114	0	0
			140	0	0
			9	0	0
			146	0	0
			147	0	0
			38	0	0
			67	0	0
			16	0	0
			49	0	0
			109	0	0
			163	0	0

```
                    6          0          0
                    61         0          0
                    62         0          0
                    63         0          0
                    16
                    8          0          0
                    16
                    9          0          0
                    17
                    1          0          0
                    12
                    8          0          0
                    17
                    3          0          0
                    17
                    4          0          0
                    17
                    5          0          0
                    11
                    3          0          0
                    17
                    9          0          0
                    18
                    0          0          0
                    83         0          0
                    18
                    2          0          0
                    18
                    3          0          0
                    93         0          0
                    98         0          0
                    18
                    6          0          0

             DESCRIPTIVE STATISTICS FOR EACH MEASURE
          1          2                              1          2
       Betweenness nBetweenness                  Betweenness nBetweenness
       ------------ ------------                  ------------ ------------
 1    Mean       31.135       2.442        1    Mean       97.348       2.543
 2  Std Dev      53.044       4.160        2  Std Dev     167.267       4.370
 3     Sum     1619.000     126.980        3     Sum     8664.000     226.332
 4 Variance    2813.680      17.308        4 Variance   27978.207      19.093
 5     SSQ   196718.313    1210.109        5     SSQ  3333486.250    2274.861
 6   MCSSQ   146311.375     900.031        6   MCSSQ  2490060.500    1699.284
 7 Euc Norm     443.529      34.787        7 Euc Norm    1825.784      47.695
 8  Minimum       0.000       0.000        8  Minimum       0.000       0.000
 9  Maximum     192.811      15.122        9  Maximum     762.862      19.928

Network Centralization Index = 12.93%      Network Centralization Index = 17.58%
Running time:  00:00:01                    Running time:  00:00:01
Output generated:  23 Oct 06 15:11:49      Output generated:  23 Oct 06 14:29:53
             Copyright (c) 1999-2005 Analytic Technologies
```

FREEMAN BETWEENNESS CENTRALITY

Network 2001-2006

ID	1 Betweenness	nBetweenness	2
	------------	------------	
13	191.651	5.007	
2	157.178	4.106	
17	143.355	3.745	
132	90.287	2.359	
48	89.495	2.338	
47	87.934	2.297	
25	83.923	2.192	
3	83.711	2.187	
7	82.91	2.166	
128	77.25	2.018	
67	75.648	1.976	
71	69.971	1.828	
82	69.843	1.825	
5	67.778	1.771	
6	67.193	1.755	
29	64.006	1.672	
10	62.187	1.625	
12	61.467	1.606	
11	60.816	1.589	
76	55.657	1.454	
83	54.852	1.433	
14	48.871	1.277	
53	46.085	1.204	
58	46.03	1.202	
77	43.127	1.127	
131	42.181	1.102	
54	39.905	1.042	
15	39.034	1.02	
74	36.631	0.957	
115	35.862	0.937	
55	31.917	0.834	
93	31.9	0.833	
81	31.326	0.818	
95	31.129	0.813	
38	30.568	0.799	
45	28.832	0.753	
112	28.353	0.741	
146	28.017	0.732	
51	27.308	0.713	
64	26.685	0.697	
90	26.667	0.697	
140	25.038	0.654	
34	24.601	0.643	
75	24.334	0.636	

19	23.515	0.614
59	22.698	0.593
40	21.815	0.57
116	21.205	0.554
72	20.141	0.526
35	18.705	0.489
142	18.312	0.478
9	17.154	0.448
136	16.392	0.428
4	16.255	0.425
43	16.252	0.425
129	15.637	0.408
73	15.491	0.405
152	14.404	0.376
68	14.215	0.371
107	13.79	0.36
18	13.471	0.352
85	13.463	0.352
49	12.44	0.325
16	12.241	0.32
56	12.027	0.314
60	10.766	0.281
113	9.636	0.252
31	9.406	0.246
52	7.928	0.207
133	7.556	0.197
8	7.146	0.187
185	6.439	0.168
147	6.305	0.165
144	6.28	0.164
125	5.416	0.141
118	3.81	0.1
164	3.743	0.098
166	3.127	0.082
87	2.482	0.065
1	2.246	0.059
109	2.242	0.059
143	1.604	0.042
184	1.373	0.036
172	1.101	0.029
181	0.196	0.005
139	0.059	0.002
178	0	0
123	0	0
159	0	0

```
DESCRIPTIVE STATISTICS FOR EACH MEASURE
                 1           2
           Betweenness nBetweenness
           ------------ ------------
 1     Mean       33.933       0.886
 2  Std Dev       35.243       0.921
 3      Sum     3020.000      78.892
 4 Variance     1242.098       0.848
 5      SSQ   213023.094     145.373
 6    MCSSQ   110546.695      75.440
 7 Euc Norm      461.544      12.057
 8  Minimum        0.000       0.000
 9  Maximum      191.651       5.007

Network Centralization Index = 4.17%
----------------------------------------
Running time:  00:00:01
Output generated:  23 Oct 06 14:23:47
Copyright (c) 1999-2005 Analytic
Technologies
```

Appendix 3. Statistical analyses

Clustering coefficient

Mann-Whitney Test and CI: 2003, 2004 clustering coefficient

```
      N  Median
2003  67  0.5220
2004  68  0.5080
Point estimate for ETA1-ETA2 is -0.0000
95.0 Percent CI for ETA1-ETA2 is (-0.0580,0.0510)
W = 4545.5
Test of ETA1 = ETA2 vs ETA1 not = ETA2 is significant at
0.9649
```

Mann-Whitney Test and CI: 2005, 2006 clustering coefficient

```
      N  Median
2005  46  1.0000
2006  83  0.8330
Point estimate for ETA1-ETA2 is 0.0000
95.1 Percent CI for ETA1-ETA2 is (-0.0000,0.0031)
W = 3112.0
Test of ETA1 = ETA2 vs ETA1 not = ETA2 is significant at
0.5502
```

Mann-Whitney Test and CI: 2003/2004, 2005/2006 clustering coefficient

```
            N  Median
2003/2004  135  0.5160
2005/2006  129  1.0000
Point estimate for ETA1-ETA2 is -0.2160
95.0 Percent CI for ETA1-ETA2 is (-0.3210,-0.1270)
W = 14371.5
Test of ETA1 = ETA2 vs ETA1 not = ETA2 is significant at
0.0000
```

Mann-Whitney Test and CI: 2003/2004, 2001-2006 clustering coefficient

```
            N   Median
2003/2004  135  0.51600
2001-2006   88  0.54750
Point estimate for ETA1-ETA2 is -
0.01300
95.0 Percent CI for ETA1-ETA2 is (-
0.04800,0.02101)
W = 14755.0
Test of ETA1 = ETA2 vs ETA1 not = ETA2 is significant at
0.4389
```

Mann-Whitney Test and CI: 2005/2006, 2001-2006   clustering coefficient

```
          N  Median
2005/2006  129  1.0000
2001-2006   88  0.5475
Point estimate for ETA1-ETA2 is 0.2940
95.0 Percent CI for ETA1-ETA2 is (0.1540,0.3610)
W = 16533.5
Test of ETA1 = ETA2 vs ETA1 not = ETA2 is significant at
0.0000
```

Degree

Mann-Whitney Test and CI: degree2003, degree2004

```
          N  Median
degree2003  71  16.670
degree2004  71  10.000
Point estimate for ETA1-ETA2 is 5.000
95.0 Percent CI for ETA1-ETA2 is (1.999,7.999)
W = 5931.0
Test of ETA1 = ETA2 vs ETA1 not = ETA2 is significant at
0.0005
```

Mann-Whitney Test and CI: degree2005, degree2006

```
          N  Median
degree2005  52   8.000
degree2006  89   6.000
Point estimate for ETA1-ETA2 is 2.000
95.0 Percent CI for ETA1-ETA2 is (-0.000,2.998)
W = 4067.0
Test of ETA1 = ETA2 vs ETA1 not = ETA2 is significant at
0.1095
```

Frequency distribution of epidermal lesions (markings) in four components in the network 2006

Chi-Square Goodness-of-Fit Test for Observed Counts in Variable:
Component Blue

```
                    Test            Contribution
Category  Observed  Proportion  Expected    to Chi-Sq
1          10   0.142857   5.42857     3.84962
2           8   0.142857   5.42857     1.21805
3           5   0.142857   5.42857     0.03383
4           4   0.142857   5.42857     0.37594
5           0   0.142857   5.42857     5.42857
6           0   0.142857   5.42857     5.42857
```

```
7             11    0.142857   5.42857       5.71805

 N  DF   Chi-Sq  P-Value
38   6  22.0526    0.001
```

Chi-Square Goodness-of-Fit Test for Observed Counts in Variable: Component Grey

```
                      Test            Contribution
Category  Observed  Proportion  Expected     to Chi-Sq
1              3    0.142857   2.14286      0.34286
2              2    0.142857   2.14286      0.00952
3              0    0.142857   2.14286      2.14286
4              3    0.142857   2.14286      0.34286
5              0    0.142857   2.14286      2.14286
6              1    0.142857   2.14286      0.60952
7              6    0.142857   2.14286      6.94286

 N  DF   Chi-Sq  P-Value
15   6  12.5333    0.051
```

Chi-Square Goodness-of-Fit Test for Observed Counts in Variable Component Black

```
                      Test            Contribution
Category  Observed  Proportion  Expected     to Chi-Sq
1              1    0.142857   2.42857      0.84034
2              1    0.142857   2.42857      0.84034
3              2    0.142857   2.42857      0.07563
4              6    0.142857   2.42857      5.25210
5              1    0.142857   2.42857      0.84034
6              0    0.142857   2.42857      2.42857
7              6    0.142857   2.42857      5.25210

 N  DF   Chi-Sq  P-Value
17   6  15.5294    0.017
```

Chi-Square Goodness-of-Fit Test for Observed Counts in Variable: Component Red

```
                      Test            Contribution
Category  Observed  Proportion  Expected     to Chi-Sq
1              1    0.142857   3.57143      1.85143
2              4    0.142857   3.57143      0.05143
3              1    0.142857   3.57143      1.85143
4              9    0.142857   3.57143      8.25143
5              2    0.142857   3.57143      0.69143
6              0    0.142857   3.57143      3.57143
7              8    0.142857   3.57143      5.49143


 N  DF  Chi-Sq  P-Value
```

```
25   6   21.76    0.001
```

Chi-Square Goodness-of-Fit Test for Observed Counts in Variable Overall network 2006

```
                         Test           Contribution
Category    Observed  Proportion  Expected     to Chi-Sq
BFS             22    0.142857   13.8571        4.7850
BP               9    0.142857   13.8571        1.7025
CL              15    0.142857   13.8571        0.0943
No lesions      32    0.142857   13.8571       23.7541
WFF              1    0.142857   13.8571       11.9293
WFS              3    0.142857   13.8571        8.5066
WP              15    0.142857   13.8571        0.0943

 N  DF   Chi-Sq  P-Value
97   6  50.8660    0.000
```

Appendix 4: Study animals

All photographs by courtesy of the Sea Watch Foundation.

001-03 S

002-03S

003-01W

004-91W

005-92W

006-01W

007-01S

008-03W

009-03S

010-01W

011-03S

012-91W


013-01S


014-01W


015-03W


016-01W


017-01W


018-03S


019-03W


020-03W


025-01W


029-03W


031-01W


034-01S


035-03W


038-91W


040-03W


043-03S


045-01W


047-01W


048-01W


049-01S


051-91W


052-03W


053-01W


054-01W

055-01W

056-01W

058-01S

059-03S

060-01W

064-01W

067-01S

068-91W

071-03S

072-03S

073-03S

074-03S


075-03W


076-01W


077-91S


081-91S


082-01W


083-03W


085-03W


087-03S


090-03S


093-01W


095-91W


107-03S


109-01W


112-01S


113-01W


115-01W


116-03W


118-03W


123-04S


125-03W


128-03S


129-03W


131-03W


132-03W


133-03S


136-04W


139-04S


140-04W


142-04W


143-04S


144-04S


146-04W


147-04W


152-05W


159-05W

Dolphins identified in 2006


032-06S


033-06S


063-06S


065-06S


161-06W


162-06S


164-06S


165-06S


166-06S


167-06S


168-06S


169-06S

171-06S

172-06S

173-06S

174-06S

178-06S

179-06S

180-06S

181-06W

182-06S

183-06W

184-06S

185-06W

186-06S