

The effect of boat disturbance on the
bottlenose dolphin (*Tursiops
truncatus*) of Cardigan Bay in Wales.

Heidi Richardson

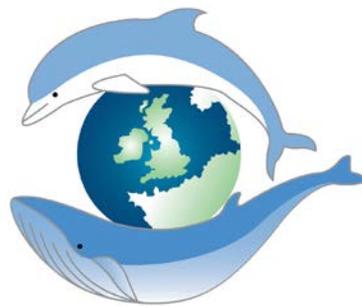
Word Count=13, 793

Thesis submitted for the degree of MSc Conservation, Dept
of Geography,

UCL (University College London)

August 2012

In association with the Sea Watch Foundation



UNIVERSITY COLLEGE LONDON

MSc Conservation

Please complete the following declaration and hand this form in with your MSc Research Project.

I,

hereby declare :

- (a) that this MSc Project is my own original work and that all source material used is acknowledged therein;
- (b) that it has been prepared specially for the MSc in Conservation of University College London;
- (c) that it does not contain any material previously submitted to the Examiners of this or any other University, or any material previously submitted for any other examination.

Signed :

Date :

Abstract

The bottlenose dolphin is a widespread, iconic species and as such is protected by law throughout Europe. Cardigan Bay in Wales has two areas designated for the protection of the bottlenose dolphin. Legislation protecting the bottlenose dolphin requires Governments to ensure factors that may adversely affect populations are limited. With respect to the bottlenose dolphins of Cardigan Bay, this factor is likely to be disturbance. Boat disturbance within Cardigan Bay has been steadily increasing due to increases in the number of recreational boats used and wildlife watching trips taken. Studies show that boat disturbance can negatively impact bottlenose dolphins, with responses ranging from moderate changes in behavior to the avoidance of preferred habitats. This study focuses on the effect of disturbance on dolphin community structure, community structure being important to increasing an individuals' fitness. Additionally, it examined the effectiveness of current management plans in decreasing the possible effects of disturbance. Cardigan Bay was split into areas of regulated and unregulated high vessel traffic and areas of low vessel traffic. The results strongly indicate that vessel traffic does impact community structure. Group size was significantly smaller in areas of high vessel traffic and results suggested individuals in high vessel traffic areas form many moderately strong bonds with many other individuals, whereas those in areas of low vessel traffic formed very strong bonds with a small number of individuals. Very similar values between areas of regulated and unregulated vessel traffic indicate that the current management plan is not being effective in reducing all of the impacts of disturbance on the dolphin population. This study recommends the continued monitoring of Cardigan Bay to increase the understanding of how disturbance may affect the bottlenose dolphins and to allow an effective management plan to be put in place.

Contents

MSc Conservation	2
Abstract	3
Tables and Figures.....	7
Acknowledgements.....	8
1. Introduction	9
1.1 Species Ecology and Current Threats	9
1.2 Bottlenose dolphin-<i>Tursiops truncatus</i>	9
1.3 Sociality of the species	10
1.4.1 Benefits and Costs of Grouping	11
1.4.2 Associations Formed within Groups	12
1.5 The Effects of Disturbance	14
1.5.1 Responses to Disturbance	15
1.5.2 Effects of Disturbance on Community Structure	16
2. Conservation of the Bottlenose Dolphin.....	16
2.1 Legislative Background	17
2.2 SAC Designation for the Bottlenose Dolphin	18
2.3 Practical Requirements of a Special Area of Conservation	19
2.4 Threats to the Bottlenose dolphins of Cardigan Bay	20
2. 5 Existing management plans	21
3. Aims and Objectives.....	23
4. Study Site: Cardigan Bay and the Cardigan Bay SAC.....	24
5. Methods.....	26
5.1 Cardigan Bay Area Divisions	26

5.2 Field Data Collection	27
5.2.1 Survey Boats	27
5.2.2 Line transect Surveys of Cardigan Bay SAC	28
5.2.3 Additional boat based and land based surveys.....	29
5.2.4 Photo-identification and group determination	29
6. Data Analysis.....	31
6.1 Effort and Reliability	31
6.3 Association strength and preferred/avoided companions.....	33
6.4 Long term Associations and Community Structure	33
6.5 Association Strength and Clustering Coefficient	34
9. Results.....	35
9.1. Effort and Reliability	35
9.2 Group Size	38
9.3 Association strength and determination of preferred and/or avoided associations	38
9.3.1 Mean Coefficient of Association (CoA)	38
9.3.2 Permutation Tests.....	39
9.4 Defining Clusters.....	41
9.4.1 Non metric multi-dimensional scaling plots	41
9.4.2 Hierarchical Agglomerative Cluster Analysis.....	43
9.5 Social Network Analysis	47
10. Discussion.....	50
10.1 Effects of Disturbance on Community Structure.....	51
10.1.1 Social Differentiation.....	51
10.1.2 Group Size, Association Index and Social Network Analysis.....	52

10.2 Interpreting Responses to Disturbance	53
10.3 Implications for management	56
10.4 Recommendations	57
11. Conclusion	58
Auto-Critique	59
12. References.....	60

Tables and Figures

		Page
Box 1	Article 2 (Directive 92/43/EEC)	17
Box 2	Favourable Conservation Status of a species	19
Table 1	Table of effort and social differentiation values	37
Table 2	Mean group size for all groups found in pooled data periods	38
Table 3	Association Index and preferred association values	40
Table 4	Strength and Cluster Coefficient Values	47
Figure 1	Study Site: Cardigan Bay	24
Figure 2	Cardigan Bay showing areas of regulated and unregulated high vessel traffic and low vessel traffic	26
Figure 3	Boats used to collect survey data	27
Figure 4	Photograph showing bottlenose dolphin dorsal fin	30
Figure 5	Representative Multi-Dimensional Scaling Plots of regulated and unregulated areas of high vessel traffic and areas of low vessel traffic	42
Figure 6	Hierarchical cluster analysis plot for years 2007-2009 for areas of regulated high vessel traffic	44
Figure 7	Hierarchical cluster analysis plot for years 2007-2009 for areas of unregulated high vessel traffic	45
Figure 8	Hierarchical cluster analysis plot for years 2001-2012 for areas of low vessel traffic	46
Figure 9	Social network for years 2007-2009 for regulated areas of high vessel traffic.	49
Figure 10	Social network for years 2007-2009 for unregulated areas of high vessel traffic.	49
Figure 11	Social network for years 2001-2012 for areas of low vessel traffic.	50

Acknowledgements

Firstly I would like to thank Dr Peter Evans for providing the opportunity to undertake this project, and for his support and guidance. Additionally, I would like to thank all those at the Sea Watch Foundation, past and present, whose hard work and data collection makes projects like this possible, with particular thanks going to those staff and volunteers who made my field work especially enjoyable and offered support when needed.

Thank you to Dr Chris Brierley for his help and guidance, as well as Cindy Elliser and David Jacoby for their advice regarding the technicalities of the SOCPROG program.

1. Introduction

1.1 Species Ecology and Current Threats

This chapter will discuss the ecology of the bottlenose dolphin *Tursiops truncatus* and the threats they face, with particular emphasis upon boat disturbance, and an overview of the known behavioural responses associated with disturbance.

1.2 Bottlenose dolphin-*Tursiops truncatus*

The bottlenose dolphin belongs to the order *Cetacea*, suborder *Odontoceti* (toothed whales) and family *Delphinidae* (IUCN, 2012). Two species of bottlenose dolphin are now recognised, the “Common Bottlenose Dolphin” *Tursiops truncatus* and the “Indian Ocean Bottlenose Dolphin” *Tursiops aduncus*. This study will focus on the former. The bottlenose dolphin is a particularly widespread, cosmopolitan species found in tropical and temperate seas of all oceans (Wells and Scott, 1999) occupying a wide range of habitats including pelagic waters, oceanic islands, and coastal habitats, including sheltered estuaries and lagoons (Leatherwood and Reeves, 1990; Connor, *et al.*, 1998; Wells and Scott, 2002). Coastal bottlenose dolphins have been recorded showing a range of movement patterns including periodic residency, year-round home ranges, seasonal migrations and both occasional long-range movements and repeated residency (Wells and Scott, 1999; Connor, *et al.*, 2000; Reynolds, *et al.*, 2000). Size of the bottlenose dolphin is varied across its distribution; off Shark Bay, Australia for example bottlenose dolphins are only 220-230cm length (Ross and Cockcroft, 1990) whereas sizes of bottlenose dolphins around the UK range between 300-410cm and therefore are some of the largest examples of the species in the world (Wilson, 2008).

Bottlenose dolphins are long lived species, females have been recorded as living for up to 50 years and some males have been recorded as reaching 45 years (Wells and Scott, 1999; 2002). Sexual and physical maturity differs with region; in general males reach maturity between 9-12 years of age and females between 5-12 years (Wells and Scott, 2002). The gestation period for calving in females is approximately 12 months, with calves being born every 3-6 years, maternal investment then extends for about 3-6 years, with many calves separating with the birth of the next calf (Wells and Scott, 1999; 2002; Reynolds, *et al.*, 2000).

1.3 Sociality of the species

Important information about species population dynamics, ecology and behaviour can be gained by studying the societies in which animals live (Whitehead, 1997; Connor, *et al.*, 2000). Kappeler and van Schaik (2002) detail that a society has three component parts: social organisation, a mating system and the social structure. The first describes a society's demography, including its group size, sex ratio, age composition and spatiotemporal cohesion. The second is concerned with describing mating interactions both genetically and behaviourally whilst the third describes the social interactions between individuals regardless of age, sex or group size. This third component, social structure, is the focus of this study. Hinde (1976) developed a framework where social relationships between a pair of individuals (a dyad) can be defined by the pattern of social interactions between them. These dyadic relationships can then be used to characterize a society's social structure. It is therefore important when studying animal social structure that interactions between individuals in a society are examined and that this is done over time to allow patterns and trends to be uncovered (Hinde, 1976; Gero, *et al.*, 2005).

Studies on bottlenose dolphin sociality have shown that the species forms complex social relationships in fission-fusion societies (Connor, *et al.*, 2000; Mann, *et al.*, 2000; Lusseau, *et al.*, 2006a). Fission-fusion societies are those where group size and composition are changeable and dynamic (Connor, *et al.*, 2000), as individuals choose to join or leave groups (Mann, *et al.*, 2000; Lusseau *et al.* 2006b), forming large communities whose members frequently change schools (White, 1992; Lusseau, *et al.*, 2006a, b).

Observing and quantifying social interactions within cetaceans however is not easy as they are primarily found underwater out of sight (Whitehead, 1997; Mann, 1999; Mann, *et al.*, 2000). Spatiotemporal groups, individuals found in the same place at the same time, have been suggested to provide a suitable proxy whereby associations within groups can be defined (Whitehead, 1997; Whitehead and Dufault, 1999; Whitehead, *et al.*, 2000). Therefore, studying the factors determining group composition, formation and individual identity are important for understanding cetacean social structure (Mann, *et al.*, 2000; Gero, *et al.*, 2005).

1.4 Grouping in Bottlenose Dolphins

It is understood that “there is no automatic benefit from group living but there are universal detriments” (Alexander, 1974), suggesting that grouping would not occur unless the benefits outweighed the costs (Connor, *et al.*, 2000). Trade-offs between the costs and benefits of grouping are thought to determine animal social systems (Mann, *et al.*, 2000; Ansmann, *et al.*, 2012), with fission-fusion societies potentially evolving to allow individuals to group when benefits outweigh the costs and disband when the situation reverses (Wrangham, *et al.*, 1982; Connor, *et al.*, 2000), so that factors affecting group formation may affect the resulting associations formed (Wiszniewski, *et al.*, 2010).

1.4.1 Benefits and Costs of Grouping

Predation and resource availability have been suggested as factors determining grouping in fission-fusion societies (Norris and Dohl 1980; Wrangham, 1982; Wiszniewski, *et al.*, 2009), with shark predation being thought the primary factor determining group size in many cetaceans (Norris and Dohl 1980; Wells, *et al.*, 1980). A variety of sharks, including tiger sharks (*Galeocerdo cuvieri*), great white sharks (*Carcharodon carcharias*), bull sharks (*Carcharhinus leucas*) and dusky sharks (*Carcharhinus obscurus*), as well as killer whales (*Orcinus orca*) are most often implicated as predators of cetaceans (Long and Jones, 1996) and several of these have been associated with attacks on near shore bottlenose dolphin populations (McBride and Hebb, 1948 in Connor, *et al.*, 2000 p.204). By grouping, individuals can enhance their survival through increasing predator detection and decreasing the rates of attack per individual. Decreased rates of attack per individual are gained through dilution and confusion effects, where rates of capture are reduced due to the synchronous movements of grouped individuals (Landeau and Terborgh, 1986; Turner and Pitcher, 1986; Miller, 1922 in Connor, *et al.*, 2000 p.206). Additional benefits include allowing some individuals to reduce their own vigilance in favour of other activities, such as foraging (Beauchamp, 2001, Davies, *et al.*, 2012).

When predation pressures are low prey availability may have a more central role in determining group size (Würsig, 1986). Cardigan Bay is free from the major predators of bottlenose dolphins and studies have shown that prey availability is probably the main determinant of range in the Cardigan Bay bottlenose dolphin population (Pesante, *et al.*,

2008a, b). Cooperation has been observed in bottlenose dolphins where fish are trapped near shore or in groups (Reynolds, 2000). Fission-fusion mammal societies have been found to respond to resource availability, with scarce resources resulting in one large well connected group that facilitates information sharing regarding unpredictable patches (Connor, *et al.*, 2000). Abundant resources have, however, been found to result in highly clustered social networks (Cross *et al.*, 2004; Sundaresan *et al.*, 2007; Chaverri, 2010; Ansmann, *et al.*, 2012). This is supported by studies showing that when resources are defensible and able to support more than one individual, group formation is favoured (Wrangham, 1980)

Grouping does not come without costs; groups can suffer increased rates of detection by predators as well as resource competition (Wrangman, 1980; Norris and Dohl, 1980, Mann, *et al.*, Ansmann, *et al.*, 2012). However, within marine environments these costs are considered to be fairly low, as detection of groups does not seem to be greater than for individuals (Pitcher and Parish 1993). Costs associated with locomotion are also considered to be lower in marine environments, thus decreasing the costs of increased foraging effort (Connor, *et al.*, 2000). Other costs associated with grouping include increased spread of parasites and disease amongst individuals (Connor, *et al.*, 2000). The flexibility of fission-fusion societies allows dolphins to react to environmental factors and, depending on the situation, to form optimal group sizes.

1.4.2 Associations Formed within Groups

Groups form when individuals come together. Whether this is a reaction to external factors such as prey availability or through genuine preferred associations is an important distinction (Lusseau, *et al.*, 2006a). Within a population individuals will encounter and associate with a number of others, forming preferred associations with specific individuals; these associations will then determine the social structure (Hinde 1976, Connor, *et al.*, 2000). Social structure then determines the genetic make up of populations (Pusey and Wolf, 1996; Sugg, *et al.*, 1996, Krutzen, *et al.*, 2003) the information transfer pathways (King, 1991, McComb, *et al.*, 2001; Leavens, 2002), the spread of diseases (Newman, 2002; Corner, *et al.*, 2003) and the way in which populations exploit their environments (Hoelzel, 1993; Baird and Dill, 1996; Connor, *et al.*, 1998). The fission-fusion societies of bottlenose dolphins are typically characterised by associations that vary in strength and stability over time (Wells, *et al.*, 1987; Gero, *et al.*, 2005; Foley, *et al.*, 2010). Strong bonds

with preferred associates are those where individuals show consistent affiliative preferences, spending more time together than would be expected by chance (Lusseau, *et al.*, 2006a). These bonds are formed primarily to increase an individual's reproductive success, varying according to ecological conditions, sex, age and social position (Connor, *et al.*, 2000).

Within bottlenose dolphins, marked sex differences have been found in the associations made by males and females (Wiszniewski, *et al.*, 2009). Males have been recorded to form very strong long term associations with one or two preferred companions; these small groups are called alliances and are usually formed to consort females (Connor, *et al.*, 2001). Such alliances are also found in chimpanzees (Mitani and Amstler, 2003). Male-male alliances in bottlenose dolphins can last for many years; for example, alliances of 20 years were found in the bottlenose dolphin (*T. truncatus*) population of Sarasota Bay, Florida, and for 12 years in the bottlenose dolphin (*T. aduncus*) population of Shark Bay, Australia (Connor, *et al.*, 1999). Complicated male alliance formation has also been demonstrated in the bottlenose dolphin population in Shark Bay where males have been found to make second order alliances (Connor, *et al.*, 1999; Connor, 2007) in order to attack, or defend against, other male alliances. Second order alliances, however, are less stable and endure for only a few years (Connor, *et al.*, 1999). These bonds within males are therefore very important in increasing those individuals' reproductive success.

Such strong alliances have not been found between females. Females naturally form very strong bonds only with their calves. Interestingly, a similar strength of association is found between males in long term stable alliances demonstrating the strength and consistency of those alliances (Connor, *et al.*, 1999). Studies have shown that female alliances are variable. Some females have no or very few strong associations whilst others seem to live in bands, with most females having associations somewhere in between (Connor, *et al.*, 2000; Lusseau, *et al.*, 2006). Observations of female grouping within the *T. aduncus* population of Port Stephens suggests that those associating closely tend to be more genetically related, but that by also having non-related associates, other factors may also play a part in determining associations (Moller and Harcourt, 2008). One factor thought to determine female associations and grouping is reproductive state, with mothers preferentially associating with other mothers (Lusseau, *et al.*, 2003). Associations between males and females are usually through reproductive consortships (Wells, *et al.* 1987).

Additionally community divisions within bottlenose dolphin populations have been found to result from individuals preferentially assorting by age, sex and behavioural state (Lusseau and Newman, 2004). Where males and females are constrained in their associations by reproductive effort and state, juveniles will group together based more on behaviours as they are less constrained by reproductive effort.

The complexity of bottlenose dolphin society has only recently begun to be understood. Bottlenose dolphins have particularly large brain sizes with respect to their body size (Connor, 2007). It is possible that this large brain size, supported by high quality diets and metabolic rate, has allowed complex social systems to evolve (Connor, 2007). Within dolphin societies, there is relationship uncertainty between individuals. Dolphins living in certain areas, including Shark Bay in Australia, can occupy large overlapping areas where, for example, dolphin A knows B, and B knows C, but A and C, whose ranges do not overlap, do not know each other (Connor and Mann, 2006; Connor, 2007). This produces relationship uncertainty, where individuals know some better than others. This suggests greater complexity than in closed primate systems where individuals can build a good knowledge of others social relationships (Connor, 2007). In addition to relationship uncertainty, imitative abilities and motion perception within bottlenose dolphins further suggests societies as complex as those within primates (Connor 2007). The complexity of open fission-fusion societies and alliance formation is thought to be facilitated by synchronous behaviours displayed between individuals (Connor, 2007).

Developing and maintaining long term associations is important for the bottlenose dolphin, as well as many animal societies, as long term associations can improve an individual's reproductive fitness. This is achieved through mechanisms including enhanced breeding success e.g. red howler monkeys , *Alouatta seniculus* (Pope, 2000), information exchange e.g. African Elephants , *Elephas maximus* (McComb *et al.*, 2001), reduced aggression e.g. spider monkeys *Ateles geoffroyi* (Asensio *et al.*, 2008) as well as reduced predation and infanticide risks e.g. (*Tursiops* spp) (Dunn, *et al.*, 2002; Wiszniewski, *et al.*, 2009).

1.5 The Effects of Disturbance

There is significant potential for conflict between some bottlenose dolphin populations and anthropogenic activities arising from the nearshore habitat preference of bottlenose dolphins (Bejder and Samuels, 2003; Bejder, *et al.*, 2006a, b, Lusseau, *et al.*, 2009).

Furthermore, within long term resident populations there is a danger of short term effects building up cumulatively. Anthropogenic activities can disrupt and threaten populations in a number of ways including entanglement in fishing nets (Vidal, 1993; Wells and Scott, 1999; Reynolds, *et al.*, 2000), increased exposure to environmental pollutants (Morris, *et al.*, 1989; Borrel, 1993) and disturbance from fishing boats, tourist trips and recreational water crafts (Evans, *et al.*, 1992; Bejder and Samuels, 2003; Bejder, *et al.*, 2006a, b; Lusseau, 2006). If bottlenose dolphin populations are to be effectively conserved the wide spread impacts resulting from anthropogenic conflicts need to be understood. This study will focus on how the anthropogenic impact of boat disturbance may affect bottlenose dolphin behaviour.

1.5.1 Responses to Disturbance

A number of studies have looked at the effects of disturbance on the physical and acoustic behaviour of dolphins (Miller, *et al.*, 2008; Lemon, *et al.*, 2006; Highman and Bejder, 2008). The preference for shallow near shore habitats by bottlenose dolphins can be attributed to prey distributions and the relative safety of shallow water habitats for raising calves (Würsig and Würsig, 1979; Wells, 1993; Barco, *et al.*, 1999), Increased boat disturbance has been reported to elicit behavioural changes (Lusseau, 2003; Constantine *et al.*, 2004) and resulted in injury and even death in some circumstances (Wells and Scott, 1997; Miller, *et al.*, 2008). Typical behavioural responses observed include changes in direction of travel (Miller, *et al.*, 2008), increased dive duration (Janik and Thompson, 1996; Lusseau, 2003), changes in dolphin behavioural state (Nowacek, *et al.*, 2001; Lusseau, 2003; Constantine, *et al.*, 2004), increased group cohesion (Bejder, 1999; Nowacek *et al.*, 2001) and increased breathing synchrony (Hastie, *et al.*, 2003). These are all responses associated with evasion (Miller, *et al.*, 2008) and are similar to responses observed to some shark predators (Tayler and Saayman, 1972; Miller, 2008). Conversely, some dolphins have been observed to approach boats, this behaviour is most common within curious, playful juvenile (Constantine, 2001) or with dolphins following fishing boats for an easy meal (Ansmann, *et al.* 2012). Cumulative short term responses to boats, either positive or negative, could have impacts on long term dolphin survival (Miller, *et al.*, 2008). By either approaching or avoiding boats, dolphins may reduce the time they would spend socializing, feeding or resting causing decreased energy acquisition and increased energy expenditure (Miller, *et al.*, 2008), potentially leading to lower individual fitness, reproductive success and thus a less viable population. The full extent of disturbance on a population

will be differentially linked to resource availability and acquisition (Bejder, *et al.*, 2006; Miller, *et al.*, 2008).

Bejder, *et al.*, (2006a) found individual bottlenose dolphins of Shark Bay in Australia will react differently to disturbance. Some individuals were found to show long lasting changes in behaviour by completely leaving a disturbed area in favour of a non-disturbed area. Those remaining in disturbed areas showed more moderate responses to disturbance. A similar effect has been noted for bottlenose dolphins in the coastal waters of Croatia, where permanent or temporary avoidance of one area of the Mediterranean was observed in response to seasonal increases in boat traffic (International Whaling Commission, 2007). Avoidance of preferred habitats has also been observed in White-tailed deer where their home ranges and activity may alter in response to disturbance (Dorrance, *et al.*, 1975).

1.5.2 Effects of Disturbance on Community Structure

It is important that the effects of boat disturbance, both their physical presence and the noise generated, are studied with respect to near shore bottlenose dolphin populations due to the continued increase in recreational boats and watercrafts leaving coastal towns (Buckstaff, 2004). This study will aim to assess the impact of boat disturbance on the community structure of the population of bottlenose dolphins inhabiting Cardigan Bay, Wales. The effects of boat disturbance will be assessed with particular respect the social networks of the bottlenose dolphins.

2. Conservation of the Bottlenose Dolphin

Within Europe, the bottlenose dolphin has been designated a species for special protection (European Union, 2007; Evans and Pesante, 2008), this designation requires that countries in which the species occurs have to protect the populations and limit the threats they face. This requirement has resulted in protected areas being designated, and management plans produced for the two main semi-resident populations of bottlenose dolphin found within the UK. The next section discusses the legislative background and management plans in place for Cardigan Bay in Wales, as this is where the present study is focused upon.

2.1 Legislative Background

Regulations and management are frequently used as a means to protect and ensure the long term survival of vulnerable species and habitats. A number of commitments have been made on conserving the world's natural biodiversity. In 1979, the UK adopted the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention), which came into force in 1982. The Bern Convention aims to ensure the protection and conservation of wild animal and plant species as well as their natural habitats, in addition to increasing cooperation between contracted countries and regulating the trade and exploitation of particular species (JNCC, 2012a).

Within Europe the European Commission developed Council Directive 92/43/EEC on the Conservation of Natural Habitats of Wild Fauna and Flora. The Directive was adopted in 1992 and is known as the European Community's Habitats Directive (EC Habitats Directive) (JNCC, 2012c). The EC Habitats Directive represents one way in which European Union member states can honour international commitments and is arguably the strongest conservation legislation within Europe. The Directive requires Member States to restore and maintain habitats and species of Community importance at favourable conservation status (JNCC, 2012c). Aims of the Directive are outlined under Article 2 of the Directive (Box 1).

Box 1. Article 2 (Directive 92/43/EEC)

1. The aim of this Directive shall be to contribute towards ensuring the bio-diversity through the conservation of natural habitats of wild fauna and flora in the European territory of the Member States to which the Treaty applies
2. Measure taken pursuant to this Directive shall be designed to maintain or restore, at favourable conservation status, natural habitats and species of wild fauna and flora of Community interest
3. Measures taken pursuant to this Directive shall take account of economic, social and cultural requirements and regional and local characteristics

(European Union, 2007)

2.2 SAC Designation for the Bottlenose Dolphin

The bottlenose dolphin (*T.truncatus*) is listed under Annex II and Annex IV of the EC Habitats Directive (European Union, 2007). The Annexes detail the habitats and species that are of European importance, listing habitats under Annex I and species under Annex II, IV or V. Regarding species designation, the Annexes afford different levels of protection and allow for some overlap in designation. As a species listed under Annex II, the bottlenose dolphin is a “species of Community interest whose conservation requires the designation of special areas of conservation (“Natura 2000 sites”)”. Under Annex IV it is a “species of community interest in need of strict protection” (European Union, 2007).

Annex II protection requires that EU Governments designate Special Areas of Conservation (SACs) for these species. SACs, together with Special Protected Areas (SPAs), designated under the Wild Birds Directive 2009/147/EC, (specifically for the protection of birds) form part of the ‘Natura 2000’ network (CCW, 2005; JNCC, 2012c; European Union, 2007). Inland sites are termed ‘European Sites’ and those including marine areas become ‘European Marine Sites’ (CCW, 2005). Protection of the species under Annex IV prevents the “deliberate capture or killing of specimens in the wild; deliberate disturbance of animals in the wild, particularly during the period of breeding, hibernation and migration; and deterioration and destruction of breeding sites or resting places”.

Within the UK there are two SACs designated primarily for the protection of the bottlenose dolphin; the Moray Firth SAC in Scotland and the Cardigan Bay SAC in Wales. For both SACs the bottlenose dolphin is designated the primary feature for the site. However, additional species present within the Cardigan Bay SAC are listed as qualifying features, including the Atlantic Grey Seal, *Halichoerus grypus*, the Sea Lamprey *Halichoerus grypus* and the River Lamprey *Lampetra fluviatilis*. Habitats present as qualifying features include reefs, submerged or partially submerged sea caves and sandbanks partially covered by sea water all the time (CCC, 2008; JNCC, 2012d). Additionally, the bottlenose dolphin is listed as a qualifying feature for the Pen Llyn a’r Sarnau SAC which is found at the northern end of Cardigan Bay (JNCC, 2012e).

Cardigan Bay and the Moray Firth have been designated as SACs for the bottlenose dolphin as they are the only sites where semi-resident populations of bottlenose dolphins can be found. Both sites have been identified as having the physical and biological factors necessary for successful reproduction, and thus sustained bottlenose dolphin populations (JNCC, 2012f). In addition to protection from SACs, a Species Action Plan for small cetacean species is also in place (JNCC, 2012f).

2.3 Practical Requirements of a Special Area of Conservation

Once an area is designated as an SAC, it is required that the features, either habitats or species, are kept in Favourable Conservation Status as defined by Article 1 of the EC Habitats Directive (Box 2) (CCW, 2005). The primary feature for Cardigan Bay SAC is the bottlenose dolphin, making it this population which must be kept in Favourable Conservation Status (CCW, 2005).

Box. 2 Favourable Conservation Status of a species

Conservation status of a species means the sum of the influences acting on the species concerned may affect the long-term natural distribution and abundance of its population within the territory referred to in Article 2.

The conservation status will be taken as 'favourable' when:

- Population dynamics data on the species concerned indicate that it is maintaining itself on a long term basis a viable component of its natural habitats(s), and
- The natural range of the species is neither being reduced, nor is likely to be reduced for the foreseeable future, and]
- There is, and will probably continue to be , a sufficiently large habitat to maintain its populations on a long-term basis

(European Union, 2007)

Favourable Conservation Status is determined using four conservation objectives (European Union, 2007). To determine Favourable Conservation Status of a species values are established, above or below which, conservation status can be considered favourable or unfavourable (European Union, 2007). Common Standards Monitoring (CSM) programs, led by the JNCC, are used to monitor these values (JNCCg, 2012) to allow accurate interpretation of performance indicators and population trends, increasing the understanding and identification of factors affecting the population (CCW, 2005; European Union, 2007). This then allows legislation and a management plans for an SAC to be developed.

2.4 Threats to the Bottlenose dolphins of Cardigan Bay

Cardigan Bay is located on the west coast of Wales. The bay is large spanning 100km from north to south and within it contains both the Cardigan Bay SAC in the south and the Pen Llyn a'r Sarnau SAC in the north.

The main threats to the dolphins of Cardigan Bay are those associated with anthropogenic activities such as recreational boating and wildlife watching tours, which result in increased noise pollution, disturbance and pollution (Pesante, *et al.*, 2003, Veneruso, and Evans, 2012). Fishing within the bay is relatively light, yet recreational boating activity is increasing as summer months attract large influxes of visitors resulting in increased water craft use and wildlife watching trips running along the coastline (Hoyt, 2001; CCW, 2005; O'Connor, 2009), as well as potential decreases in prey availability from increased recreational fishing. Short term responses to boat disturbance, such as avoidance measures, could have long term consequences on dolphin reproductive success and thus population sustainability. The degree to which damaging anthropogenic activities are affecting the Cardigan Bay bottlenose dolphins population and maintenance is not known clearly, but there is some indication that individuals within areas of high vessel activity are moving away (CCW, 2005; Pesante, *et al.*, 2008a; Veneruso and Evans, 2011a; Lohrengel *et al.*, 2012).

2. 5 Existing management plans

As stated earlier, one of the conservation objectives of the SAC is to put in place management measures to protect the species. Management of boating activities has been present along the Ceredigion Coast for over ten years. Before Cardigan Bay was designated an SAC in 1996, Ceredigion County Council had been promoting a voluntary Code of Conduct since 1992 for recreational boat users (CCC, 2009). The code of conduct advocates boating practices that minimise disturbance to seabird breeding areas, seals and dolphins (CCC, 2008). It aims to achieve this by detailing the separation distances that should be observed between visitor boats and bottlenose dolphins. Studies conducted on the effectiveness of the Code of Conduct indicate that when the code is followed, dolphins are less likely to move away from boats and it is now being followed in 90% of the encounters between boats and dolphins (Pierpoint, *et al.*,2009). Highest compliance was found around New Quay and declined toward the south. In addition to the Code of Conduct, bye-law speed limits operate on boats in the harbours and around bathing beaches, with additional voluntary speed limits stretching along the Marine Heritage Coast running from New Quay Head south toward Ynys Lochtyn (CCC, 2008).

After being initially introduced as a voluntary Code of Conduct, the code was made compulsory in 1996. Substantial effort has gone into educating both users and visitors of the bay and since the code was made compulsory, powers are present for the harbour master to give warnings and remove moorings for offenders consistently break the rules (CCC, 2010). Monitoring compliance is obviously difficult. However, at present it seems that compliance within the New Quay area is fairly high, which could be a result of many of the visitors re-visiting the Bay and being more aware of the importance of keeping their distance from marine mammals. The Welsh Government has identified Ceredigion, (the county in which Cardigan Bay is located), as an area with great economic potential from an increasing tourism industry (CCC, 2010). Despite emphasis being placed on sustainable development of the area to ensure a long term industry, the aim is to attract more tourists and the result will likely be an increase in recreational boating activity thus increasing pressures from disturbance. The fact that this area contains two SACs requires the relevant authorities to understand how factors, such as disturbance, will affect the population before developments encouraging those factors are promoted. This will help

maintain the population in favourable conservation status and prevent developments that may negatively affect this status.

3. Aims and Objectives

In the case of the bottlenose dolphin, many studies have shown that disturbance elicits a variety of reactions, including increased group cohesion, dive duration, breathing synchrony and even changes in preferred habitat (Janik and Thompson, 1996; Nowacek, *et al.*, 2001; Hastie, *et al.*, 2003 Lusseau, 2003; Constantine, *et al.*, 2004; Miller, *et al.*, 2008;) responses likened to those with predation risk, suggesting that dolphins feel threatened by boats. Behaviour could have long term effects due to changes in energy allocation and potentially result in decreased individual fitness and reproductive success.

As recreational boat usage and numbers continue to increase across the entirety of Cardigan Bay, the impact on the resident bottlenose dolphins needs to be monitored and understood. This will allow effective management to be developed and favourable conservation status maintained. The effect of disturbance on community structure has not yet been studied extensively and so the focus of this study, with the aims as follows:

- To determine if community structure differs in areas of high vessel traffic compared with areas of low vessel traffic
- To determine if community structure differs between the areas of regulated high vessel traffic and areas of unregulated high vessel traffic

The results of this study should add valuable knowledge to assessing the impact of boat disturbance on bottlenose dolphins by adding an understanding of the effects of disturbance on community structure. Furthermore, comparisons between regulated areas of high vessel traffic and unregulated areas of high vessel traffic should allow important conclusions to be drawn on whether the current management plan is being successful in reducing impacts of boat disturbance on the dolphins.

4. Study Site: Cardigan Bay and the Cardigan Bay SAC

Cardigan Bay encompasses the west coast of Wales and is the largest embayment found in the British Isles (Pesante, *et al.*, 2008b). It stretches from the Llyn Peninsula in the north to St David's in the south (Roberts *et al.*, 1998) covering a total area of 4986.86km² (Pesante, *et al.*, 2008). Within the bay there are two SACs, Cardigan Bay in the South and Pen Llyn a'r Sarnau SAC in the north (Figure. 1).

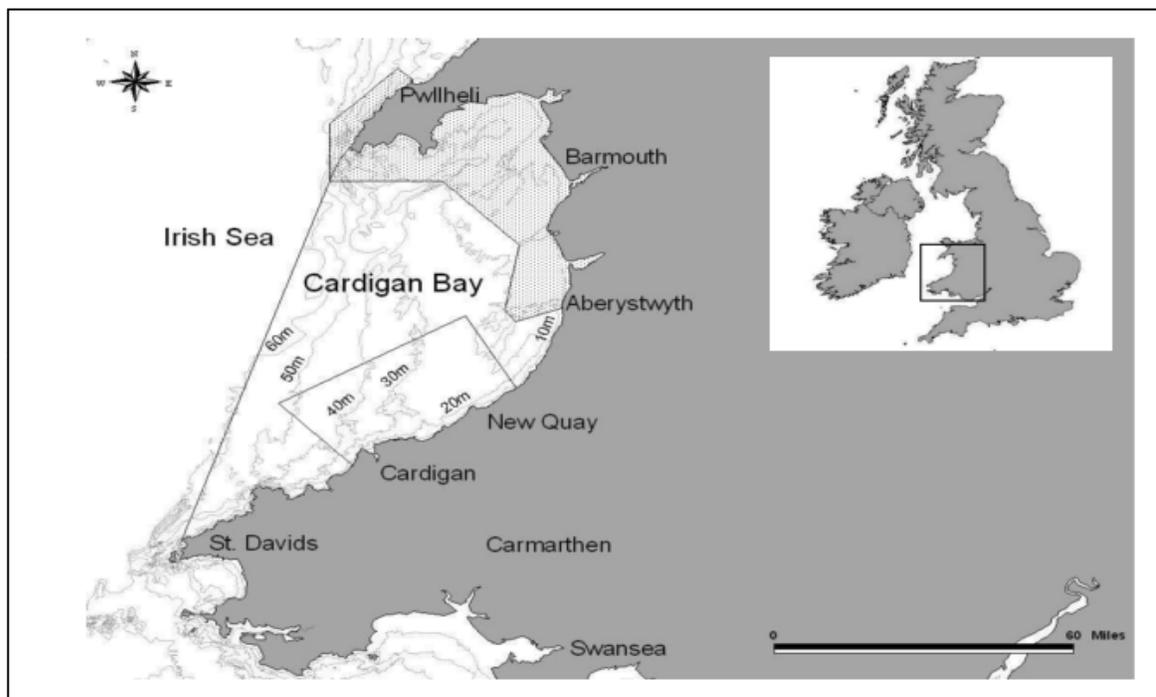


Figure 1 Study site: Cardigan Bay rectangle shows Cardigan Bay SAC, the hatched polygon shows Pen Llyn a'r Sarnau SAC with the diagonal line showing the edge of Cardigan Bay (Sourced: Pesante, *et al.*, 2008b)

The Bay is relatively shallow with gentle slopes and an average depth of 60m (Evans, 1995). Water temperatures range from 16°C offshore and 20°C inshore during August/September to minimums of 5°C in February/March (Evans, 1995; CCC, *et al.*, 2001).

Within Cardigan Bay there are three main estuaries inputting fresh water, with the potential to affect local water temperatures, salinity and quality, salinity ranges from 34.2‰ in summer and 33.3‰ in winter (Evans, 1995). Tidal current speed primarily affects the substrate, where currents are strong substrate is gravely, where current speed and energy is low, substrate is muddy. Tides within the Bay are semi-diurnal entering from the St Georges Channel (Evans, 1995).

Bottlenose dolphins are observed throughout the year within Cardigan Bay and show seasonal differences in group size and dispersion (Baines and Evans, 2009). Over summer groups tend to be small and are observed close to the coast, group size peaks in September and October as some individuals move into North Welsh waters for winter in groups of between 50-150 individuals (Baines and Evans, 2009; Veneruso and Evans, 2012). Over summer, dolphins range across the entire Bay with sightings being most common along the inshore waters from Aberystwyth to the Teifi estuary including New Quay, Ynys Lochtyn, Aberporth and Mwnt (Evans, 2000). Studies on the bottlenose dolphins in the Bay suggest that the Bay is used for breeding, socializing and feeding (Evans, 1995; Baines and Evans, 2012). Studies show the population using the Bay includes individuals of high site fidelity, those that visit occasionally and others that pass through (Pesante, *et al.*, 2008b).

5. Methods

5.1 Cardigan Bay Area Divisions

Cardigan Bay was divided into a) regulated areas of high vessel traffic, b) unregulated areas of high vessel traffic and c) areas of low vessel traffic. Areas of high and low vessel traffic were defined based on boat data collected during dedicated cetacean surveys (See chapter 5.2) for the years 2006-2011 where the number of boats present within visual range were logged every 15 minutes (Lohrengel, *et al.*, 2012). Areas of high vessel traffic were those with over 30 boats observed per hour of effort. Regulated areas were those where the Cardigan Bay Boat Management Plan is enforced and followed. They were defined independent of SAC status since not all areas within an SAC are regulated, although areas of regulated high vessel traffic did mostly fall within the Cardigan Bay SAC. Areas of low vessel traffic were defined independent of whether or not they were regulated.

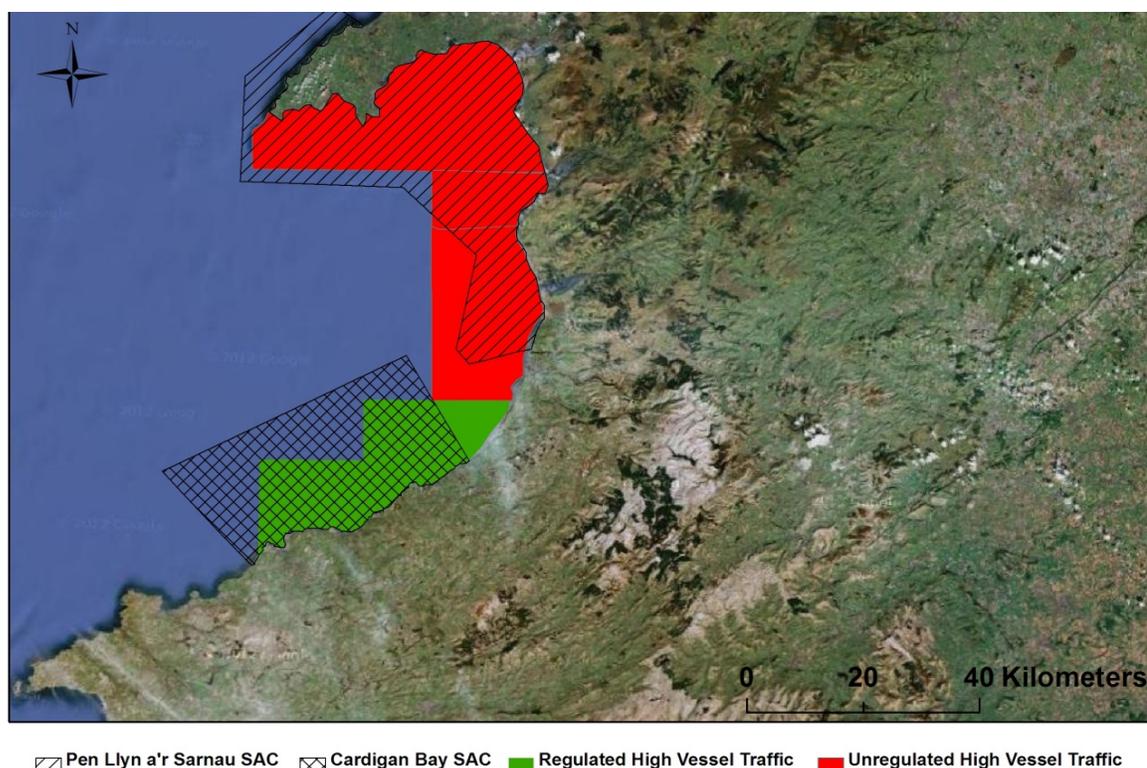


Figure 2. Cardigan Bay showing areas of regulated and unregulated high vessel traffic . Areas of low vessel traffic are those not included in areas defined as areas of regulated or unregulated high vessel traffic. Both the Cardigan Bay SAC and Pen Llyn a'r Sarnau SAC are shown (Image: GoogleMaps)

5.2 Field Data Collection

Dolphin encounter data used in the community structure analysis were collected from both land and boat based surveys between April and November, between 2001-12. Surveys would be conducted only if light conditions were good and the sea state was three or less on the Beaufort scale. The Beaufort scale grades sea state where 0 = flat glassy water, 1 = small ripples and wavelets, 2 = wavelets forming small peaks and 3 = well defined peaked wavelets with some white tops visible (Met Office, 2012). These conditions gave the best chance that dolphins, where present, would be spotted. If during a survey the visibility decreased due to heavy rain or fog, and/or the sea state rose to above three, the survey trip was terminated due to the increased possibility of unreliable sightings and a reduced chance of reliable photo identification photos being taken (Alger, 1992).

5.2.1 Survey Boats

Between 2001 and 2012, a number of different survey boats had been used for data collection, however data collection procedures were standardised across platforms. Boats were typically small motor boats of between 10 and 15 meters length, powered by one or two 100hp diesel engines. A typical example of a boat used for survey is shown in (Figure. 3). This vessel, the Dunbar Castle, was primarily used for line transect surveys out of New Quay harbour and has a cruising speed of approximately 7-8 knots (Pesante, *et al.*, 2008b).

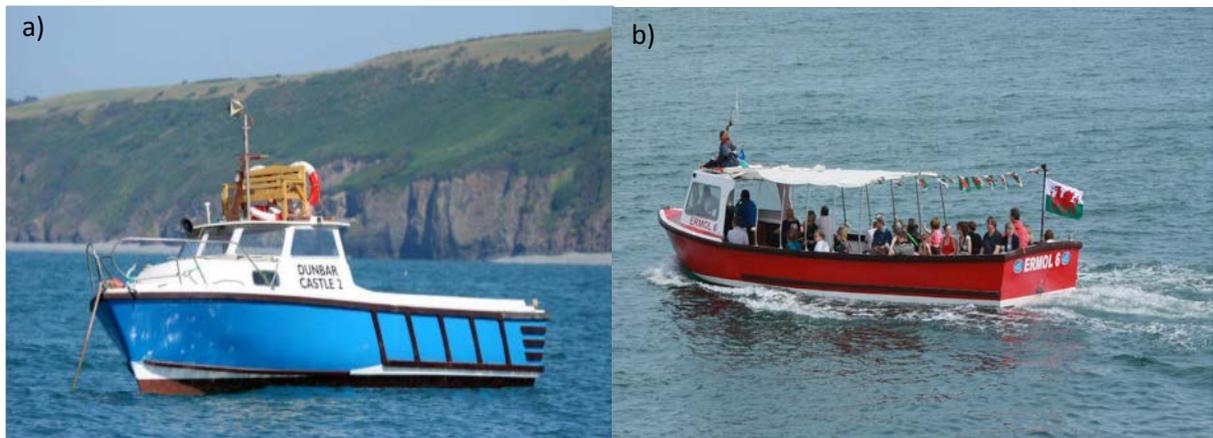


Figure 3. Boats used to collect survey data. The Dunbar Castle (a) primarily used for line transects (Sourced: Pesante, *et al.*, 2008b) and the Ermol VI (b) primarily used by volunteers for opportunistic photo ID (Photograph courtesy of M. Sostres).

5.2.2 Line transect Surveys of Cardigan Bay SAC

Boat-based surveys were conducted throughout Cardigan Bay, but with emphasis focused upon the Cardigan Bay SAC. The Cardigan Bay SAC was divided into two strata; an inshore and an offshore one. The inshore strata extended approximately 11 km from the coast, and the offshore strata ran to approximately 23 km. Line transect surveys were conducted in these areas, zigzagging from the coast to the edge of either the inshore or offshore strata. Transects were chosen at random before a survey. If a transect had to be terminated before it had been completed, it was resumed and finished at the next survey opportunity.

A minimum of 5 people were needed to conduct line transect surveys although most surveys ran with 7-10 observers aboard. Surveys were undertaken using two primary observers, two independent observers and one person to record effort. Primary observers were positioned on the roof of the boat to give them a greater field of view and searched with the naked eye, independent observers were positioned where there was good visibility, either at the front or the back of the boat, and searched using binoculars, and the person recording effort would be positioned near the independent observers. Once dolphins were sighted, information was recorded on a sightings form. Information on time, species, group size, composition and behavioural characteristics were noted and the sighting was also given a sightings reference number. Behavioural characteristics used included slow or normal swim, fast swim, feeding, suspected feeding, leaping/splashing, tail-slaps, bow-riding, resting/milling, socialising and reaction to boat.

Effort was recorded on an 'effort form' every 15 minutes and additionally when weather or boat course changed, or there was a sighting event. Entries resulting from a sighting were given a unique reference number that was also used by primary observers. Information included position (latitude and longitude), effort status (casual watch, dedicated search, photo-ID and line transect), sea state, swell height, range of visibility (0km, 1-5km, 5-10km, and 10km>), precipitation intensity and type, and the angle of any glare affecting the observers field of view.

5.2.3 Additional boat based and land based surveys

In addition to line transect surveys undertaken within the Cardigan Bay SAC, boat based surveys were undertaken ad-libitum across the Bay. These surveys covered areas within the Pen Llyn a'r Sarnau and also the southern areas of the Bay. Data collection protocols used were similar to line transect surveys, the main difference being that only two observers would search, using binoculars, at one time. Opportunistic photo-ID was also conducted from one of the wildlife watching boats; Ermol VI, which leaves New Quay and operates 1-2 hour trips long the Heritage Coast. Research volunteers joined some of these trips and conducted photo-identification where possible. Whilst the boat would not actively approach the dolphins, photo-identification could occur if the dolphins came close to the boat.

Land based photo-identification was also opportunistic. Volunteers would conduct land watches from New Quay pier monitoring dolphin presence in the harbour. If dolphins came close to the pier photo-identification was conducted.

5.2.4 Photo-identification and group determination

Once dolphins had been spotted, during line transect and ad-libitum surveys, they were approached and photo-identification was conducted, usually by two photographers at the front of the boat, following the methods of Wursig and Jefferson (1990). Photographs were taken with DSLR cameras and zoom lens. Dolphins were tracked by the remainder of the research team who would instruct the skipper and photographers on animal movement. Groups upon which photo-identification was conducted are henceforth referred to as 'encounters'. Encounters would last until

- all the dolphins had been photographed;
- dolphins were lost;
- dolphins began to show signs of avoidance such as changes in travel direction or prolonged diving;
- visibility deteriorated or
- time allowed by the licence received from Countryside Council for Wales had expired.

At this point, the encounter was terminated and the boat would leave the dolphins. Photo-identification images were taken of the animal's dorsal fin and back from a perpendicular angle (Figure 4). Attempts were made to photograph all animals observed in an encounter regardless of their markings.



Figure 4. Dorsal fin of a 'well marked' adult female showing nicks and scarring used for identification (Sourced: Pesante, *et al.*, 2008a)

All the individuals photographed in an encounter were considered to be part of the same group. A group was defined as individuals observed within 100m of each other and performing the same activity or travelling in the same direction (Wells, *et al.*, 1987). Group size was determined by counting individuals present, and then confirmed using photo-identification. Gender was determined with photographs of aerial or bow riding behaviour showing the genital area (Smolker, *et al.*, 1992). Additionally gender was suspected when adults occurred in close association with young calves (recorded as probable females) or when relatively large individuals were observed with heavy dorsal fin scarring (recorded as probable males) (Wilson, 1995). If more than one group of dolphins was sighted during a survey, the groups were recorded as separate encounters each with different unique sightings number. To separate photos of dolphin encounters, a numbered spacer photo was taken.

Photographs were downloaded onto a computer and analysed using ACDSee 5.0.1 digital imaging software, following matching protocols developed by Sea Watch Foundation. Only

high quality photos were used for identification to avoid false positive or negative errors (Scott, *et al.*, 1990). Identification was conducted based on variation of dorsal fin shape, nicks, lesions and scars (Figure) (Wilson, *et al.*, 1999), with dolphins being categorised as

- Marked - where the animal can be identified from either side from distinct markings on the dorsal fin
- Slightly marked - where the animal can be identified from either side but the markings on the dorsal fin are less distinct and can only be resolved from high quality photos
- Right - pictures taken of the right side of the dorsal fin without markings in the form of nicks, but with pigmentation patterns or scars
- Left - pictures taken of the left side of the dorsal fin without markings in the form of nicks, but with pigmentation patterns or scars

Only well marked or slightly marked individuals were included in this analysis.

6. Data Analysis

6.1 Effort and Reliability

Trade-offs are made in association studies between ensuring that data are reliable, animals are seen often enough to be representative of their associations, and that as many animals as possible are included (Elliser, *et al.*, 2012; Bejder, *et al.*, 1998). This study only included animals seen more than five times during the period 2001-12 and were considered associated if sighted in the same group. Data were then pooled into three year blocks, 2001-03, 2004-06, 2007-09 and 2010-12 to try to ensure that sufficient individuals were included in the analysis. This was particularly important in those areas designated as having low vessel traffic where encounters with individuals were low. Pooling data also allows between year studies to be undertaken, and thus long term trends to be determined, as well as allowing comparisons with other studies (Elliser, *et al.*, 2012).

6.2 Group Size and Determination of Associations

Group size was determined, and significant size differences between areas tested with a paired t-test using Minitab15.

To analyse measures of association, the Half Weight Index (HWI) was used to calculate the Coefficient of Association (CoA) (Whitehead, 2006) using the social analysis program SOCPROG 2.4 (Whitehead, 2009). A number of association indices exist for measuring association. The HWI was most appropriate for this study since it took into account possible observer bias during sampling techniques, for example surveys where it was not possible to identify all the individuals within the group (Cairns and Schwager, 1987; Lusseau, *et al.*, 2006b). Furthermore, it allows for comparisons with other bottlenose dolphin studies (e.g. Wells, *et al.*, 1987; Lusseau, *et al.*, 2003). The HWI was calculated as follows

$$HWI=X/(X+0.5(Ya+Yb))$$

Where: X = the number of times both dolphin individuals a and b were seen in the same group

Ya = the number of groups in which dolphin a was seen without dolphin b

Yb = the number of groups in which dolphin b was seen without dolphin a

Association values produced by the HWI range from 0 to 1, with 0 occurring when two individuals are never seen together, and 1 when two individuals are always seen together.

To establish the reliability of the calculated CoA values, values of social differentiation (S), $S^2 \times H$ (where H is the mean number of observed associations per individual) and the correlation coefficient (CC) were calculated (Whitehead 2008a,b; Elliser, *et al.*, 2011). These measures indicate how well the data analysed truly reflects the social system, allowing conclusions to be made on whether sufficient data have been included in the analysis. Where S is less than 0.3, the society shows slight homogeneity, whereas values over 0.5 indicate well differentiated societies and values over 2 indicate extremely differentiated societies (Whitehead, 2006). Where values of social differentiation are between 0.5 and 1, the number of associations needed to detect preferred companionships is fewer than data sets with low differentiations (Whitehead, 2008a).

Values of cluster coefficients range between 0 and 1, and indicate how well the analysis can detect the true social system; values of 1 show an exact reflection; and values of 0 indicate no reflection (Whitehead, 2008a). Standard errors were calculated using 1,000 bootstrap replicates.

6.3 Association strength and preferred/avoided companions

Pooled CoA's were calculated for all individuals included in the analysis using SOCPROG 2.4. The strength of association indices was then determined using the definition from Gero, *et al.*, (2005) and Whitehead (2008a), where strong associations are defined as those where the individual CoA was more than twice the average of the CoA of the population.

To investigate the possibility of preferred or avoided associations within the population SOCPROG was used to conduct permutation tests. The number of permutations was increased until the p-values stabilised; this occurred at 10,000 permutations with 100 flips. Following SOCPROG guidance (Whitehead, 2006), sampling periods were set to year for all analysis, and associations were weighted by "no. of groups within sample". To conduct the preferred/avoided associations, "permute groups within samples" was chosen (Whitehead, 2006).

6.4 Long term Associations and Community Structure

To determine how communities may be clustered and if disturbance has an effect on clusters non-metric multidimensional (MD) scaling was performed using SOCPROG. An MD plot shows individuals that are closely associated as being plotted close together, whereas those that are weakly associated are plotted further apart (Whitehead, 2009). A value of stress is produced with each plot, and where stress < 0.1, the plot is thought to be of good ordination (Whitehead, 2008a). The number of dimensions used to calculate plots were increased until stress was < 0.1. The starting configuration was set to random for all plots.

Hierarchical agglomerative cluster analysis was also conducted. The average linkage method was used and plots created show the degree of association on one axis and individuals on the other (Whitehead 2009). The plots are produced with a value, the

Cophenetic Correlation Coefficient (CCC), indicating how well the dendrogram matches the association matrix. CCC values > 0.8 indicate that the dendrogram is good match to the association index (Whitehead, 2008a).

6.5 Association Strength and Clustering Coefficient

Strength is the sum of associations with all other animals, and the cluster coefficient shows how well an individual's associates are associated, and therefore, the number of triads found in a network compared with the total number of triads present given the number of animals present in the network (Lusseau, 2006a). It measures the probability that if 'a' and 'b' are associated, and 'a' also associates with 'x', that 'b' and 'x' are also associated (Lusseau, 2006a), these values were calculated using SOCPROG and the information was then used to construct social networks using NetDraw (Borgatti, 2002).

9. Results

9.1. Effort and Reliability

518 days of survey were undertaken between 2001 and 2012 resulting in a total of 1559 dolphin encounters and 476 individuals identified. Of these encounters, 950 groups and 250 identified individuals were included in the analysis after fulfilling the requirements of having either a slightly or well-marked dorsal fin and being sighted at least five times. Of the included individuals, 43 were known females, 13 were known males and 194 of unknown sex. A total of 912 groups were observed in high vessel traffic areas across the Cardigan Bay; of these, 716 groups were observed in the regulated areas of high vessel traffic and 197 in the unregulated areas of high vessel traffic. A total of 39 groups were observed in low vessel traffic areas across the entire bay.

Values of social differentiation (S), H (a measure of the mean number of associations per individual), Correlation Coefficient (CC) and $S^2 \times H$ were calculated for all dolphin groups found in regulated and unregulated areas of high vessel traffic for all years (Table 1). Social differentiation values for regulated areas of high vessel traffic were very high suggesting a very well differentiated social system ($S > 1$) for all three year blocks. Correlation Coefficient values also generated for all three year blocks show that the data are a reliable representation of the social system ($CC > 0.5$). Social differentiation values could not be generated for all 3 year blocks in areas of unregulated high vessel traffic or areas of low vessel traffic, where they were generated, values for areas of regulated high vessel traffic were consistently higher. Those generated for unregulated vessel traffic show a fairly well differentiated social system in pooled years 2004-06, 2007-09 and 2001-12 ($S > 1$) with CC values showing only pooled years 2007-09 and 2001-12 are good representations of the social system ($CC > 0.5$). Therefore, hereafter all community structure comparisons made between regulated and unregulated areas of high vessel traffic will be made between years 2007-09 and 2001-12 unless otherwise stated. Regarding areas of low vessel traffic, social differentiation values could be generated only for years 2001-03 and 2001-12. Corresponding correlation coefficient values are low for the two social differentiation estimates ($CC < 0.5$), with years 2001-12 having the higher correlation coefficient ($C = 0.33$). In order to make comparisons between areas of regulated and

unregulated high vessel traffic and low vessel traffic, only social network values of low vessel traffic areas generated over the entire period 2001-12 are used.

Table 1. Total number of days surveyed, encounters and individuals included in the analysis. Also shows calculated values of social differentiation (*S*), correlation coefficient (*CC*), mean number of associations per individual (*H*) as well as $S^2 \times H$ for regulated areas of high vessel traffic (RHT), unregulated areas of high vessel traffic (UHT) and area of low vessel traffic (LT). Years with high social differentiation and corresponding correlation coefficients are in bold and will be compared in this study.

Year	Days			Encounters			Individuals			Social Differentiation (S)			Correlation Coefficient (CC)			Mean No. Associations per Individual (H)			S ² x H		
	RHT	UHT	LT	RHT	UHT	LT	RHT	UHT	LT	RHT	UHT	LT	RHT	UHT	LT	RHT	UHT	LT	RHT	UHT	LT
2001-2003	85	3	13	138	3	19	157	19	92	2.21	0	0.69	0.69	0	0.26	29.45	7.05	13.83	143.71	0	6.51
2004-2006	94	23	5	152	42	6	212	127	41	3.04	1.02	0	0.71	0.35	0	23.01	16.66	10.88	212.51	17.16	0
2007-2009	122	74	9	207	129	9	193	157	55	3.83	1.93	0	0.82	0.58	0	27.45	20.59	10.47	403.29	76.39	0
2010-2012	119	18	4	219	23	4	184	78	30	2.14	0	0	0.78	0	0	50.11	13.49	13.07	229.70	0	0
2001-2012	420	110	31	716	197	38	395	240	166	4.36	2.18	1.13	0.86	0.59	0.33	60.81	27.23	16.18	1156.50	129.64	20.07

9.2 Group Size

Group size ranged from 2 to 39 individuals with average group sizes being calculated for all pooled years (Table 2). Mean group size of regulated vs. unregulated areas of high vessel traffic, did not differ significantly. However, mean group sizes in regulated and unregulated areas of high vessel traffic were significantly smaller ($P < 0.001$ and $P < 0.5$ respectively) than groups in areas of low vessel traffic.

Table 2. Mean group size for all groups found in pooled data periods. Years and values with high social differentiation and corresponding correlation coefficients are in bold.

Year	Regulated High Vessel Traffic Areas	Unregulated High Vessel Traffic Areas	Low Vessel Traffic Areas
2001-2003	5.43	6.67	7.32
2004-2006	4.99	6.07	7.83
2007-2009	4.24	4.39	7.44
2010-2012	4.79	5.57	7.75
2001-2012	4.80	4.92	7.47

9.3 Association strength and determination of preferred and/or avoided associations

9.3.1 Mean Coefficient of Association (CoA)

When all 3 year blocks are considered, values of the mean CoA and the percentage of individuals with greater than twice the mean CoA are similar between regulated and unregulated areas of high vessel traffic (Table 3). Looking specifically at years 2007-09 this general trend is supported since mean CoA values are the same (mean CoA = 0.3) and values for percentage of individuals with over twice the mean are similar (12.95% and 15.29% respectively). Years 2001-12 show some variation on this general trend, mean CoA values remaining low for both regulated and unregulated areas of high vessel traffic (mean CoA=0.1 and 0.3), but the percentage of individuals with over twice the average

CoA being much higher in regulated areas compared with unregulated areas of high vessel traffic (24.30% and 8.33% respectively).

Comparing mean CoA's for regulated and unregulated areas of high vessel traffic with areas of low vessel traffic across all three year blocks, shows that areas of high vessel traffic have a lower mean CoA but higher percentages of individuals with greater than twice the mean CoA (Table 3). Comparing specifically between years 2001-12, mean CoA values were lower in areas of regulated high vessel traffic (mean CoA = 0.01) than in areas of low vessel traffic (mean CoA = 0.05), and had a greater number of individuals with more than twice the mean CoA (24.30%) than areas of low vessel traffic (12.05%). This was not true of comparisons between areas of unregulated high vessel traffic and areas of low vessel traffic. Mean CoA is lower in areas of unregulated high vessel traffic (mean CoA = 0.03) than in areas of low vessel traffic (mean CoA = 0.05) but the percentage of individuals with greater than the mean CoA is higher in areas of low vessel traffic (12.05%) than in areas of unregulated high vessel traffic (8.33%).

9.3.2 Permutation Tests

Permutation tests show preferred and/or avoided associations, indicated by significantly larger SD and/or CV values calculated for the data when compared to random permutation SD and/or CV ($P < 0.05$). The data show that preferred and/or avoided associations are present for pooled years 2007-09 and 2001-12 for both regulated and unregulated areas of high vessel traffic ($P < 0.05$). The data also show that significantly preferred and/or avoided associations are also present areas of low vessel traffic ($P < 0.05$).

Table 3. Mean CoA's of dolphin groups, percentage of dolphins with over twice the average mean CoA, real and random permuted SD and CV values with corresponding significance values for areas of regulated high vessel traffic, unregulated areas of high vessel traffic and areas of low vessel traffic. Years and values in bold are those with high social differentiation and corresponding correlation coefficients

Year	Regulated High Vessel Traffic					
	Mean CoA	% twice mean CoA	Real/Perm SD	P-Value	Real/Perm CV	P-Value
2001-2003	0.03 (0.02)	7.01	0.09/0.07	0.001	3.11/2.82	1
2004-2006	0.02 (0.01)	22.64	0.10/0.09	0.001	4.24/4.10	0.036
2007-2009	0.03 (0.02)	12.95	0.12/0.08	0.001	3.82/3.64	0.005
2010-2012	0.05 (0.03)	11.41	0.14/0.09	0.001	2.89/2.64	0.001
2001-2012	0.01 (0.01)	24.30	0.06/0.04	0.001	4.93/4.93	0.053
Un-regulated High Vessel Traffic						
	Mean CoA	% twice mean CoA	Real/Perm SD	P-Value	Real/Perm CV	P-Value
2001-2003	0.36 (0.12)	5.26	0.46/0.46	0.687	1.27/1.27	0.505
2004-2006	0.07 (0.05)	18.11	0.21/0.17	0.001	3.04/2.93	0.001
2007-2009	0.03 (0.02)	15.29	0.12/0.096	0.001	3.61/3.39	0.001
2010-2012	0.1 (0.07)	20.51	0.25/0.22	0.011	2.41/2.38	0.002
2001-2012	0.03 (0.02)	8.33	0.11/0.08	0.002	4.19/3.97	0.001
Low Vessel Traffic						
	Mean CoA	% twice mean CoA	Real/Perm SD	P-Value	Real/Perm CV	P-Value
2001-2003	0.09 (0.5)	2.17	0.25/0.23	0.006	2.69/2.63	0.004
2004-2006	0.24 (0.74)	0	0.40/0.39	0.007	1.68/1.69	0.792
2007-2009	0.15 (0.07)	1.81	0.32/0.32	0.481	2.16/2.15	0.151
2010-2012	0.44 (0.23)	0	0.49/0.48	0.719	1.12/1.12	0.144
2001-2012	0.05 (0.03)	12.05	0.18/0.18	0.042	3.54/3.46	0.001

9.4 Defining Clusters

9.4.1 Non metric multi-dimensional scaling plots

Non-metric multidimensional scaling plots were used to show clustering within areas (Figure 7). Representative plots from years 2007-09 were used for regulated and unregulated vessel traffic and representative plots from 2001-12 used for areas of low vessel traffic. These years were chosen due to the high social differentiation values for those years and the relatively high and similar number of individuals observed in each 3 year block (Table 1). Furthermore, stress values were lowest for these plots (Stress <0.1 indicates plots representing true ordination) when compared with plots from all other three year blocks for regulated and unregulated areas of high vessel traffic.

Plots for regulated and unregulated areas of high vessel traffic for the years 2007-09 show that clustering patterns are similar between the two areas. Closeness of individuals reflects how often individuals are seen together and thus associated. Plots of regulated high vessel traffic areas show one main cluster of individuals with four peripheral groups, whilst the plot of unregulated high vessel traffic areas shows one main cluster of closely associated individuals and two small peripheral groups with strong associations, along with some lone peripheral individuals. The MD plot for groups found in areas of low vessel traffic suggests that there are two main clusters. Within these clusters, the plots show individuals form small groups of two or three individuals each with very strong associations.

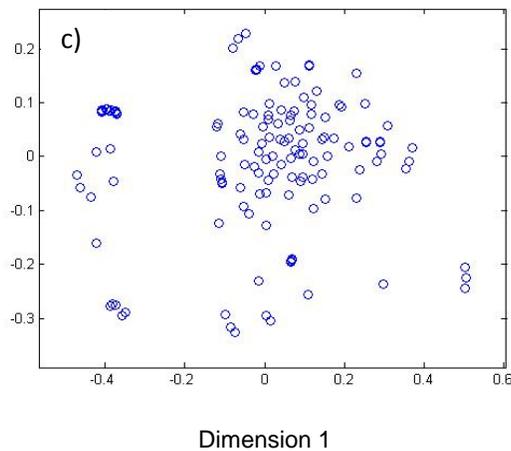
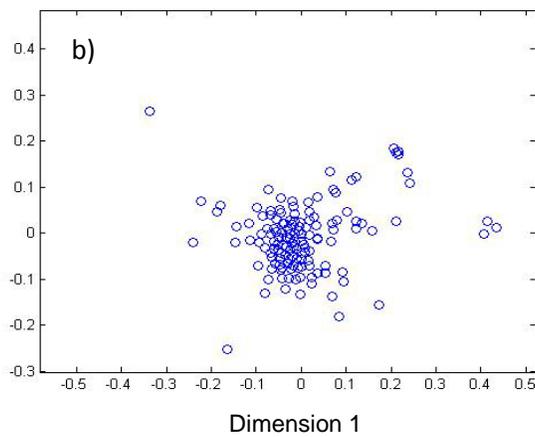
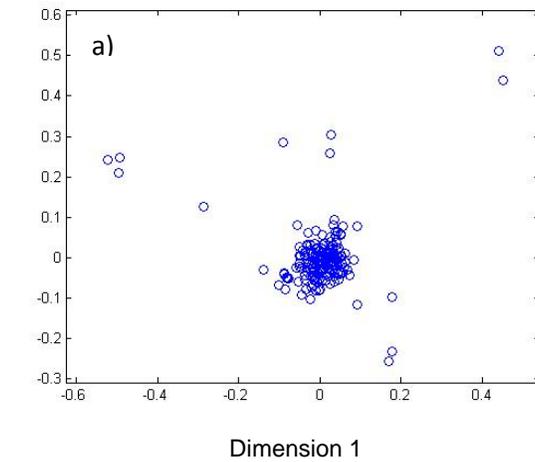


Figure.5 Representative Multidimensional Scaling Plots for years 2007-2009 for (a) regulated areas of high vessel traffic (b) unregulated areas of high vessel traffic and (c) areas of low vessel traffic. Stress (a) = 0.04, (b) = 0.05, (c) = 0.03. Stress < 0.1 shows good ordination.

9.4.2 Hierarchical Agglomerative Cluster Analysis

A comparison of hierarchical agglomerative cluster analysis for regulated (Figure 6) and unregulated (Figure 7) areas of high vessel traffic shows that grouping patterns within the cluster are similar for both areas, with groups splitting primarily at lower association index values. Groups in low vessel traffic areas contain fewer individuals and split at higher association index values than those in regulated or unregulated areas of high vessel traffic (Figure 9). Furthermore, the plot created for areas of low vessel traffic supports the non-metric multi-dimension scaling plot and suggests that within areas of low vessel traffic, two dolphin clusters have arisen. All plots had Cophenetic Correlation Coefficient (CCC) values indicating that the plots are representative of the true clustering within the data (CCC>0.8).

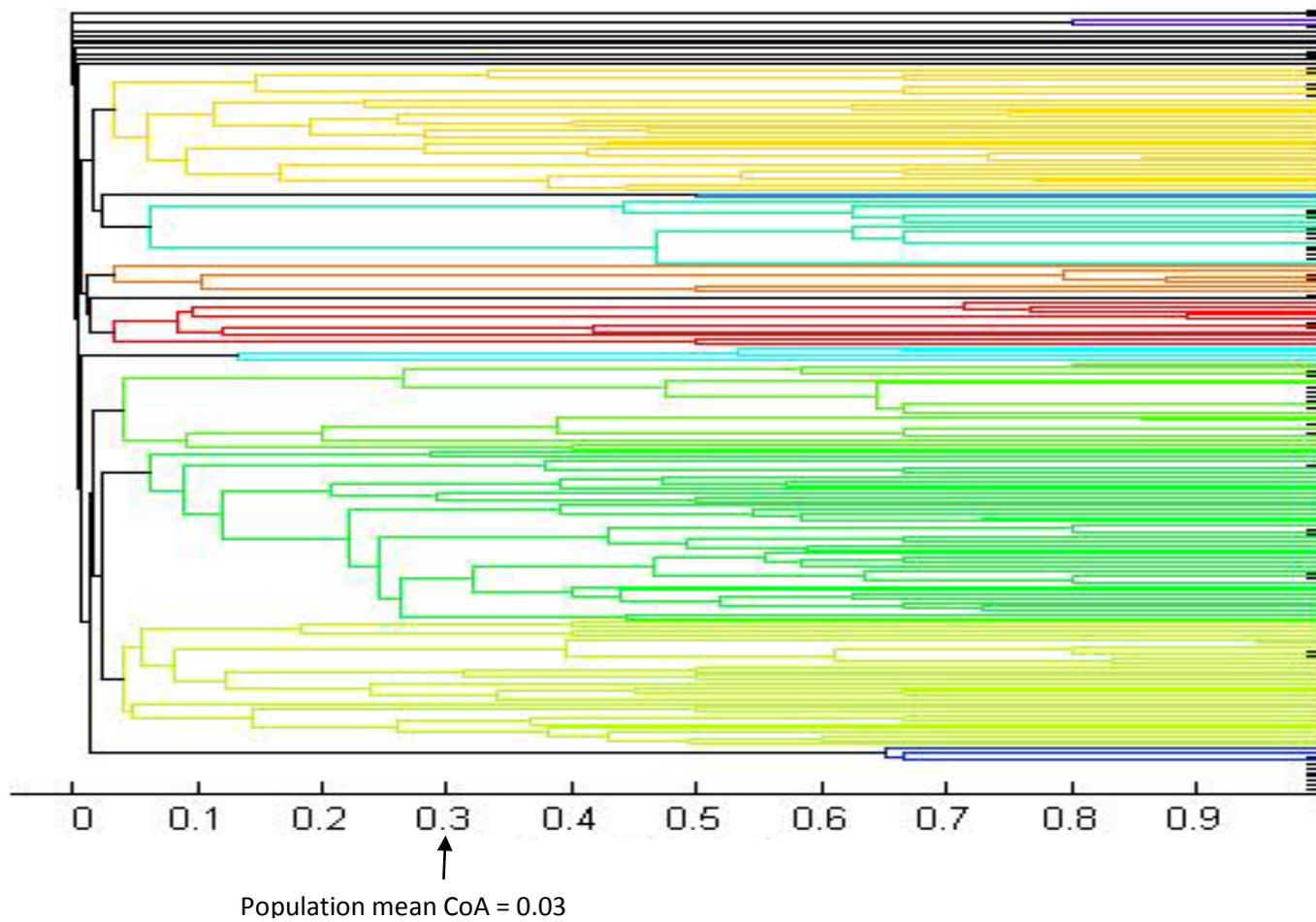


Figure 6. Hierarchical cluster analysis plot for years 2007-2009 for areas of regulated high vessel traffic CCC=0.87, CCC>0.8 shows a good representation

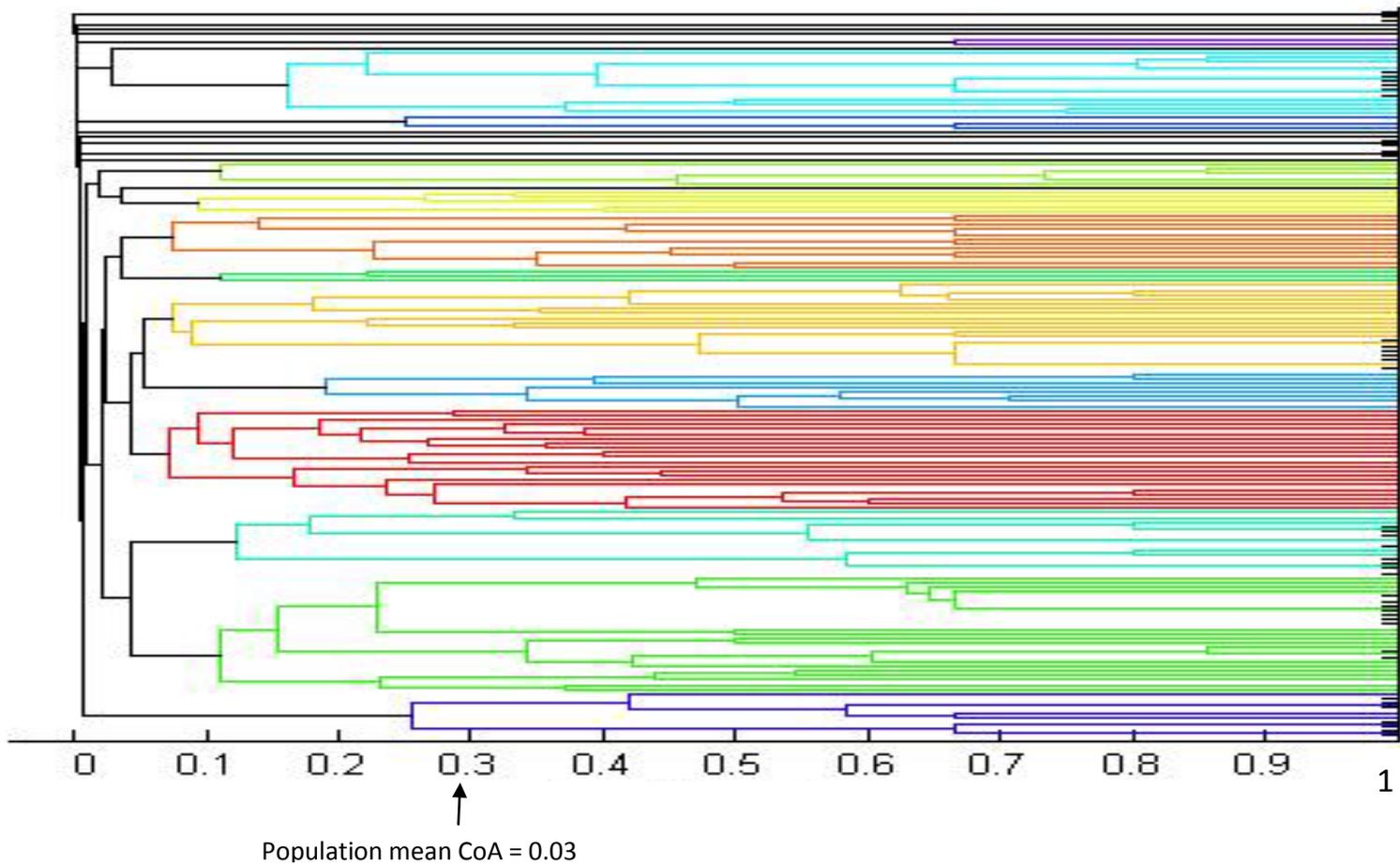


Figure 7. Hierarchical cluster analysis plot for years 2007-2009 for areas of unregulated high vessel traffic CCC=0.83, CCC>0.8 shows a good representation

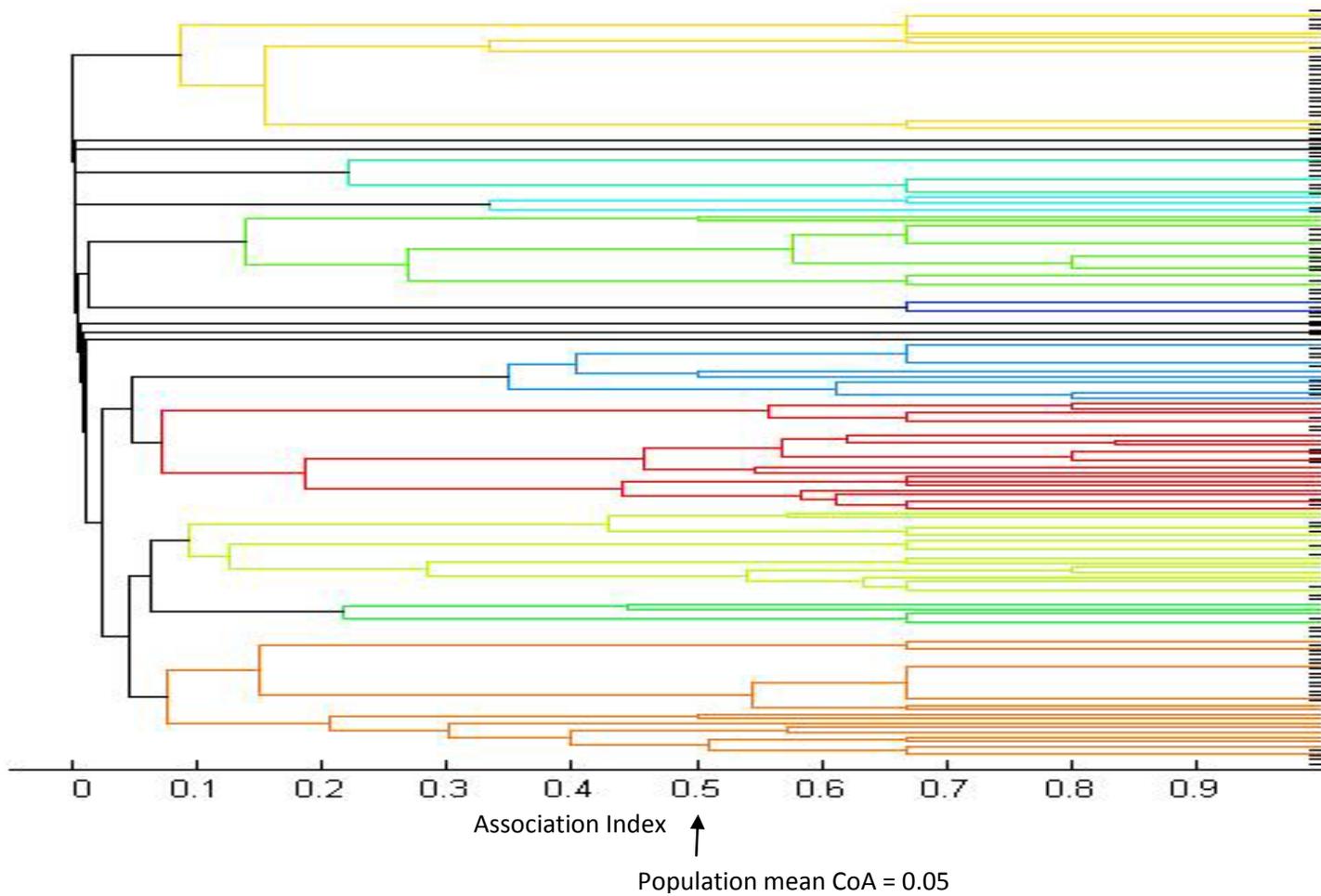


Figure 8. Hierarchical cluster analysis plot for years 2001-2012 for areas of low vessel traffic $CCC=0.878$, $CCC>0.9$ shows a good representation

9.5 Social Network Analysis

Values of association strength for regulated and unregulated areas of high vessel traffic for the years 2007-09 and 2001-12 show very similar association strength in the two areas (Table 4). When areas of regulated and unregulated vessel disturbance were compared with areas of low vessel traffic between 2001-12, values of association strength were found to be highest in low vessel traffic areas, and lowest in unregulated high vessel traffic areas (8.49 compared to 6.49 and 4.99 respectively) (Table 4).

The same is seen when considering cluster coefficients, values for regulated and unregulated areas of high vessel traffic are very similar for years 2007-09 and 2001-12. Whereas the values for low vessel traffic were higher (0.55 compared to 0.20 and 0.31 respectively) (Table 4), indicating areas of low vessel traffic to have cluster coefficients more than double that of regulated areas of high vessel traffic and almost double for areas of unregulated high vessel traffic, thus areas of regulated high vessel traffic had the lowest strength and cluster coefficient values for years 2001-12.

Table 4. Strength and Cluster Coefficient values for regulated and unregulated areas of high vessel traffic and areas of low vessel traffic. Years and values in bold are those with high social differentiation and corresponding correlation coefficients.

Year	Strength Regulated High Vessel Traffic	Strength Unregulated High Vessel Traffic	Strength Low Vessel Traffic	Cluster Coefficient Regulated High Vessel Traffic	Cluster Coefficient Unregulated High Vessel Traffic	Cluster Coefficient Low Vessel Traffic
2001-2003	4.74	6.53	8.38	0.20	0.92	0.65
2004-2006	2.98	8.9	9.53	0.31	0.51	0.86
2007-2009	5.98	5.38	8.01	0.34	0.32	0.79
2010-2012	8.75	7.92	12.64	0.31	0.59	0.98
2001-2012	4.99	6.46	8.49	0.20	0.31	0.55

Social networks produced for both regulated and unregulated areas of high vessel traffic show one main cluster of individuals. The social network for regulated areas of high vessel traffic areas shows one main cluster and two peripheral small groups (Figure 9). This supports the MD scaling plots and hierarchical cluster analysis. The two peripheral groups shown have no ties with the central cluster, indicating that they do not associate with individuals in the central cluster. Individuals are represented by symbols and the size of the symbol represents values of strength. As expected, those individuals found in the middle are larger, indicating higher strength values. Known males and females are also plotted within the diagrams, and for areas of regulated high vessel traffic, are spread throughout the cluster, both having many associations with other individuals. The network showing unregulated high vessel traffic areas again shows one main cluster (Figure 10). There is also an additional group of three individuals that does not associate with the main cluster. Both males and females are spread throughout the main cluster, although males are located more around the periphery of the cluster, whereas in regulated areas of high vessel traffic, males occur more in the centre. The social network showing areas of low vessel traffic show individuals clustering into two groups (Figure 11), and this was also indicated through MD scaling plots and hierarchical cluster analysis. Additionally, both clusters shown indicate that individuals have preferred associates and form small subgroups on the edges of the cluster yet remain well connected to the main cluster, primarily via a single individual. Again, males and females can be seen across the network both in the centre and at the edges.

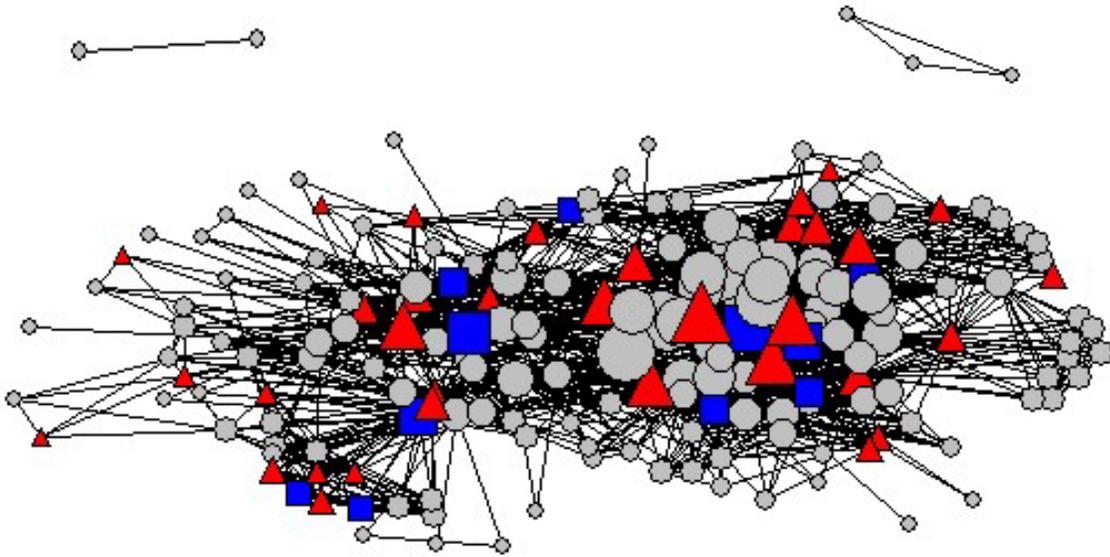


Figure 9. Social network for years 2007-2009 for regulated areas of high vessel traffic. Nodes represent individuals and edges represent associations. Females are represented as up triangles, males are represented as squares and unknown individuals are represented as grey circles. Size of individual shows number of associations (strength).

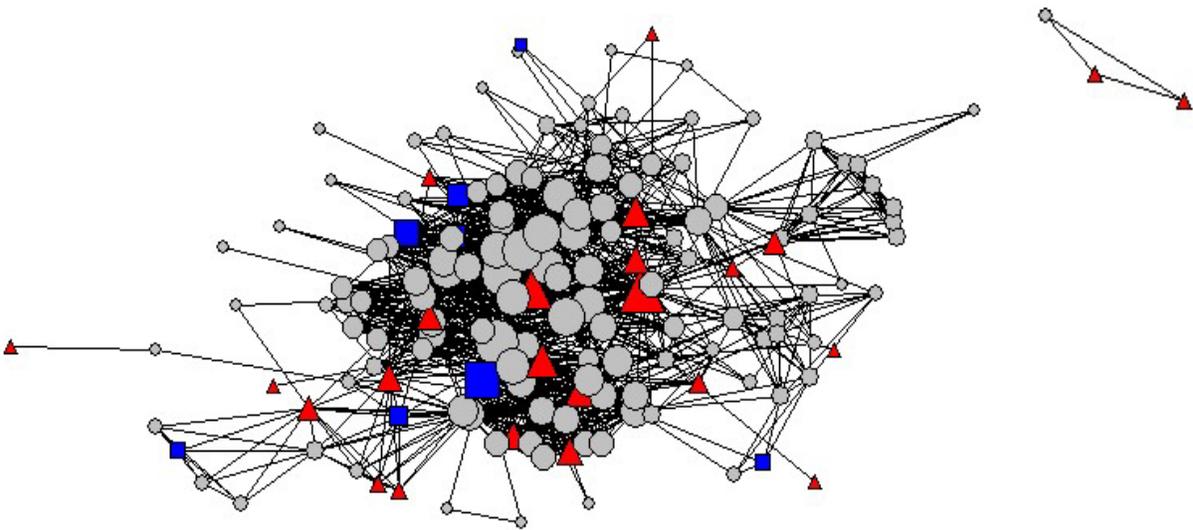


Figure 10. Social network for years 2007-2009 for unregulated areas of high vessel traffic. Nodes represent individuals and edges represent associations. Females are represented as up triangles, males are represented as squares and unknown individuals are represented as grey circles. Size of individual shows number of associations (strength).

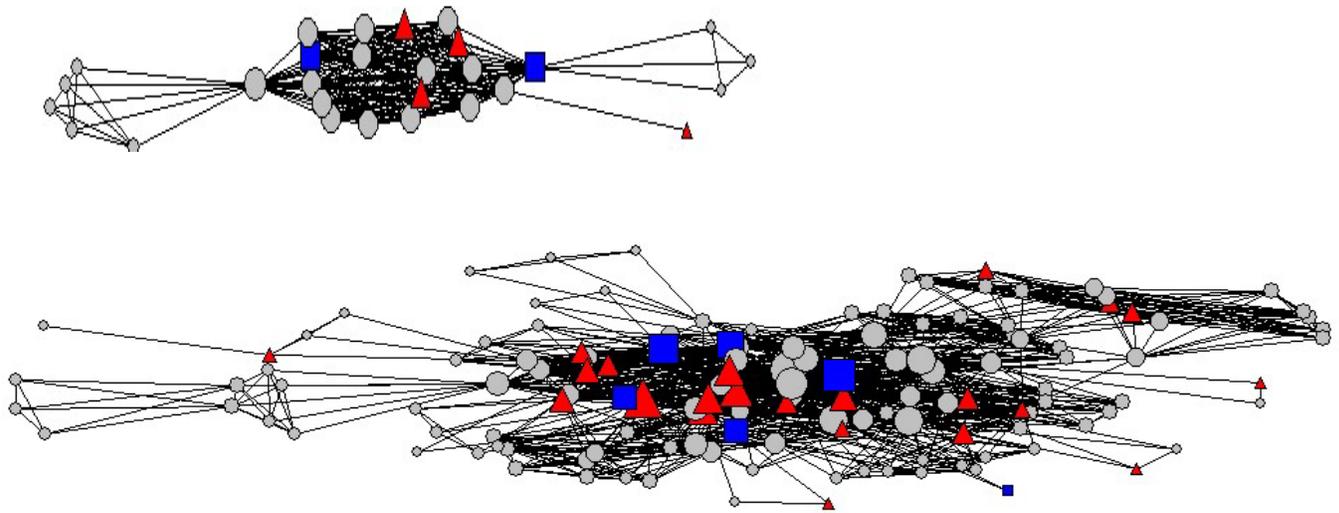


Figure 11. Social network for years 2001-2012 for areas of low vessel traffic. Nodes represent individuals and edges represent associations. Females are represented as up triangles, males are represented as squares and unknown individuals are represented as grey circles. Size of individual shows number of associations (strength).

10. Discussion

Boat disturbance in Wales from commercial wildlife watching tours and recreational boating activity within Cardigan Bay has been increasing in recent years, and continues to do so at an accelerated rate (Hoyt, 2001; Buckstaff, 2004; CCW, 2007; O'Connor, *et al.*, 2009; Lohrengel, *et al.*, 2012). This is particularly the case with Cardigan Bay, with tourism development along the Ceredigion coastline being identified as an area of unrealised economic potential in a number of strategies from the Welsh Government (CCC, 2010). Increased numbers of visitors inevitably lead to increased recreational boat usage. It is therefore important that both short and long term impacts of disturbance on species like the bottlenose dolphin within Cardigan Bay are understood

Studies show that community structure can be determined among dolphins showing long term site fidelity to a particular area (Urian, *et al.*, 2009; Elliser, *et al.*, 2011). Since a

significant proportion of the members of the Cardigan Bay bottlenose dolphin population show long term site fidelity (Pesante, *et al.*, 2008b), the population is a good candidate for studying community structure.

10.1 Effects of Disturbance on Community Structure

10.1.1 Social Differentiation

Values of social differentiation (S) were high ($S > 2$) for groups in all three year blocks in regulated high vessel traffic area, as S indicates the variation in association (Whitehead, 2008), associations in areas of regulated high vessel traffic are very varied. Correlation coefficients for groups in areas of high vessel traffic were also high, between 0.69 and 0.86, indicating that the data are a good representation of the social system (Whitehead, 2006). Social differentiation values for unregulated areas of high vessel traffic could only be generated for years 2004-06, 2007-09 and 2001-12. Correlation coefficient (CC) values for these years were low, 0.38, 0.58 and 0.59 respectively. Whereas, $CC \approx 0.4$ indicates that the data are reasonably representative of the social system, values generated from years 2007-09 and 2001-12 were primarily used in the analysis, being most representative of the social system. In areas of low vessel traffic, values could only be generated for pooled years 2001-03 and 2001-12 for which correlation coefficients were fairly low ($CC = 0.26$ and $CC = 0.33$), indicating that the social differentiation may not be a good representation of the social system (Whitehead 2006). Therefore, values generated from years 2001-12 were used in this analysis and those social structure values that were generated need to be assessed with caution.

However, if values of social differentiation do represent to some degree the social structure of the population, our results suggest that amongst dolphins in areas of high vessel traffic variation in relationships is higher than that found for dolphins in areas of low vessel traffic, with greatest social differentiation being found in those areas of high vessel traffic which are regulated.

10.1.2 Group Size, Association Index and Social Network Analysis

Both regulated and unregulated areas of high vessel traffic have group sizes that are significantly smaller than group sizes observed in low vessel traffic areas ($P < 0.001$ and $P < 0.05$ respectively), suggesting that vessel disturbance may cause dolphin group sizes to become smaller.

In areas of regulated and unregulated high vessel traffic, the mean CoA is low and percentage of individuals with over twice the mean CoA is high. This suggests that in these areas dolphins form many moderately strong associations. In areas of low vessel traffic, the mean CoA is high, but the percentage of individuals with over twice the mean CoA is low, indicating that in these areas dolphins form a small number of very strong bonds, and many weaker bonds.

When testing for preferred and/or avoided associations, permutation tests revealed that non-random preferred associations occur in regulated and unregulated areas of high vessel traffic and also in areas of low vessel traffic. This shows that dolphins preferentially assort with or avoid specific associates at both levels of vessel traffic. Non-metric multi-dimensional scaling plots consistently plotted individuals from regulated and unregulated areas of high vessel traffic within a dense singular group with few peripheral groups of individuals with strong associations. The plot for areas of low vessel traffic shows two clusters of weakly associated individuals as well many small groups of strongly associated individuals. This supports trends shown by the mean CoA values, individuals in areas of high vessel traffic have many moderate associations yet don't show many groups of individuals with strong associations, whereas in areas of low vessel traffic dolphins have weaker associations but form more small groups containing very strongly associated individuals.

Hierarchical agglomerative cluster analysis also reflects this community structure. The analysis shows that many of the groups within both regulated and unregulated areas of high vessel traffic split at lower association indices, similar to that of the mean CoA (mean CoA=0.3 for years 2007-09), whereas in areas of low vessel traffic, groups split when association indexes are higher (mean CoA=0.5 for years 2001-12). Additionally, values of strength and cluster coefficient are higher in areas of low vessel traffic; indicating that individuals within these groups have a greater number of associates and a well connected

network, whereas individuals from groups in areas of regulated and unregulated high vessel traffic had fewer associates and a less well connected network. Social networks constructed for regulated and unregulated areas of high vessel traffic and areas of low vessel traffic support those created by the non-metric multi-dimensional scaling plots. Areas of high vessel traffic show dense clusters, whereas areas of low vessel traffic exhibit two clusters and indicate subgroups occurring on the periphery but remaining connected to the main cluster.

When these results are considered together they allow for a more complete picture of the dolphin community structure. The higher social differentiation values for groups observed in regulated and unregulated areas of high vessel traffic suggest that the community structure here is well defined. This is supported by the presence of smaller group size and CoA values, suggesting that individuals seem to form many moderate associations but few very strong ones. Individuals in low vessel traffic areas seem to form larger groups where individuals have few, very strong associations, in a society that is indicated to be less varied. Low Strength and Cluster Coefficient values suggest that the community structure in regulated and unregulated areas of high vessel traffic may also be more fragmented than that of communities in low vessel traffic areas.

10.2 Interpreting Responses to Disturbance

This study shows that community structures differ in areas of high and low vessel traffic. Differences observed in community structure of groups found in areas of high vessel traffic are supported by studies on the effects of disturbance in other bottlenose dolphin populations. Dolphin groups have been observed to change their behavioural state (Nowacek, 2001; Lusseau, 2003; Constantine, et al., 2004; Ribeiro, et al., 2005), increase dive duration (Janik and Thompson, 1996; Nowacek et al., 2001; Lusseau, 2003) become more compact with increased rates of change in membership and increased cohesion (Denardo 1998, Bejder, 1999; Nowacek, *et al.*, 2001), increase breathing synchrony (Haste, 2003) as well as travelling at more erratic speeds with increased direction changes (Goodwin and Cotton, 2004; Bejder, *et al.*, 2006). These responses are generally evasive responses, and may be associated with those generated from perceived predation threats (Miller, *et al.*, 2008), similar responses having been shown in schooling fish where group cohesion increased in response to predation (Pitcher and Parish, 1993). Additionally, the results suggesting that increased disturbance causes increased rates of change in group

membership, could explain the variation in mean CoA values in the different areas of vessel traffic. Since dolphin groups are smaller in areas of high vessel traffic, yet many form moderate associations with many others, this may be the result of disturbance causing dolphins to frequently change group membership. As a result of this, however, dolphins do not develop strong associations with specific individuals as seen in dolphins in areas of low vessel traffic. Some terrestrial mammals including mountain goats *Oreamnos americanus* (Foster and Rahe, 1983) have also been observed to show unstable group membership as a result of disturbance.

Disturbance has also been observed to cause important behaviours, such as resting and socialising, to be discontinued (Lusseau 2004; Constantine 2004; Highman and Bejder 2006). Miller, *et al.*, (2008) for example found some dolphin groups would stop feeding and begin travelling if disturbed by boats. By moving around more often in areas of high vessel traffic, the opportunity for groups to come together and socialise may be reduced, whereas in areas of low vessel traffic, dolphins may form larger groups more often. In the same way that increased rates of change in group composition could impact time spent forming preferred associations, so could reduce time spent socialising and resting. Dolphins in low vessel traffic areas may have greater opportunities to exert association preferences, such as those based on gender, sex and behavioural state (Connor and Newman, 2004), than those in areas of high vessel traffic. Observed values of mean CoA and percentage of individuals with over twice the mean CoA values, for dolphins in regulated and unregulated areas of high vessel traffic, could reflect this. Dolphins from both areas were found to show preferred and/or avoided associations based on significantly high SD and/or CV values. In areas of high vessel traffic where group membership is more unstable, grouping may be determined more by the environmental pressure of boat disturbance than by preferred individuals. It may be important for dolphins to form preferred associations to increase individual reproductive fitness (Wiszniewski, *et al.*, 2009), and whilst the acquaintance level associations found in areas of high vessel traffic could be sufficient to allow bottlenose dolphins to form effective foraging groups (Gero, *et al.*, 2005), it may not be the best environment to form more stable associations.

The fission-fusion nature of bottlenose dolphin societies allows dolphins the choice of joining or leaving groups depending on the costs and benefits of the situation (Mann, 2000). Different bottlenose dolphin populations occupying different habitats show varying

degrees of behavioural flexibility with respect to social cohesion, with some populations being less fluid and more differentiated than others (Lusseau *et al.*, 2003; Karczmarski, *et al.*, 2005). As noted earlier, the effect of disturbance may cause a sub-optimal level of grouping to occur with sub-optimal associations between individuals forming. The community structure of dolphins in areas of low vessel traffic is one that is characterized by high strength and cluster coefficient values but relatively low social differentiation values, and few, but strong, associations between dyads, which is similar to that of fission-fusion societies of bottlenose dolphin populations found in other areas (Wells, *et al.*, 1987; Connor, *et al.*, 2000b; Gero, *et al.*, 2005; Foley, *et al.*, 2010; Ansman, 2012).

Besides the effects of predation, prey abundance and dispersion has frequently been found to have an impact on group size in bottlenose dolphins (Norris and Dohl, 1980). It is thought that the distribution and abundance of bottlenose dolphins in Cardigan Bay is largely determined by prey abundance and dispersion (Pesante, *et al.*, 2008b; Veneruso and Evans, 2012a). Areas of high vessel traffic within the Bay are invariably closer to the shore, where they overlap with the main distribution of dolphins, suggesting that the abundance of their favoured prey is highest here, at least in summer. It is therefore possible that the grouping nature of bottlenose dolphins could be affected by foraging activity. Additionally, observations from Cardigan Bay and others studies have shown that bottlenose dolphins tend to form small groups inshore but are found in larger groups offshore, which may help explain the higher group sizes of dolphins found in areas of low vessel traffic that are also further offshore.

Some studies indicate that mammals can become habituated to tourism disturbance, such as grey whales *Eschrichtius robustus* (Jones and Schwartz, 1984; Constantine, *et al.*, 2004) and chimpanzees *Pan troglodytes* (Jones, 1996). However, if the tourism encounters are perceived as threatening, as demonstrated or some bottlenose dolphin populations (Irvine, 1981; Constantine, *et al.*, 2001) and gorillas *Gorilla gorilla beringei* (Fossey, 1972), animals are more likely to become sensitised to encounters. Determining if habituation, defined as a reduction in responses to a stimulus over time as animals learn there are no benefits or detrimental consequences associated with it (Thorpe 1963), requires detailed assessments on sequential, longitudinal measurements of individual responses to controlled stimuli (Nisbet, 2000; Bejder, 2005). Even then it is difficult to fully ascertain if habituation has taken place, other factors can induce habituation type

responses such as deafness from exposure to disturbance (Bejder, *et al.*, 2006) or sensitive individuals having already been displaced from an area (Griffith and van Schaik 1993; Fowler 1999). Displacement of sensitive individuals has been observed in Shark Bay in Australia, where some dolphins left preferred habitats due to increased disturbance (Bejder, *et al.*, 2006). Recent results from a study on the Cardigan Bay bottlenose population suggest that fewer animals may be using the site, with more dolphin activity being seen in North Wales (Veneruso and Evans, 2012). This could be a result of sensitive individuals leaving the area, indicating the potential effects of disturbance resulting from high vessel traffic or it may also be a result of shifts in prey distributions (Veneruso and Evans, 2012) and is a factor that needs examining in more detail.

Having found differences in community structure between areas of high vessel traffic, and low vessel traffic, and that community structure is similar for both regulated and unregulated areas of vessel disturbance, it is important that these results are considered with respect to management

10.3 Implications for management

This study divided Cardigan Bay into areas of regulated and unregulated high vessel traffic, and areas of low vessel traffic. At present, the management plan for areas that are regulated focuses primarily on decreasing the direct impact of boat disturbance by increasing the distance between boats and dolphin groups, encouraging a steady speed and the continuation of the boat's predefined course without deviation towards the dolphins. Compliance with these objectives has been increasing in one particular area of the Bay (around New Quay), and as a result, the distance of boats to dolphin groups has been successfully increased (CCC, 2010). Despite this, the results of this study show that the management taking place within the regulated areas has not been effective in reducing some of the impacts of disturbance, community structure from areas of regulated high vessel traffic and unregulated areas of high vessel traffic being very similar to one another whilst differing from areas of low vessel traffic.

It is not known precisely what dolphins may perceive as disturbance. Tolerance levels in dolphins within Shark Bay Australia, have shown to vary, with no significant effects from the presence of a single tour boat, but a marked decline in numbers of animals when this was increased to two (Bejder, *et al.*, 2006). This indicates that sensitivity of bottlenose

dolphins may be more to boat number than boat speed; it also implies that some dolphins have greater tolerance levels to vessel traffic than others, since in that study not all dolphins were displaced. Aside from the physical disturbance caused by boats, there is also the impact of noise pollution generated by the boats. The frequency bands used in bottlenose dolphin whistles and vessel engines overlap, resulting in vessels having the ability to mask dolphin whistles and signals (Evans, *et al.*, 1992; Evans, 1996; Buckstaff, 2004;). Studies showed that the number of whistles emitted by dolphins was found to significantly increase as boats approached (Buckstaff, 2004), potentially being a response to attempt to increase the chance of successfully conveying information between individuals as well as possibly being used to bring individuals together (Buckstaff, 2004). Increasing group cohesion and closeness of individuals may allow increased synchrony. If increased noise pollution is a trigger for responses to vessel presence, it is possible that vessel number may again be an important factor to consider within management plans.

Management within Cardigan Bay is primarily followed and enforced within Cardigan Bay SAC (Pesante, *et al.*, 2008; Pesante and Evans, 2009; Veneruso and Evans 2012). However, evidence suggests many of the dolphins range out of the Cardigan Bay SAC throughout the summer, and form large groups in winter that disperse into North Welsh waters (Baines and Evans, 2009). As vessel traffic is increasing throughout the entire bay, particularly in the north around Barmouth, Tremadog Bay and Aberystwyth, it is important that the entire Bay is considered in management plans. The bottlenose dolphin is an Annex 2 species and as such it must be maintained in Favourable Conservation Status. For this population the mandatory attribute that requires monitoring is the 'number of dolphins using the Cardigan Bay SAC' (Veneruso and Evans, 2012). This measure will not only reflect the status of impacts from within the Cardigan Bay SAC but also those of threats occurring outside the SAC, additionally making it important that the wider area of the Bay are incorporated into the management plan.

10.4 Recommendations

Results show community structure between areas of high vessel traffic and low vessel traffic differs in the bottlenose dolphin population of Cardigan Bay. The similarity between regulated and unregulated areas of high vessel traffic suggests that the current management practice is not addressing the likely cause of the change in community structure.

Bearing in mind that survey effort has been low in certain areas, and since the correlation coefficient values suggest that data for low vessel traffic at present does not strongly reflect the social structure, this study would recommend increased survey effort and monitoring particularly in those areas in order to allow more reliable interpretation of observed trends. As high vessel traffic also coincides with areas used for feeding by the Cardigan Bay bottlenose dolphin, it is important that this relationship is investigated to determine the extent community structure is determined by prey availability. Additionally, the long-lived nature of the bottlenose dolphins requires long term studies to be undertaken in order to detect cumulative effects of disturbance upon the species. However, this study already strongly indicates that high vessel traffic impacts dolphin social networks, and therefore represents a cause for concern. In this study, high vessel traffic areas were defined as those with over 30 boats per scanning period 2006-2011. A more detailed analysis splitting Cardigan Bay into high, medium and low vessel traffic areas could allow threshold tolerance levels to be detected once more data have been collected. Furthermore, investigations into whether dolphin individuals found in areas of high vessel traffic and those of low vessel traffic are the same animals could reveal that certain individuals may be particularly sensitive to high vessel traffic disturbance and others more tolerant, possibly determined by gender, age or reproductive status. If sensitive animals have begun avoiding areas of high vessel traffic, this would have far reaching implications on conservation management within the Bay.

11. Conclusion

The semi-resident community of bottlenose dolphins found in Cardigan Bay is listed as the primary feature for the Cardigan Bay SAC designation, due to its status as an Annex II species within the EU Habitats Directive, which requires countries to designate SACs for them within the Natura 2000 network (European Union, 2007). The purpose of the SAC is to protect the species and maintain it in favourable conservation status. At present, there is insufficient information on the population to define values below which favourable conservation status would not be achieved, indicating the continued need for monitoring and data collection. Factors such as increased recreational boating activity and dolphin based eco-tourism have been identified as causes of concern for the species; factors that will need careful management for sustainable development of the area (Ugarte and Evans, 2006; Pesante *et al.*, 2008; Pierpoint *et al.*, 2009; Veneruso and Evans, 2012).

Furthermore, despite the dolphins being the primary feature within the Cardigan Bay SAC, they do not only range within this area, and therefore factors affecting them outside of it need to be taken into account when considering conservation management. As the number of recreational boats using the Bay continues to increase, so will the pressure of disturbance upon the dolphins. The designation of the two SACs in Cardigan Bay places the government under a legal obligation to protect this species, which therefore may have to consider stronger management plans that take into account the number of vessels using the Bay as well as their speed and behaviour once in the water.

Auto-Critique

This study has allowed me to gain valuable experience of marine mammal surveys and an understanding of social network analysis. With more time it would have been interesting to have investigated community structure further.

12. References

- Agler, B.A. 1992. Testing the reliability of photographic identification of individual fin whales. Report for the International Whaling Commission, 42, pp.731-737
- Alexander, R, D., 1974. The evolution of social behaviour, *Annual Review of Ecology and Systematics*, 5, pp325-83
- Ansmann, I.C. Guido. J. P, Chilvers. B . L and Lanyon, J. M., 2012. Dolphins restructure social system after reduction of commercial fisheries. *Animal Behaviour*, 84(3), pp.575–581.
- Asensio, N., Korstjens, A. H., Schaffner, C. M. and Aureli, F. 2008. Intragroup aggression, fission–fusion dynamics and feeding competition in spider monkeys. *Behaviour*, 145, pp. 833–1001.
- Baines, M.E. and Evans, P.G.H. 2009. Atlas of the Marine Mammals of Wales. CCW Monitoring Report No.68. 82pp.
- Baird, R.W. and Dill, L.M. 1996. Ecological and social determinants of group size in transient killer whales. *Behavioral Ecology*, 7 pp.408–416.
- Barco S.G., Swingle W.M., Mclellan W.A., Harris R.N. and Pabst D.A. 1999. Local abundance and distribution of bottlenose dolphins (*Tursiops truncatus*) in the nearshore waters of Virginia Beach, Virginia. *Marine Mammal Science* 15, pp.394–408.
- Bearzi, G., Notarbartolo-di-Sciara, G. and Politi, E. (1997). Social ecology of bottlenose dolphins in the Kvarneric (Northern Adriatic Sea). *Marine Mammal Science*, 13: 650-668
- Beauchamp. G., 2001. Should vigilance always decrease with group size? *Behavioural Ecology* 51(1) pp. 47-52
- Bejder, L., D. Fletcher and S. Brager. 1998. A method for testing association patterns of social animals. *Animal Behaviour* 56, pp.719–725
- Bejder L., Dawson S.M. and Harraway A. 1999. Responses by Hector’s dolphins to boats and swimmers in Porpoise Bay, New Zealand. *Marine Mammal Science* 15, pp.738–750.
- Bejder. L. 2005 Linking short term and long term effects of nature based tourism on cetaceans. Ph.D Thesis. Biology Department, Dalhousie University, Canada.

- Bejder. L., Samuels. A., Whitehead. H and Gales, N., 2006. Interpreting short-term behavioural responses to disturbance within a longitudinal perspective. *Animal Behaviour*, 72(5), pp.1149–1158.
- Borgatti, S. P., 2002. Netdraw Network Visualization. Analytic Technologies: Harvard, MA
- Borrell, A., 1993. PCB and DDTs in blubber of cetaceans from the Northeastern North Atlantic. *Marine Pollution Bulletin* 26, pp.146–151.
- Buckstaff. K. C, 2004. Effects of watercraft noise on the acoustic behaviour of bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida, *Marine Mammal Science*, 20, pp.709-725
- Cairns, S. J., and S. J. Schwager. 1987. A comparison of association indices. *Animal Behavior* 35, pp.1454–1469.
- Ceredigion County Council, the Countryside Council for Wales, Environment Agency Wales, North Western and North Wales Sea Fisheries Committee, Pembrokeshire Coast National Park Authority, Pembrokeshire County Council, D'r Cymru Welsh Water (2001) Cardigan Bay Special Area of Conservation Management Plan. 190pp.
- Ceredigion County Council, the Countryside Council for Wales, Environment Agency Wales, North Western and North Wales Sea Fisheries Committee, Pembrokeshire Coast national Park Authority , Pembrokeshire County Council, South Wales Sea Fisheries Committee and Dwr Cymru Welsh Water and EC LIFE-Nature Program (CCC), 2008. Cardigan Bay Special Area of Conservation (SAC) Management Scheme, [pdf] Available at: <http://www.cardiganbaysac.org.uk/pdf%20files/Cardigan_Bay_SAC_Management_Scheme_2008.pdf> [Accessed on 20 August 2012]
- Ceredigion County Council (CCC), 2009. *Ceredigion Recreation Boating Management Plan*, [pdf] Available at: <<http://www.cardiganbaysac.org.uk/wp-content/uploads/2009/03/flyer-draft1.pdf>> [Accessed on 20 August 2012]
- CCC, 2010. Ceredigion Recreation Boating Management Plan 2010-2020, [Online] Available at: <http://www.ceredigion.gov.uk/utilities/action/act_download.cfm?mediaid=18895andlangtoken=eng> [Accessed on 19 August 2012]
- Countryside Council for Wales (CCW), 2005. *Cardigan Bay European Marine Site*, [pdf]Available at:

<http://www.ccw.gov.uk/pdf/Reg%2033%20Cardigan%20Bay%20June%202005%20final.pdf> [Accessed on 20 August 2012]

- Chaverri, G. 2010. Comparative social network analysis in a leaf-roosting bat. *Behavioral Ecology and Sociobiology*, 64, pp.1619-1630
- Connor, R.C., Mann, J., Tyack, P.L. and Whitehead H. 1998. Social evolution in toothed whales. *Trends in Ecology and Evolution*, 13, pp.228-232.
- Connor, R.C., Heuhaus, L., Barre, L. M., 1999. Superalliance of bottlenose dolphins. *Nature* 397, pp. 571-572
- Connor, R.C., Wells, R.S., Mann, J., and Read, A.J., 2000. The Bottlenose Dolphin: Social Relationships in a Fission-Fusion Society. In: J. Mann, R.C. Connor, P.L. Tyack, and H. Whitehead eds. 2000 *Cetacean Societies: Field Studies of Dolphins and Whales*. Chicago and London: University of Chicago Press, pp. 91-126.
- Connor, R.C., Heithaus, M.R. and Barre, L.M., 2001. Complex social structure, alliance stability and mating access in a bottlenose dolphin “super-alliance”. *Proceedings. Biological sciences / The Royal Society*, 268(1464), pp.263–7.
- Connor, R. C. and Mann, J. 2006. Social cognition in the wild: Machiavellian dolphins In: S. Hurley and M. Nudds, eds. *Rational animals?* pp. 329–367. Oxford, UK: Oxford University Press.
- Connor, R.C., 2007. Dolphin social intelligence: complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 362(1480), pp.587–602.
- Constantine, R. 2001. Increased avoidance of swimmers by wild bottlenose dolphins (*Tursiops truncatus*) due to long-term exposure to swim-with-dolphin tourism. *Marine Mammal Science* 17 (4): pp.689-702
- Constantine R., Brunton D.H. and Dennis T. 2004. Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behaviour. *Biological Conservation*, 117, pp.299–307.
- Corner, L.A.L., Pfeiffer, D.U. and Morris, R.S. 2003. Social- network analysis of *Mycobacterium bovis* transmission among captive brushtail possums (*Trichosurus vulpecula*). *Preventive Veterinary Medicine*, 59, pp147–167.
- Cross, P. C., Lloyd-Smith, J. O., Bowers, J. A., Hay, C. T., Hofmeyr, M. and Getz, W. M. 2004. Integrating association data and disease dynamics in a social ungulate:

bovine tuberculosis in African buffalo in the Kruger National Park. *Annales Zoologici Fennici*, 41, pp.879-892.

- Davies. N. B., Krebs. J. R and West. S. A., 2012. An Introduction to Behavioural Ecology. Oxford: Wiley. J and Sons
- Denardo, C. 1998. Investigating the role of spatial structure in killer whale (*Orcinus orca*) behaviour. MSc. thesis, University of Aberdeen.
- Dorrance. M. J., Savage. P. J., and Huff. D. E., 1975. Effects of snowmobiles on white-tailed deer. *Journal of Wildlife Management* 39, pp.563-569.
- Dunn, D. G., Barco, S. G., Pabst, D. A. and McLellan, W. A. 2002. Evidence for infanticide in bottlenose dolphins of the Western North Atlantic. *Journal of Wildlife Diseases*, 38, pp.505–510.
- Elliser, C. R., and Herzing, D. L. 2011. Replacement dolphins? Social restructuring of a resident pod of Atlantic bottlenose dolphins, *Tursiops truncatus*, after two major hurricanes. *Marine Mammal Science*, 27(1), pp.39–59.
- Elliser, C. R., and Herzing, D. L. 2012. Community structure and cluster definition of Atlantic spotted dolphins, *Stenella frontalis*, in the Bahamas. *Marine Mammal Science*, 00(0), pp.1-12.
- Evans, P.G.H., Canwell, P.J. and Lewis, E.J. 1992. An experimental study of the effects of pleasure craft noise upon bottle-nosed dolphins in Cardigan Bay, West Wales. *European Research on Cetaceans*, 6, 43-46.
- Evans, C.D.R. 1995, Wind and Water. In: J.H. Barne, C.F. Robson, S.S. Kaznowska, and J.P. Doody, eds. 1995 *Coasts and Seas of the United Kingdom. Region 12 Wales: Margam to Little Orme*. Peterborough: Joint Nature Conservation Committee, pp.239.
- Evans, P.G.H. 1996 Human disturbance of cetaceans. In: N. Dunstone and V. Taylor 1996 eds *The Exploitation of Mammals - principles and problems underlying their sustainable use*. Cambridge Cambridge: University Press pp. 279-298.
- Evans, P.G.H., Baines, M.E., and Shepherd, B. 2000. *Bottlenose Dolphin Prey and Habitat Sampling Trials. Report to Countryside Council for Wales*. Oxford: Sea Watch Foundation
- European Union, 2007. *Guidance document on the strict protection of the animal species of Community interest under the Habitats Directive 92/43/EEC*, [pdf] Available at: <http://www.lcie.org/docs/Legislation/Art_12_guidance_final_E.pdf> [Accessed on 20 August]

- Foley, A., McGrath, D., Berrow, S. and Gerritsen, H. 2010. Social structure within the bottlenose dolphin (*Tursiops truncatus*) population in the Shannon Estuary, Ireland. *Aquatic Mammals*, 36, pp.372-381
- Fossey, D. 1972. Vocalizations of the mountain gorilla (*Gorilla gorilla beringei*). *Animal Behaviour* 20, pp.36-53.
- Foster, B. R. and Rahe, E. Y. 1983. Mountain goat response to hydro- electric exploration in northwestern British Columbia. *Environmental Management*, 7, pp.189-197.
- Fowler, G. S. 1999. Behavioral and hormonal responses of Magellanic penguins (*Spheniscus magellanicus*) to tourism and nest site visitation. *Biological Conservation*, 90, pp. 143-149.
- Gero, S. Bejder. L., Whitehead. H., Mann. J., Connor. R. C., 2005. Behaviourally specific preferred associations in bottlenose dolphins, *Tursiops spp.* *Canadian Journal of Zoology*, 1573, pp1566–1573.
- Goodwin L. and Cotton P.A. 2004. Effects of boat traffic on the behaviour of bottlenose dolphins (*Tursiops truncatus*). *Aquatic Mammals* 30, pp.279–283.
- Griffiths, M. and van Schaik, C. P. 1993. The impact of human traffic on the abundance and activity periods of Sumatran rain forest wildlife. *Conservation Biology*, 7, 623-626.
- Hastie, G.D., Wilson, B., Tufft, L.H., Thompson, P.M., 2003. Bottlenose dolphins increase breathing synchrony in response to boat traffic. *Marine Mammal Science* 19, pp.74–84.
- Higham, J. E. S. and Bejder. L., 2008. Managing Wildlife-based Tourism: Edging slowly towards sustainability? *Current Issues in Tourism*, 11 (1), pp.75-83.
- Hinde, R.A. 1976. Interactions, relationships and social structure. *Man* 11, pp. 1–17.
- Hoelzel, A.R. 1993. Foraging behavior and social group dynamics in Puget-Sound killer whales. *Animal Behaviour*, 45, pp.581–591.
- International Whaling Commission. (2007) Report of the subcommittee on whale watching. *Journal of Cetacean Research and Management*, 9(Suppl.), 326–340.
- International Union for the Conservation of Nature (IUCN), 2012. *Tursiops truncatus*, (*Mediterranean subpopulation*) [Online] Available at: <<http://www.iucnredlist.org/details/16369383/0>> [Accessed on 19 August 2012]

- Irvine A.B., Scott M.D., Wells R.S., and Kaufmann J.H. 1981. Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. *Fishery Bulletin* 79, pp.671-688.
- Janik. V.M. and Thompson P.M. 1996 Changes in surfacing patterns of bottlenose dolphins in response to boat traffic. *Tursiops truncatus (Mediterranean subpopulation)*. *Marine Mammal Science* 12, pp.597–602
- Joint Nature Conservation Committee (JNCC), 2012a. *The Convention on the Conservation of European Wildlife and Natural Habitats*. [Online] Available at: <<http://jncc.defra.gov.uk/page-1364>> [Accessed on 20 August 2012]
- JNCC, 2012b. *The Convention on Biological Diversity* [Online] Available at: <<http://jncc.defra.gov.uk/page-1365>> [Accessed on 20 August 2012]
- JNCC, 2012c. *Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora* [Online] Available at: <<http://jncc.defra.gov.uk/page-1374>> [Accessed on 20 August 2012]
- JNCC, 2012d. *Cardigan Bay/Bae Ceredigion* [Online] Available at: <<http://jncc.defra.gov.uk/ProtectedSites/SACselection/sac.asp?EUCode=UK0012712>> [Accessed on 20 August 2012]
- JNCC, 2012e. Pen Llyn a'r Sarnau/Lleyn Peninsular and the Sarnau [Online] Available at: <<http://jncc.defra.gov.uk/ProtectedSites/SACselection/sac.asp?EUCode=UK0013117>> [Accessed on 20 August 2012]
- JNCC, 2012f. Vertebrate species: mammals [Online] Available at: <<http://jncc.defra.gov.uk/ProtectedSites/SACselection/species.asp?FeatureIntCode=S1349>> [Accessed on 20 August 2012]
- JNCC, 2012g. Surveillance and Monitoring, [Online] Available at: <<http://jncc.defra.gov.uk/page-3356>> [Accessed on 20 August 2012]
- Johns, B.G., 1996. Responses of chimpanzees to habituation and tourism in the Kibale Forest, Uganda. *Biological Conservation* 78, 257–262
- Jones, M, L and Swartz. S. I., 1984. Demography and phenology of gray whales and evolution of whale-watching activities in Laguna San Ignacio, Baja California Sur, Mexico. In: M. L. Jones, S. L Swartz and S. Leatherwood, eds. 1984 *The gray whale Eschrichtius robustus*. Orlando: Academic Press

- Kappeler, P.M., and van Schaik, C.P. 2002. Evolution of primate social systems. *International Journal of Primatology* 23(4), pp.707–740.
- Karczmarski, L., B. Würsig, G. Gailey, K.W. Larson and C. Vanderlip. 2005. Spinner dolphins in a remote Hawaiian atoll: Social grouping and population structure. *Behavioral Ecology* 16, pp.675–685.
- King, B.J. 1991., Social information-transfer in monkeys, apes, and Hominids. *Yearbook of Physical Anthropology*, 34, pp. 97–115.
- Krutzen, M., Sherwin, W.B., Connor, R.C., Barre, L.M., Van de Castele, T., Mann, J. and Brooks, R., 2003. Contrasting relatedness patterns in bottlenose dolphins (*Tursiops spp.*) with different alliance strategies. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 270, pp. 497– 502.
- Landeau. L and Terborgh. J., 1986. Oddity and the confusion effect in predation, *Animal Behaviour*, 34: pp1372-1380
- Leatherwood, S. and Reeves, R. R. 1990. *The Bottlenose Dolphin*. Academic Press, London.
- Leavens, D.A. 2002. On the public nature of communication. *Behavioral and Brain Sciences*. 25, pp. 630–631.
- Lohrengel, K., Veneruso, G., Feingold, D., Pesante, G., Ugarte, F., and Evans, P.G.H. (2012) Boat traffic trends and effects on bottlenose dolphin sighting rates in Cardigan Bay, Wales. Poster, European Cetacean Society Annual Conference, Galway, Ireland.
- Long. D. J and Jones. R. E., 1996, White shark predation and scavenging on cetaceans in the eastern north Pacific Ocean. In: A. P. Klimley and D. G. Ainley, eds. *Great white sharks: The biology of Carcharodon carcharias*. San Diego: Academic Press pp.293-307.
- Lusseau, D., 2003. Male and female bottlenose dolphins *Tursiops spp* have different strategies to avoid interactions with tour boats in Doubtful Sound, New Zealand. *Marine Ecology Progress Series* 257, pp. 267–274.
- Lusseau, D. and Newman, M. E. J. 2004. Identifying the role that animals play in their social networks. *Proceedings of the Royal Society of London, Series B*, 270, pp.186–S188.
- Lusseau, D., Wilson. B., Hammond. P., Grellier. K., Durban. J. W., Parsons. K. M., Baron. T. R., and Thompson. P. M., 2006a. Quantifying the influence of sociality on population structure in bottlenose dolphins. *Journal of Animal Ecology*, 75(1), pp.14–24.

- Lusseau, D., 2006b. Evidence for social role in a dolphin social network. *Evolutionary Ecology*, 21(3), pp.357–366.
- Lemon. M, Lynch. T. P, Cato. D. H, Harcourt. R. G., 2006, Response of travelling bottlenose dolphins (*Tursiops aduncus*) to experimental approaches by a powerboat in Jervis Bay, New South Wales, Australia, *Biological Conservation* 127, pp. 363-372
- Mann, J., and Barnett, H. 1999. Lethal tiger shark (*Galeocerdo cuvier*) attack on bottlenose dolphin (*Tursiops sp.*) calf: defense and reactions by the mother. *Marine Mammal Science*, 15(2), 568–575
- Mann. J., Connor. R.C., Tyack. P. L., and Whitehead. H., 2000 *Cetacean societies: field studies of dolphins and whales*. Chicago: University of Chicago Press
- McComb, K., Moss, C., Durant, S. M., Baker, L. and Sayialel, S. 2001. Matriarchs as repositories of social knowledge in African elephants. *Science*, 292, pp.491–494
- McComb, K., Reby, D., Baker, L., Moss, C. and Sayialel, S., 2003. Long-distance communication of acoustic cues to social identity in African elephants. *Animal Behaviour*, 65, pp.317–329.
- Met Office, 2012. Beaufort wind force scale. [Online] Available at: < <http://www.metoffice.gov.uk/weather/marine/guide/beaufortscale.html>> [Accessed on 28 August 2012]
- Miller, L.J., Solangi, M. and Kuczaj, S. a., 2008. Immediate response of Atlantic bottlenose dolphins to high-speed personal watercraft in the Mississippi Sound. *Journal of the Marine Biological Association of the United Kingdom*, 88(06), pp.1139–1143.
- Mitani, J.C. and Amstler, S. 2003. Social and spatial aspects of male subgrouping in a community of wild chimpanzees. *Behaviour*, 140, pp.869–884.
- Moller, L. M. and Harcourt, R. G. 2008. Shared reproductive state enhances female associations in dolphins. *Research Letters in Ecology*, vol. 2008, Article ID 498390,
- Newman, M.E.J. 2002 The spread of epidemic disease on networks. *Physical Review E*, 66, art, no.016128
- Nisbet, I. C. T. 2000. Disturbance, habituation and management of waterbird colonies. *Waterbirds*, 23, pp.312-332.
- Norris, R. J., Law, R. J., Allchin, C. R., Kelly, C. A. and Fileman, C. F. 1989. Metals and organochlorines in dolphins and porpoises of Cardigan Bay, West Wales. *Marine Pollution Bulletin* 20, pp.512–523.

- Norris, K. and Dohl, T. P. 1980. The structure and functions of cetacean schools. In: L. M. Herman, ed. *Cetacean Behavior: Mechanisms and Functions*. pp. 211-261. New York: John Wiley and Sons.
- Nowacek S.M., Wells R.S. and Solow A.R. 2001. Short-term effects of boat traffic on bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Marine Mammal Science* 17, pp.673–688.
- O' Connor. S, Campbell. R., Cortez, H., and Knowles. T., 2009. *Whale Watching 2001: Worldwide Tourism Numbers, Expenditures and Expanding Socioeconomic Benefits*. Yarmouth Port, Massachusetts: International Fund for Animal Welfare.
- Pesante, G. and Evans, P.G.H. 2008. Sea Watch Foundation Welsh Bottlenose Dolphin Photo Identification Catalogue. CCW Marine Monitoring Report No. 66: i-xii, 1-204
- Pesante. G., Evans, P.G.H., Anderwald, P., Powell, D. and McMath, M. 2008a Connectivity of bottlenose dolphins in Wales: North Wales photo-monitoring. CCW Marine Monitoring Report No. 62: pp.1-42.
- Pesante, G., Evans, P.G.H., Baines, M.E. and McMath, M. 2008b Abundance and Life History Parameters of Bottlenose Dolphin in Cardigan Bay: Monitoring 2005-2007. CCW Marine Monitoring Report No. 61: pp.1-75
- Pierpoint. C, Allan. L, Arnold. H., Evans, P., Perry, S., Wilberforce, L., and Baxter, J. (2009). Monitoring important coastal sites for bottlenose dolphin in Cardigan Bay, UK. *Journal of the Marine Biological Association of the United Kingdom*, 89(05), pp. 1033-1043.
- Pitcher. T. J., and Parish. J. K., 1993, Functions of shoaling behaviour in teleosts. In: T. J. Pitcher, ed. *Behaviour of teleost fishes*. London: Chapman and Hall
- Pope, T. R. 2000. Reproductive success increases with degree of kinship in cooperative coalitions of female red howler monkeys (*Alouatta seniculus*). *Behavioral Ecology and Sociobiology*, 48, pp.253–267.
- Pusey, A. and Wolf, M., 1996. Inbreeding avoidance in animals. *Trends in Ecology and Evolution*, 11, pp.201–206.
- Reynolds, J.E., Wells, R.S., and Eide, S.D. 2000. *The Bottlenose Dolphin. Biology and Conservation*. Gainesville: University Press of Florida. pp.288
- Ross, J. B. and Cockcroft, V. G., 1990. Comments on Australian bottlenose dolphins and the taxonomic status of *Tursiops aduncus* (Ehrenberg, 1832). In: Leatherwood, S.

and Reeves, R.R. eds. *The Bottlenose Dolphin*. San Diego: Academic Press. pp.101 – 128

- Scott, M.D., Wells, R.S. and Irvine, A.B. 1990. A long-term study of bottlenose dolphins on the west coast of Florida. In: S. Leatherwood and R. R Reeves, eds. *The bottlenose dolphin*. pp235–244. San Diego: Academic Press
- Smolker, R.A., Richards, A.F., Connor, R.C., Pepper, J.W. 1992. Sex differences in patterns of associations among Indian Ocean bottlenose dolphins. *Behaviour*, 123, pp.38–69.
- Sugg, D.W., Chesser, R.K., Dobson, F.S. and Hoogland, J.L. 1996. Population genetics meets behavioral ecology. *Trends in Ecology and Evolution*, 11, 338–342
- Sundaresan, S. R., Fischhoff, I. R., Dushoff, J. and Rubenstein, D. I. 2007. Network metrics reveal differences in social organization between two fission-fusion species, Grevy's zebra and onager. *Oecologia*, 151, pp140-149
- Tayler C.K. and Saayman G.S. 1972. The social organization and behaviour of bottlenose dolphins (*Tursiops aduncus*) and baboons (*Papio ursinus*): some comparisons and assessments. *Annals of the Cape Provincial Museums, Natural History* 9, pp.11–49.
- Thorpe, W.H. 1963. *Learning and Instinct in Animals*. London: Methuen.
- Turner, G. F and Pitcher, T. J., 1986, Attack Abatement: A Model for Group Protection by Combined Avoidance and Dilution, *The American Naturalist*, 123(2), pp. 228-240
- Ugarte, F. and Evans, P.G.H. 2006. Monitoring of marine mammals in the Cardigan Bay SAC: surveys from May 2003 to April 2005. Marine Monitoring Report No. 23. Species Challenge Report No. 05/01/04. Countryside Council for Wales, Bangor. 38pp.
- Urian, K.W., S.Hofmann, R. S.Wells and A. J.Read. 2009. Fine-scale population structure of bottlenose dolphins (*Tursiops truncatus*) in Tampa Bay, Florida. *Marine Mammal Science* 25, pp.619–638.
- Veneruso G. and Evans P.G.H. 2012. Bottlenose dolphin and harbour porpoise monitoring in Cardigan Bay and Pen Ll_n a'r Sarnau Special Areas of Conservation. CCW Monitoring Report No. 95. 65pp
- Vidal, O. 1993. Aquatic mammal conservation in Latin America: problems and perspectives. *Conservation Biology* 7, pp. 788–795.

- Wilson, B., Arnold, H. and Hammond, P.S. 1999. Epidermal diseases in bottlenose dolphins: impacts of natural and anthropogenic factors. *Proceedings of the Royal Society of London Series B*, 266, pp.1077-1083
- Wilson, B. 2008. Bottlenose Dolphin *Tursiops truncatus*. In: S. Harris and D.W. Yalden, eds. 2008. *Mammals of the British Isles. Handbook*. Southampton: The Mammal Society. pp. 709-715.
- Wells, R. S., Irvine, A. B. and Scott, M. D. 1980. The social ecology of inshore Odontocetes. In: L. M. Herman, ed. *Cetacean Behaviour: Mechanisms and Functions* New York: John Wiley and Sons pp. 263-318.
- Wells, R. S., Scott, M. D. and Irvine, A. B. 1987. The social structure of free-ranging bottlenose dolphins. In: H. H. Genoways, ed. *Current Mammalogy*, New York: Plenum, pp. 247-305.
- Wells R.S. 1993 The marine mammals of Sarasota Bay. In: E. Roat., C. Ciccolella, H. Smith, eds. *Sarasota Bay: 1992 framework for action. Sarasota: Sarasota Bay National Estuary Program*, pp. 9.1–9.23.
- Wells R.S. and Scott M.D. 1997 Seasonal incidence of boat strikes on bottlenose dolphins near Sarasota, Florida. *Marine Mammal Science* 13, pp.475–480.
- Wells, R. S. and Scott, M. D., 1999. Bottlenose dolphin *Tursiops truncatus* (Montagu, 1821). In: S. H. Ridgway and R. Harrison eds. *Handbook of Marine Mammals, Volume VI, The second book of dolphins and the porpoises*. London: Academic Press. pp137–182.
- Wells, R.S. and Scott, M.D., 2002. Bottlenose dolphins, *Tursiops truncatus* and *T. aduncus*. In: w. Perrin., B. Würsig, and J. G. M Thewissen. eds. *Encyclopaedia of Marine Mammals*. San Diego: Academic Press. pp.122 – 128.
- White, F.J. 1992. Pygmy chimpanzee social organisation: variation with party size and between study sites. *American Journal of Primatology*, 26, pp.203–214.
- Whitehead, H. 1997. Analysing animal social structure. *Animal Behaviour*. 53, pp1053–1067.
- Whitehead, H., and Dufault, S. 1999. Techniques for analyzing vertebrate social structure using identified individuals: review and recommendations. *Advances in the Study of Behaviour*, 28, pp33–74.
- Whitehead, H., Christal, J., and Tyack, P. 2000. Studying cetacean social structure in space and time. In: J. Mann, R.C. Connor, P. Tyack, and H. Whitehead, eds. *Cetacean*

societies: field studies of dolphins and whales. Chicago: University of Chicago Press. pp. 65–87.

- Whitehead, H. 2006, Programs for analyzing social structure. [Online] Available at: <<http://myweb.dal.ca/hwhitehe/social.htm> > [Accessed on 10 June 2012].
- Whitehead, H. 2008a. Analyzing animal societies: Quantitative Methods for vertebrate social analysis. Chicago: The University of Chicago Press
- Whitehead, H. 2008b. Precision and power in the analysis of social structure using associations. *Animal Behaviour* 75, pp.1093–1099.
- Whitehead, H. 2009. SOCPROG programs: Analyzing animal social structures. *Behavioral Ecology and Sociobiology* 63, pp.765–778.
- Wiszniewski, J., Allen, S.J. and Möller, L.M., 2009. Social cohesion in a hierarchically structured embayment population of Indo-Pacific bottlenose dolphins. *Animal Behaviour*, 77(6), pp.1449–1457.
- Wiszniewski, J., Lusseau, D. and Möller, L.M., 2010. Female bisexual kinship ties maintain social cohesion in a dolphin network. *Animal Behaviour*, 80(5), pp.895–904.
- Wrangham, R. W. 1980. An ecological model of female-bonded primate groups. *Behaviour*, 75, pp. 262-300.
- Wrangham, R.W., 1982. Mutualism, kinship and social evolution. In: by King's college Sociobiology Group eds. *Current Problems in Sociobiology*, Cambridge: Cambridge University Press. pp. 269–289.
- Würsig, B. 1986. Delphinid foraging strategies. In: R. J Schusterman, J. A. Thomas., and F. G0 Woods., eds. *Dolphin cognition and behavior: A Comparative Approach*, Hillsdale: Lawrence Erlbaum pp. 347- 359.
- Würsig, B. and Jefferson, T. A. 1990. Methods of photo-identification for small cetaceans. In: P. S. Hammond, S. A. Mizroch, and G. P. Donovan, eds. *Individual Recognition of Cetaceans: Use of Photo-identification and other Techniques to Estimate Population Parameters. Report of the International Whaling Commission. Special Issue*, 12, pp.43-52
- Würsig B. and Würsig M. 1979 Behavior and ecology of the bottlenose dolphin, *Tursiops truncatus*, in the South Atlantic. *Fishery Bulletin* 77, 399–412