Associations or alliances? Comparisons of social relationships between male bottlenose dolphins (*Tursiops truncatus*) in Cardigan Bay and the Moray Firth

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In association with the Cetacean Research & Rescue Unit, and the Sea Watch Foundation

DECLARATION

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

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ABSTRACT

Mating strategies are important aspects of animal social structure, and variation in environmental conditions may drive the formation of conditional tactics which are based on an individual’s social rank, age, size or fitness. The patterns between adult male bottlenose dolphins (*Tursiops truncatus)* in the Moray Firth, northeast Scotland, and Cardigan Bay, west Wales, were investigated and compared using long-term observational data compiled by the Cetacean Research & Rescue Unit, and the Sea Watch Foundation respectively. The present study aimed to ascertain whether males in these regions formed alliance-type relationships as a mating strategy to improve reproductive success, and whether association patterns were similar between the two discrete populations. A total of 66 males from the Moray Firth, and 50 males from Cardigan Bay were identified over the study periods of 18 and 14-years, respectively.

Associations were examined using only males sighted more than twice during the study period, amounting to 62 individuals from the Moray Firth, and 47 from Cardigan Bay. Whereas non-random preferential alliances were found between certain males in both regions, they were stronger in the Moray Firth. The mean HWI was also higher between males in the Moray Firth, at 0.09± 0.05 (±SD), than Cardigan Bay at 0.04± 0.02 (±SD). Patterns of temporal stability between associations were similar, and were described as ‘casual acquaintances’ which is typical of bottlenose dolphins in a fission-fusion society. Demographic factors such as mortality, emigration and re-immigration were further shown to affect association patterns between males in both populations.

Results from the present study suggest that male bottlenose dolphins in the Moray Firth and Cardigan Bay use both alliances and solitary strategies to locate receptive females and compete for mating opportunities. The present examination ultimately allows further insight into the long-term social dynamics between male bottlenose dolphins in two semi-resident UK communities, and broadens current understanding of male mating strategies utilised in these regions, which has received limited study to date.

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1. INTRODUCTION

Mating systems and strategies in animal populations have evolved to enhance reproductive success, influencing the formation of social structures between species and within populations. While well documented in a plethora of terrestrial animals, from birds to reptiles (Chapple & Keough, 2005; Rios-Cardenas *et al*., 2007), they are less well understood in cetaceans, where only a handful of species have received extensive scientific study (Connor *et al*., 2000a; Whitehead & Mann, 2000**)**. The bottlenose dolphin (*Tursiops* spp.) is one such species which has been subject to long-term study throughout its range, subsequently highlighting a variety of different social structures utilised by geographically separate populations (Wells, 1991; Connor *et al*., 2000b; Lusseau *et al*., 2003; Eisfeld, 2003; Rogers *et al*., 2004; Gero *et al*., 2005; Magileviciute, 2006; Scott *et al*., 2012). In particular, the diversity of mating strategies used by male bottlenose dolphins varies drastically between discrete populations (Connor *et al.,* 1999; Owen *et al*., 2002; Lusseau *et al*., 2003; Wiszniewski *et al*., 2012b; Connor & Krützen, 2015), and such strategies may be integral to the frequency and type of intrasexual associations observed between individuals in social groups (Connor *et al*., 2000a; b**)**.

The present study aims to analyse the associations formed between male common bottlenose dolphins (*Tursiops truncatus)* within two UK coastal populations, in order to determine if individuals use strong alliance-type bonds as a mating strategy to improve reproductive success. Such a study, undertaken on long-term data from Cardigan Bay, Wales; and the Moray Firth, Scotland; will provide further insight into the sociality of the male bottlenose dolphins in these locales and will allow the identification of similar association patterns between the regions. Both populations are subject to increasing anthropogenic pressures, validating the importance for further study to reveal aspects of their socio-biology which have received limited attention to date.

1.1. *Animal societies*

Animals that live and interact in inter- or intraspecific groups may be said to have a social structure, with relationships of differing strengths formed between members of the group and maintained over a certain length of time (Whitehead, 2008). As such, the social structure of a same-species group of animals that cooperate with one another in an organised manner may be defined as an animal society (Wilson, 2000). A diverse range of taxa can be said to live within societies, including canids, ungulates, primates, and cetaceans (Connor, 2000; Wilson, 2000).

Animal societies may be composed of kin, unrelated individuals or a combination of both, and gain more benefits from living in close association than would be achieved from a solitary lifestyle (Wey *et al*., 2008). Such benefits may include improved survival through the acquisition of resources, or protection from predators as a result of increased vigilance (Alexander, 1974). Animals may also benefit from enhanced reproductive success by means of increased mate availability or better offspring survival (Alexander, 1974). However, group living may also invoke negative fitness trade-offs, such as increased competition for resources, or vulnerability to contagious disease, indicating that selection for group formation will only occur if benefits to the individual outweigh the costs (Slobodchikoff & Shields, 1988).

While the advantages of group living promote sociality, the development of social structure may also be heavily influenced by a number of other factors, such as individual fitness, gene flow, predation pressure, resource predictability, population distribution and density (Wilson, 2000; Wey *et al*., 2008; Whitehead, 2008). As such, societies will often have a range of grouping, spacing and mating patterns, and also show variation in relationship strength and quality between individuals (Kappeler & van Schaik, 2002). For example, pelagic dolphin species congregate within large groups in response to stochastic resource availability and the increased risk of predation in the open ocean (Gowans *et al*., 2008). Similarly, open habitats encourage the normally asocial Alaskan moose (*Alces alces gigas*) to form herds as the lowered predation risk outweighs the cost of reduced foraging efficiency (Molvar & Bowyer, 1994). Primates which coexist in larger groups can spend a greater amount of time feeding as both predation risk and inter-group competition are reduced, benefits which outweigh the costs of potential disease transfer and reduced fecundity (Majolo *et al*., 2008).

Group structures driven by dynamic interactions between social units are known as fission-fusion societies, displayed by a number of species from guppies and sticklebacks (*Poecilia reticulata* and *Gasterosteus aculeatus* respectively) (Croft *et al*., 2005) to spotted hyenas (*Crocuta crocuta*) (Ilany *et al*., 2015) and chimpanzees (*Pan troglodytes*) (Lehmann & Boesch, 2009). Fission-fusion illustrates the fluidity of the social unit as a whole, with group composition changing through time and governed by preferred associations (Connor *et al*., 1992; Wilson, 2000). This is reflected within groups of chimpanzees which frequently merge and split in response to food sources (Lehmann *et al*., 2007), or where spotted hyenas form highly labile groups whose structure is influenced by individual social rank (Smith *et al*., 2007; Ilany *et al*., 2015).

The social structure of bottlenose dolphin societies is governed by fission-fusion dynamics, thought to reduce feeding competition between group members where food is patchily distributed (Connor et al., 2000b). The associations between individuals may be largely driven by the presence or absence of other group members, resulting in a complicated variety of relationships (Connor et al, 2000b). The management of such complex social systems may be achieved through highly developed cognitive abilities, evolved as a consequence of sociality (Dunbar, 2009). Humans also display complex social behaviour, used to both communicate with and learn from individuals while simultaneously anticipating the behaviour of others (Hermann *et al*., 2007). Similar patterns of information transfer, social learning and social structure complexity have been identified in a number of non-human species, including the bottlenose dolphin. In many large-brained mammalian species, an individual’s survival within the group relies on its ability to cooperate with and manipulate other members of the community (Watts, 1998; Connor, 2007). This indicates that living within groups may require a greater level of social complexity to enable the recognition of rank among group members and the consequences of interaction with certain individuals (Connor, 2007). Indeed, primate studies have shown that species living in larger groups had an increased neocortex ratio (Kudo & Dunbar, 2001). While there are few similar studies for cetaceans, or the bottlenose dolphin, it can be inferred they too may possess greater cognitive abilities to maintain complex social structures (Dunbar, 2009; Kelley *et al*., 2014).

1.2. *The role of mating systems and strategies*

While increased encephalisation may be selected for through social complexity, societies are also heavily influenced by reproductive behaviours; namely mating systems and strategies. While mating systems determine the number of mates gained and the extent of parental care, mating strategies detail the tactics used to acquire mates, and possible inter-and intrasexual associations between individuals (Reynolds, 1996; Waterman, 2007). Females tend to invoke higher costs associated with reproduction due to pregnancy and lactation, and their distribution will be based around the availability of food and safety in which to raise offspring (Reynolds, 1996). Therefore, mating systems and strategies can be influenced by the spatial and temporal availability of certain habitats as females seek to utilise them, while males attempt to enhance their reproductive success through control of females, or the resources they utilise (Boran *et al*., 2001; Reynolds, 1996; Clutton-Brock, 2007).

A variety of mating systems are found in the animal kingdom, from monogamy; where a single mate is retained, to promiscuity; where individuals of both sexes breed with a multitude of partners (Clutton-Brock, 1989). However 90% of mammals exhibit a polygynous mating system, in which males attempt to increase their reproductive rate by mating with a large number of females within the population (Clutton-Brock, 1989). As such, polygynous systems may involve resource, or female defence by reproductive males (Emlen & Oring, 1977), creating competition between males for resource or female control. This results in large disparities between male reproductive success rates and creates the opportunity for a variety of mating strategies to arise (Emlen & Oring, 1977; Struhsaker & Pope, 1991; Shuster, 2009). Ultimately, male mating strategies enable individuals to control female distribution through the manipulation of resources, provision of safety or dominance over female groups (Clutton-Brock & Harvey, 1978; Reynolds, 1996; Clutton-Brock & Huchard, 2013).

Cetaceans have evolved mating strategies in response to the challenges of the three-dimensional marine environment, where mate and prey distribution is unpredictable, and rarely allows territorial defence of an area (Connor *et al.*, 2000a). In response to stochastic resource distribution, reproductive males typically adopt a 'roving male' strategy, where spatially dispersed females and a low cost of locomotion allow long distance movements to locate reproductive opportunities within populations (Whitehead, 1990; Connor *et al.*, 2000a). Once receptive females have been found, mate coercion or guarding may also be utilised to ensure reproductive success in toothed whale species (Boness *et al.*, 2002). Typically males will only consort with a female for as long as is necessary to guarantee successful conception, and will move on to further their mating opportunities once this has been achieved (Boness *et al.*, 2002).

1.3. *Alternative mating strategies: the male alliance*

In highly competitive societies males may adopt less common reproductive behaviours or morphologies, known as alternative mating strategies, to increase their competitive abilities against other males in a population (Krebs & Davies, 1981). Reproductive polymorphisms exist in numerous taxa, for example, small male 'sneaker' swordtails (*Xiphophorus* spp.) aggressively coerce females rather than court them like their larger competitors (Rios-Cardenas *et al.*, 2007). In contrast, alternative strategies may be conditional, and relate to an individual's size, age, social status or fitness (Dominey, 1984). This has been in observed in some male Antarctic fur seals (*Arctocephalus gazella)* which sire more pups through mating at sea than defending beach territories and female harems, which represents a more typical mating tactic (Gemmell *et al.*, 2001).

Conditional strategies may also include the formation of long-term intrasexual bonds, or alliances, between males (Möller *et al.*, 2001). Alliances depend on mutualistic behaviours, and are different to coalitions which are based only on opportunistic interactions (Möller *et al.*, 2001). Cooperative alliances as a mating strategy are unusual since copulations are indivisible, signifying that reciprocity may be an important aspect of the bond between partnered individuals and further indicating that alliance formation and maintenance may require an advanced level of social complexity and cognition (Chapais, 1995; Gowans *et al*., 2008). The extent of partner relatedness varies between species and populations; if allies are related, each receive inclusive fitness benefits from the success of the other (Parsons *et al*., 2003b), while unrelated and low-ranking males may achieve more conceptions together than if they acted alone against dominant males (Watts, 1998). The competitive fitness of individuals within an alliance may be greater than that of a solitary male, improving their ability to defend territory or females, and subsequently increasing their reproductive success (Feh, 1999).

Alliances are utilised as reproductive strategies in a range of taxa, and vary from long-term stable relationships to more dynamic alliance partner choice. For example, male lions (*Panthera leo*) of the Serengeti formed intrasexual alliances to share territories and therefore mating access to reproductive females (Grinnell *et al*., 1995). Smaller groups of bonded males were unrelated, whilst larger groups tended to be kin, improving the inclusive reproductive success of the alliance but additionally creating reproductive skew among the members (Grinnell *et al*., 1995). In the lance-tailed manakin (*Chiroxiphia lanceolata*), alliances formed between subordinate and dominant males, with the subordinate individual typically a younger bird (DuVal, 2007). Allied males performed synchronised song and dance displays to attract females at lekking sites, and alpha males often had multiple subordinate partners (DuVal, 2007).

Similarly, social rank appeared to mitigate the formation of alliances among Camargue stallions (*Equus caballus*), where low-ranking animals formed bonds of varying strength to defend reproductive females within the herd (Feh, 1999). In such alliances, one individual remained more dominant than his partner, and while the subordinate male typically risked greater injury by initiating agonistic interactions with other stallions, his reproductive success was higher than if he had acted alone to ‘sneak’ copulations (Feh, 1999). Finally, chimpanzees displayed a greater propensity for alliance formation when the male population increased, and allowed males to effectively guard periovulatory females against other competitors in 67% of observations (Watts, 1998). On the other hand, chimpanzee alliances were labile, with frequent partner switching, and mating was not equally shared between allied individuals (Watts, 1998).

1.4. *Bottlenose dolphin alliances*

The bottlenose dolphin (*Tursiops* spp.) exhibits the most complex social structure thus far described in a cetacean species (Connor, 2007), and also demonstrates a variety of alliance types. The cosmopolitan genus *Tursiops* contains two accepted species, the common bottlenose dolphin (*Tursiops truncatus)* and the Indo-Pacific bottlenose dolphin (*Tursiops aduncus),* which are distributed globally throughout temperate and tropical waters (Culik, 2011). In the fission-fusion societies typical of the species, long-term bonds between individuals can develop, but females will typically maintain temporally fluid intrasexual associations and short-term affiliations (Smolker *et al*., 1992; Connor, 2002; Lusseau *et al*., 2006).

On the other hand, long-term associations between male dolphins may be driven by unpredictable mate distribution, with alliance formation an attempt to enhance reproductive success through location and coercion of reproductive females (Whitehead, 1990; Connor *et al*., 2000a; Möller, 2012; Randíc *et al*., 2012). Long-term alliances are typically formed with preferred partners chosen as juveniles, and retained into adulthood (Connor *et al.*, 1999; Connor, 2007; Gibson & Mann, 2008). Interactions between similarly aged individuals are integral to bond formation, and male calves often show an increased tendency for play behaviour to turn aggressive (Scott *et al*., 2005), which may play a role in determining an individuals alliance suitability. The understanding of bottlenose male-male relationships has undergone frequent evolution as novel levels of associations have been revealed, and their effect upon reproductive success and individual fitness have been important in explaining their use as a mating tactic (Krützen *et al*., 2004a; Connor & Krützen, 2015**)**.

Alliances observed between males across well-studied populations of *Tursiops aduncus* are varied in their stability and strength, and are found in the population of Shark Bay, Australia (Connor & Krützen, 2015). Here, males display a variation of alliance types: stable, long-term first-order alliances which form between related pairs, triplets or quadruplets, while groups of first-order alliances may further establish labile, cooperative second-order associations in order to herd females from competitors (Connor *et al*., 1992; Krützen *et al*., 2003). The second-order alliance represents the integral mating strategy of males in this region, yet a third-order ‘super-alliance’ of 14 individuals has also been documented (Connor *et al.,* 2001; Krützen *et al*., 2004a). Males in the super-alliance were unrelated and formed fluid associations with preferred individuals in other second-order alliances to ‘steal’ females herded by other males (Krützen *et al*., 2003; Connor & Krützen, 2015).

Indo-Pacific bottlenose dolphins have also undergone long-term study in Port Stephens, Australia, revealing strong first-order and weaker second-order alliances between unrelated individuals (Wiszniewski *et al*., 2012a). In addition, a number of males in this population were solitary and competed against alliances for female access (Möller *et al*., 2001; Wiszniewski *et al*., 2012a). However, despite the presence of varied mating strategies, genetic studies have revealed that a strong first-order alliance directly increased the number of calves sired by allied individuals, improving their competitive fitness against unpaired or weakly bonded males (Wiszniewski *et al*., 2012b).

Alliances between male common bottlenose dolphins (*Tursiops truncatus*, hereafter referred as the bottlenose dolphin) have thus far only been observed in sub-tropical Sarasota Bay and St. John’s River, Florida. In Sarasota Bay, adult males establish first-order alliances with similarly aged conspecifics, while unpaired juveniles and sub-adults associate within bachelor groups, presumably establishing connections with which to form future stable alliances (Owen *et al*., 2002; Scott *et al*., 2012). First and second-order alliances have also been documented in St. John’s River (Ermak, 2014). Nonetheless, the presence of any alliance type has yet to be identified in other well-studied temperate populations; in the UK and New Zealand respectively (Wilson, 1995; Lusseau *et al*., 2003).

1.5. *The study populations*

Approximately 200 bottlenose dolphins form a semi-resident coastal population in the Moray Firth, north-east Scotland, which represents one of the northernmost communities of this species (Wilson, 1995; Cheney *et al*., 2013; Quick *et al*., 2014). Bottlenose dolphins in this region utilise a large portion of coastline, ranging from the inner Moray Firth to the Aberdeen city coastline and even beyond, as far south as Northumberland (Stockin *et al*., 2006; Robinson *et al*., 2012; Cheney *et al*., 2013). The inner Moray Firth was designated a Special Area of Conservation (SAC) in 2005 to primarily protect the bottlenose dolphin population utilising the area (Wilson *et al*., 2004; Bailey & Thompson, 2009). While a significant proportion of the population regularly utilises the SAC (Wilson *et al*., 2004), many individuals disperse far outside this protected zone, with males showing the greatest propensity to range outside the firth (Robinson *et al*., 2012; Quick *et al*., 2014). Further, Lusseau et al. (2006) suggested a division of the population into separate inner and outer firth communities, accounting for the different ranging patterns of individuals in these areas.

While it appears that the population has grown since long-term studies first began (Wilson *et al*., 2004), low genetic diversity between members of the population may indicate a potential vulnerability to inbreeding depression and fitness reduction (Parsons *et al*., 2002; Islas-Villanueva, 2010; Murray-Dickson *et al*., 2011). In addition to the potential threat of reduced genetic diversity, the population is exposed to a number of anthropogenic threats. Boat presence as a result of dolphin-watching activities has been shown to cause disturbance to normal activities, including evasive travel, increased vigilance and reduced buzzing vocalisation associated with foraging (Pirotta *et al*., 2015). Furthermore, dolphins may be also at risk from high levels of pollutants, recently shown to negatively impact the reproductive success of coastal harbour porpoises (*Phocoena phocoena*) in the UK (Murphy *et al*., 2015).

The Cardigan Bay bottlenose dolphin population is thought to number between 150 and 250 individuals (Feingold & Evans, 2014a). Like the Moray Firth population, individual dolphins tend to display different extents of residency (Pesante & Evans, 2008; Feingold & Evans, 2012), yet 15% of the population has never been observed outside of the bay (Feingold & Evans, 2014a; b). Those animals with greater home ranges appear to remain within the confines of the Irish Sea, and there is little evidence of genetic exchange with other resident or ephemeral bottlenose dolphin communities (Pesante *et al*., 2008; Feingold & Evans, 2014a).

Anthropogenic pressures on this population range from pollutants in the marine environment as a result of industrial output, boat disturbance, and the presence of renewable energy structures, such as wind-farms. Indeed, trace metal concentrations were found to be high in two bottlenose dolphin individuals autopsied from Aberaeron (Law *et al*., 1992), whilst increased boat traffic has coincided with decreased bottlenose dolphin sightings within Cardigan Bay (Pierpoint *et al*., 2009; Veneruso & Evans, 2012; Feingold & Evans, 2014a). Furthermore, recreational and tourist boat activity has been shown to change the structuring of dolphin groups, with individuals forming more associations of a moderate strength during times of increased boat traffic (Richardson, 2012). Studies on other populations have indicated that whale-watching activities may cause a reduction in energy intake as foraging behaviours decline, which may result in reduced reproductive rates (Lusseau & Bejder, 2007). This may be of importance in Cardigan Bay, as the busy tourist season running from April to October coincides with calving seasonality, and birth rates appear to show annual reductions (Feingold & Evans, 2014a).

Comparisons between social networks in the Moray Firth and Cardigan Bay analysed using identical statistical methods revealed similar social structures, where two individuals may be connected to approximately two others for short periods of time (Lusseau *et al.,* 2006; Magileviciute, 2006). Further, a study undertaken upon the Cardigan Bay community identified a stable long-term relationship between two adult males (Lott, 2004). Lott’s (2004) analysis only utilised data from a single survey season and may not be representative of longer-term associations. However, a second study conducted by Magileviciute (2006) revealed similar patterns of male intrasexual association. Furthermore, social structure analysis conducted on the community of dolphins utilising the outer Moray Firth revealed that the most closely associated animals were two adult males, while three additional individuals displayed associations akin to a triadic alliance (Eisfeld, 2003).

Specific studies on male associations are largely lacking from Cardigan Bay and the Moray Firth. Current understanding of the strength and nature of male bottlenose dolphin associations in these areas lends the hypothesis that males will form intrasexual bonds which last through time, but that the existence of alliances to enhance reproductive success through female coercion may not be utilised (Wilson, 1995; Eisfeld, 2003; Lusseau *et al.*, 2006; Magileviciute, 2006). While the inferences made thus far mirror those of temperate resident bottlenose dolphins in Doubtful Sound, New Zealand (Lusseau *et al.*, 2003), a more complete picture of intrasexual bonds and male reproductive strategies in these regions may be gained through examining longer-term datasets, and may reveal varying results.

1.6. *Research objectives*

In the present study, the resident bottlenose dolphin communities utilising Cardigan Bay and the outer Moray Firth will be investigated for the presence of stable male intrasexual associations using long-term data available for each region. In this respect the current study will focus solely on male individuals identified through photo-identification, and ascertain the strength of any present associations through social analysis techniques utilised by previous investigations on social structure in these areas.

The current study will attempt to determine and compare:

- the number of males in each population,
- the nature of male dolphin encounters across the study periods, 1997 to 2014 for the Moray Firth, and 2001 to 2014 for Cardigan Bay,
- significant preferred and avoided associations between males, and the extent of gregariousness between individuals,
- the patterns of association through hierarchical cluster analysis, and
- the stability of male-male associations across time.

Ultimately, the study aims to determine if the preferential associations formed between male bottlenose dolphins display any features which may render them akin to alliances, such as those observed within other well-studied *Tursiops* populations. The utilisation of long-term datasets to compare the formation, and function, of identified male associations will serve to highlight variations in the ecological mechanisms which control intrasexual bond ontogeny and maintenance, and further the current understanding of reproductive tactics in UK bottlenose dolphin populations.

2. METHODS

2.1. *Study areas*

2.1.1. *The Moray Firth, Scotland*

Located in north-east Scotland, the Moray Firth (57°40’N, 3°30’W) is the largest embayment in the country (Tilbrook, 1986), measuring approximately 5,230km^2 and encompassing the waters between Duncansby Head in the north-east, Inverness in the south-west and Fraserburgh in the east. The firth contains three smaller embayments known as the Beauly, Dornoch and Cromarty Firths, respectively, all of which lie within the ‘inner firth’, to the west of a diagonal line between drawn Helmsdale in the north and Lossiemouth in the south. The area to the east of this line is accordingly referred to as the outer Moray Firth (Figure 2.1) (Harding-Hill, 1993).

The outer firth environment is more akin to the open North Sea than the inner firth, with a rugged coastline dominated by cliffs and small bays (Harding-Hill, 1993). The depth gradient is also greater in this region, reaching 200m within 26km of the shore, while the sediment type ranges from boulder fields and coarse sand, to mud in the deepest areas (Irving, 1996). By contrast, the conditions within the inner firth are more protected, due to its narrow channels and inlets formed by the surrounding coast, and the large freshwater input from 10 major river systems which create salinity gradients typical of estuarine environments (Adams & Martin, 1986; Wilson *et al.*, 1997). Tidal movements subsequently create unique hydrographic features such as tidal intrusion fronts, which form twice a day upon flood and ebb tides and may influence the distribution and movement of fish species and their predators (Mendes *et al.*, 2002; Bailey & Thompson, 2010). The inner firth was designated a Special Area of Conservation (SAC) in 2005, primarily to protect the ‘resident’ bottlenose dolphin (*Tursiops truncatus*) population utilising the area.

While a diverse range of bird, fish, and invertebrate species can be found throughout the Moray Firth region, the outer firth may represent an important habitat for both commonly sighted cetaceans such as bottlenose dolphins, minke whales (*Balaenoptera acutorostrata*) and harbour porpoises (*Phocoena phocoena*) and more sporadically observed species, including killer whales (*Orcinus orca*), Risso’s dolphins (*Grampus griseus*), humpback whales (*Megaptera novaeangliae)* and common dolphins (*Delphinus delphis*) (Evans, 1996; Robinson *et al*., 2007; 2009; Robinson & MacLeod, 2009).

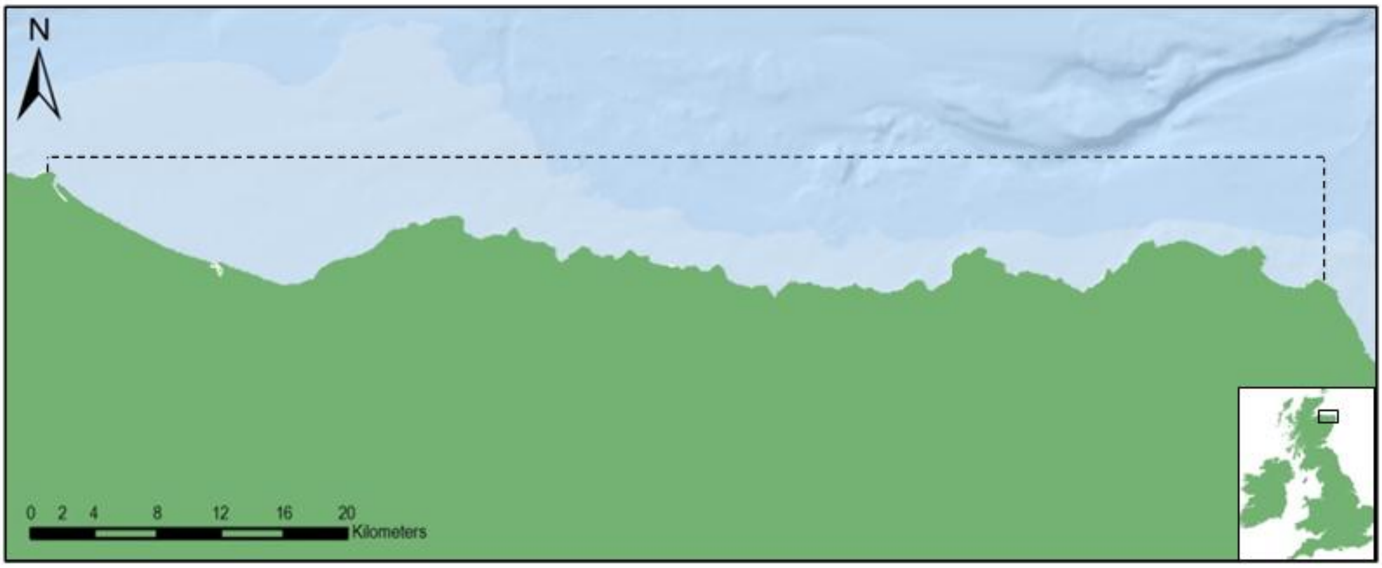

Figure 2.1. Map of Scotland showing the location of the outer Moray Firth study area from which part of the data used in the present study were collected.

2.1.3. *Cardigan Bay, Wales*

Cardigan Bay (52°28’N, 4°09’W) in Wales encompasses an area of 4,987km^2 and extends for over 60 miles from the Llŷn Peninsula in the north, to St. David’s Head in the south (Anon, 2007; Countryside Council for Wales, 2008; Feingold & Evans, 2014a). The sediment composition in the bay is variable, ranging from fine sand to cobble, and the deepest areas reach 60 metres off the Llŷn Penisula and west Pembrokeshire coasts (Evans, 1995). The area receives current speeds of up to 1.8kn, and the strongest tidal movements are typically around headlands, estuaries, and within the narrow channel between Cardigan Island and the mainland coast (Countryside Council for Wales, 2008). Several large rivers discharge freshwater into the bay, creating lower salinities closer to the coast and forming stratified pycnoclines within the water column during the summer months (Countryside Council for Wales, 2008).

In 1996, two sites within Cardigan Bay were proposed as candidate SACs which were officially implemented in 2004, namely the Cardigan Bay SAC and the Pen Llŷn a'r Sarnau SAC (Evans & Pesante, 2008). The Cardigan Bay SAC is located between Aberath and Ceibwr and covers an area of approximately 960km^2, extending 19.3km offshore (Figure 2.2) (Anon, 2007; Countryside Council for Wales, 2008). The primary feature of the SAC is to protect the semi-resident bottlenose dolphin population, however a number of other species and habitats are also protected, such as submerged or partially submerged sea caves, reefs and sandbanks, grey seals (*Halichoerus grypus),* and sea and river lampreys (*Petromyzon marinus* and *Lamptera fluviatilis* respectively) (Anon, 2007). The Pen Llŷn a'r Sarnau SAC extends between Penrhyn Nefyn and the mouth of the Afon Clarach (Pen Llŷn cSAC Plan, 2001) (Figure 2.2). This region was selected for its reefs, estuaries, mudflats and shallow bays and inlets, and also for the presence of European otters (*Lutra lutra)* (Pen Llŷn cSAC Plan, 2001*).*

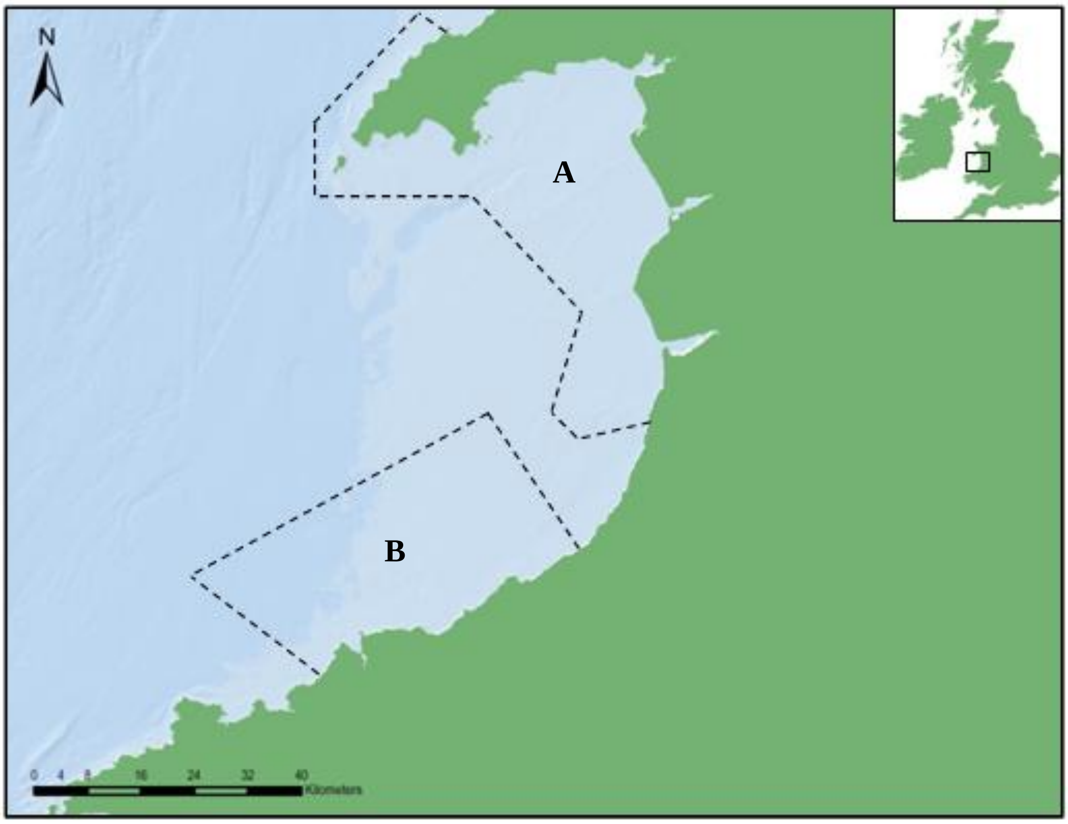

Figure 2.2. Map of Britain detailing the position of Cardigan Bay. Area **A** represents the Pen Llŷn a'r Sarnau SAC boundary, while area **B** shows the Cardigan Bay SAC boundary.

2.2. *Datasets provided*

2.2.1. *Data collection in the outer Moray Firth*

The first dataset used in the present study was collected by the Cetacean Research & Rescue Unit (CRRU) between May and October, 1997 and 2014 inclusive, during boat–based surveys in the outer southern Moray Firth. Dedicated surveys (as detailed in Robinson *et al*., 2007) were conducted using 5.4m rigid-hulled inflatable boats (RHIBs) with raised observation platforms in good weather conditions with visibility >1km and Beaufort Sea State of 3 or less. Observations were made by two experienced crew members, and up to five trained volunteers, and photo-identification of individuals within each encounter was undertaken to enable recognition of well-marked animals. During each sighting, the boat was positioned parallel to travelling animals, avoiding alterations in course unless the dolphins naturally turned and headed in the opposite direction. All interactions with the dolphins were carried out in strict accordance to formally licensed criteria agreed upon with Scottish Natural Heritage.

2.2.2. *Data collection in Cardigan Bay and surrounding areas*

The second dataset was provided by the Sea Watch Foundation (SWF) from 2001 to 2014 inclusive, compiled during dedicated line-transect and *ad libitum* surveys within Cardigan Bay and around the Welsh coast. Bottlenose dolphin surveys occurred mainly between May and September. However, a number of encounters took place outside these months, particularly off the coasts of Anglesey and mainland North Wales. All boat surveys were conducted in favourable weather conditions with minimum visibility of >1km and Beaufort Sea State of 3 or less, utilising teams of trained volunteers and SWF staff respectively.

Line-transects were conducted in the Cardigan Bay SAC, and divided into fixed inshore and offshore routes, extending to approximately 11km and 23km from the coast respectively (Ugarte & Evans, 2006; Pesante *et al*., 2008; Feingold & Evans, 2014a; Norrman *et al*., 2015). The transects were selected at random during surveys and if not completed, were continued at the next opportunity (Feingold & Evans, 2014a; Norrman *et al*., 2015). *Ad libitum* surveys were undertaken in the Pen Llŷn a'r Sarnau SAC and other regions of the bay, collecting sightings and effort data, in addition to photo-identification data (Feingold & Evans, 2014a). The same data were collected during opportunistic surveys where SWF volunteers joined dolphin-watching trips lasting up to two hours (Feingold & Evans, 2014a; Norrman *et al*., 2015).

Encounters with groups were maintained until contact was lost, all animals had been adequately identified or signs of avoidance were detected (Pesante *et al*., 2008). As with the Scottish dataset all photo-identification activities were carried out under license, in this case from Natural Resources Wales.

2.2.3. *Defining encounters and groups*

The Moray Firth and Cardigan Bay datasets utilised in the present study treated groups of animals as congregations of animals engaging in the same activity, such as travelling or foraging, with group members separated by no more than 100 metres (Wells *et al*., 1987). In each case, an encounter was taken to be the length of time spent attempting photo-identification of a group, which was continued until complete. An encounter was considered 'new' if no observations of dolphins had occurred within 15 minutes of the last sighting or if further animals were encountered greater than 2km apart. Datasets provided included encounter dates, times, and a list of the individuals identified within each encounter. Group sizes were estimated by counting individuals during an encounter, which was later verified from examination of all individuals photographed.

2.2.4. *Photo-identification and sexing of males*

Both CRRU and SWF compiled catalogues of well-marked individuals, using quality graded photographs to identify markings upon the dorsal fin and flanks, such as wounds, scarring, lesions, and dorsal edge marks (DEMs) (following Würsig & Jefferson, 1990). Attempts were made to photograph both the left and right side of each animal, which were cross-referenced and matched at a later date. From each of the CRRU and SWF databases all known males were selected for use in the present investigation of male-male associations (Figure 2.3). Adult males typically displayed more extensive scarring than females (e.g Marley *et al.*, 2013), while observation of genital slits, from aerial displays, and the lack of dependent calves over multiple sightings also further aided the host organisations in their gender confirmations.

Due to the features required for identification of known males, the sample sizes were biased towards males with the qualities previously mentioned, and it is possible some individuals were not included. Indeed, some males identified by SWF could not be identified as such with complete certainty. These represented 29 individuals where the genital region had not been observed, and were therefore sexed using the other criteria.

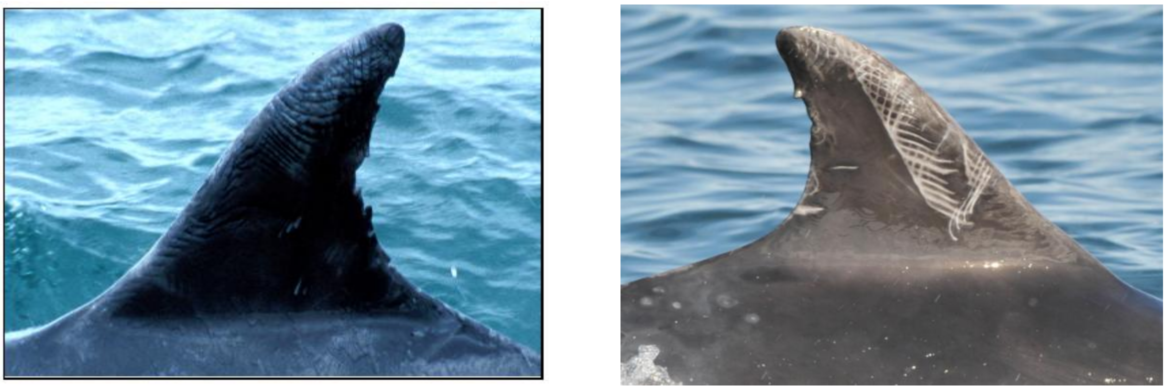

Figure 2.3. Examples of well-marked dorsal fins of known male bottlenose dolphins (from the SWF and CRRU photo-identifcation catalogues). Left image shows SWF ID #054-01W ‘Alfredo’ and the right image shows CRRU ID #021 ‘Paperclip’.

2.3. *Data analysis*

The social dynamics of male bottlenose dolphins in the study populations were analysed through the examination of association patterns, preferences, and stability, using methods utilised by studies examining social structure in other bottlenose dolphin communities. The data were analysed using the social analysis software SOCPROG v.2.6 (Whitehead, 2009) in combination with MATLAB R2012b.

Ensuring available data is applicable for the analysis of associations is important, and most studies have utilised sightings of individuals which have been positively identified at least three times from long-term surveys (Whitehead, 1995; Lusseau, 2003; Parsons *et al.*, 2003b; Mageliviciute, 2006). However, due to the relatively restricted datasets which focused solely on encounters with groups containing male animals, the present study selected individuals which had been sighted more than twice throughout each study period; 1997 to 2014 (outer Moray Firth) and 2001 to 2014 (Cardigan Bay) (following Whitehead, 2008). In addition, males under three years of age were excluded from the analysis, as associations during this period may be highly influenced by the respective associations of their mothers (Rossbach & Herzing, 1999). In the CRRU dataset males that were sighted <2 times during the study period, or were <3 years old, were ID#s 318, 407, 409 and 512. Similarly, male ID#s 177, 126, and 44 were omitted from the SWF dataset.

Analyses were undertaken on each of the two datasets provided by SWF and CRRU, and the CRRU dataset was examined in its entirety. In contrast, the data provided by SWF covered a greater area and range of months, and therefore analyses were undertaken on four versions of the available dataset to address any potential bias in the comparisons:

- (i) Full, unabridged dataset
- (ii) Only ‘definite’ male encounters
- (iii) Encounters made between May and October
- (iv) Encounters made within the Cardigan Bay SAC

The sampling period used in all calculations in SOCPROG was ‘date’, in order to capture the predicted fine-scale changes in male –male associations. All means are presented as the mean ± one SD (±SD). A range of parameters were used in the present study, and definitions may be found in Table 2.1.

Table 2.1. Definitions of parameters and measures used in the present analysis.

Parameter	Definition
Half-Weight Index (HWI)	A measure of association used to determine the strength of associations between two individuals in a population.
Monte Carlo test	A randomisation test to reject or accept the null hypothesis that animals do not form preferential associations. Involves calculation of test statistics for the observed data, which are then re-calculated a number of times, and compared to a randomly generated dataset.
Coefficient of variation (CV)	A test statistic calculated through the Monte Carlo test. If the observed statistic is significantly greater than the random, animals form preferential associations.
Standard deviation (SD) of typical group size	A test statistic calculated through the Monte Carlo test. If the observed statistic is significantly greater than the random, animals are found in consistently sized groups within the study area.
Cophenetic correlation coefficient (CCC)	Indicates how well a hierarchical cluster analysis dendrogram represents the calculated HWIs.
Standardised lagged association rate (SLAR)	The probability that, if two individuals previously associated, in the future a randomly chosen associate of one animal will be its previous associate.
Standardised null association rate (SNAR)	The probability that if two animals are associated at any time, the second individual will be a randomly chosen associate of the first after a specified time lag, if random association occurs over time.
Lagged identification rate (LIR)	The probability that an animal within the area at any time will be the same as a randomly chosen individual in the future. Assesses if demographic factors, such as mortality and emigration, have an effect on the lagged association rates of the population.

2.3.1. *Determining associations*

Through SOCPROG the sociality of male dolphins was measured using association indices, as other relationship measures (e.g. interaction rates) are difficult to achieve from cetaceans since much of their time is spent below the surface of the water (Whitehead, 2008). The use of association indices (see Table 2.2) requires the acceptance of the following assumptions: (i) that associations are symmetric, in that individual A associated with individual B at the same rate; (ii) that records are accurate for the study species; (iii) that the likelihood of individual identification is high; and (iv) that all possible associates are identified during each encounter made (Whitehead, 2008).

Table 2.2. A selection of association indices used in animal social studies. From; Whitehead, 2008; and Cairns & Schwager, 1987

Association index	Formula	Comments
Half-Weight	See text.	Least biased when pairs are more likely seen apart than together. Commonly used in studies on cetacean sociality, and good for inter-population comparisons.
Twice-Weight	$\frac{x}{x + y_{ab} + y_a + y_b}$	Least biased when pairs are more likely seen together than apart. Monotonic function of the HWI.
Simple Ratio	$\frac{x}{\sqrt{(x + y_a + y_{ab})(x + y_a + y_b + y_{ab})}}$	Often used in captive studies. Not recommended when clear sources of bias exist (e.g. identification probability changes when associates are apart, not all associates identified, or violation of other assumptions mentioned in text). Not useful for inter-population comparisons.

Occasional violation of some, or all, of the assumptions during encounters was possible due to the ephemeral nature of bottlenose dolphin groups. For this reason, the Half-Weight Index (HWI) was selected to calculate male associations in the present study, as it reduced the effect of bias in all cases of assumption violation. HWI is least biased when pairs are more likely to be seen apart than together (Cairns & Schwager, 1987) which was useful in the present study, as photographing all individuals within a group was not always achieved.

The equation for calculating HWIs is as follows:

$$\text{HWI}= \qquad x/(x+ y_{ab}+ 0.5(y_a+ y_b))$$

where:

x= the number of times both individuals ($_a$ and $_b$) were observed in the same group,

y_a= the number of encounters with individual *a* but not individual *b*,

y_b= the number of encounters with individual *b* but not individual *a*, and

y_{ab}= the number of observations including both animals in different groups at the same time (usually=0 for studies using photo-identification) (Bejder *et al.*, 1998).

The HWI approach allows pair-wise comparisons of individuals, where 0 means that two animals were never observed within the same group, and 1 suggests constant association (Bejder *et al.*, 1998). The resulting associations were constructed into HWI sociomatrices, with an index given for all male dyads (pairs) in each study population. Since the associations were symmetric, only one half of each matrix was subsequently presented (Whitehead, 2015). Dyads where the HWI was twice the mean value were highlighted, indicating that individuals were associating at least twice the value expected of a randomly selected dyad, and could be termed 'friends' (Gero *et al.*, 2005; Whitehead, 2008).

The reliability of the HWI values, and their ability to reflect the true sociality of males in each population, were estimated using a social differentiation estimate and correlation coefficient. The former indicated the proportion of time that dyads spent together and estimated the variability of the social system between males: where <0.3 is a homogeneous society; between 0.5 and 1.9 is well differentiated; and >2 is extremely differentiated (Whitehead, 2008). The correlation coefficient was used to determine if the analysis accurately represented the true social structure; where 1 is a perfect representation, and 0 is a poor one. Standard errors (±SE) were calculated through 1,000 bootstrap replicates.

2.3.2. *Preferred and avoided associates and measures of gregariousness*

Precision estimates were made on the calculated HWIs using a Monte Carlo test of random association in SOCPROG. This method tested the null hypothesis that individuals did not form preferred associations, and examined whether the identified associations differed significantly compared with what would be expected if they occurred randomly (Bejder *et al.*, 1998; Whitehead *et al.*, 2005; see also Wiszniewski *et al.*, 2009). Test statistics (see table 2.1) were calculated for the observed data, and then re-calculated for a number of permutations, and compared to a random dataset. Permutations of 10,000 and 50,000 were used to reduce the likelihood of similarity between the observed and random datasets (Bejder *et al.*, 1998; Connor *et al.*, 2000; Lusseau, 2003). The random datasets are not independent of each other or the real data, as each calculated random dataset is only marginally different. Additionally, the real dataset is the starting point for randomisation, meaning P values are biased against high values, and fewer permutations result in a more conservative test (Whitehead, 2015). Therefore, to avoid inaccurate P values, the number of permutations was increased until the P values stabilised (Whitehead, 2015). The 'permute groups within samples' option in SOCPROG was used to ensure that the temporal data were retained, and only the social data were permutated accordingly.

The Monte Carlo equation is as follows:

$$S= \qquad \sum_{a=1}^{D}\sum_{b=1}^{D}\left(o_{ab}-e_{ab}\right)^{2} / D^{2}$$

where:

D= total individuals in analysis,

O_{ab}= the HWI for individuals $_a$ and $_b$, and

$e_{ab=}$ the expected value under the expectation of random associations (Bejder *et al.*, 1998).

The test was run a number of times to ensure stability, while p-values indicated the reliability of the calculated association indices (Whitehead, 2015). The null hypothesis was rejected if 95% of the randomly calculated HWIs were less than those from the observed dataset. If the coefficient of variation (CV) was indicated as significant by $p<0.05$, associations between pairs of animals were preferential (Whitehead, 2015). Gregariousness was estimated through examination of the standard deviation (SD) of the group size. If the observed value was greater than the random value and the p value indicated significance, animals were determined to be associating in consistently sized groups (Whitehead, 2015). Finally, where the HWI between two individuals was found to be significant, as indicated by $p>0.05$, the presence of a male-male alliance was assumed.

2.2.3. *Hierarchical cluster analyses*

If preferred associations were identified from the previous analyses, the social structure of male dolphins in each study period was visualised within dendrograms using hierarchical cluster analyses (average linkage method) of the calculated HWI matrices. Clustering indicates social units within the population, and further identifies animals which preferentially associate (Whitehead, 2008). If male dolphins in the study populations were to form stable associations, dendrograms would be a useful method of identifying such relationships (Connor *et al*., 1992). The ability of the dendrogram to represent the matrix of HWIs was assessed through the cophenetic correlation coefficient (CCC). If the CCC was greater than 0.80, the dendrogram represented a good match of the calculated HWIs.

2.3.4. *Temporal patterns- Standardised lagged association rates, and lagged identification rates*

In order to understand the patterns of association between males across time, standardised lagged association rates (SLARs) were further determined. The lagged association rate is the average rate of association over time, and estimates the probability that two currently associated individuals will continue to associate after a specified time lag (Whitehead, 2007; 2008). Since this method is an integration of the available data, individuals with poor sighting histories have no disproportionate effects, and their removal may positively bias the outcome. Therefore individuals with <2 sightings were re-entered for this analysis, and all males from the CRRU and SWF dataset were used (66 and 50 males respectively).

Standardising lagged and null association rates is useful in cetacean studies where not all animals may be identified in a group and therefore account for variation in identification of both individuals and their associates within sampling periods (Whitehead, 1995; Whitehead, 2008). SOCPROG was used to calculate the standardised lagged association rate $g'(t)$, or the probability that if individuals $_{a}$ and $_{b}$ were associated, then at t time units a randomly chosen associate of $_{a}$ will be individual $_{b}$ (Whitehead, 2007). The calculated proportions were then averaged over all males in each dataset. Standard errors were calculated through jack-knifing, using a typical sampling trip of one day to run the analysis.

Calculated SLARs were then compared to the standardised null association rate (SNAR), which is the probability that under random association, two individuals which have associated at any time will again be associated after a specified time lag (Whitehead, 2008; Whitehead, 2015). Therefore, similarities between the SLAR and SNAR indicated that associations between individuals were in fact random.

The temporal patterns of association in the study populations were compared to social organisation models to interpret the presenting social structure over time (see Whitehead, 1995; 2008; 2015). Three models were chosen for comparison: (i) constant associates where individuals stayed acquainted for life; (ii) casual acquaintances where individuals rapidly disassociated; and (iv) associations that lasted for a very period of time (Whitehead, 2008). Maximum likelihood and binomial loss methods were used to select the model which best represented the data used for each population (Lusseau *et al.*, 2003).

Finally, to account for possible demographic effects upon the temporal pattern of association shown by the bottlenose dolphin populations, such as emigration or mortality, the standardised lagged identification rate was determined using the observed data. The non-social lagged identification rate (LIR) established the probability that an individual in an area at any time was the same animal if randomly chosen at t time units later (Whitehead, 2001; Whitehead, 2008). Therefore the LIR was the probability of a male dolphin remaining within the study area, divided by the total number of males (Whitehead, 2008). If demographic factors were affecting the male community within each study population, the fall in identification rate coincided with the fall in SLAR. In a similar manner to the analysis of SLAR, movement models were fitted to the observed data using maximum likelihood and binomial loss methods, to identify what pattern of movement best described the LIR and SLAR. Standard errors were calculated using 100 bootstrap replicates.

3. RESULTS

3.1. *Cetacean Research & Rescue Unit dataset*

3.1.1. *Known males*

A total of 66 males were identified by the CRRU (Table 7.1, appendix). From a total of 459 encounters with recorded bottlenose dolphin groups from 1997 to 2014, 399 groups contained one or more males, representing 86% of all encounters. A mean of five males were observed in encountered groups, with 98% of all encounters involving two or more dolphins, and only seven observations of solitary males (Table 7.1, appendix). In 57 group encounters (14%), just one male was identified, with the other animals within that encounter being female, juvenile or of unknown sex. The mean encounter rate for males was 33.7 ±27.14 times within the 18 year study period (Table 7.1, appendix). The number of encounters every hour, month and year of the study may be found in tables 7.2, 7.3, and 7.4, appendix.

3.1.2. *Patterns of association*

Of the 66 known males in the CRRU dataset, 62 were used in an analysis of associations. The distribution of HWIs (n= 3844) was skewed strongly towards lower values, with a large number of individuals maintaining no associations with others (Figure 3.1, A). HWIs ranged from 0.00 to 0.64, with an overall mean of 0.09± 0.05 (±SD). The mean and maximum HWIs for each male in the study is shown in figure 3.1 B and C, respectively. The majority of mean HWIs were below 0.2, and the most frequent value was 0.1 (n=47) (Figure 3.1, B), suggesting many associations between males were weak. The maximum HWIs for each individual ranged between 0.1 and 0.67, and the most frequently occurring value was 0.5 (n=22) (Figure 3.1, C). The mean and maximum HWIs for every individual may be found in table 7.5, appendix.

The resulting HWIs were used to form a sociomatrix, detailing the strength of association between each of the 62 males in the study (Table 3.1). The maximum HWI was 0.67, between two male pairs, ID#s 9, 10, and 326, 411. All possible dyads (n=1953) and dyads with HWIs >0.18 (twice the mean HWI) are indicated in table 3.1.

The social differentiation estimate (the proportion of time that individuals spent together) was 1.49± 0.05 (±SE), indicating a fairly well differentiated male community. The estimated correlation coefficient between the observed association indices and calculated indices was 0.95± 0.03 (±SE), suggesting that the estimation of male social structure was accurate.

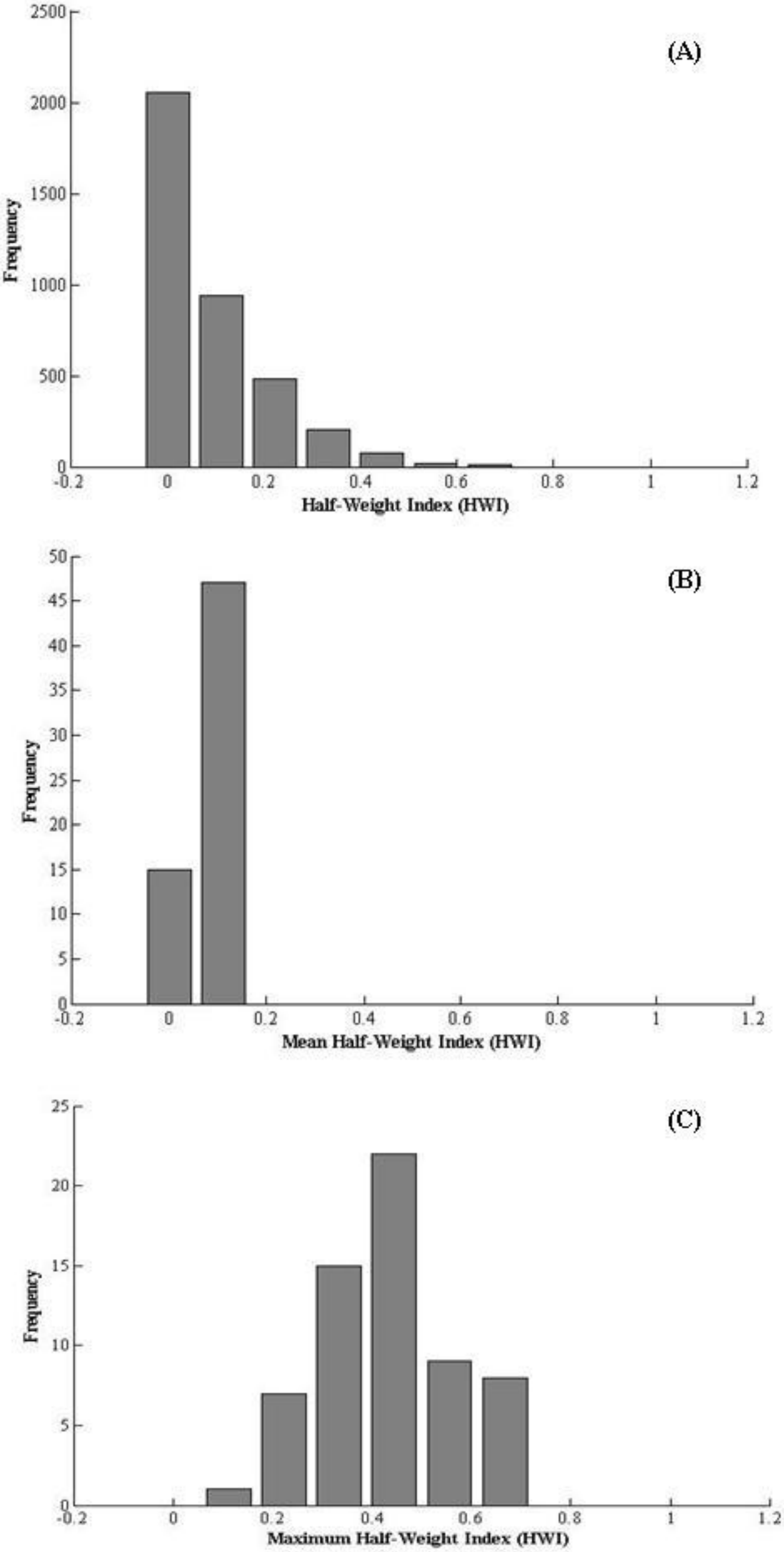

Figure 3.1. The distribution of Half-Weight Indices (HWIs) for 62 known adult males identified >2 times from 1997-2014: (A) the frequency of all pairwise comparisons (n=3844), (B) the mean HWI for each male, and (C) maximum HWIs for each male in the study.

Table 3.1. Sociomatrix detailing the strength of association between all males included in the social analysis (n=62). Values presented are Half-Weight Indices (HWIs), where 0= no association between two individuals, and 1= constant strong association between two males. HWI >0.18, at least twice the mean HWI (0.09), are highlighted **bold.** Matrix continued on pp.31

	1	10	115	134	14	144	149	165	19	198	2	20	204	21	223	238	275	279	297	298	326	329	344	347	351	354	367	380	386	395	398
1	1.00																														
10	**0.20**	1.00																													
115	0.03	0.06	1.00																												
134	0.00	0.00	0.00	1.00																											
14	0.00	0.06	0.00	0.00	1.00																										
144	0.13	**0.29**	0.04	0.00	0.00	1.00																									
149	0.00	0.06	**0.33**	0.00	**0.22**	0.04	1.00																								
165	0.13	**0.23**	0.05	0.00	0.00	**0.34**	0.00	1.00																							
19	0.11	0.08	0.00	0.00	0.09	0.00	0.09	0.04	1.00																						
198	0.11	0.08	0.00	0.00	0.00	0.03	0.00	0.11	0.00	1.00																					
2	**0.25**	**0.38**	0.06	0.00	0.07	**0.23**	0.03	**0.18**	0.08	0.03	1.00																				
20	0.17	0.14	0.13	0.00	0.00	0.16	0.15	0.07	0.15	0.00	0.08	1.00																			
204	0.15	**0.38**	0.04	0.00	0.00	**0.35**	0.00	**0.24**	0.07	0.04	**0.32**	0.13	1.00																		
21	**0.25**	**0.21**	0.02	0.00	0.00	0.13	0.02	0.11	0.06	0.13	0.17	0.15	0.12	1.00																	
223	**0.18**	**0.26**	0.00	0.00	0.03	0.12	0.03	0.14	0.13	0.05	0.17	0.12	0.08	**0.23**	1.00																
238	0.10	0.14	0.00	0.00	0.00	0.08	0.00	0.04	0.00	0.14	**0.18**	0.06	**0.32**	0.03	0.03	1.00															
275	0.17	**0.21**	0.00	0.00	0.00	**0.19**	0.00	0.13	0.03	0.16	0.06	0.03	0.12	**0.24**	0.15	0.00	1.00														
279	0.03	0.06	0.17	0.00	0.00	0.04	0.00	0.10	0.00	0.00	0.03	0.00	0.14	0.02	0.00	0.00	0.00	1.00													
297	**0.25**	**0.22**	0.00	0.03	0.00	**0.26**	0.03	0.11	0.02	0.13	**0.28**	0.15	**0.25**	**0.31**	**0.19**	0.05	**0.44**	0.00	1.00												
298	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00											
326	0.00	0.06	0.00	**0.40**	0.00	0.00	0.00	0.05	0.00	0.10	0.03	0.00	0.05	0.00	0.03	0.14	0.00	**0.29**	0.03	0.00	1.00										
329	**0.20**	**0.23**	0.00	0.00	0.00	**0.22**	0.00	0.14	0.06	**0.18**	**0.27**	0.06	0.16	**0.27**	0.13	0.03	**0.43**	0.00	**0.47**	0.00	0.00	1.00									
344	0.13	**0.25**	0.00	0.00	0.00	**0.27**	0.00	0.06	0.00	0.16	0.16	0.08	0.17	**0.27**	0.17	0.03	**0.48**	0.00	**0.46**	0.00	0.00	**0.41**	1.00								
347	0.00	0.03	0.00	**0.22**	0.00	0.00	0.00	0.05	0.00	0.08	0.16	0.00	0.09	0.00	0.03	**0.44**	0.00	0.00	0.10	0.00	**0.40**	0.07	0.06	1.00							
351	**0.20**	0.05	0.00	0.00	0.00	0.03	0.00	0.04	**0.32**	0.00	0.08	0.15	0.03	0.06	0.17	0.00	0.03	0.00	0.04	0.00	0.00	0.09	0.03	0.00	1.00						
354	**0.22**	**0.23**	0.00	0.00	0.00	0.15	0.02	0.15	0.02	0.16	0.10	0.12	0.12	**0.51**	**0.27**	0.02	**0.30**	0.00	**0.34**	0.00	0.00	**0.23**	**0.23**	0.00	0.04	1.00					
367	0.17	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.09	**0.23**	**0.19**	0.07	0.05	0.17	0.11	0.00	0.07	0.00	0.00	0.06	0.03	0.00	0.13	0.04	1.00				
380	**0.22**	0.16	0.00	0.00	0.00	**0.18**	0.00	**0.30**	0.07	0.07	0.13	0.10	**0.18**	0.16	**0.20**	0.08	0.12	0.00	0.14	0.00	0.05	0.14	0.15	0.05	0.14	0.15	0.08	1.00			
386	**0.21**	0.11	0.00	0.00	0.00	0.10	0.02	0.10	0.02	**0.20**	0.06	0.09	0.03	**0.60**	**0.26**	0.00	**0.31**	0.00	**0.34**	0.00	0.00	**0.27**	**0.26**	0.00	0.02	**0.56**	0.04	**0.18**	1.00		
395	**0.19**	**0.18**	0.00	0.00	0.00	0.14	0.00	0.12	**0.18**	**0.18**	**0.20**	0.11	0.15	0.07	0.10	**0.38**	0.00	0.00	0.02	0.00	0.11	0.06	0.03	0.09	**0.24**	0.04	0.14	0.12	0.02	1.00	
398	0.12	**0.30**	0.00	0.00	0.00	**0.27**	0.00	0.17	0.00	**0.18**	0.14	0.06	0.14	**0.21**	**0.18**	0.14	**0.40**	0.00	**0.35**	0.00	0.04	**0.27**	**0.35**	0.04	0.03	**0.27**	0.03	**0.19**	**0.27**	0.10	1.00
4	0.05	0.03	0.00	0.00	**0.40**	0.00	0.00	0.00	0.09	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.29**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
411	0.00	0.03	0.00	**0.40**	0.00	0.00	0.00	0.10	0.00	0.10	0.03	0.00	0.00	0.00	0.03	0.14	0.00	0.00	0.03	0.00	**0.67**	0.00	0.00	**0.40**	0.00	0.02	0.00	0.05	0.00	0.11	0.04
421	**0.20**	0.13	0.00	0.00	0.00	0.11	0.00	0.09	**0.34**	0.09	0.14	0.08	0.12	**0.23**	**0.22**	0.15	0.05	0.00	0.04	0.00	0.00	**0.23**	0.05	0.00	**0.29**	**0.20**	0.14	**0.18**	**0.21**	**0.50**	0.05
422	**0.20**	0.11	0.00	0.00	0.00	0.06	0.00	0.06	**0.29**	0.00	0.14	**0.23**	0.09	**0.20**	**0.35**	0.10	0.03	0.00	0.08	0.00	0.00	0.10	0.02	0.00	**0.33**	**0.22**	0.14	**0.18**	0.16	**0.18**	0.10
423	0.05	0.03	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.03	0.12	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.07	0.04	0.08	0.00	0.08	0.00	0.00
425	**0.32**	0.11	0.00	0.00	0.00	0.03	0.00	0.00	**0.38**	0.00	0.12	**0.23**	0.09	0.14	**0.26**	0.05	0.08	0.00	0.08	0.00	0.00	0.15	0.02	0.00	**0.41**	0.14	**0.23**	0.09	0.12	0.13	0.03
431	0.12	0.11	0.00	0.00	0.00	0.06	0.00	0.00	0.14	**0.18**	0.05	0.04	0.03	**0.19**	**0.20**	0.00	**0.26**	0.00	0.16	0.00	0.00	**0.18**	**0.27**	0.00	0.13	**0.21**	0.05	0.16	**0.24**	0.10	**0.25**
433	0.07	0.13	0.00	0.00	0.00	**0.22**	0.00	0.14	0.00	**0.23**	0.04	0.03	0.02	**0.30**	**0.25**	0.03	**0.53**	0.00	**0.38**	0.00	0.00	**0.34**	**0.46**	0.00	0.11	**0.30**	0.00	**0.18**	**0.39**	0.03	**0.51**
448	0.15	0.15	0.00	0.00	0.00	0.04	0.00	0.06	0.07	0.15	0.02	0.00	0.02	**0.36**	**0.39**	0.00	**0.26**	0.00	**0.28**	0.00	0.00	**0.21**	**0.29**	0.00	0.05	**0.43**	0.03	0.14	**0.41**	0.05	**0.26**
45	0.11	**0.21**	0.16	0.00	0.04	**0.19**	0.09	0.15	0.10	0.00	**0.24**	**0.25**	0.17	**0.25**	0.11	0.04	0.02	0.00	0.12	0.00	0.00	0.15	0.10	0.00	0.03	0.11	0.11	0.10	0.08	0.00	0.04
454	0.00	0.06	0.00	0.00	0.00	0.05	0.00	0.05	0.00	**0.20**	0.04	0.00	0.05	0.00	0.03	**0.31**	0.00	0.00	0.00	0.00	**0.40**	0.00	0.03	**0.22**	0.00	0.00	0.00	0.05	0.00	0.12	0.08
459	0.00	0.03	0.00	0.00	0.00	0.09	0.00	0.05	0.00	0.09	0.00	0.00	0.05	0.00	0.00	0.13	0.08	0.00	0.03	0.00	0.00	0.07	0.07	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.08
466	0.00	0.06	0.00	**0.29**	0.00	0.04	0.00	0.15	0.00	**0.26**	0.03	0.00	0.00	0.02	0.06	0.13	0.04	0.00	0.03	0.00	**0.50**	0.04	0.03	**0.33**	0.00	0.02	0.00	0.10	0.02	0.10	0.12
473	0.11	**0.22**	0.00	0.00	0.00	**0.26**	0.00	0.14	0.00	**0.22**	0.09	0.00	0.11	**0.20**	0.14	0.13	**0.49**	0.00	**0.29**	0.00	0.00	**0.30**	**0.40**	0.00	0.07	**0.20**	0.04	**0.24**	**0.23**	**0.19**	**0.60**
478	0.17	0.15	0.00	0.00	0.00	0.06	0.00	0.04	0.00	0.17	0.05	0.00	0.00	**0.41**	**0.29**	0.00	**0.32**	0.00	**0.26**	0.00	0.00	**0.20**	**0.32**	0.00	0.02	**0.36**	0.00	0.16	**0.48**	0.03	**0.29**
48	**0.29**	**0.49**	0.03	0.00	0.03	**0.28**	0.00	**0.23**	0.03	0.08	**0.35**	0.10	**0.25**	**0.19**	**0.22**	0.17	0.14	0.03	**0.29**	0.00	0.03	**0.22**	0.14	0.03	0.08	**0.23**	0.08	**0.21**	0.07	**0.22**	**0.21**
491	**0.18**	0.04	0.00	0.00	0.00	0.06	0.00	0.06	0.00	0.17	0.07	0.00	0.00	0.17	0.09	0.00	**0.32**	0.00	**0.21**	0.00	0.00	**0.25**	**0.21**	0.00	0.04	**0.29**	0.00	0.12	**0.30**	0.04	**0.23**
495	0.05	0.03	0.00	0.00	0.00	0.04	0.00	0.09	0.00	0.14	0.00	0.00	0.00	0.02	0.03	0.00	0.11	0.00	0.07	0.00	0.00	0.10	0.09	0.00	0.00	0.13	0.00	0.04	0.06	0.00	0.14
499	0.15	0.07	0.00	0.00	0.00	0.06	0.00	0.07	0.05	**0.24**	0.03	0.00	0.06	**0.19**	0.05	0.00	**0.35**	0.00	**0.27**	0.00	0.00	**0.32**	**0.22**	0.00	0.05	**0.23**	0.05	0.10	**0.22**	0.00	0.17
51	0.00	0.03	0.00	0.00	0.10	0.04	0.00	0.00	0.06	0.00	0.11	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.12	0.08	**0.18**	0.06	0.00	0.00	0.00	0.02	0.00	0.00
61	0.15	**0.22**	0.04	0.04	0.00	0.16	0.00	0.10	0.00	0.00	**0.18**	0.06	**0.26**	0.15	0.06	0.17	0.04	0.00	0.15	0.04	0.04	0.12	0.08	0.07	0.12	0.08	0.07	0.10	0.06	0.16	0.06
63	0.02	0.00	0.00	0.00	0.00	0.04	0.00	0.04	0.07	0.00	0.00	0.00	0.04	0.06	0.00	0.00	0.00	0.14	0.02	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
64	**0.27**	**0.18**	0.04	0.00	0.00	**0.25**	0.00	**0.21**	0.09	0.03	**0.21**	**0.20**	**0.21**	0.16	**0.29**	**0.20**	0.09	0.00	0.15	0.00	0.04	0.06	0.08	0.04	**0.21**	0.14	**0.20**	**0.24**	0.11	**0.29**	0.15
66	0.16	0.16	0.05	0.06	0.00	0.14	0.00	0.15	0.04	0.00	**0.19**	0.04	**0.26**	0.12	0.00	0.05	0.05	0.06	0.14	0.00	0.00	0.15	0.12	0.06	0.04	0.02	0.05	0.03	0.00	0.00	0.00
69	**0.32**	**0.29**	0.02	0.02	0.02	0.14	0.02	0.17	0.15	0.00	**0.24**	0.12	**0.18**	**0.35**	**0.42**	0.02	0.12	0.02	**0.25**	0.02	0.02	**0.23**	0.16	0.08	**0.18**	**0.30**	0.10	**0.19**	**0.23**	0.09	0.07
71	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00
74	**0.18**	**0.35**	0.05	0.00	0.03	**0.41**	0.05	**0.28**	0.05	0.11	**0.35**	0.09	**0.40**	0.15	0.17	0.17	0.12	0.05	**0.29**	0.00	0.05	**0.23**	**0.30**	0.13	0.02	0.12	0.05	**0.22**	0.12	0.14	**0.26**
77	0.13	**0.33**	0.06	0.00	0.03	**0.44**	0.10	**0.29**	0.03	0.00	**0.39**	0.16	**0.49**	0.11	0.09	0.09	0.06	0.07	**0.33**	0.00	0.04	**0.25**	**0.27**	0.13	0.00	0.10	0.03	0.11	0.06	0.03	0.08
88	0.09	**0.34**	0.06	0.00	0.00	**0.45**	0.07	**0.28**	0.03	0.08	**0.38**	0.08	**0.48**	0.11	0.13	0.12	0.10	0.07	**0.32**	0.00	0.03	**0.21**	**0.26**	0.16	0.00	0.13	0.03	0.17	0.09	0.08	**0.19**
9	**0.27**	**0.67**	0.05	0.00	0.05	**0.27**	0.05	0.17	0.07	0.02	**0.32**	0.11	**0.29**	**0.20**	**0.30**	0.10	0.17	0.03	**0.28**	0.03	0.03	**0.18**	**0.20**	0.03	0.07	**0.22**	0.14	0.17	0.06	0.14	0.14
99	0.00	0.03	0.00	0.00	0.00	0.16	0.00	**0.27**	0.00	0.00	0.03	0.00	0.04	0.00	0.03	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00

Table 3.1. continued.

4	1.00																													
411	0.00	1.00																												
421	0.00	0.00	1.00																											
422	0.00	0.06	**0.44**	1.00																										
423	0.00	0.00	0.05	0.15	1.00																									
425	0.00	0.00	**0.37**	**0.37**	0.15	1.00																								
431	0.00	0.00	**0.18**	0.14	0.00	0.14	1.00																							
433	0.00	0.00	0.05	0.05	0.00	0.05	**0.29**	1.00																						
448	0.00	0.03	**0.26**	**0.24**	0.00	0.11	**0.41**	**0.37**	1.00																					
45	0.00	0.00	0.00	0.11	0.07	0.03	0.00	0.04	0.00	1.00																				
454	0.00	**0.40**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00																			
459	0.00	0.00	0.06	0.06	0.13	0.06	0.00	0.07	0.00	0.00	**0.33**	1.00																		
466	0.00	**0.50**	0.06	0.00	0.00	0.00	0.00	0.07	0.03	0.00	**0.29**	0.00	1.00																	
473	0.00	0.00	0.15	0.09	0.00	0.00	**0.22**	**0.64**	**0.24**	0.00	0.00	0.05	0.10	1.00																
478	0.00	0.00	0.04	0.04	0.03	0.00	**0.41**	**0.48**	**0.60**	0.00	0.00	0.00	0.00	**0.30**	1.00															
48	0.00	0.07	**0.18**	0.09	0.00	0.14	0.00	0.15	0.12	**0.18**	0.03	0.03	0.10	**0.19**	0.10	1.00														
491	0.00	0.06	0.14	0.13	0.05	0.07	**0.25**	**0.30**	**0.28**	0.00	0.00	0.06	0.00	**0.27**	**0.37**	0.07	1.00													
495	0.00	0.14	0.05	0.10	0.00	0.00	0.11	0.13	**0.19**	0.00	0.00	0.13	0.13	0.17	0.08	0.09	0.15	1.00												
499	0.00	0.00	0.11	0.04	0.00	0.11	0.12	**0.32**	**0.23**	0.03	0.00	0.14	0.00	**0.30**	**0.23**	0.07	**0.33**	**0.34**	1.00											
51	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00										
61	0.00	0.04	0.11	0.08	0.00	0.00	0.00	0.02	0.00	**0.24**	0.00	0.00	0.04	0.10	0.00	0.17	0.00	0.00	0.03	0.06	1.00									
63	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.14	1.00								
64	0.00	0.04	**0.18**	**0.28**	0.03	**0.18**	0.11	0.10	0.05	0.13	0.04	0.04	0.04	0.16	0.16	**0.21**	0.13	0.00	0.06	0.03	**0.27**	0.07	1.00							
66	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.25**	0.00	0.00	0.00	0.00	0.00	0.16	0.00	0.00	0.04	**0.18**	**0.39**	**0.26**	0.13	1.00						
69	0.00	0.02	**0.25**	**0.31**	0.02	**0.20**	0.10	0.11	**0.26**	**0.25**	0.00	0.00	0.02	0.08	**0.18**	**0.25**	0.10	0.04	0.12	0.13	**0.24**	0.10	**0.24**	**0.33**	1.00					
71	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	**0.22**	0.04	0.11	0.06	1.00				
74	0.00	0.03	0.08	0.04	0.02	0.04	0.08	0.17	0.09	**0.21**	0.06	0.03	0.03	**0.24**	0.12	**0.28**	0.04	0.02	0.11	0.14	0.15	0.03	**0.20**	0.16	**0.22**	0.00	1.00			
77	0.00	0.00	0.02	0.02	0.03	0.02	0.00	0.04	0.00	**0.33**	0.00	0.00	0.00	0.02	0.00	**0.29**	0.00	0.00	0.03	0.14	**0.20**	0.06	0.14	**0.29**	**0.25**	0.00	**0.63**	1.00		
88	0.00	0.03	0.02	0.05	0.06	0.02	0.07	0.11	0.07	0.12	0.07	0.03	0.03	0.13	0.08	**0.23**	0.02	0.03	0.05	0.14	**0.19**	0.03	**0.21**	**0.23**	**0.20**	0.00	**0.58**	**0.59**	1.00	
9	0.03	0.05	0.10	0.12	0.02	0.12	0.04	0.15	0.12	**0.19**	0.03	0.05	0.03	0.17	0.08	**0.56**	0.06	0.05	0.08	0.02	**0.22**	0.00	**0.20**	**0.18**	**0.34**	0.00	**0.24**	**0.26**	**0.27**	1.00	
99	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.16	0.00	0.16	0.00	0.03	1.00
	4	**411**	**421**	**422**	**423**	**425**	**431**	**433**	**448**	**45**	**454**	**459**	**466**	**473**	**478**	**48**	**491**	**495**	**499**	**51**	**61**	**63**	**64**	**66**	**69**	**71**	**74**	**77**	**88**	**9**	**99**

3.1.3. *Preferred and avoided associates and measures of gregariousness*

The dataset of associations was randomly permuted 40,000 times with 100 flips per permutation in a Monte Carlo test. The observed CV of association index was significantly higher than the generated random CV (observed= 1.27, random= 1.26, $p<0.05$), indicating that male dolphins were forming preferential associations across the 18 year study period. However, the observed standard deviation (SD) of group size was not significantly higher than the randomly permuted SD of group size (observed= 2.19, random= 2.18, $p>0.05$). Therefore, study animals were not found in consistently sized groups, indicating that there were no differences in gregariousness within the male members of the population.

Eighteen significant dyads were isolated from the dataset, from 94 expected dyads, indicating that some males were observed together or apart more often than would be expected if random association was occurring. Twelve dyads showed significant avoidance (Table 3.2), while the five significant, preferred dyads may be found in table 3.3.

Table 3.2. The dyad ID#s for males which significantly avoided each other from 1997 to 2014. All dyads were significant for avoidance, $p<0.05$

Dyad ID#	
344	1
433	1
448	1
380	10
398	223
380	238
354	329
354	344
398	380
74	380
9	380
448	386
64	448

Table 3.3. Preferred associations in male bottlenose dolphin dyads isolated from the CRRU dataset (Cetacean Research & Rescue Unit), from 1997 to 2014. Significance is indicated by >0.05

ID #s of dyad	HWI of dyad	p value (significance >0.05)
398 433	0.51	0.97
433 473	0.64	0.98
473 398	0.60	0.99
386 21	0.60	0.98
425 1	0.32	0.97

3.1.4. *Hierarchical cluster analyses*

The cluster analysis revealed clustering within a number of dyads and triads (Figure 3.2). While some of the highest association indices were between ID#s 9 and 10 (0.67), 88, 77 and 74 (mean HWI= 0.60), and 411 and 326 (0.51), resulting in clustering, these associations were not identified as significant from the permutation tests (Tables 3.1; 3.2; 3.3). However, the significant dyad and triad between ID#s 386 and 21 (HWI= 0.60), and 398, 433 and 473 (HWI= 0.58) respectively, could be observed.

3.1.5. *Temporal patterns- Standardised lagged association rates (SLARs)*

The stability of associations across time was examined through the standardised lagged association rate (SLAR), using all 66 known males identified by the CRRU. The resulting curve showed stability over a duration of days and months (Figure 3.3). However, the association rates fell to the null association rate after around three years and thereafter showed complete disassociation (Figure 3.3). The jack-knife error bars (± 1 estimated standard error) were found to be large at the beginning of the plotted curve, which may signify that patterns of association within all groups were not fully represented at all time lags within the available data. The social-system model which best fitted the SLAR curve was found to include one level of association, described as short-term 'casual acquaintances' (Figure 3.3). The model was stable for the first three years at HWI= 0.04, which suggested generally weak but steady companionships forming between individuals after their first association, before disassociation occurred at later time lags.

3.1.6. *Temporal patterns- Lagged identification rate (LIR)*

The fitted lagged identification rate (LIR) curve showed a similar pattern to the SLAR plot, indicating that the temporal patterns in association rate between males in the outer Moray Firth were affected by demographic factors such as mortality or emigration, rather than changes in association between individuals (Figure 3.4). The LIR dropped to zero over the study period, indicating that demographic factors were permanent. The best fit movement model suggested three demographic factors influenced the observed association patterns: emigration, re-immigration, and mortality.

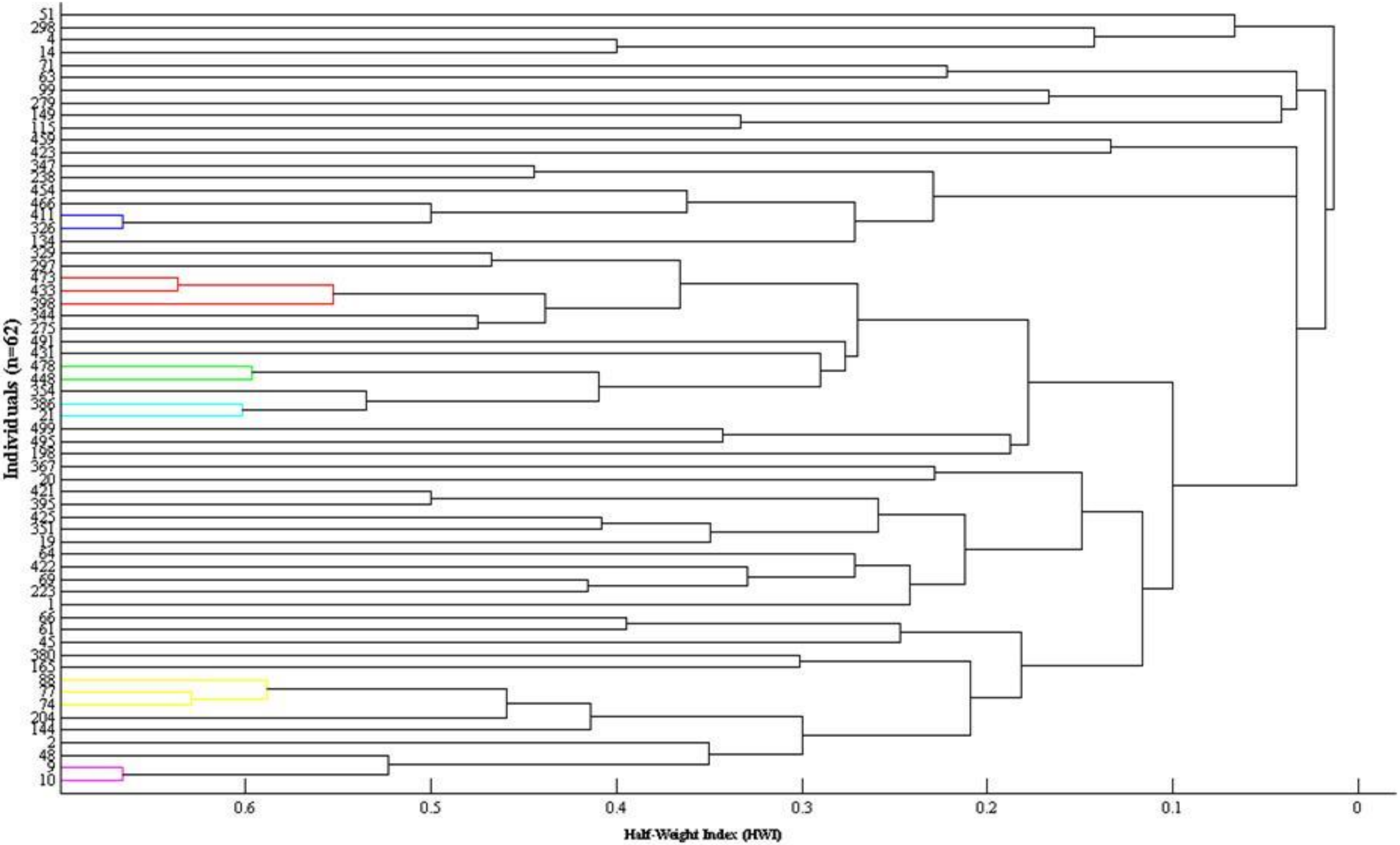

Figure 3.2. Average-linkage dendrogram for 62 males of the outer southern Moray Firth bottlenose dolphin community, observed >2 times from 1997-2014. Coloured clusters indicate animals with HWIs >0.5. Cophenetic correlation coefficient (CCC)= 0.87

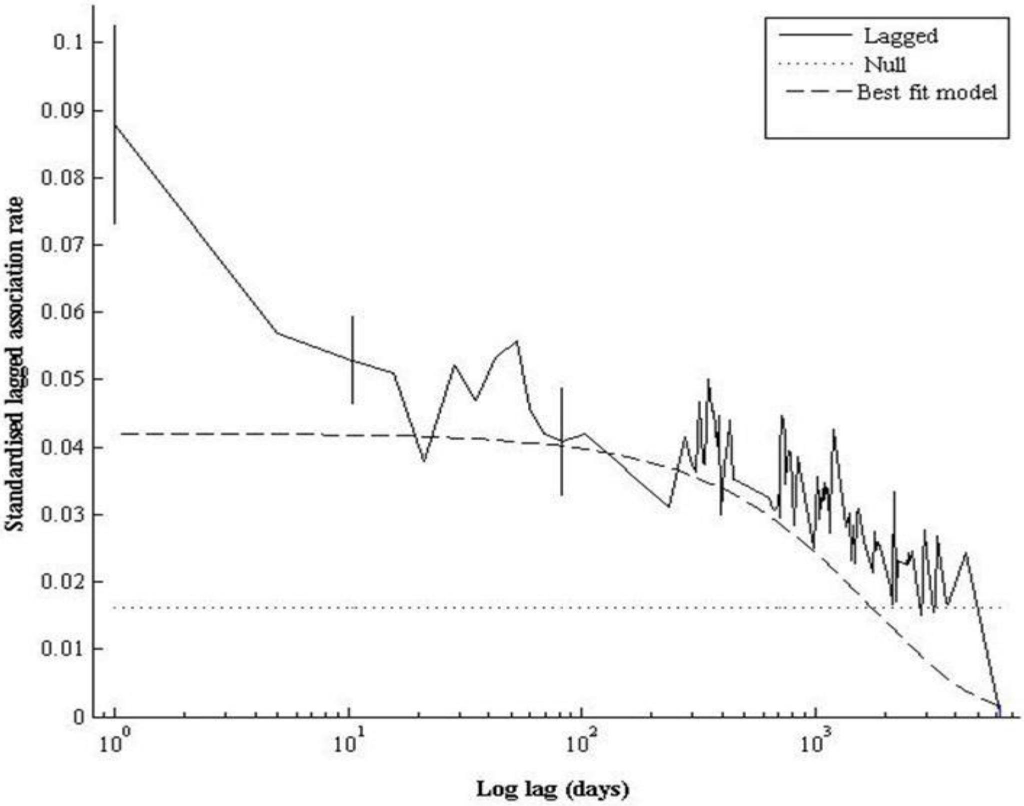

Figure 3.3. The standardised lagged association rate (SLAR) and standardised null association rate (SNAR) for all 66 known males observed in the outer Moray Firth by the Cetacean Research & Rescue Unit (CRRU), from 1997-2014. A moving average of 3,000 associations was used to smooth the curve. Vertical bars indicate approximate standard errors, which were obtained by jack-knifing. The exponential model of best fit is shown (a2*exp(-a1+td)).

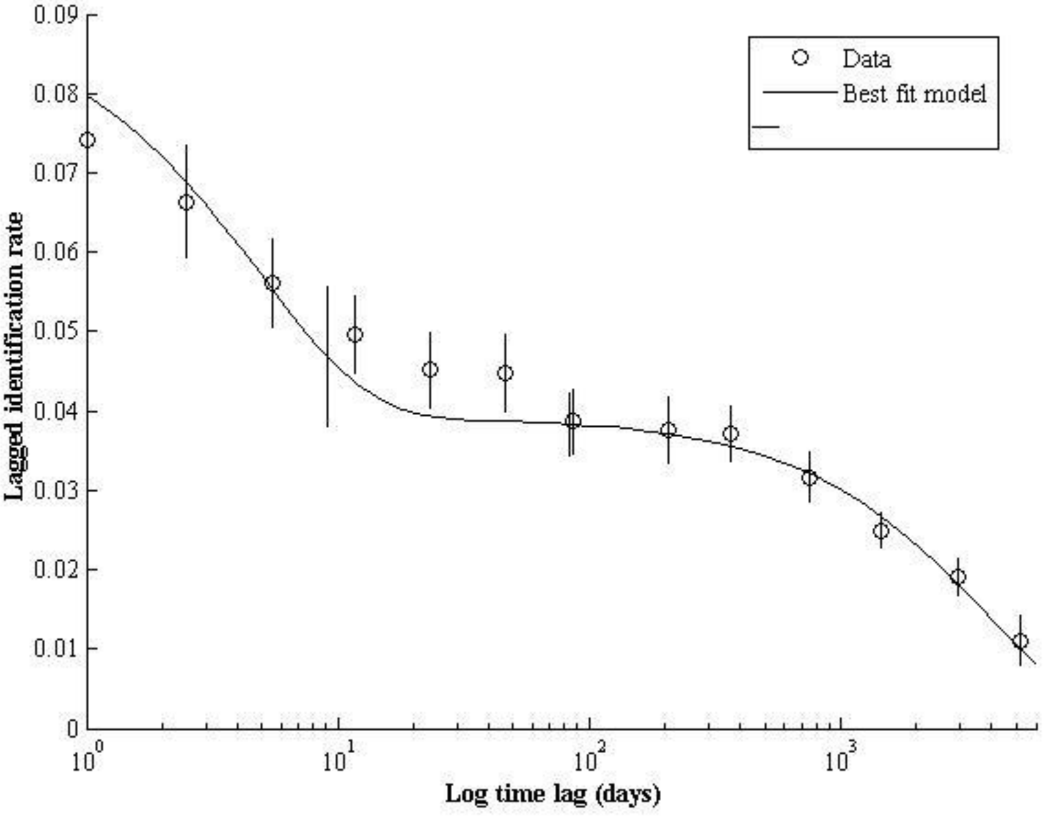

Figure 3.4. The lagged identification association rate (LIR) for all 66 known males observed in the outer Moray Firth by the Cetacean Research & Rescue Unit (CRRU), from 1997-2014. Vertical bars indicate approximate standard errors, which were obtained by boot-straps of 100 replicates. The movement model of best fit is shown (a3*exp(-a1*td)+a4*exp(-a2*td)).

3.2. *Sea Watch Foundation dataset*

3.2.1. *Known males*

A total of 50 males were identified by the SWF, with 21 being ‘definite’ males (Table 7.6, appendix). From 2001 to 2014, 5620 bottlenose dolphin encounters were recorded, with 1019 of these containing one or more male animals, representing 18% of all encounters. ‘Definite’ males were encountered 697 times. Additionally, 962 encounters occurred between May and October (94% of the 1019 encounters involving male animals). Further, 96% of all male encounters occurred within the Cardigan Bay SAC.

A mean of two males were observed across all 1019 encounters, and 78% of encounters involved one male among a group of two or more animals. Solitary males were encountered 225 times. 694 encounters (68%) involved one male, where the rest of the group members were females, juveniles or of an unknown sex. The mean encounter rate for all males over the 14-year study period was 32.06± 33.13 times (Table 7.6, appendix). Total encounters made in every hour, month and year of the study period may be found in tables 7.7, 7.8 and 7.9, appendix.

3.2.2. *Patterns of association*

(i) Full dataset

Out of the 50 males identified from the SWF dataset, 47 definite and probable males were selected for analyses of association patterns. The HWI distribution (n=2,209) for selected males was strongly skewed towards low values, many individuals maintaining no associations with other males in the population (Figure 3.5, A and B). The distribution of calculated maximum HWIs ranged between 0.00 and 0.44, with a weak mean HWI of 0.03± 0.02 (±SD). The most frequently occurring maximum HWI was 0.11 (n=17) (Figure 3.5, C). Mean and maximum HWIs for all individuals in each of the four analyses may be found in table 7.10, appendix.

The sociomatrix created from calculated HWIs showed that the strongest association was between male ID#s 54 and 56 (HWI= 0.44) (Table 3.4). All possible dyads (n=1,081) are shown in table 3.4, and dyads twice the mean HWI are also highlighted (n= 211).

The estimate of social differentiation was 1.27± 0.09 (±SD), indicating that the male dolphin community is fairly well differentiated. The estimated correlation coefficient between the observed association indices and calculated indices was 0.79± 0.01 (±SD), suggesting the analysis had detected the true social system with reasonable power (1= perfect, 0= poor fit).

(ii) ‘Definite’ males

When only definite males (n= 21) were analysed, HWI distribution (n= 441) was skewed towards lower values, and the mean HWI mirrored that calculated for all 62 probable and definite males at 0.04± 0.02. The resulting sociomatrix revealed 207 possible dyads, and 32 were at least twice the mean HWI (Table 3.5). The strongest dyad existed between male ID#s 166 and 163 (HWI= 0.38) (Table 3.5). The social differentiation estimate was similar to previous analyses at 1.31± 0.12 (±SD), while the correlation coefficient between observed and calculated HWIs was slightly higher, indicating that the power of analysis was marginally better, at 0.82± 0.02 (±SD).

(iii) Excluding months outside May-October

In order to address any potential bias in the comparisons with the CRRU dataset, months out-with May and October inclusive were excluded. Analyses included all 47 definite and probable males. The HWI distribution (n=2,209) was strongly skewed towards low values, and the mean HWI was lower than that calculated for the previous analyses at 0.03± 0.01 (±SD). For individuals, the mean HWI was 0.00, and the most frequently occurring maximum HWI was 0.22 (n=18). The sociomatrix showed 1,081 possible dyads, and 175 of these were twice the mean (>0.06). As in the former analyses of the full dataset, ID#s 56 and 54 had the largest HWI, at 0.44.

The estimate of social differentiation was 1.37± 0.10 (±SD), indicating that the male dolphin community is fairly well differentiated. The estimated correlation coefficient between the observed association indices and calculated indices was 0.77± 0.01 (±SD), suggesting that the analysis detected the true social system with reasonable power.

(iv) Cardigan Bay SAC

43 males were observed in the Cardigan Bay SAC from 2001 to 2014. Three males included in analyses of the full dataset were not observed in Cardigan Bay and were excluded, these being ID#s 23, 125 and 200, whilst ID# 121 was removed due to being sighted less than two times. Again, as in the previous analyses, the HWIs (n= 1,764) were low across the males examined. The mean HWI (0.04± 0.01) reflected that of analyses (i) and (ii). The sociomatrix revealed 861 possible dyads, and 133 were at least twice the average HWI (>0.08). Although ID#s 54 and 56 still showed the highest HWI (0.41), it was less than calculated in previous analyses (i) and (iii).

The social differentiation estimate was 1.22± 0.09 (±SD), and the estimated correlation coefficient was 0.79± 0.01 (±SD). As in the previous analyses, the male community within the Cardigan Bay SAC was fairly well differentiated and the true social system was detected through the analysis.

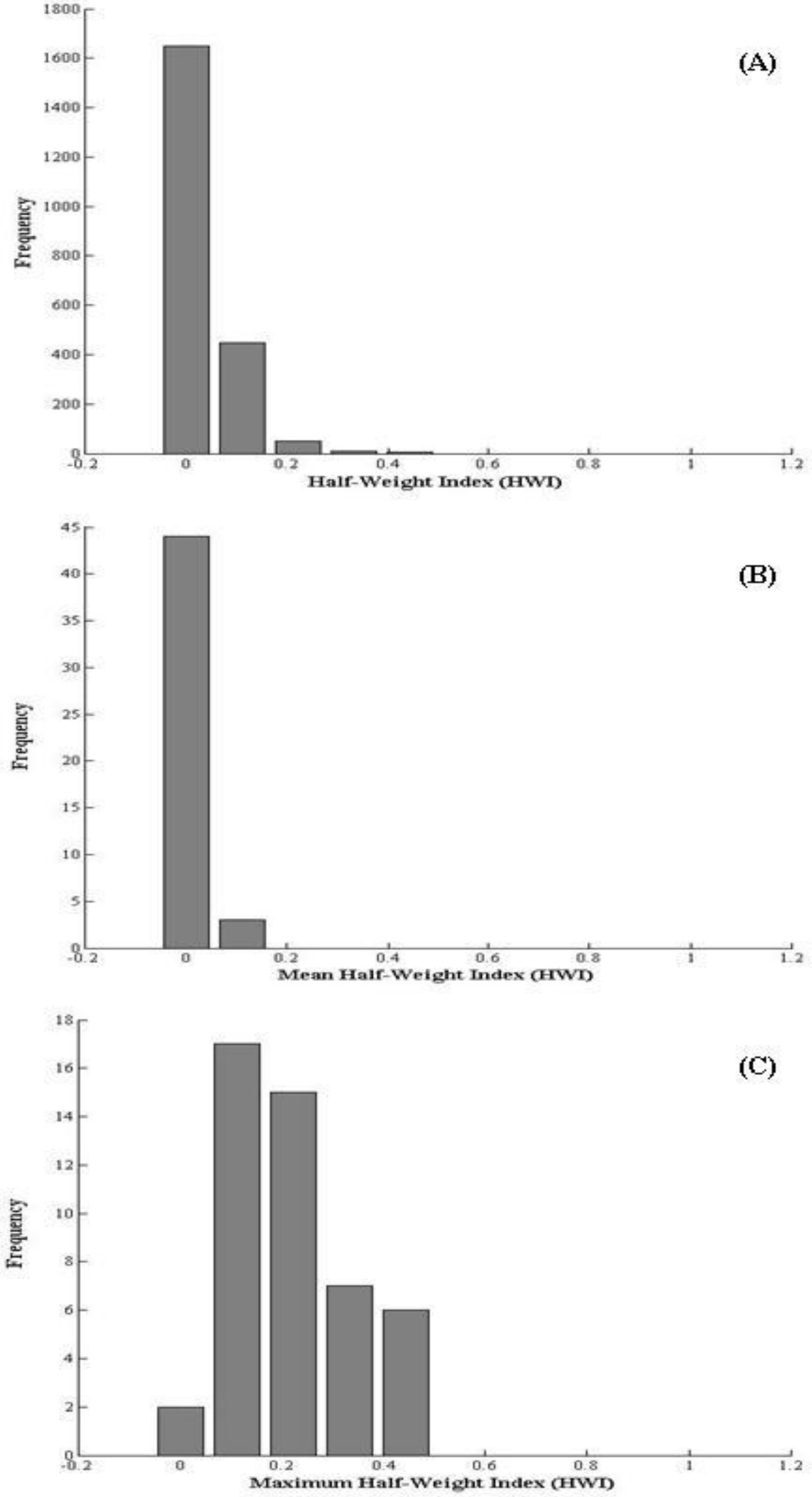

Figure 3.5. The distribution of the Half-Weight Indices (HWIs) for 47 known adult males identified >2 times from 2001- 2014, inclusive: (A) the frequency of all pairwise comparisons (n=2209), (B) the mean HWI for each male, and (C) maximum HWIs for each male in the study.

Table 3.4. Sociomatrix detailing the strength of association between all males included in the social analysis (n= 47). Values presented are Half-Weight Indices (HWIs), where 0= no association between two individuals, and 1= constant strong association between two males. HWI >0.06, at least twice the mean HWI (0.03), are highlighted **bold.**

	105	106	109	110	116	118	12	121	123	125	136	139	14	140	159	163	166	18	181	196	2	200	207	23	233	29	36	40	5	53	54	55	56	57	58	59	6	60	64	74	75	85 86	80	85	86	93	96
105	1.00																																														
106	0.00	1.00																																													
109	**0.11**	0.00	1.00																																												
110	**0.10**	0.00	0.03	1.00																																											
116	**0.06**	0.00	0.00	0.05	1.00																																										
118	**0.25**	0.00	0.03	**0.13**	0.00	1.00																																									
12	0.00	0.00	0.03	0.00	0.00	0.00	1.00																																								
121	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00																																							
123	**0.09**	0.00	0.05	**0.12**	0.00	0.03	0.00	0.00	1.00																																						
125	**0.06**	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.05	1.00																																					
136	**0.13**	**0.06**	0.05	**0.06**	0.00	**0.13**	0.00	0.00	**0.12**	0.00	1.00																																				
139	0.00	0.00	0.00	**0.07**	0.00	0.00	0.04	0.00	**0.06**	0.00	**0.07**	1.00																																			
14	0.00	0.00	0.00	**0.07**	0.04	0.05	**0.08**	0.00	0.05	0.00	**0.07**	**0.16**	1.00																																		
140	0.04	0.00	0.03	**0.07**	0.00	0.04	0.04	0.00	**0.06**	0.00	0.00	**0.08**	**0.08**	1.00																																	
159	0.05	0.00	**0.06**	0.05	0.00	0.05	0.00	0.00	0.02	0.00	0.05	0.00	0.02	0.02	1.00																																
163	0.04	0.00	**0.11**	0.00	0.00	0.04	0.00	0.00	0.00	**0.06**	0.00	0.00	0.00	0.00	**0.10**	1.00																															
166	0.04	0.00	**0.06**	0.04	0.00	**0.08**	0.00	0.00	0.00	**0.07**	0.00	0.00	0.03	0.00	**0.18**	**0.38**	1.00																														
18	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	1.00																													
181	**0.12**	0.00	**0.17**	0.00	0.00	**0.09**	0.00	0.00	0.00	**0.09**	**0.06**	0.00	0.05	0.00	**0.13**	**0.13**	**0.13**	0.00	1.00																												
196	**0.17**	0.00	**0.09**	0.04	0.00	**0.21**	0.00	0.00	0.04	**0.07**	**0.08**	0.00	0.00	0.00	**0.11**	**0.18**	**0.14**	0.00	**0.10**	1.00																											
2	**0.10**	0.00	**0.07**	0.03	0.00	**0.06**	0.00	0.00	0.00	0.00	**0.09**	0.00	0.02	0.03	**0.11**	**0.17**	**0.25**	0.00	**0.11**	**0.26**	1.00																										
200	**0.09**	0.00	**0.10**	0.04	0.00	**0.09**	0.00	0.00	0.04	**0.25**	0.04	0.00	0.00	0.00	**0.11**	**0.14**	**0.15**	0.00	**0.11**	**0.22**	0.00	1.00																									
207	0.05	0.00	**0.08**	0.02	0.00	0.02	0.00	0.00	**0.07**	0.00	0.03	0.00	0.00	0.00	0.01	0.00	0.00	0.00	**0.07**	0.02	0.03	0.00	1.00																								
23	**0.09**	0.00	0.05	0.03	0.05	**0.09**	0.00	0.00	0.03	0.05	**0.06**	0.00	**0.07**	0.00	**0.07**	**0.10**	**0.07**	0.00	**0.19**	**0.14**	**0.06**	0.04	0.03	1.00																							
233	0.00	0.00	**0.06**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	**0.40**	**0.14**	0.00	**0.07**	0.00	**0.11**	0.00	0.02	0.04	1.00																						
29	**0.35**	0.00	0.05	**0.18**	0.05	**0.13**	0.03	0.00	**0.06**	0.05	**0.09**	0.00	0.02	**0.10**	**0.07**	0.00	0.00	0.00	**0.14**	**0.15**	**0.09**	**0.12**	0.01	**0.08**	0.00	1.00																					
36	**0.17**	0.00	0.03	**0.08**	0.00	**0.25**	0.00	0.00	0.04	**0.07**	**0.08**	0.00	0.00	0.04	0.05	**0.13**	**0.09**	0.00	**0.10**	**0.40**	**0.11**	**0.22**	0.00	**0.11**	0.00	**0.15**	1.00																				
40	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.03	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	1.00																			
5	0.00	**0.06**	0.03	0.03	0.00	0.00	**0.14**	0.00	0.00	0.05	0.00	0.00	0.00	**0.07**	0.00	0.00	0.00	0.03	0.00	0.00	0.03	0.04	0.00	0.00	0.00	0.03	0.00	0.04	1.00																		
53	0.00	**0.07**	0.00	**0.14**	**0.06**	0.00	**0.12**	0.00	0.03	0.00	**0.07**	0.00	0.05	**0.08**	0.03	0.00	0.04	0.00	0.00	0.00	0.03	0.00	0.02	0.00	0.00	**0.07**	0.00	**0.25**	**0.10**	1.00																	
54	0.00	0.00	0.00	**0.08**	0.00	0.00	**0.10**	0.00	0.00	0.00	0.00	0.00	0.03	**0.09**	0.03	0.00	0.05	0.04	0.00	0.00	0.04	**0.06**	0.00	0.00	0.00	0.04	0.00	**0.13**	**0.08**	**0.14**	1.00																
55	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	**0.25**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.06**	0.04	0.05	**0.17**	1.00															
56	0.00	0.00	0.03	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.03	0.00	0.05	0.05	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	**0.21**	0.00	**0.10**	**0.44**	**0.19**	1.00														
57	0.00	**0.25**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.06**	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00													
58	0.05	0.00	0.04	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	**0.12**	**0.11**	**0.06**	0.00	**0.08**	**0.06**	0.04	**0.14**	0.02	**0.08**	0.00	0.04	**0.06**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00												
59	0.00	0.00	0.00	**0.06**	0.00	0.00	**0.13**	0.00	**0.11**	0.04	0.00	0.00	**0.07**	**0.09**	0.02	0.00	0.03	**0.26**	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.05	0.00	**0.08**	**0.06**	**0.13**	**0.11**	0.04	**0.15**	0.00	0.00	1.00											
6	0.00	0.00	0.03	0.03	0.00	0.00	**0.11**	0.00	0.00	0.00	0.00	0.03	**0.12**	**0.13**	0.00	0.00	0.00	**0.16**	0.00	0.00	0.00	0.04	0.00	**0.06**	0.00	**0.06**	0.00	0.00	**0.06**	**0.07**	**0.16**	0.00	0.04	0.00	0.00	**0.11**	1.00										
60	0.04	**0.08**	**0.09**	0.04	0.00	**0.08**	0.05	0.00	0.04	0.00	0.04	0.00	0.03	0.00	0.03	0.04	0.00	0.00	0.03	**0.15**	0.04	**0.16**	0.05	0.00	0.00	**0.11**	**0.15**	0.00	0.04	0.04	0.00	0.00	0.00	0.00	**0.06**	0.00	0.00	1.00									
64	0.00	0.00	0.05	0.03	0.00	0.00	**0.07**	0.00	0.03	0.00	0.00	0.00	**0.07**	**0.10**	0.00	0.00	0.00	**0.12**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.04	**0.15**	**0.07**	**0.08**	0.04	0.04	0.00	0.00	**0.19**	**0.12**	0.00	1.00								
74	0.04	0.00	0.04	0.01	0.00	**0.06**	0.01	0.00	0.04	0.00	**0.06**	0.01	0.03	0.01	0.03	0.02	0.01	0.00	**0.06**	0.04	0.04	0.02	**0.08**	**0.06**	0.00	0.04	0.03	0.00	0.01	0.01	0.00	0.00	0.00	0.01	0.02	0.00	0.00	0.02	0.00	1.00							
75	0.03	0.00	0.05	**0.15**	0.00	0.03	0.04	0.00	**0.12**	0.00	**0.12**	**0.14**	**0.15**	**0.07**	0.02	0.03	0.00	0.03	0.00	0.04	0.00	**0.08**	0.00	0.00	0.00	0.03	0.04	0.00	0.03	**0.10**	0.04	0.04	0.00	0.00	0.05	**0.06**	0.00	**0.07**	0.00	0.02	1.00						
76	0.00	0.05	0.00	**0.15**	0.00	0.03	**0.07**	0.00	0.03	0.05	0.03	**0.06**	**0.12**	**0.10**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.06**	0.04	**0.12**	**0.09**	**0.26**	**0.11**	0.00	**0.08**	0.00	0.00	**0.14**	**0.12**	0.04	**0.08**	0.00	**0.09**	1.00					
80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	**0.07**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	**0.10**	0.00	0.00	0.00	0.00	**0.06**	0.00	0.00	0.00	0.00	0.05 1.00	1.00				
85	**0.25**	0.00	**0.07**	**0.06**	0.05	**0.32**	0.00	0.00	**0.06**	0.00	**0.15**	0.00	0.02	0.00	**0.07**	**0.07**	**0.07**	0.00	**0.08**	0.04	0.03	**0.12**	0.00	**0.17**	0.04	**0.14**	**0.15**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.04	0.00	**0.06**	**0.06**	03 0.00 1.	0.00	1.00			
86	0.00	0.00	0.00	**0.15**	0.00	0.00	0.00	0.00	0.04	0.00	0.00	**0.13**	**0.14**	**0.17**	0.05	0.00	**0.09**	0.00	**0.07**	0.00	**0.07**	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.04	0.05	0.00	**0.06**	0.00	0.00	0.03	0.04	0.00	0.00	0.01	**0.11**	0.00 0.00	0.00	0.00	1.00		
93	0.00	0.00	0.00	**0.06**	0.05	0.00	**0.11**	0.00	0.03	0.05	**0.06**	0.00	**0.12**	**0.07**	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.04	0.02	0.00	0.00	0.03	0.00	**0.17**	**0.12**	**0.31**	**0.08**	0.00	0.00	0.05	0.00	**0.20**	**0.09**	0.00	**0.09**	0.00	**0.06**	00 0.00 0.	0.00	0.00	0.00	1.00	
96	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.04	0.00	0.04	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00 0.00	0.00	0.00	0.00	0.00	1.00

Table 3.5. Sociomatrix detailing the strength of association between definite males included in the social analysis (n= 21). Values presented are Half-Weight Indices (HWIs), where 0= no association between two individuals, and 1= constant strong association between two males. HWI >0.08, at least twice the mean HWI (0.04), are highlighted **bold.**

118	1.00																				
123	0.03	1.00																			
125	0.00	0.04	1.00																		
139	0.00	0.06	0.00	1.00																	
14	0.05	0.04	0.00	**0.16**	1.00																
140	0.04	0.06	0.00	**0.08**	**0.08**	1.00															
163	0.04	**0.12**	0.06	0.00	0.00	0.00	1.00														
166	**0.08**	0.03	0.07	0.00	0.03	0.00	**0.38**	1.00													
18	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	1.00												
2	0.03	0.05	0.00	0.00	0.02	0.03	**0.17**	**0.25**	0.00	1.00											
200	**0.09**	0.03	**0.25**	0.00	0.00	0.00	**0.14**	**0.15**	0.00	0.00	1.00										
207	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	1.00									
233	0.00	0.00	0.00	0.00	0.00	0.00	**0.27**	**0.11**	0.00	0.04	0.00	0.02	1.00								
36	**0.22**	0.00	**0.08**	0.00	0.00	0.04	**0.14**	**0.10**	0.00	**0.11**	**0.17**	0.00	0.00	1.00							
40	0.00	0.00	0.00	0.00	0.03	0.05	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	1.00						
54	0.00	0.00	0.00	0.00	0.03	**0.09**	0.00	0.05	0.04	0.04	0.06	0.00	0.00	0.00	**0.13**	1.00					
59	0.00	**0.10**	0.04	0.00	0.07	**0.09**	0.00	0.03	**0.26**	0.03	0.00	0.00	0.00	0.00	**0.08**	**0.11**	1.00				
64	0.00	0.03	0.00	0.00	0.07	**0.10**	0.00	0.00	**0.12**	0.00	0.00	0.00	0.00	0.00	0.04	**0.08**	**0.19**	1.00			
74	0.05	0.04	0.00	0.01	0.03	0.01	0.02	0.01	0.00	0.04	0.02	**0.08**	0.00	0.02	0.00	0.00	0.00	0.00	1.00		
85	**0.32**	**0.08**	0.00	0.00	0.02	0.00	0.07	0.07	0.00	0.03	**0.12**	0.00	0.00	**0.11**	0.00	0.00	0.00	0.00	0.06	1.00	
86	0.00	0.03	0.00	**0.13**	**0.14**	**0.17**	0.00	**0.09**	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.05	0.03	0.00	0.01	0.00	1.00
	118	**123**	**125**	**139**	**14**	**140**	**163**	**166**	**18**	**2**	**200**	**207**	**233**	**36**	**40**	**54**	**59**	**64**	**74**	**85**	**86**

3.2.3. *Preferred and avoided associates and measures of gregariousness*

The calculated HWIs for males in each dataset were permuted using a Monte Carlo test, and examined for differences between the observed and random test statistics, CV and SD (Table 3.6). In every case, the observed test statistic CV was significantly higher than the random CV, indicating that male dolphins from Cardigan Bay were forming preferential associations. Additionally, the observed SD for typical group size was also significantly higher than the randomly generated SD, signifying that male dolphins in Cardigan Bay were found in consistently sized groups, and that individuals showed different levels of gregariousness throughout the 14-year study period.

Table 3.6. Results of permutation tests for preferred associations and differences in gregariousness for each of the four datasets examined; full dataset with all encounters (n= 1019); 'definite' male encounters only (n= 697); excluding encounters outside May to October (n= 962); and encounters made within the Cardigan Bay SAC (n= 988). Observed/random CV= coefficient of variation. Observed/random SD= standard deviation of group size.

Dataset	Number of males	Permutations (flip number)	Observed CV	Random CV	p value	Observed SD	Random SD	p value
(i) Full	47	40,000 (100)	1.64	1.45	<0.05	0.71	0.65	<0.05
(ii) Definite males	21	20,000 (100)	1.65	1.49	<0.05	0.33	0.32	<0.05
(iii) May-October only	47	35,000 (100)	1.86	1.6	<0.05	0.57	0.49	<0.05
(iv) Cardigan Bay SAC	42	40,000 (100)	1.57	1.38	<0.05	0.55	0.5	<0.05

A number of dyads from each analysis were identified as occurring together or apart more often than would be expected under random association. Some individuals significantly avoided other males within the community (Table 3.7). Additionally, a number of significant preferred dyads were identified between individual males (Table 3.8). The association indices were low in the identified significant preferred dyads however, indicating the associations were of a moderate strength between these males.

Table 3.7. The dyad ID#s for males which significantly avoided each other within each dataset examined; (i) full dataset (47 males); (ii) 'definite' males (n=21); (iii) excluding encounters outside May-October (47 males); (iv) encounters made within Cardigan Bay SAC (42 males). All dyads were significant for avoidance, p<0.05

Dyad ID#			
(i) Full	**(ii) 'Definite' males**	**(iii) May-Oct only**	**(iv) CB SAC**
74 29	86 123	74 29	85 118
74 59	-	86 123	74 29
86 123	-	74 59	74 59

Table 3.8. The significant preferential dyads isolated from each dataset examined; (i) full dataset (47 males); (ii) 'definite' males (n=21); (iii) excluding encounters outside May-October (47 males); (iv) encounters made within Cardigan Bay SAC (42 males). Half-Weight Index (HWI) is shown, and all dyads were significant for preferential association, p>0.05

	HWI of dyad			
Dyad ID#	**(i) Full**	**(ii) 'Definite' males**	**(iii) May-Oct only**	**(iv) CB SAC**
85 105	0.25	-	0.23	0.28
85 118	0.32	0.32	0.32	-
118 105	0.25	-	0.21	0.27
29 110	0.18	-	0.17	-
75 14	0.15	-	-	-
223 163	0.40	0.27	0.45	0.39
59 18	0.26	-	0.27	0.26
56 54	0.44	-	0.44	0.41
64 59	0.19	-	0.20	-
36 29	0.15	-	-	-
76 53	0.26	-	0.21	0.25
76 6	0.12	-	0.13	-
93 59	0.20	-	0.18	-
93 6	0.09	-	0.10	0.09
36 118	-	0.22	-	-
14 139	-	0.16	-	-
76 110	-	-	-	0.15
2 196	-	-	-	0.35
223 2	-	-	-	0.11
Expected dyads	54	10	54	43
Total preferred dyads	14	4	12	10

3.2.4. *Hierarchical cluster analyses*

As in the outer Moray Firth, clustering was apparent between a number of male dyads from the SWF dataset (Figure 3.6). Two significant dyads between male ID#s 56, 54 (HWI= 0.44) and 163, 233 (HWI= 40) could be observed. Male ID#s 36, 196 (HWI= 0.40) were clustered, but these dyads were not identified as significant in previous analyses (Table 3.8, Figure 3.6). When the cluster analysis was repeated using only definite males in the population (n=21), only two males were clustered close together, ID#s 163 and 166 (HWI= 0.39). Similarly, when the data were restricted by excluding months outside May and October, and removing encounters out with the Cardigan Bay SAC, no patterns in association could be discerned.

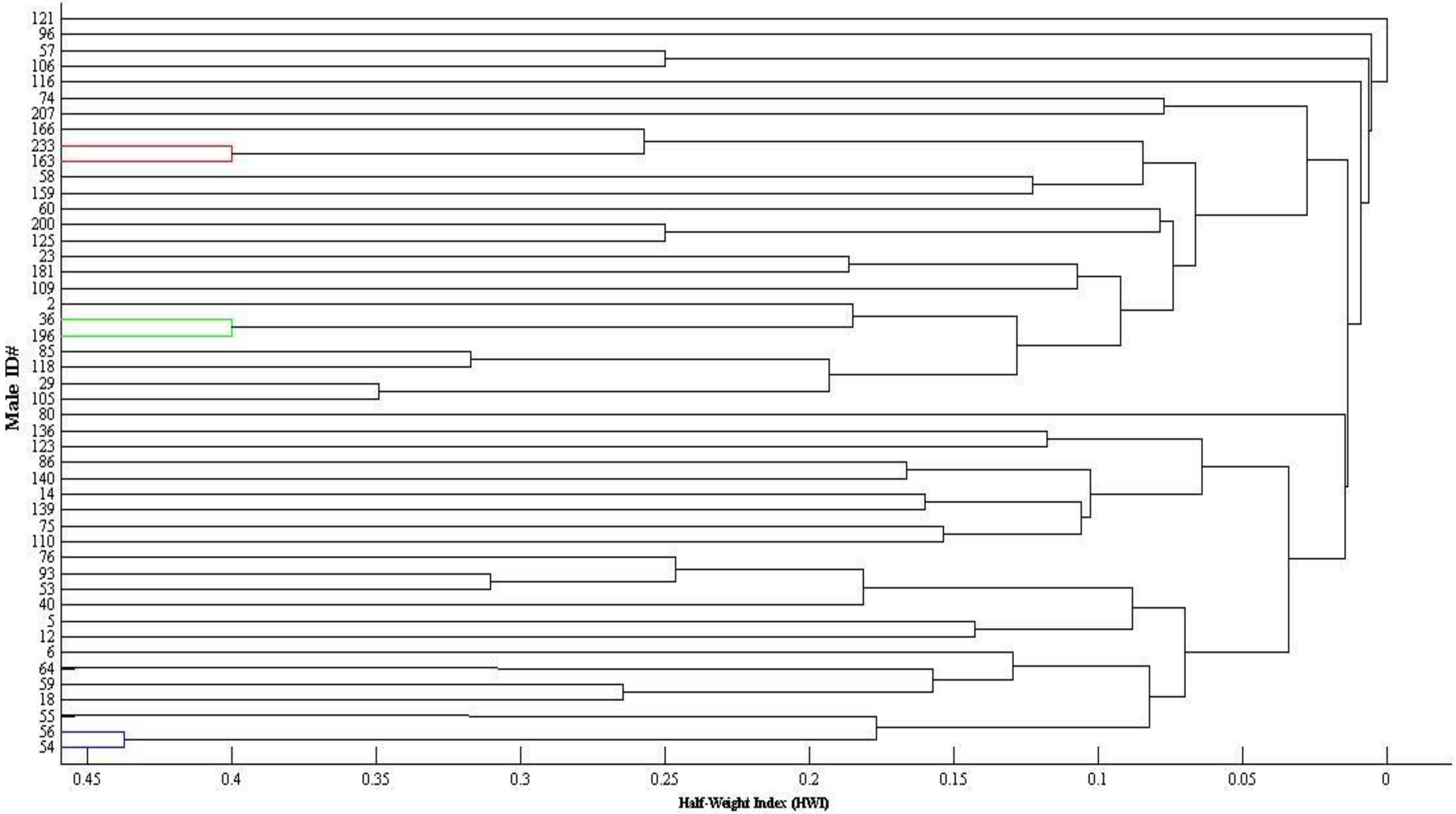

Figure 3.6. Average-linkage dendrogram for 47 males of the Cardigan Bay bottlenose dolphin population, observed >2 times from 2001-2014. Coloured clusters indicate animals with HWIs >0.35. Cophenetic correlation coefficient (CCC)= 0.80

3.2.5. *Temporal patterns- Standardised lagged association rates (SLARs)*

The social-system model found to fit all calculated SLARs described associations as ‘casual acquaintances’ (Figures 3.7; 3.8; 3.9; 3.10). The model in each case showed a gradual drop in association rate, with stable associations being retained for days and months after the first associations were made between individuals.

(i) Full dataset

The temporal patterns of association between all 50 males identified by SWF were investigated using SLARs. Unlike male-male associations in the outer Moray Firth, male association rates did not reach the null association rate, indicating that bonds between individuals remained non-random throughout the study period from 2001 to 2014 (Figure 3.7). The standardised lagged association rate fell through time, but stabilised above the null association rate, which may describe a number of possible association patterns. These may be: permanent social units, preferred but casual bonds where individuals which have previously associated are likely to associate again, or permanent groups with individuals that move between them.

(ii) ‘Definite’ males

An identical analysis was applied to 21 definite males, to observe whether excluding probable males changed the temporal pattern of association. The SLAR showed variability in the association rate, with a gradual drop in association rate which reached the null association rate at approximately 6.5 years (Figure 3.8).

(iii) Excluding months outside May-October

The SLAR was calculated for encounters made between May and October, from 2001 to 2014. The pattern of association was similar to that found previously, with a fairly stable association rate falling over time, but not reaching the null association rate (Figure 3.9). Association rate fell through time to a HWI of approximately 0.04 at around three years.

(iv) Cardigan Bay SAC

The SLAR was estimated for males (n= 42) encountered in Cardigan Bay from 2001 to 2014 (Figure 3.9). As in the analysis using the full dataset (i), and the dataset restricted by month (iii), the SLAR did not reach the null association rate, indicating that associations were non-random throughout the study period. As in the previous analyses, the association rate dropped through time to the mean HWI of approximately 0.03 at around three years.

3.2.6. *Temporal patterns- Lagged identification rates (LIRs)*

The LIR was calculated for each of the former datasets, and the curve and resulting movement model did not differ between them. Therefore, the LIR curve and movement model are presented for the full dataset in Figure 3.11. The decline in LIR over both small and large time lags coincide with those of the SLAR plots, and signify that the temporal association patterns between male bottlenose dolphins of the Cardigan Bay population were likely influenced by demographic factors such as mortality or emigration, in the same way as in the male community of the outer Moray Firth. The LIR fell to zero over the study period, indicating that such demographic factors were permanent. The best fit movement model suggested three demographic factors influenced the association patterns; emigration, re-immigration, and mortality.

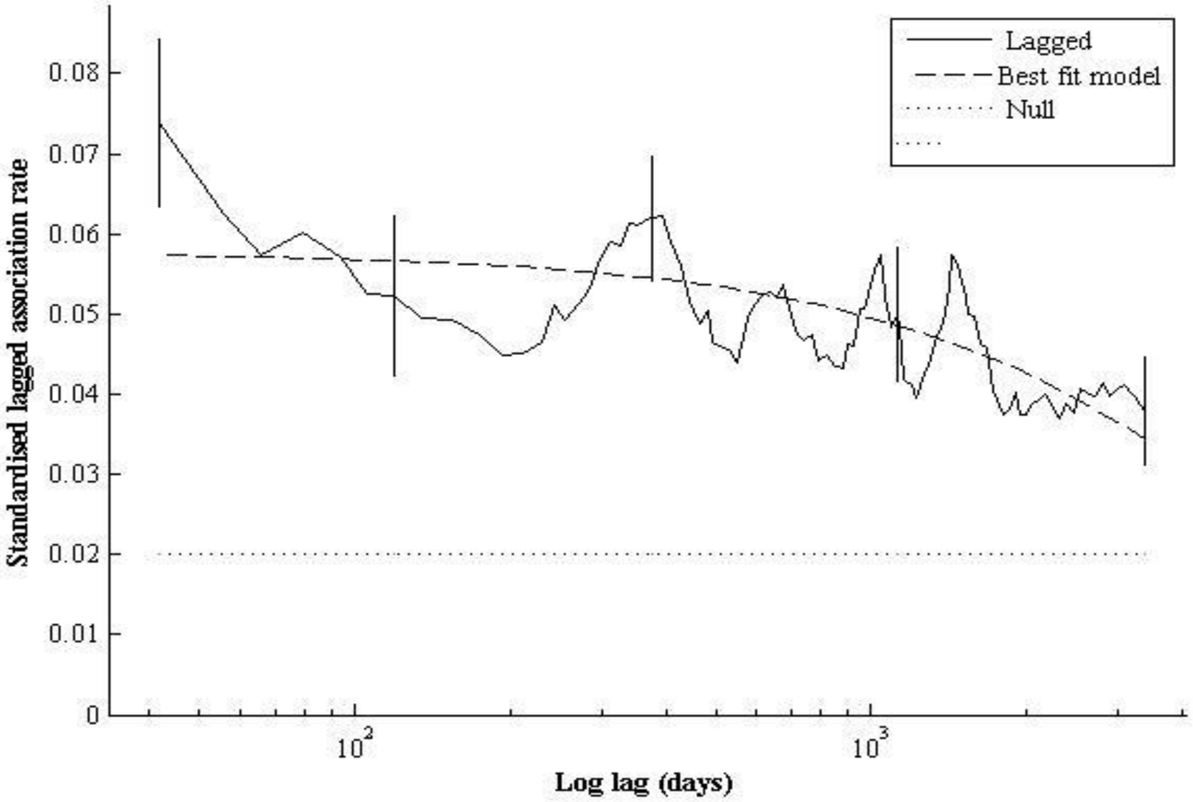

Figure 3.7. The standardised lagged association rate (SLAR) and standardised null association rate (SNAR) for all 50 males observed in Cardigan Bay and surrounding areas by the Sea Watch Foundation (SWF) from 2001-2014. A moving average of 4,000 associations was used to smooth the curve. Vertical bars indicate approximate standard errors, which were obtained by jack-knifing. The exponential model of best fit is shown (a2*exp(-a1+td)).

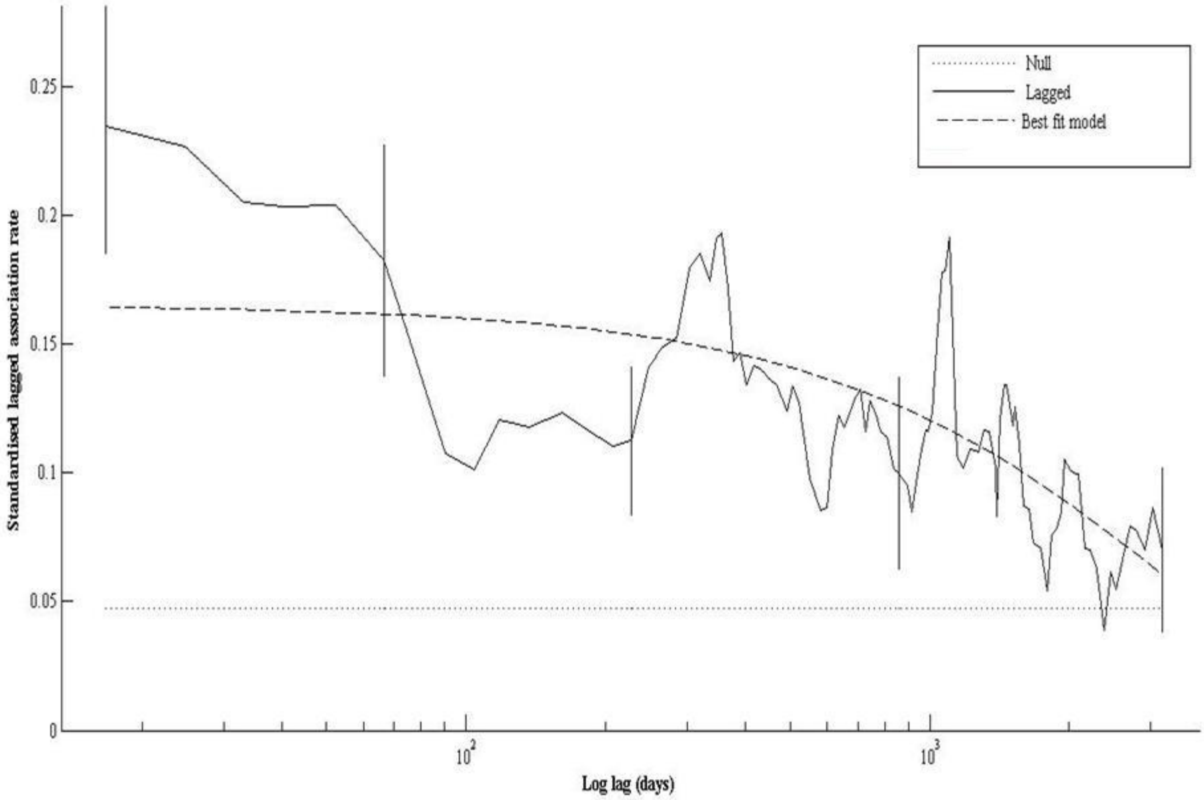

Figure 3.8. The standardised lagged association rate (SLAR) and standardised null association rate (SNAR) for 21 definite males observed in Cardigan Bay and surrounding areas by the Sea Watch Foundation (SWF) from 2001-2014. A moving average of 250 associations was used to smooth the curve. Vertical bars indicate approximate standard errors, which were obtained by jack-knifing. The exponential model of best fit is shown (a2*exp(-a1+td)).

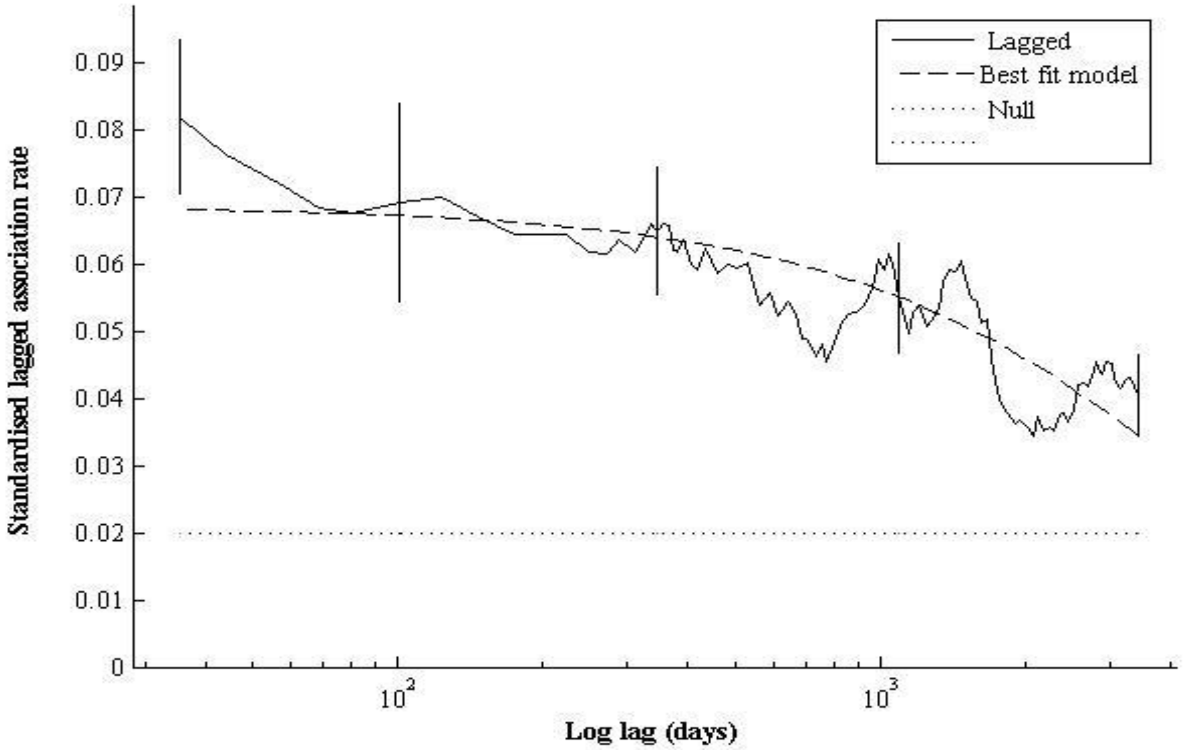

Figure 3.9. The standardised lagged association rate (SLAR) and standardised null association rate (SNAR) for 47 males observed between May and October, from 2001-2014. A moving average of 3000 associations was used to smooth the curve. Vertical bars indicate approximate standard errors, which were obtained by jack-knifing. The exponential model of best fit is shown (a2*exp(-a1+td)).

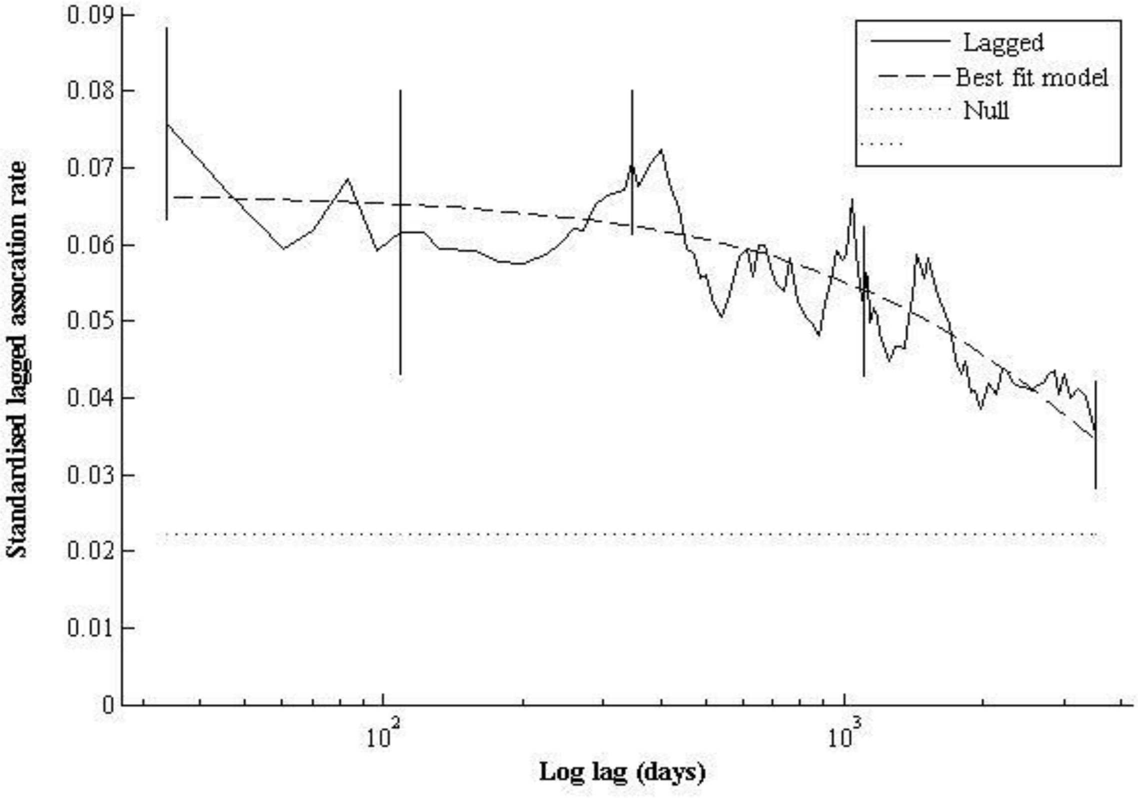

Figure 3.10. The standardised lagged association rate (SLAR) and standardised null association rate (SNAR) for 42 males observed within the Cardigan Bay SAC, between 2001-2014. A moving average of 3000 associations was used to smooth the curve. Vertical bars indicate approximate standard errors, which were obtained by jack-knifing. The exponential model of best fit is shown (a2*exp(-a1+td)).

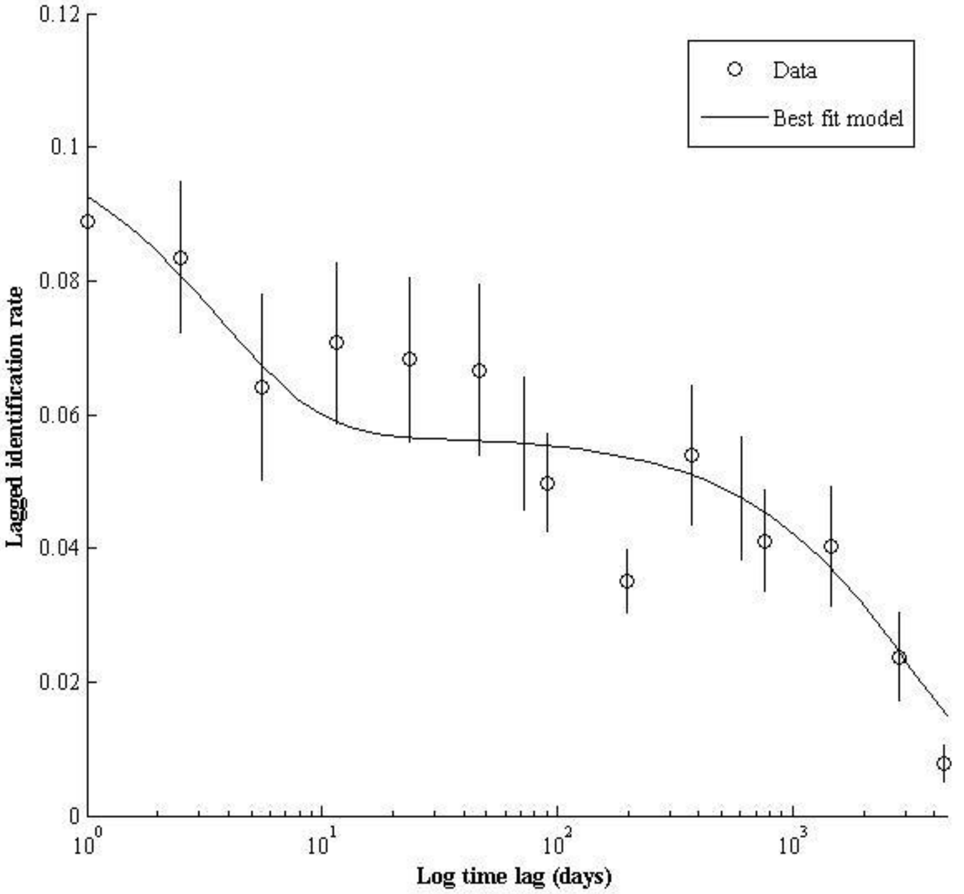

Figure 3.11. The lagged identification association rate (LIR) for all 50 males observed in Cardigan Bay and surrounding areas, from 2001-2014. Vertical bars indicate approximate standard errors, which were obtained by boot-straps of 100 replicates. The movement model of best fit is shown (a3*exp(-a1*td)+a4*exp(-a2*td).

4. DISCUSSION

The present study utilised long-term datasets to examine the associations between male bottlenose dolphins (*Tursiops truncatus*) from the Moray Firth and Cardigan Bay, and determined that a number of males within these regions formed preferential associations which remained over multiple years. Associations between males, termed alliances, were found to be weaker between individuals from Cardigan Bay. The present study examines the existence of alliances in coastal UK bottlenose dolphin populations, and offers insights into the use of these social relationships as reproductive strategies.

4.1. *The strength of association between males*

The estimation of social differentiation for the full and restricted datasets highlighted variable social patterns within the male communities from each region, with evidence for preferential associations in both study areas. The strongest male-male associations were identified between particular individuals from the Moray Firth, inferring that alliances existed between these males during the months for which data was available (May to October) at least. A triad was observed between three younger males (ID#s 398, 433, and 473), whilst two dyads were also observed between ID#s 21 and 386, 1 and 425. Another dyad of note was the non-significant association between ID#s 9 and 10, who were consistently observed together throughout the study period. After 2013, #10 was no longer encountered, and is subsequently presumed dead, which may account for the non-significance of this dyad. While alliances may be present in the Moray Firth, their strength of relationship was seen to be lower than that found in other study populations such as Shark Bay, Port Stephens, and Sarasota Bay (Connor *et al*., 1992; Owen *et al.,* 2002; Wisniewski *et al*., 2012a).

Alliances are though to ‘crystallise’ between male *T. tursiops* at approximately 20 years of age in Sarasota Bay (Owen *et al.,* 2002), while less stable alliances are known to form between sub-adult male *Tursiops aduncus* in Shark Bay (Connor *et al.*, 2011). Interestingly, in Shark Bay, young males were also shown to achieve successful matings even when competing against strongly bonded and older male alliances (Krützen *et al*., 2004a), and in a captive study a young male more frequently challenged his older male tank-mate during the breeding season (Samuels & Gifford, 1997) suggesting that on occasion younger dolphins do confront more dominant individuals for mates. The mating strategy of the male alliances between young animals observed in the present study may be akin to that observed in young low-ranking male baboons (*Papio cynocephalus*) which form coalitions to challenge mature males for mating opportunities (Noë & Sluijter, 1995). Overall, in the Moray Firth, the presence of a similarly aged companion may provide a competitive advantage to both mature and younger male dolphins competing against unallied conspecifics for access to females. Indeed, behaviours associated with such competition have been observed in this community (K. Robinson, unpublished data).

On the contrary, in Cardigan Bay, the propensity for strong intrasexual association formation between certain individuals was not evident in the present examination. While a significant number of preferred dyads were identified, they were more weakly associated at HWI <0.5. This was reflected in both the full and restricted datasets, suggesting that in general male associations were not of the same strength as those in the Moray Firth. Furthermore, strongly associated individuals previously identified by Lott (2004) and Magileviciute (2006) were not rediscovered, suggesting the short-lived nature of these associations.

In addition, a number of males examined in the present study were sub-adult or juvenile males, between which relationships may perhaps be more volatile. It is also probable that younger males in both populations are too young to compete against their larger, maturer conspecifics for female consorts, or had yet to begin associating consistently with possible alliance partners. Preferential associations between male calves have been documented in Shark Bay (Tsai & Mann, 2013), however stable alliances may not fully develop between males until sexual maturity has been reached, at around 8 to 12 years of age, as in other populations (Connor *et al*., 2000b).

The observed male intrasexual association patterns may be comparable to those found in Sarasota Bay, the Bahamas, Port Stephens and St John's River, reflecting both loosely allied and solitary males, and stronger alliances between particular males from the Moray Firth. Males in the Moray Firth had a mean HWI of 0.09, lower than the previously estimated mean HWI of 0.12 (Eisfeld, 2003). Similarly, the mean HWI was low between males from Cardigan Bay, calculated as 0.03. However, studies conducted elsewhere also recorded low mean HWIs between males, even where the presence of strong alliances between certain individuals were observed (Owen *et al.*, 2002; Parsons *et al*., 2003b; Wiszniewski *et al*., 2012a; Emak, 2014, respectively). In particular, male dolphins in the Bahamas, Port Stephens, and St. John's River displayed a range of intrasexual association strengths, including both strong and weak alliances, and unallied individuals (Parsons *et al.*, 2003b; Wiszniewski *et al*., 2012a; Ermak, 2014).

4.2. *Association stability over time*

Male social dynamics in the two study regions showed similar temporal patterns. In the Moray Firth, associations remained stable over periods of days and months and reached random association rates at approximately three years. In contrast, the null association rate was not reached in the full or temporally restricted SWF datasets, indicating non-random associations continued throughout the study period of 14 years. The null association rate was reached however when the dataset was restricted to 21 'definite' males, potentially due to a smaller sample size over the study period**.** While all individuals from both regions were likely male, the present study did not account for male age or unsexed individuals, and may have underestimated the temporal pattern of associations between older, reproductive males which may be more likely to form stable alliances.

The temporal associations within both male communities were described as 'casual acquaintances' by an exponential model of best fit. This may illustrate short-term, opportunistic alliance formation during the breeding season, which did not remain stable over the full time periods represented within the available datasets, using Connor & Whitehead's (2005) definition of an alliance as when individuals encounter resources at the same time, and subsequently cooperate to control them against other conspecifics. In this respect, they are therefore not mediated by association duration. In the Moray Firth dataset the duration of associations lasted for around three years, before disassociation occurred. Over the 14 years, the model did not fall to disassociation in the Cardigan Bay datasets, although the strength of associations declined after three years. These patterns are typical of fission-fusion social dynamics with casual associations, where males may form either weak or strong alliances, but are in general less stable than those seen in other populations (Wiszniewski *et al*., 2012a; Connor & Krützen, 2015).

Emigration, mortality and re-immigration were found to influence the temporal patterns of male associations through the application of a movement model. Indeed, six males were known or presumed to have died in the Moray Firth dataset during the study period (known = ID#s 63, 367 and 409; presumed = ID#s 10, 66 and 74), which may have contributed to the selection of the movement model and would explain why some of the stronger associations identified by Eisfeld (2003) were not observed in the present analysis. In Doubtful Sound, New Zealand, for example, the complexity of male relationships has been attributed to individual mortality, which would have a large impact on the associations of animals in such a small, closed community (Lusseau *et al*., 2003).

Another explanation for the selection of the movement model may refer to males which often travel widely between groups, as is typical of fission-fusion societies and when males adopt a ‘roving’ strategy to locate mates. Male bottlenose dolphins are known to have large ranges in other populations (Krützen *et al.,* 2004b; Rogers *et al.,* 2004; Randíc *et al.,* 2012; Sprogis *et al.,* 2015) and in Cardigan Bay and the Moray Firth, male dolphins are known to be more widely mobile than females (Baylis, 2013; Quick *et al*., 2014). It may be the case that in both regions, males enter and leave the population regularly. This would support the use of a ‘roving’ male mating strategy where males in both regions travel widely between groups of breeding females to enhance the likelihood of reproduction, and may further explain why some stronger associations identified by Eisfeld, Lott and Magileviciute (2003; 2004; 2006 respectively) were not re-identified. Interestingly, whilst the movement models presented in the current study suggest that males perhaps travel more widely, long-term, long-distance movements identified between the Moray Firth and the west coast of Ireland were found to be primarily made by reproductive females (Robinson *et al.,* 2012). Such movements by females are known to be indicative of female promiscuity in this region, which may also be the primary mating strategy of female chimpanzees (*Pan troglodytes*) (Newton-Fisher, 2014). Promiscuity is considered a tactic to allow female mate choice, and to confuse offspring paternity if males display infanticidal behaviour (van Schaik & Janson, 2000). Indeed, male bottlenose dolphins are known to attack and kill calves throughout their range, as well as within one of the study populations (Patterson *et al.,* 1998; Dunn *et al*., 2002; Kaplan *et al*., 2009; Robinson, 2014; Pertree *et al*., 2015).

4.3. *Linking male association patterns to mating strategies in the study populations*

Alliance formation as a mating strategy is believed to enhance the reproductive success in male bottlenose dolphins by improving their ability to locate and herd females (Connor *et al*., 1992), which in turn enables males to force copulations, prevent competitor access to females, and even perhaps preclude promiscuous mating by females (Connor *et al*., 2000b). Inter-population variation in alliance presence is however, highly apparent in the species. For example, in Shark Bay and Sarasota Bay, male alliances are the primary mating strategy observed (Owen *et al*., 2002; Connor & Krützen, 2015), while males in Port Stephens, St. John’s River, and the Bahamas appear to utilise a combination of both solitary and allied tactics (Parsons *et al*., 2003a; b; Wiszniewski *et al*., 2012a; Ermak, 2014), as observed in the present study. Nonetheless, establishing the mating strategies of cetaceans is inherently challenging, and may be more so in temperate bottlenose populations where adverse winter weather conditions often prevent year-round survey work. That said, male social dynamics in the Moray Firth and Cardigan Bay were evidently characterised by a typical fission-fusion structure, where solitary tactics and alliances of varying strength represent the mating strategies adopted by the males examined.

Male demographics in both study populations were found to be highly similar. A total of 66 confirmed individuals were identified from the Moray Firth dataset, whilst 50 males (21 definite; 29 suspected) were isolated from the Cardigan Bay dataset. Many individuals from both regions remain unsexed, and it is likely that some males have yet to be verified by the host organisations. Strong alliances are though to arise in conditions of elevated sexual competition, and where the Operational Sex Ratio (OSR) is biased towards males, resutling in the development of different mating strategies as individuals compete for infrequent mating opportunities (Emlen & Oring, 1977). Eisfeld (2003) suggested that in the Moray Firth, the presumed lack of male alliances was a result of reduced male-male competition, following Wilson's (1995) demographic prediction of greater female numbers within the population. While this cannot be confirmed within the current study, it would be of interest to establish the ratio of males to females within both populations via further gender confirmation, to determine if a male-biased OSR or intense intrasexual competition might explain the ontogeny of alliance formation in these temperate bottlenose dolphins.

Frequently during encounters, only one male was observed socialising with a group of females and juveniles in both the Cardigan Bay and Moray Firth populations. There was a large difference in the frequency of this type of encounter between the two areas: in the outer Moray Firth, 14% of encounters contained a single male within a group, compared to 68% in the Cardigan Bay encounters. This is unlikely to be attributed to differences in study site size, as 96% of all encounters occurred within the Cardigan Bay SAC which is comparable in area to the outer Moray Firth study region. It is therefore likely that adult males in Cardigan Bay actively either avoid the presence of other males, drive other males away from groups, herd groups away from competitors, or come together infrequently, for example when a breeding female comes into oestrous. The preferential alliances of varying strengths observed in both the SWF and CRRU datasets may be a consequence of the latter situation, where the same males congregate within temporal groups on occasion during the breeding season. Conversely, males that were frequently the only male present in a group may be older individuals, more experienced in outcompeting conspecifics. In dusky dolphins (*Lagenorhynchus obscurus*) the copulation probability of individual males decreases as other males join mating groups (Orbach *et al*., 2015), and similar disadvantages to male bottlenose dolphins in Cardigan Bay may explain the weaker male-male associations where males actively avoid one another unless competing to take control of female-juvenile groups. In the Moray Firth, associations between males were evidently much stronger, and groups usually contained at least two male individuals, which may reflect either alliances or competitors.

Solitary male dolphins were rarely encountered in either study areas. Whilst infrequent, the most encounters with solitary males were made by SWF, and may also be indicative of the weaker alliances observed between males within this region. Many solitary encounters involved ID# 74, an adult male known as Bond. Individuals encountered without the presence of other males may have been travelling between groups to feed or to find mates, typical of fission-fusion social structures. However, the ‘roving’ male strategy suggests that males will undertake frequent journeys to locate stochastic groups of reproductive females (Whitehead, 1990; Connor *et al.*, 2000a; b), and Baylis (2013) showed that bottlenose males in Cardigan Bay are more actively mobile than females. Bond however, was observed alone 105 out of 217 times (Table 7.1, appendix), and may simply be an older, more experienced male who is well practised in locating receptive females on his own.

Bond was also frequently observed solely with an adult female called Chris (ID# 004-90W). This may represent the latter stage of the roving strategy, where males will consort females and defend them from other males for a period of time to ensure conception (Boness *et al.*, 2002). In Sarasota Bay, male dolphins associate with females who are most likely to reproduce (Owen *et al.*, 2002), and Chris is known to have raised at least two calves to adulthood. Furthermore, male-female affiliative relationships have been suggested as a potential feature of mating strategies for both sexes, yet have rarely been investigated to date (Connor *et al.*, 2000b; Lusseau *et al.*, 2003). Additional investigatory analyses are evidently needed to better understand such relationships more fully in a reproductive context.

While male-male relationships were indicated in both study regions, patterns in association strength were dissimilar. The formation of alliances appears to be mediated by the level of competition experienced between males as a result of the OSR, and the reproductive availability, and density of females (Whitehead & Connor, 2005). As previously mentioned, the OSR was difficult to estimate within the study populations, but is unlikely to be drastically different considering the similar numbers of identified males in the two study sites. Similarly, the inter-birth calving interval has been estimated at an average of three years for females in both of these populations (Feingold & Evans, 2013; Sim, 2014), suggesting that the time lag between mating opportunities, and therefore the reproductive availability of females, is likely analogous.

It would also seem that large variation in female density would be unlikely to account for the differences in alliance strength between males from the Moray Firth and Cardigan Bay. The dolphins in both study areas are considered ‘semi-resident’, and those in Cardigan Bay display seasonal movements where a large proportion of the population may be found off the Anglesey coast in the winter months (Pesante *et al.*, 2008; Baines & Evans, 2012; Feingold & Evans, 2014b). Seasonal movements are also apparent in the Moray Firth, with lower dolphin abundance during the winter in the inner Moray Firth (Wilson *et al.*, 1997). Changes in residency patterns are considered a response to shifting prey availability (Wilson *et al.*, 1997), and would indicate that the distribution of females in both study regions is stochastic on a seasonal basis, resulting in similar female density and encounter rates within the two populations.

Both alliances and solitary mating strategies can be inferred through the observed association patterns in the present study, and observations made by the CRRU have indicated that males both consort females and participate in mate guarding to prevent competitor access (K. Robinson, pers. obs) as described by Connor & Vollmer, (2009). Male alliances may control the movements of reproductive females by consorting and coercing them, to improve the likelihood of either male potentially siring a calf (Connor & Vollmer, 2009). The behaviour of two males indicated as allied in the present study (ID#s 21 and 386) suggested that their attempts to consort females were frequently thwarted by older, solitary males. Recent observations suggest the dyad are now more successful at guarding females from competitors, as the males have matured and became more experienced in recent years. In Shark Bay, older, more mature alliances have been observed to show greater reproductive success (Krützen *et al.*, 2004a), and although relatively uncommon, due to female encounter unpredictability, mate guarding also has been documented in the Dall’s porpoise (*Phocoenoides dalli).* Male porpoises will guard a particular female during the breeding season, maintaining associations with her while competitively excluding other males through agonistic interactions (Willis & Dill, 2007). Considering the similarities in the factors which may drive alliance formation between the two populations, it is likely that males in Cardigan Bay also utilise a mixture of coercing and guarding strategies, although observations of such behaviours are presently lacking.

From the present results, it would seem that males of the two largest semi-resident populations in the UK each employ both allied and solitary mating strategies, yet the factors influencing the strength of associations between individuals remain largely unknown. In Cardigan Bay, some males form weak but stable associations and are distributed widely across female groups. In the Moray Firth however, multiple males are more commonly observed within groups, and males may compete as alliances or as solitary individuals to achieve mating success. A summary of male bottlenose dolphin association characteristics from other populations, in relation to the present findings, is presented in table 4.1.

Table 4.1. Characteristics of bottlenose dolphin (*Tursiops* spp.) populations, detailing habitats, known association types, and male association indices. Results from the present study are highlighted in **bold.** Adapted and extended from Ermak, 2014. ** Average HWI for whole population. *** Simple Ratio.

Study Site	Species	Male association type	Habitat type	Average HWI	Maximum HWI	Source
Outer Moray Firth, Scotland, UK	***Tursiops truncatus***	**Alliances between mature and juvenile males, and solitary individuals**	**Similar to the open North sea with an open, rugged coastline. Up to 200m deep**	**0.09± 0.05**	**0.67**	**Present study**
Cardigan Bay, Wales, UK	***T. truncatus***	**Weak alliances, and solitary individuals**	**Large embayment, reaching 60m deep in places**	**0.04± 0.02**	**0.44**	**Present study**
Shannon Estuary, Ireland	*T. truncatus*	Strong, long-term alliances but not known if male-specific	75km wide tidal estuary	-	-	Foley *et al*., 2010
Sado Estuary, Portugal	*T. truncatus*	Stable, fairly long-term population wide associations, alliances unconfirmed	Estuarine environment, up to 40m deep	0.45**	-	Augusto *et al*., 2012
Setúbal Bay, Portugal	*T. truncatus*	Possible alliances	Coastal area, with protected bays	0.28 (1998-2001) 0.63 (2007-2011)	-	Martinho et al., 2014
Normano-Breton Gulf, English Channel	*T. truncatus*	Possible alliances	Shallow coastal waters, 0-40m	0.10**	-	Louis *et al*., 2015

Sarasota Bay, Florida, USA	*T. truncatus*	Alliances between mature males and transitional solitary phases	Shallow channels and seagrass beds surrounded by barrier islands, rarely >10m	Paired- 0.03± 0.04 Unpaired- 0.01± 0.02***	0.92	Owen *et al*., 2002
St. Johns River, Florida	*T. truncatus*	First and second-order alliances	Brackish, estuarine environment, up to 18m	0.05± 0.02	1	Ermak, 2014
Panama City, Florida, USA	*T. truncatus*	First-order alliances	St Andrews Bay and coastal Gulf of Mexico, shallow with extensive seagrass beds	0.19± 0.07	0.97[1]	Bouveroux & Mallefet, 2010[1] Bouveroux *et al*., 2014
Little Bahama Bank, Bahamas	*T. truncatus*	First-order alliances	Shallow inshore waters, <7m	0.08± 0.16	1	Parsons et al., 2003b
Doubtful Sound, New Zealand	*T. truncatus*	No alliances, but complex male associations	Deep, enclosed coldwater fjords	0.49± 0.04	0.74	Lusseau *et al*., 2003
Port Stephens, Australia	*Tursiops aduncus*	First and second order alliances, and solitary males	Complex environment of sandy bays, with both estuarine and marine conditions. Approximately $166 km^2$	0.08	0.80± 0.04	Wisniewski *et al*., 2012a
Shark Bay, Australia	*T. aduncus*	First, second and third-order alliances	$1300 km^2$ shallow, enclosed bay	-	1.00[2] 0.97[3]	Smolker *et al*., 1992[2] Connor *et al*., 2011[3] Connor & Krützen, 2015

4.5. *Future directions and suggested improvements*

The present study offers a comprehensive estimation of male bottlenose dolphin mating strategies in two UK coastal populations through the use of individual sightings data collected over many years. However, while associations between males can be examined in detail by utilising encounter data, reproductive success, and therefore the effectiveness of mating strategies, can only be accurately assessed through genetic studies of calf paternity. It would certainly be of interest to assess whether the strong alliances noted between males in the Moray Firth community affect their reproductive success, or if a solitary male strategy results in more successful conceptions. Similar genetic studies on weakly associated males in Cardigan Bay might reveal conditional strategies, with animals of a certain age or social ranking achieving greater conceptions.

Such techniques could also be used to resolve the relatedness of males in each population. In Port Stephens and the Bahamas, alliances between Indo-Pacific bottlenose dolphins are not mediated by relatedness (Möller *et al*., 2001; Parsons *et al*, 2003b), while in Shark Bay, first and second-order alliance partners have a greater relatedness than would be expected through chance (Möller, 2012). Similar studies undertaken upon the UK study animals could determine if males forming alliances are indeed related. This may be important for an estimation of genetic viability of this population, which could be at risk from inbreeding (e.g. Parsons *et al*., 2002; Islas-Villanueva, 2010). However, the likelihood of genetic testing for large samples of live animals is low in the study populations, due to strict regulations associated with their protection. Nonetheless, the continuation of dedicated studies undertaken by the host organisations will serve to further improve our understanding of the social structure of these cetaceans in British waters.

5. CONCLUSIONS

The present study provides new evidence for the formation of preferential associations in male bottlenose dolphins from Cardigan Bay and the Moray Firth, and offers some explanation on how this may affect the mating strategies of individuals in these regions. In the Moray Firth, both alliances and solitary strategies were observed, whereas in Cardigan Bay the formation of male alliances was far less obvious. Animals within both regions likely utilise the ‘roving’ male strategy, travelling between groups to find reproductive females for mating. Ongoing studies of these populations and their behaviours will further our understanding of the type and longevity of male mating strategies within these semi-resident coastal populations.

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7. APPENDICES

Table 7.1. The well-marked known males identified by CRRU from 1997 to 2014 inclusive, detailing birth year, sighting histories (year inclusive), catalogue name, total encounters in the study period, number of solitary encounters and the percentage of time an individual was seen with other male animals.

ID #	Birth year (if known)	Sighting history	Catalogue name	Total encounters	Solitary encounters	% time not solitary
01		1997, 2001-2014	Sharky	71	0	100.00
02		1997-1998, 2002-2012	Barracuda	55	0	100.00
04		1997, 1999-2000	Spearhead	6	0	100.00
09		1997-1999, 2001-2014	Stardance	73	2	97.26
10		1997-1999, 2001-2012	Sailfin	61	0	100.00
14		1997, 1999, 2001	Ziggy	5	0	100.00
19		1997, 2001, 2003	Carter	18	0	100.00
20		1997-1998, 2001, 2004-2007, 2009	Trekky	23	0	100.00
21		1997, 2001-2014	Paperclip	123	0	100.00
45		1997, 2001-2007	Chicco	43	0	100.00
48		1997, 2001-2003, 2005-2014	Shrek	58	0	100.00
51		1997-1999, 2001, 2003-2004	Pluto	15	0	100.00
61		1997-1999, 2001-2008	Melbourne	48	2	95.83
63		1997-1998, 2001, 2003-2004	Chunks	10	0	100.00
64		1997-1998, 2000-2001, 2004-2011	Hubbs	48	0	100.00
66		1997-1998, 2000-2005	Goblin Seal	29	0	100.00

69		1997-1998, 2000-2006, 2008-2014	Brookie	92	0	100.00
71		1997-1998	Chanonry	9	0	100.00
74		1998-1999,2001-2002, 2004-2008, 2011-2014	George	71	0	100.00
77		1997-1999, 2001, 2003-2008	Allegranzi	54	0	100.00
88		1997-1999, 2002-2008, 2011-2012, 2014	Sparks	58	1	98.31
99		1997-1999, 2001-2002	N/A	8	0	100.00
115		1998-1999, 2001-2002	Voodoo Head	8	0	100.00
134		1998, 2006	Thunder	2	0	100.00
144		1998, 2001-2009, 2011, 2013-2014	Romeo	42	0	100.00
149		1998, 2001, 2006	Black and Decker	4	0	100.00
165		1999-2003, 2005-2011, 2014	Summer	36	0	100.00
198	2001	2008, 2012-2014	Prism	18	0	100.00
204	2000	2002-2008, 2010	N/A	40	0	100.00
223		2001, 2005-2014	Moon	62	0	100.00
238		2003, 2006-2009, 2014	Mario	11	0	100.00
275	2002	2005-2006, 2010-2014	Splash	44	0	100.00
279		1998, 2002-2003	N/A	4	0	100.00
297	2002	2004-2007, 2009-2014	Po	74	0	100.00
298		2000, 2002	N/A	2	0	100.00
318		25/06/1905	Sutor	3	0	100.00
326		2003, 2006,2 2008	N/A	50	0	100.00
329	2002	2004-2006, 2009-2014	Puff	57	0	100.00
344	2002	2004-2006, 2008-2009, 2011-2014	Richard Benjamin	7	0	100.00
347		2003-2004, 2006, 2008, 2014	Big Tear	19	0	100.00
351		2004, 2007-2013	Magic	81	0	100.00

354		2005-2007, 2009-2014	Hobbit	13	1	98.77
367		2005-2010	Marde	37	0	100.00
380		2003, 2006, 2008-2012, 2014	Miller	84	0	100.00
386		1997-1998, 2006-2007, 2010-2014	Rebel	16	0	100.00
395	2006	2008-2009, 2013	Asteroid	47	0	100.00
398		2005-2009, 2011-2014	Twister	3	1	97.87
407		2006	Sundance	29	0	100.00
409		2006	Nevis	30	0	100.00
411		2006, 2008, 2011	Beatrice	11	0	100.00
421	2006	2008-2011, 2013-2014	Avalon	30	0	100.00
422	2005	2007-2011, 2013	Olivette	27	0	100.00
423		1997-1998, 2007, 2012-2013	Fea	51	0	100.00
425		2005, 2007, 2009-2014	Gill	62	0	100.00
431	2007	2009-2013	Marina	2	0	100.00
433		2006, 2009-2014	Geo	4	0	100.00
448	2008	2010-2014	GG	5	0	100.00
454	2003	2008	Q	37	0	100.00
459		2008, 2010-2011, 2013	Couros	63	0	100.00
466		2006, 2008-2009, 2013-2014	Donald	30	0	100.00
473		2008-2009, 2011, 2013-2014	Ooti	11	0	100.00
478	2009	2011-2014	Maasie	24	0	100.00
491	2009	2011-2014	N/A	30	0	100.00
495	2009	2011-2012, 2014	N/A	11	0	100.00
499	2003	2005-2006, 2011-2014	Chocolate Bourbon	24	0	100.00
512		2012	N/A	1	0	100.00
Average encounter number (±SD)				33.70 (±27.15)		

Table 7.2. The number of bottlenose dolphin (*Tursiops truncatus)* encounters made in each hour by CRRU (Cetacean Research & Rescue Unit) from 1997-2014, in the outer Moray Firth.

Hour	**Total encounters**
06:00	3
07:00	9
08:00	8
09:00	9
10:00	18
11:00	31
12:00	53
13:00	38
14:00	47
15:00	56
16:00	47
17:00	43
18:00	20
19:00	7
20:00	9
21:00	1
Total	**399**

Table 7.3. The number of bottlenose dolphin (*Tursiops truncatus)* encounters made in each month by CRRU (Cetacean Research & Rescue Unit) from 1997-2014, in the outer Moray Firth.

Month	**Total encounters**
May	25
June	74
July	99
August	108
September	72
October	21
Total	**399**

Table 7.4. The number of bottlenose dolphin (*Tursiops truncatus)* encounters made in each year by CRRU (Cetacean Research & Rescue Unit) from 1997-2014, in the outer Moray Firth.

Year	**Total encounters**
1997	38
1998	16
1999	3
2000	2

2001	13
2002	14
2003	16
2004	9
2005	32
2006	26
2007	23
2008	19
2009	19
2010	21
2011	33
2012	38
2013	35
2014	42
Total	**399**

Table 7.5. The mean and maximum HWIs (Half-Weight Index) recorded for 62 males observed >2 times by CRRU from 1997-2014, in the outer Moray Firth.

ID#	Mean HWI	Max HWI
1	0.13	0.32
2	0.13	0.39
4	0.02	0.4
9	0.14	0.67
10	0.16	0.67
14	0.02	0.4
19	0.06	0.38
20	0.08	0.25
21	0.14	0.6
45	0.09	0.33
48	0.14	0.56
51	0.04	0.18
61	0.09	0.39
63	0.02	0.26
64	0.12	0.29
66	0.08	0.39
69	0.15	0.42
71	0.01	0.22
74	0.15	0.63
77	0.13	0.63
88	0.14	0.59
99	0.02	0.27
115	0.03	0.33
134	0.02	0.4
144	0.13	0.45
149	0.02	0.33

165	0.11	0.34
198	0.08	0.26
204	0.13	0.49
223	0.13	0.42
238	0.08	0.44
275	0.13	0.53
279	0.02	0.29
297	0.16	0.47
298	0.01	0.29
326	0.06	0.67
329	0.15	0.47
344	0.14	0.48
347	0.06	0.44
351	0.07	0.41
354	0.16	0.56
367	0.06	0.23
380	0.13	0.3
386	0.13	0.6
395	0.09	0.5
398	0.14	0.6
411	0.06	0.67
421	0.11	0.5
422	0.1	0.44
423	0.03	0.15
425	0.09	0.41
431	0.1	0.41
433	0.14	0.64
448	0.12	0.6
454	0.05	0.4
459	0.04	0.33
466	0.06	0.5
473	0.14	0.64
478	0.12	0.6
491	0.09	0.37
495	0.05	0.34
499	0.1	0.35
Overall (±SD)	**0.09 (0.05)**	**0.43 (0.14)**

Table 7.6. The well-marked males identified from the SWF dataset from 2001-2014 inclusive, detailing ID#, full SWF catalogue ID, sighting history (year inclusive), total encounters in the study period, number of solitary encounters and the percentage of time an individual was seen with other animals. 'Definite' males are marked with a ✓.

ID #	Full ID	Sighting history	Catalogue name	Total Encounters	Solitary encounters	% not solitary	Definite male?
2	002-03W	2003-2013	Flint	35	2	94.29	✓
5	005-90W	2001-2012	Rip Torn	37	2	94.59	
6	006-01W	2001, 2003-2007, 2009-2010, 2012, 2014	Tide	35	0	100.00	
12	012-89W	2001, 2003-2004, 2006-2009, 2011	Fog	23	1	95.65	
14	014-01W	2001-2004, 2006-2014	Gandalf	52	7	86.54	✓
18	018-02L/038-02R	2002-2004	N/A	31	0	100.00	✓
23	023-03W	2003, 2005-2008, 2011-2012	Voldermort	43	17	60.47	
29	029-02W	2002-2009, 2011-2013	Strata	40	3	92.50	
36	03-06W	2006-2009, 2011-2013	Comb	24	1	95.83	✓
40	040-03W	2003-2007	Gyzmo	15	1	93.33	✓
44	044-06W	2006	N/A	1	0	100.00	
53	053-01W	2001, 2003-2008, 2011-2012	Burkenzi	27	1	96.30	
54	054-01W	2001, 2003-2004, 2008, 2011-2012	Alfredo	20	1	95.00	✓
55	055-01W	2001, 2003-2004, 2006	Arian	20	2	90.00	
56	056-01W	2001, 2003-2004, 2007-2008, 2012	Mitsos	16	0	100.00	
57	057-01S	2005-2006	N/A	6	1	83.33	
58	058-04W	2004, 2007-2008, 2011	Titania	11	0	100.00	
59	059-03S	2003-2009, 2011-2013	Battleship	40	2	95.00	✓
60	060-01W	2001, 2003-2005, 2007-2008, 2010-2012	Grill	25	4	84.00	
64	064-01W	2001-2013	Jagger	42	4	90.48	✓
74	074-03W	2003-2014	Bond	217	105	51.61	✓
75	075-03W	2003-2004, 2006, 2008, 2010-2012, 2014	Max	39	5	87.18	
76	076-01W	2001-2013	Madog	36	1	97.22	

80	080-01W	2001, 2003, 2009	Dragonfly	3	0	100.00	
85	085-03W	2003, 2005-2014	Dusky	43	5	88.37	✓
86	086-06W	2007-2014	Norbert	22	3	86.36	✓
93	093-01W	2001-2008, 2010-2013	Ionikos	36	4	88.89	
96	096-05W	2005, 2007-2009, 2011-2014	Graham	18	7	61.11	
105	105-03W	2003, 2005-2014	N/A	33	0	100.00	
106	106-01W	2001	N/A	6	1	83.33	
109	109-01W	2001-2014	Riptide	51	13	74.51	
110	110-01W	2002, 2006-2008, 2010-2012	Jay	33	1	96.97	
116	116-03W	2003-2006	Razer	8	1	87.50	
118	118-02W	2002, 2006-2010, 2012-2014	Snowflake	31	2	93.55	✓
121	121-90W	2001	Wedge	1	1	0.00	
123	123-09R	2009-2013	N/A	38	0	100.00	✓
125	125-10L/121-10R	2010-2013	N/A	8	0	100.00	✓
126	126-01W	2001	N/A	1	0	100.00	
136	136-90W	2001, 2004, 2006-2014	Nippy	37	3	91.89	
139	139-91S	2003-2004, 2008-2012, 2014	Gap	30	4	86.67	✓
140	140-01W	2001, 2004-2007, 2009-2011, 2013	Roberto	33	1	96.97	✓
159	159-03W	2005-2013	Ticklefish	55	14	74.55	
163	163-05S	2005-2014	N/A	26	0	100.00	✓
166	166-05S	2005-2013	Ethan	25	0	100.00	✓
177	177-05W	2005	N/A	1	0	100.00	
181	181-06W	2006-2013	Misha	47	9	80.85	
196	196-07W	2007-2013	Vitaly	22	0	100.00	
200	200-07W	2007-2008, 2010-2012	Ty	17	0	100.00	✓
207	207-07S	2007-2014	Lumpy	121	26	78.51	✓
233	233-09R	2009-2014	N/A	22	0	100.00	✓
Average encounter number (±SD)				32.06 (±33.13)			

Table 7.7. The number of bottlenose dolphin (*Tursiops truncatus)* encounters made in each hour by SWF (Sea Watch Foundation) from 2001-2014.

Time	Total encounters
05:00	1
06:00	14
07:00	45
08:00	61
09:00	92
10:00	108
11:00	144
12:00	147
13:00	114
14:00	96
15:00	78
16:00	64
17:00	26
18:00	20
19:00	6
20:00	3
Total	**1019**

Table 7.8. The number of bottlenose dolphin (*Tursiops truncatus)* encounters made in each month by SWF (Sea Watch Foundation) from 2001-2014, in Cardigan Bay and surrounding areas.

Month	Total encounters
January	5
February	4
March	3
April	31
May	122
June	194
July	209
August	208
September	164
October	65
November	9
December	5
Total	**1019**

Table 7.9. The number of bottlenose dolphin (*Tursiops truncatus)* encounters made in each year by SWF (Sea Watch Foundation) from 2001-2014, in Cardigan Bay and surrounding areas.

Year	Total encounters
2001	29
2002	16
2003	90
2004	63
2005	37
2006	54
2007	61
2008	79
2009	71
2010	116
2011	115
2012	120
2013	110
2014	58
Total	**1019**

Table 7.10. The mean and maximum HWIs (Half-Weight Indices) for males used in association analyses between 2001-2014, for each dataset used; (i) full dataset (47 males); (ii) 'Definite' males only (n= 21); (iii) excluding encounters of males made outside the months of May-October (47 males); (iv) only including males encountered within the Cardigan Bay SAC (n= 42).

ID#	Full dataset		Definite males		May-Oct only		Cardigan Bay SAC	
	Mean HWI	Max HWI	Mean HWI	Max HWI	Mean HWI	Max HWI	Mean HWI	Max HWI
2	0.05	0.26	0.05	0.25	0.04	0.24	0.05	0.35
5	0.03	0.15	-	-	0.03	0.15	0.03	0.14
6	0.04	0.16	-	-	0.04	0.16	0.04	0.16
12	0.03	0.14	-	-	0.03	0.14	0.03	0.13
14	0.04	0.16	0.04	0.16	0.04	0.17	0.04	0.17
18	0.02	0.26	0.02	0.26	0.02	0.27	0.03	0.26
23	0.04	0.19	-	-	0.02	0.13	-	-
29	0.06	0.35	-	-	0.04	0.27	0.06	0.35
36	0.06	0.40	0.05	0.22	0.04	0.4	0.05	0.39
40	0.03	0.25	0.02	0.13	0.02	0.22	0.03	0.25
53	0.05	0.31	-	-	0.05	0.31	0.06	0.31
54	0.05	0.44	0.03	0.13	0.05	0.44	0.05	0.41
55	0.02	0.25	-	-	0.02	0.25	0.03	0.26
56	0.03	0.44	-	-	0.04	0.44	0.04	0.41
57	0.01	0.25	-	-	0.01	0.25	0.01	0.25
58	0.03	0.14	-	-	0.01	0.11	0.02	0.12
59	0.05	0.26	0.05	0.26	0.05	0.27	0.05	0.26
60	0.03	0.16	-	-	0.02	0.13	0.04	0.19
64	0.03	0.19	0.03	0.19	0.03	0.20	0.03	0.19
74	0.02	0.08	0.02	0.08	0.01	0.07	0.02	0.09

75	0.04	0.15	-	-	0.03	0.16	0.05	0.17
76	0.05	0.26	-	-	0.05	0.21	0.05	0.25
80	0.01	0.10	-	-	0.01	0.10	0.01	0.10
85	0.05	0.32	0.04	0.32	0.03	0.32	0.05	0.37
86	0.03	0.17	0.04	0.18	0.03	0.17	0.03	0.17
93	0.05	0.31	-	-	0.04	0.31	0.05	0.31
96	0.01	0.05	-	-	0.01	0.06	0.01	0.06
105	0.05	0.35	-	-	0.04	0.27	0.06	0.35
106	0.01	0.25	-	-	0.01	0.25	0.01	0.25
109	0.04	0.17	-	-	0.03	0.15	0.04	0.17
110	0.05	0.18	-	-	0.04	0.17	0.05	0.18
116	0.01	0.06	-	-	0.01	0.07	0.01	0.08
118	0.05	0.32	0.05	0.32	0.04	0.32	0.05	0.37
121	0.00	0.00	-	-	0.00	0.00	0.00	0.00
123	0.03	0.12	0.04	0.12	0.02	0.11	0.03	0.15
125	0.02	0.25	0.03	0.25	0.01	0.18	-	-
136	0.04	0.15	-	-	0.03	0.14	0.04	0.15
139	0.02	0.16	0.02	0.16	0.02	0.17	0.02	0.12
140	0.04	0.17	0.04	0.17	0.04	0.17	0.04	0.17
159	0.04	0.18	-	-	0.02	0.16	0.03	0.13
163	0.05	0.40	0.07	0.38	0.04	0.45	0.04	0.32
166	0.05	0.38	0.07	0.38	0.04	0.32	-	-
181	0.05	0.19	-	-	0.03	0.15	0.04	0.17
196	0.06	0.40	-	-	0.04	0.4	0.06	0.39
200	0.05	0.25	0.05	0.25	0.03	0.25	-	-
207	0.01	0.08	0.01	0.08	0.01	0.08	0.02	0.09
233	0.02	0.40	0.02	0.27	0.02	0.45	0.02	0.32
Overall (±SD)	0.04± 0.02		0.04± 0.02		0.03± 0.01		0.04± 0.01	