

# **Drivers of change in social networks of bottlenose dolphins (*Tursiops truncatus*) in Cardigan Bay, Wales**

A dissertation submitted in partial fulfilment of the requirements for the degree of  
Master of Science (MSc) in Marine Biology  
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This work has not previously been accepted in substance of any degree and not being concurrently submitted in candidature for any degree.

Candidate: Sophie Megan Thomson

Date: 03/09/2021

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2 **in Cardigan Bay, Wales**

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4 Running page head: Drivers of change in social networks of bottlenose dolphin

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18 **Highlights**

19 • Social differentiation within the entire social network was relatively high (Poisson:  $S =$   
20  $2.026$ ,  $SE = 0.169$ ;  $r = 0.850$ ,  $SE = 0.007$ ) demonstrating the presence of diverse, non-random  
21 social bonds.

22 • Temporal associations best fit the model of “preferred companions and casual acquaintances”  
23 (QAIC = 74290.0489) against the standardised lagged association rates (SLAR). The standard  
24 deviation (SD) and coefficient of variation (CV) values of the real association indices were  
25 higher ( $SD_o = 16.96985$ ,  $CV_o = 14.16834$ ) compared to those of random datasets ( $SD_r =$   
26  $13.17329$ ,  $CV_r = 11.30411$ ). This implies a strong presence of long-term (between-sampling  
27 period) preferred associations between individuals over time.

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29 **Key words:** Bottlenose dolphin, *Tursiops truncatus*, social network analysis, SOCPROG, photo-  
30 identification, association strength, social bonds, Cardigan Bay.

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## 35 ABSTRACT

36 Although previous studies have demonstrated the variability within delphinid social structures, it is  
37 important to analyse how association strength and patterns have changed over time and whether this  
38 correlates to fluctuations in population status, sex, social group, and changes in geographic location  
39 due to movement of individuals. This study describes the first long-term assessment, spanning almost  
40 two decades, of differences in association strength between individuals, whether preferential  
41 associations are maintained over the long-term, and the drivers of change within social networks of  
42 the bottlenose dolphin (*Tursiops truncatus*) using a compiled version of SOCPROG 2.9. A 16-year  
43 dataset was created by extracting unique identification features from high-resolution photographic  
44 images of the dorsal fin of bottlenose dolphin individuals within the Cardigan Bay, west Wales social  
45 network. Photo-identifications were collated using the research charity Sea Watch Foundation (SWF)  
46 annual monitoring database dating from 1990 to the present in the waters around Wales, but  
47 particularly within Cardigan Bay. This study identified a total of 505 dolphins. The social analysis  
48 was restricted to 305 individuals (sampled  $\geq 5$  times) which are suggested to be part of an open  
49 population as represented by the discovery curve generated using photo-identification data. Social  
50 differentiation within the entire social network was relatively high (Poisson:  $S = 2.026$ ,  $SE =$   
51  $0.169$ ;  $r = 0.850$ ,  $SE = 0.007$ ) demonstrating the presence of diverse, non-random social bonds.  
52 Temporal associations best fit the model of “preferred companions and casual acquaintances” (QAIC  
53  $= 74290.0489$ ) against the standardised lagged association rates. Most bottlenose dolphin associations  
54 were between pairs of individuals that preferentially associate which is constant over, and between  
55 pairs of individuals who associate for some time, dissociate, and may reassociate forming non-  
56 permanent associations. The present study demonstrates that among bottlenose dolphins, long-term  
57 associations are more favored over short-term non-permanent companionship, correlating to a society  
58 governed by fission-fusion dynamics. These results help develop the existing knowledge of social  
59 structure obtained for oceanic dolphin species.

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## 66 INTRODUCTION

### 67 **Animal societies**

68 A species social structure is comprised of groups of individuals living and interacting cooperatively  
69 via inter- or intra-specific relationships, in which members form associations with specific individuals  
70 of varying strength and are maintained for certain periods of time (Whitehead 2008a). Individuals are  
71 considered part of a ‘society’ when the social structure of a same-species group enables members to  
72 associate with one another in a coordinated manner (Hamilton 1964). Regardless of relatedness,  
73 members within a society benefit from close associations formed during group living in comparison  
74 to a solitary lifestyle (Croft *et al.*, 2008). Typical advantages include increased vigilance and  
75 protection from predators, higher survival rates through enhanced acquisition of resources, and  
76 greater reproductive success due to larger aggregations of suitable mates or increased offspring  
77 survival rates (Krause *et al.*, 2007). Group living can also induce detrimental fitness trade-offs such  
78 as vulnerability to infectious disease or increased resource competition. Thus, group formation will  
79 only occur if the cost-benefit analysis favours most individuals within a population (Sih *et al.*, 2009).  
80 Whilst the benefits of group living facilitate sociality, the development of social structure within  
81 animal societies is determined by a range of factors such as population distribution and density,  
82 individual fitness, and predation pressure (Wilson 2000; Croft *et al.*, 2011; Farine and Whitehead  
83 2015). The structure of social systems can influence the behaviour, ecology, biology, physiology,  
84 genetics, and rate of transmission of disease or infection within a species population (Silk 2007;  
85 Bertulli *et al.*, 2021). Consequently, societies will usually demonstrate diverse grouping, mating, and  
86 spacing patterns, and show variation in the strength and quality of relationships between individuals  
87 (Aureli *et al.*, 2008).

### 88 **Cetacean social structures**

89 Cetaceans are an excellent taxonomic group to evaluate how social networks and association patterns  
90 within a society have changed over time, as well as investigating potential drivers of change in social  
91 networks, due to the great diversification between species and the extensive continuum of sociality  
92 among delphinids (Mann *et al.*, 2000; Gero *et al.*, 2005; Rendell *et al.*, 2019; Bertulli *et al.*, 2021).  
93 Social structures vary between and within groups of cetacean species depending on a range of factors  
94 including habitat preference, environmental conditions, predator presence, and anthropogenic  
95 pressures (Gowans *et al.*, 2007). Across the broad spectrum of social structures there are: (i) long-  
96 term and constant associates with stable social bonds, as demonstrated amongst sperm whales  
97 (*Physeter macrocephalus*) and orca (*Orcinus orca*) for example, (ii) fluid societies with fission-fusion  
98 dynamics characterised by fluctuating and temporary associations, observed within striped dolphin

99 (*Stenella coeruleoalba*), and (iii) groups exhibiting social attributes of both societies, such as  
100 bottlenose (*Tursiops* spp.) and Risso's dolphin (*Grampus griseus*) (Girvan and Newman 2002;  
101 Newman 2006; Denkinger et al. 2020; Bertulli et al., 2021).

102 It is imperative to investigate the drivers of change in social networks and association patterns over  
103 time across a wide range of cetacean species, especially those inhabiting extreme or changing  
104 environments, such as the bottlenose dolphin (*Tursiops truncatus*), if one is to effectively conserve  
105 and manage populations (Newman and Girvan 2004; Bertulli *et al.*, 2021). Analysing the variation in  
106 social organisation across a population's geographic range enables us to compare social and  
107 environmental mechanisms driving the varying patterns of sociality exhibited in such species  
108 (Lusseau *et al.*, 2003).

### 109 **Social structure within bottlenose dolphin societies**

110 Social networks within bottlenose dolphin societies are governed by fission-fusion dynamics (Connor  
111 2000). Fission-fusion societies are defined as those where population group size and composition are  
112 changeable and adaptable (Connor *et al.*, 2000). Associations between individuals are partly driven  
113 by the voluntary presence or absence of group members, forming communities of individuals which  
114 frequently change pods, resulting in complex social relationships (Gero *et al.*, 2005; Pesante *et al.*,  
115 2008b). Management of these social networks is thought to be facilitated by highly developed  
116 cognitive abilities (due to large brain to body size ratio) used for communication, information transfer,  
117 social learning, and anticipation of other individuals' behaviour, evolved as a result of sociality and  
118 synchronous behaviours (Mann *et al.*, 2000; Gero *et al.*, 2005). However, as cetaceans live primarily  
119 underwater, few studies have analysed levels of social complexity and type of social interaction  
120 involved in maintaining sophisticated social network structures, as well as possible drivers of change.  
121 Therefore, it is important to explore the crucial factors influencing bottlenose dolphin group  
122 composition, formation, and individual identity when understanding bottlenose dolphin social  
123 network structure (Pesante *et al.*, 2008a; Whitehead 2009).

### 124 **Associations within bottlenose dolphin social networks**

125 Hammerschmidt and Fischer (2019) demonstrated how 'social bonds' between preferred associates,  
126 where individuals display consistent affiliative preferences, are formed to increase an individual's  
127 reproductive success. This is achieved through enhanced breeding opportunities, reduced predation  
128 and aggression, efficient information exchange, as well as decreased infanticide. Associations vary  
129 by social position, ecological conditions, age, and sex (Pesante *et al.*, 2008a; Whitehead 2009).

130 Records show that males form strong long-term associations between one or two preferred  
131 individuals. Small groups of male companions are classified as alliances and are typically established

132 to consort females (Krützen *et al.*, 2003). Bottlenose dolphin male-male alliances can potentially last  
133 many years. For example *T.truncatus* populations inhabiting Sarasota Bay, Florida, are recorded to  
134 have alliances lasting 20 years, whilst populations of *T.aduncus* within Shark Bay, Australia, are  
135 known to have alliances of at least 12 years (Parsons *et al.*, 2003). Association strength has been  
136 compared to that of mother-calf relationships, signifying the stability and consistency of male bonds  
137 (Sim 2015) Complicated male alliances have also been observed within certain populations, such as  
138 Shark Bay, in which males form second order alliances to mitigate attack and defend against rival  
139 male alliances (Sim 2015). Overall, male-male associations are fundamental in increasing the  
140 reproductive success of affiliated individuals.

141 Evidence of strong associations such as male-male alliances have not been recorded among female  
142 bottlenose dolphins. Most females have no or very limited associations, maintaining a large network  
143 of weak or moderate bonds which fluctuate regularly (Möller and Beheregaray 2004). Studies on  
144 female *T.aduncus* within Port Stephens, Australia, suggest that the majority of closely associated  
145 female bottlenose dolphins are genetically related. On the other hand, many populations have non-  
146 related female associations, indicating biological and environmental factors may also determine  
147 social bonds (Möller *et al.*, 2006). One significant factor driving female associations and grouping is  
148 their reproductive state (Parsons *et al.*, 2003; Möller *et al.*, 2006). Preferential bonds with fellow  
149 maternal kin are highly valuable, facilitating protection from predators and cooperative defence  
150 mechanisms of resources (Pesante *et al.*, 2008a.b). Alloparental care may also bond females, as  
151 observed in several odontocete species (Connor *et al.*, 1998; Wiszniewski *et al.*, 2009).

152 Calf association is the strongest bond that a female develops (Feingold and Evans 2014). Although,  
153 social behaviour develops rapidly, calves have a prolonged foraging dependence on their mother  
154 during the first 3-6 years (Feingold and Evans 2014). Association strength declines before the mothers  
155 next gestation period. However, juveniles can associate with their peers after leaving their mother  
156 (Pesante *et al.*, 2008a.b). Despite the length of juvenile postweaning and pre-reproductive stages,  
157 limited data exists on how they develop or influence the structure of social networks through  
158 behaviours such as play, sexual behaviours, and displays (Connor *et al.*, 2000).

159 Male-female associations are generally through reproductive courtships, with interactions increasing  
160 in the frequency when a female is cycling (Connor 2007). Typical patterns are: (A) solitary males  
161 defend an area used by a female, with male pairs covering a larger area, and do not stay with the  
162 female, or (B) male pairs and trios form courtships with individual females for a month (Connor *et*  
163 *al.*, 1999). Although male-female associations are not strong, mixed sex groups are not uncommon  
164 especially if they use the same natal range (Connor *et al.*, 2000).

165 *Drivers of change*

166 Although previous studies have reported the type and strength of associations within bottlenose  
167 dolphin social networks, how social networks change over time due to community divisions such as  
168 sex, behavioural state, age, and geographical location has not been fully examined (Connor 2007;  
169 Feingold and Evans 2014). For instance, male and female associations are restricted by their  
170 reproductive state and effort, whilst juveniles group together based on various behavioural  
171 characteristics as they are less constrained by reproductive effort (Connor 2007). Relationship  
172 uncertainty, where certain individuals are more closely associated compared to others due to  
173 overlapping geographical ranges, can cause change within social networks (Connor 2007). Thus, to  
174 establish how association patterns have changed over time and whether this can be related to observed  
175 changes in the status of the population, studying bottlenose dolphins within spatiotemporal groups is  
176 considered a suitable proxy as associates can be easily identified (Whitehead 2009)

177

178 Over the past decade, numerous studies have determined the gender of an increasing number of  
179 individuals, as well as establishing the nature of associations between individuals from the data  
180 collected during each individual encounter. However, few studies have undertaken a full analysis of  
181 social networks, establishing how association patterns have evolved over time and the drivers of such  
182 change. The purpose of this study was to establish whether members of the Cardigan Bay bottlenose  
183 dolphin population exhibit differences in the strength of associations shared between individuals due  
184 to their gender, social group, and geographical location. This study aimed to determine how trends in  
185 social networks and association patterns have changed over time between 2001 and 2017, and whether  
186 this can be related to environmental factors (such as changing levels of recreational disturbance),  
187 observed changes in population status, or changes in geographic location due to movements between  
188 Cardigan Bay and other parts of the Irish Sea (North Wales and the Isle of Man).

189 To analyse patterns of association, data were collected by extracting identification features (such as  
190 the unique patterns of nicks and the appearance of epidermal lesions located on the dorsal fin) from  
191 high resolution photographic images of groups of individuals which had been photo-identified in the  
192 Sea Watch Foundation (SWF) annual monitoring database, consisting of observational data from  
193 1990 to the present in the waters around Wales, but particularly within Cardigan Bay. A social  
194 network analysis using an integrated set of programs in SOCPROG (Whitehead 2009) was undertaken  
195 to establish which individuals expressed preferential associations with certain individuals, and  
196 whether these social bonds were maintained in the long-term. Levels of association were determined  
197 for all pairwise combinations of non-calf males, females, and those of undetermined gender using the



198 Half-Weight Index (HWI) in SOCPROG. These can be established for different years, geographical  
199 areas, and even seasons.

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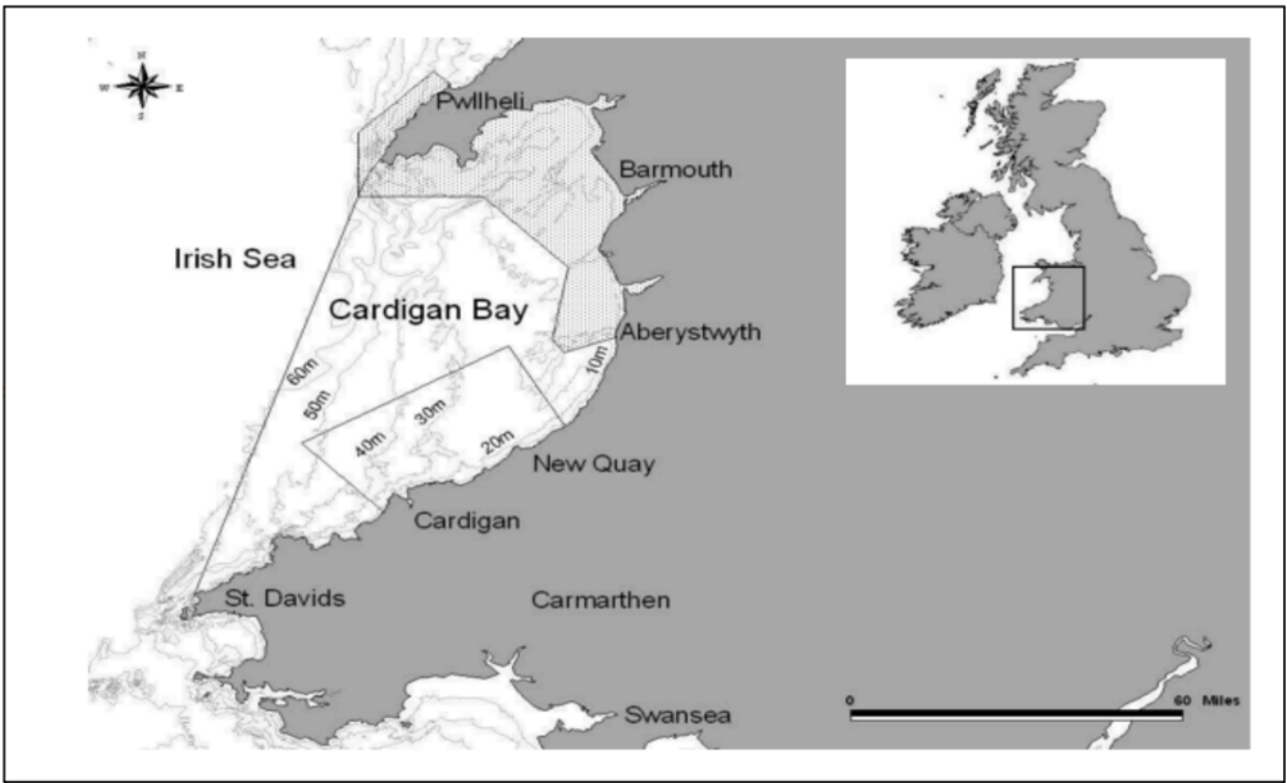
## 202 **METHODS**

### 203 **Study site**

204 Cardigan Bay is situated on the west coast of Wales (52°28'N, 4°09'W), extending from St David's  
205 head in the south to the tip of the Llyn Peninsula at Bardsey Island (Figure 1). Encompassing over  
206 100km of open coastline, Cardigan Bay is nationally recognised as one of the largest embayment's  
207 in the British Isles (Vergara-Peña, 2020). Across the bay mean annual temperatures seldom exceed  
208 11°C, although higher temperatures (20°C) are recorded in shallower near-shore regions between  
209 August-September. Lower temperatures of 5°C or less are reported from February-March (Barne  
210 1995). The large inlet is relatively shallow, with average depths failing to exceed 60m off the Llyn  
211 Peninsula and west Pembrokeshire coasts (Evans 1995). Current speeds reach up to 1.8kn, whilst the  
212 most prevalent tidal movements are usually observed around estuaries, headlands, and within St  
213 Georges Channel (Magileviciute *et al.*, 2007). Regular influxes of freshwater from three major rivers,  
214 Aeron, Ina, and Teifi, significantly influence salinity levels (33.3% in winter to 34.2% in summer,  
215 with lower salinities closer to the coast), local water temperatures, and water quality within the region  
216 (Magileviciute *et al.*, 2007). The bay's biological and physical characteristics are heavily influenced  
217 by semi-diurnal tides entering the inlet from St Georges Channel. Tidal current speed determines  
218 sediment distribution and substrate composition. Regions of strong currents, where tidal current speed  
219 and energy are high, are characterised by sandy or gravel-type substrate; the habitat most favoured  
220 by bottlenose dolphins. In comparison, areas where current speed and water energy are low, sediment  
221 composition is usually mud (Barne 1995; Evans 1995).

222 The study was primarily conducted within the Cardigan Bay SAC and Pen Llyn a'r Sarnau SACs  
223 (Figure 2). The southern Cardigan Bay SAC is situated between Aberath and Ceibwr, encompassing  
224 approximately 1039km<sup>2</sup> and extends 19.3km offshore (Barnes 2010; Vergara-Peña, 2020). The exact  
225 geographical coordinates of the study areas are shown in Table 1. SAC site selection was based upon  
226 regular sightings of semi-resident bottlenose dolphins since at least the early 1920s.

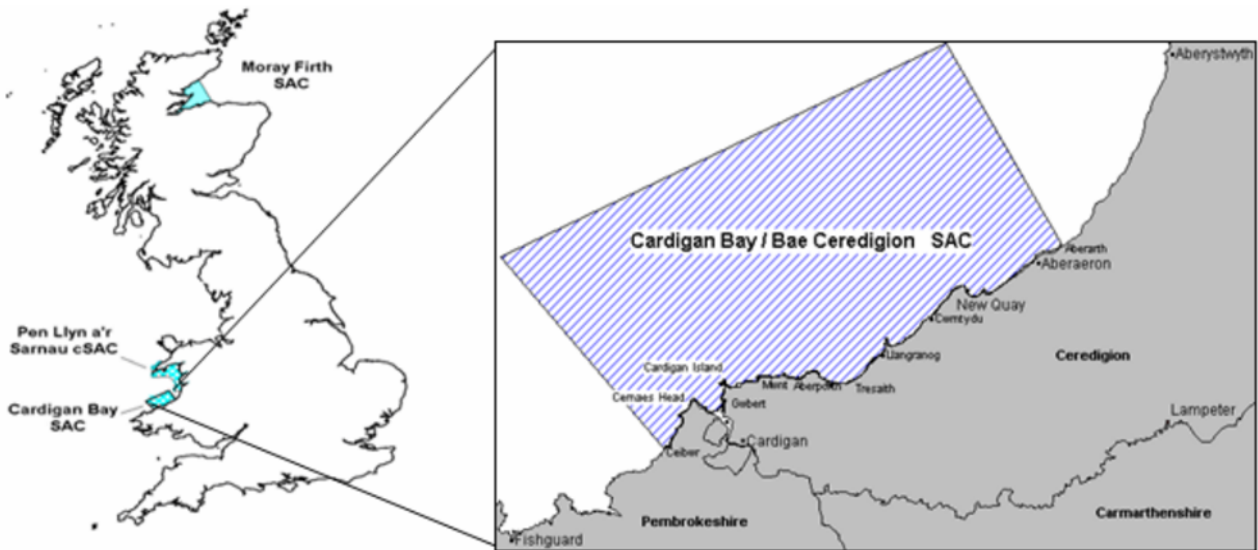
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**Figure 1:** Cardigan Bay. Rectangle shows the Cardigan Bay SAC. The hatched polygon shows Pen Llyn a'r Sarnau SAC, with the diagonal line showing the edge of Cardigan Bay (Sourced: Pesante, et al., 2008b).

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**Figure 2:** Location of the Cardigan Bay SAC, the main study area. (Sourced: Ceredigion County Council, Cardigan Bay cSAC Management Plan, 2001).

230

## 231 **Data collection**

232 Encounter data were primarily collected aboard various motorised vessels within the perimeter of the  
233 two SACs in Cardigan Bay, particularly the southernmost SAC (Table 1). Boat-based surveys were  
234 only conducted at a Beaufort scale of three or less, and only when observation conditions were  
235 suitable. Survey trips were terminated if visibility levels significantly diminished because of heavy  
236 rain or dense cloud cover, due to potential unreliable sightings and inadequate digital images for  
237 dorsal fin photo-identification.

**Table 1:** The coordinates defining the geographical boundary of the Cardigan Bay SAC study site. The boundaries of the three study regions are expressed in decimal degrees.

<b>Study area code</b>	<b>Region</b>	<b>Study area boundaries in decimal degrees</b>
<b>A</b>	Southern Cardigan Bay	<52.5 decimal degrees
<b>B</b>	Northern Cardigan Bay	52.5-53.0 decimal degrees
<b>C</b>	North Wales/northern Irish Sea	>53.0 decimal degrees

238

239 Survey effort was recorded whenever effort status fluctuated, vessel direction adjusted, every sighting  
240 event, and otherwise periodically at 15-minute intervals. Effort entries included: survey approach  
241 (methodical line-transect, casual search, dedicated search, or photo-identification), time of effort  
242 entry (hh.mm, GMT/BST), position effort entries were recorded (start and end longitude and latitude  
243 in degrees and decimal minutes), vessel speed (knots) and course of travel (degrees), angle subtended  
244 by sea surface glare obstructing the field of view, presence or absence of precipitation, level of  
245 visibility, sea state (Beaufort Scale), and height of sea swell. Every effort entry which corresponded  
246 to a sighting was assigned a unique reference number. The sighting number (encounter record ID)  
247 was transferred to a sighting survey form which correlated to an individual encounter.

248 Sighting surveys also recorded the species observed, group size, age group (classified as either new-  
249 born, calf, juvenile, or adult) and number of each sighted. Qualitative age categories were based on  
250 swimming pattern, body size, proximity to an adult, and skin colour variations. Noteworthy  
251 behavioural characteristics (or reaction to watercraft) included swim speed, breaching, bow-riding,  
252 feeding or foraging, socialising and resting.

253 Individuals, or groups of bottlenose dolphin were approached following the regulations outlined in  
254 the license to disturb granted by Natural Resources Wales regardless of group size. Suitable photo-

255 identification images were captured following Wursig and Jefferson (1990). A single encounter was  
256 defined as the total time spent photographing every individual, irrespective of how distinctive  
257 markings (dorsal nicks or skin lesions) appeared. An encounter was terminated once all individuals  
258 had been photo-identified, lost from view, or displayed avoidance behaviour.

259 Individuals belonging to the same group were classed as all the bottlenose dolphins photographed  
260 during a single encounter. Total group size was the number of associated individuals observed in a  
261 sighting, in which individuals within a spatial area of 100m were affiliated in the same behavioural  
262 activity. If multiple groups were sighted, each group was surveyed independently and recorded as a  
263 separate encounter.

264

## 265 **Data analysis**

### 266 **Photo-ID matching**

267 Photo-IDs from each encounter were analysed using ACDSee 5.0.1 following specific matching  
268 procedures developed by the Sea Watch Foundation. Only high-quality photographs were used to  
269 identify associated individuals, determined by dorsal fin shape and patterns of lesions, nicks and scars,  
270 as they are the most stable feature to use for this species (Wilson *et al.*, 2000; Bearzi *et al.*, 2009).  
271 Photographs of distinctive body features were also used if they correlated to a known individual  
272 through dorsal fin identification. Group size and age (new-born, calf, juvenile, adult) were also  
273 confirmed through photo analysis procedures. After matching to the master photo-ID database, each  
274 individual was assigned an alpha numerical code. Accurately identified individuals were used to  
275 statistically analyse social networks and spatial distribution patterns of bottlenose dolphin groups.

### 276 **Social analysis**

#### 277 *Association patterns*

278 Associated dolphins were classed as all those identified within the same group during an encounter,  
279 with a one-day sampling interval to minimise potential demographic effects (Whitehead & Dufault  
280 1999). Individuals were included in social analyses regardless of how many times they were sampled  
281 and group photo-ID coverage.

282 In SOCPROG, a one-day sampling interval was used to calculate mean associations per individuals  
283 and per dyad ( $g$ ), social differentiation ( $S$ ), and correlation coefficient ( $r$ ), by conducting Whitehead  
284 (2008a, b) likelihood approximation techniques. Accuracy of association measures utilised in

285 constructing social structure models is represented by  $r$ . Variability within the social network is  
286 defined by  $S$ , ranging from homogenous to highly differentiated (Whitehead 2008b). Combined  $r$  and  
287  $S$  values provides reassurance that the results and social network can be analysed accurately (Bertulli  
288 *et al.*, 2018). A high  $S$  value signifies less association data is required to achieve an  $r$  value closest to  
289 1, with 1 being the highest degree of accuracy the dataset processes in representing true associations,  
290 and to demonstrate the occurrence of preferred associations (Whitehead 2008a). Bootstrap methods  
291 were conducted to calculate standard errors around estimates using 10,000 replicates to increase the  
292 accuracy when working with a large dataset (Whitehead 2008b).  $S \times \bar{g}$ , where  $\bar{g}$  is the mean  
293 association per individual, was calculated to see whether the association data could detect preferred  
294 associations, acknowledging that if  $S \times \bar{g} > 5$  it is likely that individuals show tendencies to form  
295 preferred companions (Whitehead 2008a).

296 The Half weight index (HWI) was used to quantify the amount of time dolphins within a pair spend  
297 together, to accurately measure the level of association between individuals belonging to the same  
298 group on a scale from 0-1. This procedure was chosen as it significantly reduces observer bias during  
299 photo-identification and boat-based surveys (Wells 1991; Fortuna 2007). It also allows results to be  
300 compared against association patterns recorded in other bottlenose dolphin studies (Wells 1987). The  
301 HWI was cited as HWIG, as it was modified to accommodate biases induced by differences in  
302 sociality; to distinguish between associations occurring by chance during aggregations and preferred  
303 companionships (Lusseau *et al.*, 2006). A HWIG lower than 1 suggests individuals are more likely  
304 to evade each other, while a HWIG greater than 1 indicates two individuals are interacting more  
305 frequently than what would be predicted (Godde *et al.* 2013). To test whether associations were  
306 significantly higher. The Mantel test (Mantel 1967) to test whether individuals within the same region  
307 had significantly high levels of association, compared to individuals from different regions, was also  
308 run in SOCRPORG. The null hypothesis was that the rate of association between and within regions  
309 were similar.

310 ***Test for preferred and avoided companionship: long-term (between-) associations and short-term***  
311 ***(within-sampling) associations***

312 Patterns of preferred and avoided associations were tested for in SOCRPORG using a variation of the Bejder *et al.*,  
313 (1998) permutation test created by Whitehead *et al.*, 2005. The routine chosen was to “permute groups  
314 within samples” as bottlenose dolphins are known to move across the different study regions (Table 1), and as  
315 a consequence some identified individuals do not appear in each sampling period across the duration of the  
316 study. This tested the null hypotheses that individuals do not preferentially associate or avoid one another  
317 given the number of groups each individual was seen in during each sampling period (Whitehead 2008a).  
318 Associations were permuted with 10,000 trial per permutation to avoid the test being too conservative and to

319 stabilise the p-values, with association index equal to HWIG (Pearson *et al.*, 2017). If individuals develop  
320 long-term (between-sampling periods) preferential associations with other individuals the SD and CV values  
321 of the real data should be higher than the random datasets. The SD and CV real values should be lower than  
322 the random datasets if individuals preferentially associate short-term (within-sampling periods). Individuals  
323 demonstrating avoided companionship is indicated by the proportion of non-zero values being lower  
324 for the real data compared to the random (Whitehead and Dufault 1999; Blasi and Boitani 2014).

## 325 **Temporal analysis**

### 326 *Lagged association rates*

327 Standardised lagged association rates (SLAR) were calculated to analyse how a dyadic association  
328 changes over time, using all identified individuals ( $n = 505$ ) and a moving average of 400 associations  
329 (Whitehead 1995). The sampling restrictions on the number of individuals was relaxed from those  
330 sampled  $\geq 5$  times to all marked individuals, as SLAR generates an integration of all the available  
331 data. The expected SLAR values of individuals associating randomly was illustrated by the null  
332 association rate (no preferred associations; Whitehead 2009). The lagged association rate represented  
333 an estimate of the probability that if two or more individuals are associated at any time, then, after  
334 the specified time lag, the second individual is a randomly chosen associate of the first (Whitehead  
335 2019). The intercept on the y-axis (with lag 0) is an estimate of the inverse of the mean typical group  
336 size (number of associated individuals including itself) minus one (Whitehead 1995; Whitehead  
337 2015). Null and lagged association rates were standardised since during the present study it was not  
338 realistic to precisely photo-identify all social group members during an encounter (Gowans and  
339 Whitehead 2001). To corroborate whether lagged association rates were calculated with accuracy, the  
340 temporal jackknife method (Gowans and Whitehead 2001) was implemented in SOCPROG to  
341 calculate standard errors. Mathematical models were fitted to the SLAR utilising maximum likelihood  
342 procedures (Whitehead 1995) such as: (i) “preferred companions”, some pairs of individuals  
343 preferentially associate over time creating long-lasting social bonds; (ii) “casual acquaintances”, pairs  
344 who associate for some time, disassociate, and may reassociate over time forming non-permanent  
345 associations, (iii) “constant companions and casual acquaintances”, pairs with preferred and casual  
346 associations, and (iiii) “two levels of casual acquaintances” pairs with fluctuating association and  
347 dissociation stability over short and long period of time (Whitehead 2015). The best fitting model for  
348 the association data was selected by the lowest quasi Akaike Information Criterion value (QAIC;  
349 Whitehead 2015, 2019).

350

351

## 352 **Movement analysis**

### 353 *Lagged identification rate*

354 To analyse how individuals move into and out of the three different study regions (A, B, and C: Table  
355 1), the Lagged Identification Rate (LIR) was calculated. LIR is the probability that if an individual is  
356 identified within an area at any time, it is identified some time lag later in the same area during any  
357 single encounter (Whitehead 2001). If the LIR is the inverse of the population size, the population is  
358 closed. The LIR typically falls with time lag if there is mortality or emigration. LIR that rise and fall  
359 with time lag signify cyclical movements within the population. The LIR was used to determine  
360 bottlenose dolphin mean residency time “within and between” study areas, indicating the general  
361 probabilities that individuals are in the same study area or in a different area after particular time lags.  
362 The mean residency time generated by the LIR helped determine the threshold of the sampling period  
363 to classify short-term and long-term associations (see test for preferred and avoided companionship).

364

365

## 366 **RESULTS**

### 367 **Survey effort and group composition**

368 From 2001 to 2017 a total of 505 reliably marked bottlenose dolphins were photo-identified from  
369 each individual sighting (8420) across 1113 sampling days comprising 28858 hours of survey effort.  
370 The year with the most encounters was 2012 (1081), whilst the year with the least was 2002 (81). The  
371 highest number of encounters (69) was recorded on the 28<sup>th</sup> January 2012. A total of 2345 groups  
372 were encountered, in which photo-identification images were successfully taken of each group  
373 member. The total number of individuals photo-identified one or more times in southern Cardigan  
374 Bay (A) was 6238, whilst the number of sightings in northern Cardigan Bay (B) and North Wales and  
375 northern Irish Sea (C) was 1180 and 1002 respectively.

376 Of the 505 identified dolphins, 200 were excluded from the social analysis as they were associating  
377 with others less than 5 times ( $\text{Numsamp} \geq 5$ ). A total of 305 individuals were therefore used in this  
378 social analysis (sampled  $\geq 5$  times) as associations were sufficiently strong to represent social bonds  
379 accurately and reliably (Table 2). Individuals were sighted across 1106 different days from 2001 to  
380 2017. The mean number of identifications per day was 7, whereas the mean number of individuals  
381 identified per day was 6 (Table 2). Of the 305 individuals, 84 were classed as female and 23 were  
382 classed as male (Table 3).

**Table 2:** Mean number of identifications and individuals per sampling period (day) calculated from the number of individual bottlenose dolphins chosen for social analysis (sampled  $\geq 5$  times) and the frequency of sightings across the sampling period.

Number of individuals	Number of sampling periods (Day)	Number of identifications	Mean identifications per sampling period	Mean individuals identified per sampling period	Proportion of individuals identified per sampling period
305	1106	8019	7.25	6.46	0.02117

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**Table 3:** Sex of the 305 individuals selected for social analysis sampled  $\geq 5$  times. F: Female; M: Male; Probable Female: PF; Probable Male: PM; Unknown: U.

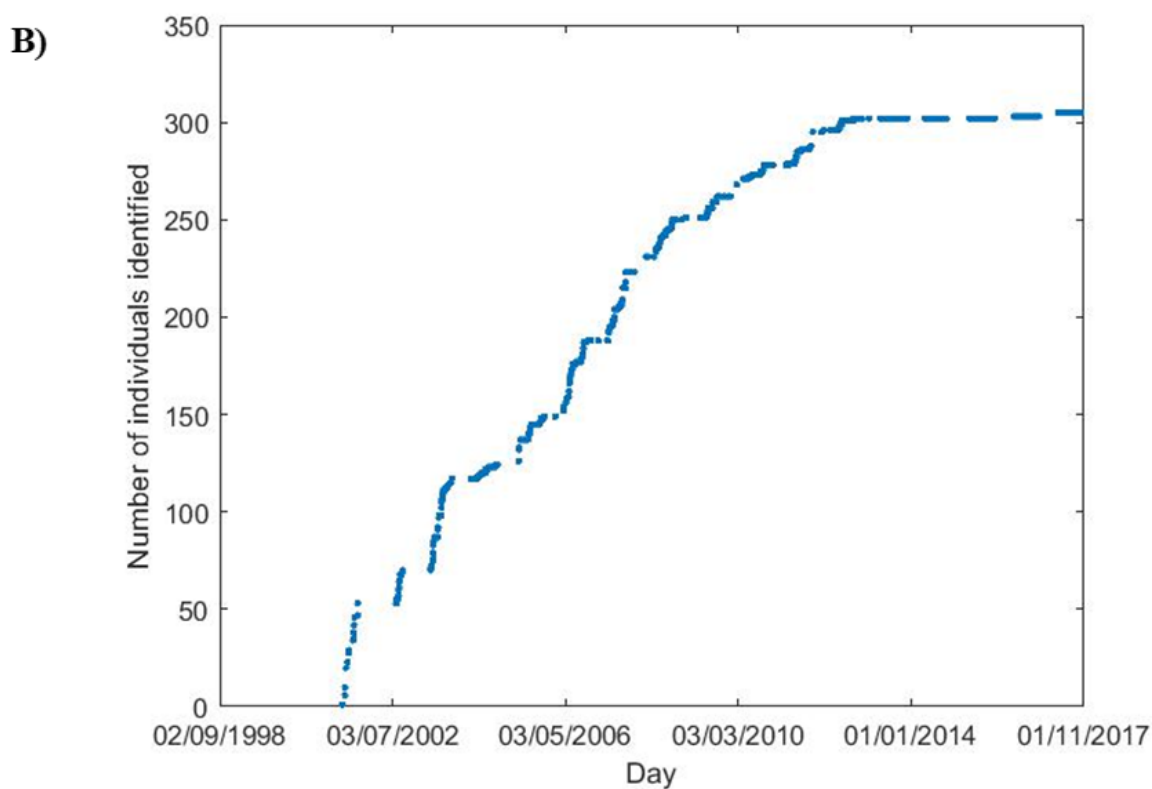
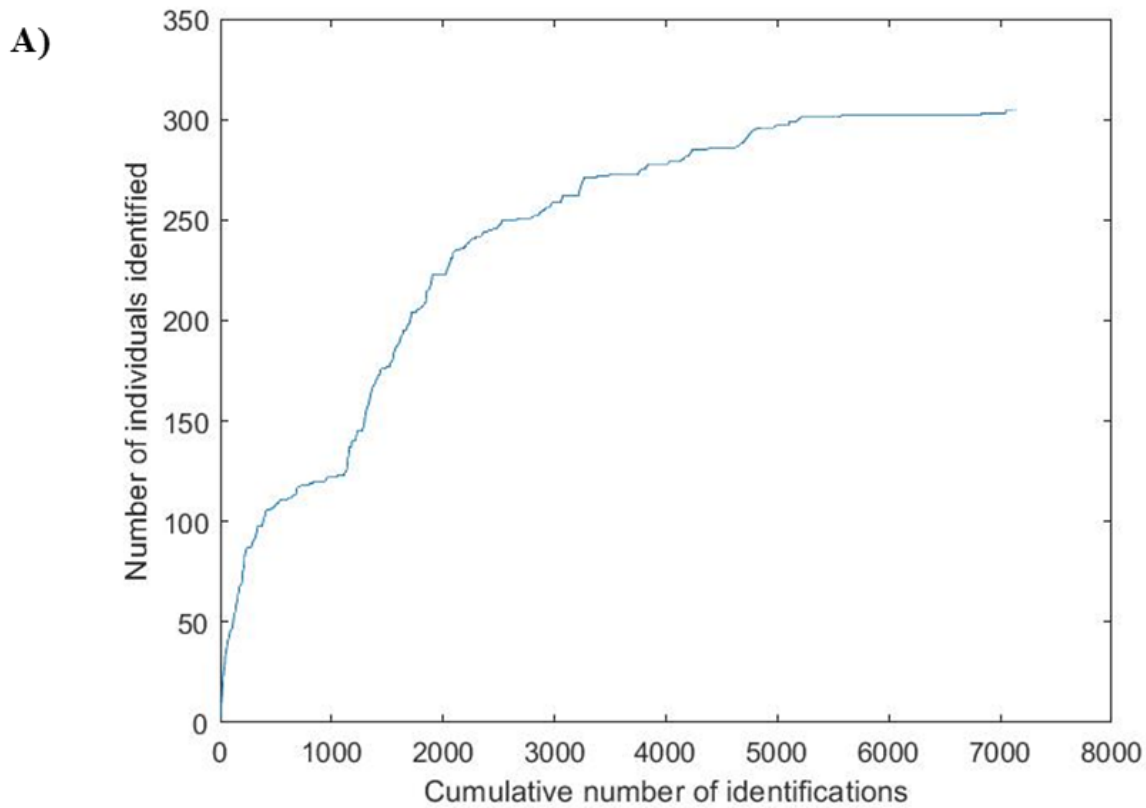
F	M	PF	PM	U
84	23	15	22	161

386

387 The discovery curve of the number of individual bottlenose dolphins identified against the cumulative  
 388 number of identifications rose progressively across the study period before plateauing in 2014 (Figure  
 389 3, A). This indicates that part of the population within the study area remained to be sampled prior to  
 390 2014 as demonstrated by previous studies conducted in the region (Pesante *et al.*, 2008a, b; Feingold  
 391 and Evans 2014, Lohrengel *et al.*, 2017)

392 The average group size across the 17-year period was six. Although 2002 had the lowest number of  
 393 sightings, 2017 had the lowest average group size (3). The year with the highest average group size  
 394 was 2012 (9).





**Figure 3:** (A) Discovery curve of number of individual bottlenose dolphins identified versus cumulative number of identifications, with year of sampling between 2001 and 2017 ( $n = 305$ ). (B) Discovery curve of number of individual bottlenose dolphins identified versus sampling period (days), with year of sampling between 2001 and 2017 ( $n=305$ ). A and B SE of social differentiation are calculated using 10,000 bootstrap replicates for greater accuracy.

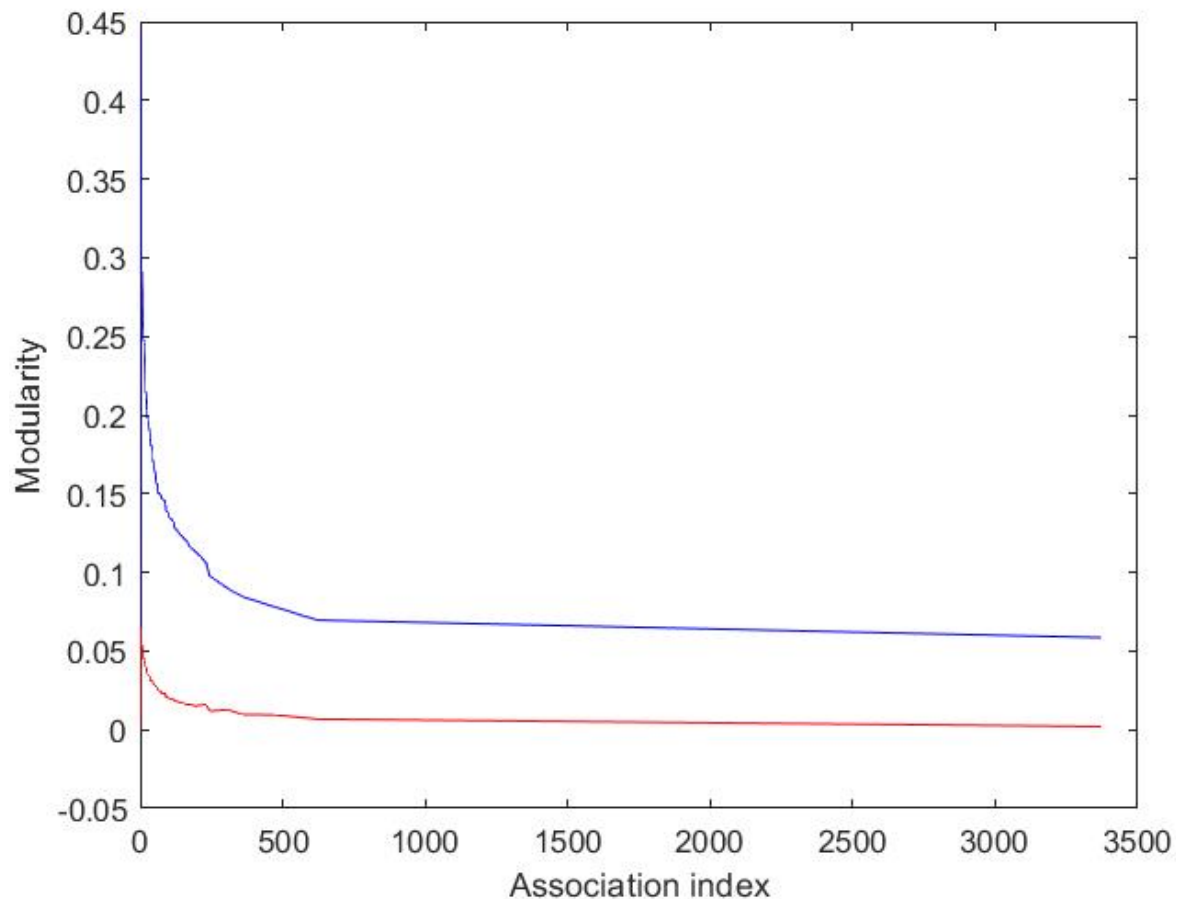
## 396 **Social analysis**

### 397 **Association patterns**

398 Mean association per dyad was  $\pm 0.64$  and per individual was  $\pm 193.40$ . The letter 'g' (1.30) represents  
399 the mean association per individual and was used to test whether association data detected preferred  
400 associations. The estimate of social differentiation ( $S$ ) using the Poisson method was 2.026  
401 ( $SE=0.169$ ), indicating that the society is differentiated. The correlation estimate between true and  
402 estimated association indices ( $r$ ) using the Poisson method was 0.850 ( $SE=0.007$ ). This suggests the  
403 power to resolve these relationships is acceptable, although limited, despite time consuming efforts  
404 in the field spanning over a decade. Standard errors were calculated from bootstrapping with 10,000  
405 replications for greater bootstrapping accuracy when analysing such an immense data set.

### 406 ***Hierarchical cluster analysis***

407 A hierarchical agglomerative cluster analysis of the association data calculated the modularity, the  
408 difference between the proportion of the total association, for the division of the population into  
409 clusters, and the expected proportion (Newman 2004; Whitehead 2008b). Modularity 1 demonstrated  
410 the expected proportion of association indices given the summed associations (from standardised  
411 gregariousness). Maximum modularity was 0.44572 and the value of the association index at this  
412 modularity (AI) was 1.2775. The cophenetic correlation coefficient (clustering using average linkage)  
413 was 0.98493 (Figure 4). Modularity 2 used the expected proportions from the number of permutations  
414 (10000 trials per permutation) of associations within samples in preferred/avoided association module  
415 routines. This controlled for gregariousness and the structure of the data (Whitehead 2019). The  
416 maximum modularity was 0.063591 at  $AI = 2.6474$ . This suggested that clusters formed had mutual  
417 association preferences as opposed to being identified together. The cophenetic correlation coefficient  
418 was 0.98493 (Figure 4). Maximum modularity of both types were greater than 0.3, suggesting useful  
419 divisions of the data (Newman 2004). The cophenetic correlation was lower than 0.8 indicating that  
420 graphing in relation to the data was reliable.



**Figure 4:** Hierarchical agglomerative cluster analysis of the association data. Modularity demonstrates the difference between the proportion of the total of the association indices, or interaction rates, within clusters and the expected proportion. Blue line (modularity 1): the expected proportions given the summed associations of the different individuals. Red line (modularity 2): the expected proportions are from the permutation (10,000) of associations within samples in the preferred/avoided association module routines.

421

#### 422 *Community division by modularity*

423 Modularity was used to assess whether the population could be usefully divided into clusters, to  
 424 evaluate whether association indices were generally higher among individuals within the same cluster  
 425 and lower with individuals from different clusters. Assignment of individuals to clusters was done  
 426 using the eigenvector-based method (Newman 2006) and modularity 1, as it was the most efficient  
 427 delineation (highest modularity) and worked the best for this procedure. All 305 individuals were  
 428 arranged into 1 of 11 individual clusters. The 6<sup>th</sup> cluster had the highest average eigenvector (0.7013)  
 429 corresponding to the final bifurcation involving that individual, which therefore had the most  
 430 uncertainty in the assignment of the individual. The cluster with the lowest average was 7 (-0.34848).  
 431 The modularity of this arrangement was 0.450. A modularity greater than 0.3 suggests there was a  
 432 useful and clear divisions of the population data.

433 *Network analysis statistics*

434 Several measures treating the matrix of symmetric association indices as a weighted network were  
 435 calculated (Table 4). The average sum of association indices of any individual with all other  
 436 individuals (strength) was 364.11 (Table 4). This high strength signifies how strong associations exist  
 437 between an individual and other dolphins within the network. The eigenvector centrality measured  
 438 the degree to which an individual is associated with others and how closely they are associated.  
 439 Although the average value was low (0.01), a highly associated individual does not necessarily have  
 440 a high eigenvector of centrality (Table 4). It could potentially mean that all associates have relatively  
 441 low or null eigenvector centrality. It is not guaranteed that an individual with a high value is greatly  
 442 linked, the individual may have few but important associates. The reach is a useful tool when  
 443 measuring a society containing behavioural contagion. A high reach (218341.34) reflected how an  
 444 individual was strongly connected indirectly (Table 4). The affinity measured the strength of an  
 445 individual's associates weighted by the association index between them. The high affinity score  
 446 (385.08) indicates an individual on average has relatively high associations with other individuals  
 447 with a high strength (Table 4). The correlation coefficients, over individuals, of strength by clustering  
 448 coefficient was 0.2376, and strength by affinity was 0.8972.

449

**Table 4:** Variety of measures treating the matrix of association indices. Strength: sum of association indices of any individual with all other individuals. Eigenvector centrality: a measure of how well an individual is associated to other individuals, and how well they are associated. Reach: a measure of indirect connectedness. Clustering coefficient: a measure of how well the associates of an individual are themselves associated. Clustering coefficient: a measure of how well the associates of an individual are themselves associated. Measures are calculated for each individual. Each measure presents the average and standard deviation (SD) for the whole population.

	<b>Strength</b>	<b>Eigenvector centrality</b>	<b>Reach</b>	<b>Clustering coefficient</b>	<b>Affinity</b>
<b>Overall means</b>	364.11 (293.34)	0.01 (0.06)	218341.34 (1015017.34)	0.00 (0.00)	385.08 (297.83)

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455 ***Distribution of association indices***

456 For each individual, the mean half-weight index (HWIG) value was  $1.20 \pm 0.96$  (mean association  
457 index with all other individuals excluding itself  $\pm$  SD). This shows there are preferred associations  
458 among individuals (Table 5). The sum of all associations (which for association indices is similar, but  
459 not identical, to the group size) was 364.11. Maximum association rate (excluding individuals with  
460 themselves) was 69.00 (Table 5). Table 5 also gives the standard deviation of such measures over all  
461 individuals and by the class variable 'sex' (each sex with all individuals, between pairs of the same  
462 sex, and within- and between- individuals of the same or different sex).

463 A Mantel test for analytical approximation was carried out on the null hypothesis that associations  
464 between study region are similar (Schnell *et al.* 1985). The t-value (with infinite degrees of freedom)  
465 was 2.876. A positive t-value indicates associations between individuals within the same region is  
466 higher. The p-value (2-sided test) was 0.0040. A p-value  $\leq 0.05$  suggests the results were statistically  
467 significant and provides strong evidence against the null hypotheses. A mantel test with 1000  
468 permutations p-value was 0.0000. As bootstrapping accuracy was increased, this result has an even  
469 greater statistical significance and supports rejecting the null hypothesis. The matrix correlation  
470 coefficient was 0.0133. Therefore, bottlenose dolphins ranging within area A, B or C (Table 1)  
471 associated significantly more with other dolphins within their geographic region than between  
472 regions.

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**Table 5:** For each individual, the mean association index with all other individuals, the sum of all associations, and the maximum association rate. Standard deviations of these measures over all individuals and by sex (each sex with all individuals, between pairs of different sex, and overall within- and between pairs of different sex).

	<b>Mean of assoc. (<math>\pm</math>SD)</b>	<b>Sum of assocs. (<math>\pm</math>SD)</b>	<b>Max. Assoc (<math>\pm</math>SD)</b>
<b>Overall</b>	1.20 (0.96)	364.11 (293.34)	69.00 (281.15)

Standard deviation in brackets

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478 *Test for preferred and avoided companionship: long-term (between-) associations and short-term*  
479 *(within-sampling) associations*

480 The routine chosen to permute the association data randomly in different ways was to “permute  
481 groups within samples” to determine whether individuals associate with the same probability with all  
482 other individuals (or among some set of them) given their availability. This tested the null hypotheses  
483 that individuals do not preferentially group together or avoid one another (preferred or avoided  
484 associations) given the number of groups in which each individual was seen during each sampling  
485 period (day). The number of trials per permutation was 10,000 to avoid the test being too conservative  
486 and an unstabilised p-value.

487 Results showed the real value, the mean of the values for the random data sets, and the number of  
488 times the test statistic from the random data was less than the real value (Table 6). The mean of the  
489 real association indices is not significantly lower than the random data (real = 1.19773, random =  
490 1.15525,  $P = 0.9600$ ). As the simulation used half-weight (standardized for gregariousness), this  
491 suggests few random short-term (within-sampling period) preferred companions. The standard  
492 deviation (SD) and coefficient of variation (CV) values of the real association indices were higher  
493 ( $SD_o = 16.96985$ ,  $CV_o = 14.16834$ ) compared to those of random datasets ( $SD_r = 13.17329$ ,  $CV_r =$   
494  $11.30411$ ). This implies there is a strong presence of long-term (between-sampling period) preferred  
495 associations between individuals over several sampling periods. The proportion of non-zero  
496 association indices for real data (0.31844) was significantly lower than the random data (0.35442,  $P$   
497  $= 0.0010$ ), representing how some individuals preferentially avoid others (Table 6). The null  
498 hypothesis was therefore rejected as the distribution of association indices from the real data was  
499 different from the distribution of association indices from many permuted data sets.

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**Table 6:** Random permutations of association data via the ‘permute groups within samples routine’. Number of trials per permutation: 10,000. Results of the tests are presented in the table giving, for each of these test statistics, the real value, the mean of the values for the random data sets, and the number of times the statistic from the random data was less than the real value. These values are translated into the p-value of a one-sided test.

	<b>Real</b>	<b>Mean (random)</b>	<b>(Real&gt;Random)</b>	<b>P(1-sided)</b>
Mean	1.19773	1.15525	(922/ 1000)	P = 0.9600
SD	16.96985	13.17329	(752/ 1000)	P = 0.1490
CV	14.16834	11.30411	(728/ 1000)	P = 0.1650
Proportion of non-zero elements	0.31844	0.35442	(1/ 1000)	P = 0.0010
Mean non-zero elements	3.76121	3.28084	(996/ 1000)	P = 0.0040
SD non-zero elements	29.91162	22.01858	(779/ 1000)	P = 0.1240
CV non-zero elements	7.95265	6.65207	(685/ 1000)	P = 0.2050
SD (typical group size)	5.10738	4.90884	(998/ 1000)	P = 0.0010

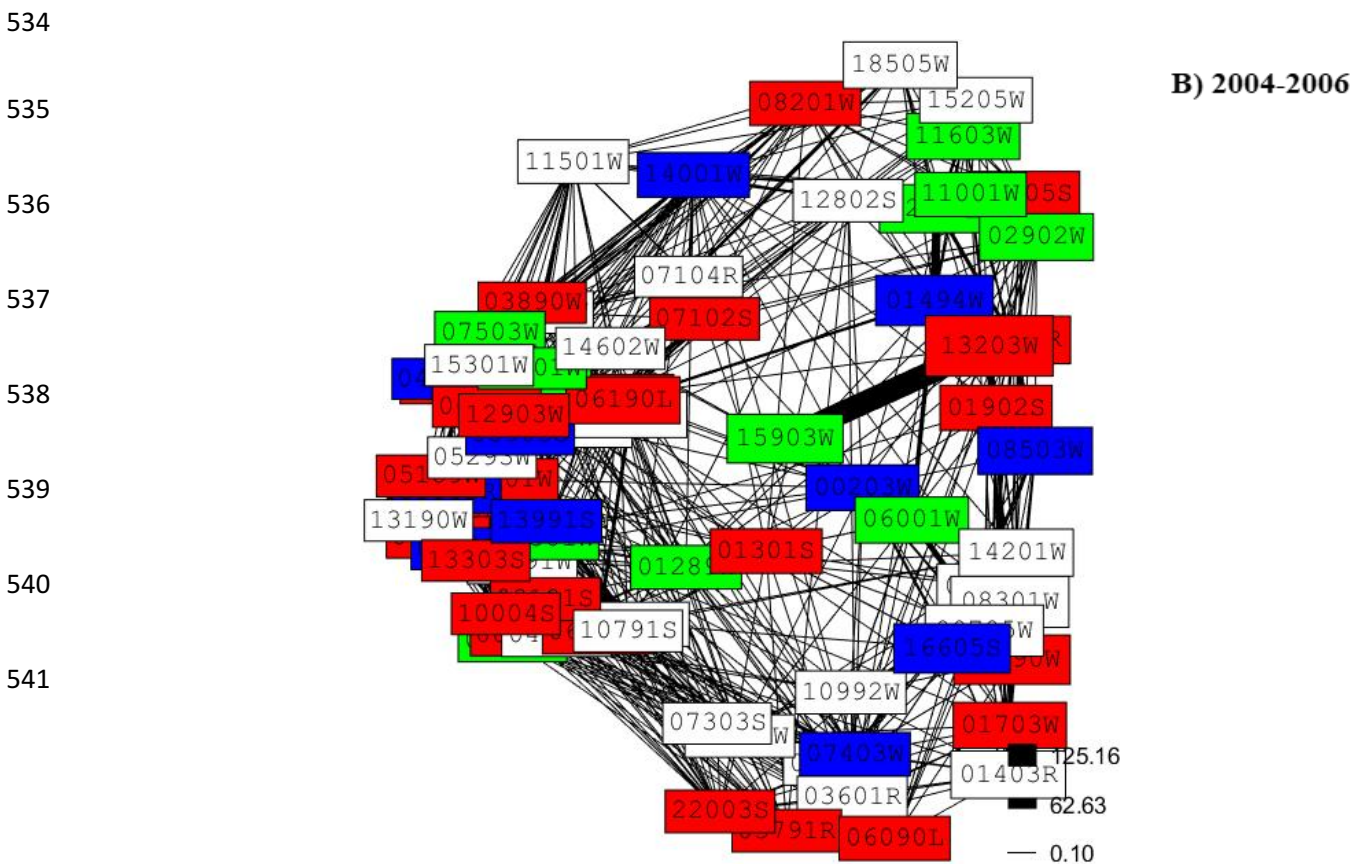
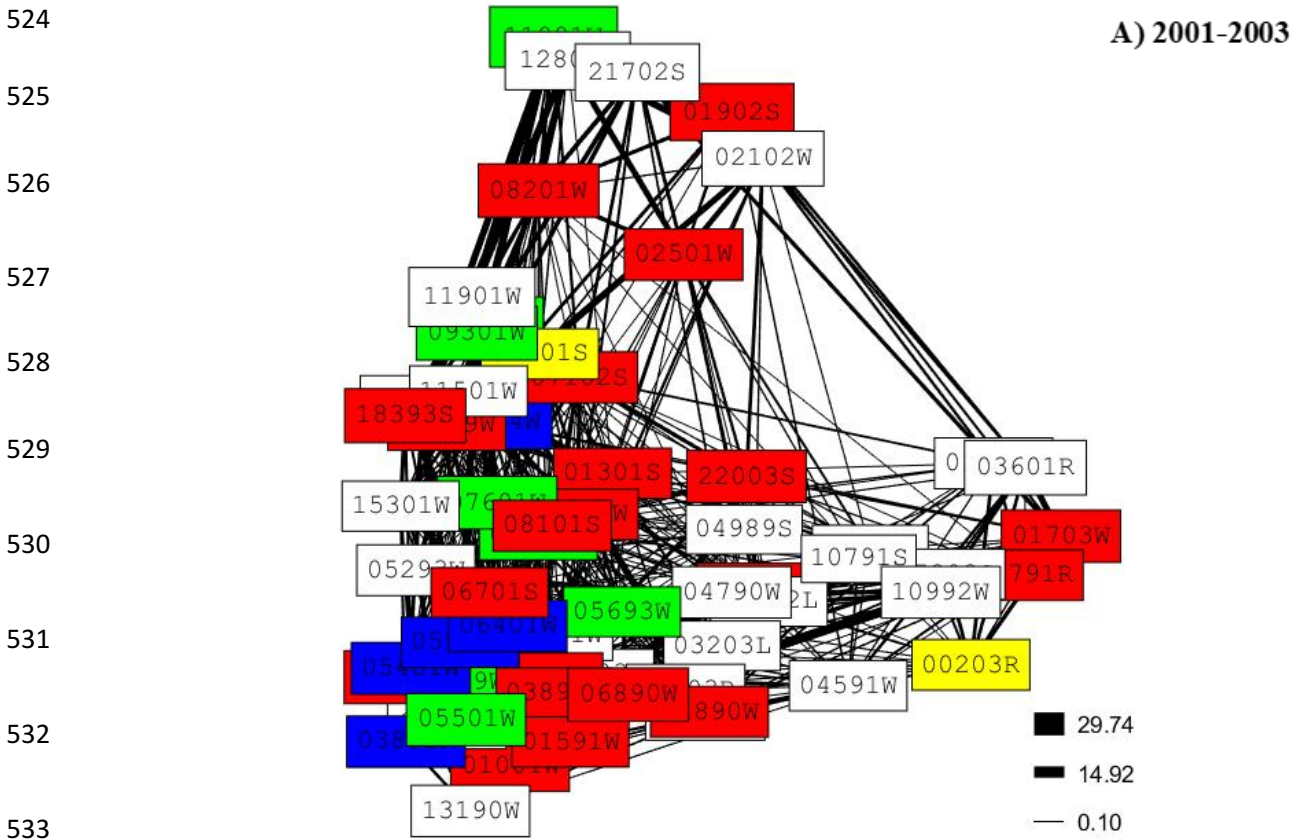
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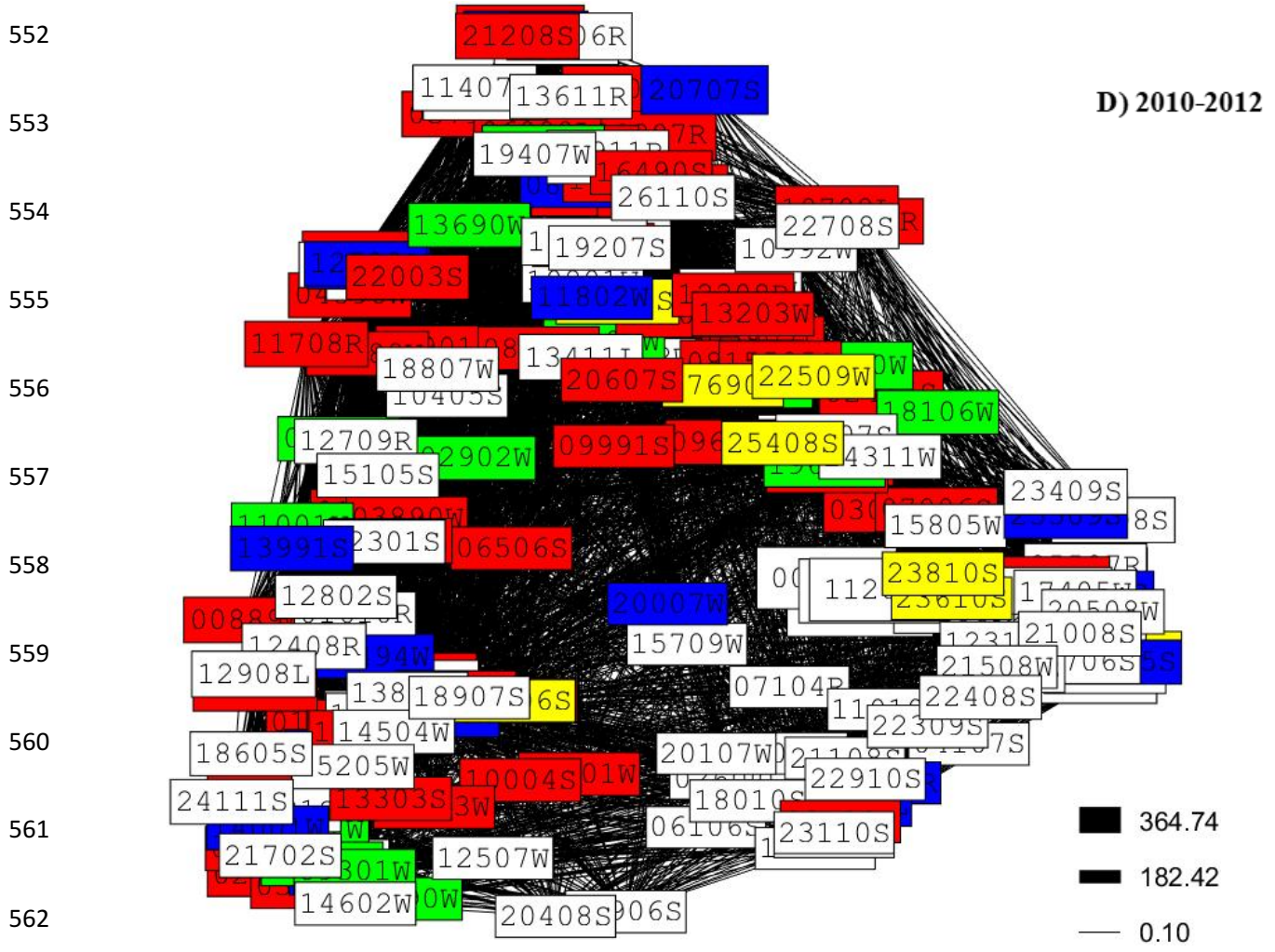
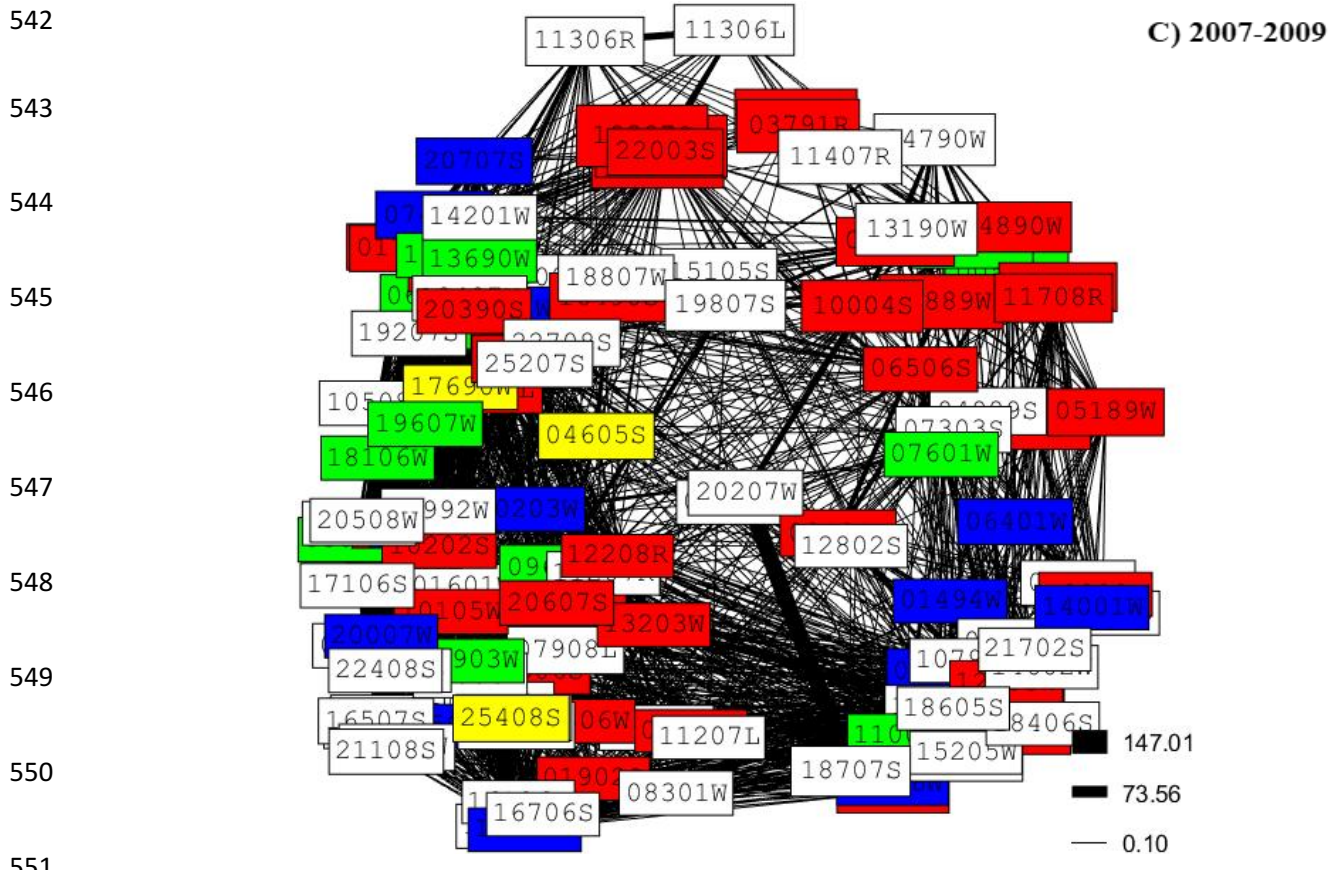
509 ***Network diagram: principal coordinates arrangement***

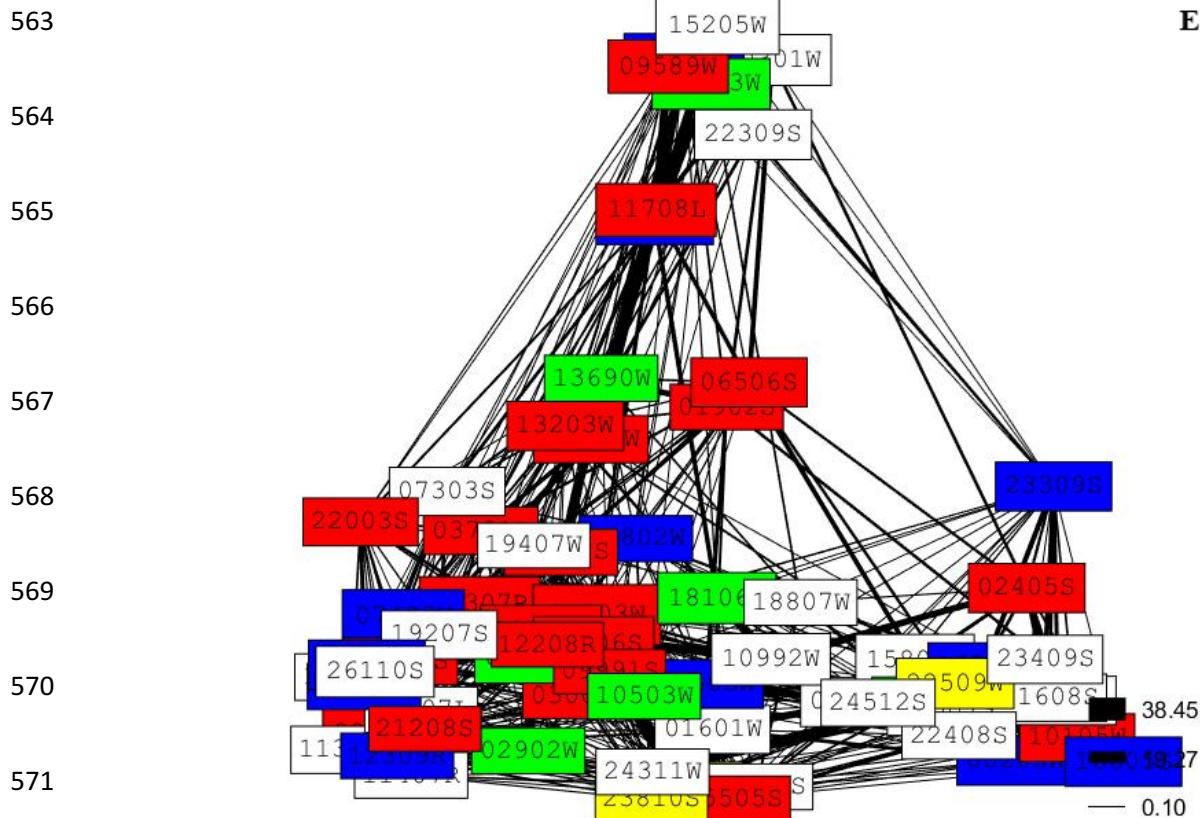
510 The network diagram (sociogram) of the matrix of association indices shows the arrangement of  
511 individuals (nodes) in two-dimensions (Figure 5). The arrangement of nodes displayed is the  
512 “principal coordinates analysis” (Whitehead 2008b). Each point represents an individual in which the  
513 unique alpha-numeric code and sex is presented. The distance between individuals is inversely  
514 proportional to their association. Therefore, the distance between each node is proportional to 1 minus  
515 the squareroot of their association index (Whitehead 2019). Strongly associated individuals are  
516 plotted together, whilst weakly associated individuals are plotted apart (Figure 5). The width of the  
517 links between pairs of nodes represents the strength of their relationship (value of association index  
518 between individuals) (Whitehead 2019). The period with the maximum level of association (364.74)  
519 was between 2010-2012 (Figure5, D), whilst the period with the second largest (147.01) was 2007-  
520 2009 (Figure 5, C). The highest median level of association (182.42) was also seen between 2010-

521 2012. The greatest range of maximum and minimum association index indices was between 2004-  
 522 2006 (125.06), 2007-2009 (146.91), 2010-2012 (364.64) (Figure 5, B, C, D). The lowest minimum  
 523 level of association for all periods was 0.10 (Figure 5).





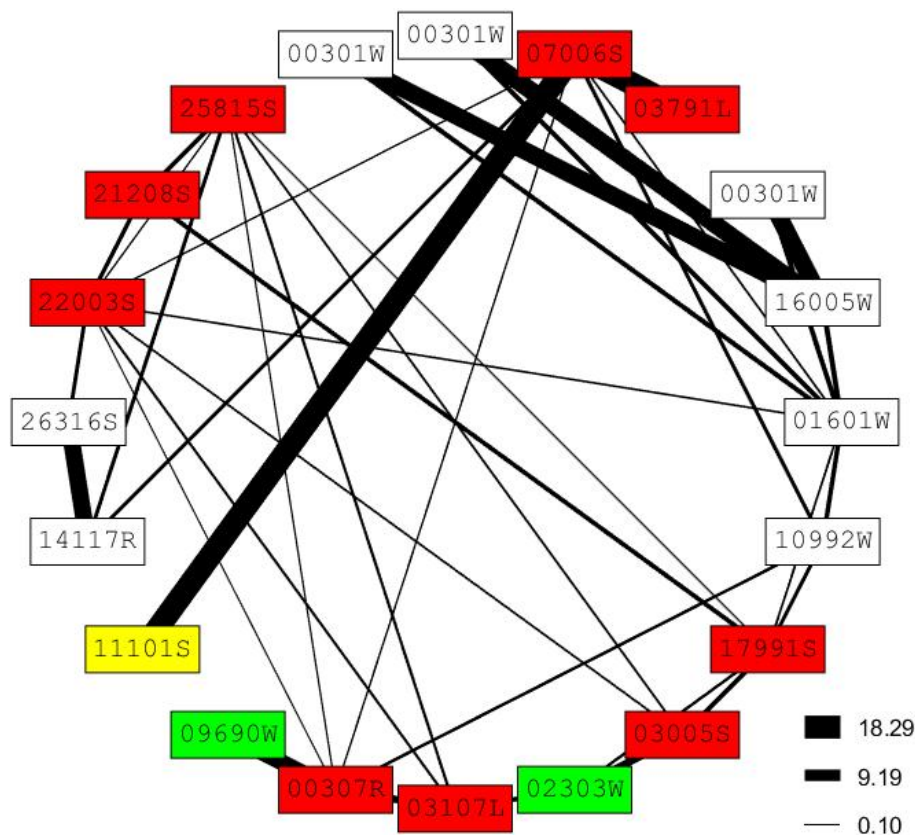




**Figure 5:** Network diagram displaying the principal coordinates arrangement of individuals between 2001-2015, in which the distance between the arrangement of nodes is inversely proportional to their association. Node size is proportional to the gregariousness of the individual (the sum of its associations). Node color represents the sex of the individual. Red: female, blue: male, probable female: yellow, probable male: green, and unknown is white. A) 2001-2003, B) 2004-2006, C) 2007-2009, D) 2010-2012, and E) 2013-2015).

#### *Network diagram: circular arrangement*

The most appropriate network diagram to represent the most recent association indices calculated for the past two years (2016-2017) was to arrange nodes in a “circular arrangement” (Figure 6). This shows the most strongly linked individuals which are usually close to one another. Similar to the principal coordinates analysis, the thickness of links between pairs of individuals demonstrates the strength of their relationship (value of association index) (Whitehead 2019). The maximum level of association was 18.29 (median = 9.19, minimum = 0.10), with an association index range of 18.19. The most closely associated individuals were 07006S (F) - 11101S (PF), 16005W (U) - 00301W (U), and 26316S (U) – 14117R (U) (Figure 6).



**Figure 6:** Network diagram displaying the circular arrangement of individuals between 2016-2017, visually representing strongly linked individuals close to one another. Node size is proportional to the gregariousness of the individual (the sum of associations).

586

## 587 **Temporal analysis**

### 588 *Lagged association rates*

589 The best fitting mathematical model for the association data, and best interpretation of bottleneck  
 590 dolphins in the study area, was “preferred companions and casual acquaintances” (QAIC =  
 591 74290.0489, Table 7; Figure 7). The standardized lagged association rate (SLAR) showed an  
 592 immediate rapid decrease, followed by a short and steady increase at approximately 10 days, before  
 593 an immediate sharp decrease at around 50 days to below 0.01. This pattern was repeated; the SLAR  
 594 peaked again at approximately 475 days before a second sharp drop, peaking again at 600 days. The  
 595 error bar fell below the null association rate approaching around 850 days, after which the general  
 596 trend is a decline in SLAR despite numerous fluctuations (SLAR, Figure 7). Although no other curve  
 597 was similar or fitted the first 100 days, the “two levels of casual acquaintances” was the next closest  
 598 fit (QAIC = 74361.5338; Table 7). This demonstrates that the majority of associations among  
 599 bottlenose dolphins are between particular pairs of individuals which have a preference for  
 600 associating (and which is constant over time), and between individuals who associate for some time,

601 dissociate, and then may reassociate (Whitehead 2019). The inverse of the intercept of the SLAR with  
 602 a lag of 0 also shows how from each day to the next, bottlenose dolphins have a mean of  
 603 approximately 6 associates.

604

**Table 7:** Model types fit to the standardized lagged association rates (SLAR) for all identified bottlenose dolphins sighted  $\geq 1$  times.

<b>Model</b>	<b>Number of parameters</b>	<b>Goodness of fit chi-squared</b>	<b>Maximum-likelihood for parameters</b>	<b>AIC</b>	<b>QAIC</b>
Preferred companions	1	50840.055	$a_1 = 0.011748$	1050667.9000	75044.8115
Casual acquaintances	2	36328.482	$a_1 = 0.00036317$ $a_2 = 0.016728$	1041833.2244	74415.6436
Preferred companions + casual acquaintances	3	36277.846	$a_1 = 0.026444$ $a_2 = 0.010546$ $a_3 = 0.038752$	1040048.8327	74290.0489
Two levels of casual acquaintances	4	35295.295	$a_1 = 2.5134$ $a_2 = 0.00035441$ $a_3 = 0.55434$ $a_4 = 0.016502$	1041023.6573	74361.5338

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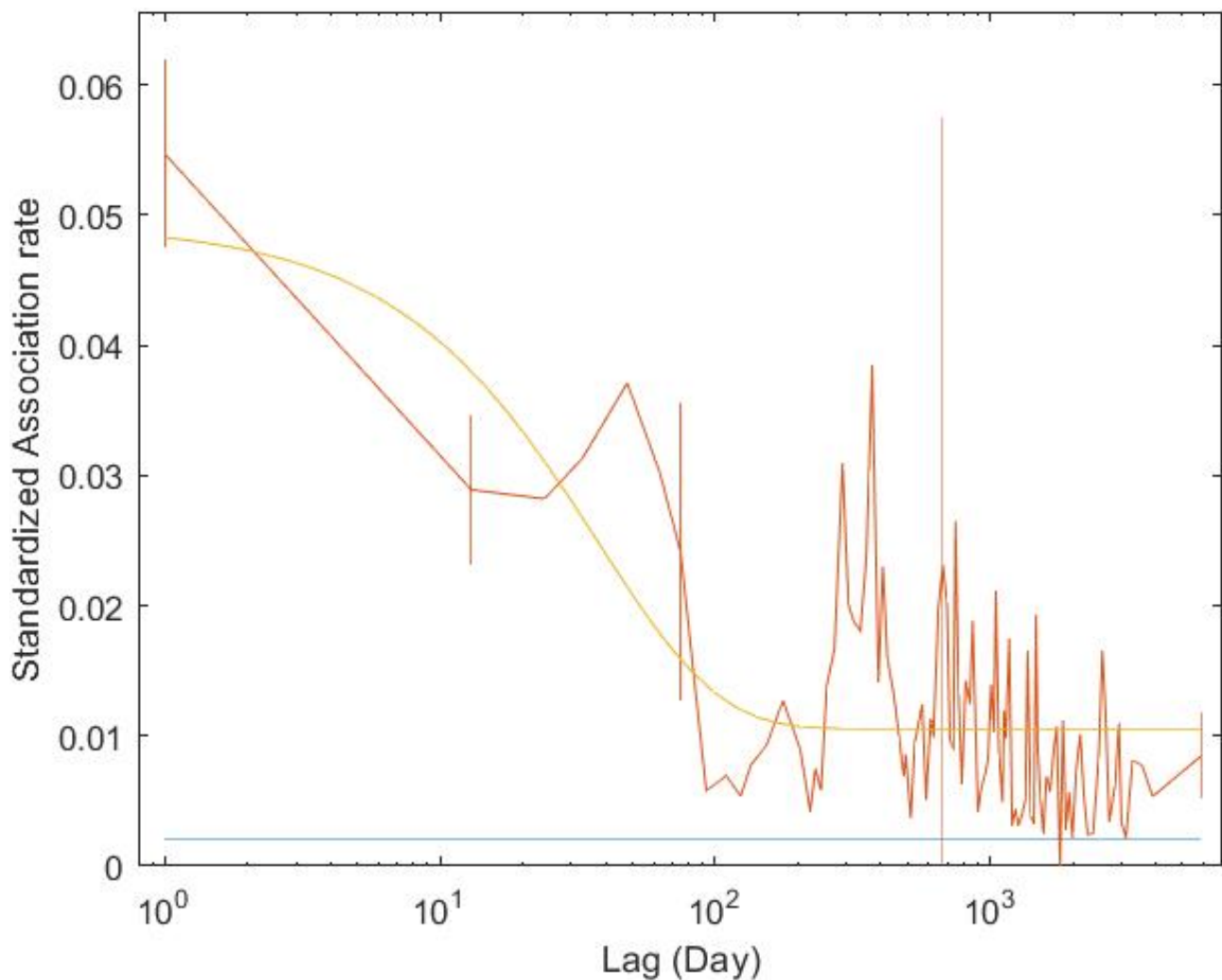
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**Figure 8:** Standardized lagged association rates (red line) for all marked bottlenose dolphins sighted within Cardigan Bay ( $n = 505$ ) with a moving average of 400 associations. Vertical bars indicate approximate standard errors calculating using the temporal jackknife method (jackknife grouping factor (in sampling units): 1, number of jackknife groupings: 1113). The best fitting model was “preferred companions and casual acquaintances”. The null association rate (orange line) is the lagged association rate expected if individuals were associating at random.

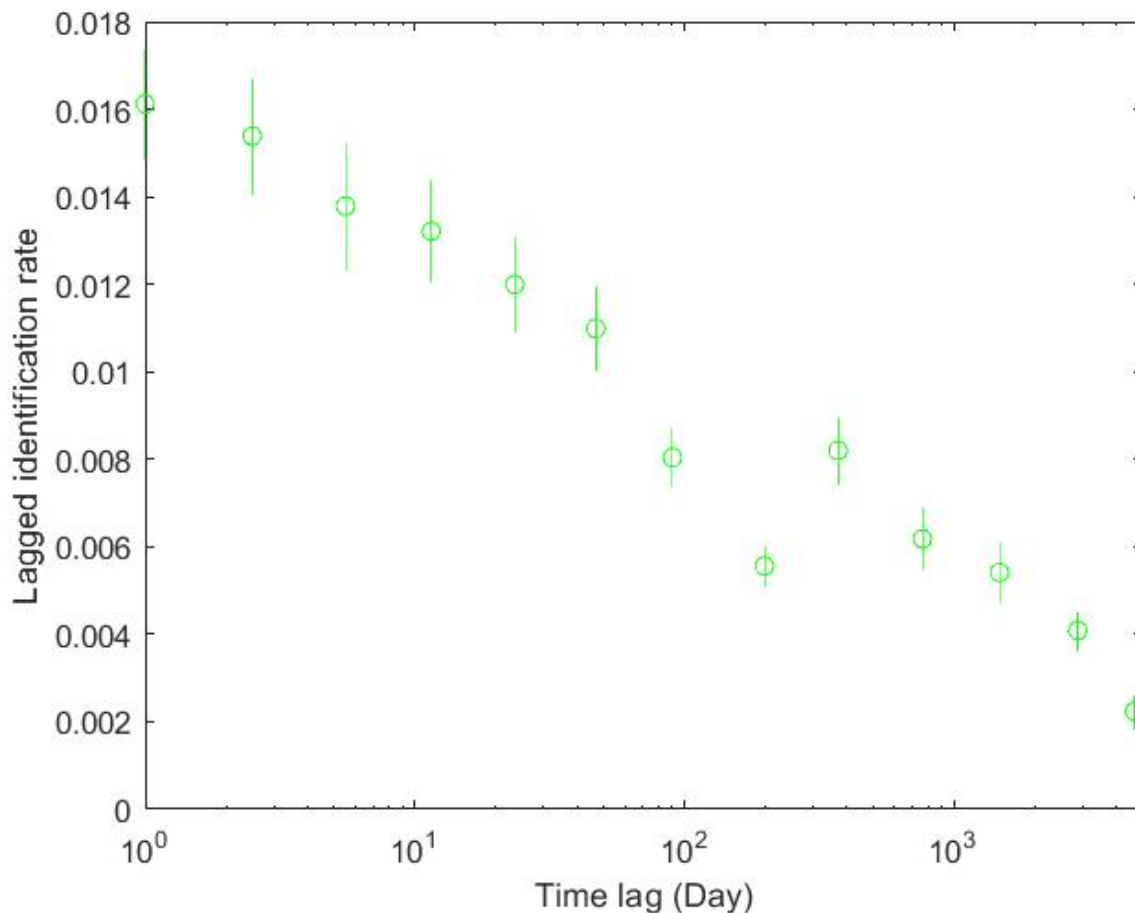
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## 613 **Movement analysis**

### 614 *Lagged identification rate*

615 As data were collected in more than one area, a movement analysis in order to analyse the movement  
 616 of individuals into and out of, and perhaps back into, the specific study areas (Table 1) were  
 617 conducted. This was examined using the ‘lagged identification rate’ (LIR). The LIR is the probability  
 618 that if an individual is identified in the area at any time, it is identified during any single identification  
 619 made in the area some time lag later (Whitehead 2001). All sampling restrictions were removed to  
 620 investigate all identified individuals. “Log x-axis” logged the x-axis (time lag) of the lagged

621 identification rate plots which was useful when considering the study's large range of time lags.  
622 10,000 bootstrap replications were used to get more precise bootstrap-estimated standard errors of  
623 the lagged identification rates, and parameter estimates for fitted models of lagged identification rates  
624 and movement parameters. Two different forms of analysis were implemented "whole study" and  
625 "among all areas". Each analysis gave a plot of lagged identification rate against time lag (in days).  
626 The "whole study" LIR analysis demonstrated the lagged identification rates for the whole study area  
627 (Figure 9). Emigration and mortality were clear within the Cardigan Bay population for the whole  
628 study area as the LIR typically fell with time lag. However, the population also exhibits cyclical  
629 movements as the LIR rose and fell with time lag (Figure 9).  
630



**Figure 9:** Lagged identification rates (LIR) against time lag (day) for individual movements of all individual bottlenose dolphins ( $n = 505$ ) within (empty circles) areas of the three study regions: A) southern Cardigan Bay ( $<52.5$  decimal degrees), B) northern Cardigan Bay ( $52.5 - 53.0$  decimal degrees), and C) north Wales/northern Irish Sea ( $>53.0$  decimal degrees). Bootstrap-estimated standard errors (bars) are calculated from 10,000 bootstrap replications.

632 The “among all areas” LIR analysis was chosen as the study area was divided into multiple areas  
633 (Table 1). Lagged identification rates were calculated and plotted for each area alone and between  
634 each pair of areas (Figure 10). Each graph visually illustrates the movement of individuals into and  
635 out of each study region, as well as the movement of individuals between each region. It demonstrates  
636 the probability that if an individual is identified within a particular study region at any time during  
637 the study period, it is identified in a later encounter either in the same area or moving between the  
638 two areas of comparison (Figure 10). The data shows that bottlenose dolphins spend time in each  
639 study region and then leave, to re-enter at a later point.

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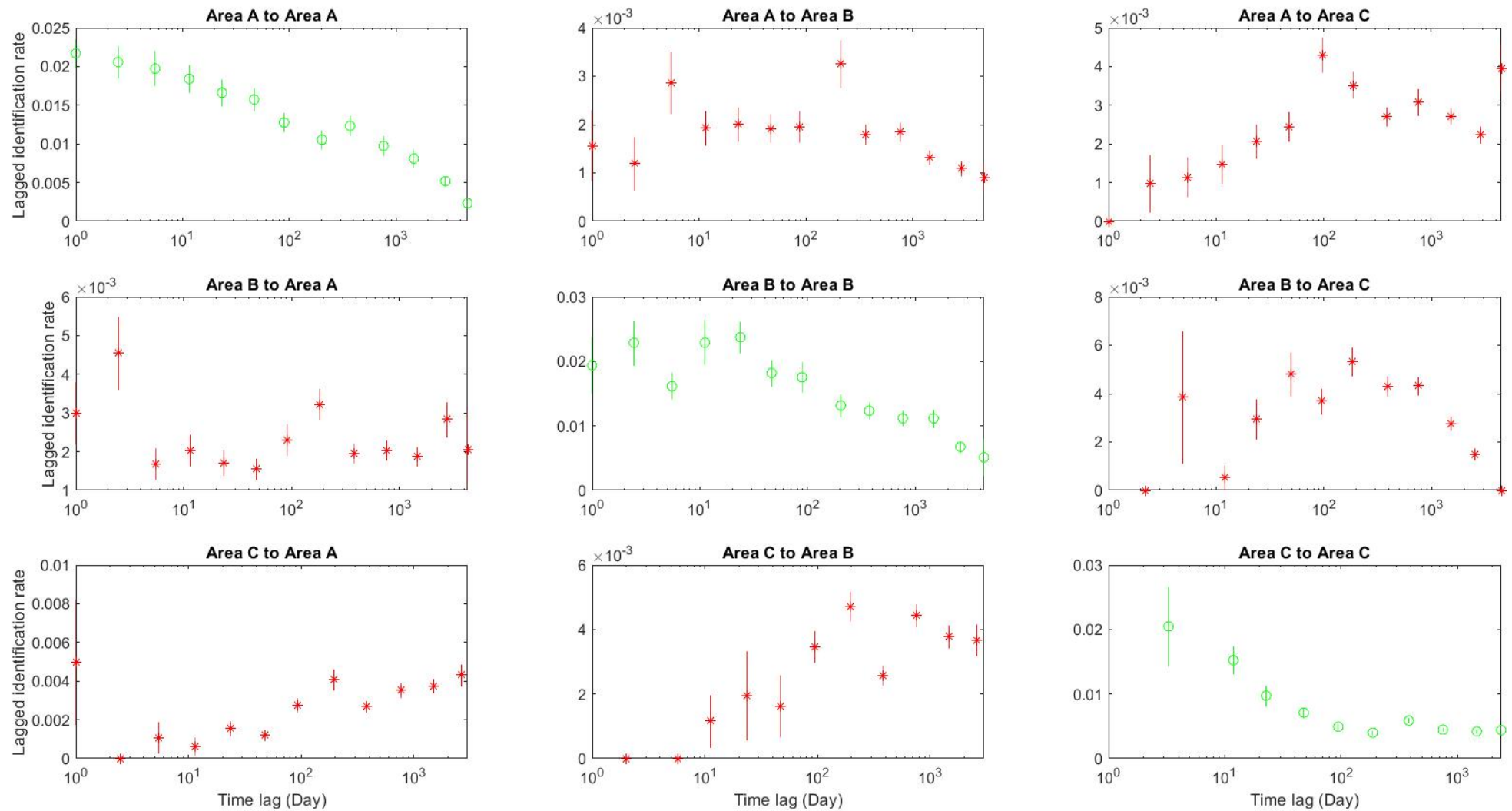
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**Figure 10:** Lagged identification rates (LIR) against time lag (day) for individual movements of all individual bottlenose dolphins ( $n = 505$ ) within (empty circles) and between (asterisks) areas of the three study regions: A) southern Cardigan Bay ( $<52.5$  decimal degrees), B) northern Cardigan Bay ( $52.5 - 53.0$  decimal degrees), and C) north Wales/northern Irish Sea ( $>53.0$  decimal degrees). Bootstrap-estimated standard errors (bars) are calculated from 10,000 bootstrap replications.



## 656 **DISCUSSION**

657 This study utilised a 17-year dataset to provide concurrent empirical evidence of how social networks  
658 and association patterns of bottlenose dolphins in Cardigan Bay have changed over time (2001-2017)  
659 due to changes in population status as well as movements between Cardigan Bay and other parts of  
660 the Irish Sea (North Wales and the Isle of Man). The present study examined differences in  
661 association strength between individuals as a result of their gender, social group, and geographical  
662 location, by applying various network analytical techniques. Whilst the power of this study is limited  
663 to resolving the social ecology of this species, partially because of the impracticalities of analysing a  
664 mobile pelagic species that moves in and out of the study area, results demonstrate that the semi-  
665 resident bottlenose dolphins live in a society governed by fission-fusion dynamics with remarkably  
666 differentiated non-random relationships consisting of intermittent short-term and preferential long-  
667 term associations. This is similar to social networks observed in several other dolphin species ranging  
668 within temperate, sub-tropical, and cold waters including from other genera such as dusky and  
669 Commerson's dolphins (Würsig and Pearson 2014; Weir *et al.*, 2018). This may indicate potential  
670 universality in the drivers of change in social patterns within networks across latitude, especially in  
671 relation to trade-offs in prey availability, group size, and predation risk (Gero *et al.*, 2005; Gowans *et*  
672 *al.*, 2007; Bertulli *et al.*, 2021).

673 The results of this comprehensive research spanning almost two decades indicated that there were  
674 numerous social groups of bottlenose dolphins, and that specific regions within the study area  
675 encompass part of their home range. In general, individuals spend the majority of their time within a  
676 particular geographic range (Table 1), and then leave, to re-enter at a later point. Individuals belonging  
677 to different social groups on average associate more with other dolphins within the same group  
678 forming long-term preferential associations (HWIG between sampling period SDo = 16.96985, CVo  
679 = 14.16834), although, interconnectivity between various groups still exists following fission-fusion  
680 dynamics. The cohesion and continuity of social bonds between individuals across the total sampling  
681 period (1106 days) is comparable to association patterns in other delphinid studies, such as Atlantic  
682 spotted dolphins (Herzing and Elliser 2013), Indo-Pacific bottlenose dolphins (Gero *et al.*, 2005),  
683 and, more recently, in white-beaked dolphins (Bertulli *et al.*, 2021), where individuals displayed  
684 consistent affiliative association preferences with others belonging to the same cluster than between  
685 clusters (Hammerschmidt and Fischer 2019)

686 Identification of central individuals within the social network, as well determining the strength of  
687 social associations within and between social groups, varied with group size. This is a particular  
688 pattern within bottlenose dolphin populations as average group size can range between 3 to >100  
689 individuals. The calculated mean group size of the Cardigan Bay network recorded in this study was

690 similar to those reported in other coastal populations of *Tursiops truncatus*. However, there is a  
691 certain level of ambiguity surrounding group classification which should be considered (Connor *et*  
692 *al.*, 2000). The average group size was comparable with group sizes for this species in the Morray  
693 Firth off the east coast of Scotland (mean = 4.50; Wilson 1995; Wilson *et al.*, 1997, 1999), along the  
694 north-eastern coast of Sardinia, Italy (mean = 4.94,  $\pm$ SD = 0.30; Díaz López 2006), and in the northern  
695 Adriatic Sea (mean = 7.40,  $\pm$ SD 0.06; Bearzi *et al.*, 1997). On the other hand, mean group sizes were  
696 larger compared to those recorded in Turneffe Atoll, Belize (mean = 3.8,  $\pm$ SD = 3.55; Campbell *et*  
697 *al.*, 2002), and near Isla del Coco, Costa Rica (mean = 3.00,  $\pm$ SD = 2.58; Acevedo-Gutiérrez and  
698 Stienessen 2004), but smaller than those estimated in the Shannon Estuary, Ireland (mean = 9.71,  
699  $\pm$ SD = 0.12; Barker and Berrow 2016). This variation in how a society is demographically structured,  
700 as a result of group size, influencing the sex ratio and spatial cohesion of social groups, determines  
701 the social organisation within a network and could therefore explain the differences in type and level  
702 of social interaction observed between individuals (Whitehead 2008a).

703 Across the literature it is considered that the risk of predation, resource availability, inter- and intra-  
704 specific competition, and areas of suitable habitat are the major factors determining grouping and  
705 therefore the type of- and strength of association associations in cetacean fission-fusion societies  
706 (Connor *et al.*, 1998; Gowans *et al.*, 2007). It is suggested that in warm waters at least, shark predation  
707 is the primary factor influencing delphinid group size (Connor *et al.*, 2000). The rate of predation is  
708 reduced by dilution and confusion tactics through synchronised swimming of grouped individuals, as  
709 well as increased vigilance amongst certain group members (Krause and Godin, 1996; Couzin *et al.*,  
710 2005). Strong associations within relatively large group sizes could therefore reflect a high predation  
711 risk, as grouping and strong social bonds can increase survival chances through enhanced predator  
712 detection, whilst allowing other individuals to reduce their own vigilance to prioritise other activities  
713 such as foraging for their survival (Wilson 2000; Davies *et al.*, 2012). However, since Cardigan Bay  
714 has no major resident bottlenose dolphin predators, previous studies have proposed the most likely  
715 factor determining group size, and consequently, association patterns and geographic range of coastal  
716 bottlenose dolphins is sources of prey, their dispersion and ecology (Pesante *et al.*, 2008a; Feingold  
717 and Evans 2014; Lohrengel *et al.*, 2017).

718 Abundance of bottlenose dolphins within Cardigan Bay increases between April and August,  
719 correlating with the seasonal appearance of migratory fish such as mackerel (*Scomber scombrus*),  
720 which may form a significant part of the population's diet at certain times of the year. In contrast,  
721 their distribution disperses over wider geographic ranges towards October as they migrate further  
722 north, occurring in significantly larger group sizes and feed on shoals of whiting (*Merlangius*  
723 *merlangius*) and herring (*Clupea harengus*) (Feingold *et al.*, 2010; Feingold and Evans, 2014). Patchy

724 or altered prey distribution is likely to dictate variations in bottlenose dolphin distribution between  
725 2001 and 2017 as well as changes in social association, which may partly explain the results of the  
726 social analysis (as well as being an important factor for their conservation). For instance, fission-  
727 fusion societies favour group formation during cooperative feeding when resources are scarce, as  
728 information transfer is better facilitated within one large well connected group in areas of patchy prey  
729 distribution (Shane *et al.*, 1986; Mann 1999; Mann *et al.*, 2000). Thus, areas of more abundant  
730 resources can result in highly clustered social networks which consist of either short-term intra-group  
731 associations, long-term preferential associations, or both. (Daura-Jorge *et al.*, 2012). Nevertheless,  
732 concluding that prey availability is a direct cause of bottlenose dolphin spatio-temporal distribution,  
733 and therefore association strength, is difficult to prove due to the realities faced in prey sampling  
734 (Mann 1999; Mann *et al.*, 2000). An alternative strategy is to relate group size and association strength  
735 to environmental factors, which in turn may determine prey distributions.

736 Recent studies conducted in Cardigan Bay used Generalised Additive Models to demonstrate how  
737 abiotic environmental variables such as bathymetry significantly influence the demographic structure  
738 of bottlenose dolphin groups over time, which could potentially explain changes in social associations  
739 (Feingold *et al.*, 2010; Lopes 2017; Nuuttila *et al.*, 2017). Bathymetry is shown to predict distribution  
740 patterns in Cardigan Bay where bottlenose dolphin presence is higher in shallow waters. Group size,  
741 however, increases with increasing distance from shore (depth). Distribution and social organisation  
742 is heavily dependent on hydrodynamic characteristics (Dinis *et al.*, 2016). Aggregations of bottlenose  
743 dolphins in Cardigan Bay are typically recorded around regions of high tidal stream energy  
744 (headlands, islands, and channels) defined by shear-lines caused by fast laminar flows and diminished  
745 eddies (Pierpoint *et al.*, 2009; Lohrengel *et al.*, 2017). Upwelling-driven nutrients (high productivity)  
746 cause dense accumulations of prey items within a concentrated area, generating an obtainable source  
747 of food for individuals or groups (Dinis *et al.*, 2016). Studies suggest differences in social  
748 organisation and association strength between shallow- and deep-water regions is a foraging strategy  
749 developed to adapt to prey distribution (La Manna *et al.*, 2016). Large deep-water groups in Cardigan  
750 Bay are observed when there are large patches of prey or during cooperative feeding. Small shallow-  
751 water groups occur prey densities are smaller as hunting alone or in limited numbers is more efficient  
752 (Cañadas and Vazquez 2017). Therefore, association strength may be influenced by the social  
753 organisation of bottlenose dolphin groups in response to prey availability. Bathymetry can be used as  
754 a proxy for prey availability and indirectly linked to spatio-temporal bottlenose dolphin distribution,  
755 thus, influencing the structure of social networks and association strength within small or large groups  
756 by determining foraging behaviour within groups of different size (Dinis *et al.*, 2016; Cañadas and  
757 Vazquez 2017).

758 The probability that two individuals are associated and will remain associated various time lags later,  
759 was relatively low for around 10 days. These patterns suggest that groups observed in Cardigan Bay  
760 are initially transient structures composed of casual acquaintances which associate for some time,  
761 then dissociate, and re-associate some time later as the standardised lagged association rate (SLAR)  
762 falls below the null association >1000 days. Subsequently, some individuals form preferred  
763 companionships in which they preferentially associate, and these are constant over time. This is best  
764 supported by the model of “preferred companions and casual acquaintances”, and loosely fits the  
765 “two levels of casual acquaintances” model. This decline in SLAR ( $\approx 850$  days) could potentially be  
766 a result of emigration and re-immigration, as some identified individuals occupy certain study areas  
767 while others sporadically transition out (Bertulli *et al.*, 2015, 2018). Long-term reassociations across  
768 the sampling period may be due to moving into seasons when prey availability is greater causing  
769 larger bottlenose dolphin aggregations, thereby reducing intraspecific competition within the large  
770 semi-resident social network (Bertulli *et al.*, 2015, 2018), although, the relatively large error bars on  
771 the SLAR should be taken into consideration. Results should be interpreted as a general trend and are  
772 not able to determine association strength and patterns for all social groups. The seasonality (largely  
773 April-October) of the data should also be considered since this likely impacts the extent of the drop  
774 between 50-100 days.

#### 775 **Potential biases, limitations, and future research**

776 There is much published literature recording the use of commercial cetacean-watching vessels,  
777 recreational watercraft, and other platforms of opportunity to facilitate research analysing cetacean  
778 association patterns to reduce expenditure (Dinis *et al.*, 2017; Baker *et al.*, 2018). However, it is  
779 acknowledged that such methods introduce their own limitations which could bias the results and  
780 interpretations. The total duration of the present study’s sampling period, as well as the size and  
781 geographic distribution of the population sampled needs to be evaluated. A potential bias was  
782 apparent in the social structure analysis by the restricted sampling area of all three regions,  
783 particularly prior to 2006 as previous years’ survey effort was largely concentrated in the Cardigan  
784 Bay SAC, considering the wider geographic distribution of bottlenose dolphins. In relation to this  
785 bias, the social network assessed in the present study relates to the photo-identified individuals where  
786 survey effort was conducted and does not strictly apply to the entire population of bottlenose dolphins  
787 in Welsh waters. The disparate coverage of the survey area could potentially be a reason for the  
788 relatively few bottlenose dolphins associating  $\geq 5$  times around North Wales and in the northern Irish  
789 Sea ( $>53.0^{\circ}$  N) where much less time was spent undertaking surveys.

790 Regarding the analysis of social structure, other factors such as seasonality, irregular photo-  
791 identification of social groups, variable behaviour of identified individuals or response to watercraft,

792 and social geography could also negatively bias results. This study relied on observational effort and  
793 sighting data in which collection in Cardigan Bay has been concentrated in the summer months  
794 (April-October), due to environmental factors such as sea states higher than Beaufort Scale 3 in winter  
795 months resulting in unsuitable survey conditions as well as low availability of survey vessels in  
796 Cardigan Bay during winter. Consequently, the ability to interpret complete annual cycles of social  
797 dynamics has been limited (Hobson *et al.*, 2013; Davis *et al.*, 2018). Occasionally, some individuals  
798 within an encounter were not identified due to a lack of reliable dorsal fin markings, challenges of  
799 accurately calculating group size in the field, and avoidance behaviour in the presence of vessels.  
800 Group size and association indices of the social network could on occasions be higher than those  
801 calculated in this study.

802 Movement within and between the three study areas indicates how the development of associations  
803 and association strength within each region could be influenced by hydrodynamic characteristics and  
804 geographical topography of each location, as well as partial spatial segregation. More detailed  
805 research comparing the frequency of bottlenose dolphin encounters to surrounding environmental  
806 conditions such as bathymetry, productivity, and water temperature could be conducted to investigate  
807 bottlenose dolphin habitat use, movement, and ultimately social patterns. Additionally, identification  
808 of prey species and their movements could be key to correlating dolphin spatio-temporal distribution  
809 and centres of activity, both of which have been discussed previously. An examination of mother-  
810 calf sighting data could also reveal different patterns in social network dynamics.

811

## 812 **CONCLUSIONS**

813 In this first study to analyse one of the largest UK bottlenose dolphin social structure dataset collected  
814 over almost two decades, the data collected in Cardigan Bay forms a good archetype analysing how  
815 association strength and patterns within a social network have changed over time due to sex, social  
816 group, and movement of individuals between Cardigan Bay and other parts of the Irish Sea (North  
817 Wales and the Isle of Man). The results have shown that the Cardigan Bay dolphin population lives  
818 in a society governed by fission-fusion dynamics with separated social groups in which association  
819 is non-random, as individuals express preferential association. Initially, short-term intra-group  
820 associations were generally random before developing preferential long-term social bonds which are  
821 constant over time. Most bottlenose dolphin associations were between pairs of individuals which  
822 preferentially associate long-term, and between pairs of individuals who associate for some time, then  
823 dissociate, but may re-associate some time later. The present study demonstrates that long-term  
824 associations are more favored over non-permanent companionships. These social patterns are similar

825 to that of many pelagic delphinids from temperate to tropical waters. This represents a good start in  
826 understanding population structure and identifying drivers of change in social networks of bottlenose  
827 dolphins in the region. To allow a more comprehensive view of differences in association patterns  
828 and how those patterns have changed over time within social networks, incorporation of techniques  
829 that evaluate several parameters (such as environmental and physical factors) may advance our  
830 knowledge towards a more complete picture of bottlenose dolphin social interactions and variable  
831 environment. Establishing kinship, sex ratio, and diet could also progress our understanding of the  
832 parameters determining bottlenose dolphin social structure. Such an approach may also be beneficial  
833 in devising management strategies contributing towards the conservation of this species and other  
834 small cetaceans.

835

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## REFERENCES

- 855 Acevedo-Gutiérrez, A. and Stienessen, S.C., (2004). Bottlenose dolphins (*Tursiops truncatus*)  
856 increase number of whistles when feeding. *Aquatic Mammals*, 30(3), pp.357-362.
- 857 Aureli, F., Schaffner, C.M., Boesch, C., Bearder, S.K., Call, J., Chapman, C.A., Connor, R., Fiore,  
858 A.D., Dunbar, R.I., Henzi, S.P. and Holekamp, K., (2008). Fission-fusion dynamics: new research  
859 frameworks. *Current Anthropology*, 49(4), pp.627-654.
- 860 Baker I, O'Brien J, McHugh K, Ingram SN, Berrow B., (2018). Bottlenose dolphin (*Tursiops*  
861 *truncatus*) social structure in the Shannon Estuary, Ireland, is distinguished by age- and area-related  
862 associations. *Marine Mammal Science* 34, 458–47.
- 863 Barker, J. and Berrow, S., (2016) January. Temporal and spatial variation in group size of bottlenose  
864 dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland. In *Biology and Environment:*  
865 *Proceedings of the Royal Irish Academy* (Vol. 116, No. 1, pp. 63-70). Royal Irish Academy.
- 866 Barne, J.H. ed., (1995). *Coasts and Seas of the United Kingdom: Region 12 Wales; Margam to Little*  
867 *Orme*. Joint Nature Conservation Committee.
- 868 Barnes, C., (2010). Social structure of bottlenose dolphins (*Tursiops truncatus*) in Cardigan Bay,  
869 Wales. Report Stage. 47p. University College Cork, Corcaigh, Ireland. doi: [http://dx. doi.](http://dx.doi.org/10.1016/j.hal.1)  
870 [org/10.1016/j. hal, 1.](http://dx.doi.org/10.1016/j.hal.1)
- 871 Bearzi, G., Notarbartolo- DI- Sciara, G. and Politi, E., (1997). Social ecology of bottlenose dolphins  
872 in the Kvarnerić (northern Adriatic Sea). *Marine mammal science*, 13(4), pp.650-668.
- 873 Bearzi, M., Rapoport, S., Chau, J. and Saylan, C., (2009). Skin lesions and physical deformities of  
874 coastal and offshore common bottlenose dolphins (*Tursiops truncatus*) in Santa Monica Bay and  
875 adjacent areas, California. *Ambio*, pp.66-71.
- 876 Bertulli CG, Tetley MJ, Magnúsdóttir EE, Rasmussen MH., (2015). Observations of movement and  
877 site fidelity of white-beaked dolphins (*Lagenorhynchus albirostris*) in Icelandic coastal waters using  
878 photo-identification. *Journal of Cetacean and Research Management* 15, 27–34.
- 879 Bertulli CG, Guéry L, McGinty N et al., (2018). Capture-recapture abundance and survival estimates  
880 of three cetacean species in Icelandic coastal waters using trained scientist-volunteers. *Journal of Sea*  
881 *Research* 131, 22–31.
- 882 Bertulli, C.G., Rasmussen, M.H. and Rosso, M., (2021). Fission–fusion dynamics of a pelagic  
883 delphinid in the arctic: the white- beaked dolphin (*Lagenorhynchus albirostris*). *Integrative Zoology*.

884 Blasi MF, Boitani L., (2014). Complex social structure of an endangered population of bottlenose  
885 dolphins (*Tursiops truncatus*) in the Aeolian Archipelago (Italy). PLoS ONE 9, e114849.

886 Campbell, G.S., Bilgre, B.A. and Defran, R.H., (2002). Bottlenose dolphins (*Tursiops truncatus*) in  
887 Tuneffe Atoll, Belize: occurrence, site fidelity, group size, and abundance. *Aquatic Mammals*, 28(2),  
888 pp.170-180.

889 Cañadas, A., and Vázquez, J.A., (2017). Common dolphins in the Alboran Sea: Facing a reduction in  
890 their suitable habitat due to an increase in Sea surface temperature. *Deep Sea Research Part II: Topical*  
891 *Studies in Oceanography*, 141, 306–318.

892 Ceredigion County Council; the Countryside Council for Wales; Environment Agency Wales; North  
893 Western and North Wales Sea Fisheries Committee; Pembrokeshire Coast National Park Authority;  
894 Pembrokeshire County Council; D'r Cymru Welsh Water (2001) “Cardigan Bay Special Area of  
895 Conservation Management Plan”, 190p.

896 Connor RC, Wells RS, Mann J, Read AJ., (2000). The bottlenose dolphin: Social relationships in a  
897 fission–fusion society. In: Mann J, Connor RC, Tyack PL, Whitehead H, eds. *Cetacean Societies*.  
898 University of Chicago Press, Chicago, USA, pp. 91–126.

899 Connor RC, Mann J, Tyack PL, Whitehead H., (1998). Social evolution in toothed whales. *Trends in*  
900 *Ecology and Evolution* 13, 228–32.

901 Connor RC., (2000). Group living in whales and dolphins. In: Mann J, Connor RC, Tyack PL,  
902 Whitehead H, eds. *Cetacean Societies: Field Studies of Dolphins and Whales*. University of Chicago  
903 Press, Chicago, USA, pp. 199–218.

904 Connor, R.C., (2007). Dolphin social intelligence: complex alliance relationships in bottlenose  
905 dolphins and a consideration of selective environments for extreme brain size evolution in mammals.  
906 *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 362(1480),  
907 pp.587–602.

908 Connor, R.C., Heithaus, M.R. and Barre, L.M., (1999). Superalliance of bottlenose dolphins. *Nature*,  
909 397: 571–572.

910 Couzin, I.D., Krause, J., Franks, N.R. and Levin, S.A., (2005). Effective leadership and decision-  
911 making in animal groups on the move. *Nature*, 433(7025), pp.513-516.

912 Croft, D.P., James, R. and Krause, J., (2008). *Exploring animal social networks*. Princeton University  
913 Press.



914 Croft, D.P., Madden, J.R., Franks, D.W. and James, R., (2011). Hypothesis testing in animal social  
915 networks. *Trends in ecology & evolution*, 26(10), pp.502-507.

916 Daura-Jorge, F.G., Cantor, M., Ingram, S.N., Lusseau, D. and Simões-Lopes, P.C., (2012). The  
917 structure of a bottlenose dolphin society is coupled to a unique foraging cooperation with artisanal  
918 fishermen. *Biology Letters*, 8(5), pp.702-705.

919 Davies. N. B., Krebs. J. R and West. S. A., (2012). *An Introduction to Behavioural Ecology*. Oxford:  
920 Wiley. J and Sons.

921 Davis, G.H., Crofoot, M.C. and Farine, D.R., (2018). Estimating the robustness and uncertainty of  
922 animal social networks using different observational methods. *Animal Behaviour*, 141, pp.29-44.

923 Denkinger J, Alarcon D, Espinosa B et al., (2020). Social structure of killer whales (*Orcinus orca*) in  
924 a variable low-latitude environment, the Galápagos Archipelago. *Marine Mammal Science* 36, 1–12.

925 Díaz López, B., (2006). Interactions between Mediterranean bottlenose dolphins (*Tursiops truncatus*)  
926 and gillnets off Sardinia, Italy. *ICES Journal of Marine Science*, 63(5), pp.946-951.

927 Dinis A, Alves F, Nicolau C et al., (2017). Social structure of a population of bottlenose dolphins  
928 (*Tursiops truncatus*) in the oceanic archipelago of Madeira, Portugal. *Journal of the Marine Biological*  
929 *Association of the United Kingdom* 98, 1141–9.

930 Dinis, A., Carvalho, A., Alves, F., Nicolau, C., Ribeiro, C., Kaufmann, M., Cañadas, A. and Freitas,  
931 L., (2016). Spatial and temporal distribution of bottlenose dolphins, *Tursiops truncatus*, in the  
932 Madeira archipelago, NE Atlantic. *Arquipélago-Life and Marine Sciences*, 33, 45-54.

933 Evans, C.D.R. (1995). Offshore Environment. In Barne, J.H., Robson, C.F., Grellier, K., Arnold, H.,  
934 Thompson, P., Wilson, B., Management Recommendations for the Cardigan Bay Bottlenose Dolphin  
935 Population. A report to the Countryside Council for Wales by University of Aberdeen, Dept. of  
936 Zoology, Cromarty. Contract Science Report 134, 68p.

937 Farine, D.R. and Whitehead, H., (2015). Constructing, conducting and interpreting animal social  
938 network analysis. *Journal of animal ecology*, 84(5), pp.1144-1163.

939 Feingold, D. and Evans, P.G., (2014). Connectivity of Bottlenose Dolphins in Welsh Waters: North  
940 Wales Photo-Monitoring Report. Natural Resources Wales Research Report.

941 Feingold, D., Vestey, C., Pesante, G. and Evans, P.G., (2010). Relationship between the bottlenose  
942 dolphin (*Tursiops truncatus*) population and ecological factors in Cardigan Bay, Wales. In Poster at  
943 the 24th Annual Conference of the European Cetacean Society, Stralsund, Germany.

944 Fortuna, C.M., (2007). Ecology and conservation of bottlenose dolphins (*Tursiops truncatus*) in the  
945 north-eastern Adriatic Sea (Doctoral dissertation, University of St Andrews).

946 Gero, S., Bejder, L., Whitehead, H., Mann, J. and Connor, R.C., (2005). Behaviourally specific  
947 preferred associations in bottlenose dolphins, *Tursiops* spp. *Canadian Journal of Zoology*, 83(12),  
948 pp.1566-1573.

949 Girvan, M. and Newman, M.E., (2002). Community structure in social and biological  
950 networks. *Proceedings of the national academy of sciences*, 99(12), pp.7821-7826.

951 Godde S, Humbert L, Côté SD, Réale D, Whitehead H (2013). Correcting for the impact of  
952 gregariousness in social network analyses. *Animal Behavior* 85, 553–8.

953 Gowans S, Whitehead H (2001). Photographic identification of northern bottlenose whales  
954 (*Hyperoodon ampullatus*): Sources of heterogeneity from natural marks. *Marine Mammal Science*  
955 17, 76–93.

956 Gowans S, Würsig B, Karczmarski L (2007). The social structure and strategies of delphinids:  
957 predictions based on an ecological framework. In: David WS, ed. *Advances in Marine Biology*.  
958 Academic Press, San Diego, CA, pp. 195–294.

959 Gowans, S., H. Whitehead, J. K. Arch and S. K. Hooker. (2000). Population size and residency  
960 patterns of northern bottlenose whales (*Hyperoodon ampullatus*) using the Gully, Nova Scotia.  
961 *Journal of Cetacean Research and Management* 2:201-210.

962 Hamilton, W.D., (1964). The genetical evolution of social behaviour. II. *Journal of theoretical*  
963 *biology*, 7(1), pp.17-52.

964 Hammerschmidt, K. and Fischer, J., (2019). Baboon vocal repertoires and the evolution of primate  
965 vocal diversity. *Journal of human evolution*, 126, pp.1-13.

966 Herzing, D.L. and Elliser, C.R., (2013). Directionality of sexual activities during mixed-species  
967 encounters between Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops*  
968 *truncatus*). *International Journal of Comparative Psychology*, 26(2).

969 Hobson, E.A., Avery, M.L. and Wright, T.F., (2013). An analytical framework for quantifying and  
970 testing patterns of temporal dynamics in social networks. *Animal Behaviour*, 85(1), pp.83-96.

971 Klaich, M.J., Kinas, P.G., Pedraza, S.N., Coscarella, M.A. and Crespo, E.A., (2011). Estimating dyad  
972 association probability under imperfect and heterogeneous detection. *Ecological Modelling*, 222(15),  
973 pp.2642-2650.

974 Krause, J. and Godin, J.G.J., (1995). Predator preferences for attacking particular prey group sizes:  
975 consequences for predator hunting success and prey predation risk. *Animal Behaviour*, 50(2), pp.465-  
976 473.

977 Krause, J., Croft, D.P. and James, R., (2007). Social network theory in the behavioural sciences:  
978 potential applications. *Behavioral Ecology and Sociobiology*, 62(1), pp.15-27.

979 Krützen, M., Sherwin, W.B., Connor, R.C., Barré, L.M., Van de Castele, T., Mann, J. and Brooks,  
980 R., (2003). Contrasting relatedness patterns in bottlenose dolphins (*Tursiops* sp.) with different  
981 alliance strategies. *Proceedings of the Royal Society of London. Series B: Biological*  
982 *Sciences*, 270(1514), pp.497-502.

983 La Manna, G., Ronchetti, F., and Sara, G. (2016). Predicting common bottlenose dolphin habitat  
984 preference to dynamically adapt management measures from a Marine Spatial Planning perspective.  
985 *Ocean & Coastal Management*, 130, 317-327.

986 Lohrengel, K., Evans, P.G., Lindenbaum, C.P., Morris, C.W. and Stringell, T.B., (2017). Bottlenose  
987 dolphin and harbour porpoise monitoring in Cardigan Bay and Pen Llŷn a'r Sarnau Special Areas of  
988 Conservation, 2014–16. NRW Evidence Report, (191).

989 Lopes, K., (2017). Habitat Preference of Bottlenose Dolphin (*Tursiops truncatus*) in Cardigan  
990 Bay (Doctoral dissertation, MSc thesis, Bangor University. 54pp).

991 Lusseau D, Schneider L, Boisseau OJ, Haase P, Slooten E, Dawson SM (2003). The bottlenose  
992 dolphin community of Doubtful Sound features a large proportion of long-lasting associations.  
993 *Behavioral Ecology and Sociobiology* 54, 396–405.

994 Lusseau, D., Wilson. B., Hammond. P., Grellier. K., Durban. J. W., Parsons. K. M., Baron. T. R., and  
995 Thompson. P. M., (2006). Quantifying the influence of sociality on population structure in bottlenose  
996 dolphins. *Journal of Animal Ecology*, 75(1), pp.14–24.

997 Magileviciute, E., Pesante, G. and Evans, P.G.H., (2007). Social networks of bottlenose dolphins  
998 *Tursiops truncatus* in Cardigan Bay, Wales (Doctoral dissertation, University of Wales Bangor).

999 Mann, J., Connor, R.C., Tyack, P.L. and Whitehead, H. eds., (2000). *Cetacean societies: field studies*  
1000 *of dolphins and whales*. University of Chicago Press.

1001 Mann, J., (1999). Behavioral sampling methods for cetaceans: a review and critique. *Marine mammal*  
1002 *science*, 15(1), pp.102-122.

1003 Mantel N (1967). The detection of disease clustering and a generalized regression approach. *Cancer*  
1004 *Research* 27, 209–20.

1005 Möller, L.M. and Beheregaray, L.B., (2004). Genetic evidence for sex- biased dispersal in resident  
1006 bottlenose dolphins (*Tursiops aduncus*). *Molecular Ecology*, 13(6), pp.1607-1612.

1007 Möller, L.M., Beheregaray, L.B., Allen, S.J. and Harcourt, R.G., (2006). Association patterns and  
1008 kinship in female Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia.  
1009 *Behavioral Ecology and Sociobiology*, 61(1), pp.109-117.

1010 Newman, M. E. J., (2004). Analysis of weighted networks. *Physical Review E* 70:056131.

1011 Newman, M. E. J., (2006). Modularity and community structure in networks. *Proceedings of the*  
1012 *National Academy of Sciences of the United States of America* 103:8577-8582.

1013 Newman, M.E. and Girvan, M., (2004). Finding and evaluating community structure in  
1014 networks. *Physical review E*, 69(2), p.026113.

1015 Nuuttila, H.K., Courtene-Jones, W., Baulch, S., Simon, M. and Evans, P.G., (2017). Don't forget the  
1016 porpoise: acoustic monitoring reveals fine scale temporal variation between bottlenose dolphin and  
1017 harbour porpoise in Cardigan Bay SAC. *Marine biology*, 164(3), p.50.

1018 Pearson HC, Markowitz TM, Weir JS, Würsig B (2017). Dusky dolphin (*Lagenorhynchus obscurus*)  
1019 social structure characterized by social fluidity and preferred companions. *Marine Mammal Science*  
1020 33, 251– 76.

1021 Pesante, G., Evans, P.G.H., Baines, M.E. and McMath, M. (2008b) Abundance and Life History  
1022 Parameters of Bottlenose Dolphin in Cardigan Bay: Monitoring 2005-2007. CCW Marine Monitoring  
1023 Report No. 61: pp.1-75

1024 Pesante. G., Evans, P.G.H., Anderwald, P., Powell, D. and McMath, M. (2008a) Connectivity of  
1025 bottlenose dolphins in Wales: North Wales photo-monitoring. CCW Marine Monitoring Report No.  
1026 62: pp.1-42

1027 Pierpoint, C., Allan, L., Arnold, H., Evans, P., Perry, S., Wilberforce, L. and Baxter, J., (2009).  
1028 Monitoring important coastal sites for bottlenose dolphin in Cardigan Bay, UK. *Journal of the Marine*  
1029 *Biological Association of the United Kingdom*, 89(5), pp.1033-1043.

1030 Rendell L, Cantor M, Gero S, Whitehead H, Mann J., (2019). Causes and consequences of female  
1031 centrality in cetacean societies. *Philosophical Transactions of the Royal Society B* 374, 20180066.

1032 Schnell, G. D., D. J. Watt and M. E. Douglas., (1985). Statistical comparison of proximity matrices:  
1033 applications in animal behaviour. *Animal Behaviour* 33:239-253.

- 1034 Shane, S.H., Wells, R.S. and Würsig, B., (1986). Ecology, behavior and social organization of the  
1035 bottlenose dolphin: a review. *Marine Mammal Science*, 2(1), pp.34-63.
- 1036 Sih, A., Hanser, S.F. and McHugh, K.A., (2009). Social network theory: new insights and issues for  
1037 behavioral ecologists. *Behavioral Ecology and Sociobiology*, 63(7), pp.975-988.
- 1038 Silk J.B., (2007). The adaptive value of sociality in mammalian groups. *Philosophical Transactions*  
1039 *of the Royal Society of London B: Biological Sciences* 362, 539–59.
- 1040 Sim, T., (2015). Associations or alliances? Comparisons of social relationships between male  
1041 bottlenose dolphins (*Tursiops truncatus*) in Cardigan Bay and the Moray Firth.
- 1042 Vergara-Peña, A., (2020). Effects of marine recreation on bottlenose dolphins in Cardigan Bay.  
1043 Bangor University (United Kingdom).
- 1044 Weir, J.S., Fiori, L., Orbach, D.N., Piwetz, S., Protheroe, C. and Würsig, B., (2018). Dusky dolphin  
1045 (*Lagenorhynchus obscurus*) Mother–calf pairs: An aerial perspective. *Aquatic Mammals*, 44(6),  
1046 p.603.
- 1047 Wells, R. S., Scott, M. D., Irvine, A. B., (1987). The social structure of free-ranging bottlenose  
1048 dolphins. In Genoways, H.H. (ed). *Current Mammalogy*, Vol. 1. pp. 247 – 305. Plenum Press, New  
1049 York.
- 1050 Wells, R.S., (1991). The role of long-term study in understanding the social structure of bottlenose  
1051 dolphin community. In Pryor, K., Norris, K.S. (eds) *Dolphin Societies: Discoveries and Puzzles*. pp.  
1052 199-225. University California Press. Oxford
- 1053 Whitehead H, Dufault S., (1999). Techniques for analysing vertebrate social structure using identified  
1054 individuals: review and recommendations. *Advances in the Study of Behavior* 28, 33–74.
- 1055 Whitehead H., (1995). Investigating structure and temporal scale in social organization using  
1056 identified individuals. *Behavioral Ecology* 6, 199–2
- 1057 Whitehead, H., (2001). Analysis of animal movement using opportunistic individual-identifications:  
1058 application to sperm whales. *Ecology* 82:1417-1432.
- 1059 Whitehead H., (2008a). *Analyzing Animal Societies: Quantitative Methods for Vertebrate Social*  
1060 *Analysis*. The University of Chicago Press, Chicago, IL.
- 1061 Whitehead H., (2008b). Precision and power in the analysis of social structure using associations.  
1062 *Animal Behavior* 75, 1093–9.

1063 Whitehead H., (2009). SOCPROG programs: Analyzing animal social structures. *Behavioral Ecology*  
1064 *and Sociobiology* 63, 765–78

1065 Whitehead, H., (2015). SOCPROG: Programs for analyzing social structure. Nova Scotia, Canada:  
1066 Dalhousie University.

1067 Whitehead H., (2019). SOCPROG: Programmes for analysing social structure. Nova Scotia, Canada:  
1068 Dalhousie University.

1069 Wilson, B. Hammond, P. and Thompson, P., (1999) Estimating Size and Assessing Trends in Coastal  
1070 Bottlenose Dolphin Population. *Ecological Applications*, 9 (1), 288300

1071 Wilson, B., (1995) The ecology of bottlenose dolphins in the Moray Firth, Scotland: a population at  
1072 the northern extreme of the species' range. PhD thesis, University of Aberdeen

1073 Wilson, B., Grellier, K., Hammond, P.S., Brown, G. and Thompson, P.M., (2000). Changing  
1074 occurrence of epidermal lesions in wild bottlenose dolphins. *Marine Ecology Progress Series*, 205,  
1075 pp.283-290.

1076 Wilson, B., Thompson, P.M., and Hammond, P.S., (1997). Habitat use by bottlenose dolphins:  
1077 seasonal distribution and stratified movement patterns in the Moray Firth Scotland. *The Journal of*  
1078 *Applied Ecology*, 34,1365–1374.

1079 Wilson, E.O., (2000). *Sociobiology: the new synthesis*. Harvard University Press.

1080 Wiszniewski, J., Allen, S.J. and Möller, L.M., (2009). Social cohesion in a hierarchically structured  
1081 embayment population of Indo-Pacific bottlenose dolphins. *Animal Behaviour*, 77(6), pp.1449-1457.

1082 Wursig, B. and Jefferson, T. A., (1990). Methods of photo-identification for small cetaceans. In: P.  
1083 S. Hammond, S. A. Mizroch, and G. P. Donovan, eds. *Individual Recognition of Cetaceans: Use of*  
1084 *Photo-identification and other Techniques to Estimate Population Parameters*. Report of the  
1085 International Whaling Commission. Special Issue, 12, pp.43-52.

1086 Würsig, B. and Pearson, H.C., (2014). Dusky dolphins: flexibility in foraging and social strategies.  
1087 In *Primates and Cetaceans* (pp. 25-42). Springer, Tokyo.