

Anthropogenic injuries disrupt social associations of common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida

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Abstract

Social connectivity is important for measuring the fitness of common bottlenose dolphins (*Tursiops truncatus*). While interactions in fission-fusion societies vary between individuals, studies show that repeated interactions enhance reproduction and foraging success. Injuries that potentially remove an individual from its association network may disrupt these interactions. Using data from the long-term resident dolphin community in Sarasota Bay, Florida, we investigated how anthropogenic injuries affect the dolphins' social associations by examining the differences before and after injury to individuals. We examined group size, strength, eigenvector centrality, clustering coefficient, and number of triangles and analyzed whether the animal's sex, age class, type of injury, or human intervention affected these values. We found that while group size did not change, injured dolphins had fewer preferred associates ($HWI > 0.14$) and were found in more fluid groups immediately after injury, but started returning to normal association levels after 2 years. This initial decrease in connectivity was not related to the age, sex, type of injury, or intervention. Despite the fluidity in individual associations, the strongest bonds remained stable, those between mothers and calves and those between male alliance partners. These findings

provide some of the first information relating injuries and social networks for animals.

KEYWORDS

anthropogenic impact, association, bottlenose dolphin, human intervention, injury, social network, *Tursiops*

1 | INTRODUCTION

Common bottlenose dolphins (*Tursiops truncatus*) in bay, sound, and estuary waters live in complex fission-fusion societies where social interactions and relationships between different individuals within that society contribute to their overall survival (Lusseau et al., 2006). Groups merge and split over time, making group composition and individual associations a dynamic property (Couzin, 2006). Yet, within these fluctuating larger networks in the community, dolphins in Sarasota Bay form more stable social units that vary with the individual's home range pattern, foraging needs, life stage, and sex (Wells, 2003; Wells, Irvine, & Scott, 1980). Adult males form long-term alliance pairs that move between adult female groups, both within and beyond the community (Wells, 2014). Juveniles often associate in fluid mixed-sex groups (Wells, 2014). Adult females maintain close associations with their most recent calves for their first 3–6 years, and tend to associate in larger nursery groups comprised of females of similar reproductive status (Irvine et al., 1981; Wells, 2003).

Reasons why common bottlenose dolphins (hereafter bottlenose dolphins) form these specific, and often long-term, relationships in a fluid fission-fusion society are varied. Gowans, Würsig, and Karczmarski (2007) suggest that potential benefits to group living for delphinids include reduced predation, increased foraging efficiency, enhanced defense of resources, increased reproductive success, and the possibility of social learning. When an animal shows a preference to associate, the cost–benefit ratio depends on its sex, reproductive state, and ecology (Gowans et al., 2007). The net benefits of close association with conspecifics must outweigh the costs (Silk, 2007). For example, while both paired and unpaired male bottlenose dolphins successfully sire calves, Wells (2003) found that males in Sarasota Bay with alliance partners sire proportionately more calves than solitary males. Seemingly, females of similar reproductive age will associate with one another to increase their reproductive success by forming a larger defense against predation and by learning from more experienced females (Wells, 2003).

Because these repeated associations are important factors for survival, events that separate the animal from its network of associates, such as an injury, pose a risk to the well-being of the animal. Close interactions with humans in the Sarasota Bay area put dolphins at risk of injuries from boat strikes and entanglements in fishing gear (Christiansen et al., 2016). Boat strikes and fishing gear injuries can harm an individual due to lacerations, loss of appendages, loss of mobility, interference with foraging, internal injuries, etc. (Wells et al., 2008). Previous studies show that boats can affect dolphin behavior, specifically by causing changes in dive length (Evans et al. 1992; Nowacek, Wells, & Solow, 2001), foraging habitat selection (Allen & Read, 2000), whistling patterns (Buckstaff, 2004), and surfacing patterns (Janik & Thompson, 1996). We hypothesize that injuries caused by boats and other anthropogenic means can also disrupt an individual's interactions with other dolphins.

Dolphin fission-fusion societies are predominantly comprised of short-term casual acquaintances lasting up to only a few days, with a smaller number of associations lasting for years (Lusseau et al., 2006). These transitory associations often make it difficult to understand the relationships between individuals because individuals may only associate a handful of times in a given year. Applying social network analysis allows for a more complete picture of how an animal fits into a dynamic community (Rubenstein, 2015). We examine several network metrics (strength, eigenvector centrality, clustering coefficient, and the number of triangles) to quantify the extent to which anthropogenic injuries impact the social connectivity of bottlenose dolphins. We evaluate whether the sex and age class of the injured animal, the type of injury, and presence of human intervention are related to features of the individual's

direct association network. Given that injuries are known to impact the overall fitness and behavior of bottlenose dolphins along the west coast of Florida (Wells et al., 2008), we hypothesized that animals suffering from injury will have fewer associates compared to noninjured animals and will exhibit lower network connectivity and greater solitary behavior (Janik & Thompson, 1996; Nowacek et al., 2001; Powell & Wells, 2011).

2 | METHODS

2.1 | Study site and population

The Sarasota Bay region of the central west coast of Florida encompasses Sarasota and Manatee counties (Figure 1) and is home to a well-known long-term resident dolphin community (McHugh, Allen, Barleycorn, & Wells, 2011). The Sarasota Dolphin Research Program has studied this community since 1970, documenting characteristics and life-history patterns of individual resident animals through photo-identification and temporary capture-release efforts (Wells, 2009, 2014). Current estimates indicate that there are about 170 known dolphins spanning up to as many as five concurrent generations living within a 125 km² home range from southern Tampa Bay to Venice Inlet (McHugh et al., 2011; Wells, 2003; Tyson & Wells, 2016). Based on longitudinal observations and periodic health assessments, 96% of the dolphins residing in Sarasota Bay and nearby waters are easily identifiable and over 90% of the resident dolphins are of known age and sex, as well as maternal lineage, paternal lineage, or a combination of the two (Christiansen et al., 2016; Wells, 2003, 2009). Ages of animals were determined by long-term sighting histories of individuals known since birth or from examining growth layers in dolphin teeth extracted under local anesthesia during dolphin health assessments (Wells, 2009). Sex was determined either by direct observation of the genital region, genetics, or for some females, repeated sightings with a dependent calf (Wells, 2009). Calves were defined as individuals still associated with their mothers (mother-calf HWI > 0.5; Gibson and Mann, 2008; Mann, Connor, Barre, & Heithus, 2000). Juveniles were defined as socially independent, postweaning individuals (mother-calf HWI < 0.5) who had not yet reproduced (McHugh et al., 2011). Males were categorized as adults if they were over the age of 10 (Wells & Scott, 2017). Females were categorized as adults if they had given birth to a calf or were above the age of 10 (Schwacke et al., 2010). Presence of injury was observed directly in the field during routine surveys, opportunistic sightings, capture-release efforts, or rescue missions (Christiansen et al., 2016).

2.2 | Data collection

Observational data on the associations and life history patterns of 24 animals from Sarasota Bay that suffered from an anthropogenic injury were gathered during boat-based monitoring surveys and health assessments from 1982 to 2018 (Table 1). Individuals were identified using photographic identification based on unique dorsal fin and body markings (Wells, 2003). Photo-identification processes followed the methods of Würsig and Jefferson (1990). For each sighting, which consisted of visualization of at least one dolphin in a given area, an attempt was made to photograph all individuals present in the group. A group was defined as all individuals within an approximate radius of ~100 m, moving in the same direction and generally involved in the same activity (Wells, Scott, & Irvine, 1987). Identity of individual animals was confirmed if possible during field observations. For uncertain identifications, photos were reviewed in a laboratory and compared against a database of known dorsal fins. Sightings included in analyses were those recorded 1 year prior to injury, 1 year postinjury, and 2 years postinjury for each individual. The sampling period was set as 1 day, so resightings of the same group on the same day were only counted once (Ansmann, Parra, Chilvers, & Lanyon, 2012). Data were restricted to include only those individuals seen on at least five different occasions to reduce bias introduced by low resighting rates, eliminate nonresident individuals, and avoid spurious associations (Titcomb, O'Corry-Crowe, Hartel, & Mazzoil, 2015; Whitehead, 2008). For one individual, sighting data were not available before injury. For two individuals, sighting data were not available after injury.

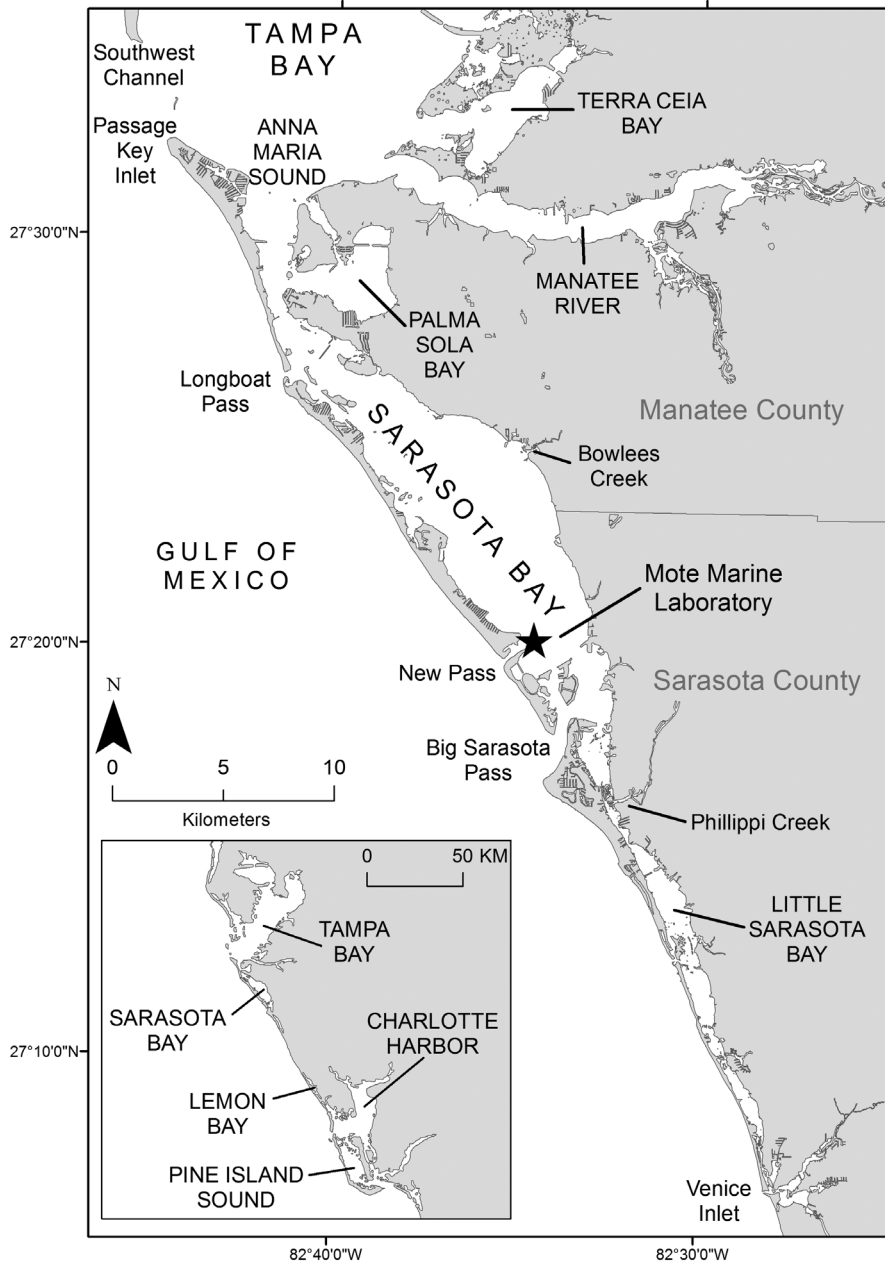


FIGURE 1 Sarasota Bay study area, which extends on the western coast of Florida from southern Tampa Bay to Venice Inlet.

2.3 | Study animals

Dolphins ranged in age from 1 month to 42 years. Sources of injury considered were entanglements and boat strikes. Entanglements were identified based on observations of hooks, lures, monofilament, crab trap floatlines, or from scarring patterns consistent with wounds from lines (Christiansen et al., 2016). Boat strikes were identified based on the occurrence of deep, evenly spaced, parallel cuts, and/or indications of severe blunt trauma (Wells et al., 2008).

TABLE 1 Summary characteristics of injured animals.

ID	Sex	Age class	Injury type	Days between last sighting and injury	Date injury first observed	Intervention	Days until intervention
1351	Unknown	Calf	Entanglement	21	June 10, 2011	Yes	0
C797	Male	Calf	Entanglement	33	March 18, 2011	Yes	91
F103	Female	Calf	Boat	2	July 8, 1988	No	NA
F108	Male	Juvenile	Boat	1	June 24, 1984	No	NA
F111	Female	Adult with calf	Boat	1	July 16, 1997	No	NA
F113	Female	Adult with calf	Entanglement	5	May 23, 2012	Yes	58
F118	Male	Adult	Entanglement	13	October 26, 2003	No	NA
F175	Female	Juvenile	Entanglement	20	April 16, 1998	No	NA
F188	Male	Adult	Boat	13	July 19, 2012	No	NA
F201	Female	Calf	Entanglement/boat	196	December 12, 2006	Yes	49
F209	Female	Calf	Boat	27	January 8, 2005	No	NA
F221	Female	Calf	Entanglement	66	February 19, 2010	Yes	10
F222	Male	Juvenile	Entanglement	1	July 21, 2005	No	NA
F222	Male	Adult	Boat	27	July 1, 2015	No	NA
F248	Male	Juvenile	Entanglement	6	June 29, 2006	Yes	35
F262	Male	Adult	Entanglement	17	February 29, 2016	Yes	1
F286	Male	Calf	Entanglement	15	October 16, 2014	Yes	0
FB03	Female	Juvenile	Entanglement	5	June 4, 1996	Yes	2
FB09	Female	Adult with calf	Boat	14	July 9, 1996	No	NA
FB11	Female	Calf	Entanglement	4	June 27, 1985	Yes	0
FB16	Male	Juvenile	Entanglement	84	December 16, 1988	No	NA
FB28	Male	Adult	Entanglement	14	June 22, 2007	Yes	14
FB66	Male	Adult	Boat	6	July 15, 2013	No	NA
FB78	Male	Adult	Boat	NA	July 2, 1983	No	NA

We did not consider any individuals with crescent-shape scars or wounds, as these are consistent with a shark jaw and could be potential shark bites (Wilkinson, Wells, Pine, & Borkhataria 2017). Intervention was defined as any rescue attempt by humans in which an animal received assistance in the water or on land in a rehabilitation center (Moore et al., 2007). All individuals were paired with control animals that were matched to be of the same sex and age class at the time of injury. This was to establish a baseline for the behavior of an individual and to minimize the number of external factors that could contribute to differences in associations.

2.4 | Defining association

For Sarasota Bay dolphins, the association level between pairs of individuals is typically described by using the half-weight index (HWI), which is defined by the equation $x/(1/2)(n_a + n_b)$, where x is the number of times that individual A and B were located together in the same group; $n_a = x + y_a + y_{ab}$ and $n_b = x + y_b + y_{ab}$, where y_a is the number of times only individual A is located, y_b is the number of times only individual B is located, and y_{ab} is the number of times individual A and B were located separately (Cairns and Schwager, 1987). We calculated

the HWI for each interaction between two distinct individuals with software program SOCPROG 2.8 (Whitehead, 2009).

2.5 | Preferred associates

The overall mean HWI obtained from all interactions between injured and noninjured animals during the specified time periods was 0.03. Preferred associations were defined by those interactions with a HWI greater than twice the mean HWI (0.06) (Titcomb et al., 2015; Whitehead, 2008). To focus on the true associations within the population (HWI > 0) and eliminate all nonexisting associations between individuals (HWI = 0), we further filtered associations by removing all HWI values of zero from the population and recalculated the mean HWI (0.07). Preferred associations by this method were those associations with a HWI greater than twice the mean HWI (0.14).

2.6 | Social network measures

We calculated individual social network metrics and association matrices showing pairwise relationships between animals using SOCPROG 2.8 (Whitehead, 2009) and Gephi 0.9.2 (Bastian, Heymann, & Jacomy, 2009). Network metrics calculated included strength, eigenvector centrality, clustering coefficient, and number of triangles, which evaluate different aspects of connectedness between individuals in a given area (Titcomb et al., 2015; Whitehead, 2008). Strength is a measure of the connections of an individual calculated as the sum of its HWI. Eigenvector centrality is the sum of the centralities of an individual's neighbors (Farine & Whitehead, 2015). Clustering Coefficient is a measure of how well associates of one individual are themselves associated (Whitehead, 2008). Number of triangles refers to the connections between nodes that form complete triangles, thereby measuring the degree to which the animal of interest's associates are associates of one another (Hunter, Goodreau, & Handcock, 2008).

Association matrices were visualized as social networks using Gephi 0.9.2 (Bastian et al., 2009). To simplify graphic visualization, the population networks were filtered to ego networks of the injured or control animal. Filtering eliminated all animals in the population without direct connections to the specified individual. However, the graphs maintain the ties, if present, among the alters, which are the nodes to whom the ego animal is directly connected. For comparisons of preferred associates, the ego networks were further filtered to only include those individuals with a HWI > 0.14 with the injured/control animal.

The mean group size was found by averaging the group size for all sightings for a given individual during the specified time period.

2.7 | Statistical tests

We applied a Shapiro–Wilk test for normality to all data. Data were not normal, so all tests used were nonparametric. We applied a paired one-sample Wilcoxon signed-rank test against zero for comparisons of group size and network metrics before and after injury, as well as for comparisons between injured and control animals. Paired one-sample Wilcoxon signed-rank tests were also used to determine how the sex of the animal, the type of injury, and the presence of intervention affected the network metrics. We applied a paired one-way Kruskal-Wallis test to determine how the age class affected the network metrics. For tests comparing the network metrics before injury and 1 year or 2 years after injury, those individuals that were not seen for the full extent of the time period were removed from analysis. For tests focusing on the sex of the animal, the single individual with unknown sex was removed from analysis. For tests focusing on the age class of the animals, all adults were combined regardless of reproductive status.

Unless otherwise noted, comparisons for network metrics only consider 1 year before injury and 1 year after injury. All statistical tests were run in JMP Pro 12 (Version 12; SAS Institute Inc., Cary, NC).

3 | RESULTS

At the time of injury, eight dolphins were categorized as calves, six as juveniles, and 10 as adults. Thirteen of the animals were males, 10 were females, and the sex of one animal was unknown. Of the 10 adults, only three were females, and all adult females were associated with calves. Of the 24 injured animals, nine received injuries from a boat strike, 14 were entangled, and one suffered from a boat strike and an entanglement. 13 individuals did not receive any form of human intervention after injury. For the 11 that did, there were on average 23.54 days between the first sighting of injury and any form of intervention ($SD = 27.82$, range 0–91). On average, there were 23.17 days between the last sighting and the first sighting with injury ($SD = 41.53$, range 1–196) (Table 1). Only three animals were not seen within a month prior to the first injury sighting (Table 1). Removing them from analyses did not change the overall patterns demonstrated.

Bottlenose dolphins were found in groups of similar size (Figure 2) and had similar number of sightings, associates, and number of associates per sighting before and after injury (Table 2, Table 3). They also did not differ in either mean or maximum association strength (HWI) with other individuals in the community network before or after injury (Table 3). We compared the preinjury and 1-year postinjury network metrics within the subsets of injured and control animals to determine if the individual interactions changed after injury (Table 4). For the full unfiltered network connections and with all connections filtered to $2\times$ mean HWI (0.06) there were no significant differences observed in any metrics for injured or control animals. Within the networks of preferred associates of $HWI > 0.14$ ($2\times$ mean nonzero HWI), we found that strength ($df = 20$, $T = -65.50$, $p = .0093$), eigenvector centrality ($df = 20$, $T = -52.50$, $p = .0332$), clustering coefficient ($df = 20$, $T = -66.00$, $p = .0088$), and number of triangles ($df = 20$, $T = -61.00$, $p = .0150$) decreased in the year after injury. For control animals, clustering coefficient also decreased ($df = 20$,

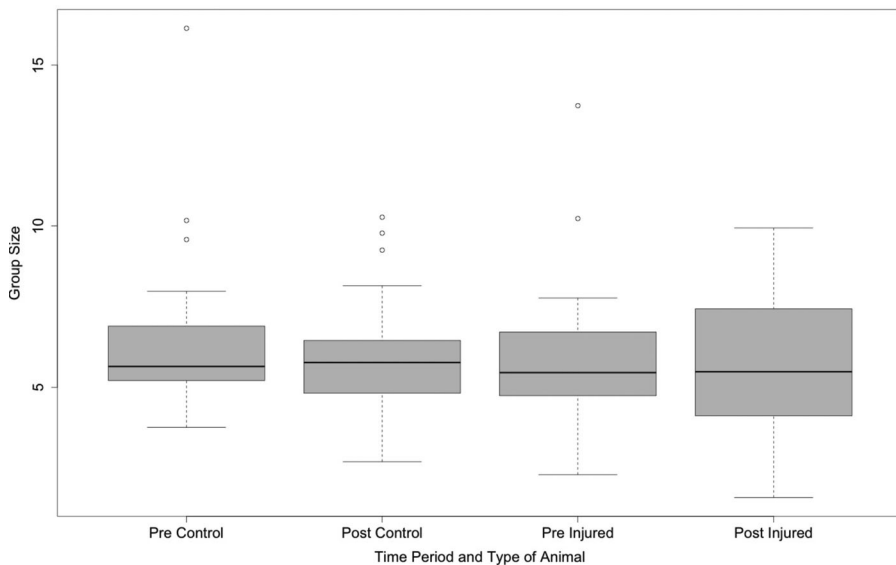


FIGURE 2 Boxplot of group size for control and injured animals before and after injury. Lines in boxes denote medians. Lines above and below boxes denote upper (Q3) and lower quartiles (Q1). Outer limits include $Q3 + 1.5 \times IQR$ and $Q1 - 1.5 \times IQR$.

TABLE 2 Summary of central tendencies for injured and control animals. All values reported are raw. M is the median value. Two years postinjury values were only evaluated for network metrics that exhibited differences between injured and control animals (Table 3).

	Preinjury			Postinjury			Two years postinjury			
	Injured		Control	Injured		Control	Injured		Control	
	M	IQR	M	IQR	M	IQR	M	IQR	M	IQR
Group size	5.481	3.106	6.000	1.659	5.455	2.421	5.645	2.055		
Number of sightings	25.00	12.00	27.00	18.00	23.00	25.00	29.00	14.00		
Number of associates (No Filter)	52.00	30.00	57.00	21.00	48.00	30.00	53.00	27.00		
Number of associates (HWI > 0.06)	25.00	16.00	31.00	13.00	27.00	13.00	31.00	14.00		
Number of associates (HWI > 0.14)	6.00	7.00	8.00	7.00	4.00	10.00	9.00	7.00		
Mean HWI	0.020	0.010	0.020	0.020	0.020	0.010	0.030	0.020		
Max HWI	0.520	0.670	0.080	0.510	0.800	0.470	0.820	0.520		
Strength (no filter)	4.540	1.390	5.320	2.220	4.970	2.550	5.750	2.490		
Eigenvector centrality (no filter)	0.030	0.090	0.040	0.090	0.060	0.070	0.050	0.060		
Clustering coefficient (no filter)	0.100	0.090	0.090	0.040	0.100	0.070	0.090	0.040		
Number of triangles (no filter)	665.0	573.0	819.0	498.0	689.0	699.0	864.0	634.0		
Strength (HWI > 0.06)	5.718	1.512	5.989	1.873	5.224	2.838	6.484	2.153		
Eigenvector centrality (HWI > 0.06)	0.374	0.338	0.563	0.258	0.434	0.392	0.564	0.324		
Clustering coefficient (HWI > 0.06)	0.495	0.267	0.458	0.120	0.473	0.274	0.467	0.150		
Number of triangles (HWI > 0.06)	160.0	136.0	210.0	147.0	165.0	188.0	255.0	226.0		
Strength (HWI > 0.14)	3.879	1.971	4.091	1.582	3.593	2.392	4.773	1.637	3.689	1.637
Eigenvector centrality (HWI > 0.14)	0.086	0.251	0.081	0.394	0.101	0.156	0.138	0.303	0.022	0.034
Clustering coefficient (HWI > 0.14)	0.434	0.191	0.400	0.148	0.333	0.477	0.303	0.180	0.189	0.373
Number of triangles (HWI > 0.14)	10.00	31.00	11.00	20.00	5.00	23.00	20.00	25.00	9.500	14.75
									16.50	17.75

TABLE 3 Paired one-sample Wilcoxon signed-rank test comparing injured and control animals 1 year before and 1 year after injury. M is median difference between the two time periods.

	No HWI filter				
	<i>df</i>	<i>T</i>	<i>p</i>	<i>M</i>	<i>IQR</i>
Mean group size injured	20	18.50	.7333	0.3289	2.427
Mean group size control	20	5.000	.5665	0.000	1.960
Number of sightings injured	20	-10.00	.3685	-2.000	22.00
Number of sightings control	20	-16.00	.2952	-2.000	15.50
Number of associates injured	20	-30.00	.1542	-2.000	35.50
Number of associates control	20	-40.00	.0849	-9.000	35.50
Number of associates per sighting injured	20	-15.50	.3012	-0.1558	1.026
Number of associates per sighting control	20	-11.50	.3498	-0.3677	1.798
Mean HWI injured	20	7.000	.5991	0.000	0.015
Mean HWI control	20	-8.500	.3824	0.000	0.015
Max HWI injured	20	31.50	.8580	0.000	0.390
Max HWI control	20	-22.50	.2234	-0.010	0.120

$T = -50.50$, $p = .0392$). We compared the preinjury and 2 years postinjury network metrics ($HWI > 0.14$) to determine if a longer time period would be sufficient for an injured animal to rebuild its social networks (Table 4). Results show that there is a trend toward returning to preinjury network metric values. However, the animals do not return to their preinjury baseline levels.

A paired one sample Wilcoxon signed-rank test was conducted to evaluate the relationship between network metrics ($HWI > 0.14$) and the animal's sex, type of injury, and presence of intervention (Table 5). A one-way Kruskal-Wallis test was used to evaluate the relationship between network metrics and age class (Table 5). No major differences were noted.

For preferred associations ($HWI > 0.14$) animals had with specific individuals before injury, on average, injured animals maintained 17.17% and controls maintained 16.74% of preferred associations with the exact same individuals after injury. Due to the decrease in metrics after injury for the preferred networks associated with this continuity, we were interested in determining if the most stable social pairing structures documented in Sarasota Bay would remain despite injury. Therefore, we compared the association between mothers and calves as well as the association between male alliance partners before and after injury. In six of the eight documented cases in which calves were injured, the mother remained the strongest associate before and after injury. For the other two cases, one calf was not sighted after injury and the other was not sighted with any dolphin after injury with a $HWI > 0.14$. Figure 3 depicts the continuity of the relationship between FB11, an injured calf, and its mother. FB11 was only 1 year old at the time of injury and had the same number of sightings before and after injury, making it an ideal representative calf. Similarly, in two of the three cases in which mothers still with calves were injured, the calves remained the strongest associate before and after injury. In the third case, the calf remained one of the five strongest associates. Aligning with the behavior of control animals, both before and after injury, calves and mothers predominantly remained in nursery groups, consisting of other mothers and calves.

Male alliance pairs also demonstrated continuity in relationships. In two of the three documented cases in which males had confirmed alliance partners, the strongest relationship in both time intervals was with the alliance partner. For one male, the HWI before and after injury was equal to one, meaning that the alliance partner was always sighted with the injured animal. All other relationships for this animal had a $HWI < 0.25$. For the third male with a confirmed alliance partner, the alliance partner was the strongest associate prior to injury, but the injured individual

TABLE 4 Paired one-sample Wilcoxon signed-rank test evaluating changes in network metrics for injured (I) and control animals (C) 1 year before and 1 year after injury. M is median difference between time periods.

	No HWI filter					HWI filter 0.06				
	df	T	p	M	IQR	df	T	p	M	IQR
Strength I	20	-0.500	.4933	-0.400	2.960	20	-23.50	.2137	-0.4016	2.480
Strength C	20	1.000	.5134	-0.290	2.605	20	-8.500	.3878	-0.1671	2.508
Eigenvector centrality I	20	19.50	.7476	0.000	0.030	20	-10.50	.3623	-0.0346	0.3630
Eigenvector centrality C	20	14.50	.6910	0.000	0.040	20	-19.50	.2556	-0.0723	0.2276
Clustering coefficient I	20	-38.50	.0927	-0.010	0.045	20	-26.50	.1849	-0.0417	0.2617
Clustering coefficient C	20	-31.00	.1451	-0.010	0.040	20	14.50	.6869	-0.0495	0.2222
Triangles I	20	17.50	.7220	33.00	890.5	20	4.500	.5599	-3.000	277.5
Triangles C	20	21.50	.7658	199	983.5	20	9.500	.6250	26.00	269.5
	HWI filter 0.14					HWI filter 0.14 2 years postinjury				
	df	T	p	M	IQR	df	T	p	M	IQR
Strength I	20	-65.50	.0093*	-0.6396	1.302	15	-30.00	.0649	-0.0496	1.228
Strength C	20	0.500	.5067	-0.0785	2.043	15	-13.00	.2641	-0.1092	1.283
Eigenvector centrality I	20	-52.50	.0332*	-0.0219	0.0984	15	-42.00	.0145*	-0.0316	0.2430
Eigenvector centrality C	20	32.50	.8656	0.0362	0.1302	15	-57.00	.0008*	-0.0475	0.2427
Clustering coefficient I	20	-66.00	.0088*	-0.0952	0.3031	15	-36.00	.0316*	-0.1741	0.3714
Clustering coefficient C	20	-50.50	.0392*	-0.0867	0.2756	15	7.500	.6422	0.0630	0.3341
Triangles I	20	-61.00	.0150*	-6.000	27.5	15	-28.00	.0791	-6.500	14.75
Triangles C	20	17.50	.7222	1.000	24.00	15	-0.500	.4945	0.000	17.00

* $p < .05$.

did not survive postinjury. Figure 4 depicts injured male F188 and its alliance partner. F188 was chosen as a representative male due to his numerous sightings and associations both before and after injury. For males that did not have a confirmed alliance partner, most associated with a few other adult males and an occasional adult female, though the specific individuals varied. These findings were consistent for both injured and control animals.

4 | DISCUSSION

4.1 | Group size and social connectivity

Dolphins in Sarasota Bay and many parts of the world are susceptible to anthropogenic injuries that impact the formation and stability of their social relationships. Our results show that while injured animals were found in groups of approximately the same size as prior to injury (Figure 2), the composition of the relationships, particularly the strongest relationships, varied. Within the subset of preferred associates (HWI > 0.14), strength decreased for individuals after injury, suggesting that the animals had fewer preferred associates after injury despite maintaining the size of

TABLE 5 Paired one-sample Wilcoxon signed-rank test to evaluate relationship between network metrics (HWI > 0.14) and animal's sex, type of injury, and presence of intervention. One-way Kruskal-Wallis test to evaluate relationship between network metrics and age class.

	Sex			Age class							
	df	χ^2	p	Mean rank score		df	χ^2	p	Mean rank score		
				Male	Female				Calf	Juvenile	Adult
Strength	1	0.9719	.3242	9.600	12.27	2	0.8957	.6390	13.29	11.29	10.13
Eigenvector centrality	1	0.0229	.8798	10.30	10.70	2	1.1243	.5700	12.57	11.50	9.250
Clustering coefficient	1	0.0198	.8880	11.20	10.82	2	0.2114	.8997	11.00	12.43	11.13
Triangles	1	0.5485	.4589	9.950	11.95	2	0.3007	.8604	12.00	12.14	10.50
	Type of injury			Presence of intervention							
	df	χ^2	p	Mean rank score		df	χ^2	p	Mean rank score		
				Boat	Entangle				Yes	No	
Strength	1	0.0769	.7815	11.00	10.23	1	0.3891	.5327	10.64	12.36	
Eigenvector centrality	1	0.0392	.8430	10.14	10.69	1	0.0050	.9439	10.90	11.09	
Clustering coefficient	1	0.5667	.4516	11.86	9.769	1	2.2823	.1309	9.409	13.59	
Triangles	1	0.016	.9684	10.43	10.54	1	0.0530	.8180	11.18	11.82	

their larger population-wide community (Rubenstein, 2015). The decrease in eigenvector centrality and clustering coefficient suggest that injured animals associate with a greater variety of less well-connected individuals, thereby decreasing their global reach (Rubenstein, 2015). The decrease in the number of triangles after injury suggests that injuries may lead animals to be found in more isolated and less tightly knit groups (Hunter et al., 2008). Therefore, our prediction that animals would exhibit greater solitary behavior after incurring an injury applies only within the subset of strong associates rather than overall associates as previously assumed (see Supplementary Data). Injured animals do not suffer from a decrease in the overall sizes of the groups in which they are found, but they do show a decrease in the size of the smaller network of individuals with whom they were previously strongly associated. After 2 years, the animals continue associating with a greater variety of less well-connected individuals. They do not return to their preinjury network values, but there is a positive trend in strength and number of triangles suggesting there is opportunity for postinjury recovery for their associations.

These behavioral patterns may result from injured animals' attempts to maintain the size of their larger social network by having more variable and transient associations. However, it may also be that dolphins interpret injury as a sign of weakness and are less likely to associate with an injured animal repeatedly, thereby increasing the variety of associates for the injured animal. While this is not confirmed in marine mammals, other species such as the ring-tailed lemur (*Lemur catta*) distinguish weaker individuals through changes in their pheromones and adapt their behavior accordingly (Harris et al., 2018).

4.2 | Effect of sex, age class, type of injury, and human intervention

We did not observe any changes in social relationships due to the sex or age class of the injured animal or the type of injury (Table 5). Age class and sex describe characteristics of the individual animal, not the injury. A lack of relationship between these characteristics and any resulting behavioral change suggests that it may be the presence or severity of the injury rather than the attributes of the animal itself that are contributing to the noted change. Further

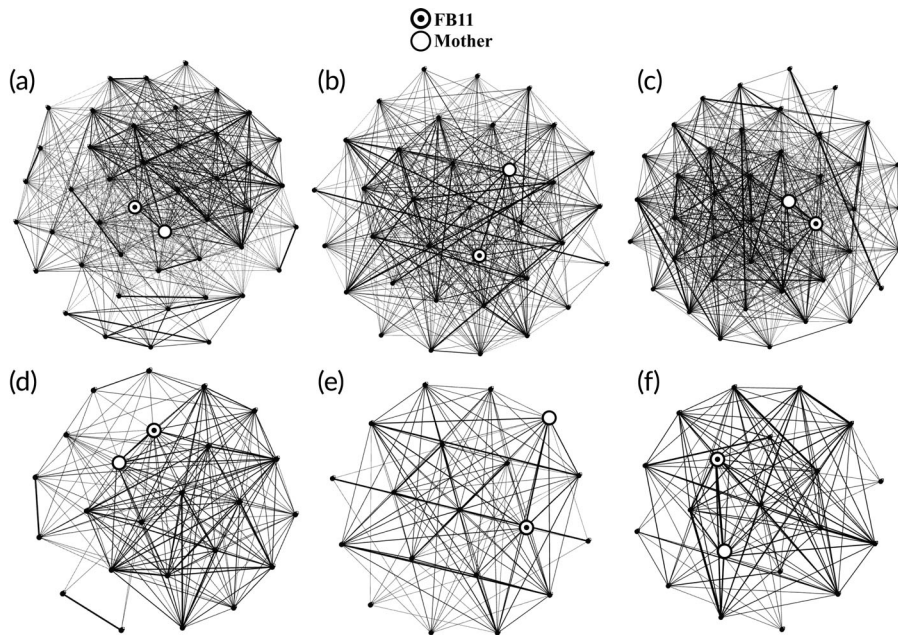


FIGURE 3 Ego networks of representative calf FB11 and its mother nonfiltered before (a), 1 year after (b) and 2 years after injury (c) as well as filtered to $HWI > 0.14$ before (d), 1 year after (e) and 2 years after injury (f). Line thickness notes the strength of the association, where thicker lines represent greater HWI values. FB11 strength nonfiltered preinjury 8.77 (population mean 4.77) and postinjury 8.37 (population mean 4.88). FB11 strength filtered to $HWI > 0.14$ preinjury 8.74 (population mean 4.51) and postinjury 8.63 (population mean 4.05).

analysis comparing social association changes against the location of the injury on the body, the severity of the injury, and how the injury affects functionality may be more informative.

Our results suggest that interventions to rescue and rehabilitate injured animals do not negatively impact the social connectivity of an injured animal. Along with the findings of the importance of interventions for survival of injured dolphins (Wells et al., 2013), this fact provides additional encouragement for rescue teams to continue providing assistance to injured animals.

4.3 | Group composition

Despite the decrease in the number of strong associates noted for dolphins in Sarasota Bay after injury, mother-calf pairs and adult male pairs demonstrated strong continuity in their associations. In Sarasota Bay, calves are closely associated with their mothers for the first few years after birth. Calves require nutritional support from their mothers for at least their first year, though most remain closely associated for 3–6 years on average (Wells, 2003). Previous studies explain that the majority of behavioral and social learning in bottlenose dolphins occurs from mothers teaching their calves (Mann & Sargeant, 2003; Nowacek, 2002; Wells, 2003). Our findings support the importance of strong mother-calf bonds, since mothers and calves in our study stay together despite injury to either party.

The relationships with the longest duration in the Sarasota Bay community consist of adult males (Wells, 2003). Most males form alliances once they reach sexual maturity, and more than 93% have typically formed alliances by the age of 20 years (Owen, Hofmann & Wells, 2002; Wells, 1991, 2003). These bonds are often maintained through life, or until one member in the pair dies (Wells, 2003). Forming new bonds after death was of particular importance for this study since injury could have been interpreted as a sign of impending death, with the potential to remove an

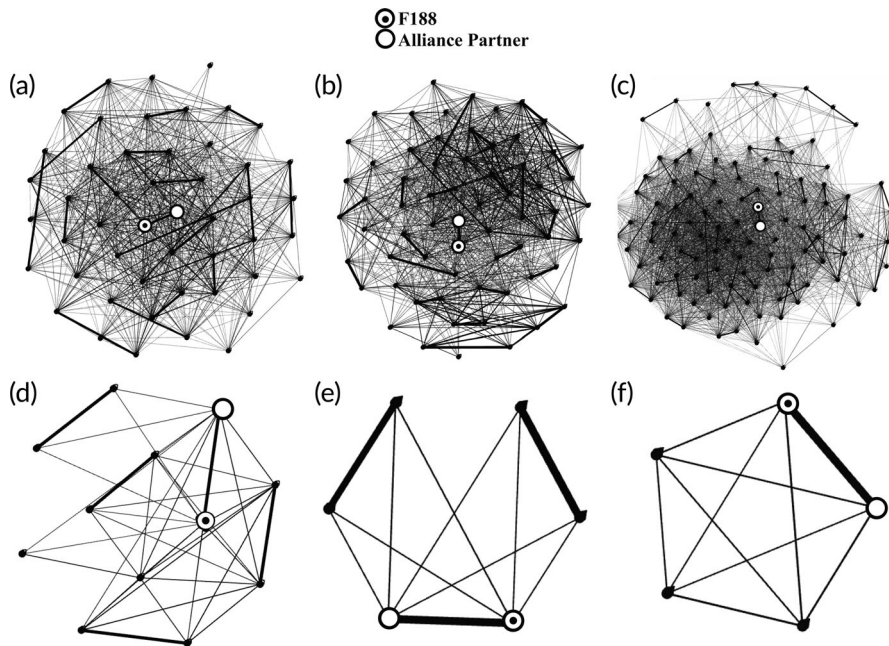


FIGURE 4 Ego networks of representative male F188 and his alliance partner nonfiltered before (a), 1 year after (b) and 2 years after injury (c) as well as filtered to $HWI > 0.14$ before (d), 1 year after (e) and 2 years after injury (f). Line thickness notes the strength of the association, where thicker lines represent greater HWI values. F188 strength nonfiltered preinjury 5.19 (population mean 4.77) and postinjury 5.05 (population mean 4.88). F188 strength filtered to $HWI > 0.14$ preinjury 4.82 (population mean 45.1) and postinjury 3.63 (population mean 4.05).

individual from the population. If the noninjured animal incorrectly assumed his partner had died, he could have sought a new bond, thereby disrupting the social relationships of the injured animal. In our study, the two animals with a confirmed alliance partner did not receive any form of intervention. Mazzoil et al. (2008) found that two bottlenose dolphin males from the Indian River Lagoon reunited after 6 months of separation due to rehabilitation of one of the partners. Therefore, there is potential for these bonds to reform after an out-of-habitat intervention. However, it is still unclear if there is a specific length of intervention that will simulate death and cause the non-injured partner to seek a new companion.

Because this study relied on opportunistic sightings, some animals were seen frequently over the study period while others were seen only occasionally. Our analyses are sensitive to numbers of sightings, though we attempted to maintain similarities between paired control and injured animals (Table 3). Despite Sarasota Bay being a well-studied population, the distinctiveness of individuals could also impact their ability of being identified. Yet, the combination of residency, monthly survey effort, presence of mothers and/or calves, presence of male alliances, and the appearance of injuries enhances the ability for resighting an animal, minimizing the concern. Additionally, the recorded date for each injury may not accurately reflect the true date of injury occurrence. For the purposes of this study, the date of injury was determined by the first day in which the animal was sighted with visible signs of injury.

Injuries included in this study were only external and readily visible. Internal injuries potentially caused by boat strikes and entanglements or hooking were not considered. It is likely that these injuries also cause debilitating effects, which could impact the way in which they associate with others in the population. The inclusion of internal injuries could further clarify the extent to which human interactions disrupt the social behavior of dolphins, but a method to identify these types of injuries for animals not involved in interventions is not available.

4.4 | Conclusion

Bottlenose dolphins in Sarasota Bay live in a complex and highly dynamic fission-fusion society. Animals in this type of community rely on one another for survival. Our findings conclude that injuries disrupt the social interactions of the animals and decrease the number of preferred associates with whom they successfully form associations within the first year after injury. Because dolphins rely on these relationships for survival, increased occurrence of injury from boating and fishing may put the animals at greater risk for long-term survival, including making them more vulnerable to predation. To reduce the frequency of these animals incurring anthropogenic injuries, boaters and fishermen should adhere to best practices recommendations such as *Marine Life Viewing Guidelines and Dolphin Friendly Fishing and Viewing Tips* (https://mote.org/media/uploads/files/dolphin_friendly_tips.pdf). For instance, staying at least 50 yards away from marine mammals, avoiding excessive speed or changes in directions when animals are nearby, removing fishing gear from the water when dolphins are present, and refraining from feeding wild animals can mitigate the potential for dangerous dolphin-human interactions.

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AUTHOR CONTRIBUTIONS

Michelle Greenfield: Conceptualization; formal analysis; funding acquisition; investigation; methodology; project administration; resources; validation; visualization; writing-original draft; writing-review and editing. **Katherine McHugh:** Conceptualization; data curation; funding acquisition; investigation; methodology; project administration; resources; supervision; writing-review and editing. **Randall Wells:** Data curation; funding acquisition; resources; writing-review and editing. **Daniel Rubenstein:** Conceptualization; formal analysis; funding acquisition; methodology; supervision; writing-original draft; writing-review and editing.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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