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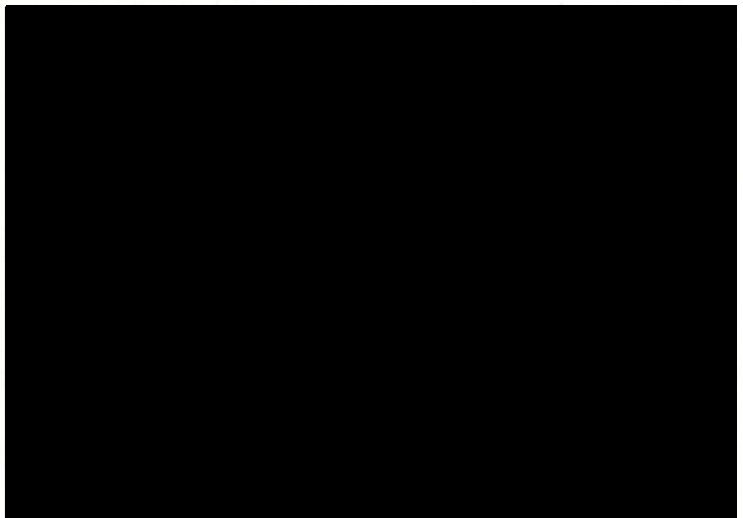
SITE FIDELITY AND ASSOCIATION PATTERNS OF BOTTLENOSE DOLPHINS
(*TURSIOPS TRUNCATUS*) IN THE MISSISSIPPI SOUND

by

Angela Dawn Mackey

A Thesis
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ABSTRACT

SITE FIDELITY AND ASSOCIATION PATTERNS OF BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*) IN THE MISSISSIPPI SOUND

by Angela D. Mackey

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The current study examined the site fidelity and association patterns of a community of 678 wild bottlenose dolphins (*Tursiops truncatus*) in the Mississippi Sound (Sound) over a three-year period (May 2004 - April 2007). Using photo-identification techniques, 74% (n = 498) of the identified dolphins were classified as transients, while 10% (n = 71) were classified as year-round residents, and 16% (n = 109) were classified as seasonal residents based on their sighting histories. Thirty-nine “select” dolphins (n = 17 seasonal residents, n = 22 year-round residents) that were sighted five or more times over the study period were used to calculate the coefficients of association (COAs) using the Half-weight index. Non-zero COAs ranged from 0.10 to 0.91 ($M = 0.25$), with a majority (91%) falling below 0.40. Select dolphins had an average of 55.6 associates, and 21% of the associations between two dolphins were repeated associations.

Social networking analyses were used to investigate the substructure of this network. The network was filtered such that only associations greater than the mean COA were represented, and only individuals with more than one association were included (n = 36). The Girvan-Newman algorithm revealed three distinct communities within the network. A randomized test of autocorrelation provided evidence that the dolphins in this network do not

preferentially associate with individuals of the same residency classification. However, individuals of high degree (number and weight of network neighbors) were more likely to associate more closely with other individuals of high degree. As individuals with high measures of centrality (degree and betweenness) were removed from the network, the network began to break apart, but not prior to the removal of several individuals, suggesting the structure of the network is maintained by multiple individuals. Networks created for each of the three barrier islands and the channel revealed distinct differences in social structure at those locations. Network centrality measures were also calculated for a group of dolphins sighted two or more times before and after Hurricane Katrina, to examine its effects on the social structure of dolphins in the Sound. Most of the measures of centrality were significantly higher after the hurricane, suggesting that the dolphins in the network were more strongly connected at this time.

Finally, I want to thank my family and friends for their love and support. The last few years have been full of highs and lows, but I have always been able to count on each of you to listen patiently and give advice when needed. Thank you for your encouragement to pursue my dreams. I'll never be where I am without you!

Funding for this project was provided by the Department of Commerce and the Institute for Marine Mammal Studies. Research effort for the current study was conducted under NMFS permit #1041-1701.

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Finally, I want to thank my family and friends for their love and support. The past few years have been full of highs and lows, but I have always been able to count on each of you to listen patiently and give advice when needed. Thank you for your encouragement to pursue my dreams; I'd never be where I am without it!

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CHAPTER I

INTRODUCTION AND REVIEW OF LITERATURE

Bottlenose dolphins (*Tursiops* sp.) are the best-known cetaceans in the ocean. Not only is this species common in aquaria, it is ubiquitous along the coasts of nations worldwide (Leatherwood & Reeves, 1990). The bottlenose dolphins' proximity to humans in near shore waters has allowed researchers to collect a vast amount of ecological and behavioral data on this species. Long term studies in Sarasota Bay, Florida and Shark Bay, Australia, have provided much insight into the social world of the bottlenose dolphin.

Unfortunately, proximity to humans has made the bottlenose dolphin susceptible to anthropogenic disturbances including contaminants (e.g. Cardellicchio, 1995; Storelli & Marcotrigiano, 2000), noise pollution (e.g. Perry, 1998; Weilgart, 2007), over-fishing (e.g. Bearzi et al., 2005), and harassment (e.g. Samuels & Bejder, 2004). Such disturbances have been shown to have an effect on dolphin health, behavior, and habitat usage (Bearzi et al., 2005; Bejder et al., 2006; Constantine, Brunton, & Dennis, 2004; Lusseau, 2005). Some disturbances may lead to long-term site avoidance, and thus impact dolphin social structure (Bejder et al., 2006).

Within the Mississippi Sound (Sound), bottlenose dolphins are exposed to a variety of human activities including shipping, commercial and recreational fishing, oil and gas development, dredging, and recreational boating (Hubard, Maze-Foley, Mullin, & Schroeder, 2004). Little research has been conducted to determine to what extent these activities affect bottlenose dolphins in this area. However, Miller, Solangi, and Kuczaj (2008) examined the effect of high-speed

personal watercraft on bottlenose dolphin behavior in the Sound. They reported immediate impacts, such as increases in dive duration, group cohesion, and breathing synchrony, each of which may be behavioral responses to a possible threat. Additional impacts included an increase in traveling behavior and decreased feeding behavior, which suggests that dolphins were attempting to avoid high-speed watercraft.

Due to the bottlenose dolphin's long-life span, wide coastal distribution, and status as a top-level predator, this species may serve as a barometer of the health of coastal marine ecosystems (Wells et al., 2004). As Wells et al. (2004) point out, "[d]olphin health and population status not only reflect the effects of natural and anthropogenic stressors on the species, but they serve as sentinels of the health and status of lower trophic levels..." (p. 247). As shrimping and commercial fishing are common activities in the Mississippi Sound, it is worthwhile to take a proactive approach to identifying how dolphins utilize the area, rather than waiting for a potentially devastating event (e.g. mass stranding) to take place. Thus, the purpose of the current study is to investigate the site fidelity and association patterns of bottlenose dolphins in the Mississippi Sound for the years 2004-2007. In addition, this study takes advantage of a natural disaster (Hurricane Katrina) that occurred during the study period, to examine its potential effects on the social structure of dolphins in the area.

Site Fidelity

Site fidelity is best defined as "the return to and reuse of a previously occupied location" (Switzer, 1993, p. 533). Although a majority of studies regarding site fidelity focus on migratory birds (see review by Greenwood, 1980),

site fidelity has also been observed in a variety of other species, including mammals (e.g. harbor seal, *Phoca vitulina*, Yochem, Stewart, DeLong, & DeMaster, 1987; humpback whales, *Megaptera novaeangliae*, Craig & Herman, 1997; caribou, *Rangifer tarandus*, Schaefer, Bergman, & Luttich, 2000), fish (e.g. goatfish, *Parupeneus porphyreus*, Meyer, Holland, Wetherbee, & Lowe, 2000), reptiles (e.g. loggerhead sea turtle, *Caretta caretta*, Avens, Braun-McNeill, Epperly, & Lohmann, 2003; Clark & Gillingham, 1990), amphibians (e.g. natterjack toad, *Bufo calamita*, Sinsch, 1992), and insects (e.g. carpenter bee, *Xylocopa varipuncta*, Alcock, 1993).

Unfortunately, as Switzer (1993) points out, literature on the topic of site fidelity reflects a lack of consistency in the use of the term "site". In some studies, site refers to a general area (e.g. Raveling, 1979; Schaefer et al., 2000), whereas in others it is a specific location (e.g. Lewis, 1995, Rydell, 1989). Moreover, return to the site in question may occur on a daily basis, such as the return to a particular shelter or rest site (e.g. Clark & Gillingham, 1990; Meyer et al., 2000) or seasonally, as is often the case with migration or breeding sites (e.g. Haas, 1998; Harvey, Greenwood, & Perrins, 1979; Lewis, Campagna, & Quintana, 1996).

An animal's decision to settle in a particular habitat is influenced by a variety of ecological factors. These factors include population density (Greenwood, 1980), territoriality of conspecifics (Brown, 1969), proximity of water and food sources (Orians & Wittenberger, 1991), and reproductive success within the habitat (Fretwell & Lucas, 1970; Harvey et al., 1979). In basic habitat selection models, an animal chooses a particular habitat after evaluating all

possible habitats based on these factors (Switzer, 1993). If a higher quality habitat (i.e. one that results in high reproductive success) becomes available, the optimal decision is for the individual to switch to the new location (Switzer, 1993).

In order to explain why some individuals exhibit site fidelity and others do not, Switzer (1993) developed a general model that accounts for factors such as heterogeneity in territory quality, cost of changing territories, probability of adult mortality, and predictability of the habitat. A predictable habitat is one in which "the probability that this period's [reproductive] outcome on a given territory will be the same as the outcome on that territory in the last period" (Switzer, 1993, p.550).

Several predictions about site fidelity can be made based on Switzer's (1993) model. First, site fidelity should be related to the cost of switching habitats; as the cost of changing territories increases, the likelihood of an individual switching to the new territory decreases (Switzer, 1993). Relocation costs may be incurred through searching costs (e.g. time and energy spent searching for a suitable environment), establishment costs (e.g. competition between territorial residents), lost-opportunities costs, or the loss of potential benefits of alternative behaviors that an animal might engage in if it were not relocating (Jakob, Porter, & Uetz, 2001). However, an individual may compensate for the high cost of switching if there is enough expected gain to lifetime fitness (Switzer, 1993).

For this reason, Switzer (1993) proposes that age and lifespan may also be predictors of site fidelity. A young animal with a long lifespan, for example, has a greater number of potential reproductive events, and thus may make-up for

the costs incurred from moving to a new territory. In contrast, older animals, or those with a short lifespan, may have fewer reproductive opportunities, and should exhibit site fidelity. Adult mortality, which has a similar effect as lifespan, may predict site fidelity as well. An animal living in a habitat with high adult mortality rates will likely live a shorter life than those in areas with low mortality rates, regardless of average lifespan (Switzer, 1993).

Switzer (1993) also identifies habitat predictability (as previously defined) as a potential factor affecting site fidelity. Switzer (1993) states that individuals are likely to exhibit site fidelity when two territories are similar in quality, regardless of habitat predictability. However, when previous reproductive outcome is taken into consideration, site fidelity will differ between predictable and unpredictable habitats. In predictable habitats, individuals should base their habitat selection on previous reproductive outcomes, moving only when the previous outcome was poor, or following a good outcome only if a higher quality territory is available (Switzer, 1993). Individuals in unpredictable habitats, however, should not base their settlement decisions on previous reproductive outcome. Rather, these individuals should base their decisions on differences in territory quality (Switzer, 1993).

Site Fidelity in Bottlenose Dolphins

Site fidelity has been observed in bottlenose dolphins (*Tursiops* sp.), but the type of site fidelity is dependent on the area. Additionally, more than one type of site-fidelity can occur within a location (Defran, Weller, Kelley, & Espinosa, 1999). Year-round site fidelity has been reported in coastal populations worldwide, including Sarasota, Florida (e.g. Wells, Scott, & Irvine,

1987), Grand Bahama Island, Bahamas (Rossbach & Herzing, 1999), Shark Bay, Australia (e.g. Smolker, Richards, Connor, & Pepper, 1992), Amakusa, Japan (Shirakihara, Shirakihara, Tomonaga, & Takatsuki, 2002), Moray Firth, Scotland (Wilson, Thompson, & Hammond, 1997), Golfo San José, Argentina (Wursig, 1978), Gulf de Guayaquil, Ecuador (Felix, 1997), and Doubtful Sound, New Zealand (e.g. Williams, Dawson, & Slooten, 1993).

Although these sites report year-round usage of the respective areas, many bottlenose dolphin populations exhibit seasonal movements within the study area, often with low numbers of dolphins in the winter and population peaks in the summer and autumn (Hubard et al., 2004; Wilson et al., 1997). In Sarasota Bay, for instance, dolphins utilize shallow grassflats during the summer months and deeper passes, channels and shallow areas of the Gulf of Mexico in the winter months (Irvine, Scott, Wells, & Kaufmann, 1981). Similar movements were reported by Maze and Wursig (1999) for dolphins in San Luis Pass, near Galveston, Texas.

Along the northeastern coast of the United States, bottlenose dolphins show seasonal patterns of residency (Barco, Swingle, McLellan, Harris, & Pabst, 1999), ranging as far north as Long Island, New York during the summer (Kenney, 1990). Lower abundance and a southerly sighting distribution during the winter months suggest that these animals migrate south at this time (Kenney, 1990). Studies along the coasts of Virginia (Barco et al., 1999; Fearnbach, 1997) and South Carolina (Zolman, 2002) have reported a high number of transient animals, which may be a result of the migratory patterns of this population.

Little to no site fidelity has been observed in populations off the coast of

southern California (Defran & Weller, 1999). Dolphins in this area often make repeated travel movements ranging from 50-470km, which have been interpreted as non-migratory movements (Defran et al., 1999). Defran et al. (1999) suggest such movements may be related to an unpredictable distribution of prey in the Southern California Bight, evidenced by the fact that the population shifted its northern boundary by 450 km during the 1983 El Niño event (Hansen, 1990).

Site fidelity patterns in bottlenose dolphins may be affected by a variety of factors. For many populations, it is hypothesized that these seasonal changes in habitat usage are a result of changes in prey distribution (Irvine et al., 1981; Maze & Wursig, 1999) and/or predator abundance (Gowans, Wursig, & Karczmarski, 2007; Wells, Scott, & Irvine, 1987). However, anthropogenic disturbances can result in changes in site fidelity. For instance, Lusseau (2005) observed that bottlenose dolphins in Milford Sound, New Zealand spent less time in the fjord during times of increased boat traffic, both on a daily and seasonal basis.

Understanding the site fidelity of a species may be important for management decisions, particularly when it comes to the control of anthropogenic disturbances. A study on the effects of tour vessel activity on dolphin presence in Shark Bay found a significant decline of one per seven individuals (14.9%) in dolphin abundance as the number of vessels increased from zero, to one, to two (Bejder et al., 2006). The authors suggest that while such a decline may not have severe impacts on large populations, a similar decline could be devastating to less genetically diverse populations (e.g. small, closed, resident, or endangered cetacean populations).

Additionally, the displacement of some individuals due to anthropogenic disturbance may impact the social structure of dolphins. Research indicates that site fidelity may play a role in the establishment of social relationships (Michod, 1999; Wolf & Trillmich, 2007). Individuals that regularly return to a particular area have increased opportunities to interact with others that have done the same. Non-random associations, formed when animals spend long periods of time in close proximity, can lead to social bonds, and, in turn, active (preferred) associations (Michod, 1999). When individuals with lower tolerance levels relocate in response to disturbance, these individually specific social relationships may be disrupted (Bejder et al., 2006).

Social Living

Benefits of Group Living

Protection from predators. Animals that form long-term social groups do so because they derive benefits from living in such groups (Alexander, 1974; Gowans et al, 2008). One of the most important advantages to forming social groups is a reduction in predation risk (van Schaik, 1983; Inman & Krebs, 1987). Inman and Krebs (1987) discuss two mechanisms through which groups can provide protection from predation: the encounter effect and the dilution effect. The encounter effect assumes that a predator is not proportionally more likely to detect groups of prey than solitary individuals (Connor, 2000; Inman & Krebs, 1987). On the other hand, the dilution effect provides protection by decreasing an individual's probability of being the victim of an attack once detection has occurred (Inman & Krebs, 1987). Therefore, the risk to each individual in a group of size n is $1/n$; assuming individual predation risk is spread evenly among group

members (Lindstrom, 1989), though this may not be the case for older individuals or females with young.

The encounter and dilution effects provide optimal predator protection when working in tandem (Inman & Krebs, 1987). A group of n individuals, for example, has an individual predation risk of $1/n (x \cdot y)$ (where x is the probability of a predator encounter and y is the probability of any one individual being attacked once the group is encountered) when the two operate together, whereas this risk increases to $x \cdot y$ when either of these effects act alone (Inman & Krebs, 1987). However, Inman and Krebs (1987) argue that each effect can generate advantages when operating alone, such as when a group forms for reasons other than predator avoidance. For example, if 50 individuals aggregate around a common food source and neither the dilution nor the encounter effect is in operation, each individual has a predation risk 50 times greater than a solitary individual. When either of these effects function alone, this risk is reduced to that of a solitary individual (Inman & Krebs, 1987).

Group formation can also reduce individual predation risk by increasing the likelihood that a predator will be detected prior to an attack (Pulliam, 1973). With a greater number of individuals in a group, more eyes are alert for predators. When a member of the group detects a predator, the rest of the group is simultaneously informed either through alarm calls or conspicuous behavior (Dehn, 1990).

Interestingly, many studies have shown that individual vigilance actually decreases as group size increases (see Elgar, 1989 for a review). This phenomenon is similar to that of social loafing in human social psychology, in

which individuals exert less effort when working together as a group than when working alone (Ingham, Levinger, Graves, & Peckham, 1974; Latane, Williams, & Harkins, 1979).

Roberts (1996) provided several hypotheses that may explain why vigilance decreases as group size increases. First, individuals in larger groups can take advantage of the vigilance of group-mates and allocate more time to other activities such as feeding, socializing, and resting (Pulliam, 1973; Dehn, 1990). This hypothesis has often been referred to as the “many eyes effect” (Powell, 1974) or the “detection effect” (Dehn, 1990). Second, if vigilance varies with predation risk and that risk decreases as group size increases (due to encounter and dilution effects), vigilance should, in turn, decrease with an increase in group size (Roberts, 1996). A third hypothesis accounts for other factors related to group size that affect vigilance. For example, if animals aggregate around a high quality food supply, they may spend more time feeding and less time alert for predators (Roberts, 1996).

Many factors affect whether vigilance changes with group size. Burger and Gochfeld (1994) reported that for several species of African animals (including African elephant, *Loxodonta africana*; Burchell's zebra, *Equus burchelli*; Cape buffalo, *Syncerus caffer*; wildebeest, *Connochaetes taurinus*; impala, *Aepycerus melampus*; and Uganda kob, *Kobus kob*), females with young were more vigilant than either their young or other females without young. They also observed few sex differences in the level of vigilance in most of the species studied; the exceptions being zebra, wildebeest and waterbuck. In these

species, males were more vigilant than females, perhaps due to increased alertness for competitive males.

The most important determinant of vigilance level is an animal's position within the group (Burger & Gochfeld, 1994). Burger and Gochfeld (1994) observed that individuals located near the edges of the group devoted more time to scanning for predators than those in the center, regardless of sex or maternal status. However, females with young were more vigilant than males or lone females and may be a result of either vigilance for predators or to prevent their young from straying.

Although the phenomenon of vigilance decreasing with group size is well documented, there may be a threshold above which any increase in group size will not result in a further decrease in vigilance (Burger & Gochfeld, 1994). Though Burger and Gochfeld (1994) did not indicate what this threshold may be, they suggested that it may be dependent on the species and herd structure. For example, they observed that large, migrating herds that extended over more than a kilometer (e.g. zebra and wildebeest) did not exhibit a negative correlation between group size and vigilance, while small, non-migrating herds (e.g. impala) did.

For bottlenose dolphins (*Tursiops sp.*), the greatest predation threat is sharks (Shane, Wells, & Wursig, 1986). Dolphin remains have been found in the stomachs of several shark species (Cockcroft, Cliff, & Ross, 1989), including the bull shark (*Carcharhinus obscurus*), dusky shark (*Carcharhinus obscurus*), tiger shark (*Galeocerdo cuvieri*), and great white shark (*Carcharodon carcharias*). Large species such as these are the most common predators of bottlenose

dolphins, yet smaller species have been implicated in attacks as well. For example, Gibson (2006) observed an attack on a bottlenose dolphin calf by a small (~0.9m), unidentified carcharhinid shark, which resulted in the calf losing half of its tail fluke.

Dolphin calves are at the highest risk of shark attacks due to their small size and limited defenses (Gibson, 2006). However, mothers of young calves may be at risk as well. In Moreton Bay, Queensland, 25% (5 of 21) of females with calves aged less than eighteen months bore fresh shark wounds (Corkeron, Morris, and Bryden, 1987). In Shark Bay, Heithaus (2001a) reported no significant differences in the presence of scars among adult females with calves and those without calves. This may be a result of a higher overall predation risk by sharks in this area, which is supported by a higher calf mortality rate (Heithaus, 2001b) and higher scarring frequency (74.2%; Heithaus, 2001a) than has been observed in other areas.

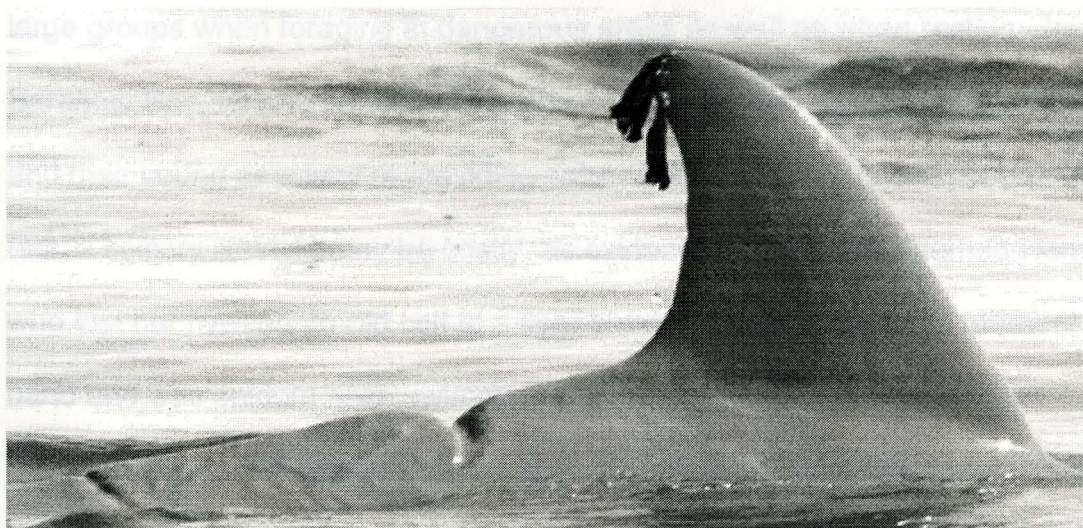


Figure 1. Image of possible shark bite on the peduncle of a bottlenose dolphin in the Mississippi Sound. (Photograph by Marine Mammal Behavior and Cognition Lab)

Killer whales (*Orcinus orca*) are another predator of bottlenose dolphins. These whales are the ocean's top predator and have been observed in all oceans of the world (Baird, 2000). This wide distribution makes killer whales a threat to bottlenose dolphin populations around the globe, with one exception being populations that live in protected coastal habitats (Jefferson, Stacey, & Baird, 1991). Though there have been no documented accounts of killer whales preying on bottlenose dolphins (Connor, Wells, Mann, & Read, 2000), there is evidence that they pose a threat. For example, in Golfo San José, Argentina, Wursig and Wursig (1979) observed a group of bottlenose dolphins rapidly swimming away from a group of killer whales. Additionally, they photographed an individual with scars that appeared to be caused by killer whale teeth.

Bottlenose dolphins can reduce their risk of predation by forming groups, particularly during the warm summer months when predation risk is highest. For example, in Shark Bay, Heithaus and Dill (2002) observed that dolphins formed large groups when foraging in dangerous areas as well as when resting. In Sarasota Bay, female bottlenose dolphins often form bands with other females and their young as a way of providing safety from predators (Wells, 1991). In fact, a solitary lifestyle may be costly, as evidenced by a female named Hannah, who lost her five-month-old calf to a tiger shark. Hannah was not a member of a band and was seldom seen swimming with other females (Wells, 1991).

Resource protection. Resource protection is another factor that influences social living. Food is a very important resource and may require defense from either conspecifics or members of another species. When food sources are widely and uniformly distributed, groups are less likely to form and intergroup

interactions are non-aggressive (Kinnaird, 1992; Gowans et al., 2007). On the other hand, when food sources are patchy and difficult for individuals to locate on their own, group formation is favored (Alexander, 1974; Gowans et al., 2007).

Kinnaird (1992) observed that when two groups of Tana River crested mangabeys (*Cercocebus galeritus galeritus*) fed on uniformly dispersed species of fruit, interactions between groups were generally peaceful. Groups remained discrete but often intermingled. However, though the total fruit biomass was similar, when fruit resources were patchily distributed, aggressive interactions were common.

Territorial food resource defense has not been reported in cetaceans, a fact likely due to the mobility of the prey species, the wide-ranging habits of cetaceans, and the three-dimensional underwater environment (Connor, 2000; Gowans et al., 2007). Thus, food is not likely a resource that is protected by bottlenose dolphin groups.

However, food is not the only defensible resource that can result in group formation. For males, females are a very important resource as mating access to females promotes reproductive success (Cheney, Seyfarth, & Smuts, 1986). In species in which females preferably mate with dominant males, lower ranking males may gain access to sexually receptive females via the formation of alliances that allow them to overpower high-ranking males (e.g. savanna baboons, *Papio cynocephalus*, Cheney et al., 1986). Alliances in baboons are typically formed between individuals who are familiar with each other (though not necessarily related) and whose combined fighting ability will lead to success in a fight with a higher ranking male (Noe & Sluijter, 1995). In most cases, the male

who initiated the alliance formation is the one to mate with the female (Packer, 1979).

Alliances in chimpanzees (*Pan troglodytes*), on the other hand, are often formed as a way of acquiring and maintaining the top-ranking position in the group, which results in exclusive copulatory access to estrous females (Nishida, 1983). Because male chimpanzees remain in their natal group (Morin et al., 1994), it is thought that alliances are formed between close kin (Cheney et al., 1986).

As is the case in many primate species, male bottlenose dolphins may form alliances to gain access to females. In Shark Bay, males regularly form groups of 2-3 individuals (Connor, Smolker, & Richards, 1992). Connor et al. (1992) observed that such alliances form to herd females for mating purposes, which is evidenced by the fact that 1) all herded individuals that were sexed were female, and 2) pregnant females were herded significantly less than non-pregnant, potentially estrous females. The social bonds between alliance members are very strong, with association coefficients equal to females and their nursing young, and these associations remain stable for several years (Connor et al., 1992).

Connor et al. (1992) describe two levels of alliances formed by bottlenose dolphins in Shark Bay. At the basic level are first-order alliances, consisting of pairs or trios of males who cooperatively work together to form and maintain companionships with females. When three males form a first-order alliance, only two of them cooperatively herd a female at a time. These two males are referred to as "partners" and the third individual is the "odd man out". Partner changes, in

which the odd male out becomes closely associated with one of the partners while the other partner becomes the odd male out occur frequently, but typically only occur when males are not herding a female (Connor et al., 1992).

The second level of alliance described by Connor et al. (1992) is a second-order alliance, which is formed when two first-order alliances join together to aggressively steal females from other alliances. Some observations suggest that an alliance may even "recruit" other alliances to participate in the theft (Connor et al., 1992). Though both alliances participate, only one of the alliances herds the female after the attack and in some cases, the assisting alliance may already be in possession of a female consort. One explanation for this may be reciprocal altruism-- the assisting alliance will be "repaid" by the other alliance in the future (Connor, Wells, et al., 2000).

Although high levels of association between males have been observed in other study areas (e.g. Sarasota, FL, Wells et al., 1987; Doubtful Sound, New Zealand, Lusseau et al., 2003), alliances similar to those seen in Shark Bay have not been reported (Connor, Wells, et al., 2000). Connor, Wells, et al. (2000) discuss several factors that may explain why this reproductive strategy is not utilized in other bottlenose dolphin populations. First, the rate of interaction between males may correlate with the presence of alliances, which may be influenced by population density, male to female ratio, day range, and openness of the habitat. Areas with a higher rate of interaction between males should favor the formation of alliances between males. Second, predation risk may drive alliance formation. In areas that have higher predation risk, solitary males may be more vulnerable to predation while taking advantage of mating opportunities

than males in a pair or trio. Resource distribution has also been suggested as having an influence on alliances. If resources are widely or patchily distributed, the cost of foraging may increase enough to make grouping unfavorable. Lastly, the degree of sexual dimorphism between males and females could affect alliance formation. Males who are only slightly larger than females (as is the case in Shark Bay) may have difficulty coercing females without assistance.

Cooperation. Hunting is one of the most prevalent cooperative behaviors seen in social groups (Packer & Rutten, 1988). Animals benefit from cooperative hunting in a variety of ways. They may experience greater capture success and be more likely to capture larger, more energetically valuable, prey (Bednarz, 1988; Blundell, Ben-David, & Bowyer, 2002). In a study on hunting in African wild dogs, Creel & Creel (1995) observed that in addition to greater hunting success and prey mass, the probability of multiple kills increased as the number of adults in the hunting group increased. They also found that the distance prey was chased prior to capture decreased with an increase in group size. In this situation, the overall amount of energy saved and total meal size gained likely outweighed the cost of sharing the catch with other group members, promoting cooperative hunting.

The optimal group size for a cooperatively hunting species may be determined by intra-group competition for resources. Packer et al. (1990) found that when prey was scarce, daily food intake rate for female lions in groups of 2-4 individuals was significantly lower than that for solitary females or females in groups of 5-7 individuals. Although solitary females obtained the same amount of food as those in groups of 2-4, they could consume the entire meal

themselves, thus gaining larger meals. Groups of 5-7 females had to divide the meal amongst all members of the group, but these groups were able to take down much larger carcasses (typically Cape buffalo) than groups of 2-4 females and consequently had larger per capita meal sizes.

Cooperative hunting in bottlenose dolphins is likely related to the type of prey upon which they are feeding. Bottlenose dolphins in Sarasota Bay, for example, typically feed on non-schooling fish species and thus tend to feed alone or in small groups (Barros & Wells, 1998). However, in Amakusa, Japan, bottlenose dolphins are often found in groups of >100 individuals, presumably as an adaptation for feeding on schooling prey such as striped mullet (*Mugil cephalus*) and shad (*Clupea punctatus*; Shirakihara et al., 2002). Large groups of individuals are able to combine their search efforts in order to locate patchy prey, such as schools of fish (Norris & Dohl, 1980).

Many different cooperative hunting strategies have been observed in bottlenose dolphins. Bel'kovich, Ivanova, Yefremenkova, Kozarovitsky, & Kharitonov (1991) described several of these strategies as seen in bottlenose dolphins in the Black Sea. In one technique (which has several forms), a group of dolphins surrounds a school of fish and forces the fish into a ball that is gradually tightened by the dolphins swimming around the mass of fish. The dolphins might then swim into or under the ball to feed. Another technique described by Bel'kovich et al. (1991) involves driving fish into a barrier of some sort (e.g. the shore, fishermen's nets, or a wall of dolphins). The barrier serves to slow down the movement of a school of fish and prevents large solitary fish from escaping.

Perhaps one of the most fascinating cooperative hunting strategies used by dolphins is shore-feeding, which was first observed in bottlenose dolphins in marshes along Georgia (Hoese, 1971), but has also been seen in South Carolina (Duffy-Echevarria, Connor, & St. Aubin, 2008). This type of feeding is typically limited to within 30 minutes before or after a low tide, and occurs when several dolphins in pursuit of fish rush up on the exposed mud bank, pushing a large bow wave ahead of them. This wave breaks on the bank, stranding the fish that were caught in the wave, which the dolphins quickly eat with agile biting movements of their head (Hoese, 1971). As Hoese (1971) points out, this feeding behavior requires precise coordination of the individuals involved, which is remarkable since the water in which this behavior occurs is too turbid for the use of vision.

Cooperation by bottlenose dolphins may also be involved in the search for prey. Bel'kovich et al. (1991) observed bottlenose dolphins in the Black Sea synchronously hunting-- either as a whole herd, or in smaller groups spread out over a wider area. Additionally, scouts made of groups of 2-4 dolphins were spotted searching for fish several kilometers from the rest of the group. When fish were detected, the rest of the herd would join them. It is likely that acoustic signals, such as bray calls, were used to inform the herd of the location of food. Janik (2000) found that low frequency bray calls produced by feeding bottlenose dolphins were followed by fast approaches to the area by conspecifics.

Another cooperative behavior that influences group living is cooperative breeding. In cooperative breeding, individuals in a social group assist in the rearing of young that are not their own, a behavior known as alloparenting (Solomon & French, 1997). Individuals engaging in this type of behavior are

often non-breeding adults and sub-adults; however, reproductive adults may also share in the care of young (Solomon & French, 1997). Alloparental behaviors include babysitting (Glander, 1971; Whitehead, 1996), grooming (Gould, 1997), food provisioning (Emlen et al., 1991), and carrying of young, which is most common in primates (Kohda, 1985; Stanford, 1992).

Mothers benefit greatly from the helping behavior of group-mates. Since alloparental behavior provides relief from maternal caregiving behaviors, mothers receiving such help are able to produce larger litters and may experience shorter inter-birth intervals (Fairbanks & McGuire, 1995; Mitani & Watts, 1997). Mothers are also able to spend a longer period of time foraging than if they were solely responsible for the care of their infant (Mitani & Watts, 1997).

Mothers are not the only individuals that can benefit from cooperative parenting behaviors. Group members engaging in alloparental behavior also gain from this type of care giving. These individuals may benefit from gained experience in infant care, inheritance of a breeding position within the group, increased access to breeding female (for alloparenting males), or inclusive fitness gains from the survival of relatives (Tardif, 1997).

Allomaternal care has been observed in a variety of odontocetes (toothed whales) both in captive facilities and in the wild (Whitehead & Mann, 2000). In sperm whales, alloparenting often involves members of the social group taking turns "babysitting" a calf, while its mother and other group members forage (Whitehead, 1996). In the same way, bottlenose dolphin mothers may benefit from the presence of other dolphins by being able to separate from their calves and forage more efficiently (Mann, 1997; Shane, 1990). Though some mothers

may take advantage of the separation from their calves, Mann and Smuts (1998) found no evidence that mothers forage more when another dolphin escorted their calves.

The benefits of alloparenting in bottlenose dolphins may be greater for those providing the care than for the mother. Mann (1997) observed that immature females and females who had lost infants in the first few months of life are highly attracted to infants, and, other than the mother, tend to be the calves' most common social partners. This provides support for a 'learning to parent' hypothesis in which young or inexperienced females (including those who lost infants) are able to practice appropriate maternal behaviors, which may be applied to the care of future offspring (Mann & Smuts, 1998).

Defense against harassment. A final advantage to group formation is defense against harassment. This aspect most often benefits females and their offspring. Infanticide, the killing of the immature young of a species is common in several species of non-human primates (Crockett & Sekulic, 1984; Soltis, Thomsen, Matsubayashi, & Takenaka, 2000; Newton, 1988), social carnivores (e.g. lions, *Panthera leo*, Packer & Pusey, 1983), and rodents (Menella & Moltz, 1988). In fact, infanticide has been observed in at least 91 mammalian species as well as other vertebrates and invertebrates (Ebensperger, 1998).

Acts of infanticide may be performed by a variety of perpetrators, including the mother, other females, males, members of other groups, and siblings (Packer & Pusey, 1983). Yet, infanticide most often occurs as a male reproductive strategy. Immigrating males will often kill an unfamiliar female's infant in an attempt to stop the female from investing in her current infant. By doing so, the

new male shortens the period during which she is sexually unreceptive and can mate with her sooner, thus ensuring that his own genes are passed on (Fairbanks, 1993). Palombit, Seyfarth, and Cheney (1997) reported that all observed infanticides in a group of chacma baboons (*Papio cynocephalus ursinus*) were committed by adult males who were not resident to the group at the time of conception and who had also achieved alpha male status. Within 2 months of their infants' deaths, the mothers were once again ovulating. Eventually they copulated with the male who had killed their infant. Similarly, Packer and Pusey (1983) reported that an infanticidal male lion was able to sire cubs 8 months sooner than if he had waited for the cubs from another male to be weaned.

Females can employ several tactics to reduce the risk of infanticide for their infants. One method is to mate promiscuously, even during pregnancy, thus confusing the infant's paternity (Hrdy, 1977; van Schaik & Kappeler, 1997). Females can also shorten the inter-birth interval by weaning their infants early when new males immigrate into the social group (Fairbanks, 1993). Finally, forming relationships with resident males can be an effective strategy for reducing infanticide (Hrdy, 1977; van Schaik & Kappeler, 1997). In the case of baboons, females gain protection from infanticidal males by forming relationships with males who had likely fathered their infant (Palombit et al., 1997).

Although infanticide is not a common phenomenon in bottlenose dolphins, some evidence exists to suggest that it does occur. Patterson et al. (1998) were the first to report possible infanticide in a group of bottlenose dolphins along the northeast coast of Scotland. Bottlenose dolphins in the Moray Firth have been directly observed attacking harbor porpoises in the area (Ross & Wilson, 1996).

Post-mortem examinations of 5 stranded bottlenose dolphin calves revealed the same excessive damage as has been reported in harbor porpoises that have been attacked (Patterson et al., 1998). Following the account from Patterson et al. (1998), Dunn, Barco, Pabst, and McLellan (2002) also reported evidence of similar traumatic injuries in 9 bottlenose dolphin calves that stranded off the coast of Virginia.

Bottlenose dolphins share many characteristics that have been suggested to contribute to the risk of infanticide among other mammals. First, breeding in bottlenose dolphins is only moderately seasonal (Mann, Connor, Barre, & Heithaus, 2000). Females are receptive to males and can produce offspring throughout the year, though most calving takes place in the spring and early summer, with a second peak in the early fall (Scott, Irvine, & Wells, 1990). Second, females typically produce a calf every 2-4 years, but if a female loses her calf, she becomes attractive to males again within 1-2 weeks (Connor, Richards, Smolker, & Mann, 1996). Third, bottlenose dolphins nurse their young for 2-8 years (Mann et al., 2000), thus females cannot use postpartum mating as a strategy for reducing the risk of infanticide as seen in primates (van Schaik & Kappeler, 1997).

As is the case for many primate species, such as the savannah baboons previously discussed, female bottlenose dolphins are seen in year-round association with males (e.g. Wells et al., 1987). This association may serve as a strategy to avoid infanticide by strange males (Connor, Read, & Wrangham, 2000).

In addition to protection against infanticide, female bottlenose dolphins

may form groups with other females in order to protect against harassing males. This is particularly likely to be the case in areas, such as Shark Bay, where the herding of females by groups of males for mating purposes is common. In these situations, males engage in highly aggressive behaviors such as chasing, charging, biting and body slamming, in order to coerce the female to mate (Connor, Smolker, & Richards, 1992). Agonistic interactions between males and females are rarely observed in areas such as Sarasota, where herding is not a male reproductive strategy (Connor, Wells, et al., 2000), and females in these areas may join together for other reasons such as predator protection and calf survivorship (Wells, 1991).

The factors that drive group formation in animals are varied, but one thing is constant: for groups to stay together, the benefits derived from grouping must outweigh the costs. Costs and benefits may be immediately experienced by individuals in the group, but they can also be measured by the influence they have on an individual's lifetime reproductive fitness (Gowans et al., 2007).

Association Patterns

Social Structure

In addition to studying why groups form, it is important to identify the social structure, or organization, of a group. Ecological factors, such as those described in the previous section, contribute to the establishment of a particular social structure. Likewise, social structure defines ecological relationships between conspecifics (Whitehead, 1997), such as mortality, reproductive success, and dispersal (Whitehead, 2008). Thus, social structure is an important element in the population biology of a species (Wilson, 1975).

Additionally, social structure complexity has been linked to the advancement of cognitive abilities in animals. Among primates, for example, the ability to “distinguish group members as individuals and as kin, remember their relative ranks and past affiliations and, in some cases, remember even the personal histories of help given and received from various others” (Byrne, 1996, p. 175) allows individuals to maximize their inclusive fitness by behaving appropriately with other group members. Such cognitive abilities require considerable memory capacity (Byrne, 1996), thus increased neocortex size in social mammals has been linked with social complexity (e.g. group size, Dunbar, 1992).

Hinde (1976) proposed a conceptual framework for the analysis of social structure in non-human primate species, which has been adapted for the investigation of social behavior in a variety of animal species. This framework consists of three levels: interactions between individuals, relationships between individuals, and group social structure. Interactions between individuals are considered to be the foundation of the social structure of a species and involve sequences of behaviors performed by two or more individuals. As these individuals continue to interact with one another over time, a relationship emerges between them. In turn, the patterning of relationships among individuals in a group gives rise to social structure.

Use of this framework requires detailed information on the interactions occurring between individuals in a population (Whitehead & Default, 1999). For example, Hinde (1976) suggests that the description of interactions between individuals should not only involve the content of the interaction (i.e. what the

individuals are doing together), but also the quality of the interaction: "It must include understanding not only of the behavioural propensities of each of the participants..., but also of how each reacts with that particular other... to produce the behavior observed" (p. 4). Thus the successful application of Hinde's (1976) framework has been limited to species that live in situations where it is possible to collect such detailed data (Whitehead, 1997).

Unfortunately, species in which interactions between individuals occur out of the view of an observer are relatively inaccessible for this type of detailed analysis (Whitehead, 1997). Cetaceans, for example, spend a large portion of their time underwater, out of the view of observers (particularly in turbid waters). Therefore, in order to analyze the social structure of cetaceans, such as bottlenose dolphins, cetologists have relied on coefficients of association (COA's) as a substitute for detailed records of interactions (Whitehead & Default, 1999).

Two assumptions provide the rationale behind the use of such measures: a) social interactions are most likely to occur while animals are in close spatial proximity, and b) interactions between individuals are likely to take place among animals that are associated (i.e. in the same group; Brager, 1999). This second assumption is related to what Whitehead and Default (1999) refer to as the "gambit of the group"—the assumption that animals in a cluster (spatial or temporal) are interacting. The gambit of the group can be problematic, especially for cetologists, because definitions for grouping may not involve all members of the group (e.g. some members may be acoustically linked, though spatially separate; Whitehead, Christal, & Tyack, 2000). Additionally, membership in observed groups may have little to do with interactions; several individuals may

be clustered for non-social reasons, such as prey distribution or refuge from predators (Whitehead & Default, 1999).

Although problematic, Whitehead & Default (1999) suggest that the gambit of the group may be warranted in instances in which all, or most, of the interactions take place within a group. In the case of cetaceans, clusters of individuals seem to interact strongly with members of their group, thus the gambit of the group may be justified (Whitehead et al., 2000) and can be used to create a model of social structure (Whitehead & Default, 1999).

Association Indices

A variety of COA's can be calculated to determine how often two individuals are associated. Three of the most commonly used indices of association are: the Half-Weight Index, the Twice-Weight Index, and the Simple Ratio Index (Cairns & Schwager, 1987). Though each of these COA's use the same basic data set to calculate the association index, the sampling procedures used to collect the data can affect the accuracy of the chosen index (Cairns & Schwager, 1987).

In an effort to describe the conditions under which each of the indices results in an accurate measure of association, Cairns and Schwager (1987) used two simple models to compare each index to a maximum-likelihood estimator. The first of these models assumes that the population is divided into k groups, j of which are located by the observer. Under this model the maximum-likelihood estimator and the Half-Weight Index both accurately estimate p (the probability that a given pair will be together in the same group at the same time). The Twice-Weight Index and the Simple Ratio Index each underestimate p .

The second model proposed by Cairns and Schwager (1987) follows the same assumption as the first, but additionally assumes that one group has a different probability of being observed than all the others. Again, the Half-Weight Index performed better than both the Twice-Weight Index and the Simple Ratio Index, but it was less accurate than the maximum-likelihood estimator at estimating p .

In both models, the maximum-likelihood estimator was shown to be less biased than the other three indices. Unfortunately, as Cairns and Schwager (1987) point out, it may not always be possible to derive a maximum-likelihood estimator for the parameter of interest. Therefore, they suggest that researchers determine whether a sampling bias exists in the probability of locating a pair, either separately or together, prior to choosing a COA. If no bias exists, the Simple Ratio Index should be used. If a bias exists and is in favor of locating a pair when they are together, the Twice Weight is optimal, while if the pair is more likely to be located when they are in separate groups, the Half-Weight Index will be most accurate.

Coefficients of Association in Bottlenose Dolphins

Bottlenose dolphins worldwide exhibit fission-fusion social patterns. In this fluid system, group composition changes frequently as small groups fuse together to form larger groups and then break apart (Connor, Wells, et al., 2000; Cross, Lloyd-Smith, & Getz, 2005). The frequency and duration of the associations in such groups may be indicative of the strength of associations between individuals (Whitehead, 1999). Due to the nature of the fission-fusion social system, pairs of dolphins are more likely to be observed apart than

together. Therefore, the half-weight index (HWI) is commonly used in analysis of their social structure. This measure (once called the association index) was developed by Dice (1945) to quantitatively measure the co-occurrence of different plant species in a particular area. Eventually, zoologists adopted it as a measure of the association between individual animals (Brager, 1999). The HWI is calculated using the following formula:

$$2N / (n_a + n_b)$$

where N represents the number of observations in which both individuals a and b were present, n_a represents the total number of observations in which a (but not b) was observed, and n_b represents the total number of observations in which b (but not a) was observed (Cairns & Schwager, 1987; Rogers et al., 2004). The COA's resulting from the HWI indicate the strength of the association between two animals and ranges from 0.0 (two individuals never seen together) to 1.0 (two individuals always seen together). A high COA between a pair indicates a stronger association.

One caveat to the use of the HWI as a measure of association is that it can be affected by group size. There are two potential sources of bias when group size is large. The first is that large schools are more likely to be incompletely sampled, with some members of the group not being identified (Chilvers & Corkeron, 2002). This would drive down the number of joint sightings of a pair and affect the value of the HWI. Another source of bias stemming from group size is that the larger the group, the more likely two individuals are to be found together rather than separate. This increases the number of joint sightings and, in turn, affects the value of the index.

Studies of association patterns in bottlenose dolphins worldwide have revealed similarities as well as differences among populations. Typically, associations between individuals are weak and short-term, yet strong, long-term bonds have been observed. Females tend to form strong bonds (COA's near 1.0) with their calves (Rogers, Brunnick, Herzing, & Baldwin, 2004; Smolker et al., 1992; Wells et al. 1987) an association that remains high for the first three years of life (Wells et al., 1987). Female-female associations, on the other hand, are highly variable. While in some areas (e.g. Cedar Keys, Florida, Quintana-Rizzo & Wells, 2001) these associations are rather weak, in other areas (e.g. Sarasota Bay, Wells et al., 1987; Gulf de Guayaquil, Ecuador, Felix, 1997) females are often strongly associated with other females, forming "bands" that last for many years. Reproductive status is one factor that can influence the strength of association between females, with females forming associations with other females of similar status (Rogers et al., 2004). This is likely the result of similar energetic or defense needs (Cockroft & Ross, 1990).

Associations between adult males are generally low (Quintana-Rizzo & Wells, 2001; Rogers et al., 2004), but high degrees of association have been observed in several areas. As described previously, males in Shark Bay form alliances that result in COAs above 0.7 (Connor et al., 1992; Connor, Wells, et al., 2000) and strong bonds are also formed between adult males in Sarasota Bay (Wells et al., 1987). Interactions between males and females are less frequent than within sex class (Wells et al., 1987) and are strongly influenced by female reproductive state (Connor, Wells, et al., 2000; Rogers et al., 2004).

Besides forming associations with individuals of the same age/sex class,

bottlenose dolphins may have behaviorally specific associations. In an analysis of behavior state and association patterns, Gero, Bejder, Whitehead, Mann, and Connor (2005) found that dolphins form three general types of associations: dolphins that have preferred associations across all behavior states (affiliates), dolphins that never form preferred associations, but associate in at least one behavior state (acquaintances), and dolphins that form preferred associations in at least one, but not all behavior states. Affiliates were rare and typically involved adult males (5.7% of the study animals) while behavioral associates were more common (28.9%), but were most often formed between juveniles.

Unfortunately, as associations among individuals in a population vary naturally, COA's alone do not provide much information about social structure (Whitehead, 1999). For this reason, it is important to account for associations that occur at random and distinguish them from those that arise from preferred associations or avoidances (Bejder, Fletcher, & Brager, 1998). Bejder et al. (1998) created an algorithm that uses Monte Carlo simulations to statistically test whether the association index for a pair is greater than would be expected by chance alone. The algorithm randomly generates alternative data sets by "randomly selecting two individuals and two groups so that each individual is seen in only one of the groups, and each group contains only one of the individuals" (Whitehead, 1999, p. 26). The group allocations are then switched which creates a new association matrix with the same row and column totals. Randomly switching individuals in this way provides a means of retaining the number of times an individual was sighted and the group size so that it matches the original data set (Bejder et al., 1998). However, use of this algorithm requires

a sufficient number of permutations (typically 1,000 to 10,000) in order to avoid bias that may be a result of the randomized data matrices being too close to the original data set (Bejder et al., 1998).

New Techniques for Social Structure Analysis

Recently, tools that were created to study human social networks have been applied to the analysis of bottlenose dolphin social structure. Such techniques have not only provided information on community and sub-community structure, but have also allowed researchers to examine how these divisions within networks arise. For example, Lusseau and Newman (2004) observed that the communities found in a population of bottlenose dolphins in Doubtful Sound, New Zealand were formed via assortative mixing, whereby individual animals tend to associate with others who are like them (e.g. same age/sex class).

One such tool is the Girvan-Newman algorithm (Girvan & Newman, 2002), which uses centrality measures to define natural divisions within a network. This algorithm breaks the network into communities, ranging from one to n (n = the number of individuals in the network). This division is determined by the modularity index, Q , which measures the proportion of edges between individuals that are within a community in relation to the proportion of edges between communities (Croft, James, & Krause, 2008; Newman & Girvan, 2004). The best division is the one that results in the highest value of Q (Croft, James, & Krause, 2008). The centrality measure used in this algorithm is betweenness (Freeman, 1977), which is a measure of how often an individual (node) is encountered when traveling along the shortest path between all possible pairs in a network (Lusseau, 2007). The shortest path is determined by calculating the fewest

number of nodes one must pass through when moving along the edges (which represent associations between pairs) between one individual and another (Lusseau et al., 2006).

Another measure of centrality often used in network analysis is degree, which is the number of associates (edges) a dolphin has. It has been suggested that a dolphin's degree can function as a "measure of how much influence an individual can have on its peers" (Lusseau, 2007, p. 361). An individual with high degree is connected to many other individuals, and thus has a higher influence (Lusseau, 2007).

Dolphins with the highest betweenness values are often the individuals at the boundary between communities. Thus, when these individuals are removed from the network, tight knit communities emerge (Lusseau et al., 2006). The dolphins located at the boundaries between communities may function as brokers of information and may be responsible for maintaining the cohesiveness of the network (Lusseau & Newman, 2004). However, Whitehead (2008) argues that these individuals may just be young, highly exploratory individuals that, ultimately, have no effect on social bonds.

There is evidence to support the idea that dolphins at the boundaries between communities may play a role in maintaining network cohesiveness. Lusseau and Newman (2004) observed a decrease in interactions between two communities when the individual with the highest betweenness value temporarily disappeared. Upon the return of this individual, interactions between the two communities resumed. Thus, Lusseau and Newman (2004) suggested that management efforts geared toward the "preservation of certain key individuals

within a community may be crucial to maintaining its cohesion" (p. 480).

Bottlenose Dolphins in the Mississippi Sound

Stock Structure

Bottlenose dolphins inhabiting the United States coastal waters of the Gulf of Mexico are currently divided into 33 discrete stocks from the bays, estuaries and sounds, and these divisions have been supported by genetic data (Waring, Josephson, Fairfield-Walsh, & Maze-Foley, 2007). The bottlenose dolphins within the Mississippi Sound study area may be comprised of several "stocks". These stocks are referred to as communities (Wells et al., 1987) rather than populations, however, as there is often genetic exchange between neighboring areas (Waring et al., 2007). The genetic mixing and behavioral variability of dolphins along the Gulf coast make it difficult to create appropriate management strategies at a large-scale level (Waring et al., 2007). Thus, it has been suggested that management actions should focus on protecting local resident communities (Waring et al., 2007).

Previous research in the Mississippi Sound

A vast majority of the studies that have previously been conducted on dolphins in the Mississippi Sound have focused on population assessments. One of the first population assessments was an aerial survey of the coastal waters of Alabama, Mississippi, and eastern Louisiana in the summer of 1974 (Leatherwood & Platter, 1975). Several years later, Solangi and Dukes (1983) captured, freeze-branded, and released 50 bottlenose dolphins from the Mississippi Sound in an attempt to gather information on ranging patterns and collect baseline biological data. Immediately following this study, Lohoefer,

Hoggard, Ford, and Benigno (1990) used mark-recapture methods to estimate the abundance of dolphins in the area.

The most recent population assessment in the Sound was conducted by Hubard et al. (2004) who used boat-based line-transect methods to estimate abundance on a seasonal basis. These authors reported a peak in abundance in the summer, with an estimated abundance of approximately 2,000 dolphins. Estimates of the winter abundance were around 1,000 dolphins. Hubard et al. (2004) also reported site fidelity over various time scales in the area.

As previously mentioned, the Mississippi Sound is an area that is utilized for multiple human activities, each of which may have potential impacts on the bottlenose dolphins that also utilize the area. The previous research on bottlenose dolphin abundance in the Mississippi Sound can help assess how human disturbance may contribute changes in population size (Hubard et al., 2004). However, little work has been done to understand the residency patterns and social dynamics of the dolphins in the Sound, so it is difficult to assess the impact of human activities on these dimensions.

Human activities may result in some animals migrating away from the area (Bejder et al., 2006) or, in the worst case scenario, death of some individuals (Waring et al., 2007). Both of these outcomes could potentially lead to changes in residency and disrupt the social dynamics of the animals. Thus it is important to have a basic understanding of which animals are utilizing the area on a regular (seasonal or year-round) basis, as these animals may be most sensitive to anthropogenic disturbances.

Hurricane Katrina

In August of 2005, Hurricane Katrina swept through the Gulf coast causing massive damage to many coastal communities in Louisiana, Mississippi, and Alabama. In addition to the damage caused to homes and businesses, Katrina resulted in damage to many commercial and recreational vessels, resulting in a decrease in commercial and recreational traffic in the waters of the Mississippi Sound (Miller, Mackey, Hoffland, Solangi, & Kuczaj, in press).

The decrease in vessel traffic, coupled with a possible increase in prey abundance due to the reduction of fishing activities (Miller et al., in press), may have resulted in changes in the social interactions of the bottlenose dolphins that utilize the Mississippi Sound. The current study takes advantage of this natural disaster, to examine these potential effects.

Project Goals

The main goal of this project was to examine the residency patterns and associations of bottlenose dolphins in the Mississippi Sound region of the northern Gulf of Mexico. Specifically, my objectives were to:

- 1) Determine what proportion of identifiable individuals in the Mississippi Sound are year-round residents, seasonal residents, or transient animals.
- 2) Determine the average level of association for identifiable individuals by calculating the HWI between select individuals.
 - 2a) Compare the association values of year-round and seasonal residents to determine if there is a significant difference between the two residency classifications.

- 2b) Compare the number of associates among year-round and seasonal residents.
- 2c) Determine if associations among individuals in the area are different from random and whether there are preferred associations among individuals.
- 3) Employ social networking techniques to examine community structure of bottlenose dolphins in the Mississippi Sound.
 - 3a) Detect the presence of communities in the network by calculating the modularity index, Q , using the Girvan-Newman algorithm.
 - 3b) Calculate the betweenness and degree for each individual to identify the individuals that may play a role in maintaining the cohesion of the network.
 - 3c) Determine if dolphins in this area mix assortatively by residency classification or degree.
 - 3d) Examine the differences in network structure for networks of dolphins created based on sighting locations throughout the Sound.
- 4) Determine if Hurricane Katrina had any immediate effects on the social structure of the dolphins in the area by looking for differences in network centrality measures before and after the hurricane.

Figure 2. Map of the Mississippi Sound study area

CHAPTER II

METHODOLOGY

Study Site

The study site (Figure 2) was a 1496 km² portion of the Mississippi Sound (Sound) that extends from Pass Christian, MS at the west boundary (89° 10' W) to the Mississippi/Alabama border at the east boundary (88° 23' W). The southern boundary of the study area was the south side of the barrier islands that separate the Sound from the Gulf of Mexico (30° 5' N).

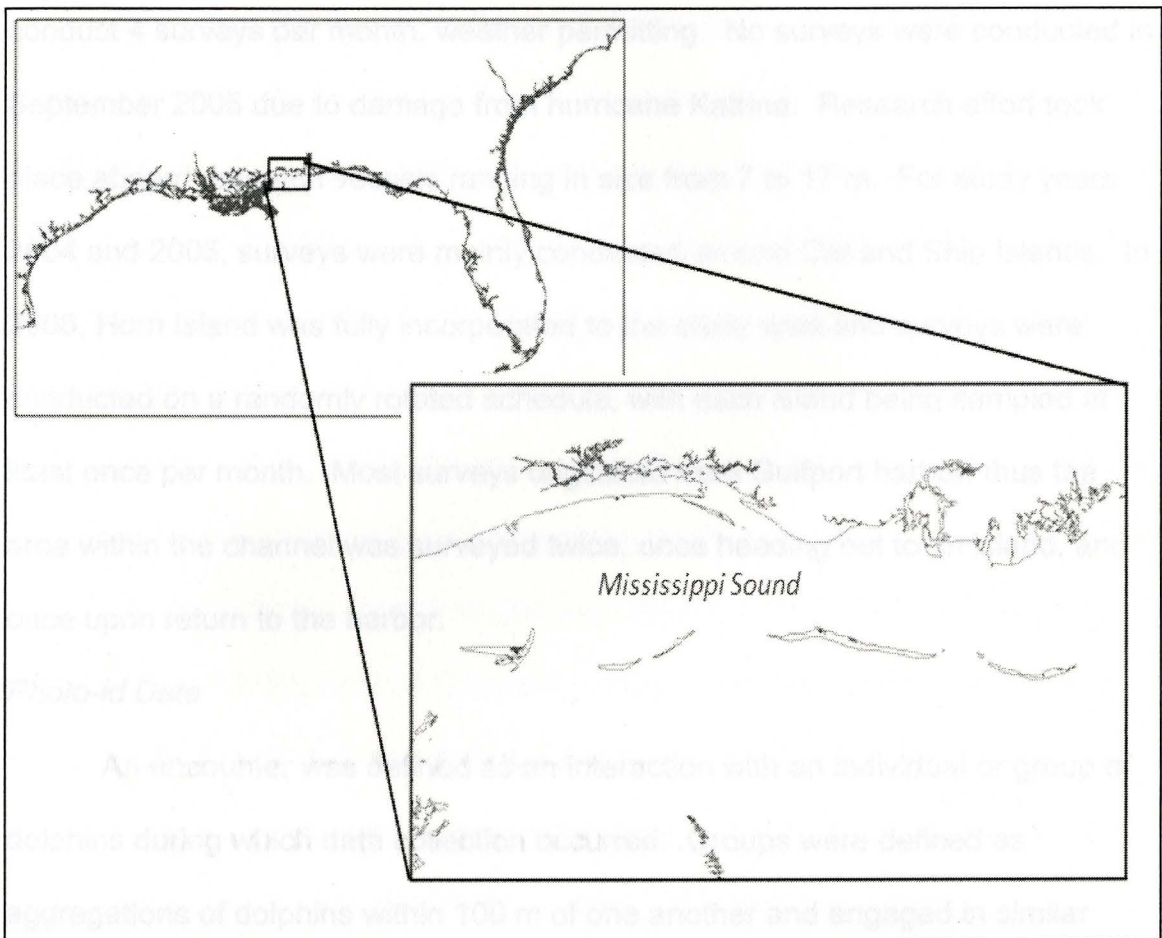


Figure 2. Map of the Mississippi Sound study area.

The average water depth in the Sound is 3 m (Chigbu, Gordon, & Strange, 2004), though there are two deep (~8m) shipping channels (Pascagoula and Gulfport) within the Sound. During the study, water temperature ranged from a mean low of 14.9° C in the winter to a mean high of 31.8° C in the summer.

Data Collection

Opportunistic surveys were conducted year round over a three-year period from May 2004 to April 2007. Each year of the study began in May and ended in April of the following year (e.g. May 2004 to April 2005). The goal was to conduct 4 surveys per month, weather permitting. No surveys were conducted in September 2005 due to damage from hurricane Katrina. Research effort took place aboard research vessels ranging in size from 7 to 17 m. For study years 2004 and 2005, surveys were mainly conducted around Cat and Ship Islands. In 2006, Horn Island was fully incorporated to the study area and surveys were conducted on a randomly rotated schedule, with each island being sampled at least once per month. Most surveys originated from Gulfport harbor, thus the area within the channel was surveyed twice, once heading out to an island, and once upon return to the harbor.

Photo-id Data

An encounter was defined as an interaction with an individual or group of dolphins during which data collection occurred. Groups were defined as aggregations of dolphins within 100 m of one another and engaged in similar activities (Lusseau et al., 2006; Wells et al., 1987). When a group of dolphins was sighted the boat was maneuvered toward the group and an attempt was made to take photographs of each dolphin's dorsal fin. Dorsal fins were

photographed using a Canon EOS 10D digital camera with a 400-mm zoom lens. Photos were cropped using Adobe Photoshop 7.1 so that a single dorsal fin was the focus of the frame. Individual fins were assessed for quality in five categories: focus, contrast, angle, fully visible, and distinctiveness. Photos of high quality were used to create a catalog of identifiable fins. Individuals were identified and matched based on distinctive markings on their dorsal fins (Wursig & Jefferson, 1990; Wursig & Wursig, 1977) and were verified by a second researcher trained in photo-identification.

Photo-identification is the standard method used by cetologists to differentiate individual dolphins. Dolphins can be identified by long-lasting dorsal fin features, such as nicks, notches, shape, and coloration (Wursig & Wursig, 1977; Wursig & Jefferson, 1990). Although other methods of identification exist (e.g. radio tagging, freeze-branding), they are often expensive and may pose risks to both dolphins and researchers (Scott, Wells, Irvine, Mate, 1990). Photo-id, on the other hand, is an inexpensive, non-invasive technique, that has allowed researchers to examine daily and long-range movements (e.g. Wells et al., 1990; Wood, 1998), determine home-ranges (e.g. Wursig & Wursig, 1977; Ballance, 1992; Defran, Weller, Kelly, & Espinosa, 1999), estimate population sizes (e.g. Hansen, 1990; Wilson, Hammond, & Thompson, 1999), and study individual associations and social structure (e.g. Brager, Wursig, Acevedo, & Henningsen, 1994; Smolker et al., 1992; Wells et al., 1987) of bottlenose dolphins.

While the validity of photo-identification has been addressed (Scott et al., 1990), it is difficult to assess the reliability of this method. Several factors contribute to the successful identification of individual dolphins, including sea

state, individual and group behavior, group size, light conditions, and photographer experience/ability.

Survey Data

In addition to photographing individual dorsal fins, environmental and behavioral data were collected. At the start of each encounter, time, location (using a Garmin GPSmap 76 global positioning device), and environmental variables (weather condition, Beaufort sea state, depth, salinity, glare, and water and air temperature) were recorded. Throughout the encounter, behavioral states (e.g. travel, feed, etc.) and events were recorded.

An encounter ended when 1) photographs were taken of most or all individuals and a minimum of 15 minutes of behavioral data was collected, 2) the dolphins disappeared from view, or 3) weather conditions deteriorated. At the end of an encounter, the time, GPS location, group size (minimum, maximum, and best estimate) and group composition (i.e. presence or absence of calves) were recorded. Additionally, the start and end frame numbers for the digital camera were recorded for the encounter.

Missing data. On occasion, data were not recorded properly, due to equipment malfunction or human error. In such situations, estimates were used. Survey distance and survey time were estimated by calculating the average distance and time for similar surveys (i.e. same islands were visited). Best group size for an encounter was estimated by averaging the minimum and maximum values for this measurement (which has a correlation of $r(337) = .97, p < .001$). If either the minimum or maximum value (or both) was missing this encounter was not included in the analysis.

Data Analyses

Residency

Residency patterns were determined based on the seasonal presence or absence of identifiable dolphins. Seasons in Mississippi are indistinct; thus, two seasons were defined based on a twenty-year history of sea surface temperature (SST; NOAA National Data Buoy Center): winter included the six months with the lowest mean SST (November-April), while summer included the six months with the highest mean SST (May-October).

The months in which each individual was sighted were determined and each individual was assigned to one of three residency categories, similar to those of Zolman (2002): year-round residents, seasonal residents, or transient/other. Year-round residents were defined as individuals identified in the study area in both seasons, independent of year. Seasonal residents were defined as individuals identified in the study area during the same seasonal timeframe over multiple years. Transient animals were defined as individuals sighted once or sighted in only one season in a single year. The number of individuals in each residency category was divided by the total number of identified individuals and multiplied by 100 to determine the percentage of dolphins in each residency classification.

Individual Identifications

A discovery curve (cumulative number of newly identified fins) was created to assess how many new dolphins were identified over the course of the study. In addition, a discovery curve was created for each residency classification to determine the identification patterns for each category. The

number of new identifications was analyzed for seasonal variation. The data did not satisfy the assumptions of an independent measures t-test, so non-parametric statistics were used.

Association Patterns

Association patterns were analyzed using the compiled version of SOCPROG 2.4 (Whitehead, 2009), which uses sighting information of individuals to compute the coefficient of association (COA) between two or more animals. Individuals sighted (photographed) within the same group were considered to be associated. To ensure independent sampling, only sightings that were at least one day apart were included in the analysis. Additionally, if an individual was sighted in more than one group in a single day, only the associations in the first sighting were analyzed for that individual.

Currently, there is a lack of consensus among those who study social association concerning a suitable minimum number of sightings required for inclusion in association analysis. Chilvers and Corkeron (2002) argued the importance of maintaining a balance between including individuals with low resighting frequencies and limiting inclusion to individuals with high resighting frequencies. The former ensures the data are representative, while the latter ensures reliability. While there is no agreed-upon standard, many studies have used five as the minimum number of sightings for inclusion in association analysis (Appendix A). Thus, the selection criterion for the current study was set at individuals sighted five or more times in the study period. These individuals are referred to as "select dolphins" from this point forward (following Fearnbach, 1997).

The half-weight index (HWI) was calculated as the coefficient of association (COA) for each possible pair (dyad) of dolphins. This index is frequently used in cetacean studies because it compensates for bias when individuals are more likely to be identified when separate than together (Cairns & Schwager, 1987) or if not all individuals present in the group are identified (Whitehead, 2008). As previously described, the HWI can range from 0.0 (two dolphins never seen together) and 1.0 (two dolphins always seen together). The HWI is calculated using the following formula (e.g. Rogers et al., 2004):

$$2N / (n_a + n_b)$$

N = number of observations in which a and b were present in same group

n_a = number of observations in which a was observed, but not b

n_b = number of observations in which b was observed, but not a

All non-zero COA values were used to calculate the mean and maximum COA for each select dolphin. From this, the overall mean COA and mean maximum COAs were calculated. Each COA was classified into one of five categories as used by Quintana-Rizzo & Wells (2001): low (0.10–0.20), low-moderate (0.21–0.40), moderate (0.41–0.60), moderate-high (0.61–0.80), and high (0.81–1.00). The COA's of year-round residents were compared to seasonal residents to determine if there are differences in associations among dolphins between these categories. The assumptions of an independent-samples t-test were not met, thus non-parametric statistics were used.

The total number of associates was determined for each select dolphin, as well as the mean number of associates for all select individuals combined. Any dolphin sighted in the same encounter as a select individual was considered an

associate and was included in this part of the analysis. The number of associates for year-round residents was compared to that of seasonal residents. The data met the assumptions of normality and homogeneity of variance, thus an independent measures t-test was used for this comparison.

The calculated COA values were tested for preferred/avoided associations, which was accomplished by creating randomized association matrices (as previously described) and calculating the COA for each dyad following each permutation. The “permute associations within samples” test was chosen because it controls for both movement into or out of the study area as well as differences in gregariousness among individuals (Whitehead, 2008). A monthly sampling period was used to ensure that a) associations between sampling periods were independent, and b) enough data was available within each sampling period to allow for a variety of possible permutations (Whitehead, 2008). If the standard deviation and coefficient of variability of the real associations is significantly larger than that of the randomly produced associations, then the null hypothesis that individuals are associating randomly can be rejected (Whitehead, 2008).

Network Structure

It has been suggested that for the purpose of simply describing social structure (without assuming the spread of information), a weighted network is more useful than the binary network previously described (Whitehead, 2008). In this case, the degree of an individual is calculated by summing the weights (COA's) on the edges connected to the node, rather than the number of edges connected to the node. Betweenness is determined by making the “length” of an

edge the inverse of its weight. Since there was no assumption of the transfer of information or disease in the current study, a weighted network was used to examine the social structure of bottlenose dolphins in the Sound.

Prior to analysis, the network of select individuals was filtered such that only dyads with a COA greater than the mean COA were included. This removed weak associations from the network and allowed the analysis to focus on the “core” component (Croft et al., 2008). Additionally, any individuals that had one or fewer associates after filtering were removed from the analysis. NetDraw (Borgatti, 2002) was used to create a visual display of the network, in which each individual is represented as a point (or node) and the associations between dyads are represented by lines connecting the nodes. The thickness of the line is an indication of the strength of the relationship (COA) of a dyad.

The Girvan-Newman algorithm was used to examine the structure of the network by calculating the modularity index, Q . The highest calculated value of Q was chosen as the best community division for the network.

Centrality measures (betweenness and degree) were calculated for each individual in the network, and the mean for each measure was obtained. Individuals with high values are expected to play large roles in keeping the network connected, possibly controlling the flow of information to others in the network either by being connected to many other individuals in the network (measured by degree; Lusseau et al., 2006) or by being located in between clusters, or communities in the network (measured by betweenness; Lusseau et al., 2006). Individuals with high betweenness and high degree values were

removed from the network one by one to examine what role that these individuals play in the Mississippi Sound network.

The types of associations formed by individuals in the network were also examined. In order to determine if the dolphins in the Sound preferentially associate based on residency classification, a randomized autocorrelation using a chi-square test was performed in Ucinet (Borgatti, Everett, & Freeman, 2002). Similarly, a randomized autocorrelation was performed to determine whether individuals of high degree tend to form associations with other individuals of high degree. Assorting by degree is common among human networks (Croft et al., 2008), though it has not been demonstrated with dolphins (Lusseau & Newman, 2004). This autocorrelation was performed using Moran's I statistic, which was originally used to measure geographic spatial correlation, but has been adapted in social networking to measure the network distance between individuals (Hanneman & Riddle, 2005). Dolphins closer to one another in the network are presumed to interact more closely with one another (Croft et al., 2008).

Social networks were also created based on the location of sightings of individuals. Dolphins that were sighted two or more times were included in this analysis. A separate network was created for each island (Cat, Ship, and Horn) as well as Gulfport channel, hereto referred to as the channel. If an individual was sighted at a particular island or within the channel, they were included in the network for that location. For this analysis, a binary network was used such that the edges represent whether a pair was observed in the same group at the location at any time.

In order to examine the effects of Hurricane Katrina on the social structure of bottlenose dolphins in the study area, a variety of centrality measures were calculated using 2.4 (Whitehead, 2009). These measures included strength, eigenvector, reach, clustering coefficient, and affinity. Appendix B provides a description of each of these measures based on Whitehead (2008). Individuals were only included in the analysis if they were sighted two or more times over a ten month period (October to August) both before and after Hurricane Katrina. The criterion of two sightings in each condition was chosen in order to minimize the inflation of HWI values due to individuals being sighted only once.

($F(2, 126) = 1.36, p = .26$) as well as across seasons ($F(1, 127) = 2.14, p = .15$). Likewise, the total distance surveyed was consistent between years ($F(2, 126) = 0.07, p = .93$) and seasons ($F(1, 127) = 1.04, p = .31$). Table 1 presents the survey effort for all three years while Tables 2-4 present monthly summary data for each year.

Table 1

Summary of Yearly Survey Effort

Year	Number of Surveys	Total Survey Hours	Total Distance Surveyed (km)	Total Encounters
2004	43	218.52	3278.1	166
2005	41	222.65	3214.8	191
2006	45	218.87	3461.4	229

CHAPTER III

RESULTS

Survey Effort

Overall, 129 boat-based surveys were completed from May 2004 to April 2007. No surveys were conducted in September 2005 due to damage from Hurricane Katrina. Approximately 660 survey hours were logged, covering a total of approximately 9,955 km. Fifty-eight percent (384.6 hours) of the survey time was spent actively searching for dolphins, while the remaining time was spent in direct observation of dolphins. Surveys lasted an average of 5.1 hours ($SD = 1.5$) and survey duration was statistically similar between all three years of the study ($F(2, 126) = 1.36, p = .26$) as well as across seasons ($F(1, 127) = 2.14, p = .15$). Likewise, the total distance surveyed was consistent between years ($F(2, 126) = .07, p = .93$) and seasons ($F(1, 127) = 1.04, p = .26$). Table 1 presents the survey effort for all three years while Tables 2-4 present monthly summary data for each year.

Table 1

Summary of Yearly Survey Effort

Year	Number of Surveys	Total Survey Hours	Total Distance Surveyed (km)	Total Encounters
2004	43	218.55	3278.1	168
2005	41	222.85	3214.8	191
2006	45	218.67	3461.4	229

Table 2

Summary of Monthly Survey Effort for 2004

Effort variables	May	June	July	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	Total
Number of surveys	5	4	4	4	4	4	4	3	2	2	3	4	43
Total survey hours	18.9	18.3	20.3	20.7	19.9	22.0	23.3	16.3	10.7	12.3	16.1	19.9	218.7
Average daily survey hours	3.8	4.6	5.1	5.2	5.0	5.5	5.8	5.4	5.4	6.2	5.4	5.0	62.2
Km traveled	221.6	254.5	294.7	332.3	326	355.6	320.6	181.4	180	203.2	289.4	318.8	3278.1
Total number of encounters	19	19	18	20	8	18	14	12	4	9	9	18	168
Total hours with dolphins	8	8.5	11.6	8.6	3.9	7.8	7.3	7.1	3.4	5.4	4.5	8.3	84.4
Average daily hours with dolphins	1.6	2.1	2.9	2.2	1.0	2.0	1.8	2.4	1.7	2.7	1.5	2.1	23.9
Estimated number dolphins encountered	84	93	118	115	72	141	69	57	20	24	42	77	912

Table 3

Summary of Monthly Survey Effort for 2005

Effort variables	May	June	July	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	Total
Number of surveys	4	4	6	4	--	2	3	2	4	4	4	4	41
Total survey hours	20.9	21	49.9	22.7	--	10.7	14	5.6	18.3	16.5	24.3	19	22.9
Average daily survey hours	5.2	5.3	8.3	5.7	--	5.4	4.7	2.8	4.6	4.1	6.1	4.8	56.8
Km traveled	290.6	244.9	556.9	285.2	--	143.6	200.7	115.5	420.3	314.1	370.9	272.3	3215
Total number of encounters	16	14	40	19	--	12	12	4	12	14	29	19	191
Total hours with dolphins	9.7	12.8	23.1	10.6	--	5	7.3	1.4	6.3	4.9	11.7	8.3	101.1
Average daily hours with dolphins	2.4	3.2	3.9	2.7	--	2.5	2.4	0.7	1.6	1.2	2.9	2.1	25.6
Estimated number dolphins encountered	136	207	626	234	--	147	133	17	53	43	143	162	1901

Note. No data were collected in September 2005 due to Hurricane Katrina

Table 4

Summary of Monthly Survey Effort for 2006

Effort variables	May	June	July	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	Total
Number of surveys	2	4	4	4	4	3	4	3	3	7	4	3	45
Total hours of effort	10.3	24.4	21.6	17.9	22.5	15.5	21.6	14.7	8.5	26.5	22.4	12.9	218.8
Average daily hours effort	5.2	6.1	5.4	4.5	5.6	5.2	5.4	4.9	2.8	3.8	5.6	4.3	58.7
Km traveled	177.1	377.8	308.6	269.6	285.9	192.6	332.4	268.9	158.1	473.8	387.1	229.5	3461.4
Total number of encounters	13	25	22	20	23	11	24	14	10	28	25	14	229
Total hours with dolphins	4	12.2	9.1	9.3	11.2	4.2	6.3	4.5	2.2	7.6	6.1	4.6	81.3
Average daily hours with dolphins	2.0	3.1	2.3	2.3	2.8	1.4	1.6	1.5	0.7	1.1	1.5	1.5	21.8
Estimated number dolphins encountered	69	297	259	274	229	138	116	81	26	103	166	107	1865

Figure 3. Map of sighting locations over the study period (May 2004 – April 2007, N = 190).

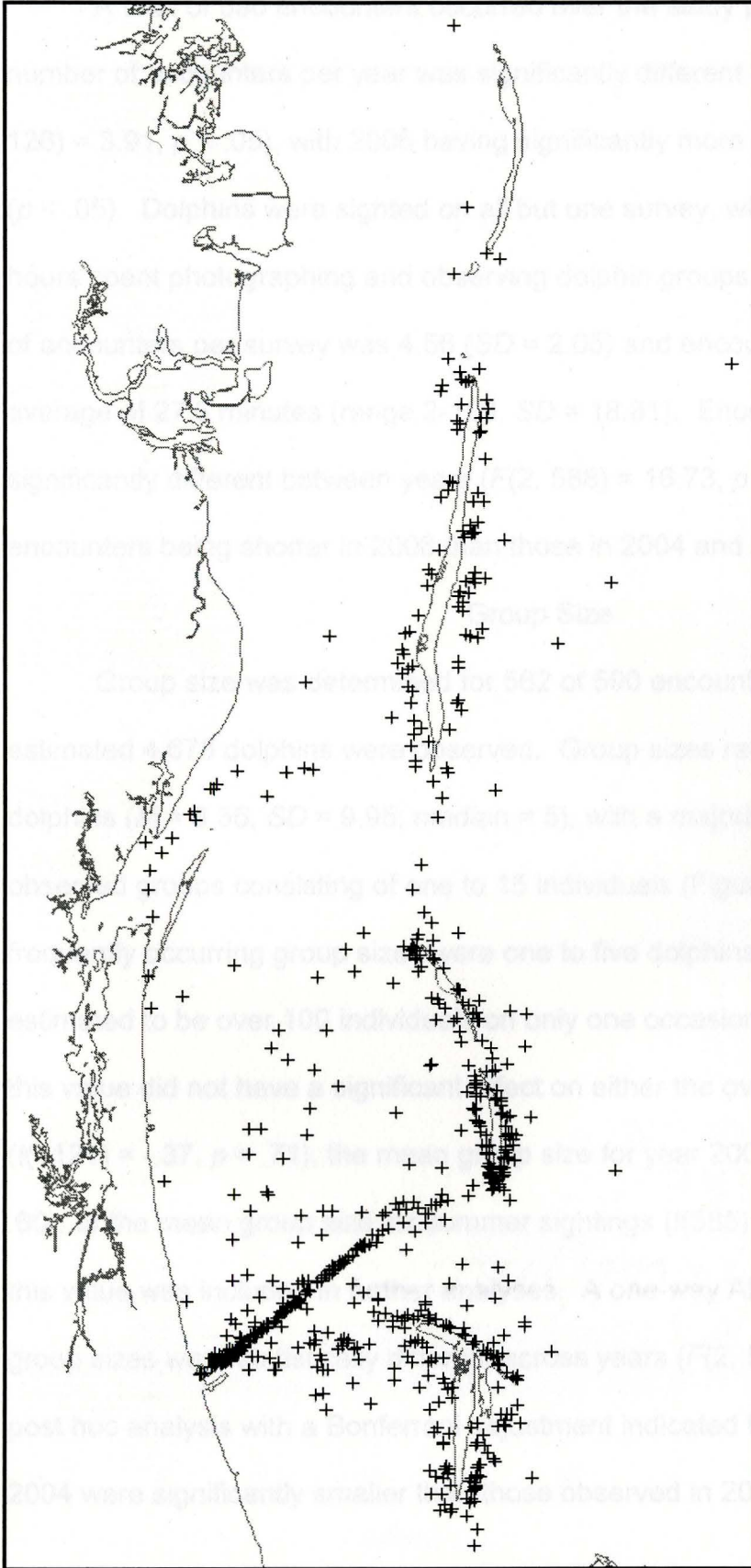


Figure 3. Map of sighting locations over the study period (May 2004 – April 2007; N = 590).

A total of 590 encounters occurred over the study period (Figure 3). The number of encounters per year was significantly different between years ($F(2, 126) = 3.91, p < .05$), with 2006 having significantly more encounters than 2004 ($p < .05$). Dolphins were sighted on all but one survey, with approximately 275.7 hours spent photographing and observing dolphin groups. The average number of encounters per survey was 4.56 ($SD = 2.05$) and encounters lasted an average of 27.5 minutes (range 2-103, $SD = 18.81$). Encounter duration was significantly different between years ($F(2, 588) = 16.73, p < .001$), with encounters being shorter in 2006 than those in 2004 and 2005 ($p < .001$).

Group Size

Group size was determined for 562 of 590 encounters (95%) and an estimated 4,678 dolphins were observed. Group sizes ranged from one to 125 dolphins ($M = 8.35, SD = 9.95$; median = 5), with a majority (87.2%) of the observed groups consisting of one to 15 individuals (Figure 4). The most frequently occurring group sizes were one to five dolphins. Group size was estimated to be over 100 individuals on only one occasion (July 2005); however, this value did not have a significant effect on either the overall mean group size ($t(1121) = -.37, p = .71$), the mean group size for year 2005 ($t(369) = -.53, p = .60$), or the mean group size for summer sightings ($t(585) = -.43, p = .67$), thus this value was included in further analyses. A one-way ANOVA revealed that group sizes were statistically different across years ($F(2, 559) = 7.27, p < .01$). A post hoc analysis with a Bonferroni adjustment indicated that groups observed in 2004 were significantly smaller than those observed in 2005 ($p < .01$).

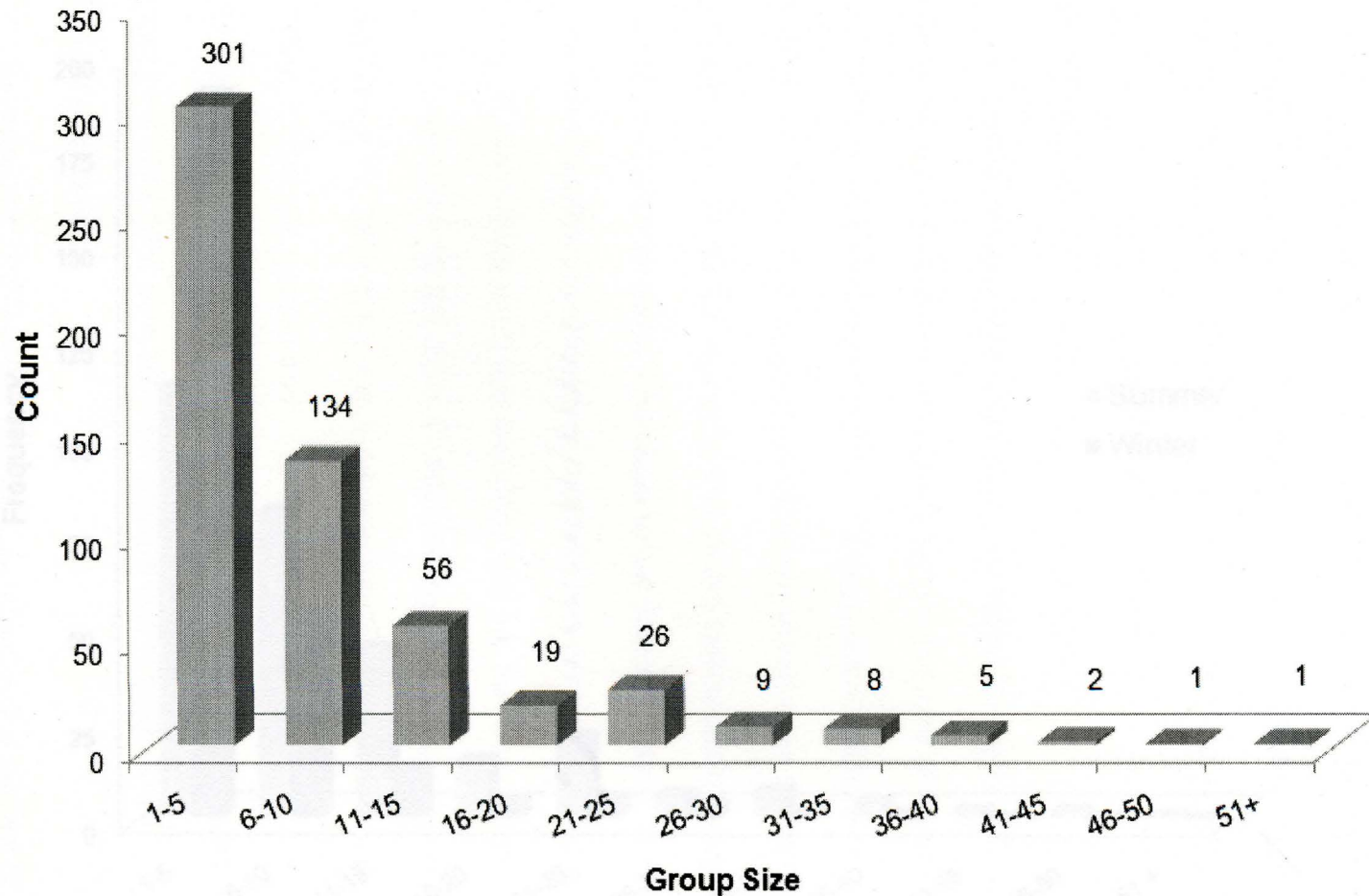


Figure 4. Frequency distribution of group size for all sightings for which group size was determined (n = 562).

Figure 5. Frequency distribution of group size by season (summer, n = 204, winter, n = 358).

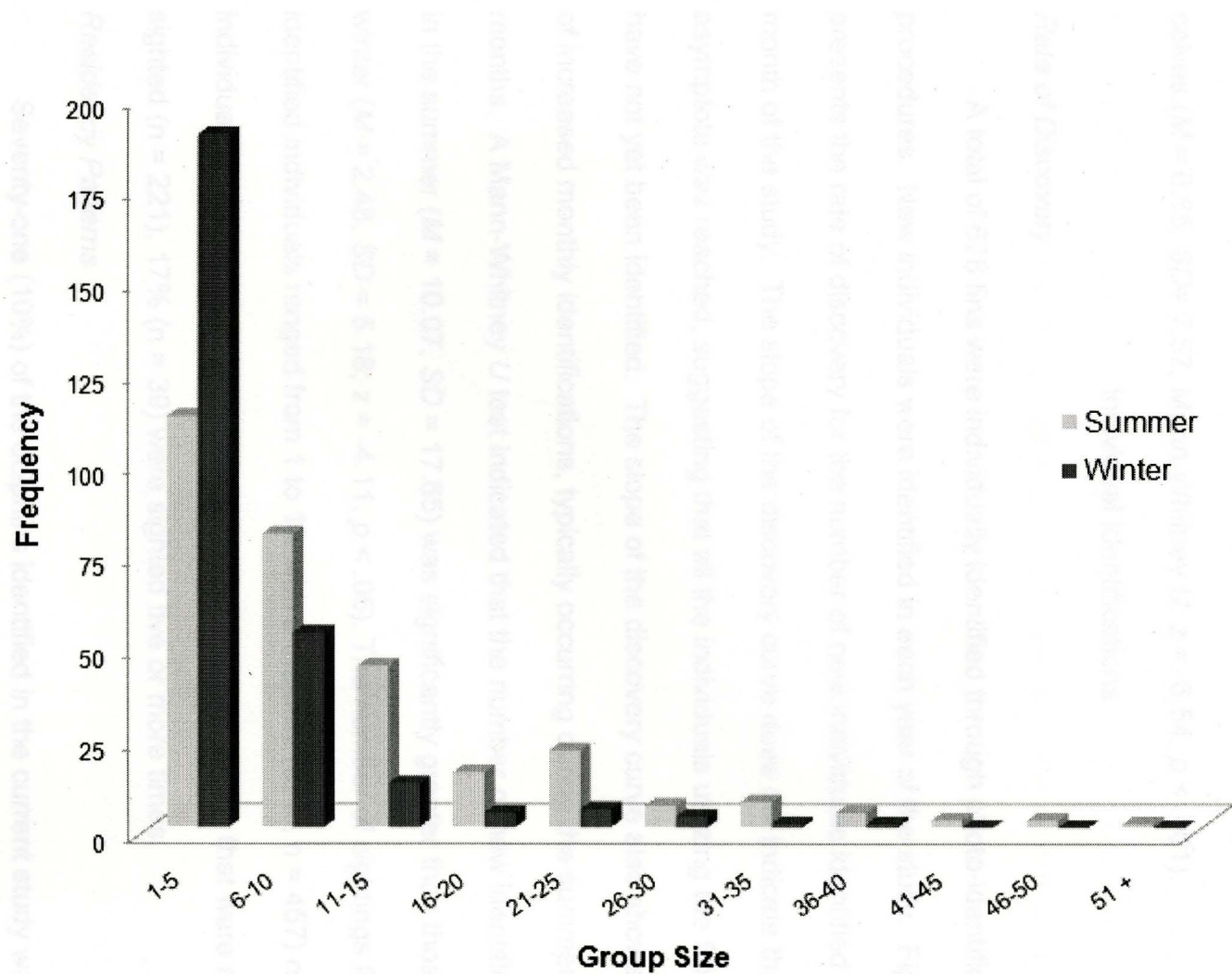


Figure 5. Frequency distribution of group size by season (summer, n = 294; winter, n = 268).

Group size was also influenced by both season and group composition. Groups of dolphins observed in the summer months ($M = 11.06$, $SD = 11.94$) were significantly larger than those observed during the winter ($M = 5.37$, $SD = 5.88$; Mann-Whitney U : $z = -8.11$, $p < .01$). Figure 5 presents a frequency distribution of group size by season. Groups in which at least one calf was present ($M = 10.90$, $SD = 12.01$) were significantly larger than groups without calves ($M = 6.65$, $SD = 7.57$; Mann-Whitney U : $z = -6.54$, $p < .001$).

Individual Identifications

Rate of Discovery

A total of 678 fins were individually identified through photo-identification procedures. New individuals were identified in each year of the study. Figure 6 presents the rate of discovery for the number of new individuals identified each month of the study. The slope of the discovery curve does not indicate that an asymptote was reached, suggesting that all the individuals utilizing the Sound have not yet been identified. The slope of the discovery curve also shows spurts of increased monthly identifications, typically occurring during the summer months. A Mann-Whitney U test indicated that the number of new identifications in the summer ($M = 10.07$, $SD = 17.65$) was significantly greater than those in the winter ($M = 2.48$, $SD = 5.18$; $z = -4.11$, $p < .05$). The number of sightings for identified individuals ranged from 1 to 10, with a majority (67%, $n = 457$) of the individuals being sighted only once (Figure 7). Of the dolphins that were re-sighted ($n = 221$), 17% ($n = 39$) were sighted five or more times.

Residency Patterns

Seventy-one (10%) of the dolphins identified in the current study were

classified as year-round residents based on their sighting histories. The number of re-sightings of year-round residents ranged from 2 to 10 ($M = 3.76$, $SD = 2.05$), with considerable variability in the amount of time separating re-sightings (range: 0 - 34 months, $M = 5.70$, $SD = 5.52$). A total of 21 (29.6%) year-round residents were sighted in each year of the study. Ninety-three percent ($n = 66$) of year-round residents had first been identified by the end of the second year of the study (April 2006). Figure 8 shows the discovery curve of individuals identified over the study period based on residency classification. The identification of individuals classified as year-round residents had a low slope and reached an asymptote by September 2006.

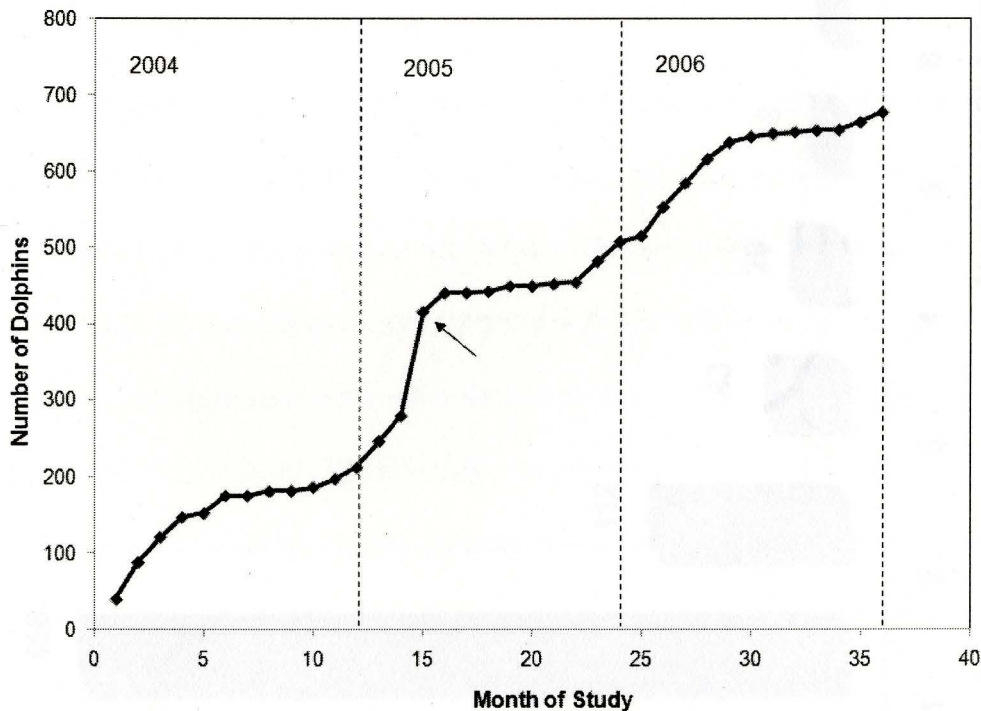


Figure 6. Discovery curve for new identifications in each month of the study period. Arrow indicates when Horn Island was added to the study area (July 2005).

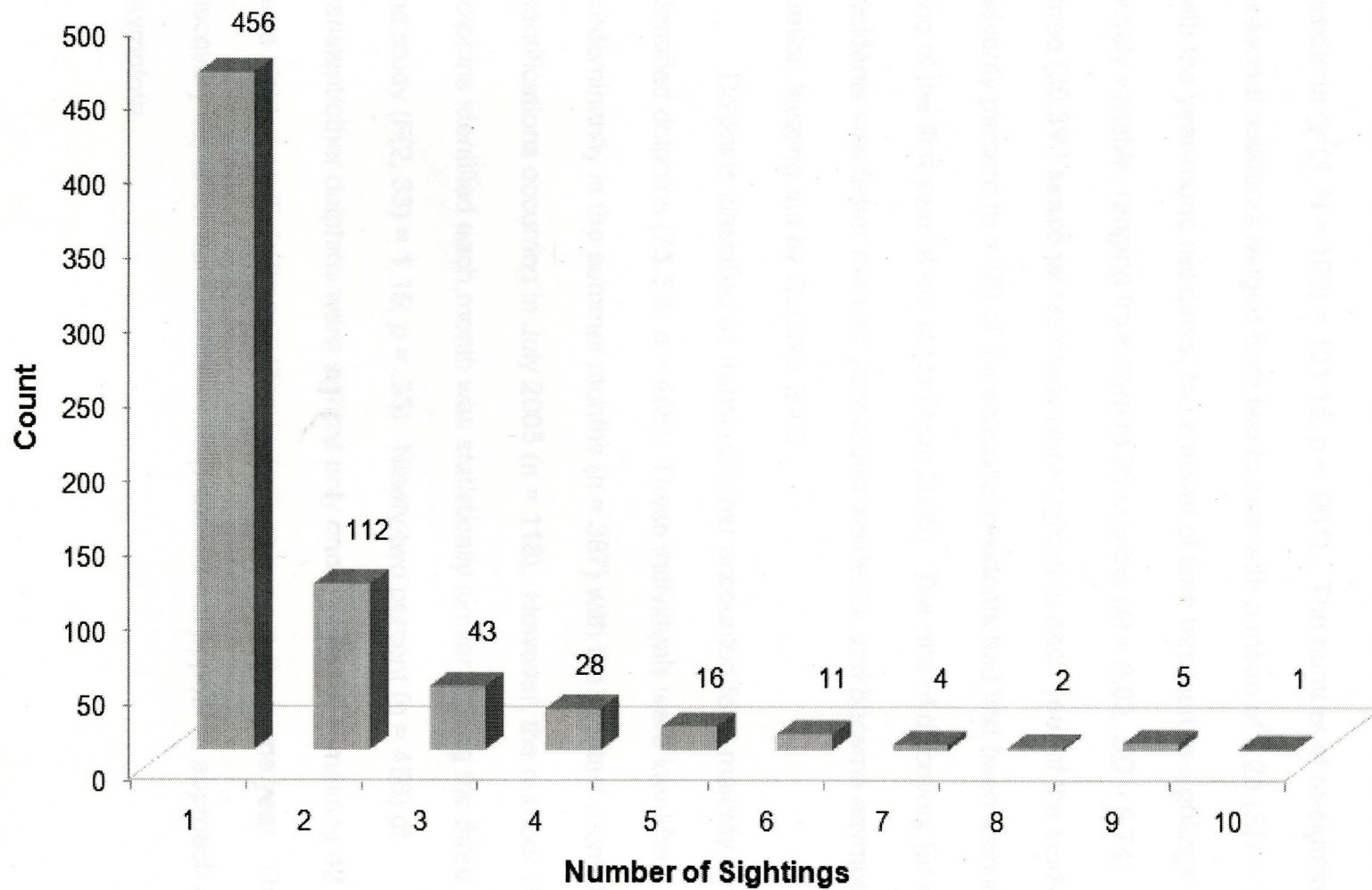


Figure 7. Frequency distribution of number of sightings for bottlenose dolphins in the Mississippi Sound (N = 678).

Approximately 16% ($n = 109$) of the identified dolphins were classified as seasonal residents. A majority of these ($n = 107$) were seasonal residents during the summer months, while two dolphins were classified as winter seasonal residents ($\chi^2(1, N = 109) = 101.15, p < .001$). The number of re-sightings of seasonal residents ranged from two to nine with a mean of 3.25 ($SD = 1.57$). As with the year-round residents, the amount of time between re-sightings was widely variable, ranging from zero to 26 months ($M = 8.02, SD = 6.74$). Thirty-three (30.3%) seasonal residents were sighted in each year of the study. Seventy percent ($n = 76$) of the seasonal residents had first been identified by the end of the first year of the study (April 2005). The rate of discovery for seasonal residents was faster than for year-round residents, and became asymptotic earlier, leveling out by October 2005.

Dolphins classified as transient/other accounted for a majority of the identified dolphins (73.5%; $n = 498$). These individuals were identified predominantly in the summer months ($n = 387$) with the greatest monthly identifications occurring in July 2005 ($n = 118$). However, the number of transient dolphins identified each month was statistically similar among the three years of the study ($F(2, 33) = 1.15, p = .33$). Ninety-two percent ($n = 456$) of transient/other dolphins were sighted only once, while the remaining 42 dolphins were sighted multiple times within a single season in the same year. The discovery curve for transient/other dolphins did not appear to approach an asymptote.

Association Patterns

Thirty-nine dolphins met the selection criteria of five or more sightings for inclusion in the analysis of association patterns. The mean number of sightings for select dolphins was 6.3 (range: 5 - 10, $SD = 1.5$). Seventy-nine percent ($n = 31$) of the select dolphins were sighted in each year of the study period. Of the remaining eight select dolphins, four were sighted in the first two years of the study, three were sighted in the last two years of the study, and one was sighted in the first and last years of the study.

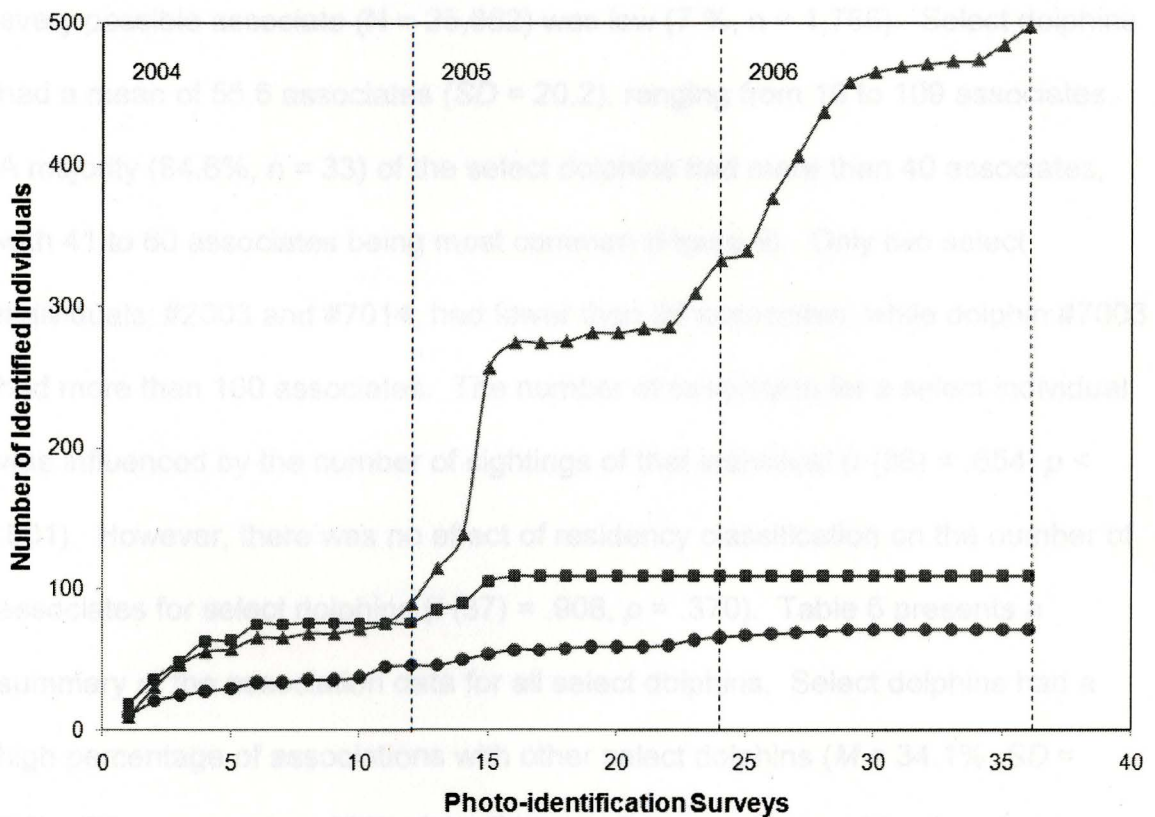


Figure 8. Discovery curve of new dolphin identifications by residency classification.

Note. Circles represent year-round residents ($n = 71$), squares represent seasonal residents ($n = 109$), and triangles represent transient/other individuals ($n = 498$).

Select dolphins were observed in groups ranging from 3 to 45 dolphins. Since select dolphins were often sighted in groups with other select dolphins, the overall mean group size for select dolphins could not be determined. However, the mean group size for each select individual is presented in Table 5.

Number of Associates

Of the 39 select dolphins, 22 (56.4%) were classified as year-round residents while the remaining 17 (43.6%) were classified as summer seasonal residents. The percent of associations observed between select dolphins and every possible associate ($N = 25,662$) was low (7 %, $n = 1,786$). Select dolphins had a mean of 55.6 associates ($SD = 20.2$), ranging from 16 to 109 associates. A majority (84.6%, $n = 33$) of the select dolphins had more than 40 associates, with 41 to 60 associates being most common (Figure 9). Only two select individuals, #2003 and #7014, had fewer than 25 associates, while dolphin #7003 had more than 100 associates. The number of associates for a select individual was influenced by the number of sightings of that individual ($r(38) = .654, p < .001$). However, there was no effect of residency classification on the number of associates for select dolphins ($t(37) = .908, p = .370$). Table 6 presents a summary of the association data for all select dolphins. Select dolphins had a high percentage of associations with other select dolphins ($M = 34.1\%$, $SD = 5.3$). Fifty percent ($n = 372$) of the 741 possible pairwise combinations between any two select individuals were observed.

Table 5

Mean, Standard Deviation, and Range of Group Size for Select Dolphins

Dolphin ID (No. of groups analyzed)	Residency	Mean group size	SD	Range
1002 (9)	seasonal	25.1	9.9	10 - 40
2002 (5)	seasonal	15.2	9.8	5 - 25
2003 (6)	year-round	11.7	7.6	5 - 25
2010 (5)	year-round	20.2	12.0	11 - 40
2014 (7)	seasonal	26.6	10.3	12 - 40
2020 (5)	year-round	19.8	13.2	6 - 40
5003 (6)	year-round	15.8	7.2	6 - 25
5007 (6)	seasonal	24.5	12.0	10 - 40
5016 (5)	seasonal	26.6	12.7	15 - 40
6001 (8)	year-round	19.0	11.2	3 - 40
6006 (5)	seasonal	23.0	10.9	12 - 40
6011 (6)	year-round	15.5	7.0	8 - 25
6019 (5)	year-round	13.6	4.2	9 - 20
6031 (8)	year-round	15.3	6.9	7 - 25
6040 (5)	seasonal	20.2	6.6	13 - 25
6041 (5)	seasonal	19.8	6.4	13 - 25
6054 (5)	year-round	23.4	15.4	9 - 40
6055 (5)	year-round	21.2	11.9	8 - 40
6099 (5)	seasonal	20.4	12.4	10 - 40
7002 (9)	year-round	16.4	10.1	7 - 40
7003 (9)	seasonal	25.3	14.4	7 - 45
7005 (6)	year-round	14.0	7.4	3 - 25
7011 (6)	seasonal	23.3	12.3	10 - 40
7013 (5)	year-round	19.4	11.0	7 - 35
7014 (5)	seasonal	14.0	12.3	4 - 35
7015 (6)	year-round	23.8	10.7	10 - 40
7025 (5)	year-round	14.2	4.3	9 - 20
7026 (6)	year-round	14.0	7.1	6 - 25
7027 (6)	seasonal	19.0	6.2	9 - 25
7030 (6)	year-round	15.2	12.6	6 - 40
7042 (6)	year-round	18.3	13.0	6 - 40
7055 (8)	year-round	20.3	12.0	6 - 40
7058 (9)	seasonal	24.3	10.3	10 - 40
7060 (10)	year-round	19.1	10.4	6 - 40
7077 (7)	seasonal	22.0	9.8	10 - 40
7093 (5)	seasonal	21.0	4.2	15 - 25
8003 (5)	year-round	23.6	14.4	8 - 40
8004 (5)	seasonal	15.4	6.4	6 - 25
8013 (7)	year-round	11.7	6.2	4 - 23

Number of Associates

Of the 39 select dolphins, 22 (56.4%) were classified as year-round residents while the remaining 17 (43.6%) were classified as summer seasonal residents. The percent of associations observed between select dolphins and every possible associate ($N = 25,662$) was low (7 %, $n = 1,786$). Select dolphins had a mean of 55.6 associates ($SD = 20.2$), ranging from 16 to 109 associates. A majority (84.6%, $n = 33$) of the select dolphins had more than 40 associates, with 41 to 60 associates being most common (Figure 9). Only two select individuals, #2003 and #7014, had fewer than 25 associates, while dolphin #7003 had more than 100 associates. The number of associates for a select individual was influenced by the number of sightings of that individual ($r(38) = .654$, $p < .001$). However, there was no effect of residency classification on the number of associates for select dolphins ($t(37) = .908$, $p = .370$). Table 6 presents a summary of the association data for all select dolphins. Select dolphins had a high percentage of associations with other select dolphins ($M = 34.1\%$, $SD = 5.3$). Fifty percent ($n = 372$) of the 741 possible pairwise combinations between any two select individuals were observed.

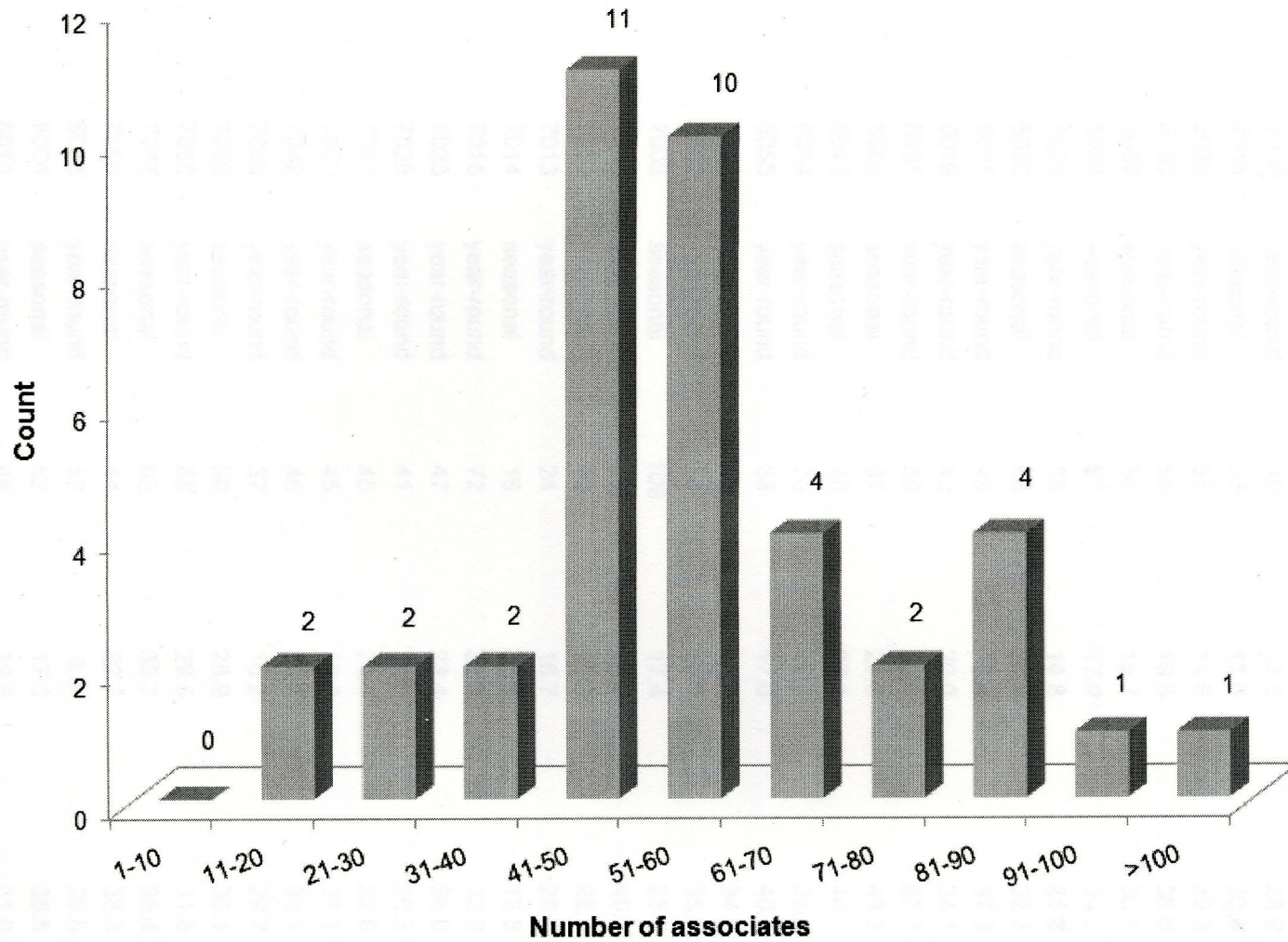


Figure 9. Frequency distribution of the number of associates for select dolphins (n = 39).

Table 6

Summary of Association Data for Select Individuals (n = 39).

Dolphin ID	Residency	Number of associates	Percent repeat associates	Percent of select associates
1002	seasonal	79	32.9	34.1
2002	seasonal	55	29.0	40.0
2003	year-round	20	5.0	35.0
2010	year-round	40	12.5	28.9
2014	seasonal	59	13.6	36.8
2020	year-round	55	14.5	39.3
5003	year-round	56	19.6	38.6
5007	seasonal	57	19.3	36.4
5016	seasonal	67	17.9	34.3
6001	year-round	88	14.8	25.8
6006	seasonal	68	30.9	32.4
6011	year-round	49	18.4	37.3
6019	year-round	40	20.0	34.1
6031	year-round	60	25.0	37.7
6040	seasonal	37	27.0	43.2
6041	seasonal	48	27.1	44.7
6054	year-round	70	15.7	35.2
6055	year-round	53	17.0	40.4
6099	seasonal	53	1.9	34.5
7002	year-round	84	11.9	35.3
7003	seasonal	109	17.4	25.7
7005	year-round	28	17.9	40.7
7011	seasonal	49	16.3	26.5
7013	year-round	24	16.7	28.0
7014	seasonal	16	31.3	18.8
7015	year-round	72	22.2	32.9
7025	year-round	47	23.4	38.0
7026	year-round	41	2.4	26.2
7027	seasonal	45	24.4	32.6
7030	year-round	45	15.6	31.1
7042	year-round	46	30.4	39.1
7055	year-round	37	16.2	29.7
7058	seasonal	90	28.9	30.1
7060	year-round	88	29.5	31.8
7077	seasonal	63	39.7	35.4
7093	seasonal	44	22.7	33.3
8003	year-round	57	8.8	35.8
8004	seasonal	52	17.3	38.5
8013	year-round	46	19.6	31.8

Select dolphins were often observed with repeated associates, with recurring individuals being sighted from 2 to 7 times together. Sixty-seven percent ($n = 26$) of the select dolphins had between 6 and 15 repeat associates. On average, 21% of a select individual's associates were repeated associations (range: 1.82 – 42.4%; $SD = 0.09$). Seasonal select dolphins had a higher mean percent of repeated associates than year-round select dolphins ($t(37) = 2.52$; $p < .05$). However, a Mann-Whitney U test revealed no statistical difference between the two residency classifications regarding the number of times of repeated associates were observed ($z = -.78$, $p = .44$).

Strength of Associations

The non-zero COA values for associations between select dolphins ranged from 0.10 to 0.91, with a mean COA value of 0.25 (range: 0.10 – 0.91, $SD = 0.13$). Appendix C shows a matrix of the associations among the select dolphins. Most of the observed associations were in the low level (59.4%; $n = 221$) and moderate-low level (31.7%; $n = 118$) categories, while 7.0% ($n = 26$) were categorized as moderate. Very few COA's were considered moderate-high level (1.3%; $n = 5$) or high level (0.5%; $n = 2$) (Figure 10).

Figures 11 and 12 show the distribution of mean and maximum COA values for select individuals based on residency classification, respectively. On an individual level, all 39 select dolphins had a mean COA with other select dolphins less than 0.40. Twenty-six percent ($N = 10$) of the select dolphins had a mean COA in the low level category, while the remaining select individuals ($N = 29$) had a mean COA in the moderate-low category. Maximum COA's for select dolphins ranged from 0.25 to 0.91 ($M = 0.55$, $SD = 0.20$), with a majority of the

maximum COA values falling into the moderate-low (41.0%) and moderate (30.8%) categories. Following an arcsine transformation, it was determined that seasonal residents had significantly higher mean COA values (Mann-Whitney U : $z = -2.17$, $p < .05$) as well as maximum COA values (Mann-Whitney U : $z = -2.79$, $p < .01$) than year-round residents.

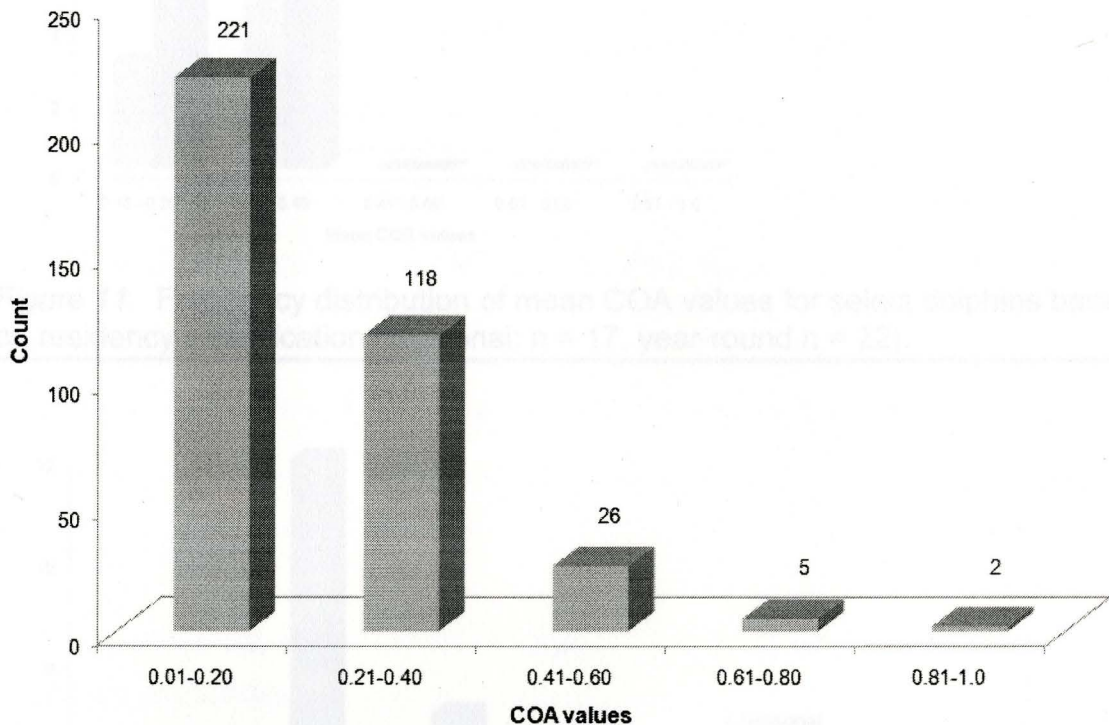


Figure 10. Frequency distribution of observed non-zero COA values for associations between the 39 select dolphins (N = 372).

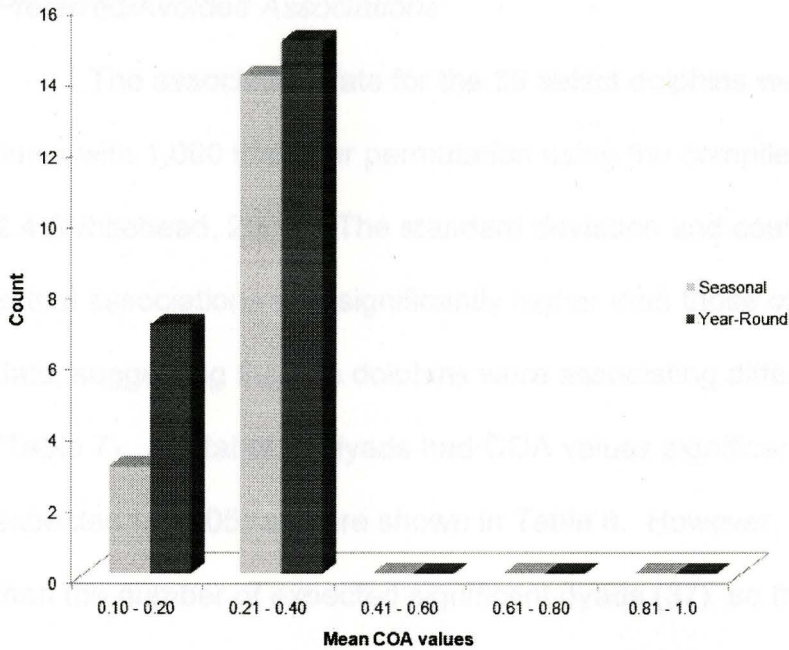


Figure 11. Frequency distribution of mean COA values for select dolphins based on residency classification (seasonal: n = 17, year-round n = 22).

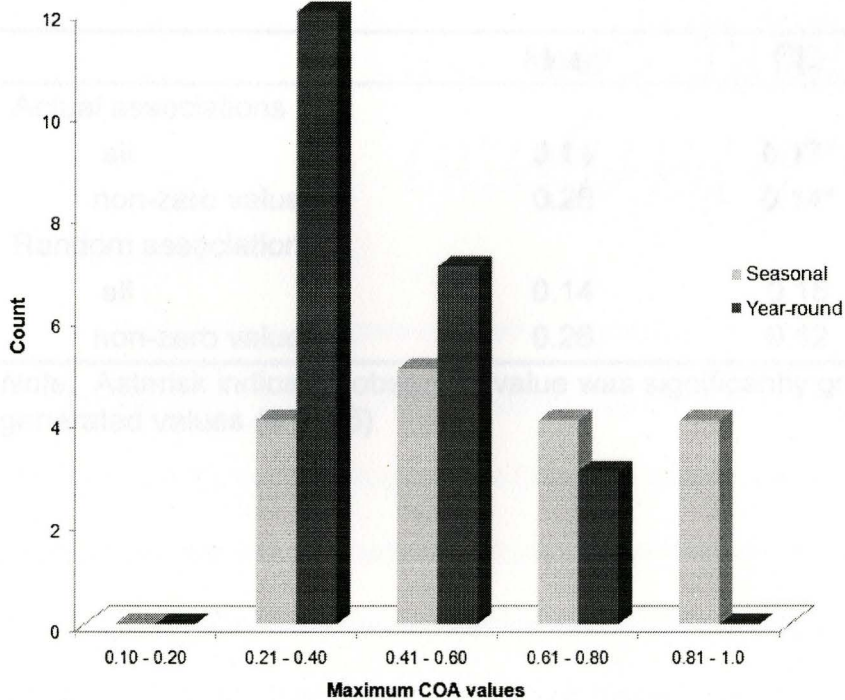


Figure 12. Frequency distribution of maximum COA values for select dolphins based on residency classification (seasonal: n = 17; year-round n = 22).

Preferred/Avoided Associations

The association data for the 39 select dolphins were randomized 15,000 times with 1,000 trials per permutation using the compiled version of SOCPROG 2.4 (Whitehead, 2009). The standard deviation and coefficient of variation for the actual associations was significantly higher than those of the randomly generated data, suggesting that the dolphins were associating differently from random (Table 7). A total of 17 dyads had COA values significantly greater than expected ($p < .05$) and are shown in Table 8. However, this number was less than the number of expected significant dyads (37), so these significant dyads should be viewed with caution (Whitehead, 1999; Rogers et al., 2004).

Table 7

Results of Permutation Test for Preferred/Avoided Associations

	Mean	SD	CV
Actual associations			
all	0.14	0.17*	1.23*
non-zero values	0.28	0.14*	0.51*
Random associations			
all	0.14	0.15	1.10
non-zero values	0.26	0.12	0.45

Note. Asterisk indicates observed value was significantly greater than randomly generated values ($p < .05$)

Table 8

Significant Dyads Identified by Permutation Test

Dyad	P-value	COA
1002 - 7058	0.9767	0.91
2014 - 7011	0.9858	0.33
2014 - 7055	0.9949	0.46
5003 - 7027	0.9873	0.33
5003 - 7093	0.9857	0.36
5007 - 8003	0.9997	0.60
6006 - 7015	0.9944	0.80
6019 - 7025	0.9780	0.80
6040 - 6041	0.9974	0.89
6099 - 7026	0.9935	0.22
7005 - 7027	0.9753	0.17
7005 - 7093	0.9764	0.18
7011 - 7013	0.9999	0.55
7011 - 7014	0.9993	0.36
7011 - 7055	0.9895	0.31
7013 - 7014	0.9995	0.40
7027 - 7093	0.9999	0.91

Social Network Analysis

Overall Network

After filtering, the core network consisted of 36 select individuals. A total of 132 dyads was present in the network, with 40 associations occurring between seasonal residents, 34 associations between year-round residents, and 58 associations between seasonal and year-round residents.

The Girvan-Newman algorithm was used to divide the network into two to ten communities. The resulting Q values ranged from 0.109 to 0.319, with the highest value corresponding to a division of 3 communities (Figure 13). Each community consisted of several individuals and included a mix of seasonal and

year-round residents. A randomized autocorrelation (10,000 permutations) revealed that dolphins in the network did not preferentially associate with other dolphins of the same residency classification ($\chi^2 = 45.93$, $p = .13$). It is important to note that the autocorrelation provides an estimate of the chi-square distribution, and as such, is not dependent on degrees of freedom.

Betweenness and degree were calculated for each individual in the network. The mean betweenness value was 44.50 ($SD = 71.35$), while the mean degree was 2.87 ($SD = 1.75$). Dolphins with high values of betweenness were removed from the network, one by one, resulting in a breakdown of the network into three components before the mean value was reached (9 individuals removed; Figure 14). Similar results were achieved when dolphins of high degree were removed from the network one at a time (13 individuals removed; Figure 15), with the network breaking apart into five components.

The network was also analyzed to determine whether dolphins were assorting by degree (i.e. do dolphins of high degree tend to form associations with other dolphins of high degree). A randomized autocorrelation (10,000 permutations) revealed that dolphins in the network were significantly more likely to form an association with other dolphins of similar degree value (Moran's $I = .48$, $p < .001$). As this result may have been biased by the filtering of the network, the same process was repeated using all associations among all 39 select dolphins. The magnitude of the correlation was slightly lower, but remained statistically significant (Moran's $I = .33$, $p < .001$).

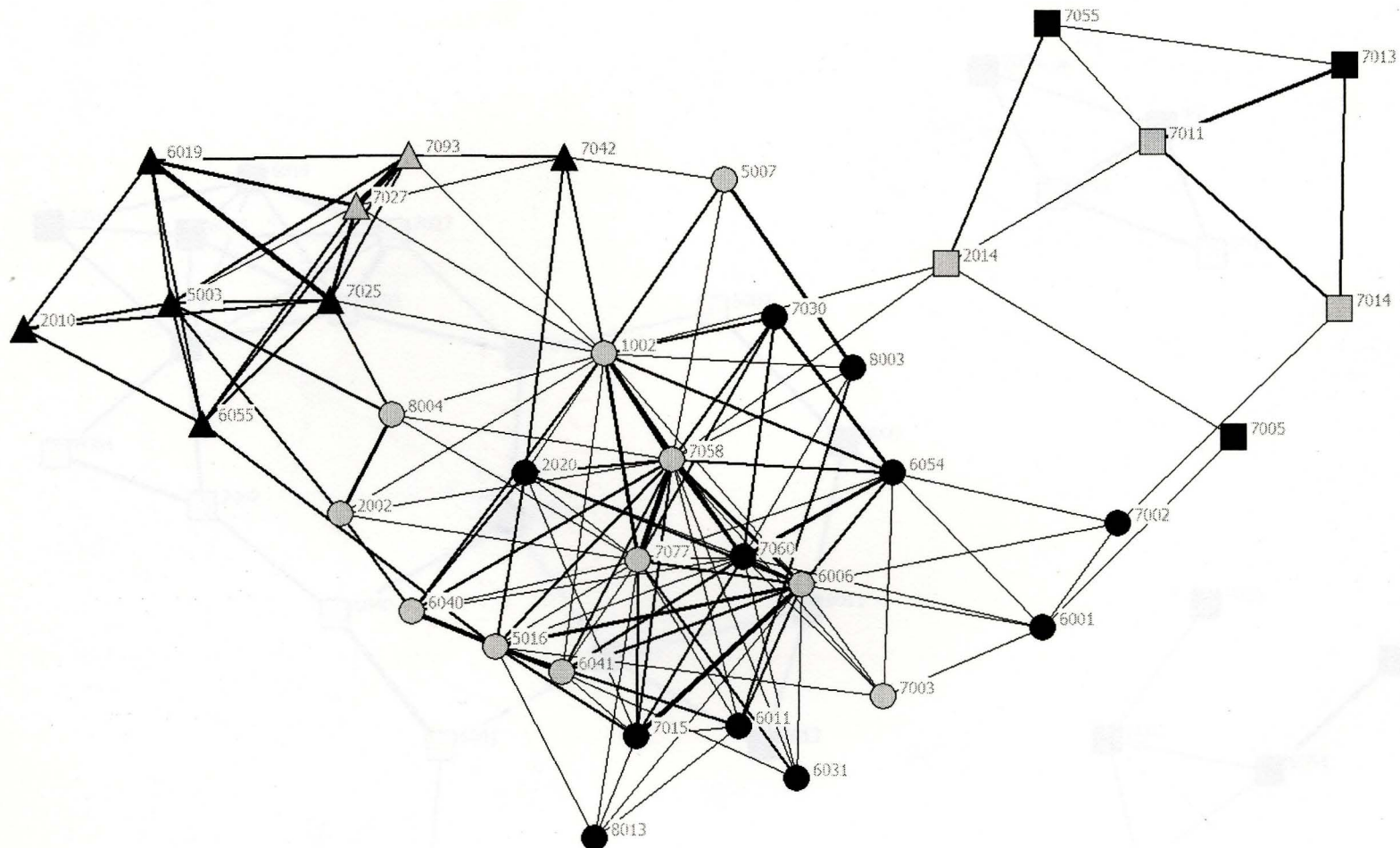


Figure 13. Social network of bottlenose dolphins in the Mississippi Sound.

Note. Each node represents an individual, while the edges represent the associations between dyads. The thickness of the line represents the strength of the association, with thicker lines being stronger. The shape of the node represents the community to which it belongs, while the color of the node indicates the residency classification of the individual (gray: seasonal resident, black: year-round resident).

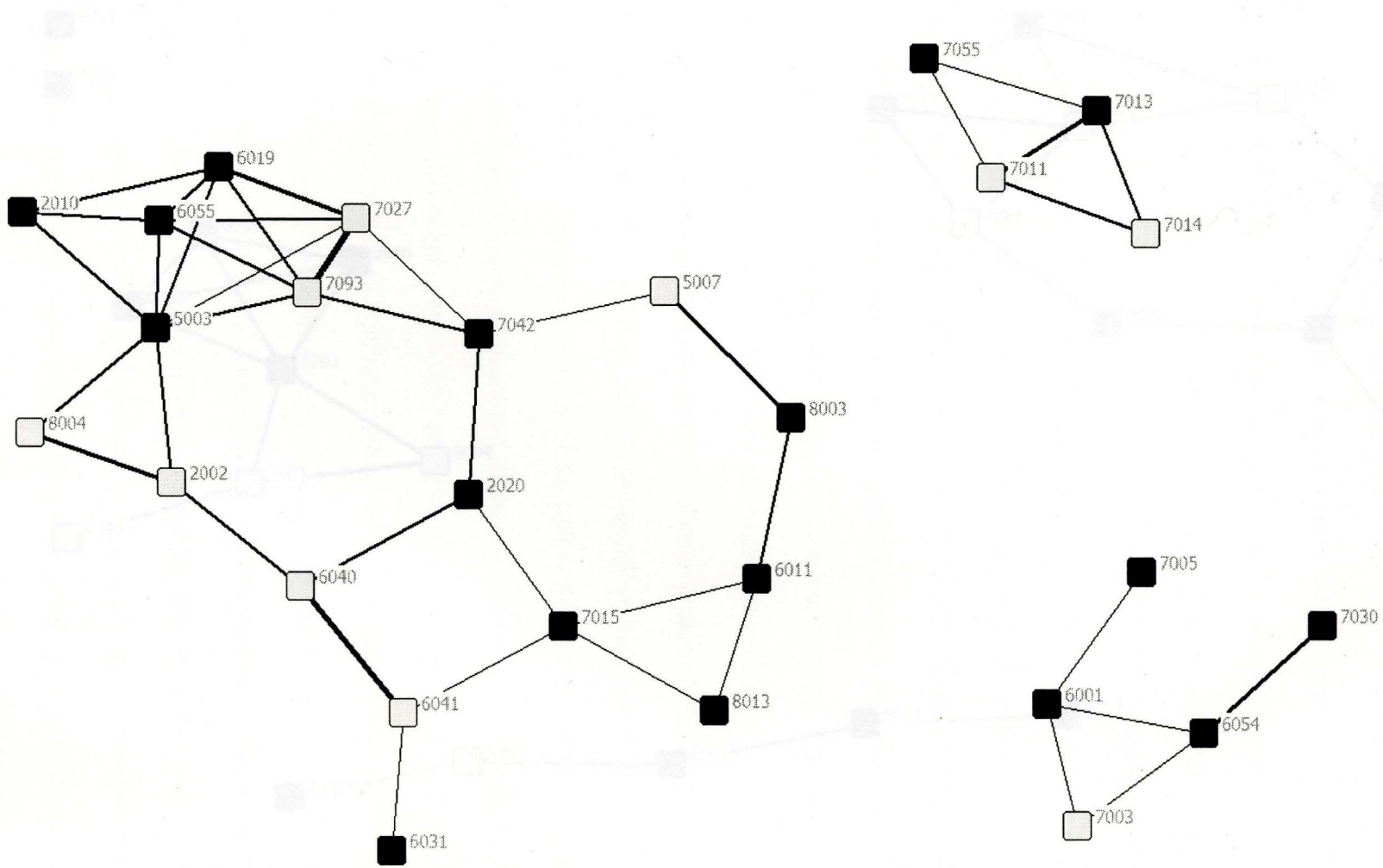


Figure 14. Social network after dolphins with highest betweenness ($n = 9$) have been removed.

Note. Color of node represents residency classification with gray representing seasonal residents and black representing year-round residents.

6031
 7030

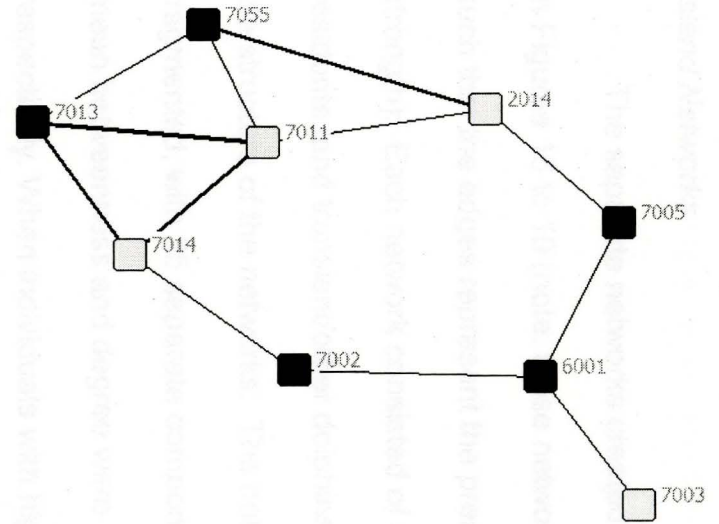
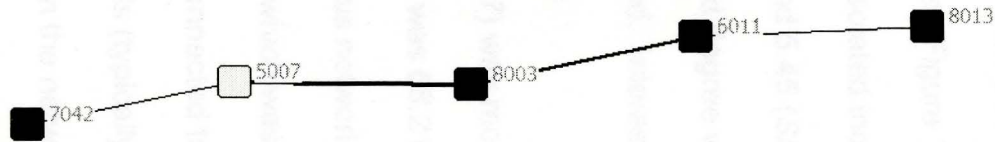
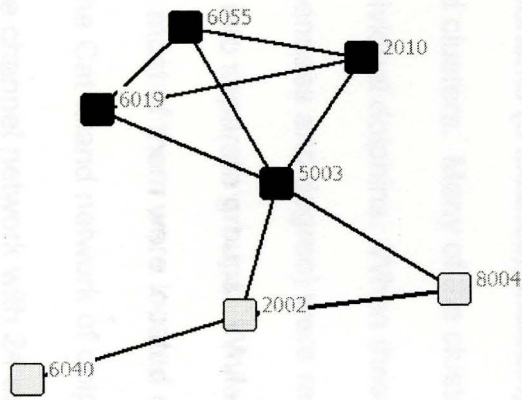


Figure 15. Social network after dolphins with the highest degree ($n = 13$) have been removed.

Note. Color of the node represents residency classification with gray representing seasonal residents and black representing year-round residents.

Island Networks

The separate networks created for each island and the channel are shown in Figures 16 to 19 (note: these networks were created using a binary network, such that the edges represent the presence of an association rather than its strength). Each network consisted of a mixture of seasonal residents, year-round residents, and transient/other dolphins. However, there were clear differences in the structure of the networks. The network for the channel (Figure 16) was highly fragmented, with 35 separate components, including 18 isolated individuals. The mean betweenness and degree were 4.34 ($SD = 3.56$) and 5.45 ($SD = 23.82$), respectively. When individuals with high betweenness and degree were removed from this network it quickly became even more fragmented. Interestingly, only one select individual was included in the channel network.

The structure of the Horn Island network (Figure 17) was more organized than the channel network. The mean betweenness value was 68.21 ($SD = 203.54$) and the mean degree was 11.55 ($SD = 8.74$). This network consisted of 17 separate components (8 isolates), including the core, which was made of several connected clusters. Many of the clusters were connected to each other via one or two individual dolphins. When these individuals (typically those having the highest betweenness and degree) were removed from the network, the clusters broke off into separate groups. While this network consisted of several select individuals, most of them were located on the periphery of the network.

Similarly, the Cat Island network of dolphins (Figure 18) was more organized than the channel network with 24 separate groups (15 isolates) including the core. However, unlike Horn Island, select dolphins that were part of

this network tended to be located within the core of the network. Additionally, the dolphins in this network were not often connected to the “core” via a single individual; rather, there were multiple connections. Thus, when individuals with the highest betweenness and degree were removed from the network, the network did not break apart very quickly. The mean betweenness for this network was 88.15 ($SD = 261.6$) and the mean degree was 8.77 ($SD = 8.21$). The network for Ship Island (Figure 19) was by far the most densely connected network of all of the island networks, with one large core and 9 smaller components, including 7 isolated individuals. The average betweenness was 120.29 ($SD = 275.47$), while the mean degree was 23.20 ($SD = 19.65$). The Ship Island network consisted of many select individuals and these dolphins were mainly located at the center of the network. Because of the vast number of connections within this network, the removal of individuals with high betweenness and degree did not greatly affect the network structure.

Hurricane Katrina

Only seventeen dolphins were sighted two or more times in the ten months (October to August) both before and after Hurricane Katrina. Thirteen of these individuals were select dolphins, while the remaining four were not. The strength, eigenvector, reach, clustering coefficient and affinity were calculated for each individual using the bootstrap method with 10,000 bootstraps (see Appendix B for a description of these measures).

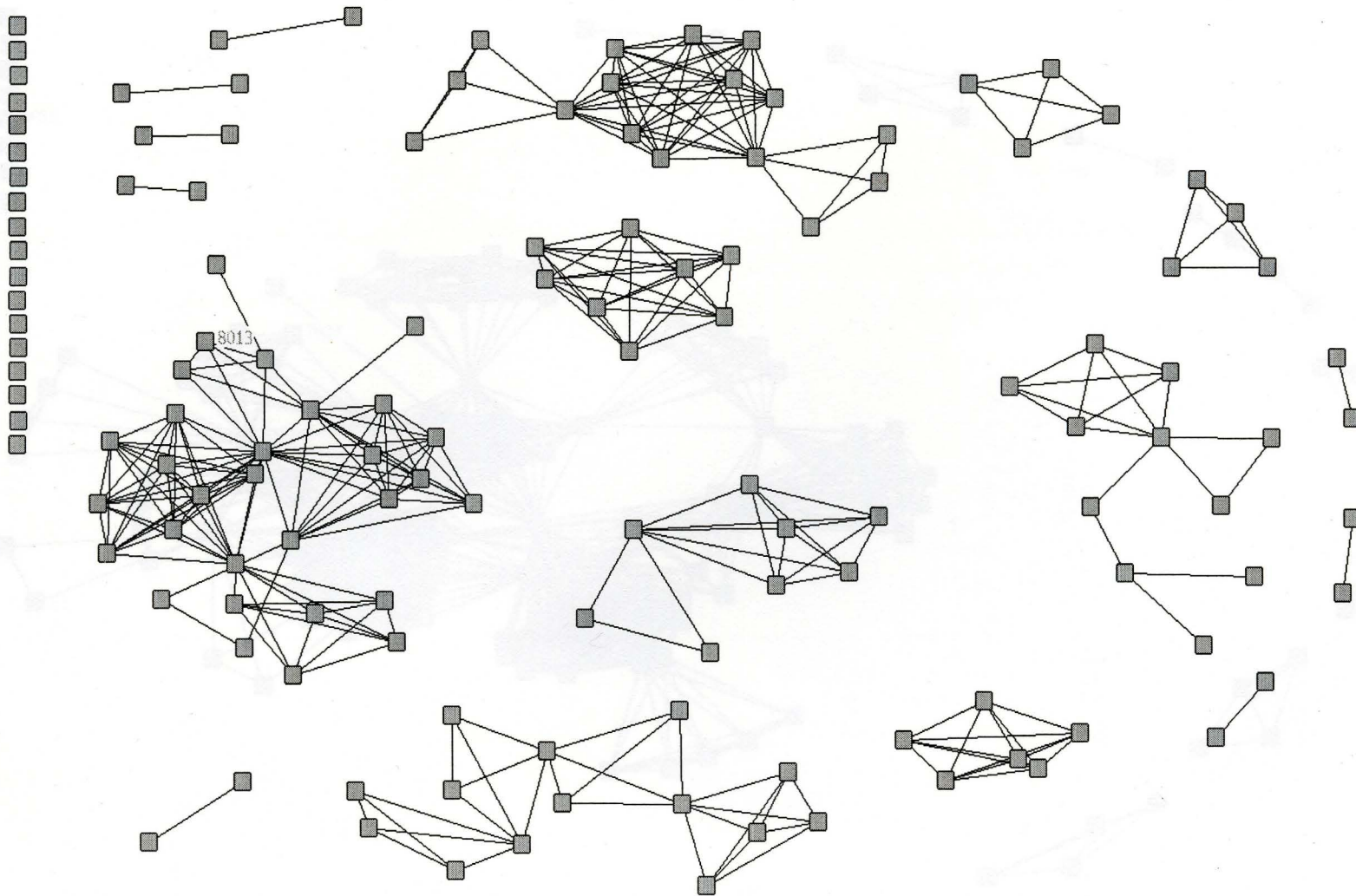


Figure 16. Social network of bottlenose dolphins sighted two or more times in the channel.

Note. Nodes represent individual dolphins, while edges represent presence of an association between a dyad. Select dolphins are labeled.

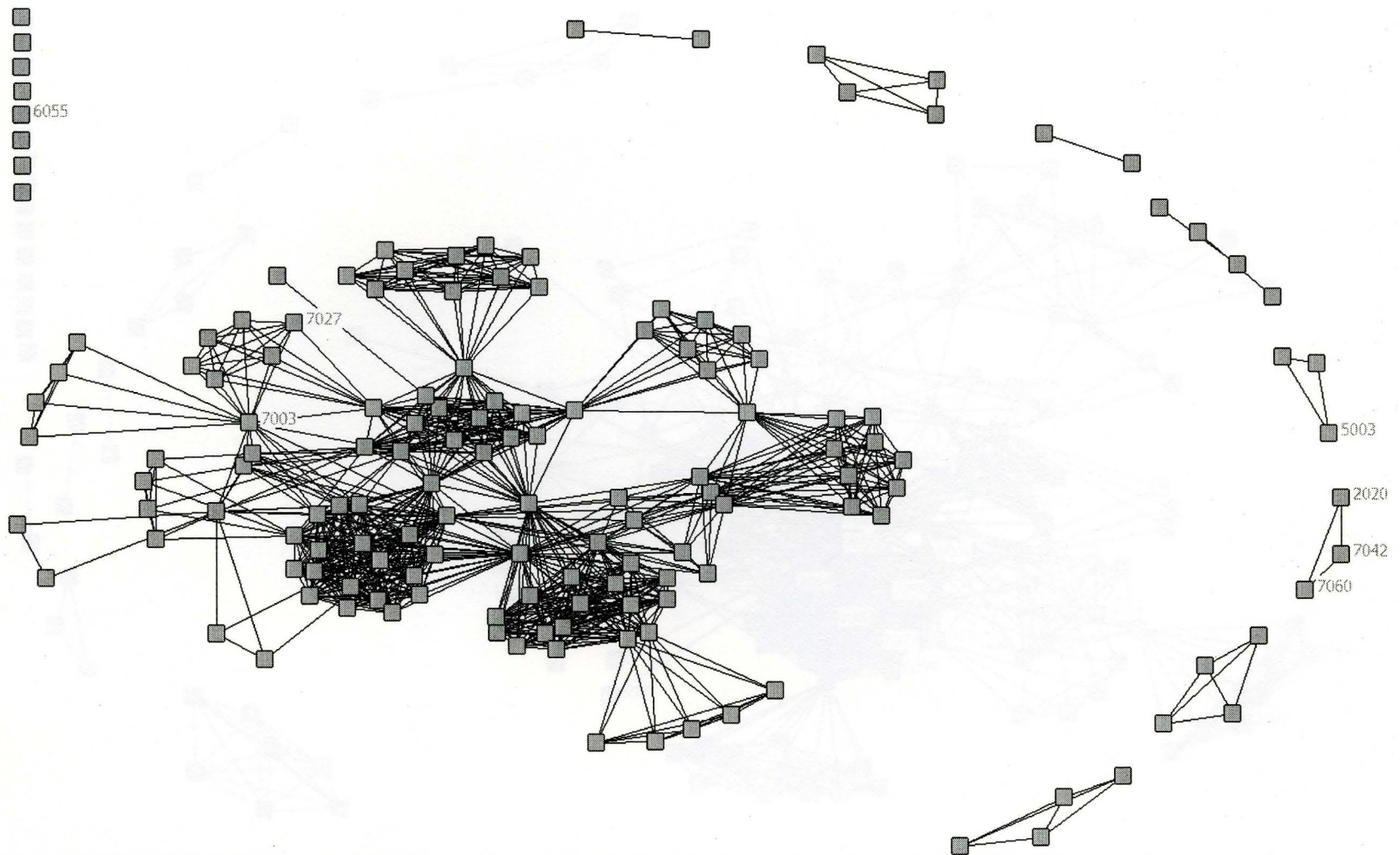


Figure 17. Social network of bottlenose dolphins sighted two or more times at Horn Island.

Note. Nodes represent individual dolphins, while edges represent presence of an association between a dyad. Select dolphins are labeled.

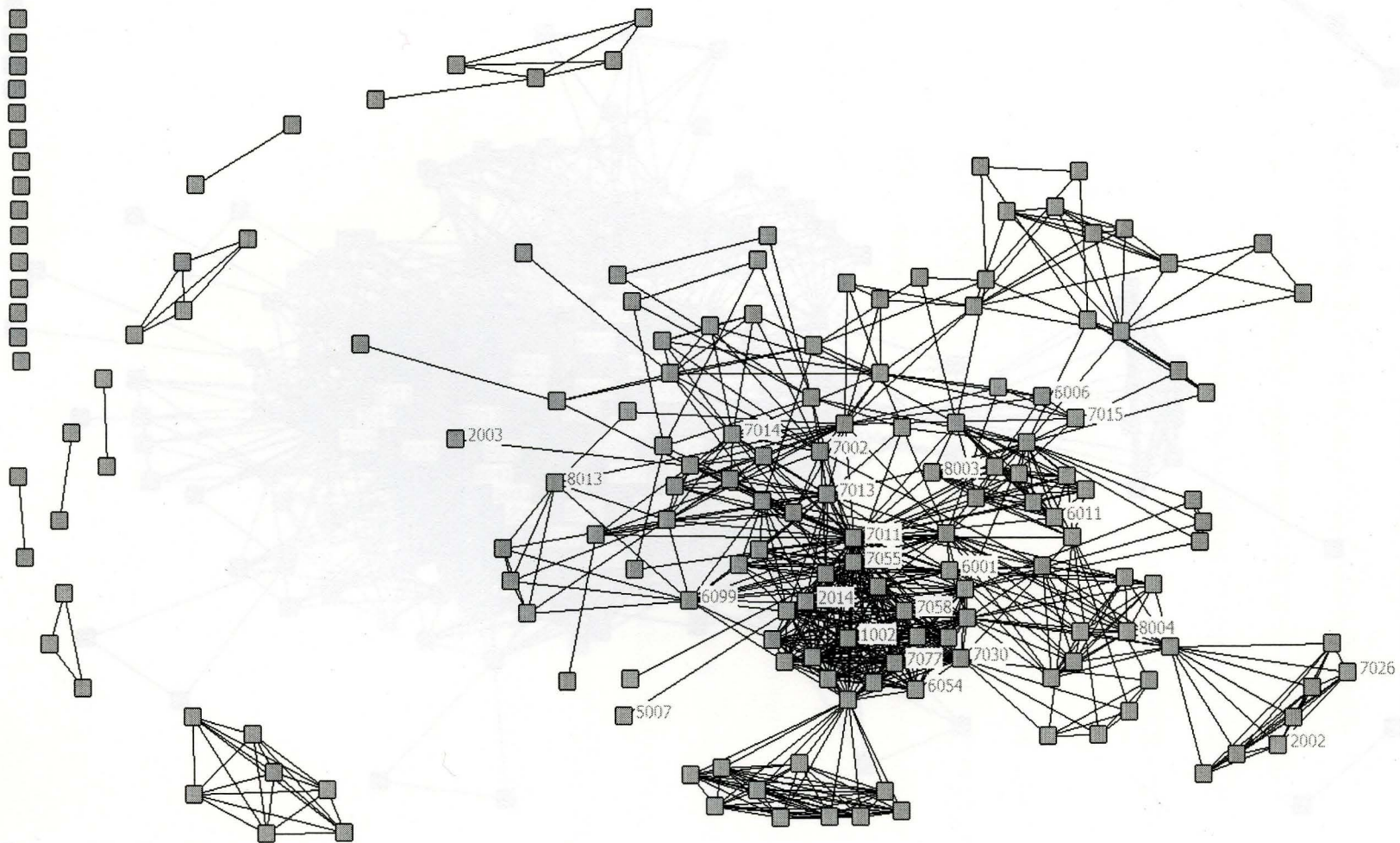


Figure 18. Social network of bottlenose dolphins sighted two or more times at Cat Island.

Figure 18. Social network of bottlenose dolphins sighted two or more times at Cat Island.

Note. Nodes represent individual dolphins, while edges represent presence of an association between a dyad. Select dolphins are labeled.

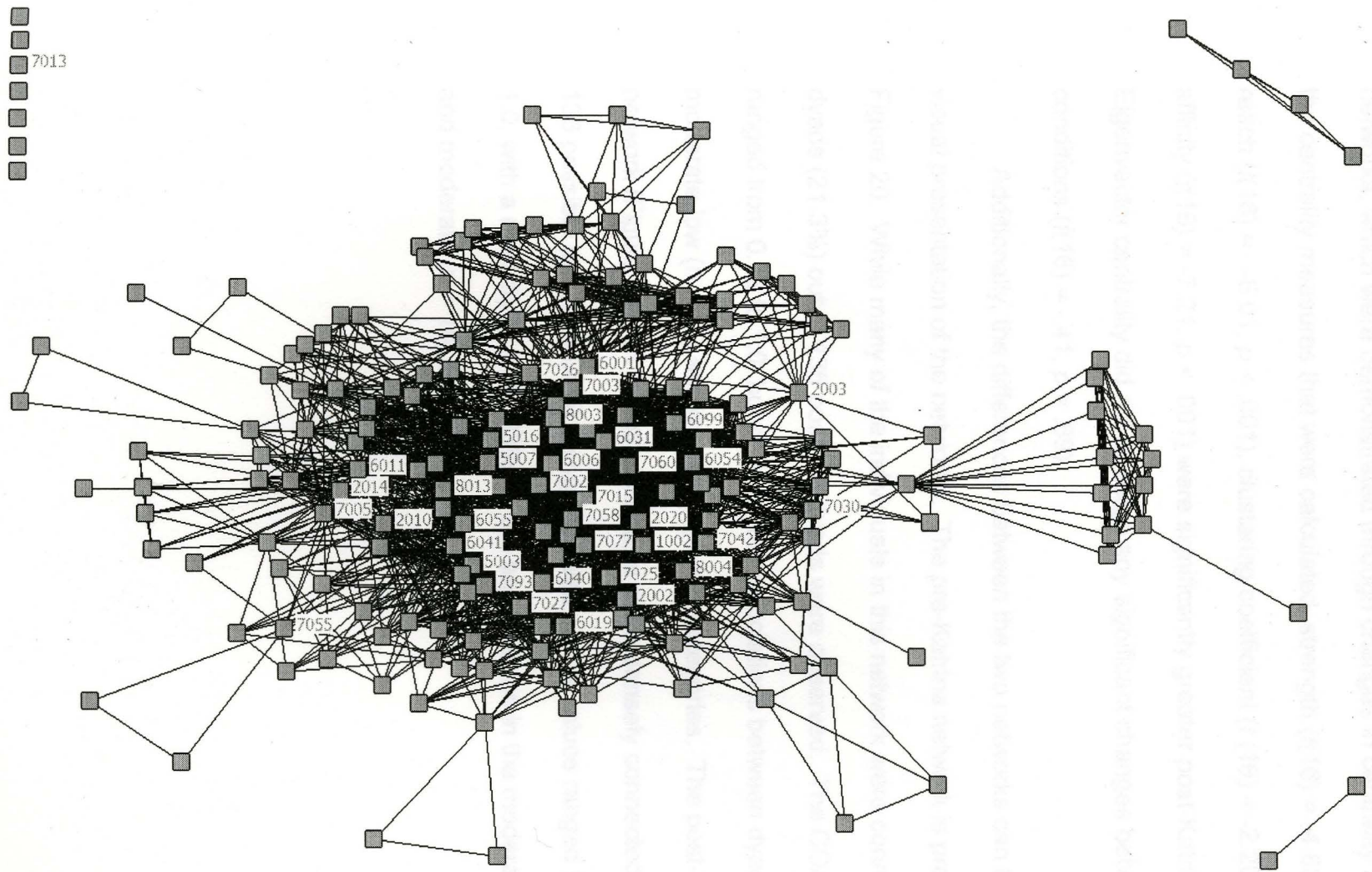


Figure 19. Social network of bottlenose dolphins sighted two or more times at Ship Island.

Note. Nodes represent individual dolphins, while edges represent presence of an association between a dyad. Select dolphins are labeled.

There were substantial differences between the pre- and post-Katrina networks, which were demonstrated through changes in centrality measures. Of the centrality measures that were calculated, strength ($t(16) = -4.88, p < .001$), reach ($t(16) = -6.01, p < .001$), clustering coefficient ($t(16) = -2.29, p < .05$) and affinity ($t(16) = -7.21, p < .001$) were significantly greater post-Katrina. Eigenvector centrality did not undergo any significant changes between the two conditions ($t(16) = -.41, p = .69$).

Additionally, the differences between the two networks can be seen in the visual presentation of the networks. The pre-Katrina network is presented in Figure 20. While many of the individuals in this network were connected, only 29 dyads (21.3%) out of 136 possible dyads were observed. The COA values ranged from 0.18 to 1.0, but most of the associations between dyads were in the moderate-low ($n = 15$) and moderate ($n = 9$) categories. The post-Katrina network (Figure 21), on the other hand, is more densely connected, with 59 of 136 possible dyads (43.4%) being observed. COA values ranged from 0.33 to 1.0, with a majority ($n = 49, 83\%$) of the associations in the moderate low ($n = 34$) and moderate ($n = 15$) categories.

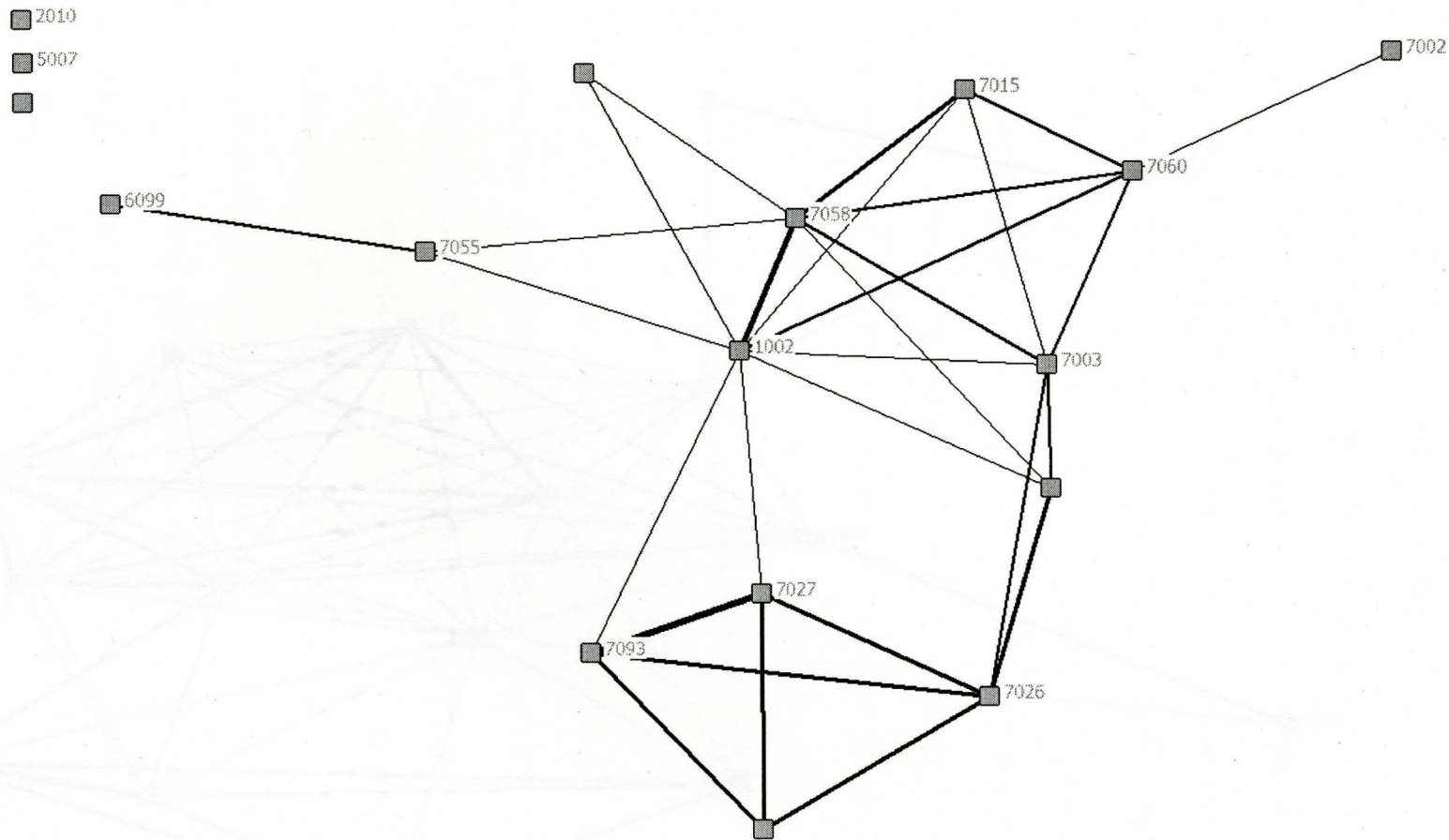
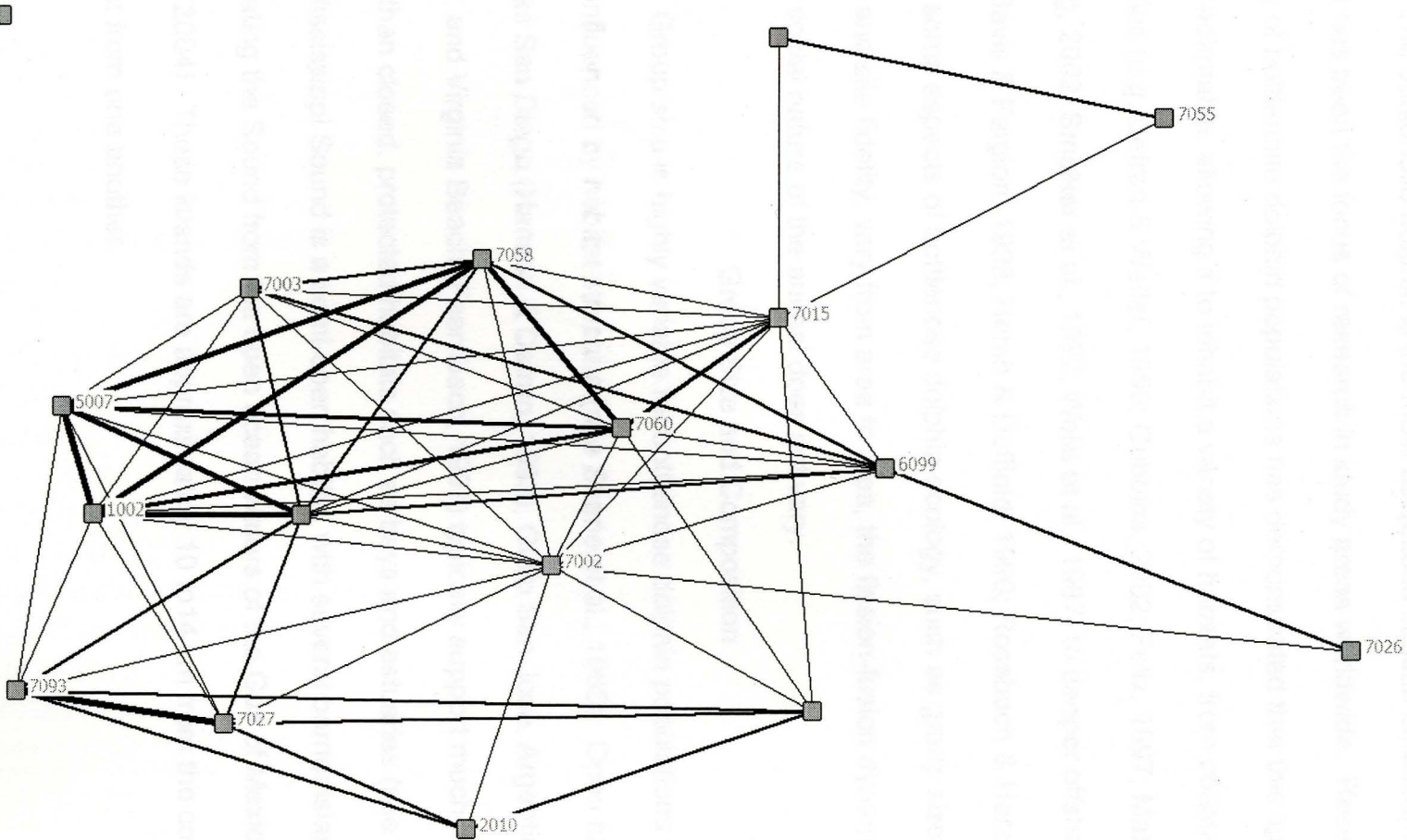


Figure 20. Social network of bottlenose dolphins sighted two or more times ($n = 17$) in the 10-month period before Hurricane Katrina (October 2004 to August 2005).

Note. Nodes represent dolphins, while edges represent the association between a dyad. The thickness of the line represents the strength of the association with thicker lines being stronger. Select dolphins are labeled.



21. Social network of bottlenose dolphins sighted two or more times ($n = 17$) in the 10-month period after Hurricane Katrina (October 2005 to August 2006).

Note. Nodes represent dolphins, while edges represent the association between a dyad. The thickness of the line represents the strength of the association with thicker lines being stronger. Select dolphins are labeled.

Figure

CHAPTER IV

DISCUSSION

The bottlenose dolphin is the most ubiquitous coastal cetacean, and as such it has been the focus of research in study areas worldwide. Research on a variety of bottlenose dolphin populations has demonstrated that this species is highly adaptable, allowing it to inhabit a variety of habitats, from coastal bays and estuaries (e.g. Defran & Weller, 1999; Gubbins, 2002; Felix, 1997; Maze-Foley & Wursig, 2002; Smolker et al., 1992; Wells et al., 1987) to deeper offshore waters (e.g. Davis & Fargion, 1998; Hersh & Duffield, 1990; Rossbach & Herzing, 1999). While some aspects of bottlenose dolphin ecology, such as group size, home range and site fidelity, vary from area to area, the fission-fusion dynamics and highly social nature of the animal does not vary.

Group Size and Composition

Group size is highly variable for bottlenose dolphin populations and is often influenced by habitat structure (see Shane et al., 1986). Open habitats, such as San Diego (Hanson & Defran, 1993), Golfo San Jose, Argentina (Wursig 1978), and Virginia Beach (Fearnbach, 1997) typically support much larger group sizes than closed, protected habitats such as bays and estuaries (see Table 9). The Mississippi Sound is a semi-open habitat, with several barrier islands separating the Sound from the open ocean waters of the Gulf of Mexico (Hubard et al., 2004). These islands are approximately 10 to 14 km from the coastline and 8.5 km from one another.

Table 9

Mean Group Size of Inshore Bottlenose Dolphin (Tursiops sp.) Groups Reported from a Variety of Study Sites

Study site	Habitat Structure	Mean Group Size	Citation
North Adriatic Sea	closed	7.4	Bearzi et al., 1997
Moreton Bay, Australia	closed	10.4	Corkeron, 1990
Gulf de Guauaquil, Ecuador	closed	25.4	Felix, 1997
Sarasota Bay, FL	closed	4.8	Irvine et al., 1981
Shark Bay, Australia	closed	4.8	Smolker et al., 1992
Sarasota Bay, FL	closed	7	Wells et al., 1987
Kino Bay, Baja CA	open	15	Balance, 1992
Santa Monica Bay, CA	open	8.8	Bearzi, 2005
San Diego, CA	open	19.8	Defran & Weller, 1999
Virginia Beach, VA	open	22	Fernbach, 1999
San Deigo, CA	open	18	Hansen, 1990
Grand Bahama Island, Bahamas	open	10.6	Rogers et al., 2004
Gulfo San Jose, Argentina	open	14	Wursig, 1978
Ionian Sea	semi-open	6.8	Bearzi et al., 2005
Mississippi Sound	semi-open	6.5	Hubard et al., 2004
Drowned Cayes, Belize	semi-open	2.9	Kerr et al., 2005

As such, this area is not as protected as semi-enclosed bays and estuaries (Hubard et al., 2004). Thus, it was expected that the mean group size in this area would be similar to that reported for other open habitats. However, the mean group size for dolphin groups in the study area was considerably smaller than expected ($M = 8.35$), with the most frequently occurring group sizes ranging between one and 15 individuals.

One explanation for the relatively small mean group size in the current study is the criteria used to determine group size. Shane et al. (1986) suggested that much of the variability in group sizes reported for bottlenose dolphins may be due to differing definitions of the term "group". Some studies have been quite inclusive in the definition of a group: individuals passing the shore at the same time (Wursig, 1978), all dolphins in a particular area (e.g. Kino Bay; Ballance, 1990), any aggregation of one or more dolphins (Hansen, 1990). Other studies have defined groups based on behavior, such as moving in the same direction and engaging in similar behaviors (e.g. Brager et al., 1994; Shane, 1990), while still others have used distance as a criterion for inclusion, though these distances differ from study to study (e.g. Wells et al., 1987, Lusseau et al., 2006; Smolker et al., 1992). For the current study, dolphins were considered to be part of a group if they were within a 100 m of one another and engaged in similar activities.

On the other hand, the mean group size for dolphins in the Sound may be related to its depth. While the Sound is a semi-open environment, its average depth is only 3 meters. Many studies have reported that dolphin group sizes tend to be smaller in shallow waters (reviewed by Shane et al., 1986). The factors commonly attributed to this finding are prey distribution and predation

risk. In deep waters, prey is more likely to be patchily distributed, requiring individuals to combine their search efforts in order to locate and capture their prey (Norris & Dohl, 1980; Shane et al., 1986; Wursig, 1978). However, in shallow coastal waters, prey is more evenly distributed and often consists of non-schooling individuals (Shane et al., 1986), which may reduce the need for cooperative foraging efforts (Gowans et al., 2007). Shallow waters also reduce the three dimensional space that must be monitored for predators (Wells et al., 1980), which may in turn diminish the need for group formation.

There was no correlation between group size and water depth in the current study. This suggests that prey distribution and predation risk are not markedly influenced by water depth in the Mississippi Sound. However, group size did vary significantly by season, with observed group sizes being much larger in the summer months. This may be related to an increase in foraging opportunities due to the migration of schooling prey species. Mullet and menhaden have been identified as prey of bottlenose dolphins in the Sound (Leatherwood, 1975; Barros & Odell, 1990), and both species have been reported to migrate into the area in the summer after heading to deeper, warmer waters to spawn in the winter (Wells et al., 1980).

Similarly, the presence of predators may also increase in the summer. Most of the shark species identified in the Mississippi Sound are smaller species, such as blacktip sharks, *Carcharhinus limbatus*, and finetooth sharks, *Charcharhinu isodon* (Hoffmayer & Parsons, 2003). Such small sharks may not pose a risk to adult bottlenose dolphins, yet they may be dangerous to small calves (see Gibson, 2006). Thus, group composition, specifically the presence of

calves, has often been reported as an important factor for group size in bottlenose dolphins (e.g. Felix, 1997; Hubbard et al., 2004; Maze-Foley & Wursig 2002; Rogers et al., 2004; Weller, 1991; Wells et al., 1987). The results of the current study support this, with dolphin groups being significantly larger when at least one calf was present.

Individual Identification and Residency Patterns

Six hundred seventy-eight individual dolphins were identified over the three year study period. New identifications were significantly more likely to occur during the summer months, represented by an increase in the slope of the discovery curve at these times. This seasonal increase in new dolphin identifications is likely a result of increased dolphin abundance in the Mississippi Sound, which peaks in the summer (Hubbard et al., 2004). However, it must be noted that methodological changes may have resulted in the large number of new identifications (N = 137) in July 2005, the time at which Horn Island was incorporated into the study area. As this area was not surveyed prior to this time, most of the dolphins sighted were “new”, though a few had been previously identified in other regions of the study area.

The lack of an asymptote in the discovery curve, particularly considering the size of the photo-id catalog, may reflect the transient nature of this population of dolphins. Nearly three-quarters of the identified dolphins were classified as transient/other, while 10% were classified as year-round residents and 16% were classified as seasonal residents. The discovery curves for both year-round and seasonal resident dolphins in the study area did reach an asymptote, indicating that most of the individuals in these residency categories have been identified.

Individuals classified as transient/other, however, did not appear to reach an asymptote, which suggests that more dolphins in this residency category utilize the study area than have been identified up to this point.

There was considerable variability in the number of months between re-sightings of both seasonal and year-round resident dolphins. For seasonal residents, the typical sighting pattern was several sightings within a single season in a single year, then a several-month lapse (on average, 8 months) in sightings until the same season the following year. It is likely that these individuals left the study area altogether during the intervening months, possibly heading out to the warmer, deeper waters of the Gulf of Mexico. Several authors have suggested that bottlenose dolphins may migrate seasonally based on the seasonal movements of their prey items, which move toward deeper waters during the winter months (Norris, 1967; Irvine et al., 1981; Maze-Foley & Wursig, 2002; Wells et al., 1980). As Hubbard et al. (2004) hypothesized, when prey species migrate during the winter, the Mississippi Sound may not be able to support as many bottlenose dolphins, resulting in a part of the population moving out of the area at this time.

Year-round residents, on the other hand, had an average of 5.7 months between sightings. The time between sightings may be evidence that the study area is only part of the home range of some year-round dolphins. Individuals whose home range extends far beyond the boundaries of the study area are less likely to be sighted with any regularity. A variety of studies have demonstrated the considerable variability in bottlenose dolphin home ranges. In Matagorda Bay, Texas, for example, dolphins had a mean range of 140 km² (Lynn & Wursig,

2002). Felix (1997) reported home ranges of 30 to 45km along the coast for five communities of bottlenose dolphins in Ecuador, whereas Defran et al. (1999) reported individual dolphin home ranges between 50 and 483 km along a 0.5 km wide strip of California coastline.

As with group size, a dolphin's home range may be influenced by the structure of the habitat. The area available for dolphins to utilize is greater in open habitats than in closed habitats (Leatherwood, 1975). As the Mississippi Sound is a semi-open habitat, it is likely that the home ranges of the dolphins in the Sound are quite large and extend beyond the boundaries of the study area. A comparison of photo-identification catalogs with neighboring study areas is needed to determine to what extent the dolphins in the Mississippi Sound range along the Gulf coast.

From the present data, it is clear that there is some level of site fidelity to the Mississippi Sound. One hundred eighty individuals were sighted in at least two years of the study (54 of which were sighted in all three years), suggesting, at minimum, short-term site fidelity to the area. However, some individuals in this population may exhibit long-term site fidelity. Two individuals (#3000 and #12005) identified in the current study had visible freeze-brand marks on their dorsal fins or lateral side, which were originally branded more than twenty years ago (Solangi & Dukes, 1983). While it is not known whether these particular individuals were present in any of the intervening years, it is possible that they were. Both of these individuals have been sighted in the study area since the end of the current study, and two other individuals freeze-branded in 1982 were identified near Horn Island in 1996 by Hubard et al. (2004).

Limitations. The results for individual identification and residency classification in the current study are subject to a variety of confounding factors. In regard to individual identification, the most likely error is the mis-identification of individuals. Incorrect “new” identifications may stem from numerous sources. For example, individuals with relatively clean fins (i.e. free of identifiable marks) in an initial encounter may acquire marks allowing them to be identified in a future sighting (Maze & Wursig, 1999). Likewise, fins that were previously identified may undergo major changes that obscure previously existing identifying marks (Wursig & Jefferson, 1990).

Alternatively, individuals may have been present in the area, but were not identified because they were not encountered, not photographed, or, if photographed, the photos were of poor quality and subsequently excluded from the analysis (Maze & Wursig, 1999; Zolman, 2002). This last point is particularly likely to be the case in the winter months when the sea state is much worse, making it difficult to sight and photograph dolphins (Chilvers & Corkeron, 2002; Maze & Wursig, 1999).

Residency classifications were made based on the sighting history of each individual, and are thus subject to similar confounds. For example, an individual classified as a seasonal resident may have been present year-round, but was not identified in both seasons due to one of the previously described factors (Zolman, 2002). This may be the case for the two individuals classified as winter seasonal residents, who may have been present year-round, but were not identified in the summer months.

Additionally, changes in habitat use may also have led to mis-

classifications of residency. A newly identified individual classified as transient/other in the final year of the study may have been an animal that immigrated into the study area but afterwards began to utilize it on a year-round or seasonal basis (Zolman, 2002). Analysis of data collected in the years following the current study will help to determine which classifications (if any) need to be adjusted.

Other methodological issues may have contributed to bias in the results of the current study. The re-sighting frequency for dolphins in the study area was relatively low, with a majority of the dolphins (N = 456, 67%) being sighted only once, and 90% (N = 611) sighted fewer than 4 times. Such a low rate of re-sighting may have resulted in the mis-classification of some individuals, such as those who utilize the area on a regular basis, or whose home range only slightly overlaps the study area.

Moreover, survey effort was not equally distributed throughout the study area. Most surveys focused on the area around the barrier islands, resulting in fewer sightings in area between the islands and the coast. This is excepting the channel, which was often surveyed twice, once leaving the harbor and once upon return. Additionally, Horn Island was not a regular part of the study area until summer of 2005. Thus, individuals sighted in this part of the study area may be underrepresented, resulting in incorrect residency classifications.

Association Patterns

Number of Associates

Select dolphins had an average of 55.6 associates, with a majority of select dolphins having between 41 and 60 associates. Only two individuals had

fewer than 25 associates. When viewed in the light of the total number of individuals potentially available for interaction, the percentage of associates (mean number of associates divided by total number of identified individuals \times 100) for select dolphins was relatively low (8%). Other study areas have reported much higher percentages of associates (e.g. San Luis Pass, Texas, 30%, Maze-Foley & Wursig; 2002; Cedar Keys, Florida, 24%, Quintana-Rizzo & Wells; Bahamas, 23%, Rossbach & Herzing, 1999). However, the total number of identified individuals in these study areas was considerably lower than that of the current study (71, 233, and 211, respectively).

While the total number of identified individuals may have contributed to the low percentage of associates in the current study, there are several other factors that may have influenced this value. One such factor is the high number of transient/other individuals identified in the Sound. As transient individuals are only in the area on a temporary basis, they have limited opportunities to associate with other individuals in the area (Fearnbach, 1997). It is probable that the select dolphins actually have a higher percentage of associates, but because associations with transient individuals are brief, they were not always observed.

Habitat structure may also play a role in the low percentage of associates. Closed habitats often consist of narrow, constricted areas, such as channels, inlets, and passes, which limit the movements of animals (Irvine et al., 1981) and thus preclude the spatial separation of groups sharing the same area. As the population density increases in these areas, individuals are more likely to encounter one another (Connor et al., 2000) and may be more likely to interact, though this does not always occur (see Lusseau et al., 2006). The Mississippi

Sound, however, is a semi-open habitat, with very few constricted areas and groups of dolphins are able to maintain separation from other groups, if desired.

In a similar manner, habitat usage may contribute to the percent of associates of an individual dolphin. Individuals may change the way they utilize an area based on a variety of ecological factors such as migration, prey distribution, and the distribution of possible mates (Defran et al., 1999; Gowans et al., 2008; Scott et al., 1990). These factors may bring individuals to the same area at the same time, and although interactions between individuals aggregated around resources are not guaranteed to occur (see Lusseau et al., 2006), the possibility of such social interactions is nonetheless increased.

Strength of Associations

The distribution of COA's for bottlenose dolphins in the Mississippi Sound is similar to that reported for other study areas (Chilvers & Corkeron, 2002; Fearnbach, 1997; Smolker et al., 1992; Weller, 1991; Wells et al., 1987). A majority (91%) of the COA's fell below 0.40, while very few associations were above 0.80. Such low levels of association are not surprising given the fission-fusion dynamics of bottlenose dolphins. Within a fission-fusion social structure, group membership is fluid and highly variable (White, 1992), thus most associations are not long-lasting.

It is possible that the few high level associations observed in the current study are between a female and her offspring, strongly bonded males, or females in a similar reproductive state, as has been reported for bottlenose dolphins elsewhere (e.g. Rogers et al., 2004; Connor et al., 1992; Wells et al., 1987).

Unfortunately, there is currently little information on the sex of individual dolphins

in this study area. As a result, it is impossible to determine whether sex-class is an ecological aspect producing these high level associations. Future effort in this study area should incorporate genetic sampling to determine what sexes are forming these strong associations.

Limitations. The selection criteria for inclusion in the analysis may have affected the results of the association analysis. Individuals were only recorded as present for the first group that they were sighted in on a single day. If that group joined another, the new associations were not represented. Likewise, sightings were only included if they were separated by at least one day to assure independence. The combination of these factors may have resulted in an underestimation of the percentage of associates for the select dolphins.

The selection criteria may have also had an influence on the strength of associations reported for the current study. While an association may have existed between a pair of dolphins, if they were not included in the analysis due to the selection criteria, the proportion of joint sightings would be reduced, ultimately lowering the COA value of the dyad.

Several other factors may have contributed to an error in the COA values for this study, including group size. Large group size can affect COA values in two ways. First, the likelihood that two individuals will be observed in the same group increases with group size, resulting in a higher COA value for the pair. Secondly, it can be difficult to ensure that a photograph has been taken of each individual in a large group. Thus, large groups are less likely to be completely sampled (Chilvers & Corkeron, 2002), resulting in lower COA values. Select dolphins were commonly sighted in groups of 15 or more dolphins, thus it is

possible that either of these two sources of bias could have affected the results of the current study.

In a similar way, COA values can be affected by the mis-identification or non-identification of individuals. The factors leading to such errors were previously described for residency classification. Additionally, non-identification of an individual may be influenced by the behavior of the individual or that of the group. For example a female with a young calf may avoid interactions with boats, making it difficult for a researcher to photograph her (Fearnbach, 1997).

Finally, the number of sightings of a dolphin can affect the value of the COA of any dyad involving that individual. Since the COA used in this study (HWI) takes into account both the number of joint sightings *and* the number of separate sightings for a pair of dolphins, if one individual has a large number of sightings, this can bias the calculated index (Fearnbach, 1997). Consequently, individuals with a large number of sightings often have lower COA values, regardless of the number of joint sightings (Fearnbach, 1997).

Preferred/Avoided Associations

The results of the permutation test indicated that dolphins in the Mississippi Sound associate non-randomly. This result may not only be obtained due to social factors, however. Demographic effects, such as habitat use, migration, birth or death can produce a significant non-random result as well (Whitehead, 1999). The contribution of these factors was eliminated in the current study by permuting the groups within a sampling period and using a sampling period short enough that it was unlikely that migration into/out of the study area occurred within this interval (Whitehead, 2008).

Not all of the dyads that were determined to be associating significantly more than expected by chance had high COA values. In fact, two of the 17 significant dyads had COA values of 0.18, while several non-significant dyads had much higher COA values. However, significance is determined based on the observed group size and number of sightings of each individual (Bejder et al., 1998), which makes these results possible, though perhaps not intuitive. Analysis of association data for the years following the study period will determine whether these significant dyads remain significant over time and may also reveal new preferred associations.

Network Analysis

The Girvan-Newman algorithm detected three different communities within the network of dolphins in the Mississippi Sound. While the observed modularity index, Q , corresponding to this division was within the range that is considered to be a strongly structured community (0.3 to 0.7, Newman & Girvan, 2004), it is toward the low end of the range, suggesting that there are multiple connections between members of different communities. This is typical for a social structure consisting of fission-fusion social dynamics, in which there is a high degree of turnover in group membership, leading to few intra-community associations (Croft et al., 2008).

Lusseau et al. (2006) discuss the importance of associations between members of different communities. They suggest that such relationships may be important for the facilitation of rapid information transfer (e.g. food availability) within the overall network, which may be ecologically advantageous to individuals in the network. Inter-community associations may also be important for ensuring

gene flow, preventing genetic inbreeding and promoting the spread of genes from individuals that may be advantageous if environmental changes occur (Slatkin, 1987).

The division of communities may be related to a variety of ecological factors. Lusseau and Newman (2004) identified two communities in a network of bottlenose dolphins in Doubtful Sound, New Zealand, which were further divided into sub-communities. These authors suggested that these community divisions may have resulted from assortative mixing by age- and/or sex-class. They further suggested that genetic relatedness may play a role in the formation of the communities in the area. In Moray Firth, Scotland, on the other hand, Lusseau et al. (2006), determined that community divisions were related to geographical ranging patterns arising from differences in habitat use (e.g. foraging strategies).

Based on the results of Lusseau et al. (2006), the current study examined whether the relationships among dolphins in the Mississippi Sound were related to differences in residency patterns. There was no evidence that this is the case; dolphins in the network were just as likely to associate with a member of a different residency classification as with those of the same classification. As suggested previously for inter-community associations, inter-residency associations may be important for genetic exchange among dolphins in the Sound.

Another possible mechanism of community division tested in the current study was preferential assorting by degree. Dolphins in the Sound were found to associate more closely with other individuals of like degree. Similar results were reported for the dolphins in the Moray Firth (Lusseau et al., 2006) but no such

assortative mixing was detected in Doubtful Sound (Lusseau & Newman, 2004). As Lusseau et al. (2006) indicate mixing by degree can occur from two different interaction patterns: a) two individuals become friends because they share a common friend, or b) new individuals in the network associate with others that already have a high number of associates. It is unclear which of these may be the foundation for associations in the Mississippi Sound.

The removal of individuals of high centrality from the network resulted in a breakdown of the network into separate components. However, before these components appeared, several individuals had to be removed (9 and 13 for betweenness and degree, respectively). The removal of only one or two individuals with the highest centrality measures did not seem to cause disruption to the network, suggesting that there are multiple individuals that maintain the structural integrity of the network.

This is not to say that there is no effect on the network with the removal of only a few key individuals. It is possible that the presence of one individual in a group is related to that of another. For example, every time #7093 was sighted, #7027 was a part of the group. Every time #7077 was sighted, so was #7058. Therefore, if #7027 and #7058 are removed from the network, all associations involving #7093 and #7077 would be removed as well. This effect is not accounted for in the visual display of the network. Thus, some individuals may have a stronger effect on the maintenance of the network than reflected simply by the network statistics.

There are two possible sources of removal from a network: 1) death or 2) migration out of the area utilized by the network. Each of these sources may

occur under natural circumstances (such as death from disease or migration due to changes in prey distribution) or as the result of anthropogenic factors.

Regardless of the source of removal, the impacts on the social network may be significant. Specific social bonds may be destroyed (Bejder et al., 2006) and in some cases, the interactions between communities in the network may be restricted (Lusseau & Newman, 2004).

Limitations. The network was filtered with the intention of removing the effect of associations due to the “gambit of the group” on the network values, allowing for a clearer picture the network structure (Croft et al., 2008). While previous studies have used dyad significance values as a method of filtering the network (e.g. Lusseau & Newman, 2004), Whitehead, Bejder, and Ottensmeyer (2005) point out that these values do not provide a measure of the strength of the relationship between individuals. Thus, for the current study, the value of the association index was used as a filter, with associations being represented in the network only if they were above the mean value. This threshold was arbitrary, and a different threshold value may have produced very different network values, leading to a completely different interpretation of the data.

Ultimately, the results that would be most highly affected by filtering are those that incorporate specific values calculated from the network, such as betweenness and degree. The removal of even one association has the potential to have an effect on these centrality measures. Therefore, the community divisions identified in the current study may have been different if no filtering had taken place. Additionally, the disintegration of the network as highly

central animals were removed may have been reduced if some of the associations had not been removed.

Island Networks

The network analyses for each of the island locations (including the channel) revealed some very interesting differences between locations. The network for the channel was highly disjointed, with many distinct clusters. This may be a reflection of the fact that dolphins often use the channel for feeding and then move to other locations within the study area (personal observation).

The island networks were much more structured than the channel. The networks for Horn and Cat Islands were similar, but the connections between individuals at Horn Island were often more isolated, with clusters of individuals being connected through only one or two individuals. There were no distinct connected clusters of individuals in the Cat Island network, however. Individuals were often connected to others in the network through several pathways, which is reflected in a higher average betweenness.

Ship Island was the most highly connected network, which is reflected in its high mean betweenness and degree. On average, individuals in this network were associated with 23 other dolphins, while at Cat and Horn islands, individuals had a much lower average of 9 and 12 associates, respectively. The highly structured network of Ship Island, as well as the presence of a large portion of select individuals suggests that this island may be ecologically relevant to dolphins in the Mississippi Sound. Often, groups with young calves have been observed in the shallow areas around the west end of the island (personal observation), which may serve as a nursery area similar to those observed by

Scott et al. (1990) in Sarasota Bay. It is also possible that the distribution of prey items at Ship Island facilitates group formation, thus increasing the likelihood of two dolphins being connected.

Limitations. Because the island networks were constructed using a binary network, the strength of the relationships between connected individuals is not represented. Therefore, while one network may appear more structured than another, the relationships between individuals in that network may not be as strong as those in a less structured network.

Additionally, the structure of the network at Horn Island, specifically, may be an artifact of the sampling methods used in the study. As previously mentioned, Horn Island was not a regular part of the study area until July 2005. Analysis of data collected in the years following the study period will help determine whether this structure is accurate.

Hurricane Katrina

Network analyses of the seventeen dolphins sighted at least two times before and after Hurricane Katrina revealed interesting changes in the network between the two conditions. Each of the calculated measures of centrality except eigenvector increased following the hurricane. Following the hurricane, there was a much higher proportion of observed associations between the seventeen dolphins. Prior to the hurricane only 21% of the possible associations were observed, while 43% were observed after the hurricane. This change can be seen in the visual display of the network, but is also reflected in a significantly higher clustering coefficient post-Katrina.

Not only were there more connections between individuals after Hurricane

Katrina, but the strength of these associations was significantly higher as well. Interestingly, eigenvector centrality was not affected by increases in strength. This centrality measure represents the relationship between an individual's strength and the strength of its associates (Whitehead, 2008). As this value did not change significantly, dolphins with strong associations were not more likely to associate with other dolphins that had strong associations following the hurricane.

The ultimate cause of the increase in the number and strength of the associations among these 17 individuals is not clear. However, it is possibly due to a change in the use of the study area brought on by changes in habitat structure. Most sightings of the 17 dolphins in the post-Katrina condition were at Ship Island. Quite possibly, the hurricane made substantial changes to the habitat, such as the distribution of prey or potential mates, which led to increased utilization of this location.

Another possible cause for increased associations post-Katrina may be the reduction of human disturbances in the area. Previous work has shown that dolphins in the Sound increase their traveling behavior and decrease foraging in the presence of high-speed watercraft. However, the hurricane damaged many vessels, including those used for recreational and commercial purposes, which led to an overall reduction of vessel traffic (Miller et al., in press). Additionally, fishing activities were significantly reduced, possibly resulting in a higher abundance of prey (Miller et al., in press). Consequently, reduced disturbance from vessel traffic and increases in prey abundance may have resulted in increases in foraging and socializing behaviors among dolphins in the area.

Limitations. The selection criterion for this analysis may have had an effect on the results. To be included, an individual had to be sighted twice both before and after the hurricane, a condition that only 17 individuals satisfied. This limited the number of associations that were represented in the network. Changing the criterion to individuals sighted at least once before and once after the hurricane would have allowed for many more individuals to be included in the analysis and may have given a better picture of changes in the number of associations. However, the strength of the associations, and consequently the value of the network statistics, would have been biased by a higher number of associations with a COA value of 1.0.

Conclusions

The results of the current study may have implications for how the stocks that utilize the Mississippi Sound are managed. It is clear that the area is ecologically important for bottlenose dolphins on a seasonal and year-round basis. The Sound is also highly valuable for human activities and special attention should be paid to the potential effects that anthropogenic disturbance may have on the animals in the area. The current study was able to capitalize on a natural disaster that resulted in a reduction of anthropogenic disturbances and provides a foundation for future research on the subject.

Table A1

Inclusion Criteria From a Variety of Studies on Association Patterns in Tursiops sp.

Study Area	Criteria	Study Period	Citation
Galveston Bay, TX	≥ 4	each yr / 2 yrs	Brager et al., 1999
Point Lookout, Australia	≥ 4	2 yrs	Chilvers & Corkeron, 1987
Virginia Beach, VA	≥ 5	3 of 6 yrs	Fearnbach, 1997
Gulfo de Guayaquil, Ecuador	≥ 5	2 yrs	Felix, 1997
San Luis Pass, TX	≥ 5	1 year	Maze-Foley & Wursig, 2002
Cedar Keys, FL	≥ 5	1 yr	Quintana-Rizzo & Wells, 2001
Grand Bahamas	≥ 3	10 yrs	Rogers et al., 2004
Grand Bahamas	≥ 5	3 yrs	Rosbach & Herzing, 1999
Shark Bay, Australia	≥ 10	each yr / 5 yrs	Smolker et al., 1992
Beaufort, NC	≥ 5	10 yrs	Thayer, 2007
San Diego, CA	≥ 5	6 years	Weller, 1991

	6041	6054	6055	6099	7002	7003	7005	7011	7013	7014	7015	7025	7026	7027	7030
1002	0.29	0.43	0.14	0.14	0.11	0.22		0.13			0.25	0.29		0.27	0.4
2002	0.2		0.2		0.14						0.17	0.2	0.18	0.18	
2003		0.18													0.17
2010			0.4		0.14							0.4		0.18	
2014	0.17	0.17	0.17	0.17			0.31	0.31	0.17						0.15
2020	0.2	0.2		0.2	0.14	0.14					0.33				
5003	0.18		0.36		0.13	0.13	0.17				0.15	0.36	0.17	0.33	
5007	0.18	0.18		0.18	0.13	0.13					0.15			0.17	
5016	0.2	0.2	0.4	0.2	0.14	0.29					0.5				
6001		0.31		0.31	0.35	0.35	0.29	0.14	0.15		0.13		0.14		
6006	0.36	0.36	0.18	0.18	0.27	0.27					0.77				
6011	0.18	0.18	0.18		0.13	0.13		0.17			0.31				
6019	0.2		0.4		0.14							0.8	0.18	0.55	
6031	0.29	0.14	0.14		0.22	0.22					0.25	0.14	0.13		0.13
6040	0.8						0.18				0.17				
6041	—		0.2			0.14	0.18				0.33				
6054	—	—		0.2	0.29	0.29		0.18			0.17	0.2			0.55
6055			—		0.14	0.14					0.17	0.4		0.36	
6099				—	0.14	0.14		0.18	0.2		0.17		0.18		
7002					—	0.22	0.13	0.13	0.14	0.29	0.13	0.14	0.13	0.13	
7003						—	0.13				0.25	0.14	0.13	0.13	0.13
7005							—						0.17	0.17	
7011								—	0.55	0.36					0.17
7013									—	0.4					
7014										—					
7015											—				0.15
7025												—	0.18	0.55	0.18
7026													—	0.33	
7027														—	
7030															—
7042															
7055															
7058															
7060															
7077															
7093															
8003															
8004															
8013															



0



0.1-0.20



0.21-0.40























0.41-0.60



0.61-0.80



0.81-1.00

	7042	7055	7058	7060	7077	7093	8003	8004	8013
1002	0.4	0.12	0.78	0.42	0.63	0.29	0.29	0.29	
2002			0.29	0.13	0.33	0.2		0.6	
2003				0.25				0.18	
2010						0.2		0.2	
2014		0.4	0.25	0.12	0.14		0.17		
2020	0.36		0.43	0.27	0.33		0.2	0.2	0.17
5003			0.13	0.13	0.15	0.36		0.36	0.15
5007	0.33		0.27	0.25		0.18	0.55		
5016	0.18		0.43	0.27	0.33		0.2		0.33
6001	0.14	0.13	0.12	0.33			0.15	0.15	
6006	0.17		0.53	0.5	0.46		0.18		0.31
6011			0.27	0.25	0.31		0.36		0.31
6019	0.18					0.4		0.2	
6031			0.33	0.32	0.38			0.14	0.25
6040			0.43	0.27	0.33		0.2	0.2	
6041			0.43	0.4	0.33		0.2		0.17
6054	0.18	0.15	0.43	0.53	0.33		0.2	0.2	
6055	0.18		0.14	0.13	0.17	0.4		0.2	0.17
6099	0.18	0.15	0.14	0.13			0.2		0.17
7002	0.13		0.11	0.21		0.14	0.14	0.14	
7003	0.13		0.33	0.32	0.25	0.14	0.14	0.14	0.13
7005		0.14				0.18			
7011		0.29	0.13		0.15		0.18		
7013		0.31							
7014									
7015	0.15	0.13	0.5	0.47	0.43		0.17		0.29
7025	0.18		0.14	0.13	0.17	0.4		0.4	
7026						0.18			
7027	0.33					0.91		0.18	
7030		0.14	0.4	0.38	0.46			0.18	
7042	—		0.13	0.25		0.36	0.18		
7055		—	0.12		0.13				
7058			—	0.53	0.88		0.29	0.29	0.25
7060				—	0.35		0.27	0.13	0.12
7077					—			0.33	0.29
7093						—		0.2	
8003							—		
8004								—	
8013								—	

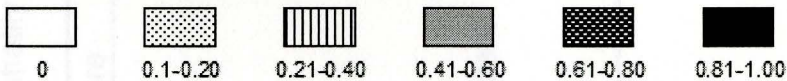


Table A3

Description of centrality measures calculated by SOCPROG 2.4 as defined by Whitehead (2008).

Centrality measure	Definition
Strength	How well connected an individual is to other individuals
Eigenvector	How well connected an individual is to other individuals in terms of the number and strength of connections; individual can have high eigenvector centrality because it has high strength or because it is connected to other individuals of high strength
Reach	Overall strength of an individual's neighbors
Clustering coefficient	How well connected neighbors are to one another
Affinity	Average weighted strength of neighbors; calculated as an individual's reach divided by its strength

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