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Characterization of Association Patterns of Coastal Migratory Bottlenose Dolphins, *Tursiops truncatus*, in the Nearshore Waters of Virginia Beach, Virginia

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CHARACTERIZATION OF ASSOCIATION PATTERNS OF COASTAL MIGRATORY BOTTLENOSE DOLPHINS, *TURSIOPS TRUNCATUS,* IN THE NEARSHORE WATERS OF VIRGINIA BEACH, VIRGINIA

by

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ABSTRACT

CHARACTERIZATION OF ASSOCIATION PATTERNS OF COASTAL MIGRATORY BOTTLENOSE DOLPHIN IN VIRGINIA BEACH, VIRGINIA

Holly Fearnbach
Old Dominion University, 2004
Director: Dr. Mark Butler

Bottlenose dolphins, *Tursiops truncatus*, commonly occur in fission-fusion social systems. For this study, I analyzed photo-identification data from 1994 to 1999 to describe association patterns of bottlenose dolphins in the nearshore waters of Virginia Beach, Virginia. Bottlenose dolphins are present seasonally (late April until early November) in these waters and individuals are considered to be members of the North Atlantic coastal migratory stock. I selected 78 individuals for detailed analyses from the 972 dolphins identified in the study area. Those chosen as "select" dolphins had been sighted at least five times in three of the six study years; all 972 identified individuals were included in analyses as possible associates. The mean group size for all identified dolphins was 22 (range: 2 - 200; SD = 20), whereas the mean group size for select dolphins was 35 (SD = 12). Select individuals had a mean number of 93 associates (range: 18-243; SD = 48), and almost 13% of associations between individuals were repeat associations. Associations were measured using the Half Weight Index (HWI), which ranges from 0 when animals are never associated to 1 if they are always associated. Only 10.5 %, or 6216/64090, of all calculated HWI values were greater than 0. The mean HWI value for select individuals was 0.18 (range: 0.01 - 0.75; SD = 0.05). "Definite" and "probable" females were identified based on the number of times they were sighted with young of year (YOY). A loose network was evident for all definite and probable females and associations were influenced by reproductive state. Four (18%) females had another female as their highest associate and 13 (59 %) had another female as one of their five highest associates. Groups containing YOY were significantly larger than groups without YOY and 100% of all select individuals associated with at least one YOY. In conclusion, this study was the first to concentrate on purely migratory bottlenose dolphins. Social patterns were consistent with those observed for bottlenose dolphins in various habitats throughout the world, with individuals exhibiting a high degree of social fluidity with mostly weak and few strong associations between individuals.

For Michael and Emily

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TABLE OF CONTENTS

Page

TABLE OF CONTENTS (cont.)

TABLE OF CONTENTS (cont.)

Page

LIST OF TABLES

Table Page

LIST OF FIGURES

LIST OF FIGURES (cont.)

LIST OF FIGURES

LIST OF APPENDICES

INTRODUCTION

The study of mammalian social organization, particularly field studies of free-ranging mammals, has greatly enhanced our overall understanding of social systems (Heimlich-Boran 1993). Wells et al. (1987) stated that an accurate description of the social structure of a species is the first step towards understanding its social organization. Interactions between pairs of individuals are the basic elements of social structure and social systems represent the outcome of an individual's behavioral interactions and strategies (Hinde 1976). One way to accurately characterize the social structure of a population or species is to examine these interactions or associations among individuals (Wells et al. 1987; Smolker et al. 1992).

Associations between individuals can be defined as the frequency with which two individuals are present in the same group at the same time (Cairns and Schwager 1987). When group membership changes at frequent intervals, the level of association between individuals can also vary widely (Cairns and Schwager 1987). Variation in association patterns arises when individuals change groups at random, sometimes showing no preference for a particular companion. Individuals can occur in small cliques that form sub-units of a larger, changeable group, or as a pair that occurs together on a specific day (Cairns and Schwager 1987). In some species, an individual almost always associates with the same set of conspecifics, whereas in others, an individual may rarely associate with the same conspecific (Smolker et al. 1992). Long-term studies are therefore necessary to show which features of social organization are consistent over time (Wrangham 1986).

The journal model for this thesis is the Canadian Journal of Zoology.

Variables affecting social patterns

Group formation in mammalian systems has been proposed to be a result of three main factors: resource availability, access to mates, and predation (Eisenberg et al. 1972; Jarman 1974; Crook et al. 1976; Bertram 1978; van Shaik 1983; Lott 1984; Pulliam and Curaco 1984; Andelman 1986; Clark and Mangel 1986). Lott (1984) suggests that population density, and thus potential habitat saturation, may also cause intraspecific variation in social patterns. Wrangham and Rubenstein (1986) report that the effects of intraspecific competition, which may be mediated by ecological constraints, are often expressed differently in different species. Such effects may therefore account for the evolution of complex social groups, even when no other factors favor social grouping (Wrangham and Rubenstein 1986).

Relationships between individuals reflect behavioral strategies that have been selected to maximize inclusive fitness (Wrangham and Rubenstein 1986; van Shaik 1989; Kappeler 1999a). In primates, energetic costs of reproduction differ between sexes because female reproductive success is usually limited by ecological resource quality and availability, whereas male reproductive success is usually limited by social resource availability, such as mates (Andelman 1986). Selection pressures on females ultimately determine the effect of ecological variables (e.g., predation, resource distribution) on social systems (Bradbury and Vehrencamp 1977; Emlen and Oring 1977; Wrangham 1980; Rubenstein 1986). Therefore, the distribution of females often determines the reproductive options that are available to males, whose main focus is the optimization of mating success, and whose strategies can in turn influence female grouping patterns (Rubenstein 1986; Wrangham 1987; van Schaik 1989; van Hoof and van Shaik 1994).

Primates, the best studied of the large social mammals, often serve as a model for other large and more difficult to study social mammals, such as cetaceans. Norris and Dohl (1980b) placed group formation (schooling) in open-water social species of cetaceans into six functional categories: food gathering, reproduction and growth, social integration and communication, learning, defense, and response to environmental cycles. Individuals decide whether they lead a solitary life or form permanent groups, and thus determine which group size and composition is optimal under a given set of ecological conditions (Kappeler 1999b). Different species, and even different populations of the same species, often show variability in their social organization in response to variations in environmental conditions such as availability and distribution of food resources, density of predators, and physical characteristics of the habitat (Wells et al. 1980). However, much of the variability observed within primate social organization has been correlated with the interaction of both ecological and social pressures (Wrangham 1986; Wrangham and Rubenstein 1986).

In ecology, a population is typically defined as a group of individuals of one species in an area, whereas a community is defined as an assemblage of species populations that occur together in time and space (Begon et al. 1996). However, for bottlenose dolphins in Sarasota, Florida, Wells et al. (1987) defined a dolphin community as all groups of dolphins (and individuals that clearly did not belong to a group) that share a large portion of their range and interact with each other to a greater extent than with members of similar units in adjacent waters. The use of this terminology is commonplace in cetacean studies and Brager (1999) comments that a community of Wells et al. (1987) is probably the same as a local population. For Virginia Beach dolphins, all animals are referred to as the study population. References to both communities and populations throughout this thesis were made according to definitions from individual study areas.

Fission-fusion social systems

A frequently observed social pattern in mammals is the fission-fusion system. Members of this system display frequent changes in group membership as individuals form temporary groups that fuse together and then break apart (Kummer 1971; Struhsaker and Leland 1979). Both social and ecological factors can cause such changes in group membership (Wrangham 1986). Mammals exhibiting this system include the African lion, *Panthera leo* (Schaller 1972; Packer 1986; Packer et al. 1990), spotted hyena, *Crocuta crocuta* (Holecamp 1997), golden jackal, *Canis aureus* (MacDonald 1979), wolf, *Canus lupus* (Mech 1987) and coyote, *Canus latrans* (Bekoff and Wells 1981); primates such as the common chimpanzee, *Pan troglodytes* (Goodall 1968, 1986; Wrangham 1986), pygmy chimpanzee or bonobo, *Pan paniscus* (Badrian and Badrian 1984; Wrangham 1986) and spider monkey, *Ateles geoffri* (Chapman 1990); ungulates such as the eland, *Tragelaphus oryx* (Hillman 1987) and many antelopes (Jarman 1974); marsupials including the gray kangaroo, *Macropus giganteus* (Jarman and Southwell 1986) and red-necked wallaby, *Macropus rufogriseus banksianus* (Johnson 1989); and cetacean species such as the bottlenose dolphin, *Tursiops truncatus* (Saayman and Tayler 1973; Wursig 1978; Wursig and Wursig 1977, 1979; Wells et al. 1987; Ballance 1990; Brager et al. 1994; Fertl 1994a, b; Wilson 1995; Bearzi et al. 1997; Rossbach and Herzing 1999; Quintana-Rizzo and Wells 2001; Zolman 2002; Chilvers and Corkeron

2002), spinner and spotted dolphins, *Stenella longirostris sp.* and *Stenella frontalis/attenuata sp.* (Norris and Dohl 1980a, 1994; Ostman 1994; Herzing and Brunnick 1997), Hector's dolphin, *Cephalorhynchus hectori* (Slooten et al. 1993; Bedjer et al. 1998; Brager 1999) and sperm whale, *Physeter macrocephalus* (Whitehead and Arnbom 1987; Whitehead and Weilgart 2000).

Fluidity of association patterns in delphinid species appears to increase as body size decreases (Bedjer et al.1998). Resident (fish-eating) killer whales are recognized as having the most stable cetacean societies; some community memberships have remained unchanged (excluding births and deaths) for more than 30 years (Bigg et al.1990). Pilot whales fall next on the continuum; most members remain in their natal pods throughout their lives, only briefly associating with other groups for breeding purposes (Heimlich-Boran 1993; Amos et al.1991, 1993). Bottlenose dolphins follow; multiple studies have reported fluid systems with many weak and few strong associations among individuals (Wells et al. 1987; Ballance 1990; Weller 1991; Smolker et al. 1992; Brager et al. 1994; Wilson 1995; Richards 1996; Felix 1997; Rossbach and Herzing 1999; Quintana-Rizzo and Wells 2001; Zolman 2002; Chilvers and Corkeron 2002; Maze-Foley and Wursig 2002). Spinner dolphins are next; individuals associate intermittently with almost every other member of their school (often more than 250 animals), but still form long-term, strong bonds with certain individuals (Norris and Dohl 1980a; Ostman 1994). Hector's dolphins, with the most fluid social system, appear to fall at the bottom of the cetacean social continuum. Like spinner dolphins, individuals associate with most other group members, but most of these associations are random and few long-term bonds have been observed (Slooten et al. 1993; Bedjer et al. 1998; Brager 1999).

Background on bottlenose dolphins

Bottlenose dolphins, *Tursiops spp.*, are the most widely studied cetacean species due to their coastal distribution worldwide and their high abundance in nature and captivity. Bottlenose dolphins are distributed worldwide and studies have been conducted in a variety of habitats, ranging from rivers and estuarine systems to pelagic oceanic systems. Bottlenose dolphins have been studied in the United States, along both the east coast and in the Gulf of Mexico and associated waters (Shane 1990; Wells et al. 1987; Scott et al. 1990; Fertl 1994a, b; Brager et al. 1994; Zolman 2002; Barco et al. 1999a; Maze and Wursig 1999; Quintana-Rizzo and Wells 2001; Gubbins et al. 2002a, b; Maze-Foley and Wursig 2002), the Bahamas (Rossbach and Herzing 1999; Parsons 2002) and the west coast and in the Gulf of California, Mexico (Hansen 1990; Ballance 1987, 1990; Weller 1991; DeFran et al. 1999; Defran and Weller 1999); Australia (Corkeron et al. 1987; Corkeron 1990; Smolker et al. 1992; Connor et al. 1992; Richards 1996; Chilvers and Corkeron 2002); New Zealand (Williams et al. 1993); the United Kingdom in Scotland (Wilson et al. 1997, 1999) and Cornwall (Wood 1998); along the coast of South Africa (Saayman and Tayler 1973); Ecuador (Felix 1997); and Argentina (Wursig 1978; Wursig and Wursig 1977, 1979).

Long-term studies on residential populations of bottlenose dolphins have been conducted in Sarasota Bay, Florida, where ~100 animals have been studied since the 1970s (Irvine et al. 1981; Wells et al. 1987; Scott et al. 1990), and Shark Bay, Australia, where ~380 animals have been studied since the mid-1980s (Smolker et al. 1992; Connor et al. 1992; Richards 1996). These two studies have produced the bulk of the information pertaining to the social structure, life-history patterns, and behavioral interactions of free-ranging bottlenose dolphins. Both Sarasota and Shark Bay are closed estuarine systems and their resident bottlenose dolphin populations have strikingly similar patterns of social organization (Wells et al. 1987; Smolker et al. 1992; Richards 1996). Individuals have extremely fluid social systems with many weak and few strong associations. Long-term associations among individuals are frequent and, although mixed sex associations occur, the highest associate of an individual is most commonly a member of the same sex (Wells et al. 1987; Smolker et al. 1992; Connor et al. 1992; Richards 1996). Associations are based largely on age, sex, behavior, and reproductive status (Wells et al. 1987; Smolker et al. 1992).

Short-term studies have been conducted in both open and closed habitats and most results are consistent with those found in Sarasota and Shark Bay. Associations among individual dolphins were predominantly weak and short-term, with few strong and long-term bonds (Ballance 1990; Weller 1991; Brager et al. 1994; Felix 1997; DeFran et al. 1999; Defran and Weller 1999; Quintana-Rizzo and Wells 2001; Gubbins 2002b). Both Brager et al. (1994) and Fertl (1994a) suggest that a high incidence of low-level associations among individuals is most likely the result of interactions between residents and either animals simply moving through the area or individuals with overlapping home ranges. DeFran et al. (1999) and DeFran and Weller (1999) suggest that the variability in the sighting history, site fidelity, and movement patterns observed for bottlenose dolphins along the coast of San Diego, California could be attributed to variability in the open habitat structure of the California coastline compared to more protected study areas such as Sarasota or Galveston Bay.

Residency patterns of dolphins in many study areas (both open and closed) differ from those in Sarasota and Shark Bay because they involved dolphins of "mixed" residency strategies, including both resident and non-resident dolphins (Baker 1978; Sinclair 1983; Swingland 1983). Resident dolphins often display a high degree of site and association fidelity, whereas non-residents often display low site and association fidelity (Quintana-Rizzo and Wells 2001; Gubbins 2002a). Associations between resident and non-resident dolphins are often observed, but these associations occur less frequently than associations between dolphins of similar residency status (Felix 1997; Quintana-Rizzo and Wells 2001; Gubbins 2002b).

Smolker et al. (1992) proposed that bottlenose dolphins in different habitats could exhibit widely differing social organization because factors such as increased predation or resource availability could exert markedly different pressures on individual association patterns. Shane (1980) found that bottlenose dolphins in Texas had both seasonal and year-round home ranges and Caldwell and Caldwell (1972) suggested that bottlenose dolphins have seasonal home ranges joined by a traveling range. Prey movements may cause large-scale dolphin movements in open ocean and bay systems as proposed for Argentina, the Gulf of California, Mexico and San Diego (Wursig 1978; Wursig and Wursig 1977, 1999; Ballance 1990; Hansen 1990; Weller 1991; DeFran et al. 1999; DeFran and Weller 1999) and small-scale movements and/or changes in habitat use in estuarine and bay systems (Scott et al. 1990; Bearzi et al. 1997; Quintana-Rizzo and Wells 2001; Gubbins 2002a).

Stomach content analyses of stranded bottlenose dolphins along the Atlantic coast indicate a preference for prey species in the family Sciaenidae (Barros and Odell 1990;

Mead and Potter 1990; McGurk 1997). Barco et al. (1999a) noted that certain sciaenid fishes present in the Chesapeake Bay in the spring and summer undergo a migration into deeper or warmer waters in the fall and suggested that water temperature may indirectly affect dolphin migration by directly affecting prey movements. Barco (1995) found a positive correlation between dolphin abundance and water temperature, but her limited prey data did not support a correlation between dolphin abundance and prey availability. Future studies should aid in understanding both the movement patterns and population structure of bottlenose dolphins along the east coast.

Stock definition

Bottlenose dolphins included in this study are present seasonally (mid-April through mid-November) in the nearshore waters of Virginia Beach, Virginia (Barco et al. 1999a). The Virginia Marine Science Museum has been conducting photo-identification surveys in this area since 1989 and individual dolphins are considered to be members of the Western North Atlantic coastal migratory stock (Hohn 1997; NMFS 2002).

The stock structure and movement patterns of Atlantic coastal migratory bottlenose dolphins were evaluated following a mass-mortality event in 1987-88 that potentially reduced the coastal bottlenose dolphin population by as much as 50% (Scott et al. 1988). Stranding patterns suggest that the epizootic (morbillivirus) involved in the "die-off" was potentially spread by contact between individuals as they migrated along the coastline.

The existence of a single coastal migratory stock, composed of subsets of permanent residents, transients and seasonal migrants that inhabit estuarine, coastal and offshore waters from Florida to New Jersey was first suggested by Scott et al. (1988).

However, because it is currently believed that there is a complex mosaic of stocks that range along the east coast rather than a single stock (Hohn 1997; NMFS 2002), seven management stocks have been established (NMFS 2002). The range of these dolphins extends from as far south as central Florida to as far north as Long Island, New York (Scott et al. 1988; Kenney 1990; NMFS 2002). These dolphins display variable degrees of residency, ranging from small, year-round residential populations to large transient populations that migrate on a seasonal basis (Wang et al. 1994; Hohn 1997; Zolman 2002; NMFS 2002).

Virginia Beach dolphins (seasonal transients) have been sighted as far north as Cape May, New Jersey and as far south as Manteo, North Carolina (~360 km), but the data set is far from being complete. Sightings of individual bottlenose dolphins from study sites along the east coast have been collected opportunistically and all matches are housed in the Mid-Atlantic Bottlenose Dolphin Catalog (MABDC) (Urian et al. 1999). Almost 400 individuals from Virginia Beach are included in the catalog and matches for individual dolphins among and between several study areas support the idea that individuals move long distances along the coastline. Both the exact proportion of the population involved in these movements and the amount of time individuals occur in each study region have not been determined, but these and other issues are being investigated.

Objectives

The goal of this project was to characterize the association patterns of bottlenose dolphins that occur seasonally in the nearshore waters of Virginia Beach. Similarities in associations have been reported for bottlenose dolphins from a variety of habitat types with a wide range of residency patterns. But no study has concentrated on purely migratory dolphins, although one might predict that similarities would exist between coastal migratory bottlenose dolphins in the Virginia Beach study area and bottlenose dolphins exhibiting variable residency patterns in other study areas. Specifically, I attempted to describe social structure and underlying association patterns of 78 individual bottlenose dolphins, *Tursiops truncatus,* for which sufficient sighting data existed. Please refer to Methods for a more detailed description of all objectives and associated analyses.

METHODS

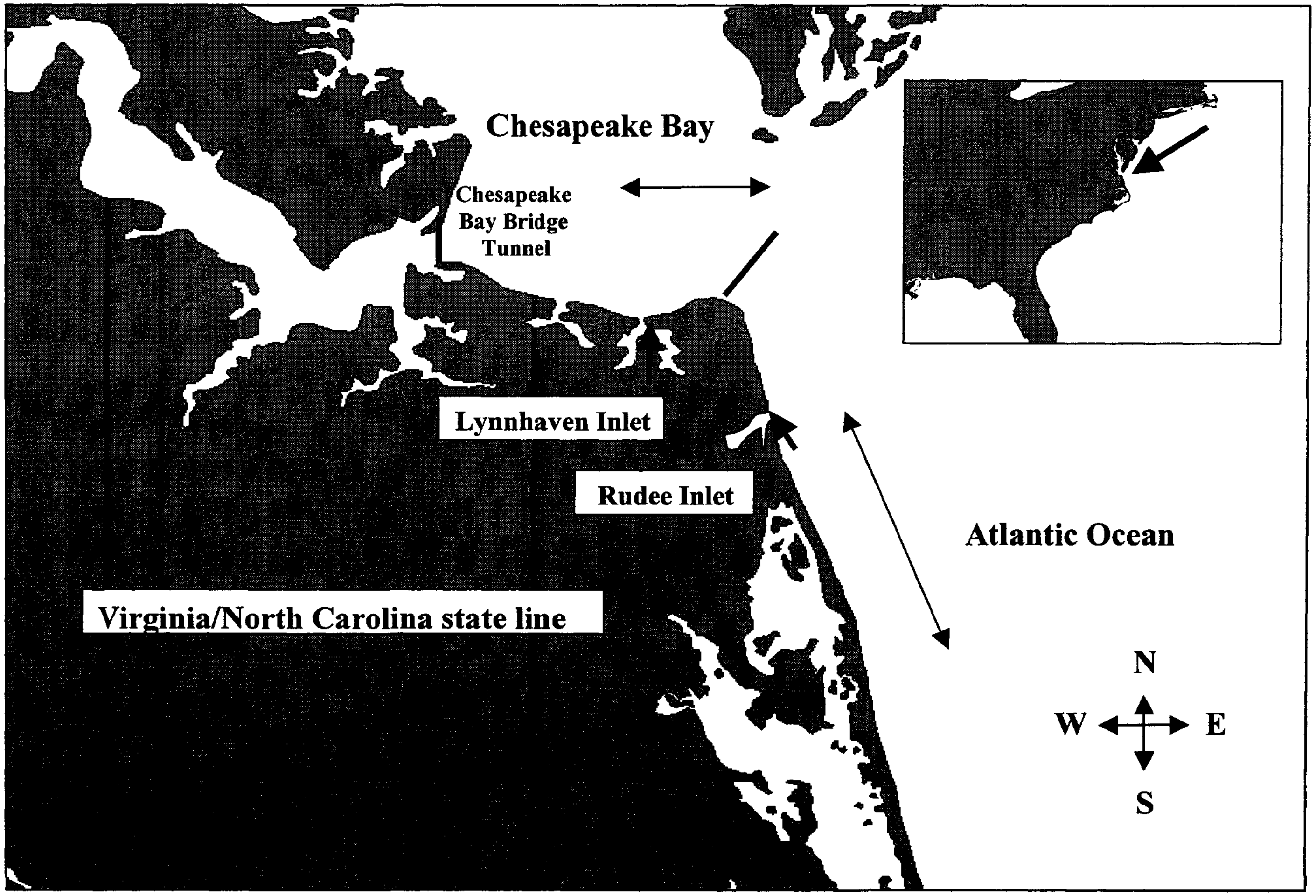
Study area

This study examined the association patterns of coastal migratory bottlenose dolphins in the nearshore waters (<1 km from shore) of Virginia Beach, Virginia (USA). The study area covered approximately 24 km^2 and ranged from 3-5 km south of Rudee Inlet (36° 39.0 W, 75° 53.0 N) to the Chesapeake Bay Bridge Tunnel (36°55.5 W, 76°7.4 N) (Fig.1). Surveys were rarely conducted farther than 1 km offshore, although animals were frequently sighted beyond the boundary of the study area (Barco et al. 1999a; personal observation). Following the methods of Barco et al. (1999a), the study area was divided into two sections: 1) bay; a portion of the Chesapeake Bay running east-west from the mouth of the Chesapeake Bay to the Chesapeake Bay Bridge Tunnel and 2) ocean; an area running north-south along Virginia Beach in the Atlantic Ocean and southeast of the mouth of the Chesapeake Bay. Following Ballance (1990), the Virginia Beach study area can be defined as an open system; waters have no protection from winds or storms and are defined by few geographical features (*i.e.,* gently sloping beaches with sand bars and low wave energy). The bottom topography is predominantly loose, small grain sand and silt. The mean water temperature in Virginia Beach from April through November is 20 °C (range: 12 to 28 °C) (NOAA 1994-1999).

Surveys

The Virginia Marine Science Museum conducted boat-based photo-identification (photo-id) surveys from 1994 through 1999. The number of surveys conducted each week

FIG. 1. Map of the Virginia Beach study area. Surveys ranged from several km south of Rudee Inlet to the Chesapeake Bay Bridge Tunnel (<1 km from shore). Note the separation between bay and ocean waters.



varied, although every effort was made to conduct at least two surveys per week in 1994 and 1997-1999. Overall effort was lower in both 1995 and 1996 due to limited crew, funding, and boat availability.

Most surveys were conducted using the Virginia Marine Science Museum's 6.4 m Boston Whaler, but private watercraft (< 8m in length) were used opportunistically when the museum boat was not available. Surveys usually began in the morning (~ 0900) and the length of the survey depended on the number and activity of the dolphins encountered and overall weather and light conditions. Surveys originated from either Rudee Inlet, heading north or south, approximately 150 m from the ocean shoreline or Lynnhaven Inlet, heading east, approximately 150 m from the Chesapeake Bay shoreline. Daily survey routes were chosen based on weather conditions or the frequency of previous sightings within the study area. The boat crew consisted of at least one photographer, one boat operator and one data recorder/observer, although the optimal crew included an additional observer/photographer.

Data collection

An "encounter" was defined as any research-oriented interaction with an individual or group of dolphins. A "sighting" was defined as the photographic documentation of an individual dolphin and a "group" of dolphins was defined, following Shane (1990), as any number of dolphins observed in apparent association, moving in the same direction and often times, but not always, engaged in the same activity (Appendix A). When a group of dolphins was observed, the boat slowly approached and moved parallel to the group, at a speed just faster than the dolphins. Two SRL 35 mm Sigma cameras (both with f 2.8-4.5, 75-300 mm zoom lenses) were used to photograph individuals. Either Kodachrome 64 or 200 or Ektachrome 100 color slide film was used.

Bottlenose dolphins can be distinguished individually by nicks and notches on their dorsal fins. Due to the relative permanence of these distinctive features, individuals can be recognized for long periods of time from photographs of their dorsal fins (Wursig and Wursig 1977). Attempts were made to photo-identify all individuals within the group and the survey was ended when most or all individuals were believed to have been photographed, the behavior of the group became erratic or drastically changed from the start of the encounter, or weather conditions deteriorated.

Survey data

In addition to photographing individuals, both encounter and environmental data were recorded. An encounter data sheet was completed for each encounter and all data except for group estimates and final location were recorded at the start of the encounter (Appendix B). Encounter data fields included total trip, survey effort and encounter times (start and end), vessel, crew, group size (minimum, maximum and best estimate), group composition (presence of young of year and neonates), group heading (where possible), group behavior and initial and final encounter locations (latitude and longitude). Both group size and group composition estimates were recorded at the end of the encounter after all animals observed during the encounter could be accurately evaluated. Estimates were the observer's "best guess" of the group size for each encounter. Minimum, maximum and best estimates were recorded for group size and composition for each encounter group. All group size and composition estimates were determined by a consensus of everyone on the vessel. Estimates of large groups (>50 animals) were more difficult to assess. The group was scanned during the initial approach and throughout the encounter and subgroup estimates were combined to determine overall group size. Latitude and longitude were recorded using a global positioning system (GPS). Environmental data included water depth, temperature, salinity, sea state (Beaufort sea scale), swell, tidal state, and overall weather conditions (*i.e.*, cloudy, rain, clear). Water depth was recorded by a depth sounder and both water temperature and salinity were recorded using a standard refractometer. The start and end frame exposure numbers of each film roll were recorded for the encounter. The photographer's initials were photographed as a "blank" to mark the start of the encounter and the completed datasheet was photographed as a "blank" to mark the end of the encounter.

Slide analysis

All photographs were developed and taken into the lab for analysis. All slides were stamped, separated by encounter date and placed in archival slide sleeves. The slides were then divided into either identifiable ("id") or non-identifiable ("non-id") categories. Identifiable dolphins were individual dolphins with distinct notches or markings on their dorsal fins that enabled them to be distinguished from other dolphins. Non-identifiable dolphins were individual dolphins without any distinct notches/markings on their dorsal fins or with *Xenobalanus sp.* (a pseudo-stalked, commensal barnacle) obscuring some or all of their dorsal fins. All "id" slides were separated by individual for every encounter and the dorsal fin of each individual was sketched to allow for easy comparison. All encounters within a season were compared for possible matches of individuals between or among encounters and a slide analysis data sheet was completed and then proofed for every encounter (Appendix C). Individuals were then separated into categories based on scar/notch/abnormality patterns of leading edge (LE) or trailing edge (TE) (Appendix D). After all individuals had been categorized and matched within season, they were compared to the main catalog of animals. When a match was made (at least three people in agreement), the sightings for that individual for the current season were integrated into the main catalog. If no match was found within the main catalog, a new number was assigned to that individual and it was added to the appropriate category. Only the best quality slides, showing distinctive features of each identified individual, were included in the main catalog (Urian and Wells 1996).

Selection criteria

The Virginia Marine Science Museum photo-id catalogs contain 1006 individuals, of which 972 (97 %) were sighted post-1994. For this study, I selected 78 individuals from these 972 individuals. Individuals qualified if they had a minimum of five sightings in three of the six (1994-1999) study years. Mother/calf associations were not included in analyses based on both the assumption that such associations are 100 % and the low degree of scarring and thus low recognizability of calves. The select 78 individuals were included in all analyses; all 972 individuals were included in association analyses as possible associates. Because more than three-quarters (741/972 = 76.2 %) of the individuals in the photo-id catalog were only sighted one time (557/972 = 57.3 %) or multiple times in a single year (184/972 = 18.9 %), only individuals with more than one sighting were included in small-scale population analyses. This reduced the occurrence of high association values caused by a low number of individual sightings instead of a high number of joint sightings between two individuals.

The sex of most dolphins in the Virginia Beach study area was not determined because of the turbidity of the water, large group sizes, and rough seas. Because the genital region of dolphins was rarely visible, females could only be identified if they had a minimum number of three sightings (photographs) in close proximity to a YOY or neonate. I classified these females as “definite females.” I classified individuals as “probable females” if they had two sightings in close proximity of a neonate or YOY, and as “possible females” if they had a single sighting with a neonate or YOY or multiple sightings with a calf. YOY were characterized by having at least three of the following traits: fetal folds, close proximity to the mother, size of less than half of that of the presumed mother, and extreme buoyancy, the latter a physical trait of juveniles. Neonates were considered a subset of YOY and were characterized by having at least three of the following traits in addition to the characteristics of a YOY: dark coloration, floppy dorsal fin, extreme thinness and equal length of the upper and lower jaw (Urian and Wells 1996). Both YOY and neonates were combined in field counts from 1994-1998, but neonates were recorded as a separate category starting in 1999. To maintain consistency in analyses, both YOY and neonatal counts were combined for all years and I will hereafter refer to them as YOY.

Data processing

All sighting and encounter data were maintained in Excel spreadsheets. The encounter database included all fields previously listed for the encounter data sheets. The sighting database included each individual dolphin’s catalog number, encounter date and number, the year the dolphin was first sighted, the year (if applicable) the individual had a calf and the main catalog notch category.

Analysis of association data

Animals were considered to be associates if they were sighted (photographed) in the same encounter. All sightings of individuals from these encounters were included in association analyses. Association indices were developed to describe the co-occurrence of species within a community or habitat (Dice 1945), but during the past 20 years they have been adopted to measure social structure in vertebrates (Schaller 1972; Wells et al. 1987; Ballance 1990; Smolker et al. 1992; Slooten et al. 1993; Brager et al. 1994; Wilson 1995; Bejder et al. 1998; Brager 1999; Rossbach and Herzing 1999; Quintana-Rizzo and Wells 2001; Chilvers and Corkeron 2002; Maze-Foley and Wursig 2002). The underlying assumptions of these indices are that physical proximity (membership of the same group) signifies social affiliation, and that the amount of time spent together correlates with the strength of association (Bejder et al. 1998). The Half-Weight Index (HWI) was used to describe and quantify the level of associations between select individuals.

The formula for the HWI is:

$$\mathbf{HWI = 2N / n1 + n2}, \text{ where}$$

N = the total number of joint associations between individual 1 and individual 2

n1 = the total number of sightings for individual 1

n2 = the total number of sightings for individual 2

The HWI coefficients of association range from 0, where two individuals are never seen together, to 1, where individuals are always seen together. HWI values were calculated for every possible dyad and minimum, maximum, and mean values were determined for each individual.

According to Cairns and Schwager (1987), the choice of association index formula should be based on the sampling method used. They argue that the HWI is least biased if pairs are more likely to be sighted apart than together. This is often the case because individuals have to be sighted and photographed together in the same sighting. When animals are apart, they can be recorded in another group, whereas if they are together, they can only be documented in one group (Slooten et al. 1993). Ginsberg and Young (1992) suggest that researchers should use another index, the simple ratio (SR) index, over the half weight and other indices. The SR index divides the total number of joint sightings for dolphins 1 and 2 by the sum of all joint sightings of dolphins 1 and 2 and the total number of sightings for both dolphins. They point out that sampling biases may differ from one pair of individuals to the next and the arbitrary weightings of indices reflect the direction but not the extent of the sampling bias (Slooten et al. 1993). Cairns and Schwager (1987) suggest that the SR be used if sampling is random.

Among cetacean researchers, the HWI was used by Wells et al. (1987), Weller (1991), Smolker et al. (1992), Connor et al.(1992), Brager et al. (1994), Felix (1997), Brager 1999, Quintana-Rizzo and Wells (2001), Chilvers and Corkeron (2002) and Maze-Foley and Wursig (2002), whereas the SR was used by Heimlich-Boran (1993), Wilson (1995), Rossbach and Herzing (1999) and Owen et al. (2003). Both indices were used, and compared, by Slooten et al. (1993) and Wilson (1995).

Due to both the variability in sighting patterns of individuals and the migratory nature of the population as a whole, I felt it was more likely that individuals would be seen apart than together and that the HWI was best suited for this study. Comparisons of results to other studies must be made with caution. Rossbach (1997) points out five factors that complicate a straightforward comparison, including: the association index applied, the choice of data applied to the index, the sampling method of data collection used, the method used to identify dolphins, and the location of the sampled area in relation to the range of the dolphins.

I placed all calculated HWI values into one of six categories: no association (0), low level (0.01-0.20), moderate-low level (0.21-0.40), moderate level (0.41-0.60), moderate-high level (0.61-0.80) and high level (0.81-1.0). I used modified Monte Carlo simulations (Manly 1995, 1997; Bedjer et al. 1998) to determine whether associations between individuals were significantly different from random (Whitehead 1997, 1999b; Bedjer et al. 1998).

Objectives

My objectives were:

(1) To determine the mean group size and composition (presence of YOY) for all 78 select individuals. These values were calculated using the "best estimate" values recorded for both group size and composition from encounter data.

(2) To determine both the total and mean numbers of identifiable associates for all select individuals, using sighting data. All identified individuals sighted in an encounter with the select individual were considered associates and were included in analyses. Total and mean values were determined by calculating the sum and mean numbers of all associates for each select individual.

(3) To determine the relative strengths of associations among all select individuals and their identifiable associates. These were calculated using the Half Weight Index (HWI). HWI values were calculated for every associate of each select dolphin (n=78).

(3a) To determine whether associations between individuals were significantly different from random. This was tested using SOCPROG 5.1 (Whitehead 1999a). Alternative data sets were generated with the same number of dolphins and groups as the observed data. Monte-Carlo simulations (10,000) were then applied to determine whether associations between individuals were significantly different from random (Manly 1995, 1997; Bejder et al. 1998; Whitehead 1999b). Associations were deemed significantly different from random if the calculated p-value was < 0.05. (Smolker et al. 1992; Slooten et al. 1993).

(4) To determine grouping patterns of dolphins in the study area (both large- and small-scale).

(4a) To determine whether large-scale grouping patterns of individuals existed within the study population. Whitehead (1997) recommended the use of cluster analyses or multidimensional scaling as a single measure method of displaying the patterning of relationships. SOCPROG 5.1 was used for both hierarchical cluster analyses (Heimlich-Boran 1993; Slooten et al.1993; Rossbach and Herzing 1999) and multi-dimensional scaling (Smolker et al.1992; Rossbach and Herzing 1999). The hierarchical method of cluster analysis results in a dendogram indicating clusters of closely associated individuals. These methods use interval data (squared Euclidean distance) with the average linkage between groups cluster method (Heimlich-Boran 1993). Multi-dimensional scaling (MDS) also uses interval data and produces a scatterplot of individuals. If groups or close associations exist, they are apparent by the position of the individual on the plot. Individuals close to the 0,0 coordinates have little association with other individuals. Due to the large number of associates for all select individuals, both the dendrograms and MDS scatterplots produced were unwieldy and too difficult to interpret. Therefore, I created a separate database for all select definite and probable females and both a dendrogram and scatterplot were produced from this dataset. Thus, these analyses became small-scale and results will be discussed accordingly.

(4b) To determine whether small-scale grouping patterns existed for individuals within the study population. Subgroups of strongly associated individuals were identified based on association indices and were placed into dyads, triads, quartets, or larger networks (including both direct and indirect associations) following Smolker et al. (1992). A dyad was defined when one individual was the other individual's highest associate. A triad resulted when the third individual had: both dyad members as its highest associates, the third individual was the second highest associate for both of the dyad members and the mean association value for the third animal and each of the dyad members was equal to or less than 0.20 away from the calculated association value of the dyad (Smolker et al. 1992). A quartet was formed by adding a fourth member in a similar manner (Smolker et al. 1992).

(5) To determine whether variations in association patterns exist based on the sex or reproductive status of an individual. The total number of associates, mean group size, group composition and HWI values were calculated for all select definite ($n = 18$) and probable females (n = 4). Either Mann-Whitney U test or Kruskal-Wallis analysis was applied to determine whether group size, group composition and number of associates were significantly different between and among all identified females, all select females, all definite females, all probable females and all identified dolphins. These tests were also used to determine whether associations and group sizes of females were significantly different based on the reproductive status of the female. Females were considered to be "reproductive" during a range of years, from the year before the first sighting with a neonate until the last year sighted with a calf. Sighting data were analyzed to determine whether the number of associates for select females was significantly different among reproductive years and two sociograms were created to access small-scale grouping and the degree of fluidity of associations for select females (definite and probable).

(6) To determine whether temporal variations in associations exist for individuals within the study population. Bottlenose dolphins are present seasonally in the Virginia Beach study area and have variable site fidelity (Barco et al. 1999b). Variations in associations between individuals could be attributed to variations in individual occurrence patterns in the study area. Again, either a Mann-Whitney-U test or Kruskal-Wallis analysis was applied to determine whether dolphin occurrence was significantly different among months and years.

RESULTS

Effort

In all, 253 boat-based surveys were conducted between April 1994 and October 1999. Surveys lasted an average of 1.9 hours and 453 hours of effort were logged. Dolphins were observed on 96 % of the surveys and 323 hours were spent in direct observation of dolphin groups. A total of 506 encounters of 10,680 dolphins was recorded (group size was determined for only 479 of the 506 encounters). The number of encounters and dolphins observed was highest in 1994 and lowest in 1995; number of encounters ranged from 70-79 in all other years (1996-1999). Line transect surveys were conducted during 1994. All dolphin groups were not approached, resulting in an increase in the number of encounters and dolphins observed. The number of surveys in 1995 was low due to limited boat and crew availability. Peak survey months (June-August) coincided with peak dolphin abundance in most years. Table 1 summarizes photo-id effort for all survey years and Tables 2-7 present summary data for effort for each survey year.

Group size and composition

Group size for all encounters (n = 479) ranged from two to 200, with a mean of 22 (SD = 20). Overall, more than three-quarters (82 %) of all observed groups numbered between two and 30 individuals. Within that range (2-30), group size of two to five was least common, whereas group size of six to ten was most common. Group size exceeded 100 individuals only four times (Fig. 2).

Table 1. Summary of annual effort for photo-id surveys (1994 - 1999). An encounter is defined as a research-oriented interaction with an individual or group of dolphins.

Year	Total # encounters	Total dolphins encountered
1994	149	2839
1995	59	821
1996	79	1117
1997	73	1828
1998	76	1961
1999	70	2114
TOTAL=	506	10680

Table 2. Summary of 1994 photo-id effort

1994	April	May	June	July	August	September	October	November	Total
Total days surveyed	1	10	14	10	7	10	5	1	58
Total hours of effort	0.6	9.8	16.5	12.8	9.0	9.8	2.2	0.6	61.2
Average daily hours of effort	0.6	1.0	1.2	1.3	1.3	1.0	0.4	0.6	7.4
Total number of encounters	1	18	29	35	36	25	5	1	149
Total hours with dolphins	0.6	9.8	16.5	12.8	9.0	9.8	2.2	0.6	61.2
Total dolphins encountered	27	235	503	660	775	537	78	24	2839

Table 3. Summary of 1995 photo-id effort

1995	April	May	June	July	August	September	October	November	Total
Total days surveyed	0	5	9	9	4	2	2	0	31
Total hours of effort	0	4.9	4.5	16.9	1	2.3	0	0	29.6
Average daily hours of effort	0	1.0	0.5	1.9	0.3	1.2	0	0	4.8
Total number of encounters	0	9	13	30	2	5	0	0	59
Total hours with dolphins	0	4.9	4.5	12.5	1	2.3	0	0	25.2
Total dolphins encountered	0	165	180	320	44	112	0	0	821

Table 4. Summary of 1996 photo-id effort

1996	April	May	June	July	August	September	October	November	Total
Total days surveyed	**1**	**5**	**7**	**10**	**11**	**8**	**0**	**0**	**42**
Total hours of effort	**0**	**7.6**	**21.6**	**21.7**	**22.6**	**8.6**	**0**	**0**	**82.1**
Average daily hours of effort	**0**	**1.5**	**3.1**	**2.2**	**2.05**	**1.1**	**0**	**0**	**9.9**
Total number of encounters	**0**	**4**	**17**	**22**	**25**	**11**	**0**	**0**	**79**
Total hours with dolphins	**0**	**3.2**	**14.6**	**14**	**15.2**	**5.7**	**0**	**0**	**52.7**
Total dolphins encountered	**0**	**39**	**239**	**316**	**392**	**131**	**0**	**0**	**1117**

Table 5: Summary of 1997 photo-id effort

1997	April	May	June	July	August	September	October	November	Total
Total days surveyed	**0**	**5**	**8**	**6**	**11**	**6**	**1**	**0**	**37**
Total hours of effort	**0**	**7.3**	**21.4**	**16.5**	**32.2**	**15.5**	**3.3**	**0**	**96.2**
Average daily hours of effort	**0**	**1.5**	**2.7**	**2.75**	**2.9**	**2.6**	**3.3**	**0**	**15.8**
Total number of encounters	**0**	**4**	**23**	**14**	**21**	**10**	**1**	**0**	**73**
Total hours with dolphins	**0**	**1.9**	**13.9**	**8.5**	**19.7**	**11.2**	**.75**	**0**	**56**
Total dolphins encountered	**0**	**51**	**312**	**314**	**563**	**538**	**50**	**0**	**1828**

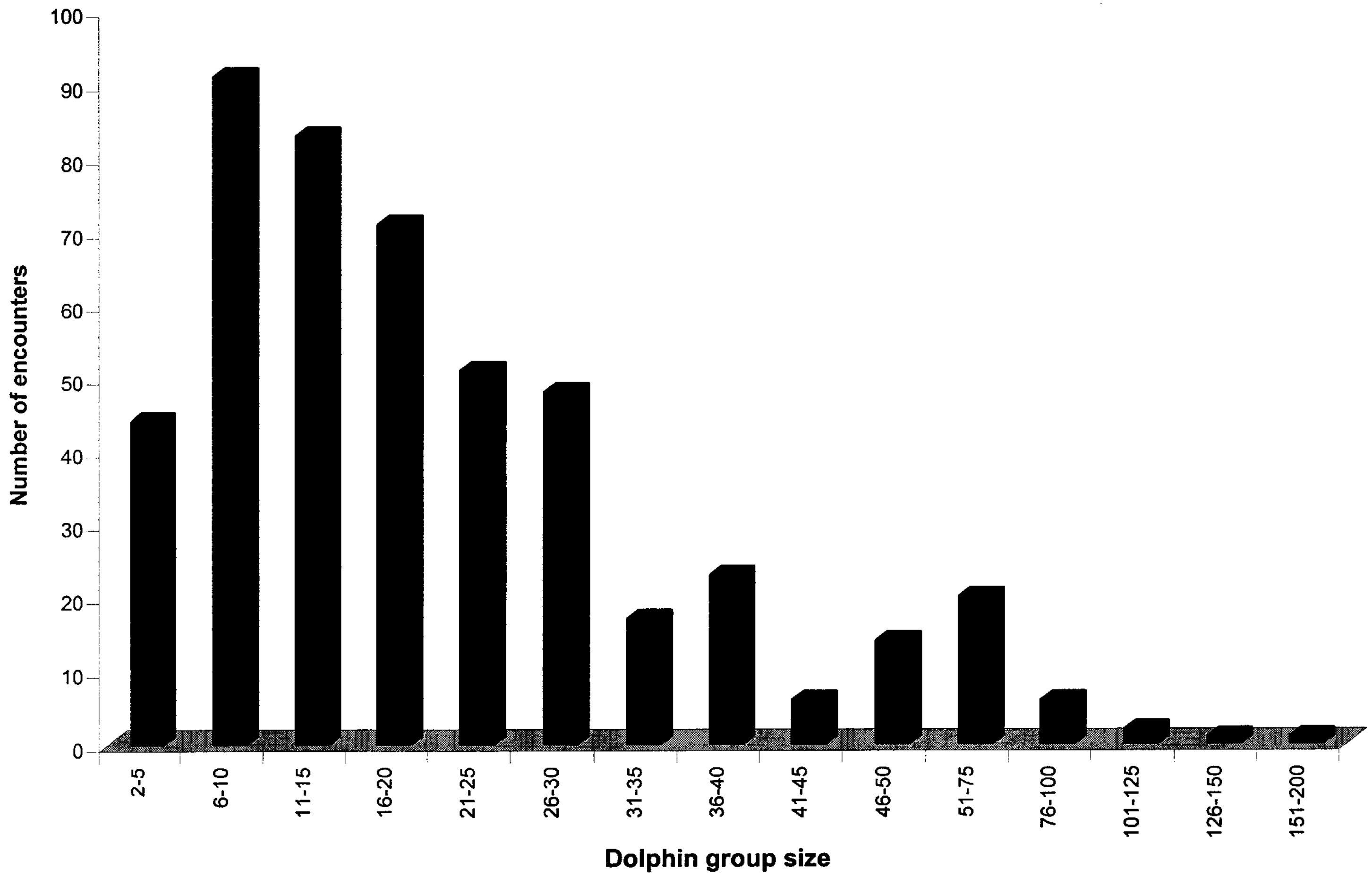
Table 6: Summary of 1998 photo-id effort

1998	April	May	June	July	August	September	October	November	Total
Total days surveyed	**5**	**7**	**7**	**11**	**5**	**6**	**2**	**0**	**43**
Total hours of effort	**3.5**	**14.5**	**13.9**	**23.9**	**13.8**	**5.8**	**5.5**	**0**	**80.9**
Average daily hours of effort	**0.7**	**2.1**	**2**	**2.2**	**2.8**	**1**	**2.8**	**0**	**16.4**
Total number of encounters	**1**	**10**	**11**	**26**	**12**	**10**	**6**	**0**	**76**
Total hours with dolphins	**0.2**	**7.6**	**9.8**	**19.8**	**11.2**	**5.4**	**5.6**	**0**	**59.6**
Total dolphins encountered	**22**	**209**	**276**	**637**	**449**	**311**	**57**	**0**	**1961**

Table 7: Summary of 1999 photo-id effort

1999	April	May	June	July	August	September	October	November	Total
Total days surveyed	**4**	**3**	**7**	**13**	**10**	**3**	**2**	**0**	**42**
Total hours of effort	**5.5**	**4.5**	**17.2**	**40.2**	**27.1**	**6.8**	**0.32**	**0**	**101.6**
Average daily hours of effort	**1.4**	**1.5**	**2.5**	**3.1**	**2.7**	**2.3**	**0.16**	**0**	**17.8**
Total number of encounters	**0**	**3**	**14**	**26**	**19**	**6**	**2**	**0**	**70**
Total hours with dolphins	**0**	**2.8**	**12.2**	**28.8**	**19**	**5.7**	**0.32**	**0**	**68.8**
Total dolphins encountered	**0**	**112**	**218**	**961**	**538**	**269**	**16**	**0**	**2114**

FIG. 2. Distribution of dolphin group size for all 479 encounters (1994 -1999). Best estimates of group size (by all observers) for all dolphin groups approached were used in analyses.



Overall, 64 % (of 479) of all groups contained at least one YOY, but 100 % of select individuals associated with a mean number of at least one YOY (Fig. 3a). Mean group size containing YOY was 25 (range: 4-140; SD = 19.3) and mean group size without YOY was 12 (range: 2-50; SD = 8.5). Groups with YOY were significantly larger than groups without YOY (Mann-Whitney U = 9.184, $p < 0.001$). Group size with YOY was also significantly larger after YOY were subtracted from estimates and base group sizes were compared (Mann-Whitney U= 8.953, $p < 0.001$). For the 78 select individuals, mean group size was 35 (range: 4-97; SD = 12)(Fig. 3b) and mean number of YOY was four (range: 1–6; SD = 1) (Fig. 3a). Mean group size was highest for dolphins ID 0010 and ID 0244, and lowest for ID 0254 and ID 0257. Both ID 0010 and ID 0254 were select definite females (Fig. 3b). Refer to Appendix B for a summary table of all select individuals.

Individual identification

Of all identified dolphins (1006), 972 individuals (97 %) were sighted post-1994 and included in this study. A rate-of-discovery curve was created to illustrate the number of new individuals that were photo-identified each year. New individuals were identified during each year of the study, with the highest number of new individuals being identified in 1999 (Fig. 4). The consistent positive slope of the discovery curve and lack of an asymptote indicated that the majority of the individuals within the population have yet to be identified. Fluctuations in the slope of the discovery curve are, in part, the result of variable effort among years. Figure 5 shows the number of dolphins observed

FIG. 3a. The mean number of YOY (young of year, including neonates) for select individuals (n = 78) for all encounters in all study years (1994-1999). Select individuals were sighted at least 5 times in 3 of the 6 study years. Best estimates of the number of YOY were used in analyses.

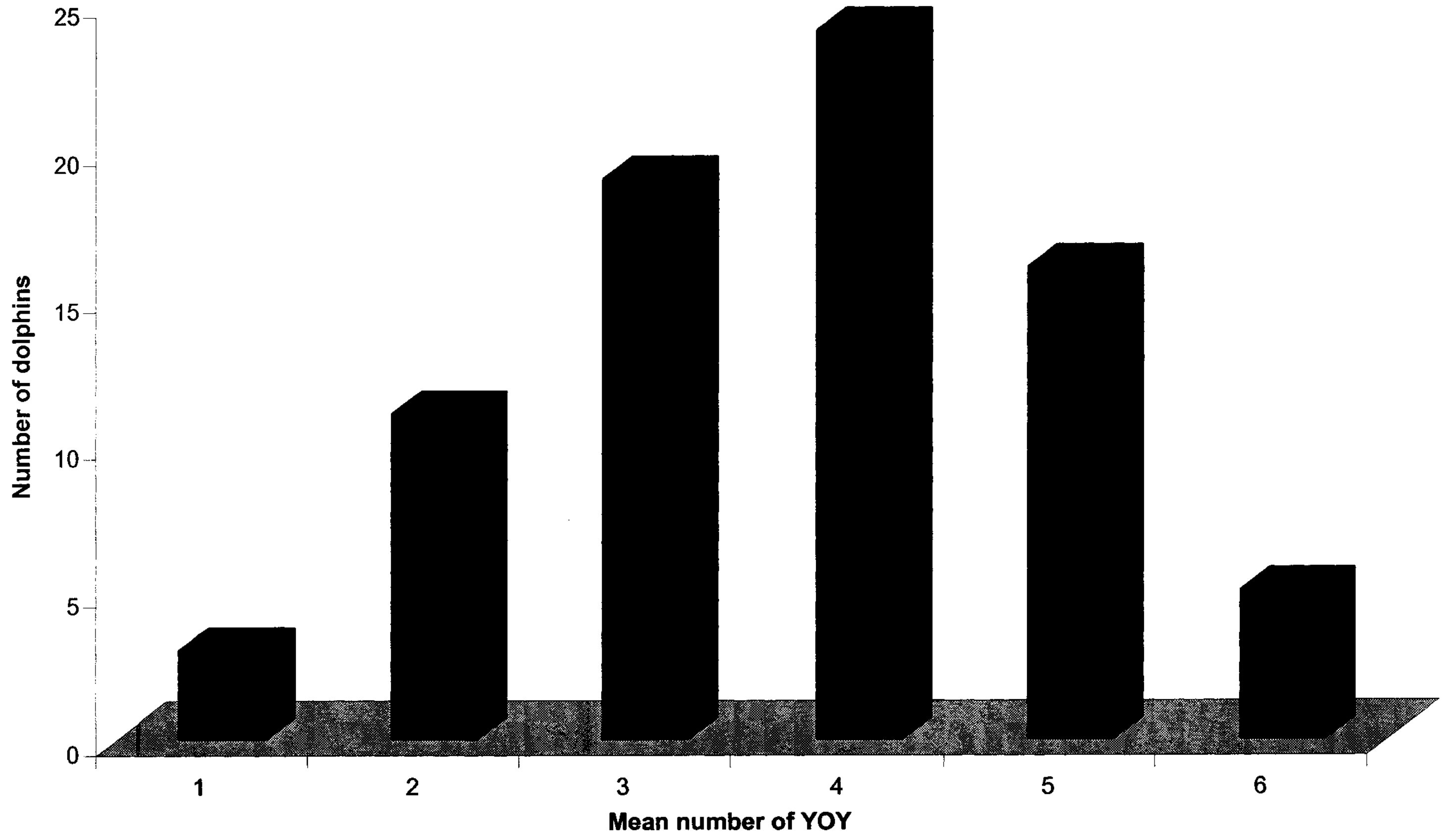


FIG. 3b. The mean group size for select individuals (n=78) for all encounters in all study years (1994-1999). Best estimates of group size were used in analyses. Select individuals were sighted at least 5 times in 3 of the 6 study years.

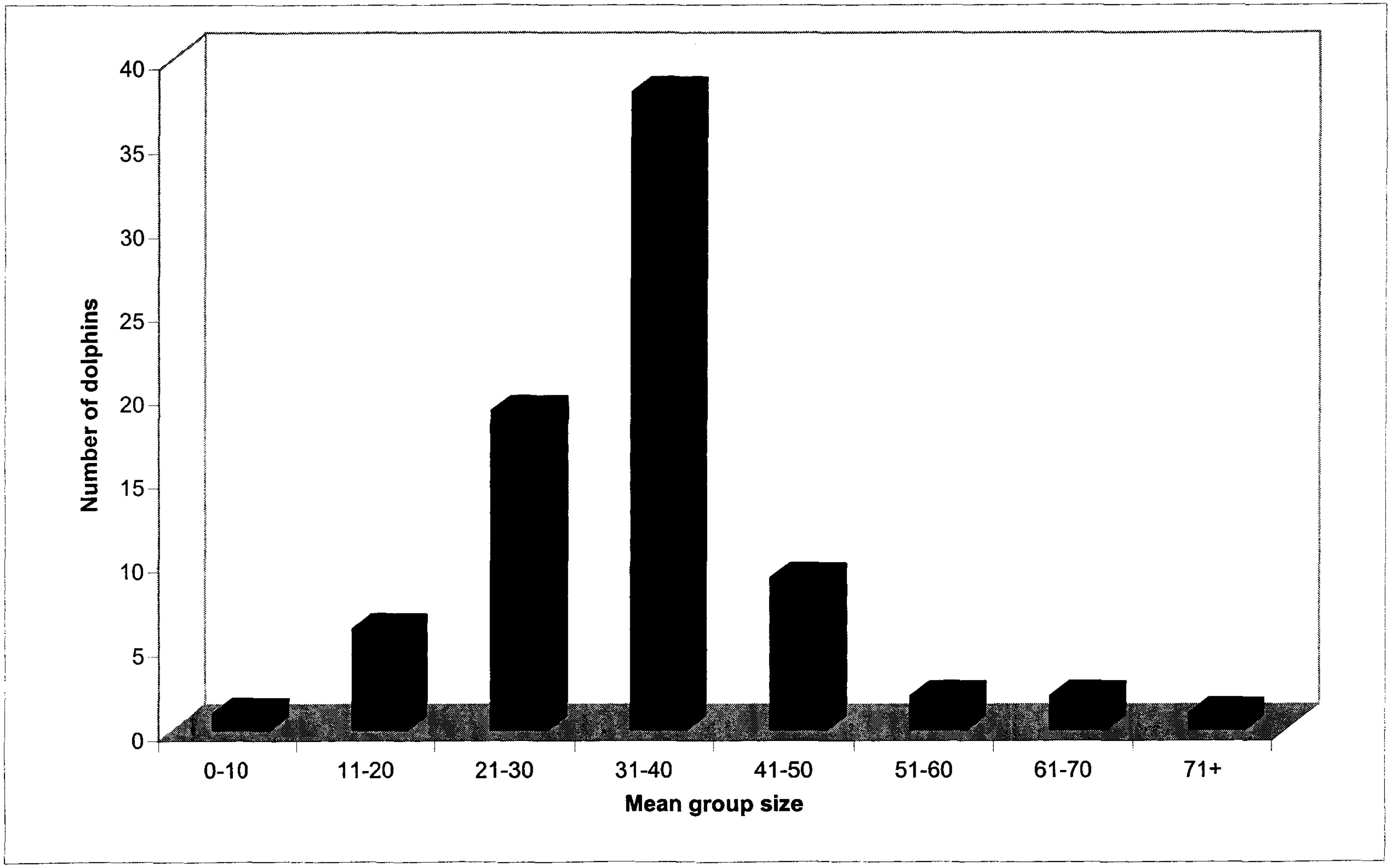


FIG. 4. Discovery curve: the number of new photo-identified individuals observed off Virginia Beach, Virginia each year and added to the photo-id catalog. The catalo (through 1999) includes 1006 individuals; 972 were included in analyses.

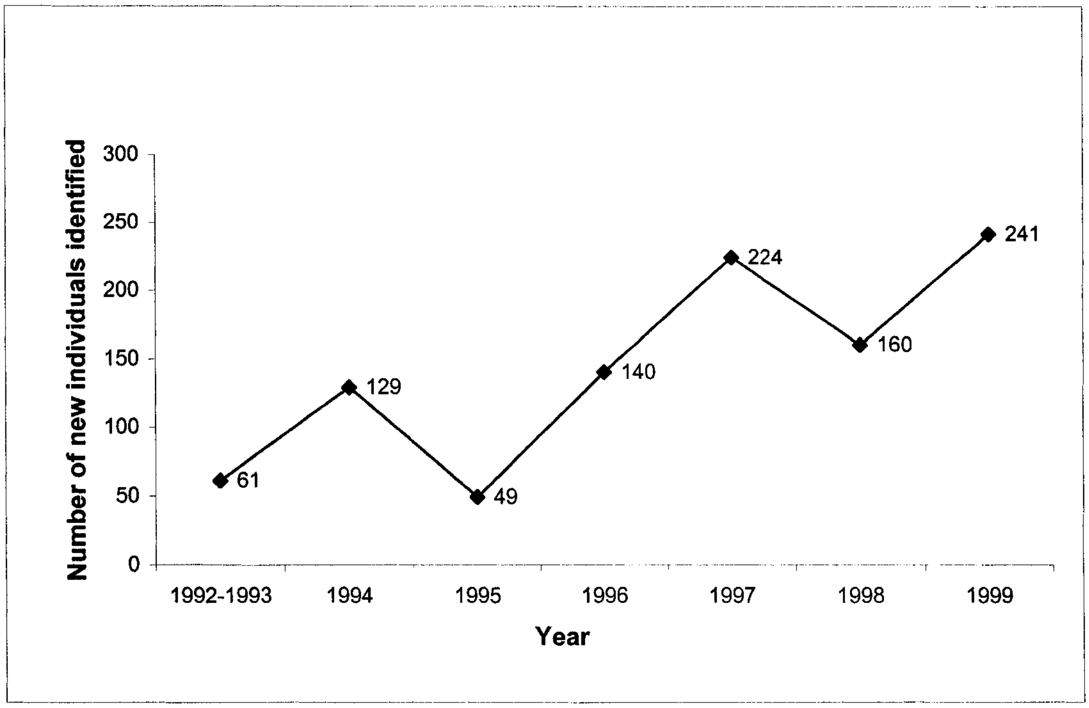
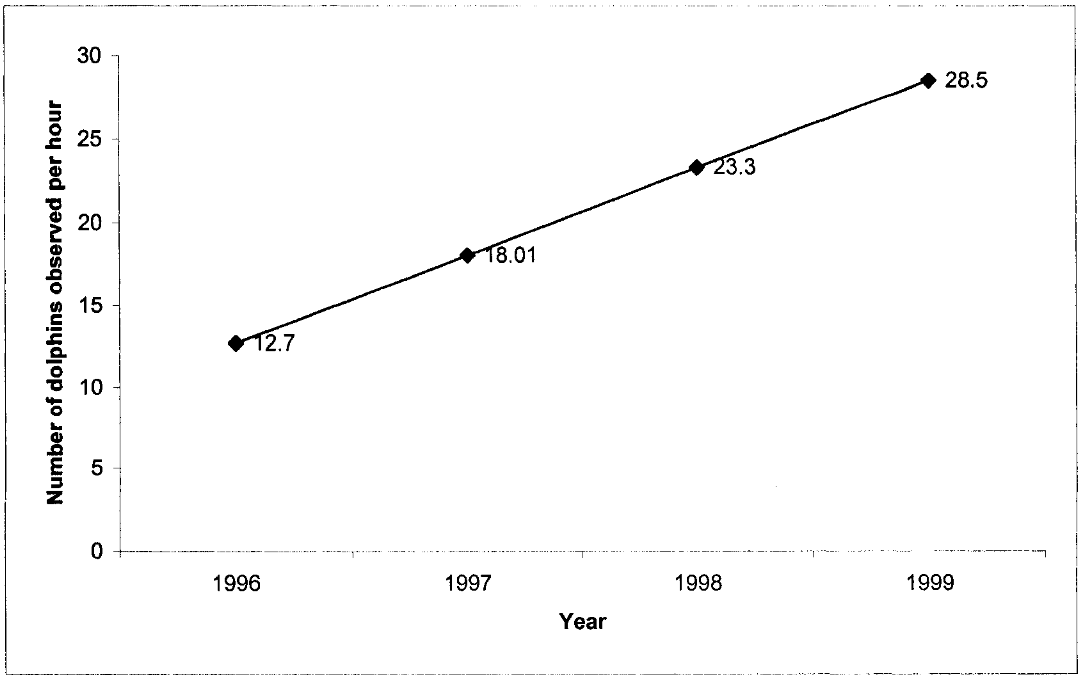


FIG. 5. Number of photo-identified dolphins observed per hour for 1996-1999. Both 1994 and 1995 were excluded due to variations in data collection methodology.



per hour per year and, again, a steady increase in the number of animals identified throughout the study is evident.

Association Patterns

Number of associates

The mean number of identified associates for select dolphins in the Virginia Beach study area was 93.1 (range: 18-243; SD = 47.6) (Fig. 6). The majority of select individuals (78%) had 125 or fewer associates, but only one individual had less than 25 associates. More than one quarter of select individuals (24 or 31%) had 51-75 associates, whereas only four individuals (5%) had more than 125 associates (Fig. 6). There were 64,090 possible pair-wise combinations for the 78 individuals and all possible associates, but only 6216, or 10.5 %, were observed. One adult female (ID 0254) had the lowest number of associates with 18, and an individual of unknown sex (ID 0016) had the highest number of associates with 243. Select individuals had a high percentage of other select dolphins as associates (mean: 27.5%; range: 14-48.3%; SD = 5.7). Select individuals had repeat associations with a mean of 12.9 % of their associates (range: 0-28.4; SD = 6.9).

Association values

HWI analyses

The mean HWI value for select individuals was 0.18 (range: 0.04-0.75; SD = 0.05) (Fig. 7). Sixty-eight percent (53) of select individuals had mean HWI values in the low category (0.01-0.20) and the remaining 32% (25) had mean HWI values in the

FIG. 6. Distribution of the total number of associates for all select individuals (n = 78). Individuals were considered to be associates if they were photographed in the same encounter group. Select individuals included all dolphins sighted at least 5 times in 3 of the 6 study years.

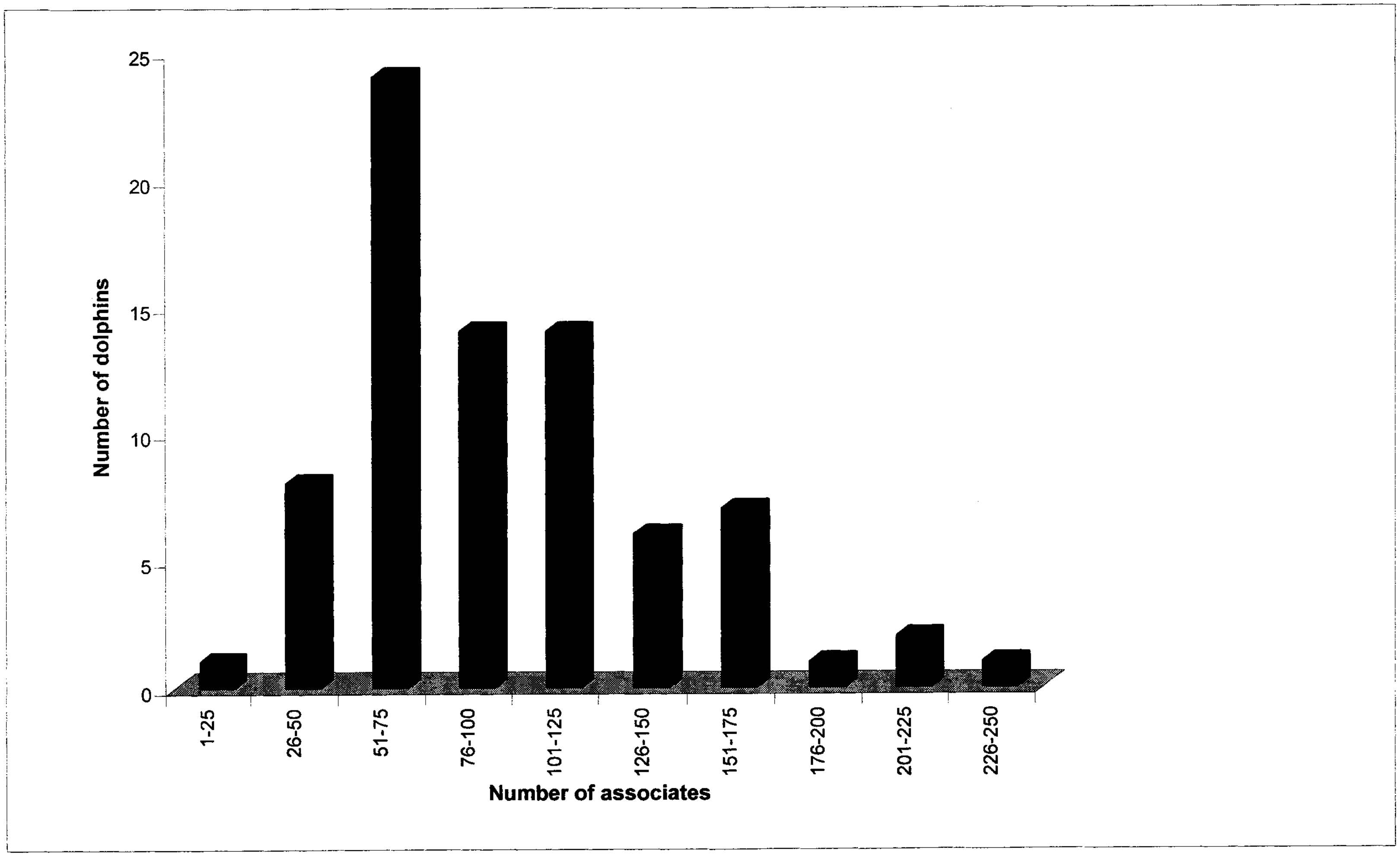
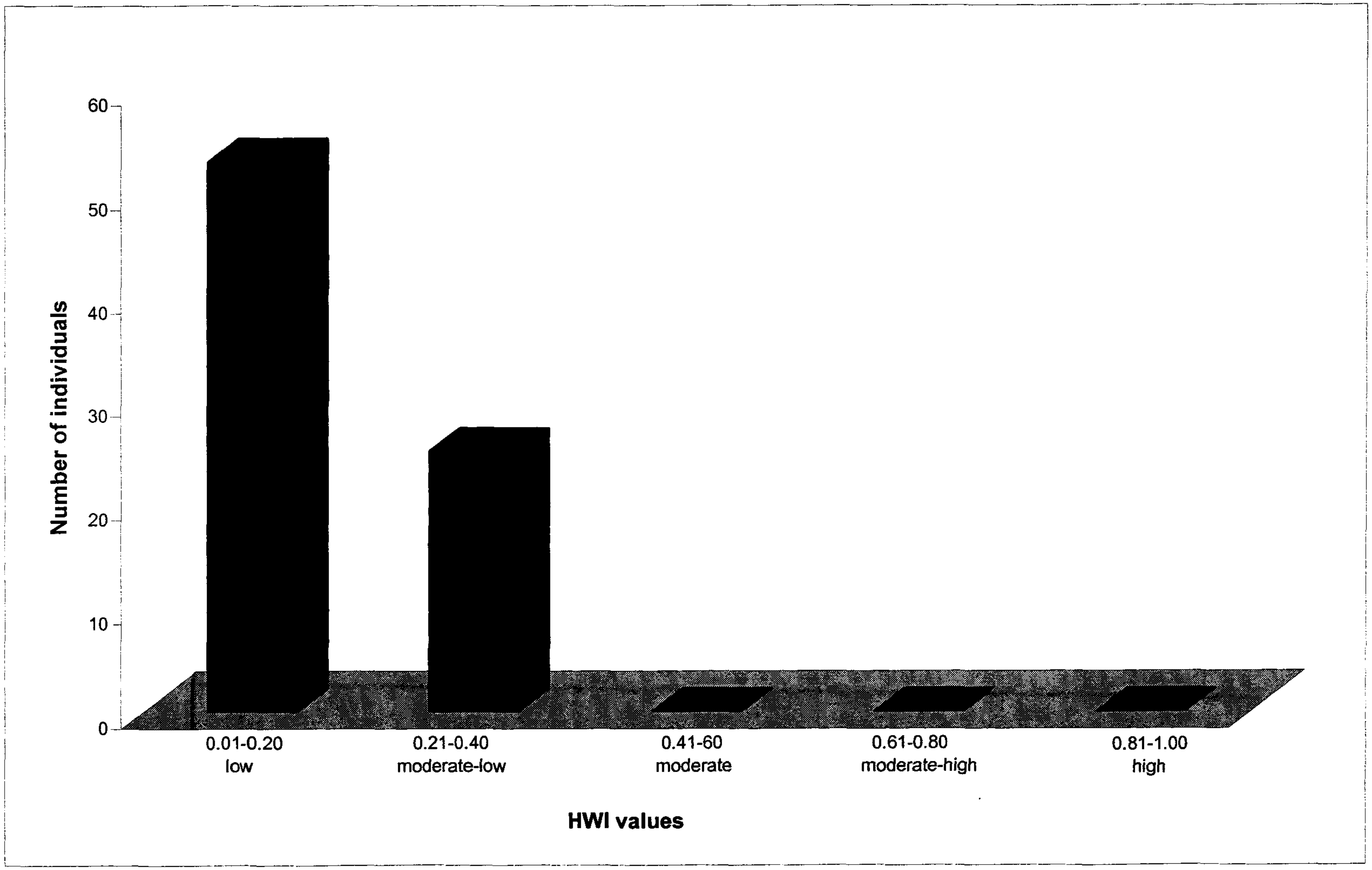


FIG. 7. Frequency distribution of mean calculated Half Weight Index (HWI) values for select individuals (n = 78) in each HWI category. HWI values were calculated for each dolphin dyad and the mean values for each select individual were used.



moderate-low category (0.21-0.40) (Fig. 7). No select individuals had mean association values greater than 0.40. The mean maximum HWI value was 0.39 (range: 0.15-0.75; SD = 0.11) (Fig. 8). The majority (62.8%) of maximum HWI values for select individuals fell into the moderate-low category. In addition, 29.5 % of calculated maximum HWI values fell in the moderate category, resulting in 92.3% of all maximum values occurring in the moderate-low to moderate range (Fig. 8). In all, 53,004 of calculated HWI values were zeros and these values are excluded from the ranges and other statistics. The following are the placement results for calculated HWI values for all dyads: 79.3 % (or 5684) in the low level category (0.01-0.20), 20.0 % (or 1433) in the moderate-low level (0.21-0.40), 0.60 % (or 43) in the moderate level (0.41-0.60), 0.06 % (or 4) in the moderate-high level (0.61-0.80) and no values in the high level (0.81-1.0) (Fig. 9). Few strong associations (>0.40) were calculated for dyads. Appendix C is a matrix table of all calculated HWI values for associations among select individuals.

Randomizations

Ten-thousand Monte Carlo simulations were run using SOCPROG 5.1 to determine whether associations were nonrandom (Whitehead 1999a). HWI values were used for all dyads and thirty-six dyads (out of 6216 observed dyads) resulted in calculated p values < 0.05. These dyads were determined to be significantly different from random. Seven definite and one probable female were members of seven of the 36 non-random dyads; one dyad included two definite select females.

FIG. 8. Frequency distribution of maximum calculated Half Weight Index (HWI) values for select individuals (n = 78) in each HWI category. HWI values were calculated for all dolphin dyads and maximum HWI values were used.

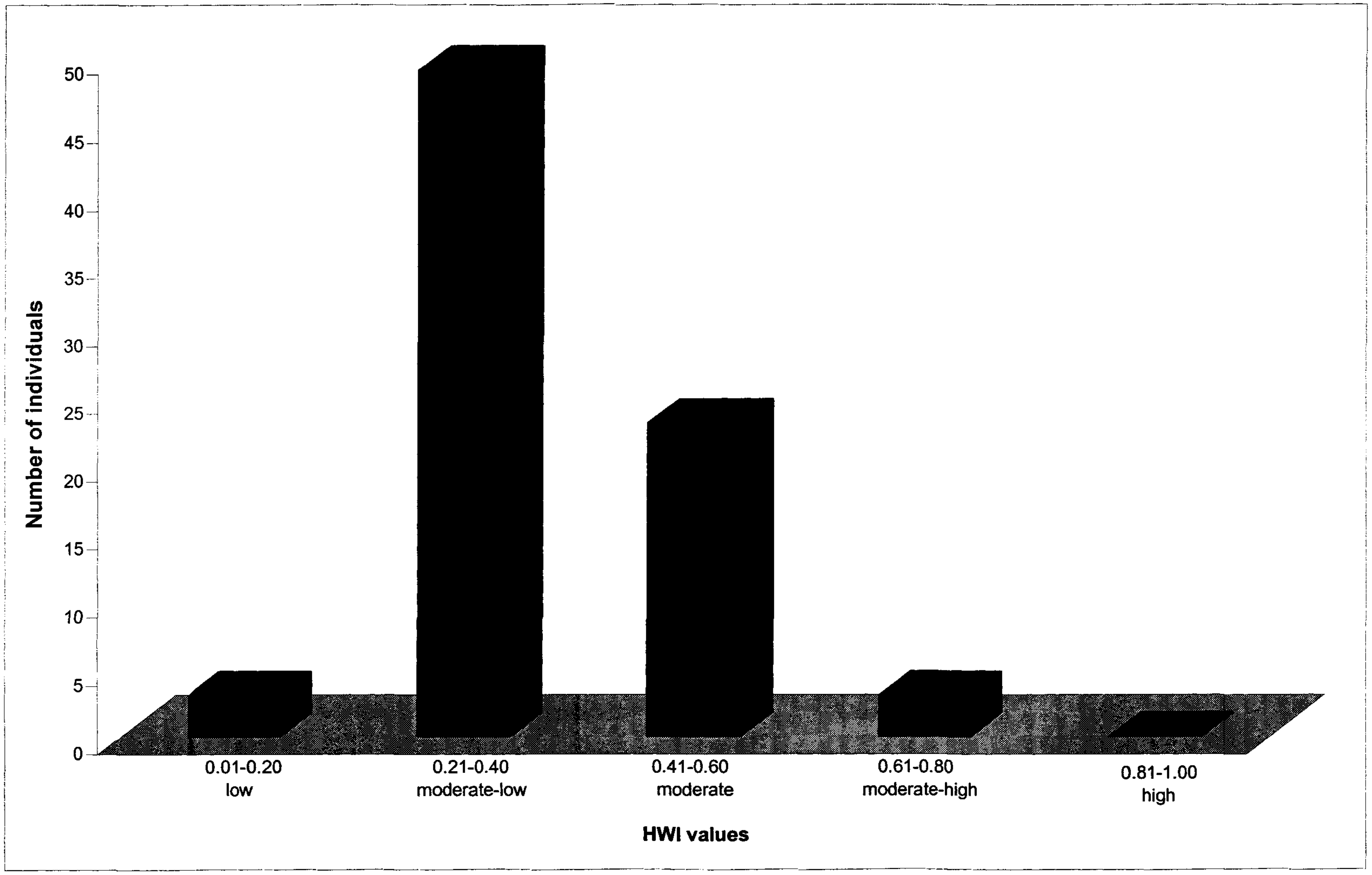
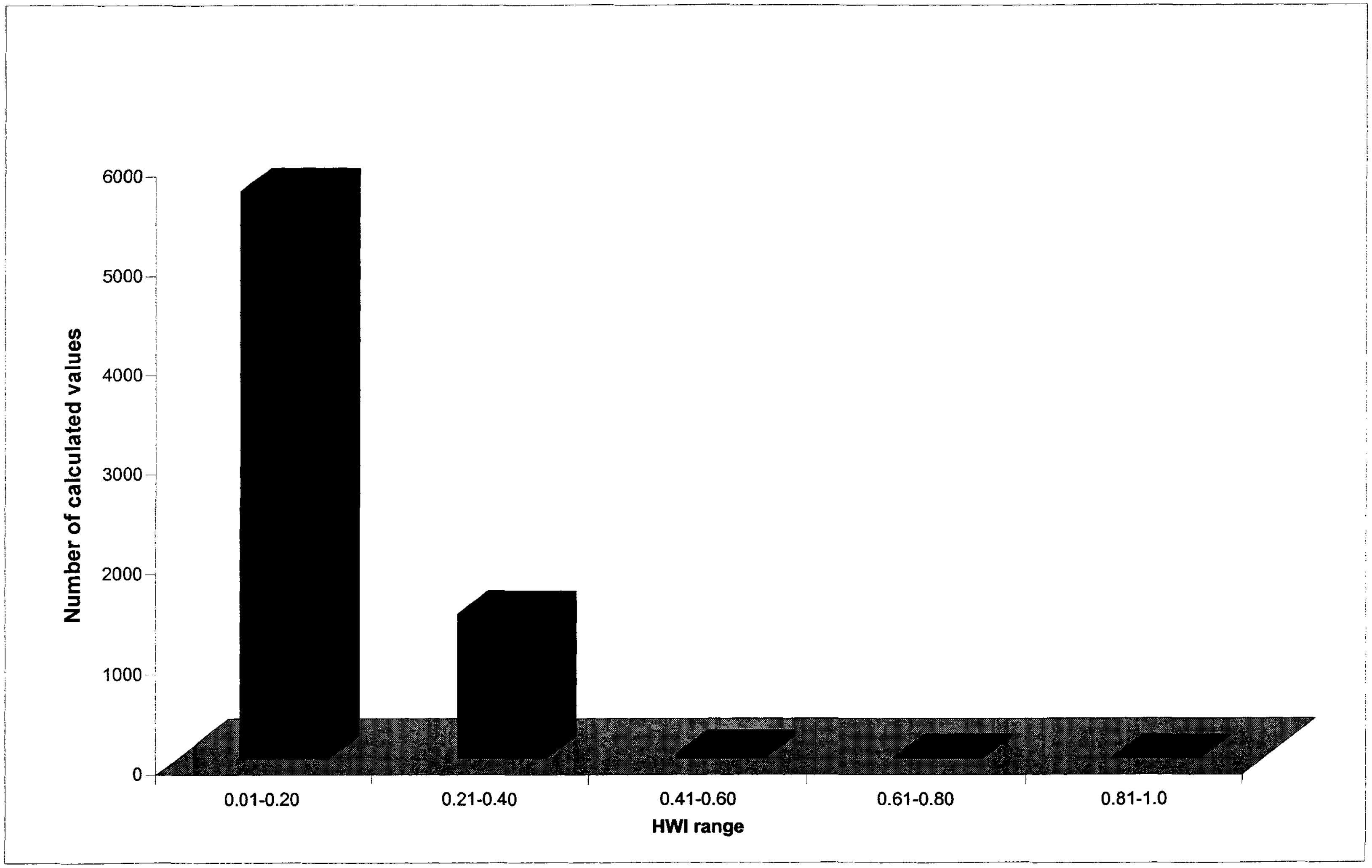


FIG. 9. Distribution of calculated Half Weight Index (HWI) values in each category for all select individuals (n = 78). HWI values were calculated for all dolphin dyads and all values were used.



Grouping patterns

Following Smolker et al. (1992), 28 dyads, two triads and one quartet of associated individuals were identified (Appendix D). The mean HWI value among dyad members was 0.45 (range: 0.27 – 0.75; SD = 0.134). The number of associates for dyad members (mean: 101.2; range: 35-206; SD = 45) did not differ significantly from the number of associates for non-dyad members (mean: 89.5; range: 18-243; SD = 45.6) (Mann-Whitney U = 1.768, p = 0.08). One triad (IDs 0855, 0899, 0181) almost qualified as a quartet with the addition of ID 0204. ID 0204, the third highest associate for all three members of the triad, had the highest number of joint associations with both ID 0855 and ID 0181, but exceeded the required 0.20 difference from the HWI value between the primary dyad (difference was 0.33) (Appendix D). Some dyads were associated in all six study years, whereas others were only associated during one season.

A loose network of select females was evident in the study population and two sociograms were produced using HWI values to illustrate the existence of a fluid network of females. Each female was connected either by a direct or indirect (an associate of an associate) association with every other select female. Figure 10 is a sociogram of all select definite females (n = 18); Figure 11 includes both definite and probable select females (n = 22). Four same-sex dyads were documented. Some associations were dependent upon the reproductive status of females, but many still occurred independently of reproductive status. Both sociograms demonstrate the fluidity of associations present for females. Note that most associations were low-level (0.01-0.19) and as indicated in Figure 6, ID 0254 has the lowest number of associates.

FIG. 10. Sociogram demonstrating associations among select definite females (n = 18). Half Weight Index (HWI) values were calculated for all dolphin dyads. HWI values between all select definite females were used. Strengths of associations vary based on the thickness of the HWI value line. Select definite females were sighted at least 5 times in 3 of the 6 study years; three of those sightings had to be with a YOY.

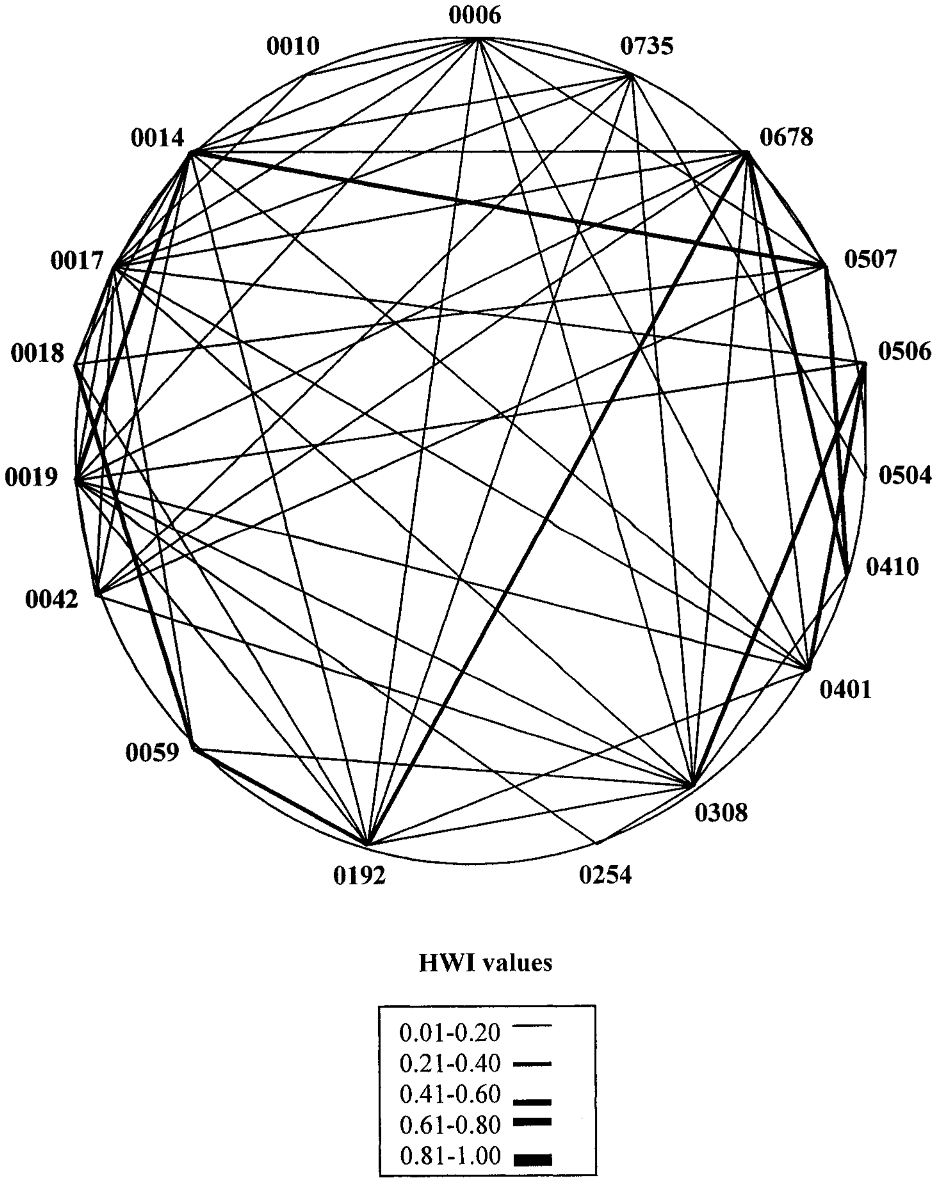


FIG. 11. Sociogram demonstrating associations among select definite females (n = 18) and probable females (n = 4;* / dashed). Half Weight Index (HWI) values were calculated for all dolphin dyads. HWI values between all select definite and probable females were used. Strengths of associations vary based on the thickness of the HWI value line. Select individuals were sighted at least 5 times in 3 of the 6 study years; definite females required 3 sightings with a YOY and probable females required at least 2 sightings with a YOY.

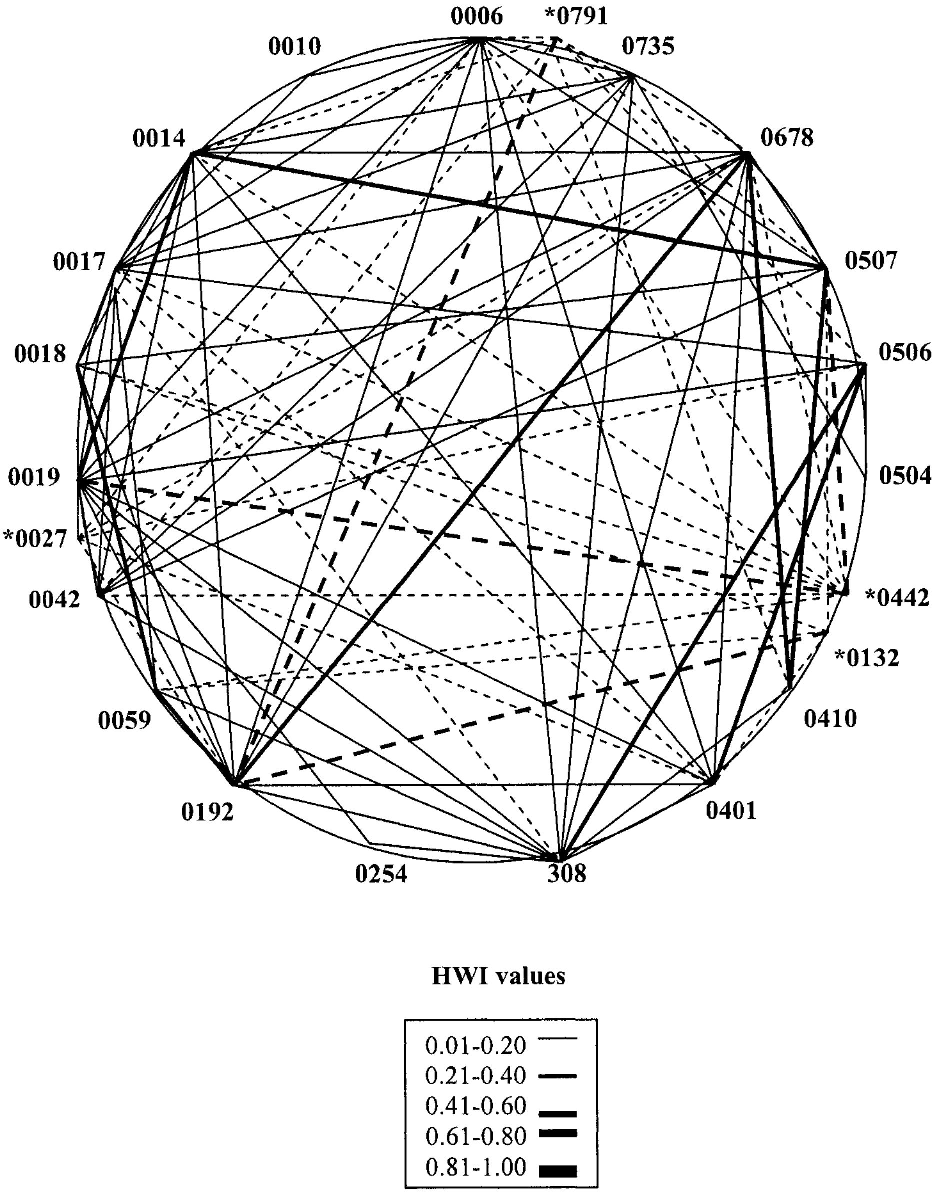


FIG. 12. Cluster analysis dendogram of calculated Half Weight Index (HWI) values for definite and probable select females (n = 22). Note that several smaller groupings and a high degree of fluidity were evident among all females. Each female was either directly or indirectly linked to all other females. Select individuals require at least 5 sightings in 3 of the 6 study years (1994-1999). Definite females require at least 3 sightings with a YOY and probable females require 2 sightings with a YOY.

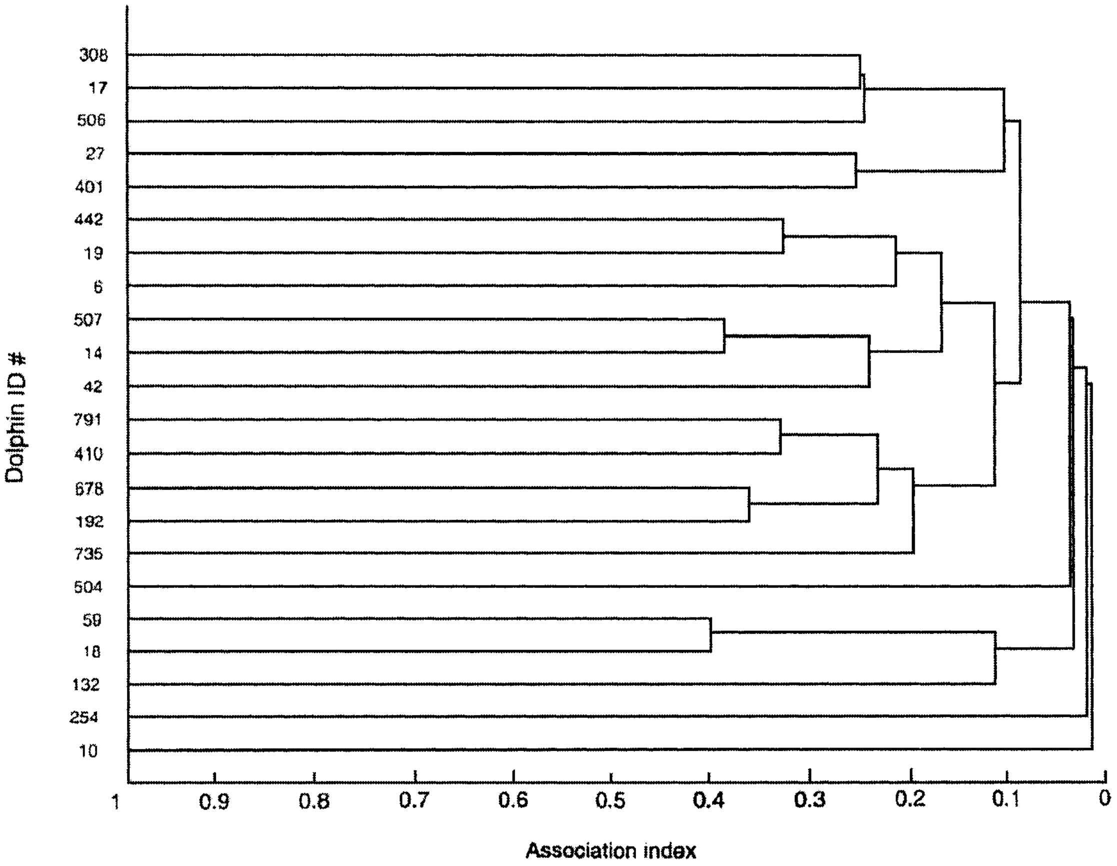


FIG. 13. Multi-dimensional scaling (MDS) of calculated Half Weight Index (HWI) values for definite and probable select females (n = 22); shows the relative distance between HWI values for all select females. Clusters of individuals indicate strong association, while individuals close to the 0,0 coordinates have no strong association with other individuals. Select individuals were sighted at 5 times in 3 of the 6 study years (1994-1999). Definite females required at least 3 sightings with a YOY and probable females required at least 2 sightings with a YOY.

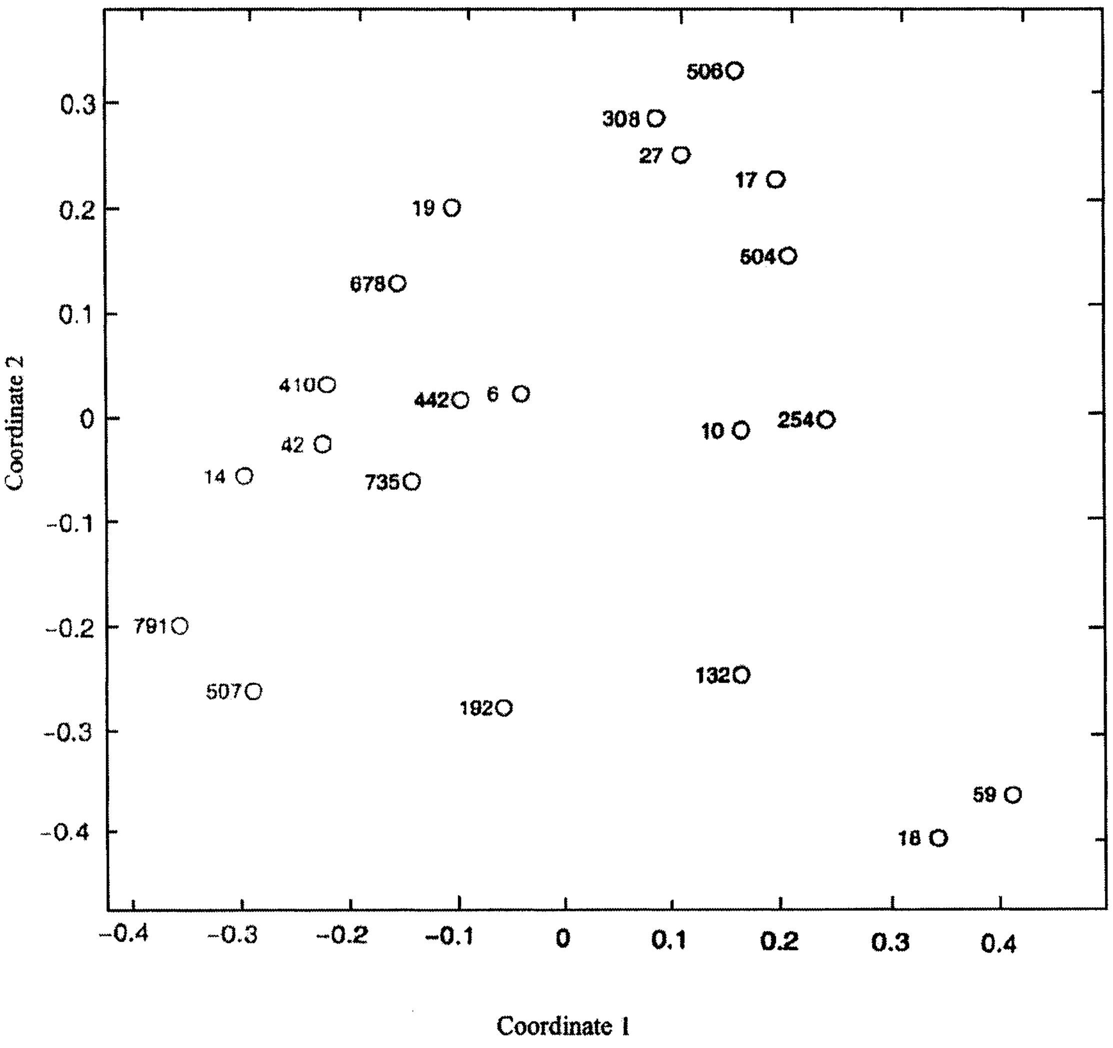


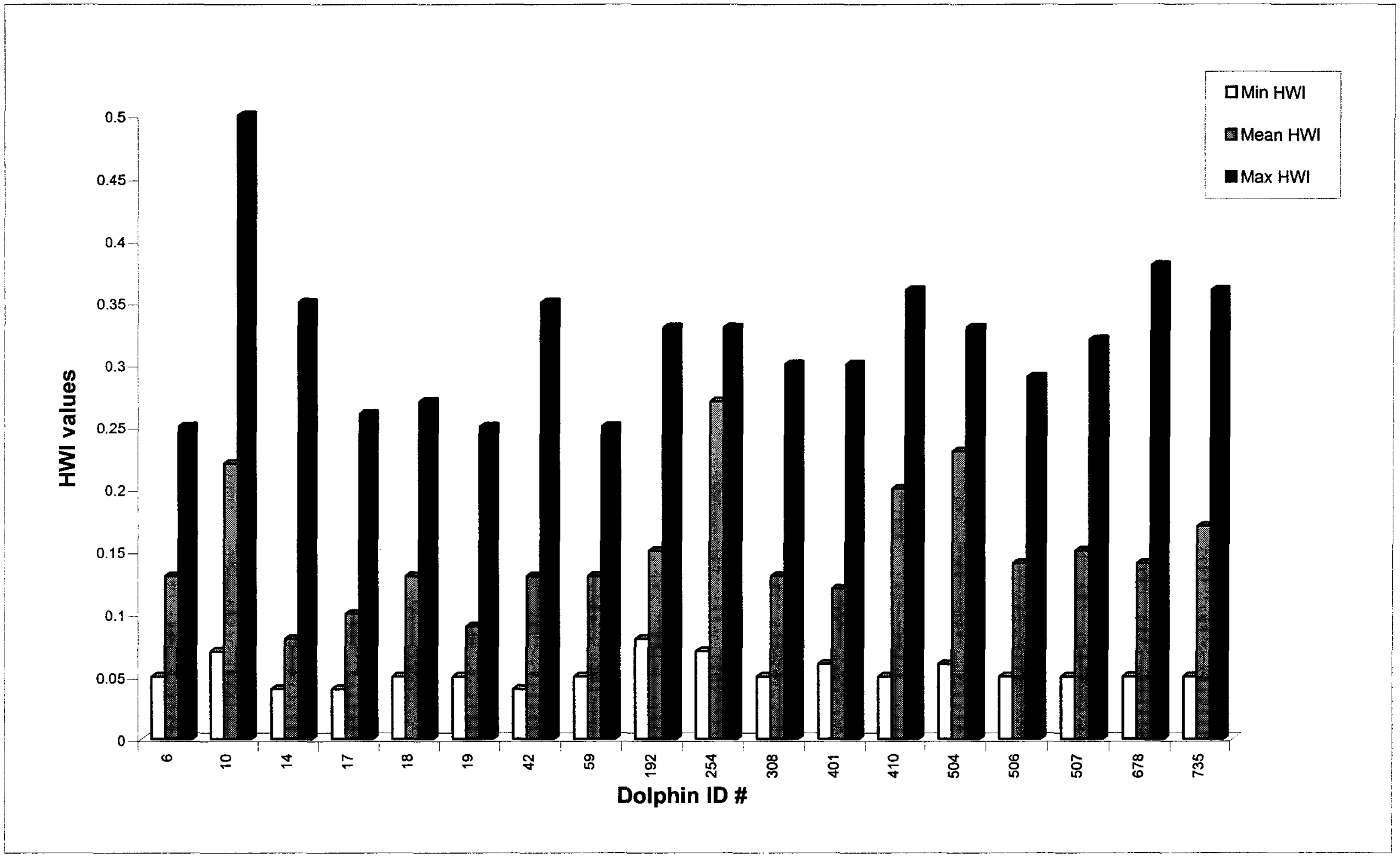
Figure 12 is a cluster dendogram created for all select definite and probable females. HWI values were used to determine groups and closeness of associates. Several small groups were apparent, but most importantly, the fluidity among all individuals and groups was clearly demonstrated. Figure 13, a multidimensional scatterplot, was also created using HWI values. Clusters of individuals indicated strong associations and that individuals close to the 0,0 coordinates were not closely associated with other individuals. Several clusters of weakly associated individuals were apparent, as well as several strong dyads, including IDs 0059 and 0018 and a cluster with IDs 0410, 0308 and 0506.

Effects of sex

Thirty-six definite (≥ 3 sightings with a neonate/YOY), 24 probable (two sightings with a YOY) and 45 possible females (at least one sighting in close proximity to a YOY) were identified from the 972 photo-identified individuals. Stranding records provided sex identification for two females and one male. Based on body length measurements for North Atlantic bottlenose dolphins, all three individuals were adults (262-274 cm) (NC Stranding Records; Mead and Potter 1990). The sex of one of the two females (ID 0254) had already been determined from multiple sightings with a calf (NC Maritime museum: K. Rittmaster and N. Bowles). Eighteen (23.1 %) of the 78 select individuals were definite females and four (5.1 %) were probable females.

The mean HWI value for definite select females was 0.15 (range: 0.08-0.27; SD = 0.05) (Fig. 14) and 0.19 (range: 0.15-0.23; SD = 0.03) for probable females. ID 0254 had

FIG. 14. Minimum, mean and maximum Half Weight Index (HWI) values for select definite females (n = 18). HWI values were calculated for all select individuals (at least 5 sightings in 3 of the 6 study years); definite females had at least 3 sightings with a YOY. Minimum, mean and maximum HWI values were used.



the highest mean HWI value with 0.27 and ID 0010 had the highest maximum HWI value with 0.50 (Fig. 14). For select individuals, there was no significant difference among the HWI values for all individuals (n = 78; mean: 0.18; range: 0.04-0.75; SD = 0.05) vs. definite females (n = 18; mean: 0.15; range: 0.08-0.27; SD = 0.05) vs. probable females (n = 4; mean: 0.19; range: 0.15-0.23; SD = 0.03) vs. all females (n=22; mean: 0.16; range: 0.08-0.27; SD = 0.05) (Kruskal Wallis = 3.182, p = 0.09) or between definite (n = 18) vs. probable (n = 4) females (Mann-Whitney U = 1.788, p = 0.07).

Select definite females had a mean of 97.6 associates (range: 18-162; SD = 44.8), whereas select probable females had a mean of 53.8 associates (range: 44-64; SD = 9.0) (Fig. 15a). IDs 0014 and 0017 had the highest number of associates with 162 and ID 0254 had the lowest number of associates with 18 (Fig 15a). The number of associates for select definite versus probable females was not significantly different (Mann-Whitney U = 1.169, p = 0.2422). Combined, all select females (definite and probable) had a mean number of 90.9 associates (range: 18-162; SD = 4.7). Other females comprised 5.1-22.4 % of the total number of associates for a female.

Mean group size was 40 (range: 4-200; SD = 29) for all definite females (n = 36), 31 (range: 4-200; SD = 14.8) for all probable females (n = 23), 32 (range: 20-65; SD = 9.6) for select definite females (n = 18) (Fig. 15b), and 29 (range: 7-65; SD = 18) for select probable females (n = 4). ID 0010 had the highest mean group size with 65 and ID 0254 had the lowest mean group size with 3.6 (Fig. 15b). For select individuals, there was no significant difference between group size for definite (n = 18) vs. probable (n = 4) females (Mann-Whitney U = 0.979, p = 0.3276) or between all females (n = 22) vs. all individuals (n = 78) (Mann-Whitney U = 1.1417, p = 0.1566). There was also no

FIG. 15 (a-d). Number of associates, mean group size, mean number of YOY and % repeat associates for select definite females (n=18). For select definite females: a) the total number of associates; b) the mean value of best estimate of group size from all encounters c) the mean number of YOY for all encounter groups; d) the mean percentage of repeat associates. Select individuals had at least 5 sightings in 3 of the 6 study years (1994-1999); definite females require at least 3 sightings with a YOY.

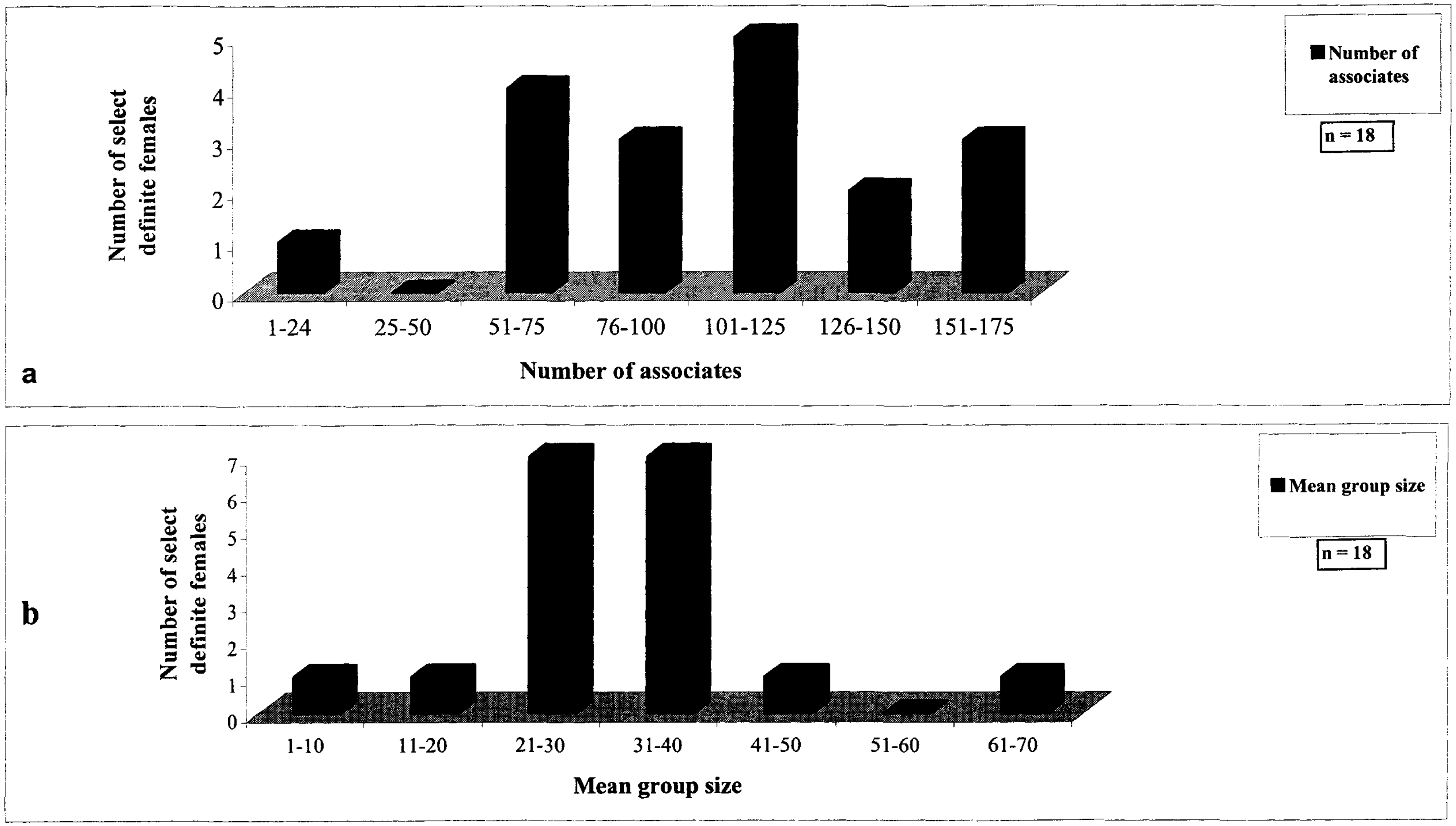
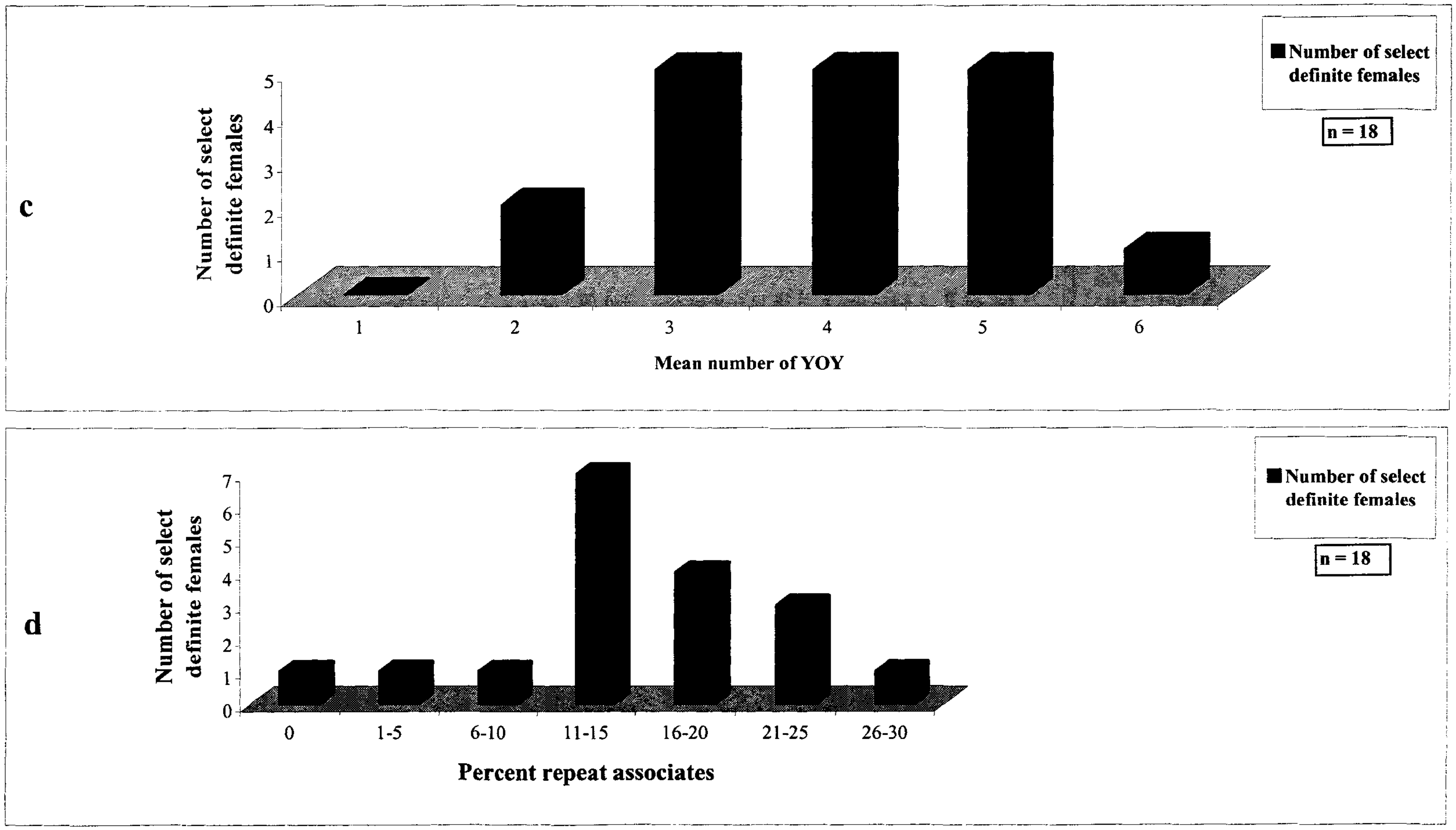


FIG. 15 (a-d)(cont.). Number of associates, mean group size, mean number of YOY and % repeat associates for select definite females (n=18). For select definite female: a) the total number of associates; b) the mean value of best estimate of group size from all encounters c) the mean number of YOY for all encounter groups; d) the mean percentage of repeat associates. Select individuals had at least 5 sightings in 3 of the 6 study years (1994-1999); definite females require at least 3 sightings with a YOY.



significant difference between group size for all individuals vs. definite females vs. probable females vs. all females (Kruskal-Wallis = 5.36, p = 0.1473). Both definite and probable females had a mean number of four YOY per group [definite female range: 2-6; SD = 1.1 (Fig. 15c, Table 8); probable female range: 1–13; SD = 2.8], whereas all known females had a mean of five YOY per group (range: 1–13; SD = 2). ID 0678 had the highest mean number of YOY for all sightings with six and IDs 0254 and 0059 tied for the lowest number of YOY with two (Fig. 15c). There was no significant difference between the number of YOY observed per group between select definite and probable females (Mann-Whitney U = 0.189, p = 0.8501) or between all select females vs. all definite females vs. all probable females vs. all select individuals (Kruskal-Wallis = 3.182, p = 0.3645).

Select definite females had a mean of 14.7 % repeat associates (range: 0–28.4; SD = 7.4) (Fig. 15d), whereas select probable females had a mean value of 11.5 % repeat associates (range: 3.1 – 24.1; SD = 9.8). ID 0014 had the highest number of repeat associates with 28.4% and ID 0254 had the lowest number with no repeat associates (Fig. 15d). There was no significant difference between repeat associate values for all select definite vs. probable females (Mann-Whitney U = 24, p = 0.6710). Combined, all select females (definite and probable) had a mean of 12 female associates (range: 2-22; SD = 5.2) and 14.1 % (range: 0-28.4; SD = 7.5) of those associates were repeats.

The mean HWI value was 0.14 (range: 0.09-0.21; SD = 0.03) for select females and all female associates and 0.13 (range: 0.04-0.25; SD = 0.07) for select females and their select female associates. Four (18.2 %) definite females had another female as their

Table 8. Mean Half Weight Index (HWI), mean group size, mean number of YOY, mean number of associates and % repeat associates for select definite females (n=18). Select definite females had at least 5 sightings in 3 of the 6 study years (1994-1999), with a minimum number of 3 sightings with a YOY. Mean group size and number of YOY used best estimates from all observers.

Individual ID #	Mean HWI	Mean grp size	Mean # YOY	Total # associates	% repeat assoc.
6	0.13	30	4	104	12.5
10	0.22	65	3	98	8.2
14	0.08	29	5	162	28.4
17	0.1	35	4	162	17.9
18	0.13	30	4	63	11.1
19	0.09	29	4	130	21.5
42	0.13	29	4	104	16.3
59	0.13	20	2	62	17.7
192	0.15	33	5	113	25.7
254	0.27	20	2	18	0
308	0.13	29	3	121	14.9
401	0.12	32	5	139	18
410	0.2	38	6	63	11.1
504	0.23	37	4	63	1.6
506	0.14	34	3	97	11.3
507	0.15	29	6	87	13.8
678	0.14	36	6	119	22.7
735	0.17	41	5	154	11
GRAND MEAN=	**0.15**	**32**	**4**	**106**	**14.7**

Table 9. Calculated Half Weight Index (HWI) values among select females (definite and probable combined) (n = 22). Select dolphins had at 5 sightings in at least 3 of the 6 study years. Definite females had a minimum of 3 sightings with a YOY and probable females had at least 2 sightings with a YOY. HWI value color codes listed below table for below table for categories 0 - 0.39.

ID	0006	0010	0014	0017	0018	0019	0027	0042	0059	0132	0192	0254	0308	0401	0410	0442	0504	0506	0507	0678	0735	0791
0006	-				▨			▨	▨	▨		▨			▨		▨	▨		▨		
0010	0.11	-	▨		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
0014	0.14	0	-			■	▨		▨	▨		▨	▨	▨	▨		▨	▨				
0017	0.06	0.07	0.04	-			▨			▨	▨	▨			▨		▨		▨			▨
0018	0	0	0.05	0.06	-	▨	▨	▨	■			▨	▨	▨	▨		▨	▨		▨	▨	▨
0019	0.17	0	0.25	0.09	0	-	■		▨	▨					▨	■	▨		▨		▨	
0027	0.10	0	0	0	0	0.06	-	▨	▨	▨		▨	▨		▨	▨	▨		▨		▨	▨
0042	0	0	0.18	0.12	0	0.11	0	-	▨	▨	▨	▨		▨	▨		▨	▨				
0059	0	0	0	0.18	0.24	0	0	0	-		■	▨		▨	▨		▨	▨	▨	▨	▨	▨
0132	0	0	0	0	0.12	0	0	0	0.11	-	■	▨	▨		▨	▨	▨	▨		▨	▨	▨
0192	0.08	0	0.14	0	0.08	0.11	0.10	0	0.24	0.24	-	▨			▨	▨	▨	▨	▨	■		■
0254	0	0	0	0	0	0.07	0	0	0	0	0	-		▨	▨	▨	▨	▨	▨	▨	▨	▨
0308	0.08	0	0	0.18	0	0.05	0	0.07	0.08	0	0.08	0.11	-			▨	▨	■	▨		▨	▨
0401	0.07	0	0.17	0.11	0	0.15	0.08	0	0	0.10	0.15	0	0.07	-	▨	▨	▨	■	▨		▨	▨
0410	0	0	0	0	0	0	0	0	0	0	0	0	0.11	0	-	▨	▨	▨	■	■	▨	
0442	0.20	0	0.10	0.07	0.10	0.25	0	0.09	0.10	0	0	0	0	0	0	-	▨	▨	■		▨	▨
0504	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-		▨	▨		▨
0506	0	0	0	0.19	0	0.06	0.10	0	0	0	0	0	0.24	0.22	0	0	0.12	-	▨	▨	▨	
0507	0.09	0	0.19	0	0.09	0	0	0.08	0	0.13	0	0	0	0	0.24	0.21	0	0	-		▨	
0678	0	0	0.05	0.18	0	0.11	0.09	0.07	0	0	0.24	0	0.08	0.14	0.21	0.19	0	0	0.08	-	▨	
0735	0.10	0	0.05	0.07	0	0	0	0.09	0	0	0.19	0	0.18	0	0	0	0.14	0	0	0	-	▨
0791	0.11	0	0.11	0	0	0.06	0	0.19	0	0	0.21	0	0	0	0.15	0	0	0.11	0.11	0.10	0	-

HWI Category Color Codes = ☐ = 0 ▨ = 0.01-0.20 ■ = 0.21-0.39

highest associate, whereas 13 (59 %) had another female as one of their top five associates. Females had significantly more associates in reproductive years as compared to non-reproductive years (reprod. mean: 40.4; range: 1-109; SD = 28.1 vs. nonreprod. mean: 21.4; range: 1-75; SD = 20.5) (Mann-Whitney U =3.130, p = 0.017), as well as a significantly different number of female associates in years when they were with a YOY vs. years when they were without a YOY (with YOY: mean: 6.3; range:0-17; SD = 4.9 vs. w/o YOY: mean: 3.8; range: 0-12; SD = 3.3) (Mann-Whitney U = 2.143; p = 0.033). Tables 8 and 9 show calculated HWI values for associations among all select females (definite and probable).

One outlier for the females was ID 0254, a select definite female observed multiple times with a calf and then later recovered as a dead, stranded animal. She had no repeat associates, the lowest mean group size (20 vs. the mean value of 32 for select definite females), her average HWI value was the highest of all females at 0.27 (partially a result of a low total number of sightings), and she had the lowest number of associates (18 vs. a mean value of 97.6 for select definite females). She also had one of the lowest mean YOY values (two vs. a mean value of four for select definite females). Number 0254 was sighted six times in five years (1993 to 1998) and her carcass was recovered in North Carolina in 1999.

Site fidelity and seasonal occurrence

Site fidelity patterns for Virginia Beach dolphins were variable. The amount of time between the first and last sightings of individuals during a single season ranged widely, from one to 155 days. Some individuals were first sighted early in the season

FIG. 16. Distribution of the total number of years all photo-identified individuals (n=972) were sighted during all study years (1994-1999).

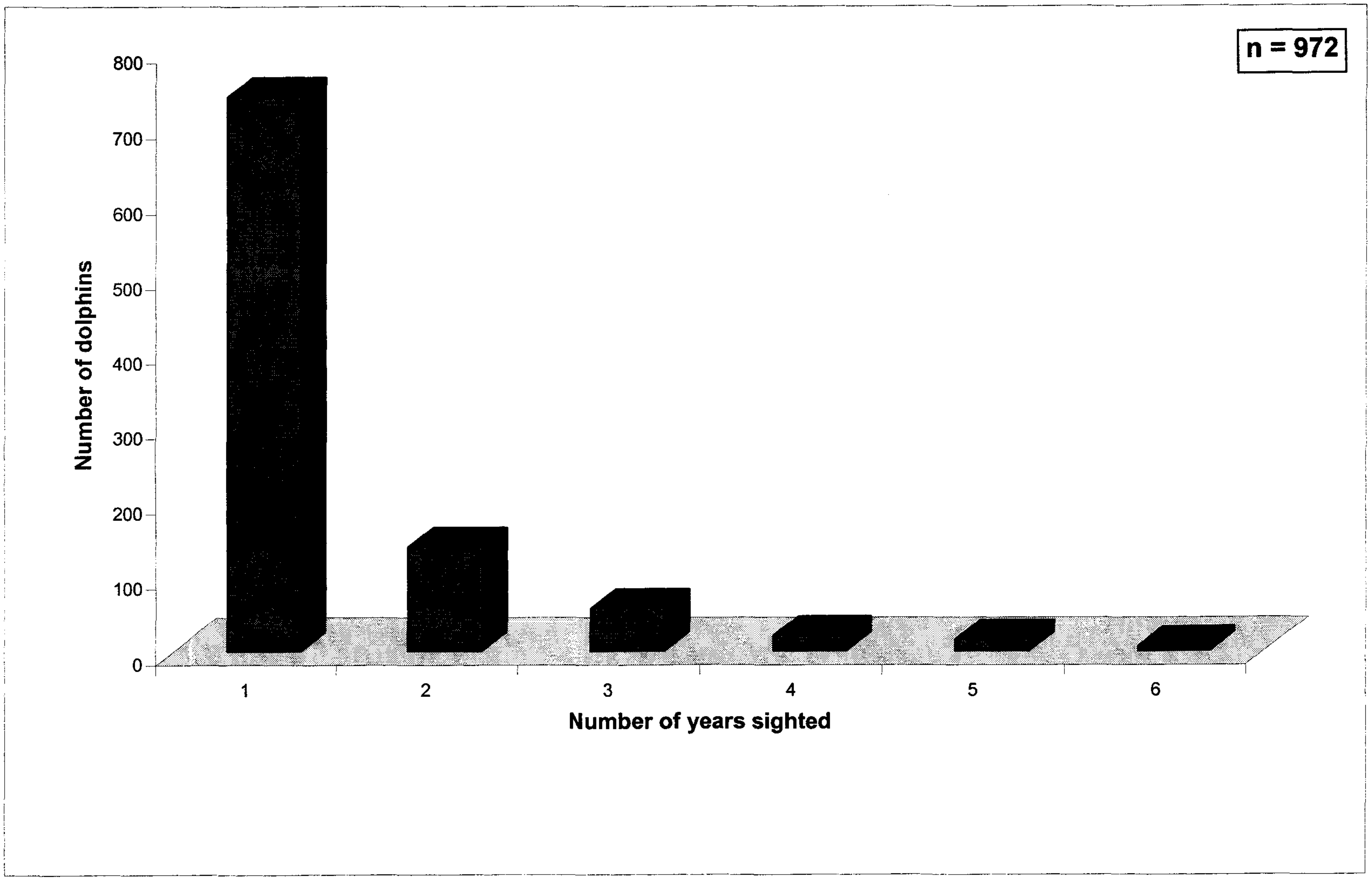
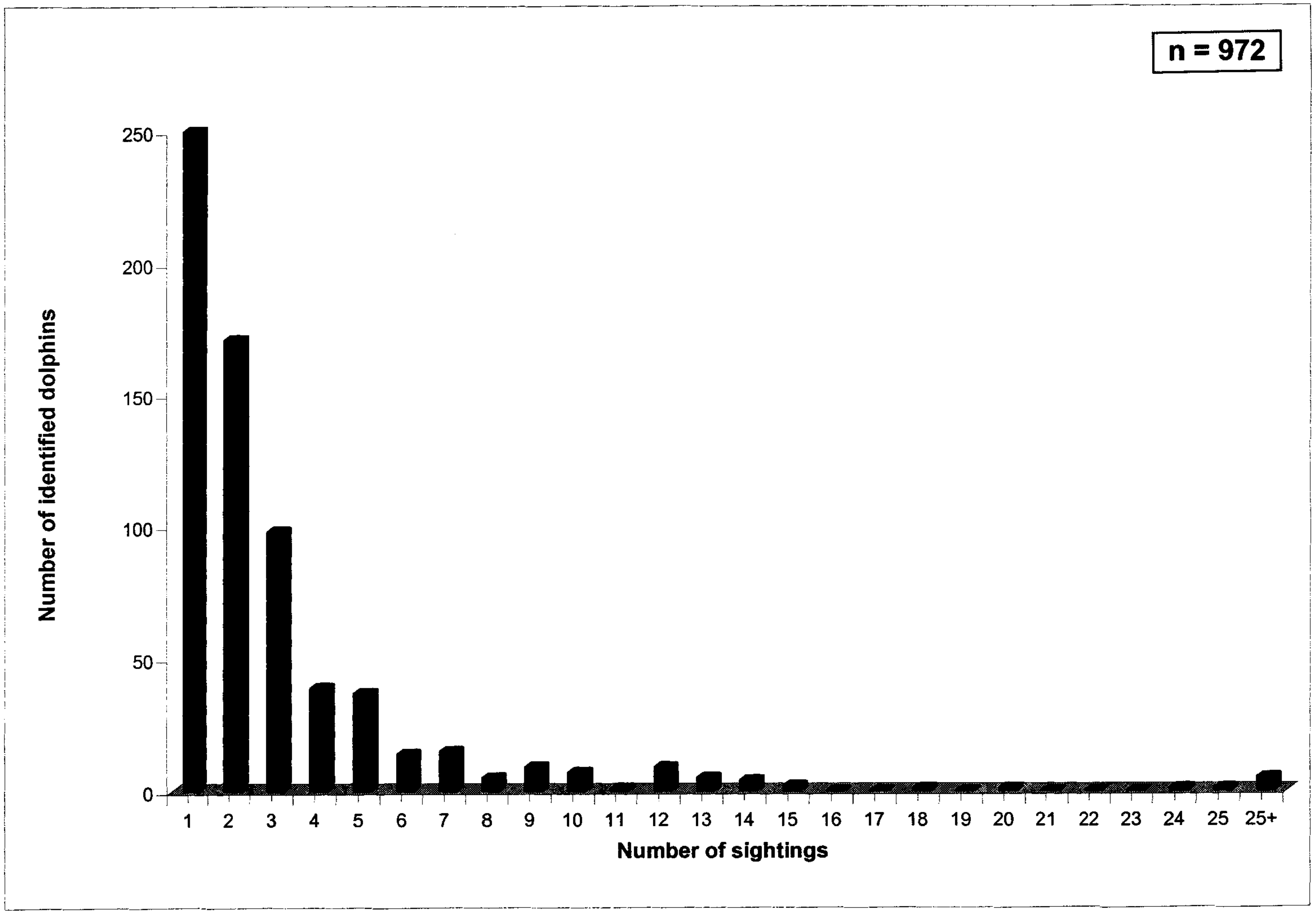


FIG. 17. Distribution of the total number of sightings for all photo-identified individuals (n=972) during all study years (1994-1999).



(late April/early May) and were not resighted until late September/early October, whereas others were sighted repeatedly during several months. Some individuals were sighted five as few as times in three of the six study years, to as many as 31 times in all six years (Appendix E). Sighting data collected before 1994 were used to examine site fidelity. The mean number of years identified individuals were recorded was 1.4 (range: 1-6; SD = 0.89) (Fig. 16). Ninety-three percent of all identified dolphins were sighted in one year (Fig. 16). All identified individuals had a mean number of 2.4 sightings (range: 1-31; SD = 3.2) (Fig. 17). Fifty-seven percent (554) of all identified dolphins were sighted once, 24.5 % (238) were recorded in multiple years, and 75.5 % (734) were seen one or more times in a single year. The mean number of sightings for the select 78 individuals was 10.7 (range: 5–31; SD = 6) (Fig. 18). Thirty-two (41%) of all select dolphins had 5-7 sightings, 18 (23.1%) had 8-10 sightings and 16 (20.5%) had 11-13 sightings (Fig. 18). In all, almost 85% of select dolphins were sighted 13 or fewer times (Fig. 18). Although most select individuals were only recorded in a single year (once or multiple times), several had extensive sighting histories. Five individuals were sighted in all six of the study years and 14 were seen in five of the six years.

Individuals were seen during a mean of two months for each field season (range: 1-5 months; SD = 0.77). Peak sightings for select individuals varied among study years, but July and August were consistently peak abundance months for all identified individuals, all select individuals and all select females (Figs. 19-21). A significant difference in group composition was found among months for 1994-1999 (Kruskal-Wallis = 27.922, $p < 0.0001$) (Fig. 22). The number of YOY observed in July 1999 was almost twice that of all previous years with 141 (Fig. 22).

FIG. 18. Distribution of the number of sightings for select individuals (n = 78) during all study years (1994-1999). Select individuals were dolphins sighted at least 5 times in 3 of the 6 study years.

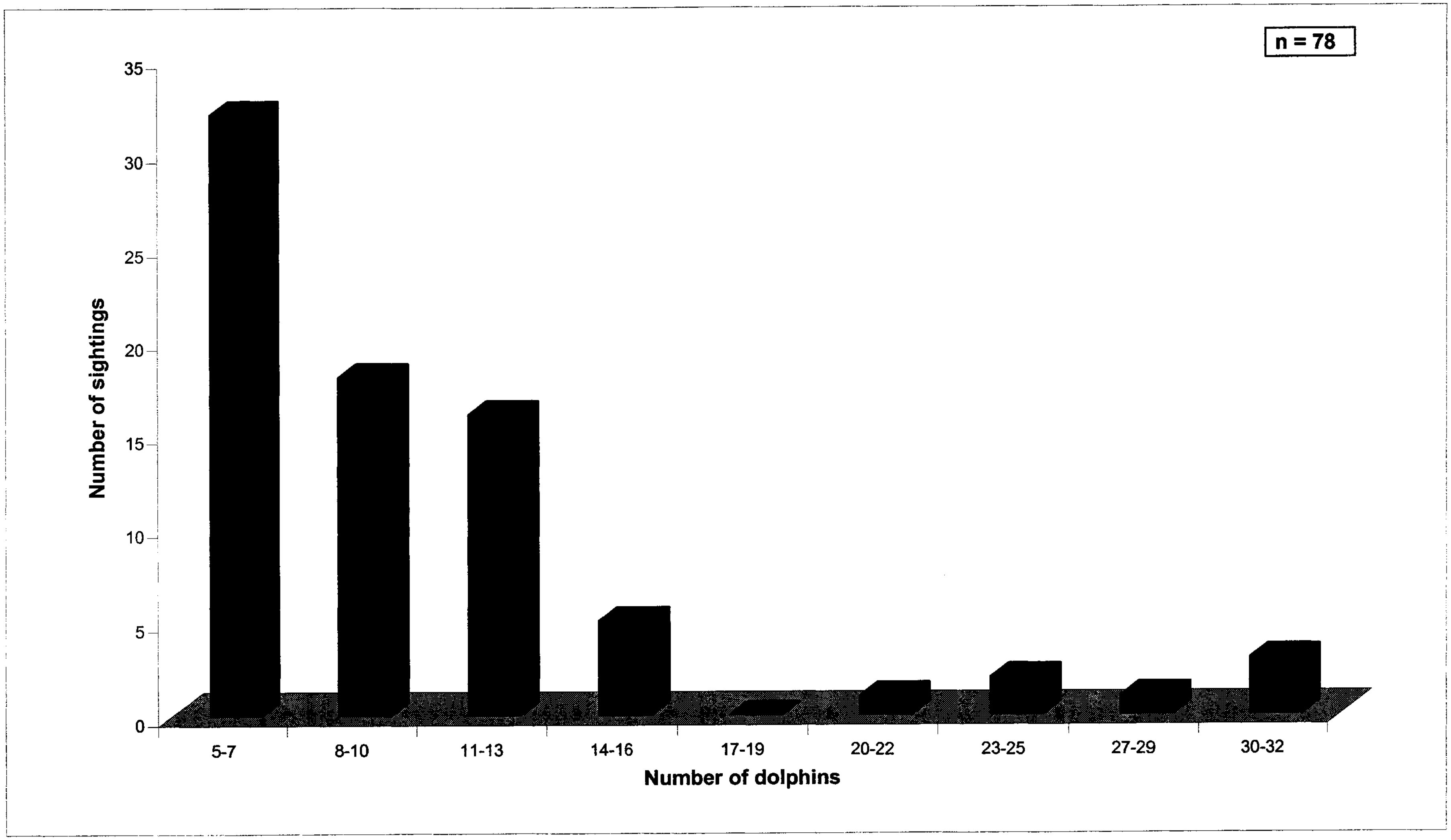


FIG. 19. Number of select individuals (n = 78) sighted during each month of all study years (1994-1999). Select individuals were dolphins sighted at least 5 times in 3 of the 6 study years.

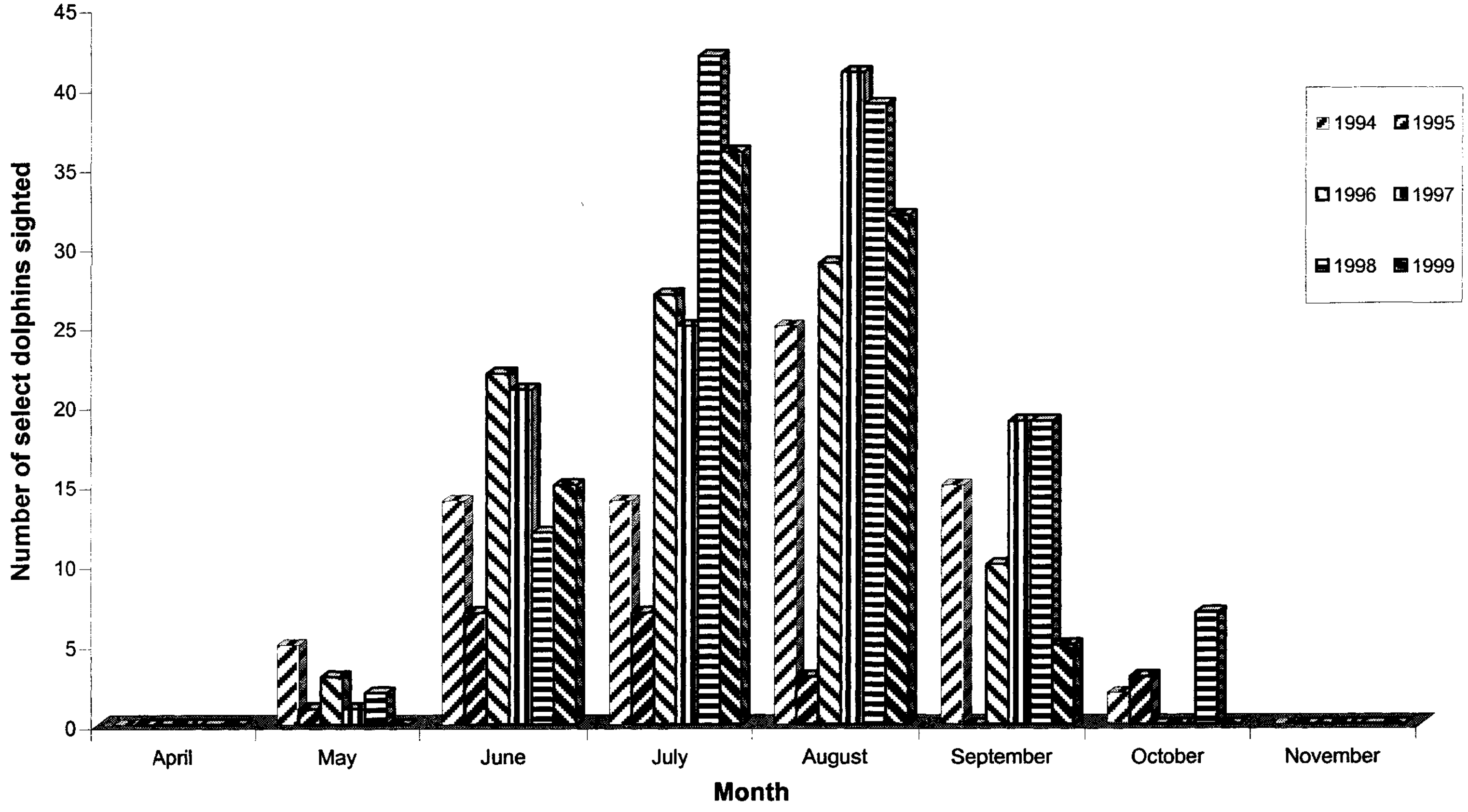


FIG. 20. Number of select definite and probable females (n = 22) sighted during each month for all study years (1994 - 1999). Select dolphins were sighted at least 5 times in 3 of 6 study years. Definite females had at least 3 sightings with a YOY and probable females had at least two sightings with a YOY.

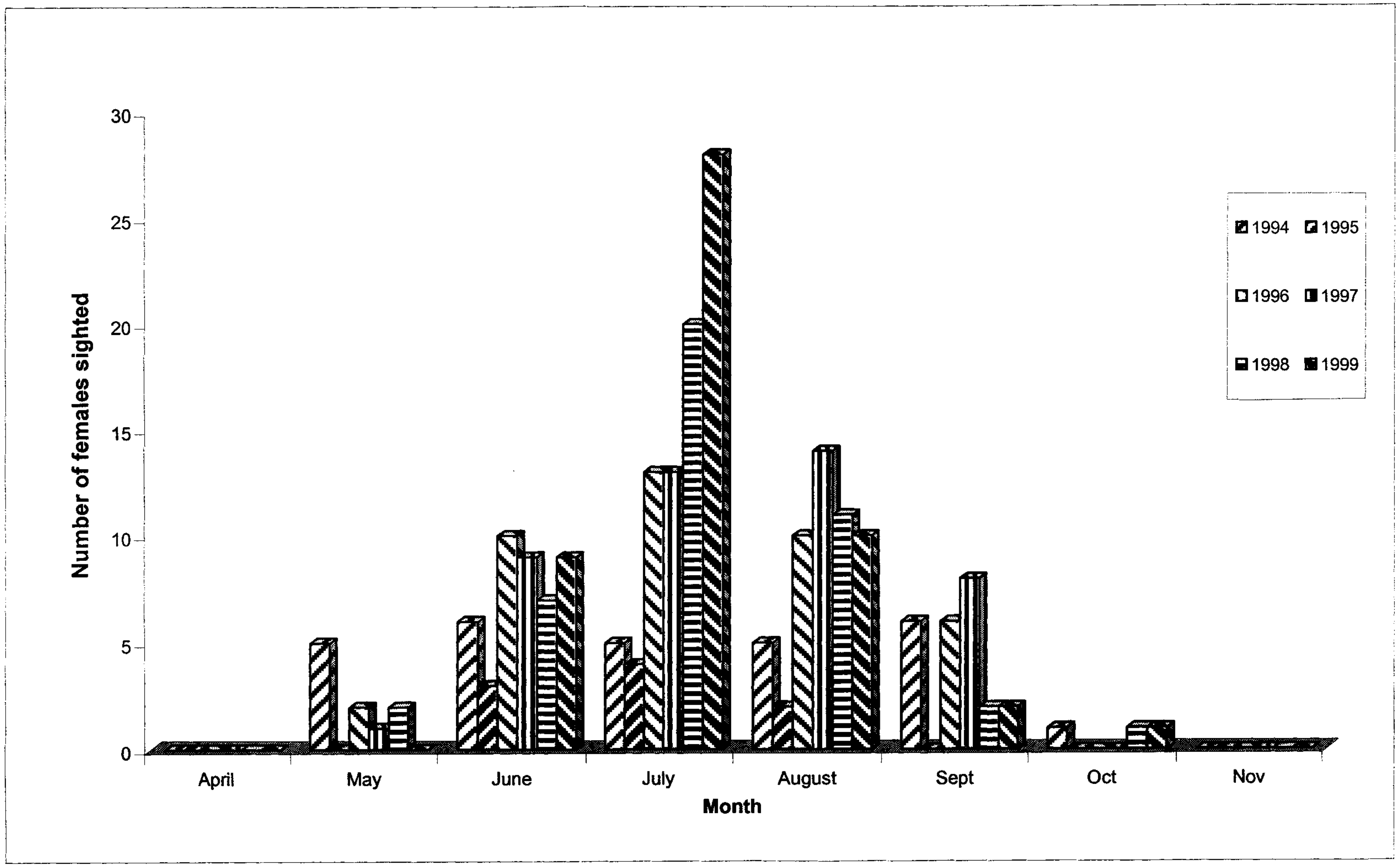


FIG. 21. Monthly distribution of select definite females (n = 18) for all study years (1994-1999). Select definite females had at least 5 sightings in at least 3 of 6 study years with a minimum of 3 sightings with a YOY.

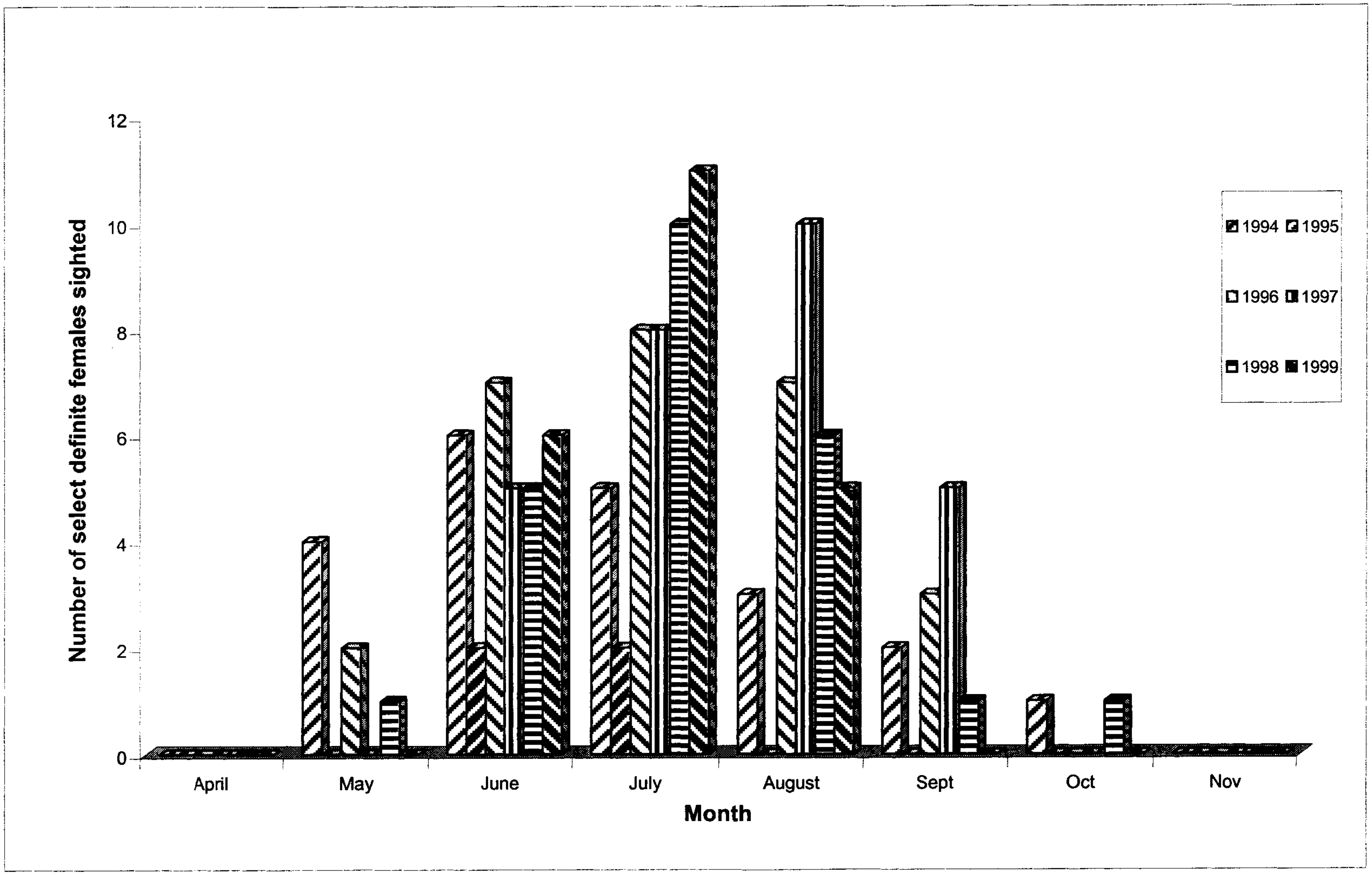
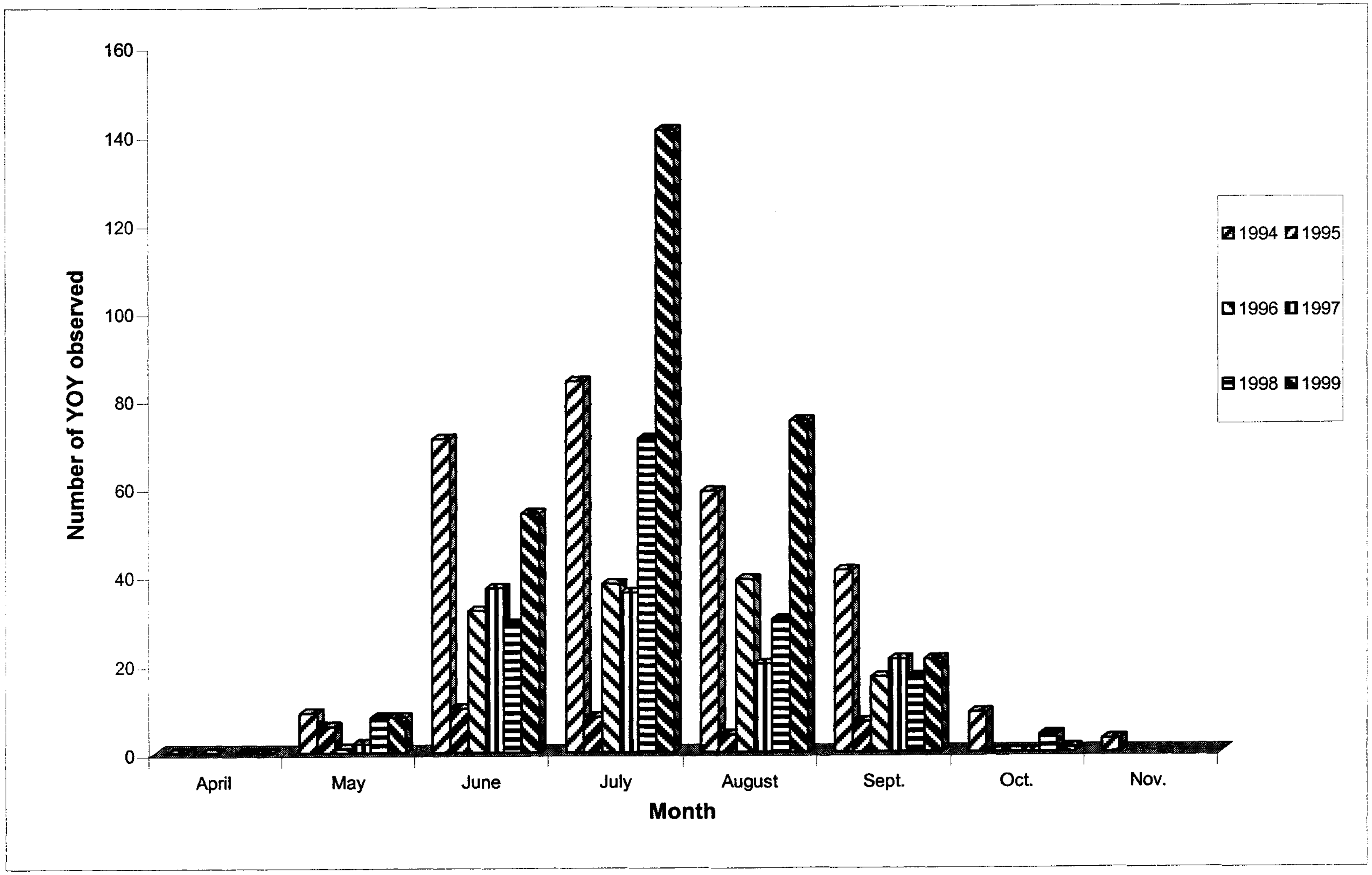


FIG. 22. Monthly distribution of the number of YOY (including neonates) observed in all encounter groups during all study years (1994 -1999) .



DISCUSSION

This section is divided into two parts. In Part I, I compare Virginia Beach bottlenose dolphins and other bottlenose dolphin populations around the world. Then, in part II, I discuss major ecological and social influences on group formation in mammalian systems with a focus on cetaceans.

Part I: A comparison of Virginia Beach dolphins with other bottlenose dolphin populations

Group size and composition

The Virginia Beach study area is an open system, being comprised of unprotected ocean and bay waters (Barco 1995). A dolphin group size of six to ten was most common, with the majority of sighting groups (82%) ranging between two and 30 individuals. Mean group size (22) for all encounters of Virginia Beach dolphins was most similar to mean group sizes calculated for both San Diego (mean: 19.8) (Weller 1991) and Argentina (mean: 14.5) (Wursig 1978; Wursig and Wursig 1977, 1979), two open ocean study areas. There was no significant difference in group size among these three study areas (Kruskal Wallis = 2; p = 0.367). However, these results must be viewed with caution because the definition of group varies among most studies (Shane et al. 1986).

Shane et al. (1986) state that group size is highly variable for bottlenose dolphins, ranging from one to more than 100, with individuals most commonly occurring in relatively small groups of two to 15. Lott (1984) noted that the formation of social groups of variable size and composition may be beneficial because it enabled the exploration of new opportunities that may have been created by changes in climate, prey availability, or the number of competitors or predators present. Conversely, Shane et al. (1986) suggested that group size in bottlenose dolphins may fluctuate based on habitat structure. Observations supporting such intraspecific variation have been documented in multiple populations of bottlenose dolphins (Wursig and Wursig 1977, 1979; Wursig 1978; Wells et al. 1987; Ballance 1990; Williams et al. 1993; Brager et al. 1994; Wilson 1995; Felix 1997; Rossbach and Herzing 1999; DeFran and Weller 1999; Gubbins 2002a, b; Parsons 2002). Protected habitats often foster relatively small school sizes, variable degrees of regional site fidelity, and limited movement patterns (Shane 1980; Wells et al. 1987; Smolker et al. 1992; Wilson 1995; Bearzi et al. 1997; Maze and Wursig 1999; Parsons 2002), whereas semi-open and open habitats often sustain larger school sizes, diminished levels of site fidelity, and more expansive home ranges (Wursig 1978; Wursig and Wursig 1977, 1979; Saaymen and Tayler 1973; Ballance 1990; Hansen 1990; Weller 1991; Defran and Weller 1999; DeFran et al. 1999; Barco et al. 1999a; Chilvers and Corkeron 2002; Parsons 2002). Open habitats may increase exposure to potential predators (Norris and Dohl 1980b; Shane et al. 1986, Parsons 2002) and require cooperation in feeding among individuals (Wursig 1978; Wursig and Wursig 1977, 1979; Saayman and Tayler 1973; Shane et al. 1986; Shane 1990; Fertl 1994a; Waples 1995; Parsons 2002).

Saayman and Tayler's (1973) study of a population of Indian Ocean bottlenose dolphins, *Tursiops aduncus*, in a closed habitat serves as a prime example of variability in the definition of a "group." Dolphins occurred in large schools of up to 1000 individuals

(63% contained > 50 dolphins) that were usually fragmented into four or five subgroups and dispersed over several square km (mean: 140.3)(Saayman and Tayler 1973). Excluding Saayman and Tayler's (1973) study, group size was significantly smaller in closed habitats compared to open habitats (Mann U Whitney = 18; $p < 0.005$) (Table 10).

Group composition (relative numbers of adults and YOY) also appeared to affect group size. Again, results in the Virginia Beach study area were consistent with results from other study areas. Groups containing YOY were significantly larger than groups without YOY (Wells et al. 1987; Ballance 1990; Weller 1991; Smolker et al. 1992; Fertl 1994a; Zolman 2002; Felix 1997; Quintana-Rizzo and Wells 2001; Gubbins 2000). Mean values for group composition were also comparable to other study areas, with a mean of three YOY per group for all encounters and four YOY per group for all encounters involving select 78 individuals. Although only 64% of all encounter groups contained YOY, 100% of all select individuals had a mean value of at least one YOY for all encounters. This suggests the occurrence of mixed sex groups because of the unlikely probability that all select dolphins are females. Large group size for females and their young may provide increased protection for calves, resulting in greater survival of the young and thus increased fitness of the mother and other related individuals in the group. Genetic relatedness is not known for Virginia Beach dolphins, but has been shown to be a factor in associations for females in Sarasota, Florida (Duffield and Wells 1991).

In all, Virginia Beach bottlenose dolphins appeared to follow a pattern typical of an open environment, where group size is large and associations transient as animals move through the region. Therefore, the occurrence of large less cohesive groups is not surprising due to a high number of dolphins moving through an area of high dolphin density.

Individual identification

Figures 4 (rate-of-discovery curve) and 5 (number of dolphins identified per hour) demonstrate that all dolphins in the Virginia Beach study area have not yet been identified. An asymptote would be apparent if most individuals had been identified. The highest number of new individuals identified, the highest number of hours of effort logged, and the second highest number of dolphins encountered all occurred in 1999. Although the highest number of dolphins was logged for 1994, all dolphins were not approached for photo-identification. Therefore, the peak in the discovery curve for new animals identified in 1999 was most likely the result of an increase in both effort and the number of dolphins present in the study area. The absence of an asymptote after so many years, and with such a large working photo-id catalog, may also be attributed to the transient nature of the study population. The low number of sightings recorded for most identified individuals supports the hypothesis that dolphins are using different strategies in different years. Some individuals demonstrate high site fidelity and predictable patterns of occurrence in the Virginia Beach study area, but it appears that most individuals alter annual movement patterns based on existing social and/or ecological conditions.

Number of associates

The mean number of associates for the 78 select individuals in my study was 93.1 (range: 18-243; SD = 47.6). The majority of select individuals (78%) had 125 or fewer associates, but only one animal had less than 25 associates. Thirty-one percent of all select dolphins had between 51-75 associates. Compared to other study populations, these values are high. Again, the high number of associates is most likely a result of the large size of the Virginia Beach population. However, the actual proportion of associates (mean number of associates as a proportion of the number of identified individuals) was much smaller at 9.6 % compared to 61 % for Sarasota (Wells et al. 1987), 19.3 % for Cedar Keys (Quintana-Rizzo 1999) and 23 % for the Bahamas (Rossbach 1997). Such a low proportion of associates may be attributed to the transient nature of Virginia Beach animals. Most individuals only briefly occurred in the study area and thus only temporarily associated with other animals also present in the region.

Connor et al. (2000b) commented that differences in the population density of a study area should correlate with encounter rates and alliance formation in dolphins within that site. A high degree of fluidity in associations is often observed between residents and non-residents (Felix 1997; Quintana-Rizzo and Wells 2001; Gubbins 2002b). Thus, variations in movement patterns of both individuals and groups, could explain the fluctuations observed in the number of associates for individuals. The calculated percentage of actual versus possible associates was 10.5 % for Virginia Beach dolphins, compared to 17 % for dolphins in the Bahamas (Rossbach and Herzing 1999) (Table 10). Individuals in the Sarasota community showed a high degree of fluidity in the number of associates, with 95.8 % of all possible female-female associations, 76.2 % of all male-

Table 10. A comparison of bottlenose dolphin studies throughout the world.

Study site	Habitat type	Group size		# identified individuals	# Associates		Mean COA	Site Fidelity	Mixed Residency Strategies?
		mean	range		mean	range			
Sarasota, Florida	closed	4.8; 7	1-39	100	60.55	25-91	HWI; 0.20	high	N
Stono River Estuary, South Carolina	closed	3.4	1-16	112	ND	ND	ND	high/mixed	Y
Hilton Head, South Carolina	closed	25; 27	ND	478	10/2	1-21/0-6	ND	high/mixed	Y
Shark Bay, Australia	closed	4.8	2-20	400	ND	ND	HWI; 84% ≤ 0.20	high	N
Kvarneric (Northern Adriatic Sea)	closed	7.4	2-65	106	ND	ND	ND	high/mixed	Y
Moray Firth, Scotland	closed	6.5	1-46	129	males:52 females:42	ND	SR; 95% < 0.25	high	N
SE Cape Coast, South Africa	closed	140	2-1000	ND	ND	ND	ND	ND	ND
Gulf de Guayaquil, Ecuador	closed	25.4 (all); 2.3 (subad.)	comm:115 rge:56-60	441	39;76;30 *see below	0-83;0-79;48-96	HWI; 0.32	high/mixed	Y
Galveston Channel, Texas	closed	2.9 w/calf; 3.2 w/o calf	1-15	240	ND	ND	mom/calf pair w/other; most freq. 0.08-0.12	high; mixed	Y
Moreton Bay, Australia	closed	10.4	1-37	334	ND	ND	ND	ND	
Galveston Bay, Texas	open	4.4	2-30	200	39.3	8-78	HWI; 0.19	low	Y
Cedar Keys, Florida	open	4.1	2-28	233	55	10-85	HWI; 93.5%≤0.40	high/mixed	Y
Point Lookout, Australia	open			550	14-27		HWI; 0.04-0.12	high	
Gulfo San Jose, Argentina	open	14.9	8-22	53	ND	ND	ND	low/mixed	Y
Gulf of California, Mexico	open	15	1-125	155	ND	ND	JC; most < 0.20	low	Y
San Diego, California	open	18	1-139	173-240		1-32	ND	low	Y
San Diego, California	open	19.8	2-90	373	signif.: 16	25-259	HWI; 0.21	low	Y
Grand Bahama Island	open	5.8	2-28	211	48	32-77	SR; 0.58	high	Y
Virginia Beach, Virginia	open	22	2-200	1006	99	13-258	HWI; 0.18	low	N

ND= no data found HWI= half weight index SR= simple ratio index JC= Jaccard's index

*Ecuador: adult female; adult male; subadult

Table 10 (cont.). A comparison of bottlenose dolphin studies throughout the world.

Study Site	**Associated Citations**
Sarasota, Florida	Irvine et al. 1981; Wells et al. 1987; Scott et al. 1990
Stono River Estuary, South Carolina	Zolman 1996, 2002
Hilton Head, South Carolina	Gubbins 2000; Gubbins 2002 a, b
Shark Bay, Australia	Smolker et al. 1992; Connor et al. 1992; Richards 1996; Connor et al. 1999; Connor et al. 2000 a, b
Kvarneric (Northern Adriatic Sea)	Bearzi et al. 1997
Moray Firth, Scotland	Wilson 1995; Wilson et al. 1997; Wilson et al. 1999
SE Cape Coast, South Africa	Saayman and Tayler 1973
Gulf de Guayaquil, Ecuador	Felix 1997
Galveston Channel, Texas	Fertl 1994 a,b
Galveston Bay, Texas	Brager et al. 1994
Moreton Bay, Australia	Corkeron 1990
Cedar Keys, Florida	Quintana-Rizzo 1999; Quintana-Rizzo and Wells 2001
Point Lookout, Australia	Chilvers and Corkeron 2002
Gulfo San Jose, Argentina	Wursig 1978; Wursig and Wursig 1977, 1979; Wursig and Harris 1990
Gulf of California, Mexico	Ballance 1987; Ballance 1990
San Diego, California	Hansen 1990
San Diego, California	Weller 1991; DeFran and Weller, 1999; DeFran et al. 1999
Grand Bahama Island	Rossbach 1997; Rossbach and Herzing 1999
Virginia Beach, Virginia	Barco 1997; Barco et al. 1999a, b; current study

male associations and 83.7 % of all male-female associations being recorded during five years of study (Wells et al. 1987).

Large estimated local population sizes could potentially be an artifact of the inclusion of dolphins using differing residency strategies that occur in a certain region at the same time. Dolphin associations in both open and closed populations are fluid, with individuals either directly or indirectly associating with most other members of the study population (Wells et al. 1987; Weller 1991; Smolker et al. 1992; Brager et al. 1994; Quintana-Rizzo and Wells 2001; Gubbins 2002b). Therefore, it is interesting that the proportion of associates for Virginia Beach dolphins was so low. One would assume that associations among individuals within the limited range of the study area would readily occur unless individuals actively avoided one another or were temporally separated. Again, pulses of animals moving through the study area would help explain such a low proportion of actual versus possible associations. It would also support the existence of mostly low-level associations occurring among different migratory groups, as well as many stronger, long-term associations between other individuals possibly migrating together.

Strengths of association

The half-weight index (HWI) was used to calculate strengths of associations for Virginia Beach dolphins. The HWI was more applicable to the Virginia Beach study area because individual members of a dyad were more likely to be sighted separately than together. Although most associations (79.3%) between individuals in the Virginia Beach study area fell into the low-level category (0.01 - 0.40), with no recorded high-level

(0.81 - 1.0) associations, 20% were placed in the moderate-low level category. No select individuals had a mean association value greater than 0.40 and the mean maximum association value was 0.39. Such results demonstrate that, although most associations were low-level, stronger associations did occur between individuals and among groups for Virginia Beach dolphins. An abundance of low-level association values could also be a result of individuals not being photographed in a sighting group. Every effort was made to photograph all individuals within a group, but due to large group size, turbid waters and high sea state, it was likely that a many individuals were present but not documented in any given period of observation. It is also likely that the temporal separation of individuals passing through the study area was a major factor influencing the associations of individuals.

A caveat of the use of association indices is that individuals with a high total number of sightings often had lower calculated association indices compared to individuals with a low total number of sightings, regardless of the number of joint associations. In several cases, two individuals had more than four joint sightings, but were not each other's highest associate because one of the two associating individuals had an extremely high number of individual sightings. The likelihood of an individual being photographed also varied. For example, mothers with calves may actively avoid the research vessel (= low sighting record), while other individuals, such as juveniles, may readily approach the research vessel (= high sighting record). All associates of select individuals were included in HWI calculations, regardless of their sighting history, but individuals with only one sighting were not included in analyses when evaluating individuals for small-scale grouping patterns (dyads/triads/quartets). Calculated HWI values for individuals with only one sighting were often the highest association value for the associate due to their low number of sightings rather than a high number of joint associations.

Many low-level, weak associations with few high-level associations are the norm for most studies, independent of habitat type and site fidelity (Wells et al. 1987; Ballance 1990; Weller 1991; Smolker et al. 1992; Fertl 1994a; Brager et al. 1994; Wilson 1995; Bearzi et al. 1997; Felix et al. 1997; Rossbach and Herzing 1999; Quintana-Rizzo and Wells 2001; Gubbins 2002b; Chilvers and Corkeron 2002; Zolman 2002). Strong associations do regularly occur between and among individuals, but usually include only a small proportion of the total associations within the population. Associations appear to be influenced consistently by age, sex and reproductive status (Wells et al. 1987; Smolker et al. 1992; Richards 1996; Felix 1997; Rossbach and Herzing 1999; Quintana- Rizzo and Wells 2001), as well as genetic relatedness (Duffield and Wells 1991, 2002; Kruetzen et al. 2003).

Associations in Virginia Beach were extremely fluid, and although mostly low-level, weak associations were observed, several strong, long-term associations were also recorded. A low proportion of possible associations was also observed, suggesting that individuals may preferentially associate with a more limited group within the study population. The sex of Virginia Beach dolphins was determined for only a small percentage of the population and the genetic make-up and exact age of individuals was almost completely unknown.

Determining whether associations are significantly different from random

Association indices are readily used to describe and quantify relationships between individuals, but both Whitehead (1997) and Bedjer et al. (1998) discuss the limitations of only using association indices for analyses. Another method, randomizations, can be applied to datasets to determine whether associations are significantly different from a random occurrence (Manly 1995, 1997; Bedjer et al. 1998). Bedjer et al. (1998), who describes a modification of Manly's (1995, 1997) Monte Carlo method, suggests that researchers apply such a test to their data before they can make any inferences from their association indices. Associations are deemed significantly different from random if the calculated p-value is less than 0.05, although Bedjer et al. (1998) noted that the failure to reject this hypothesis simply means that there is no evidence against random association in the data. Smolker et al. (1992) found many significant associations when using Monte Carlo simulations to study sex differences in associations for bottlenose dolphins in Shark Bay.

Individual sighting records for Virginia Beach dolphins were affected by variable sighting patterns, large group size and environmental conditions. It is likely that these conditions prevented total photographic coverage of all dolphins, in turn affecting calculated association values and the outcome of randomization analyses based on sighting data. This raises the question of how applicable certain statistical analyses may be to large populations with irregular movement and sighting patterns and limited survey conditions. Chilvers and Corkeron (2002) noted that association analyses have limitations, particularly for study areas where animals live at high densities or a significant proportion of the animals lives in large schools or lacks distinguishing marks.

The way data are collected for large dolphin schools may inherently be more likely to produce results that suggest randomness of associations, when definite partners actually exist. Chilvers and Corkeron (2002) point out that associations between individuals are often not apparent until a strong history is established.

Nonetheless, 36 dyads were deemed to be significantly different from random for Virginia Beach bottlenose dolphins. These dyads are important because they demonstrate that nonrandom associations, including one same-sex significant dyad, do occur in coastal migratory bottlenose dolphins. Again, following Bedjer et al. (1998), a lack of statistically nonrandom associations can be interpreted as no evidence against random associations rather than a lack of significant associations. I have demonstrated that long-term associations do exist for Virginia Beach dolphins, many at a low-moderate level, and future data may support the existence of additional nonrandom associations. It is likely that many dolphins associate randomly as they move through the study area, but the existence of 36 nonrandom dyads supports the notion that all Virginia Beach dolphins were not mediated solely by random, temporary associations. Continued photo-id effort in the study area will greatly assist in future examinations of associations.

Grouping patterns

Large-scale grouping patterns of coastal bottlenose dolphins are something many researchers are trying to understand. Distinct dolphin communities (as defined by Wells et al. 1987) have been documented in several coastal study sites, some containing multiple associating communities (Quintana-Rizzo and Wells 2000; Gubbins 2002b). Initial efforts to extrapolate large-scale grouping patterns for Virginia Beach dolphins proved to be difficult with unwieldy results due to the high number of associates for select dolphins. Therefore, small-scale analyses were applied to Virginia Beach dolphins.

Small-scale groupings or subgroups of strongly associated individuals often exist within larger dolphin populations or communities. Smolker et al. (1992) defined these subgroups as pairs, trios and quadruplets (here referred to as dyads, triads and quartets). Many of these subgroups fuse to form large aggregations of both directly and indirectly linked individuals, including bands or networks of females (Wells et al. 1987; Smolker et al. 1992; Wilson 1995; Richards 1996; Felix 1997; Rossbach and Herzing 1999; Quintana-Rizzo and Wells 2001) and a superalliance of males (Connor et al. 1999). A loose network was found for Virginia Beach female dolphins. Associations were extremely fluid, and most associations were low to moderate level. Every select definite and probable female in the Virginia Beach study area was either directly or indirectly associated. Both a cluster analysis dendogram and a multi-dimensional scatterplot were generated from HWI values for select females. Several clusters of individuals were apparent in the figures and the fluidity of associations for females was obvious. Twenty-eight dyads, two triads and one quartet were identified for Virginia Beach dolphins, supporting the existence of strong reciprocal associations between individuals. Small-scale analyses were clearly a useful tool for deciphering large-scale patterns for large open populations like Virginia Beach.

Effects of sex

Frequently, the sex of individual dolphins cannot be determined in study areas with turbid waters and large group size, or where biopsy sampling is not an option

(Ballance 1990; Weller 1991; Brager et al. 1994; Fertl 1994a, b; Felix 1997; Zolman 1996; Barco 1995; Quintana-Rizzo 1999; Gubbins 2000; Chilvers and Corkeron 2002; Maze-Foley and Wursig 2002). However, researchers in several study areas with excellent water conditions (allowing for enhanced viewing and increased sampling opportunities) have been able to determine the sex of most individuals in their study population (Wells et al. 1987, Smolker et al. 1992; Rossbach and Herzing 1999).

Thirty-six definite and 24 probable females were identified in the Virginia Beach study area. Positive female identification required multiple sightings in close proximity of a YOY or neonate, but such identification was difficult because the young animal was often absent in the photograph of the mother due to it being either underwater or obscured by larger animals. In addition, many of the probable and possible females were newly identified and simply did not have the sighting history to meet the requirements of definite females. Eighteen definite and four probable females were considered “select” and included in further analyses. All select definite (n = 18) and probable (n = 4) females were linked, either by direct association or through indirect association with another known female (Figs. 10 and 11), but only four (18.2 %) select females had other identified females as their highest associate. However, 13 (59 %) had other identified females as one of their top five associates. These results support the presence of several strongly associated dyads of females and a network among these associated females. Multiple same-sex dyads were also documented, supporting a trend of sex-influenced associations.

Although variability exists (and sample sizes are often quite small), overall patterns of association based on sex appear to be consistent among study areas. The highest associate for bottlenose dolphins (excluding mother and calf pairs) is most frequently a member of the same sex (Wells et al. 1987; Smolker et al. 1992; Richards 1996; Felix 1997; Rossbach and Herzing 1999; Quintana-Rizzo and Wells 2001). Associations among males are often the result of cooperative interactions among individuals in an attempt to gain access to females (Wells et al. 1987; Smolker et al. 1992; Connor et al. 1992, 1999, 2000b; Richards 1996; Felix 1997; Connor 2000) and associations among females have been suggested to form in order to thwart these coercive male efforts and increase the fitness of the mother through increased protection of offspring (Smolker et al. 1992; Connor et al. 1992; Richards 1996).

Female bottlenose dolphins often occur in small bands or cliques of highly associated individuals and may form a larger network of more loosely associated (directly and indirectly) individuals, although all members have never been observed together at one time (Wells et al. 1987; Smolker et al. 1992; Richards 1996; Felix 1997; Rossbach and Herzing 1999; Quintana-Rizzo and Wells 2001). Both Wells et al. (1987) and Quintana-Rizzo and Wells (2001) found groups containing females to be significantly larger than those containing males, but Bearzi et al. (1997) found no significant difference in group size between the sexes. Home ranges of females overlap in most study areas (Wells et al. 1987; Smolker et al. 1992; Wilson 1995; Richards 1996; Rossbach and Herzing 1999; Quintana-Rizzo and Wells 2001; Gubbins 2002a). Wells (1991) stated that home ranges were likely determinants of association patterns among individuals, as dolphins that stayed within their home ranges would limit their number of possible associates. Wilson (1995) further supported this idea when he suggested that associations between identified females with calves are in part a result of overlapping ranges.

Due to both the transient nature of dolphins in the Virginia Beach study area and a low mean number of sightings, it was not possible to determine temporary home ranges for select females. Wells (1978) recommends using individuals with at least 15 sightings for home range calculations, but only four select females met this criterion in my study. All encounters of select females were plotted and most occurred in a small fraction of the Virginia Beach study area. Sighting areas of females appeared to overlap, which could increase associations and group fluidity, but such a statement is purely speculative.

Only one male (with few sightings) was identified from all photo-identified individuals in the Virginia Beach study area and no males were identified from the 78 select individuals. The sex of the single male was determined from a stranding event in North Carolina. Although this male did not meet the sighting requirements for a "select" individual, he was sighted in an encounter with several known females. The occurrence of this male in a group with known females, coupled with the fact that all select individuals had a mean value of at least one YOY for all encounters, supports the occurrence of mixed sex groups for the Virginia Beach study area. Mixed sex groups are common in most study areas, occurring in 31% of all encounters in Sarasota (Wells et al. 1987), 49% of all encounters in Shark Bay (Smolker et al. 1992) and 65.3% of all adult groups in the Kvarneric Sea (Bearzi et al. 1997). Almost all possible male/female associations were observed for two communities in the Bahamas (Rossbach and Herzing 1999) and Waples (1995) also found that both males and females in Sarasota most frequently occurred in mixed sex groups.

Male bottlenose dolphins in Sarasota may adopt one of two ranging patterns to ensure access to females: a single resident male remains in areas frequented by a large number of females and associates with many of them or roving multi-male groups range over large areas and associate with small numbers of adult females (Wells et al. 1987). Adult males in Ecuador did not show a preference for a particular female band, but ranged between bands searching for receptive females (Felix 1997). Males in Shark Bay are rarely found solitarily and exhibit two levels of alliance formation (Connor et al. 1992a): males in dyads or triads ("1st order alliances") cooperate to form coercively maintained consortships with individual females (Connor et al. 1992, 1996) and teams of two or more alliances ("2nd order alliances") cooperate in attempts to take female consorts from other alliances or to defend against such attacks (Connor et al. 1992). Male-male bonds in Shark Bay are extremely strong (some sustained up to13 years) and each dyad or triad maintains moderately strong associations with one or two other dyads or triads (Smolker et al. 1992). Connor et al. (1999) documented a superalliance of 14 males in Shark Bay comprised of multiple unstable 1st order alliances. Associations within this superalliance were fluid as 39 different alliances were observed over a three-year period (Connor et al. 1999). Males often have a higher number of associates than do females (Wells et al. 1987; Smolker et al. 1992; Rossbach and Herzing 1999; Brager 1999; Quintana-Rizzo and Wells 2001) and male-male associations appear to increase the fitness of both individuals as associations are prolonged and associates are often replaced when lost (Wells et al. 1987; Smolker et al. 1992).

Male dyads in Sarasota have not been observed to form cooperative alliances (Wells et al. 1987; Connor 2000) and as noted, strong bonds between males in the Moray

Firth appear to be altogether absent from the population (Wilson 1995). Sexual dimorphism has been suggested to be more apparent for dolphins in the Moray Firth and associations between males (to gain access to females) may therefore not be necessary to acquire and maintain reproductive access to females. Males generally have larger home ranges than females (Wells et al. 1987; Smolker et al. 1992; Wilson 1995; Richards 1996; Bearzi et al. 1997; Felix 1997; Rossbach and Herzing 1999; Quintana-Rizzo and Wells 2001) and Owen et al. (2003) found that male dyad members in Sarasota had significantly larger ranging patterns and core areas than males that were not members of a dyad. Increased home range has been theorized to equate to an increase in mating success; males are likely to meet a greater number of females if they roam within a wider area searching for receptive females (Eisenberg 1966; Wells et al. 1987; Quintana-Rizzo and Wells 2001).

Temporal variation in site fidelity

Movements of Virginia Beach dolphins were strongly seasonal, being observed only from late spring to early fall. Individual photo-id matches have been made among study sites along the east coast, some sites being separated by nearly 400 km. There is frequently a several-month lapse in sightings of individuals between northern and southern sites and animals are presumed to be traveling between study sites during this period. Barco et al. (1999b) analyzed data from 1989 to 1997 and found that 66 % of all identified individuals were seen only once. Analyses of sighting data from 1994-1999 showed that 57 % of the study animals were sighted once, 24.5 % were sighted in multiple years and 76 % were sighted more than one time in a single year. Sightings of individuals ranged from one to 31 (mean: 2.4; SD = 3.2).

Many individuals displayed long-term site fidelity, with sighting histories far exceeding the six years included in this study (sighting data date back to 1989), whereas others were only seen once or multiple times within a single year. Some individuals remained in the study area for up to three months, others appeared one month, disappeared and then reappeared several months later (possibly on their return from more northerly waters) and some were only observed once within the season. Sighting patterns indicated that not all dolphins moved synchronously along the coast, although coordinated movements were apparent for some individuals.

Barco et al. (1999a) found a significant difference for group composition between months (1994-1996), with peak YOY abundance in August. Similar results were found for this study (1994-1999), although July was the peak month for YOY abundance. Barco et al. (1999a) also found that seven known females spent significantly more time in the Virginia Beach study area during the year their calf was born than in other years and suggested that the Virginia Beach study area served as a nursery area for some individuals. Both female-female and male-female associations are often affected by the reproductive status of an individual (Wells et al. 1987; Smolker et al. 1992; Richards 1996), and associations among individuals and group movement patterns (Barco et al. 1999a, b) may vary from year to year based on the reproductive status of a few animals within the group. Associations for females in the Virginia Beach study area did vary based on reproductive status and both the number of sightings and the duration of time spent in the Virginia Beach study area increased for reproductive females.

Individuals were often sighted for several month periods in more than one study area, suggesting that these dolphins may be using each study area equally, essentially maintaining one large home range and varying their distributions between sites due to social or ecological factors (e.g., the availability of food resources). The notion that the Virginia Beach study area is an extension of a home range or one of two "home ranges" connected by a traveling range (Caldwell and Caldwell 1972) needs to be considered. Large-scale movement patterns could be influenced by ecological factors such as food availability, but small-scale group fluctuations could be affected by both social and ecological factors. It was difficult to determine exact migratory patterns for Virginia Beach bottlenose dolphins, but seasonal movements appeared to occur in pulses and monthly sighting patterns for some individuals were consistent throughout the years.

Bottlenose dolphins show a great deal of variability in movement and site fidelity (Shane et al. 1986; Ballance 1990; Defran et al. 1999; Quintana-Rizzo and Wells 2001). Some study areas contain dolphins with year-round residency and long-term site fidelity (Wells et al. 1987; Smolker et al. 1992; Wursig and Harris 1990; Fertl 1994a; Bearzi et al. 1997; Rossbach and Herzing 1999; Quintana-Rizzo and Wells 2001; Chilvers and Corkeron 2002), some may have a mix of both transient and resident dolphins with some individuals having strong, long-term site fidelity, and others may contain individuals with short-term or no site fidelity (Brager et al. 1994; Fertl 1994a; Felix 1997; Maze and Wursig 1999; Quintana-Rizzo and Wells 2001; Gubbins 2002a; Zolman 2002). Other study areas include seasonal or year-round residents or transients with low site fidelity (Wursig and Wursig 1977, 1979; Wursig 1978; Ballance 1990; Weller 1991; Bearzi et al. 1997; Defran and Weller 1999; Barco et al. 1999a, b). Many times, the majority of individuals identified in a study area are considered to be transient and the resident community (following Wells et al. 1987) is actually only a small proportion of the study population.

Wursig (1978) commented that fluctuations in group size for bottlenose dolphins in Argentina were the result of a continual flux of animals joining and leaving subgroups. Some individuals were observed during certain months of the year in the same vicinity and others were resighted > 300 km from their initial sighting location (Wursig 1978; Wursig and Wursig 1977, 1979). Wursig (1978) suggested that his study area was part of an extended home range for these dolphins. Several additional studies have also suggested that their study areas include only a portion of the home range of some or all of their study dolphins and researchers have attempted to define variable sighting and movements patterns for individuals or groups (Ballance 1990; Hansen 1990; Weller 1991; Brager et al.1994; Fertl 1994a; Zolman 2002; Felix 1997; Bearzi et al. 1997; Defran and Weller 1999; DeFran et al. 1999; Quintana-Rizzo and Wells 2001; Gubbins 2002 a). Please refer to Appendix H for definitions and study details on residency patterns observed for several dolphin populations.

For many open systems, like Argentina (Wursig 1978), San Diego (Hansen 1990; Weller 1991; DeFran and Weller 1999; DeFran et al. 1999) and Virginia Beach, dolphins make long-distance movements and site fidelity is often low. Wells et al. (1987) suggested that the Sarasota population is a closed community, but associations (17%) with non-community members were still frequently observed (Wells et al. 1987). Shark Bay, Australia is regarded as a closed habitat system, but the population appears to be open with a regular exchange of individuals (Smolker et al. 1992; Connor et al. 1992;

Richards 1996; Connor 2000; Connor et al. 2000a). Bottlenose dolphin populations throughout the United Kingdom have been found to have relatively high degrees of residency in certain core areas, such as Cornwall and the Moray Firth, Scotland (Wood 1998; Wilson et al. 1999). Bearzi et al. (1997) suggested that an extension of home range and movements within a study area is the result of the availability of suitable habitats for activities such as feeding, resting and rearing offspring.

If residential populations of bottlenose dolphins limited their associates to individuals sharing similar residency patterns, a high degree of inbreeding would most likely occur. Both the temporary and permanent dispersal of individuals from their natal groups may be a method of preventing inbreeding within small populations (Greenwood 1980). A high frequency of associations between resident and non-resident individuals, either as a result of individuals associating within a resident's home range, or from individuals traveling outside of their home range helps to ensure genetic exchange within the population. Quintana-Rizzo (1999) observed mating attempts between residents and non-residents on several occasions and Duffield and Wells (2002) documented measurable reproductive exchange between Sarasota Bay residents and non-residents. Duffield and Wells (2002) therefore concluded that non-residents interact with Sarasota residents reproductively as well as socially. But there are exceptions. Wilson (1995) studied a population of 129 bottlenose dolphins in the Moray Firth, Scotland and defined this population as a closed community; Parsons et al. (2002) confirms that minimal genetic exchange between Moray Firth dolphins and adjacent populations.

Gubbins (2002b) found that associations among resident dolphins in South Carolina did not change when transients migrated into the study area, but noted an overall increase in group size and suggested that resident and transient groups temporarily joined and then separated. Such associations between these South Carolina residents and transients further support the notion that inter-population reproductive interactions may minimize the consequences of the isolation of small populations. Zolman (2002) also observed an influx of animals into his study area during winter months, but little has been documented on the location of those animals during summer months. Zolman (2002) suggested that the seasonal residents observed in his South Carolina study area are members of the North Atlantic coastal migratory stock. Further investigation into stock movement patterns along the East coast will help determine stock membership and occurrence patterns.

Part II: A comparison of ecological and social influences on group formation in mammals

Ecological processes

Predation

The Virginia Beach study area is an open, exposed habitat. Shark bites and scars were observed on dead stranded dolphins and crescent-shaped scars were visible on a low percentage of individuals within the study population (personal observation; Virginia Marine Science Museum stranding records). Mead and Potter (1990) reported that, although there was no direct evidence of mortality by predators, several dolphins along the Mid-Atlantic coast bore wounds (some fresh) or scars from previous encounters with sharks. Predation pressure is not a factor influencing bottlenose dolphin associations in San Diego (an open system with similar patterns in group formation), but (Weller 1991) suggests that it might play a role in the occurrence of large groups with calves (significantly larger than groups without calves). Similarly, groups containing YOY were also significantly larger than groups without YOY in the Virginia Beach study area. The large group size observed for Virginia Beach dolphins may simply be an artifact of an open system, resulting in an overlap of individual daily ranges, but predation pressure is a possible factor. Individuals may have found larger groups to be an effective deterrent against predators.

The consensus on hypotheses of mammalian sociality is that defense against predators is one of the major benefits of group living. It is commonly viewed as the driving force in the evolution of groups (Crook 1972; Eisenberg et al. 1972; Alexander

1974; Altmann 1974; Wilson 1975; Bertram 1978; Wrangham 1980; Rubenstein 1986). The survival benefits of joining a group are especially great when predators are concentrated (Pulliam 1973; Treisman 1975; Bertram 1978; Rubenstein 1986; Dunbar 1986; Jarman and Southwell 1986). Intraspecific associations may boost defense against predators by providing increased cover and amplifying overall group attentiveness; if intraspecific associations are not possible, interspecific associations may develop to serve the same function (Crook et al.1976; Terbough 1983; Chapman and Chapman 2000). Researchers commonly observe interspecific associations in more exposed habitats (primates: Goldizen 1987, Chapman and Chapman 2000; ungulates: Jarman 1974, Hillman 1987) and bottlenose dolphins have been observed to increase overall group size through interspecific associations in pelagic waters (Kenney 1990).

Habitat type, and thus the amount of available refuge, is also a major factor for group formation. Terrestrial primate species, presumably more exposed to the dangers of predation due to decreased refuges, tend to occur in larger groups than do arboreal species (reviewed by Clutton-Brock and Harvey 1977; Dunbar 1988) as larger groups may provide a more effective defense against potential predators (Struhsaker 1969; Bertram 1978; Pusey and Packer 1987; Packer et al.1990). Gelada baboons (terrestrial) are commonly observed in small bands, but aggregate in large numbers in gorges (little available cover) for safe sleeping refuges from predators (Dunbar 1986). The formation of large groups for predatory defense in open habitats and small groups in more protected habitats is also observed in ungulates, although group stability varies among species (e.g., antelopes: Jarman 1974; elands: Hillman 1987).

Analogous patterns are found for cetaceans. Dolphins inhabiting more open pelagic waters (and thus more susceptible to predators) generally form large groups (Norris and Dohl 1980b; Wells et al.(1980), Shane et al.(1986) and Scott et al.(1990). Again, group living not only reduces the chance of an individual being attacked and killed, but also increases the chance of detecting a predator before an attack occurs (Norris and Dohl 1980b; Pulliam and Caraco 1984; Connor 2000). Shane et al.(1986) noted that group formation in dolphins would be important if their physical environment provided little protection from predators. In Cedar Keys, Florida, female bottlenose dolphins with young calves are rarely sighted in gulf waters where animals are potentially more exposed to predators compared to more protected inshore waters (Quintana-Rizzo 1999).

Norris and Dohl (1980b) comment that the degree of variation observed in cetacean school size is exactly what would be predicted if predation were the basis for schooling tendency (Hamilton 1971). Large group size is common among many smaller odontocete species such as spinner, spotted and bottlenose dolphins, which are susceptible to predation as demonstrated by the presence of scars from shark attacks (Wood et al.1970; Norris and Dohl 1980b; Wells et al.1987; Ostman 1994; Fertl 1994a; Zolman 1996, 2002). Leatherwood (1971) suggest that fast-swimming dolphins either outmaneuver most sharks in open water or that attacks that do occur are fatal. By contrast, Wells et al. (1980) suggests that the larger groups formed by pelagic species are a relatively effective deterrent to attack. Leatherwood et al. (1971) reports a low number of shark bite scars on pelagic dolphins and Wood et al. (1970) reports a higher frequency of shark bite scars on inshore dolphins as compared to dolphins frequenting offshore waters. Shark scars were observed on 10.3% of bottlenose dolphins in South Africa (Cockcroft et al. 1989), as compared to 36.5 % in Australia (Corkeron et al. 1987; Corkeron 1990) and 21.7% in non-calves in Sarasota (Wells et al. 1987). Killer whale attacks on both small odontocetes and large baleen whales are frequently documented in areas of medium to high density of killer whales. Killer whale sightings along the mid-Atlantic are rare and therefore are not considered to be a threat for coastal bottlenose dolphins.

Wells (1991) found that males that regularly occurred in dyads often acquired more scars than those living solitarily, but tended to live longer, suggesting they were able to recover from injuries whereas solitary individuals were not [presumably due to protection by their partner (Connor 2000)]. Solitary living may be more advantageous than occurring in a group for mating purposes, but is definitely not more advantageous in high-risk habitats because vulnerability to predators would be greatly increased (Connor 2000; Connor et al. 2000b). Ostman (1994) suggests that predator avoidance causes the formation of the strong male-male bonds observed in her study population of spinner dolphins off the Kona coast of Hawaii. In contrast, Wilson (1995) and Wilson et al. (1997) found bottlenose dolphins in the Moray Firth, Scotland, a closed estuarine system, to be virtually free of potential predators and proposed that the absence of strong pair-bonds between individuals of similar size (presumed to be adult males) is a direct result of the absence of predators and thus a lack of the need for increased protection provided by the presence of a close affiliate. Parsons (2002) studied bottlenose dolphins in two contrasting environments in the Bahamas and observed larger, more stable groups in the in the exposed habitat with an increased abundance of sharks, and smaller, less stable groups in the protected habitat with a lower abundance of sharks.

Resource acquistion

Group living, and thus associations among individuals, may also be a result of individual feeding requirements. Saayman and Tayler (1973), Wursig (1978) and Wrangham (1986) suggests that the abundance and distribution of food resources may be related to the density of consumers using an area, and that food availability may be a major determinant of subgroup size and stability. If group stability depends on resource stability (Estes 1969), and the number of animals in a particular area depends largely on the density of available resources, then large unstable groups are likely to form in areas of high resource density (e.g., gelada baboons: Crook and Gartlan 1966) and small cohesive groups may evolve in areas of low resource density (e.g., chimpanzees: Reynolds and Reynolds 1965; Chapman et al. 1996). Large groups may be detrimental to individuals when resources are low and foraging in such groups may therefore only be adaptive if food occurs in clusters or units that can feed more than one animal (Wrangham 1980; Wrangham and Rubenstein 1986). Consequently, resource availability and patchiness may set an upper limit on group size and density (Wrangham 1980; Baird and Dill 1996; Williamson and Dunbar 1999) and lead to interspecific variability (e.g., pygmy and common chimpanzees: Badrian and Badrian 1984; Nishida and Hiraiwa-Hasegawa 1987).

Changes in social organization such as the formation of feeding aggregations and establishment of territories are commonly observed adaptations to changes in the abundance and distribution of resources (e.g., golden jackals: MacDonald 1979; African lions: Pusey and Packer 1983, Packer 1986, Packer et al.1990; equids: Rubenstein 1986; chimpanzees: Chapman et al.1996; black bears: Rogers 1987; gorillas: Stewart and Harcourt 1987; vervets: Chapman et al.1988; spider monkeys: Chapman 1990; orangutans: Mitani et al.1991). Patchy or clumped distribution of resources may cause a decrease in overall group size (e.g., chimpanzees: Chapman et al.1996; black bears: Rogers 1987; spider monkeys: Chapman 1990) or stability through an increase in inter-animal distance due to increased travel (e.g., red-necked wallabies: Johnson 1989). Cetaceans appear to be exempt from such constraints because they have relatively low travel costs due to streamlined bodies and other adaptations for their aquatic environment. Cetaceans should therefore be able to travel in larger groups with fewer constraints than do terrestrial species of comparable size (Connor 2000).

Fish schools can be regarded as resource patches and cetacean abundance should therefore be affected by the size and distribution of these schools. Indeed, both the quality and abundance of food resources have been found to impact dolphin abundance and movement patterns (Shane et al.1986; Williams et al.1993; Ostman 1994; Bearzi 1997). Several studies have found bottlenose dolphins to discriminate among ecologically different patches (natural or man-made; e.g., trawlers) in their environment, often altering group size (Shane 1990; Corkeron 1990; Weller 1991), home ranges (Scott et al.1990; Gubbins 2002a) or moving long distances (up to 670 km) from well-established home ranges (Wells et al.1990).

Large groups may form when individuals or coalitions merge to acquire food items requiring cooperation (e.g., rhesus macaques: Kaplan 1978, Datta 1983; chacma baboons: Cheney 1977). Alexander (1974) suggested that cooperative hunting may be an adaptation to group living. Benefits of group hunting potentially include an increase in the rate at which prey are encountered, an increase in prey capture success, an increase in the ability of groups to defend prey during group conflicts, and a decrease in prey handling time (Baird 2000). Bottlenose dolphins have been observed to form large feeding aggregations in deep, open waters worldwide, including Argentina (Wursig 1978; Wursig and Wursig 1977, 1979), South Africa (Saayman and Tayler 1973) and the Gulf of Mexico (Wells et al. 1980; Irvine et al. 1981). Bottlenose dolphins in an exposed shallow water habitat (adjacent to deeper waters) south of Abaco Island in the northeastern Bahamas specialized on large schools of prey and used cooperative feeding strategies, but such feeding methods were not observed in a nearby shallow water protected habitat east of Abaco Island (Parsons 2002). Cooperative feeding was observed for approximately 16% of all identified individuals in shallow waters in the northwestern Bahamas (near Grand Bahama Island) (Rossbach 1997). The common occurrence of cooperative feeding in large groups may increase the fitness of individuals in the group, but seems to vary dependent on habitat type.

Intraspecific variation in cetaceans includes differences in prey preference, feeding strategies and movement patterns. Bottlenose dolphins may alter their home ranges to accommodate different feeding strategies, thus influencing the degree of sociality and grouping among individuals (Richards 1996; Smolker et al. 1997; Rossbach and Herzing 1999). Killer whales in British Columbia are an excellent example of intraspecific divergence as two distinct ecotypes are currently recognized based primarily on feeding strategy: fish-eaters or “residents” and mammal-eaters or “transients” (Bigg et al. 1990; Baird and Dill 1995, 1996; Baird 2000). Although the target prey items vary, both ecotypes may benefit through cooperative food searching (Ford 1989; Hoelzel 1991, 1993; Baird and Dill 1996; Baird 2000).

Defense of territory

Individuals primarily establish and maintain territories to guard resources (Rubenstein 1986; Cheney 1987). A small amount of food distributed over an area would probably not justify territorial defense, but abundant food supplies make territoriality profitable if the cost of defense isn't too high and increased reproductive benefits are a possible result (Jarman 1974; Lott 1984). Rubenstein and Wrangham (1986) suggested that it was often more beneficial for a male to defend a resource (against other males) that attracted a higher number of females than to adopt alternative strategies. In contrast, defense of similar resources by females (against other females) was beneficial only if it would increase their net gain in productivity.

Territorial resource defense has been reported infrequently in cetaceans and is not a viable option for an open-ocean habitat due to mobile prey and large home ranges of individuals in a three-dimensional environment (Connor 2000). Both male and female bottlenose dolphins establish home ranges of variable sizes, but most have overlapping boundaries (Wells et al. 1987; Richards 1996; Rossbach and Herzing 1999; Quintana-Rizzo 1999; Gubbins 2002a). Individuals frequently associate amicably across these boundaries, indicating that these boundaries are not closed to non-community members (Wells et al. 1987; Wells 1991; Richards 1996; Quintana- Rizzo 1999; Rossbach and Herzing 1999; Gubbins 2002a, b). However, agonistic interactions between resident males and large, heavily scarred (probable males) individuals from adjacent communities have been observed at the Sarasota community boundary, which suggests that some males may actively defend the community boundary (Wells 1991). Wilson et al. (1997) suggested that area defense by individuals or social groupings could explain both the stratified movement patterns of dolphins in the Moray Firth and the lack of mixing between groups. As a result of such stratified movements, the Moray Firth appears to be a closed community with little interchange between adjacent populations (Wilson et al.1997; Parsons et al.2002).

Mate guarding is also rare for cetaceans, perhaps because most species appear to have a promiscuous mating system (Wells et al.1987; Slooten et al.1993). Sexual dimorphism is not a prominent feature of many delphinid species, including bottlenose dolphins, making it difficult to impossible for males to control a harem of females. This inability to control females is only magnified in bottlenose dolphins because females do not readily occur in groups of fixed composition (Wells et al.1987; Smolker et al.1992; Connor et al.1992; Richards 1996; Quintana-Rizzo and Wells 2001). Therefore, coalitions between males may form to increase mating success (Smuts 1985; Connor et al.1992; Felix 1997; Connor et al.2000b). Felix (1997) documented a cooperative alliance between two male bottlenose dolphins in Ecuador and on two occasions aggressive interactions were observed between this highly associated dyad and other individuals. Both encounters involved a female, although one involved a solitary individual and the other involved a dyad of unknown sex (suspected to be males due to large size/heavy scarring) (Felix 1997). Felix (1997) suggested that bottlenose dolphins in Ecuador occur in a polygynous mating system and certain males appear to control access to females.

Primates with small defendable home ranges, as well as those living in monogamous groups or groups with a single breeding female, commonly defend territories (Cheney 1987). Chapman (1990) reported seeing male spider monkeys near the edge of their community and suggested that close alliances among males may be important for territorial defense (also found in chimpanzees: Nishida and Hiraiwa-Hasegawa 1987). Cheney (1987) noted that dominance hierarchies are less common when primate groups are territorial and that interspecific associations (separate troops) of primates have been observed to defend a single joint territory in Peru (Terborgh 1983). MacDonald (1979) interpreted the establishment of territories by golden jackals as an adaptation to the distribution and abundance of food. Pack formation in coyotes appears to be an adaptation of group defense of both food and territory rather than for the previously suggested idea of aiding in the capture of large prey items (Bekoff and Wells 1981). Jarman and Southwell (1986) suggested that, for gray kangaroos, a lack of social organization was the result of a high abundance of resources and thus an absence of territories and competition for resources.

Mate guarding is common in equids and shifts in individual territories are observed as a direct result of female behavior (which is usually a result of resource availability) (Rubenstein 1986). Male primates often form coalitions to defend their territories (and thus harems) against challenging bachelors (Rubenstein 1986), whereas coalitions of male lions defend female prides rather than a specific territory and large coalitions may control several adjacent prides simultaneously (Bygott et al.1979; Pusey and Packer 1983; Packer 1986). Per capita reproductive success has been shown to be higher in larger coalitions (Bygott et al.1979; Packer 1986; Packer et al.1991).

Both territorial defense and mate guarding would be difficult for Virginia Beach dolphins due to their brief duration in the study area. Sightings of many individuals are limited and temporary ranges of individuals still need to be examined.

Social Processes

Effects of sex and reproductive status

Although the sex of most dolphins in the Virginia Beach study area was unknown, fluid associations between known females, as well as the occurrence of a large network of associated females (both directly and indirectly linked), supports the existence of some degree of sexual segregation. Several females had another female as one of their highest associates and both the total number of associates and the number of female associates varied based on reproductive status.

Breeding success, and thus ensured fitness, is a primary concern of mammals (Rubenstein 1986). Wrangham (1980) suggests that the principal motivation of males is access to females, whereas the principal concern of females is gaining access to food resources. Males therefore pattern their lifestyles after the patterns of females, who may in return shape their lives after the males (Wrangham 1980; Rubenstein 1986). Males must determine whether it would be more beneficial to adopt either a “roving” strategy in search of females in estrus or a strategy in which they guard either a group or individual to enhance mating access (Rubenstein 1986). This decision often depends on several factors such as the number females available, the length of the female’s estrous cycle or calving interval and the degree of sexual dimorphism exhibited by the species (Rubenstein 1986).

Often times, group members of one sex will disperse (either to live solitarily or join another group), but members of the other sex will remain with their natal group and form small, closely associated groups. Dispersal is usually described as a method of preventing inbreeding among kin and ensuring genetic diversity (Greenwood 1980). Rogers (1987) suggested that an individual may also disperse if it would increase mating opportunities, reduce food competition or increase the inclusive fitness of the individual's natal group by reducing food competition within the group. Fission-fusion properties are still observed in these small groups as members often break off to forage with and travel in smaller subgroups. Greenwood (1980) noted that male-biased dispersal is commonly observed in polygynous mating systems, probably to increase the likelihood of mating.

Association patterns for many mammalian species also vary based on the reproductive state of individuals (for both males and females) (e.g., orang-utans: Mitani et al. 1991; red-necked wallabies: Johnson 1989; equids: Rubenstein 1986; gray kangaroos: Jarman and Southwell 1986). Primate social patterns are variable and either sex may constitute the core social unit for any given species. Although overlapping home ranges are still observed, female spider monkeys usually disperse from their natal groups to either live solitarily or form small groups, whereas males form cohesive social units (although they often associate with subgroups of mixed age or sex during certain behaviors) (Fedigan and Baxter 1984). Common and pygmy chimpanzees are similar in that they form all age-sex groups (Badrian and Badrian 1984; Nishida and Hiraiwa-Hasegawa 1987), but differ because mixed-sex groups are predominant in pygmy chimpanzees (Nishida and Hiraiwa-Hasegawa 1987) and single-sex parties are predominant in common chimpanzees (Wrangham 1986). Both male and female gorillas may disperse from their natal group following weaning, but form stable, bisexual breeding groups. These groups usually consist of one or two silverback males, and group cohesion is often determined by the relationship of the dominant silverback and the adult females (Stewart and Harcourt 1987).

Adult females form the core social units in both baboons and lemurs (Smuts 1985; Dunbar 1986) and may remain in their natal groups throughout their lives. With the exception of gelada baboons (Dunbar 1986), male baboons disperse from natal groups at sexual maturity (Smuts 1985; Kappeler 1999a). Male gelada baboons may form stable all-male groups of mixed-age and/or alliances to aid in agonistic interactions with other males (Dunbar 1986) or to gain access to females (Smuts 1985). Male primates show a higher degree of variability in their number of associates compared to females (Smuts 1985) and females tend to associate more often with other females than with males (Gouzoules and Gouzoules 1987).

Numerous parallels in sex influenced social patterns are apparent between cetaceans and primates. At least some degree of sexual segregation has been documented in most odontocete species including, but not limited to: bottlenose dolphins (Wells et al. 1987; Smolker et al. 1992; Connor et al. 1992; Rossbach and Herzing 1999; Quintana-Rizzo and Wells 2001), spotted dolphins (Pryor and Shallenberger 1990; Herzing and Brunnick 1997), spinner dolphins (Norris and Dohl 1980a; Norris et al. 1994; Ostman 1994), Hector's dolphins (Slooten et al. 1993), pilot whales (Amos et al. 1993; Heimlich-Boran 1993; Kasuya and Marsh 1984), sperm whales (Best 1979; Whitehead and

Arnbom 1987; Whitehead and Waters 1990; Whitehead et al. 1991, Christal et al. 1998) and killer whales (Bigg et al. 1990; Heimlich-Boran 1986; Baird 2000). Both male and female bottlenose dolphins tend to disperse from their natal group near or at weaning to form juvenile groups (often mixed-sex) (Wells et al. 1987; Smolker et al. 1992). However, Richards (1996) found that both sexes of bottlenose dolphins in Shark Bay may not truly disperse, but rather may "dissociate" and continue to maintain overlapping home ranges with their natal groups throughout their lives. Maintenance of overlapping home ranges is referred to as natal philopatry (Appendix A) and is commonly observed in mammalian populations (e.g., black bears, elephants, wolves, primates). Females may return to their natal pod after reaching sexual maturity, but males usually maintain progressively smaller groups as they mature until they eventually form small, strongly bonded groups or live solitarily (Wells et al. 1987; Smolker et al. 1992).

Pod members of fish-eating killer whales appear to have the highest degree of natal philopatry of all cetaceans and both sexes remain with their natal pod (Bigg et al. 1990). Since neither sex disperses in fish-eaters, out-breeding is thought to occur during multi-pod associations (Heimlich-Boran 1986; Baird 2000). In contrast, dispersal by both sexes of mammal-eating killer whales has been observed, although some mother/calf bonds are retained into adulthood (Bigg et al. 1990; Baird and Whitehead 2000; Baird 2000). Other individuals have been observed within their natal range following dispersal, but were never observed associating with their natal group, demonstrating site rather than filial philopatry (Baird 2000). These individuals usually travel alone, but may briefly associate with pods with potentially reproductive females (Baird and Whitehead 2000). Associations among solitary males were not observed in British Columbia (Baird and

British Columbia (Baird and Whitehead 2000), but Hoelzel (1991) noted long-term adult male-male bonds in mammal-eaters in Argentina. Female mammal-eaters have never been documented to travel alone and it appears that following dispersal, a female may briefly associate with a number of different groups containing an adult male (Baird and Whitehead 2000). Baird and Whitehead (2000) suggested that such brief associations were tolerated due to increased mating opportunities for male group members, resulting in an increase in the inclusive fitness of the group.

Both long- (Amos et al.1991, 1993) and short-finned pilot whales (Heimlich-Boran 1993) also appear to remain in their natal groups throughout their lives. Natal philopatry for female pilot whales exists, but the longevity of bonds between males and their natal group is still in question because some individuals (predominantly males) have been suggested to disperse after reaching sexual maturity (Shane and McSweeney 1990; Kasuya and Marsh 1984; see Connor et al.2000a). Low levels of association among males and females from their own pod (along with high levels of association with females from neighboring pods) support the idea that mating may not occur within pods. This may imply that that the benefits of social cohesion in pilot whales are not reproductive (Heimlich-Boran 1993).

For sperm whales, immature males disperse from their natal groups and migrate to high latitudes where they remain until they reach sexual maturity, whereas females remain in low latitudes in groups of female relatives and their offspring (Best 1979; Whitehead and Weilgart 2000). Best (1979) suggested that two possible functions of close, permanent bonds among female sperm whales were the care of calves and cooperative feeding. Sexual segregation has also been reported for spinner dolphins off

Kona, Hawaii (Ostman 1994). A network of males was observed, with core groups of three to six individuals, but no such network was observed for females (Ostman 1994). Female spinner dolphins appeared to actively compete for positions near males (thereby increasing mating opportunities), suggesting that males may be the central members of the school around which the female social organization was organized (Ostman 1994).

Both the testis size and lack of substantial sexual dimorphism support a polygamous mating system for bottlenose dolphins (Harcourt et al.1981; Kenagy and Trombulak 1986; Scott et al.1990; Connor et al.2000b). Wells et al.(1987) stated that a polygamous mating system for bottlenose dolphins is supported by fluid associations between individuals, in conjunction with high sperm-producing capabilities of males. Smolker et al.(1992) and Connor et al.(1992) documented a female in Shark Bay mating with as many as 12 males during a single breeding season. Females in cetacean systems are joined by males more frequently during their reproductive cycles than at other times (Wells et al.1987; Smolker et al.1992; Slooten et al.1993; Herzing and Brunnick 1997) and females in both Sarasota and Shark Bay were more apt to associate with one another if they were in similar reproductive states (Wells et al.1987; Smolker et al.1992; Richards 1996). Owen et al.(2003) found that Sarasota males often formed associations with females before receptive periods and commented that it may be difficult to form such an association once a female is reproductive and male-male competition increases (as suggested by Goodall 1986 and Connor et al.1996).

The formation of male alliances or coalitions to gain access to mates is commonly observed in mammalian systems (Smuts 1985; Wells et al.1987; de Waal 1987; Bercovitch 1988; Noe 1992; Smolker et al.1992; Connor et al.1992; Felix 1997) and male coercion of females may have a profound effect on the observed pattern of sociality in a species (Wrangham 1979; Packer and Pusey 1983; Packer et al.1990). Such coalitions are often a result of dominance ranking as two lower ranked individuals may form a coalition to challenge a more highly ranked individual (de Waal 1987; Smolker et al.1992; Connor et al.1992; Connor et al.1999).

Many similarities are found between lions and bottlenose dolphins. Female lion prides, much like bottlenose dolphin bands (Wells et al.1987; Smolker et al.1992), are comprised of related individuals and members are often scattered throughout a pride's range. It is rare to find all pride members together (Packer 1986) and Schaller (1972) found that, on average, any two females of the same pride only spent 20-30% of their time together. Some females are highly philopatric, with pride members rearing similar-aged cubs together (Schaller 1972; Packer 1986), whereas others are solitary as a result of either being the sole survivor of a pride or from being evicted by incoming males before she had reached sexual maturity (Packer 1986). Lion prides usually consist of from two to 18 related females, their dependent offspring and a coalition of from one to seven adult males that have entered the pride from elsewhere (Schaller 1972; Packer and Pusey 1982; Packer 1986). Unrelated females have never been observed joining together to form a pride, but males frequently form coalitions with unrelated males (Packer 1986; Packer et al.1991). Large male coalitions gain higher reproductive success because they are more likely to gain control of a pride, acquire larger prides and control prides for longer periods (Bygott et al.1979; Packer 1986; Packer et al.1990).

Associations between males and mom/calf pairs are observed in both primate and cetacean populations (Smuts 1985; Wrangham 1986; Wells et al.1987; Ostman 1994;

Quintana-Rizzo 1999). Connor et al.(2000a) lists several examples of male-female friendships in Shark Bay, although males (adult and subadult) were observed with calves only six percent of the time. Male-female-calf triads were frequently observed in spinner dolphin schools and while in these triads, calves spent an average of 24 % (range: 1-71 %) with the adult male (Ostman 1994). In contrast, bottlenose dolphin calves in Sarasota were never seen associating with males away from their mother during their first year and few instances of male-female-calf associations were recorded (Wells et al.1987). Benefits for both females and infants from male-female-infant associations in baboons include: increased protection from harassment by other troop members, protection of infants from predators and other baboons, increased foraging efficiency and alternative care-giving (Smuts 1985). Benefits for males from male-female-infant associations include: increased chances of forming a consortship with this female in the future, use of females/infants as buffers during agonistic interactions of other males, increased opportunity for investment in his own likely offspring and possible integration into a new group (females decide if a male joins a group) (Smuts 1985).

Effects of age

Age is another major factor influencing group formation in mammals. Similar-sized individuals were frequently observed associating in the Virginia Beach study area, but exact age confirmation was not possible. Dolphins in Virginia Beach were classified as adult, YOY or neonate based on size and several physical and behavioral characteristics (Appendix A). Barco et al.(1999a, b) suggest that the Virginia Beach study area serves as a nursery based on sighting patterns for several females. Select individuals

individuals had a mean number of four YOY per group and group size was larger for groups with YOY compared to groups without YOY, both indicating that aggregations of females and YOY were common for Virginia Beach dolphins.

Cetaceans of the same age class frequently associate, although associations among members of all age classes, for both sexes, still readily occur (e.g., killer whales: Heimlich-Boran 1986; Bigg et al. 1990; bottlenose dolphins: Wells et al. 1987; Smolker et al. 1992; Richards 1996; Rossbach and Herzing 1999; spotted dolphins: Herzing and Brunnick 1997; Hector's dolphins: Slooten et al. 1993; and sperm whales: Whitehead and Arnbom 1987; Whitehead and Weilgart 2000). Parallels were found between Shark Bay and Sarasota bottlenose dolphin juveniles. Females associated with their mother, her associates (and potentially their offspring) and juvenile males, but juvenile males tended to remain in juvenile parties (Wells et al. 1987; Smolker et al. 1992; Richards 1996). Wells et al. (1987) found a tendency for group size to decrease with increasing age until the individual bottlenose dolphins approached sexual maturity, a trait also found in sperm whales (Best 1979; Whitehead and Weilgart 2000). Association patterns of male bottlenose dolphins appear to be strongly dependent on the ages of the individuals, whereas female bands are often comprised of several generations of individuals (Wells et al. 1987; Duffield and Wells 1991, 2002). Both Quintana-Rizzo and Wells (2001) and Felix (1997) observed groups of mixed age in the Cedar Keys, FL and Ecuador, respectively. Same-age associations for juveniles are most common for bottlenose dolphins in Sarasota, Florida (Wells et al. 1987) and spinner dolphins in Kona, Hawaii (Ostman 1994)

Effects of kinship

Kinship is another major determinant of association patterns and group formation in mammals. Individuals may choose one or more of the following patterns: remain in their natal groups throughout their lives (natal philopatry) (e.g., female gelada baboons: Dunbar 1986, Smuts 1985; dwarf mongoose: Rood 1986; fish eating killer whales: Bigg et al.1990; pilot whales: Amos et al.1991,1993; Heimlich- Boran 1993), disperse from their natal group, but establish a territory adjacent to or overlapping with their natal home range (e.g., bears: Rogers 1987; wolves: Mech 1987; bottlenose dolphins: Wells et al.1987; Smolker et al.1992; Richards 1996; mammal-eating killer whales: Baird 2000; rhesus monkeys: Chepko-Sade and Sade 1979), or permanently disperse from their natal groups (e.g., male sperm whales: Best 1979; male lions: Packer 1986; dwarf mongoose: Rood 1986; wolves: Mech 1987; gorillas: Stewart and Harcourt 1987; male spotted hyenas: Holecamp et al.1997). Wrangham and Rubenstein (1986) note that cooperation may be more extensive among individuals of the same sex that remain together as kin.

For bottlenose dolphins, associations based on kinship have been documented in female bands in Sarasota Bay, Florida (Duffield and Wells 1991). Both genetic analyses and observational data indicate that members of male dyads in Sarasota are often not closely related (Duffield and Wells 2002; Owen *et al.*2003), whereas Kruetzen et al.(2003) found many male bottlenose dolphin associates in Shark Bay to be related. Males occurring in stable 1st order alliances and the derived 2nd order alliances were often closely related, but members of the superalliance were no more closely related than expected by chance (Kruetzen et al.2003). The genetic makeup and thus, relatedness of identified individuals, was not available for Virginia Beach dolphins.

Both male and female fish-eating killer whales in British Columbia/Washington State exhibit natal philopatry (Bigg et al.1990). Social organization of killer whales is based on a matriarchal hierarchy and pods may include from one to 11 matrilines (Bigg et al.1990). Male-male associations observed in fish-eating pods appear to be based on kinship (Heimlich-Boran 1986). Mammal-eating killer whales may also exist in pods based on kinship, but these pods generally consist of a single matriline (Baird and Whitehead 2000). Genetic testing has determined that fish-eating killer whales mate outside of their natal pod to prevent inbreeding (Bigg et al.1990; Amos et al.1993) and the same has been suggested for pilot whales (Amos et al.1991, 1993; Heimlich-Boran 1993; see Connor 2000). Genetic analyses demonstrated that male pod members of long-finned pilot whales were closely related (Amos et al.1991, 1993) and Heimlich-Boran (1993) documented strong male-male associations.

Sperm whale females also live in matrilineal social systems in which females and their offspring form stable groups (Best 1979; Whitehead and Weilgart 2000). These nursery groups or "family units" are thought to be the fundamental elements of sperm whale society (Best 1979; Rice 1989; Whitehead et al.1991; Whitehead and Weilgart 2000). Genetic studies have determined that these units may contain more than a single matriline (Christal et al.1998) and paternal relatedness between grouped matrilines has been suggested (Whitehead and Weilgart 2000).

Gelada baboons associations are heavily influenced by kinship. Females separate into small clusters and relationships within the unit depend on their degree of relatedness

(Dunbar 1986). These female coalitions may aid in maintaining high dominance ranks and it is likely that the tendency for females to group together in matrilines is a result of the reproductive costs suffered by the formation of large groups (Dunbar 1980, 1986). Similar strategies are observed for the spotted hyena, where associations among females are influenced by the both degree of relatedness and rank of other individuals (Holecamp et al.1997). These associations most likely result in an increased fitness of individuals through cooperation in obtaining and defending food resources and maintaining positions in the social hierarchy (Holecamp et al.1997).

In many species of primates, infants and juveniles regularly associate with relatives other than their mothers (e.g., macaques: Gouzoules 1980; yellow baboons: Altmann 1980; chimpanzees: Goodall 1968, 1986; gorillas: Fossey 1979; tamarins and marmosets: Goldizen 1987). Both immature and senescent females may assist mothers with the care of their offspring. This behavior, often referred to as babysitting, occurs in a variety of mammalian societies (e.g., lions: Packer 1986, Packer et al.1990; mongoose: Rood 1986, 1987; killer whales: Heimlich-Boran 1986; bottlenose dolphins: Wells et al.1987, Shane 1990; primates: Goldizen 1987; spinner dolphins: Ostman 1994; sperm whales: Whitehead 1986; Whitehead and Weilgart 2000). Babysitters benefit both themselves and their group in two ways: increased learning/experience in the rearing of young and increased fitness through the survival of the offspring (if there is genetic relatedness) (Smuts 1985). Mothers benefit from the increased care of their offspring and, as a result, there is a reduction in the likelihood of predation or potential infanticide of the offspring (Packer 1986;Wells et al.1987; Goldizen 1987; Packer et al.1990; Whitehead and Weilgart 2000). Calf survivorship appears to be related to group size and stability as shown by a higher probability of success in rearing calves by band members compared to non-band members (Wells 1991; Richards 1996).

Table 11. A comparison of life history patterns among mammalian systems.

Species	Study area	Dispersal	Sexual Dimorphism	Mating System	Territorality	Reprod. Status *	Other
Chimpanzee	various	female	Y	promiscuous	Y	Y; M/F	babysitting
Baboons	various	male	Y	promiscuous; harem		Y; M/F, F/F	babysitting
Gorilla	various	both	Y	harem	N	Y; M/F	babysitting
Orang-utan	various	both	Y	promiscuous	Y	Y; M/F	ND
Mongoose	various	both	Y; slight	monogamous;promiscuous	Y	Y; M/F, F/F	babysitting in some sp.
Horses/zebras	various	both	N; slight in some	harem	Y	Y; M/F; F/F	ND
Wallaby/ kangaroo	various	both	Y	promiscous	N	Y; M/F, F/F	babysitting
Lions	Serengeti Ntl. Park	male	Y	harem	Y	Y; M/F, F/F	babysitting
Bottlenose dolphins	various	both;natal philopatry	N	promiscuous	N	Y; M/F, F/F	babysitting
Killer whales- fish-eaters	British Columbia, Washington state	neither	Y	promiscuous	N	Y; M/F, F/F	babysitting
Killer whales- mammal-eaters	British Columbia, Argentina	both	Y	promiscuous	N	Y; M/F, F/F	babysitting
Spotted dolphins	Bahamas	male	Y; slight	promiscuous	N	Y; M/F, F/F	babysitting
Pilot whales	various	males?	Y	promiscuous	N	Y; M/F, F/F	babysitting
Sperm whales	Galapagos; various	male	Y	promiscuous	N	Y; M/F, F/F	babysitting

* associations occur based on reproductive status

Table 11 (cont.): A comparison of life history patterns among mammalian systems.

Species	Reference
Chimpanzee	Goodall 1968, 1986; Wrangam 1986; Chapman *et al.* 1996;
Baboons	Smuts 1985; Dunbar 1986
Gorilla	Stewart and Harcourt 1987; Bean 1999
Orang-utan	Mitani *et al*. 1981
Mongoose	Rood 1986,1987
Horses/zebras	Rubenstein 1986
Wallaby/ kangaroo	Johnson 1980; Jarman and Southwell 1986
Lions	Schaller 1972; Packer 1986; Packer *et al.* 1990; Packer *et al*. 1991
Bottlenose dolphins	Wursig 1978; Wells *et al*. 1987; Ballance 1990; Weller 1991; Smolker et al. 1992; Quintana-Rizzo and Wells 2001
Killer whales- fish-eaters	Bigg *et a*l. 1987; Baird 2000
Killer whales- mammal-eaters	Hoelzel 1991; Baird and Whitehead 2000; Baird 2000
Spotted dolphins	Pryor and Shallenberger 1991; Herzing and Brunnick 1997
Pilot whales	Kasuya and Marsh 1981; Amos 1991; Amos et al. 1993, Heimlich-Boran 1993
Sperm whales	Best 1979; Whitehead 1986; Christal et al. 1998; Whitehead and Weilgart 2000

CONCLUSIONS

Group formation in mammals may be influenced by a myriad of factors, both social and ecological. Among social mammals, similar patterns of group formation are observed. For example, there is a general trend for an increase in group size in more open, exposed habitats, ranging from primates and ungulates to cetaceans, and a decrease in group size in less exposed habitats (e.g., heavily forested regions for primates; small protected bays for dolphins). These patterns are consistent among different types of mammals, probably in response to predation. Other ecological factors that may influence group formation, such as resource acquisition, may be directly correlated to social factors such as reproductive state and mate availability.

The primary influences on cetaceans appear to be predator avoidance, prey availability and reproduction, but factors such as kinship are integral for some species. For bottlenose dolphins, some patterns are consistent regardless of habitat type, such as associations based on sex and kinship, whereas others, such as group size and habitat use, vary among habitat types. Group size increases in more exposed habitats such as open oceans or bays, and dolphins usually exhibit low site fidelity as a result of increased home range and movement. In contrast, group size often decreases in more protected habitats where dolphins usually exhibit high site fidelity with decreased home ranges and movement. Same-sex associations are observed in most study areas, although the degree of small-scale grouping varies. Both large- and small-scale movements are regularly associated with fluctuations in the distribution and abundance of prey items.

Virginia Beach, Virginia is an intriguing study site. Dolphins are considered to be members of the North Atlantic Coastal Migratory Bottlenose Dolphin Stock. It was initially proposed that these coastal dolphins belonged to a single stock, but variability in sighting, stranding and movement patterns suggest a different picture. Data from multiple large-scale studies, including both aerial and boat-based surveys, combined with more localized photo-identification and tagging studies, resulted in the recognition of seven management units. However, long-term, small-scale studies, such as this one, are extremely important because they provide insight into daily movements, activities and patterns of aggregation among individual dolphins from the larger study population.

My analyses of sightings of Virginia Beach dolphins demonstrate the consistency of social patterns in bottlenose dolphins, regardless of habitat type, residency pattern or region. Group size in Virginia Beach was large, and was most similar to those in exposed habitats such as San Diego and Argentina. Site-fidelity patterns were consistent with other open habitat populations as individuals exhibited variable degrees of site fidelity, with most individuals having low site fidelity. Several individuals had extensive sighting histories (up to 31 sightings in all six study years), but the majority of all identified animals were observed either one time or multiple times in a single year. Associations among Virginia Beach bottlenose dolphins were mostly weak with few strong associations and both sex and reproductive status influenced group formation. Females were more apt to associate with other females when in similar reproductive states, although associations among all females were consistently fluid. Groups containing YOY were larger than groups without YOY and 100% of all select individuals associated with a mean number of at least one YOY. Although small in number, several dyads, including one of the same-sex, were identified in which associations were significantly non-random.

My study was one of the first to concentrate solely on migratory dolphins. Unfortunately, such spatial and temporal transience only provides researchers with a “snapshot” of the lives of dolphins and cooperative analyses of datasets from multiple study sites are needed to provide a more complete picture of the annual cycle of these dolphins. Still, it is remarkable that strong patterns were apparent for individuals within the Virginia Beach population and that these patterns were consistent with those observed for bottlenose dolphins and social mammals throughout the world.

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Appendix A. Glossary

Ab libitum- events recorded as they occurred

Calf- size approximately 2/3 of an adult; still associates closely with mother (adult) as well as other individuals within the group

Community (Begon *et al.* 1996)- an assemblage of species populations that occur together in time and space

Community (Wells *et al.* 1987 for bottlenose dolphins)- all groups of dolphins (and individuals who clearly do not belong to a group) that shared a large portion of their range and interacted with each other to a greater extent than with members of similar units in adjacent waters

Definite female- sighted at least three times in close proximity of a neonate or YOY

Encounter- research-oriented observations of an individual or group of dolphins

Group (Shane 1990)- all animals within 100 meters, moving in the same direction, but not necessarily engaged in the same activity

Sighting- photographic documentation of an individual dolphin

Migration- a life history adaptation caused by climatic changes which may indirectly affect a population through reduced resource availability such as food or shelter from extreme conditions or predators; the passing (usually periodically) from one region or climate to another for feeding or breeding purposes

Natal philopatry- the tendency for an individual to return to/stay near their birth group

Neonate (subset of YOY)- size approximately one third of the body length of an adult; dark coloration, extreme buoyancy; fetal folds obvious; little to no separation from mother

Non-resident- variable for study sites; ** often refers to transients; usually sighted once in the study area

Population (Began *et al.* 1996)-- a group of individuals of one species in an area (size arbitrarily changes based on the study)

Probable female- sighted at least two times in close proximity of a neonate or YOY

Resident- variable for study sites; usually sighted in the study area during each season of the year

Sciaenid species: members of Family Sciaenidae (drum); examples and preferred prey items for *Tursiops* include weakfish (*Cynoscion sp.*), Atlantic croaker (*Micropogon undulates*), spot (*Leiostomus xanthurus*) and silver perch (*Bairdiella chrysura*); found in Barco *et al.* (1999a)

Select individual- has at least 5 sightings in three of the six study years

Site philopatry- the tendency for an individual to return to/stay near a specific place

****Transient-** variable for study sites; usually only sighted in the study area once or during one or two seasons of the year

Young of year (YOY)- size approximately one half the body size of an adult; fetal folds light to absent; interanimal distance between mother may increase but still closely associated; light color

Appendix B. Summary table for all select individuals (n = 78).

ID #	1st year sighted	Total # years sighted	94	95	96	97	98	99	Total sightings	Total assoc.	% repeat	Mean HWI	Gender	Mean group	Mean YOY
1	1993	5	8	3	0	1	1	1	14	58	3.4	0.11	U	30	3
5	1994	4	2	0	2	1	0	1	6	106	9.4	0.23	U	40	3
6	1992	4	2	0	1	4	5	0	12	104	12.5	0.13	F	30	4
8	1994	4	5	0	4	4	0	2	15	80	11.3	0.11	U	20	3
10	1993	3	2	0	0	3	2	0	7	98	8.2	0.22	F	65	3
14	1993	6	2	1	1	9	11	7	31	162	28.4	0.08	F	29	5
16	1989	6	5	1	2	6	6	5	25	243	21.4	0.09	U	40	4
17	1994	5	7	0	4	2	4	3	20	162	17.9	0.1	F	35	4
18	1993	4	7	1	3	1	0	0	12	63	11.1	0.13	F	30	4
19	1994	5	4	0	9	3	5	3	24	130	21.5	0.09	F	29	4
21	1994	5	3	0	1	2	1	3	10	55	14.5	0.15	U	29	4
24	1994	3	2	0	1	2	0	0	5	35	5.7	0.27	U	14	1
25	1994	3	4	0	0	1	4	0	9	70	21.4	0.19	U	27	2
27	1994	4	1	0	4	3	1	0	9	44	4.5	0.15	PF	20	1
28	1992	3	2	0	0	2	5	0	9	113	17.7	0.19	U	42	3
29	1992	6	2	1	7	9	6	6	31	206	24.8	0.08	U	31	3
30	1993	5	2	1	1	1	1	0	6	57	7	0.22	U	33	3
32	1996	3	0	0	3	2	2	0	7	89	7.9	0.19	U	40	3
34	1992	6	3	3	2	9	12	2	31	164	24.4	0.08	U	30	4
36	1993	6	3	1	7	7	4	6	28	214	22.9	0.08	U	30	4
40	1994	3	1	0	3	0	1	0	5	76	1.3	0.2	U	33	3
42	1994	5	2	0	1	2	5	4	14	104	16.3	0.13	F	29	4
44	1994	4	2	0	1	0	2	4	9	94	5.3	0.17	U	31	3
45	1994	5	3	0	2	1	1	1	8	71	11.3	0.18	U	22	4
48	1994	4	2	0	2	2	7	0	13	134	17.2	0.13	U	33	4
50	1993	3	3	1	0	0	0	3	7	93	2.2	0.21	U	40	6
56	1990	4	2	0	1	3	4	4	14	158	19	0.11	U	37	4

Appendix B (cont.): Summary table for all select individuals (n = 78).

ID #	1st year sighted	Total # years sighted	94	95	96	97	98	99	Total sightings	Total assoc.	% repeat	Mean HWI	Gender	Mean group	Mean YOY
57	1994	4	3	1	1	1	0	0	6	35	5.7	0.2	U	23	2
58	1990	3	6	0	0	1	5	0	12	99	20.2	0.16	U	29	2
59	1994	3	7	2	4	0	0	0	13	62	17.7	0.13	F	20	2
62	1994	5	2	0	2	1	1	2	8	51	5.9	0.16	U	37	2
63	1994	3	2	0	0	0	3	1	6	106	17	0.24	U	29	2
71	1994	4	2	0	1	0	1	2	6	75	6.6	0.21	U	33	3
73	1989	3	0	2	4	0	4	0	10	71	14.1	0.15	U	27	2
79	1993	3	0	1	2	0	2	0	5	61	6.6	0.25	U	32	2
108	1996	3	0	0	2	2	5	0	9	87	8	0.16	U	44	5
132	1996	3	0	0	3	1	0	1	5	64	3.1	0.23	PF	20	3
154	1996	3	0	0	2	0	5	6	13	164	21.3	0.15	U	39	5
159	1994	4	1	0	0	1	2	1	5	55	10.9	0.23	U	38	5
166	1996	3	0	0	5	0	1	2	8	74	9.5	0.18	U	29	4
192	1989	5	1	0	2	2	2	5	12	113	25.7	0.15	F	33	5
204	1994	5	1	0	1	2	2	3	9	138	18.2	0.19	U	52	6
211	1994	4	1	0	1	2	1	0	5	57	12.3	0.26	U	37	3
223	1994	5	1	0	1	1	4	2	9	120	7.5	0.15	U	34	3
226	1994	3	1	1	0	3	0	0	5	50	10	0.25	U	34	2
242	1992	5	1	1	3	0	0	0	5	40	15	0.27	U	36	3
244	1989	5	1	1	1	1	1	0	5	55	1.8	0.28	U	97	4
254	1994	4	2	0	1	1	1	0	5	18	0	0.27	F	20	2
257	1996	3	0	0	5	4	1	0	10	58	19	0.16	U	15	2
258	1994	5	2	0	4	2	5	1	14	117	17.9	0.12	U	50	5
266	1996	4	0	0	1	1	2	1	5	57	12.3	0.24	U	48	4
272	1994	5	1	0	1	2	4	2	10	154	11	0.16	U	36	5
290	1995	3	0	1	0	5	1	0	7	122	12.3	0.23	U	62	4
308	1996	4	0	0	3	4	5	1	13	121	14.9	0.13	F	29	3

Appendix B (cont.): Summary table for all select individuals (n = 78).

ID #	1st year sighted	Total # years sighted	94	95	96	97	98	99	Total sightings	Total assoc.	% repeat	Mean HWI	Gender	Mean group	Mean YOY
316	1996	4	0	0	1	1	3	2	7	77	7.8	0.19	U	38	4
401	1995	5	0	1	2	5	5	2	15	139	18	0.12	F	32	5
410	1996	3	0	0	1	0	1	4	6	63	11.1	0.2	F	38	6
418	1995	3	0	1	0	2	2	0	5	48	4.2	0.25	U	45	3
442	1996	3	0	0	2	4	0	2	8	58	24.1	0.18	PF	30	5
470	1995	3	0	1	3	1	1	0	6	45	4.4	0.21	U	30	2
504	1996	3	0	0	2	2	0	1	5	63	1.6	0.23	F	37	4
506	1996	4	0	0	5	5	1	1	12	97	11.3	0.14	F	34	3
507	1996	3	0	0	3	5	0	3	11	87	13.8	0.15	F	29	5
510	1996	3	0	0	3	4	3	0	10	113	22.1	0.17	U	37	5
612	1997	3	0	0	0	1	3	5	9	106	19.8	0.18	U	44	5
615	1997	3	0	0	0	1	1	3	5	57	8.8	0.21	U	39	6
622	1997	3	0	0	0	3	4	7	14	196	18.9	0.13	U	38	4
667	1997	3	0	0	0	5	3	4	12	99	20.2	0.14	U	28	4
676	1996	3	0	0	1	4	0	7	12	122	12.4	0.14	U	35	5
678	1997	3	0	0	0	1	3	9	13	119	22.7	0.14	F	36	6
686	1997	3	0	0	0	1	3	1	5	57	5.3	0.21	U	32	4
691	1997	3	0	0	0	1	3	1	5	79	13.9	0.27	U	39	4
733	1997	3	0	0	0	3	1	8	12	142	12	0.14	U	33	4
735	1997	3	0	0	0	1	3	5	9	154	11	0.17	F	41	5
740	1997	3	0	0	0	1	1	3	5	92	7.6	0.25	U	49	5
746	1997	3	0	0	0	2	2	5	9	127	15.7	0.16	U	51	6
791	1997	3	0	0	0	1	1	5	7	49	14.3	0.2	PF	42	5
1161	1994	3	1	0	0	0	3	2	6	57	7	0.2	U	34	4

Appendix C. Matrix of calculated Half Weight Index (HWI) values between all select individuals (n = 78).

ID	1	5	6	8	10	14	16	17	18	19	21	24	25	27	28	29	30	32	34	36	40	42	44	45	48	50
1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	0	0.11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	0	0.10	0.07	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10	0	0.31	0.11	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
14	0	0	0.14	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
16	0.05	0.13	0.11	0	0.19	0.04	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
17	0	0	0.06	0	0.07	0.04	0.13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
18	0.08	0.11	0	0	0	0.05	0	0.06	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
19	0	0	0.17	0.05	0	0.25	0.08	0.09	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
21	0	0	0	0	0	0.10	0	0	0	0.12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
24	0	0	0	0.10	0	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
25	0	0.13	0	0	0.13	0	0	0.07	0	0	0.11	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
27	0	0	0.10	0.08	0	0	0.12	0	0	0.06	0	0	0.11	-	-	-	-	-	-	-	-	-	-	-	-	-
28	0	0	0	0	0.13	0.10	0.06	0	0	0	0.11	0	0.22	0	-	-	-	-	-	-	-	-	-	-	-	-
29	0.04	0.05	0	0.09	0	0.23	0.04	0.04	0.14	0.11	0.10	0	0	0	0.05	-	-	-	-	-	-	-	-	-	-	-
30	0	0	0	0.10	0.15	0	0.13	0	0	0	0	0	0.13	0.13	0.27	0	-	-	-	-	-	-	-	-	-	-
32	0	0.17	0.22	0	0	0	0.26	0.15	0.11	0.07	0	0	0	0	0	0.05	0	-	-	-	-	-	-	-	-	-
34	0.09	0	0.09	0.43	0	0.35	0.07	0.08	0.05	0.22	0.05	0	0.05	0.15	0.05	0.19	0	0	-	-	-	-	-	-	-	-
36	0.05	0	0.05	0.14	0	0.10	0.08	0.08	0.10	0.08	0.05	0	0	0	0	0.14	0.06	0.06	0.10	-	-	-	-	-	-	-
40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.13	0.05	0	0	0	0.06	-	-	-	-	-	-
42	0	0	0	0.07	0	0.18	0.05	0.12	0	0.11	0	0	0	0	0	0.04	0.10	0	0.09	0.05	0	-	-	-	-	-
44	0	0.40	0	0.08	0	0	0	0.07	0	0	0	0	0.11	0	0	0.05	0	0	0.05	0	0	0	-	-	-	-
45	0	0.14	0	0	0	0	0	0.07	0.10	0.06	0	0	0	0	0	0.05	0	0.13	0.23	0.06	0.14	0.18	0	-	-	-
48	0.07	0.11	0.08	0.07	0	0.14	0.05	0.12	0	0.11	0.09	0	0	0	0.09	0.14	0	0	0.23	0.05	0.11	0.07	0.09	0	-	-
50	0	0.15	0	0	0	0	0.06	0.07	0	0	0	0	0.13	0	0	0	0	0	0	0	0	0.10	0.13	0	0	-
56	0	0	0.07	0	0	0	0.14	0.05	0.07	0.05	0.07	0	0.22	0	0.30	0	0.08	0.16	0.04	0.04	0.29	0	0	0	0.06	0.08
57	0	0	0	0	0	0	0.06	0	0	0	0	0	0	0	0	0	0	0	0	0	0.08	0	0.13	0	0	0
58	0	0.11	0	0	0.11	0	0.16	0.06	0	0	0.09	0	0.57	0	0.29	0	0.11	0	0	0	0.11	0	0.10	0	0.08	0
59	0	0.21	0	0.21	0	0	0.05	0.18	0.24	0	0	0	0	0	0	0.09	0	0.10	0	0.05	0.11	0	0.09	0.19	0	0
62	0	0	0.10	0	0	0.10	0	0	0	0.06	0	0	0	0	0	0	0	0	0.10	0.06	0	0.09	0	0	0.10	0
63	0.10	0	0	0	0.15	0	0.06	0.07	0	0	0	0	0.40	0	0.27	0	0.17	0	0	0.06	0.17	0	0	0	0.11	0
71	0	0	0	0	0	0	0.06	0	0	0	0	0	0	0	0.13	0.05	0	0	0	0	0.17	0	0	0	0.11	0
73	0	0.13	0	0.08	0.12	0.10	0	0.13	0	0	0	0.13	0.10	0	0	0.05	0	0	0.10	0.05	0	0	0.21	0	0.17	0
79	0.11	0	0	0	0	0	0	0	0	0	0	0	0	0	0.14	0	0	0.17	0	0	0.18	0.12	0	0	0.11	0
108	0	0	0.19	0.08	0	0.05	0.06	0	0	0	0.11	0.14	0.22	0	0.11	0	0	0.13	0.10	0	0	0	0.11	0	0	0
132	0	.18	0	0	0	0	0	0	.12	0	0	0	0	0	0	0.06	0	0.17	0	0.06	0	0	0	0.15	0.11	0
154	0.15	0.11	0	0.07	0	0.18	0.05	0	0.08	0.16	0	0	0	0	0	0.23	0	0.10	0.09	0.20	0	0.07	0.09	0.10	0.15	0
159	0	0	0	0	0	0	0.07	0.08	0	0.07	0	0	0	0	0	0.11	0	0	0.06	0.06	0	0.21	0	0.31	0.11	0
166	0	0	0	0.09	0	0.10	0.06	0.07	0	0.06	0	0	0	0.12	0.12	0.10	0	0.13	0.05	0.06	0	0	0	0	0	0
192	0	0.11	0.08	0.15	0	0.14	0.11	0	0.08	0.11	0	0	0	0.10	0	0.14	0	0.11	0.09	0.10	0.11	0	0	0.20	0.08	0
204	0	0.27	0.10	0	0.25	0	0.12	0.07	0	0	0	0	0.11	0	0.22	0	0.13	0	0	0	0.13	0	0	0	0.09	0.13
211	0	0	0.12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.06	0.06	0	0	0.14	0	0	0
223	0	0.25	0	0.08	0	0	0.06	0	0.09	0	0	0	0	0	0.11	0.05	0	0.12	0.05	0	0	0.08	0.32	0.11	0.09	0
226	0	0	0	0	0	0	0	0	0	0	0	0	0.14	0.14	0.14	0.06	0	0	0.06	0	0	0	0	0	0.11	0
242	0	0	0	0	0	0	0.07	0.16	0	0.07	0	0	0	0.14	0	0	0	0.17	0	0.12	0.18	0	0	0	0	0
244	0.11	0	0	0	0.17	0	0.07	0	0	0	0	0	0	0	0	0	0.18	0	0	0	0	0.11	0	0	0	0
254	0	0	0	0	0	0	0	0	0	0.07	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
257	0	0	0.09	0.08	0	0.05	0	0	0	0.12	0	0	0	0	0	0.10	0	0	0	0.16	0.13	0	0	0	0.17	0
258	0	0.20	0.15	0.14	0.10	0.04	0.10	0.06	0	0.05	0	0.11	0	0	0	0.04	0	0.10	0.09	0.14	0.10	0	0.17	0.09	0.07	0
266	0	0.18	0.12	0	0.17	0	0.13	0	0	0.07	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
272	0.08	0.13	0.09	0.08	0	0.05	0.06	0.07	0.09	0.12	0	0	0	0	0.11	0.05	0	0.12	0.05	0.11	0.13	0.08	0	0.11	0.26	0
290	0	0.15	0.11	0	0.29	0	0.19	0	0	0	0	0	0.13	0.13	0.25	0.05	0.15	0	0.11	0	0.15	0	0	0	0.10	0
308	0	0	0.08	0	0	0	0.21	0.18	0	0.05	0.09	0	0	0	0	0.05	0	0.30	0	0.15	0.21	0.07	0	0.10	0	0
316	0	0	0	0	0	0	0.06	0	0	0	0	0	0	0	0.13	0	0	0	0.05	0	0.15	0.10	0	0	0.10	0
401	0	0	0.07	0	0	0.17	0.15	0.11	0	0.15	0	0	0.08	0.08	0.08	0.09	0	0.09	0.13	0.14	0	0	0	0	0.21	0.09
410	0	0	0	0	0	0	0.06	0.15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
418	0	0.18	0.12	0	0.17	0	0.07	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
442	0	0.14	0.20	0.09	0	0.10	0	0.07	0.10	0.25	0.11	0	0	0	0	0.05	0	0	0.10	0	0	0.09	0.12	0.13	0	0
470	0	0.17	0.11	0	0.31	0	0.06	0.08	0	0.07	0	0	0.13	0	0	0	0	0	0	0	0	0	0	0	0	0
504	0.11	0	0	0.20	0	0	0.07	0	0	0	0	0.20	0	0	0	0.06	0	0	0	0.06	0	0	0	0	0	0
506	0.08	0	0	0	0	0	0.11	0.19	0	0.06	0	0	0.10	0.10	0	0.05	0	0.21	0.05	0.20	0.11	0	0	0	0	0
507	0	0	0.09	0	0	0.24	0	0	0	0	0	0	0	0	0	0.05	0	0	0.14	0.05	0	0.08	0	0	0.08	0
510	0	0.13	0.18	0	0	0.15	0.06	0.07	0.27	0.12	0	0	0	0	0	0.15	0	0.12	0.20	0.21	0	0.08	0	0.22	0.26	0
612	0	0	0	0	0	0.05	0.18	0.14	0	0.06	0	0	0	0.11	0	0.10	0	0	0.05	0	0	0.09	0.11	0	0	0.13
615	0	0	0	0	0	0.06	0.07	0.08	0	0.07	0	0	0	0	0	0.11	0	0	0.06	0.06	0	0	0	0	0.11	0
622	0.07	0.10	0.15	0	0.10	0.04	0.21	0.06	0	0	0	0	0	0	0.09	0.09	0	0.10	0	0.10	0.10	0	0.17	0.09	0.15	0
667	0	0	0.08	0.15	0	0.19	0.05	0	0.08	0.06	0	0	0	0	0	0.19	0	0	0.19	0.20	0	0.08	0.10	0	0.08	0
676	0	0	0	0.07	0	0.19	0.05	0.06	0	0.11	0.18	0	0.10	0.10	0	0.09	0	0	0.09	0.15	0.11	0	0	0.10	0	0.11
678	0	0	0	0.07	0	0.05	0.11	0.12	0	0.11	0.17	0	0	0.09	0	0.09	0	0	0.09	0.05	0	0.07	0	0	0.15	0.10
686	0	0	0	0	0	0	0.07	0	0	0	0	0	0.14	0	0.14	0.06	0.18	0	0.11	0.12	0	0	0	0	0.11	0
691	0	0	0	0.10	0	0	0.07	0	0	0	0	0	0.29	0	0.29	0	0.18	0	0	0	0.18	0	0	0	0.11	0
733	0.08	0	0.08	0	0	0.09	0.05	0	0	0.06	0	0	0	0	0	0.05	0	0	0	0.40	0	0.08	0	0	0	0
735	0.09	0	0.10	0	0	0.05	0.18	0.07	0	0	0	0	0	0	0.11	0.05	0	0.13	0	0.05	0.13	0.09	0	0	0.09	0
740	0.11	0	0	0	0	0	0.13	0.16	0	0	0	0	0	0	0.14	0	0	0	0	0	0.18	0	0.14	0	0.22	0.17
746	0.08	0.13	0.09	0	0.12	0.10	0.11	0.07	0.09	0.06	0.10	0	0	0	0	0.10	0	0	0.05	0.05	0	0.08	0	0	0	0
791	0	0	0.11	0	0	0.11	0	0	0	0.06	0	0	0	0	0	0.11	0	0	0	0	0	0.19	0	0	0	0
1161	0	0	0	0	0	0.16	0	0	0	0.07	0	0	0	0	0.13	0.27	0	0	0	0	0	0.10	0	0	0	0

Appendix C (cont.). Matrix of calculated Half Weight Index (HWI) values between all select individuals (n = 78).

56	57	58	59	62	63	71	73	79	108	132	154	159	166	192	204	211	223	226	242	244	254	257	258	266	272	290
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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0.08	0.15	0.11	0.11	0	0.17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0	0	0.09	0.09	0	0.13	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.09	0	0.12	0	0	0.18	0.18	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.07	0	0.19	0	0.12	0	0	0.11	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0	0.17	0	0.11	0.15	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0	0	0	0.08	0	0.11	0	0.09	0	0	0.11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0	0	0.12	0	0	0	0	0	0	0	0	0.11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.08	0	0	0	0	0	0	0	0	0	0	0.19	0.15	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0	0	0	0.24	0	0	0	0	0	0	0.24	0.16	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-
0.15	0	0.19	0	0	0.27	0.27	0	0.14	0.11	0	0	0	0	0.09	-	-	-	-	-	-	-	-	-	-	-	-
0	0.33	0.12	0	0	0	0	0.13	0	0.17	0.20	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-
0.07	0.12	0	0.17	0	0	0.13	0.20	0.13	0.11	0.13	0.09	0	0	0	0.11	0.13	-	-	-	-	-	-	-	-	-	-
0.17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.13	-	-	-	-	-	-	-	-	-
0.09	0	0	0	0	0	0	0.27	0	0	0	0	0	0.31	0	0	0	0	0	-	-	-	-	-	-	-	-
0	0	0	0	0	0	0	0	0	0	0	0.11	0	0	0	0	0	0	0.20	0	-	-	-	-	-	-	-
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0	0	0	0	0.11	0	0	0	0	0	0.13	0	0	0	0	0	0.13	0	0	0	0	0	-	-	-	-	-
0	0	0	0	0	0	0	0.17	0	0.43	0	0.07	0	0	0.08	0.17	0.11	0.17	0	0	0	0	0	-	-	-	-
0	0	0	0	0.25	0	0.18	0	0	0	0	0	0	0	0	0.29	0	0.27	0	0	0	0	0	0.11	-	-	-
0.07	0.12	0.09	0.09	0	0.13	0.13	0	0.13	0	0.20	0.17	0	0	0.27	0.11	0.27	0.10	0	0	0.13	0	0.10	0	0	-	-
0.08	0	0.11	0	0	0.16	0.15	0	0.17	0	0	0	0	0	0.11	0.25	0	0	0.17	0	0	0	0	0.10	0.17	0.12	-
0.06	0	0	0.08	0	0	0	0	0.11	0.09	0	0	0	0.10	0.08	0.09	0	0.09	0	0.11	0	0.11	0.09	0.15	0	0	0
0.24	0	0.11	0	0	0.15	0.15	0	0.33	0	0.17	0	0	0	0	0.13	0	0.12	0	0	0	0	0	0	0	0.12	0.15
0.06	0	0	0	0.09	0	0.10	0	0	0	0.10	0.07	0	0	0	0	0	0	0.20	0	0	0	0	0.07	0.10	0.08	0.10
0.08	0	0	0	0.14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0.09	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.14	0	0	0	0	0	0	0	0.11	0.20	0	0.18
0.08	0	0	0.10	0.13	0	0	0.11	0	0.12	0	0	0.15	0	0	0	0	0.11	0	0	0	0	0.11	0.09	0	0	0
0	0	0.11	0	0	0.17	0	0.13	0	0	0	0	0	0	0	0.13	0	0	0	0	0	0.18	0	0.10	0.18	0	0.17
0	0	0	0	0	0.18	0	0	0	0.14	0	0.11	0	0.15	0	0	0	0	0	0	00	0	0	0.11	0	0	0
0.07	0.11	0	0	0	0	0	0.09	0	0	0	0.08	0	0.10	0	0	0.12	0	0.12	0.24	0.12	0	0	0.08	0	0.09	0.11
0.07	0	0	0	0.32	0	0	0	0	0.10	0.13	0.08	0	0	0	0	0	0	0	0	0	0	0.19	0	0	0	0
0	0	0	0.09	0.11	0	0	0	0	0.11	0.13	0.26	0.27	0	0.18	0	0.13	0.10	0	0	0	0	0.30	0	0	0.30	0
0	0	0	0	0	0	0	0	0.14	0	0	0.18	0	0	0.19	0	0	0.11	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0.11	0.20	0.15	0.12	0	0	0	0	0	0	0	0	0	0	0.13	0
0.13	0	0.08	0	0	0.20	0.20	0.08	0.11	0	0	0.30	0.11	0.18	0	0.26	0.11	0.17	0	0	0	0	0.08	0.07	0.32	0.17	0.20
0	0	0	0	0	0	0	0	0	0	0	0.24	0	0	0.08	0	0	0	0	0	0	0	0	0.08	0	0.09	0.11
0	0	0	0.08	0	0	0	0	0	0	0	0.08	0	0	0.33	0	0	0	0.12	0	0	0	0	0.08	0	0.09	0.11
0.06	0	0	0	0.10	0	0.11	0	0	0	0	0.08	0	0.10	0.24	0	0	0	0	0	0	0	0	0	0	0.26	0
0.09	0	0.12	0	0	0.18	0	0	0	0	0	0	0.20	0	0	0.14	0	0	0	0	0	0	0	0	0	0	0
0.17	0	0.47	0	0	0.36	0.18	0	0.20	0.14	0	0	0	0	0	0.29	0	0	0	0	0	0	0	0	0	0.13	0.17
0	0	0	0	0	0.11	0.11	0	0	0	0.12	0.24	0	0	0.17	0.10	0.12	0.09	0		0	0	0.18	0.08	0.12	0.09	0
0.07	0	0.10	0	0	0.27	0.13	0	0.14	0.11	0	0.18	0	0	0.19	0.11	0	0.11	0		0	0	0	0.09	0	0.11	0.27
0.09	0	0.12	0	0	0.18	0.18	0	0.20	0	0	0	0	0	0	0.14	0	0	0		0	0	0	0	0	0.13	0.18
0	0	0	0	0.11	0.13	0	0	0	0	0	0.26	0	0.11	0	0.11	0	0	0		0	0	0	0.08	0.27	0	0.13
0	0	0	0	0.13	0	0	0	0	0	0	0.10	0	0	0.21	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0.21	0.18	0.14	0.11	0	0	0	0		0	0	0	0	0	0	0

Appendix C (cont.). Matrix of calculated Half Weight Index (HWI) values between all select individuals (n = 78).

308	316	401	410	418	442	470	504	506	507	510	612	615	622	667	676	678	686	691	733	735	740	746	791	1161
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0.11	0.15	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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0.24	0	0.22	0	0	0	0	0.12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0	0	0	0.24	0	0.21	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0	0	0.08	0	0	0.33	0	0	0	0.29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.18	0.25	0.08	0.13	0	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0	0	0.10	0.18	0	0	0	0	0	0	0.13	0	-	-	-	-	-	-	-	-	-	-	-	-	-
0.07	0.10	0.07	0.20	0.11	0	0.10	0.11	0.08	0.08	0.08	0	0.11	-	-	-	-	-	-	-	-	-	-	-	-
0	0	0.15	0	0	0.10	0	0	0	0.17	0.18	0.10	0.12	0	-	-	-	-	-	-	-	-	-	-	-
0.16	0	0.15	0	0	0.10	0	0	0.17	0.09	0	0.19	0.12	0	0.08	-	-	-	-	-	-	-	-	-	-
0.08	0	0.14	0.21	0	0.19	0	0	0	0.08	0.09	0.18	0.22	0.07	0.08	0.24	-	-	-	-	-	-	-	-	-
0.11	0.17	0.14	0.18	0	0	0	0	0.12	0	0.13	0.14	0	0	0	0	0	-	-	-	-	-	-	-	-
0	0.17	0	0	0	0	0	0	0	0	0	0	0	0.11	0	0	0	0.20	0	-	-	-	-	-	-
0	0	0.07	0	0	0	0	0.12	0.08	0	0.09	0.10	0	0.23	0.08	0.08	0	0	0	-	-	-	-	-	-
0.18	0.13	0	0	0	0	0	0.14	0	0	0	0.29	0	0.17	0	0.10	0	0	0.29	0.10	-	-	-	-	-
0	0.17	0.10	0	0	0	0	0	0	0	0	0	0	0.11	0	0.12	0	0	0.20	0	0.14	-	-	-	-
0	0	0.08	0.13	0.13	0.22	0.13	0.13	0	0.10	0.10	0.11	0.13	0.25	0.09	0.09	0.26	0	0	0.09	0.11	0	-	-	-
0	0	0	0.15	0	0	0	0	0.11	0.11	0	0.13	0	0	0	0.11	0.10	0	0	0.11	0	0	0.12	-	-
0	0	0.10	0	0	0	0	0	0	0	0	0.13	0.18	0.10	0	0.11	0	0	0	0.11	0	0	0	0.15	-

Appendix D. Summary table of small-scale grouping results.

Dyads	Joint HWI value	Sex
0401 w/ 0951	0.3	F w/ F
0062 w/0507	0.32	F w/ F
0735 w/ 1103	0.33	F w/ F
0410 w/ 0818	0.37	F w/ PoF
0010 w/ 0470	0.31	F w/ U
0014 w/ 0034	0.36	F w/ U
0192 w/ 0676	0.33	F w/ U
0418 w/ 0630	0.5	PoF w/ U
0746 w/ 0635	0.38	PoF w/ U
0029 w/ 1161	0.27	PoF w/ U
0406 w/ 0002	0.66	PrF w/ U
0032 w/ 0308	0.3	U w/ F
0025 w/ 0058	0.57	U w/ PoF
0028 w/ 0595	0.63	U w/ PoF
0242 w/ 0412	0.6	U w/ PrF
0005 w/ 0044	0.4	U w/ U
0036 w/ 0733	0.4	U w/ U
0079 w/ 0511	0.75	U w/ U
0108 w/ 0258	0.44	U w/ U
0154 w/ 1220	0.38	U w/ U
0159 w/ 0049	0.5	U w/ U
0377 w/ 0769	0.66	U w/ U
0226 w/ 0338	0.44	U w/ U
0244 w/ 0234	0.5	U w/ U
0470 w/ 0351	0.67	U w/ U
0612 w/ 0621	0.46	U w/ U
0667 w/ 0796	0.35	U w/ U
0740 w/ 0832	0.44	U w/ U

F = female
PrF = probable female
PoF = possible female
U = unknown

0025 w/ 0058 w/ 0063 U w/ PoF w/ U

Triads	25	58	63
25	-	-	-
58	0.57	-	-
63	0.4	0.44	-

0855 w/ 0899 w/ 0181 U w/ U w/ U

Triads	855	899	181	***204**
855	-	-	-	-
899	0.66	-	-	-
181	0.57	0.57	-	-
***204**	**0.5**	**0.5**	**0.46**	-

*** 204 (U) highly associated but didn't meet requirements for a quadruplet.**

0448 w/ 0771 w/ 0442 w/ 0510 F w/U w/PrF w/ U

Quartets	448	771	442	510
448	-	-	-	-
771	0.6	-	-	-
442	0.46	0.46	-	-
510	0.4	0.4	0.33	-

Appendix E. Examples of site fidelity definitions and patterns in several study areas.

San Diego, California
Hansen (1990); Weller (1991); Defran *et al.* (1999); DeFran and Weller (1999)
373 individuals identified
Overall low site fidelity (although some dolphins were sighted in all four seasons)
Sighting frequency ranged from one to 24 (mean = 4.6), with 24% sighted once and 67% seen greater than six times.
It was suggested that the study area was only a small portion of an extended home range for the dolphins and that movements were influenced largely by prey availability.

Kino Bay, Gulf of California, Mexico
Ballance (1990)
155 individuals identified
Resident (94): sighted more than one time in the study area
Non- resident (61): sighted once in the study area
Almost 50% of the non-resident sightings were in large groups of > 40 dolphins of mixed residency patterns.
Thirty-nine percent of the dolphins were sighted once with a time interval between the first and last sighting ranging from two to 195 days (mean = 80).
***Associations were observed between residents and non-residents.

Galveston Bay, Texas
Brager *et al.* (1994)
1000 individuals identified, but only 200 regularly used the study area
Residents and transients

Galveston ship channel, Texas
Fertl (1994a)
240 individuals identified
Residents and transients
Forty-two percent were sighted in one year, 34% during two years and 23% during three years.
Sighting frequency ranged from one to 115 and 75% of the animals were sighted more than once.

San Luis Pass region of Galveston Bay estuary system, Texas
Maze and Wursig 1999; Maze-Foley and Wursig 2002
71 individuals identified
Less than 50% were sighted more than once.
Year-round residents (Bay) (37): sighted in bay sections or in both bay and Gulf of Mexico sections
Transients (Gulf) (34): sighted only in the Gulf of Mexico section of the study area
***Associations were observed between residents and transients.

Cedar Keys, Florida
Quintana- Rizzo (1999); Quintana-Rizzo and Wells (2001)
233 individuals identified; 217 used for residency analyses
Resident (41 individuals): sighted in at least half of the survey months
    Common (26): sighted in at least eight months
    Frequent (15): sighted in a minimum of four months, but no more than seven months
Non-resident (176): sighted from one to five months
    Occasional (43): sighted in a minimum of three, but no more than five months
    Rare (143): sighted in a minimum of one, but no more than two months
Twenty percent of the sightings involved mixed strategy groups, but residents associated with non-residents less frequently than the associated with other residents.
***Associations were observed between residents and non-residents.

Appendix E (cont.): Examples of site fidelity definitions and patterns in several study areas.

Charleston, South Carolina (Stono and Folly Creeks)
Zolman (1996, 2002)
112 individuals identified
Residents (21): sighted at least once in all four seasons
Seasonal residents (9): sighted during the same season in consecutive years, but not during intervening seasons
Transients (72): sighted during a single season or in two consecutive seasons
Thirty-two% were sighted once and 28% were sighted five or more times.
This study was determined to be part of the home range of a year-round resident population and it was suggested that the migratory behavior was correlated with environmental variables that may affect the distribution of prey.
***Associations were observed between individuals exhibiting variable residency patterns.

Gulf de Guayaquil, Ecuador
Felix (1997)
441 individuals identified; population estimate of 2500
All communities contained between 56-160 individuals.
Resident (3 communities): sighted with the same frequency year round
Non-resident (2 communities): sighted only a portion of the year (absent during several months)
Non-resident communities were larger than resident communities.
***Associations between all communities were observed.

Hilton Head, South Carolina
Gubbins (2000), Gubbins (2002 a, b)
478 individuals identified;
Residents (52 animals): sighted in all seasons; two communities identified
Creek dolphins (27 individuals)
Sound dolphins (25 individuals)
Transients (426 animals): only sighted during one or two seasons
Sighting frequency ranged from ten to 115 for residents and one to eight for transients.
***Associations were readily observed between residents and transients.

Cornwall, United Kingdom
Wood (1998)
44 individuals identified
Most individuals were classified as resident, but had extended home ranges of up to 650 km.
An obvious trend in the movement patterns of dolphins was found and residency was described as flexible, with a number of animals using the region intermittently.
Sighting frequency varied from one to 81 sightings (mean = 24).

Moray Firth, Scotland
Wilson *et al.* (1997)
128 individuals identified
Residents
Sighting frequency ranged from one to 31 and individuals were classified as common, frequent, occasional and rare.
Stratified short-term seasonal movements observed as individuals used certain habitats preferentially during certain times of the year. It was suggested that the seasonal migration of prey species may influence this seasonal migration of the study animals.

Curriculum Vitae

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EDUCATION.

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Marine Mammal Observer Photo-ID Project Leader June 25 – November 4, 2004
SPLASH (Structure of populations, levels of abundance and status of humpbacks)
NOAA Southwest Fisheries Science Center (SWFSC)- La Jolla, California

North Atlantic Right Whale Aerial Observer 2004 (Northeast Fisheries Science Center), 2003 (New England Aquarium), 2002 (Wildlife Trust)

Endangered Species Observer 2002-2004 Coastwise Consulting

Marine Mammal Observer Photo-id Specialist July 26 – December 10, 2003
STAR (Stenella Abundance Research Cruise) NOAA SWFSC- La Jolla, California

Chief Scientist Bottlenose Dolphin Mark Recapture Photo-id Project July 2003
Georgetown, South Carolina Site- NOAA/NMFS Beaufort, North Carolina Lab

Marine Mammal Observer September 4 – December 8, 2002 HICEAS (Hawaiian Island Cetacean and Ecological Assessment Survey) NOAA SWFSC- La Jolla, California

Research Associate/Photographer 2002, 2001
Bottlenose Dolphin Biopsy Project NOAA/NMFS - Beaufort, North Carolina Lab

Research Associate, Wild Dolphin Project May 2000 – August 2001

Co-project Leader (2000) and Project Leader (2001) Pacific Whale Foundation , Maui

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Virginia Marine Science Museum - Virginia Beach, Virginia

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ABSTRACTS & PRESENTATIONS

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