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BRIEF REVIEW

Learning From Nature: Bottlenose Dolphin Care and Husbandry

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The world's longest-running study of a wild dolphin population, operated by the Chicago Zoological Society since 1989, has focused on the multi-generational resident community of about 160 bottlenose dolphins in Sarasota Bay, Florida, since 1970. Observational and capture-release research on the biology, behavior, life history, ecology, and health of individually identifiable bay residents of up to 59 years of age and spanning five generations has helped to inform collection managers at the Brookfield Zoo and partner institutions. Age, sex, and genetic compositions of colonies at cooperating institutions have been based on observations of social structure and genetic paternity testing in Sarasota Bay to optimize breeding success. Breeding success, including calf survivorship, is evaluated relative to individual wild dolphin reproductive histories, spanning as many as nine calves and four decades. Individual rearing patterns for wild dolphins provide guidance for determining how long to keep mothers and calves together, and help to define the next steps in the calves' social development. Health assessments provide data on expected ranges of blood, milk and urine values, morphometrics, and body condition relative to age, sex, and reproductive condition. Calf growth can be compared with wild values. Target weights and blubber thicknesses for specific age and sex classes in specified water temperatures are available for wild dolphins, and caloric intakes can be adjusted accordingly to meet the targets. A strength of the program is the ability to monitor individuals throughout their lives, and to be able to define individual ranges of variability through ontogenetic stages. Zoo Biol 28:1–17, 2009. © 2009 Wiley-Liss, Inc.

Keywords: health assessment; social structure; captive breeding; reproductive success; life history

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INTRODUCTION

The public display of common bottlenose dolphins (*Tursiops truncatus*) has been occurring for more than 125 years, with the first exhibition in 1883 at the Brighton Aquarium, followed by the first display in the United States in 1914 at the New York Aquarium [Wells and Scott, 1999]. The first long-term colony of bottlenose dolphins for public display was established in 1938, with the opening of Marine Studios (later Marineland of Florida) in St. Augustine, Florida, followed over the next several decades by the development of a number of dolphinaria around the coast of the U.S. where natural seawater was readily available [Reeves and Mead, 1999]. The first inland dolphinarium opened to the public in 1961, at the Chicago Zoological Society's Brookfield Zoo [Ross, 1997]. Today, nearly 30 facilities in the United States display bottlenose dolphins to the public.

Until the 1980s, dolphinaria (along with research and military facilities) were stocked largely with dolphins collected from the wild, resulting in the documented removal of nearly a thousand bottlenose dolphins from U.S. waters [Leatherwood and Reeves, 1982]. In the early years of public display programs in the U.S., collections were maintained primarily by replacing animals lost through mortality with new individuals obtained through additional live-capture removals from the wild. Advances in medical and husbandry knowledge [e.g., Ridgway, 1972; Dierauf and Gulland, 2001] have contributed to improved longevity of collection dolphins, to the point where survivorship approaches that estimated or measured for wild populations [DeMaster and Drevenak, 1988; Duffield and Wells, 1993]. Increased captive breeding success has allowed many facilities to maintain or expand their collections without needing to resort to live-captures in recent years. In fact, no bottlenose dolphins have been collected from U.S. waters since the late 1980s. The cessation of bottlenose dolphin-collecting practices in the U.S. not only favorably reflects significant improvements in care and husbandry, but it also provides conservation benefits to the wild populations from which dolphins were collected, as removals likely reduce the reproductive success of the animals remaining in those populations [Wells, 2000].

The medical care and husbandry of collection dolphins has been advanced through the integration of various efforts, including decades of experience with maintaining and treating dolphins in collections, improvements in medical technology, necropsies and rehabilitation attempts through stranding response programs [Moore et al., 2007], and field research. The focus of this paper is on the contribution of one long-term field research program toward the care and husbandry of bottlenose dolphins. Since 1989, the Chicago Zoological Society (CZS) has supported the operations of the Sarasota Dolphin Research Program, the world's longest-running study of a wild dolphin population. The resident dolphin community of bottlenose dolphins inhabiting Sarasota Bay, Florida, has been under study since 1970 [Scott et al., 1990a; Wells, 1991, 2003]. Data on health and physiology, behavior and social patterns, mortality, and reproductive success gathered over more than 38 years and across at least five generations of resident dolphins have provided unique insights into the lives and needs of these animals, and the basis for developing expectations and targets for collection animals. Of particular value has been the ability to monitor individual dolphins longitudinally, through life history stages from the time they are born until they die, as they demonstrate a full range of individual variation, and provide the basis for establishing normal values based on life in the wild. Long-term continuity and consistency of data collection, as provided by the ongoing support from CZS, has been crucial for deriving reference values. The data resulting from the long-term research program are available to those who maintain collections of bottlenose and other dolphins, to enhance the care and husbandry of the animals.

METHODS

The bottlenose dolphins of Sarasota Bay, Florida, have been studied since October 1970, when dolphin tagging efforts were initiated by scientists based at Mote Marine Laboratory [Irvine and Wells, 1972]. Repeated sightings of dolphins tagged during 1970 and 1971 suggested residency to the region from southern Tampa Bay, southward to about Venice Inlet, and within several kilometers of shore (Fig. 1). Additional tagging combined with radio-tracking during 1975–1976 confirmed multi-year, year-round residency to the area, with 92% of the Sarasota Bay dolphins tagged during 1970–1971 re-identified in the same area during 1975–1976 [Wells et al., 1980; Irvine et al., 1981]. As of 2008, 25% of the original tagged dolphins were still alive and in the area, more than 38 years after their initial identifications.

Overall, the approximately 160 current residents of Sarasota Bay span five generations, and range in age from newborns up to 59 years (Fig. 2). The long-term, multi-generational, year-round site fidelity of bottlenose dolphins to the Sarasota Bay area creates a "natural laboratory" situation where selected individuals or members of specific age/sex/reproductive classes may be found predictably. Individual community members can be observed, measured, and sampled throughout their lives, and the community as a whole can be monitored over periods of decades [Scott et al., 1990a; Wells, 1991, 2003].

Research on the Sarasota Bay dolphins involves various methods, but the approaches of greatest relevance to generating data for application to the care and husbandry of collection dolphins come from: (1) photographic identification surveys, (2) focal animal behavioral observations, (3) capture-release for health assessment and life history research, and (4) stranding response, including carcass recovery/necropsy and rehabilitation. Systematic small-boat surveys are conducted regularly to locate and identify dolphins and record associated environmental and activity data. Digital photography is used to document distinctive dorsal fin shapes and patterns of nicks and notches [Scott et al., 1990b; Wells, 2002]. The photo-identification approach, in which 96% of the local dolphins are recognizable, allows us to investigate ranging patterns and habitat selection at the level of the individual animal or demographic group [Wells, 1991, 2003; Wells et al., 1987], provides census-level data for absolute abundance measurements [Wells and Scott, 1990], and provides crucial information on the presence or absence of associated calves for measures of fecundity, birth rates, and calf survivorship. Identification and survey data are available since 1970, but the most consistent, year-round survey efforts have occurred since 1993. The sighting database includes more than 36,000 dolphin group sightings since 1970, involving more than 105,000 identifications of more than 3,400 recognizable individuals found in the waters from Tampa Bay through Charlotte Harbor and Pine Island Sound (Fig. 1).

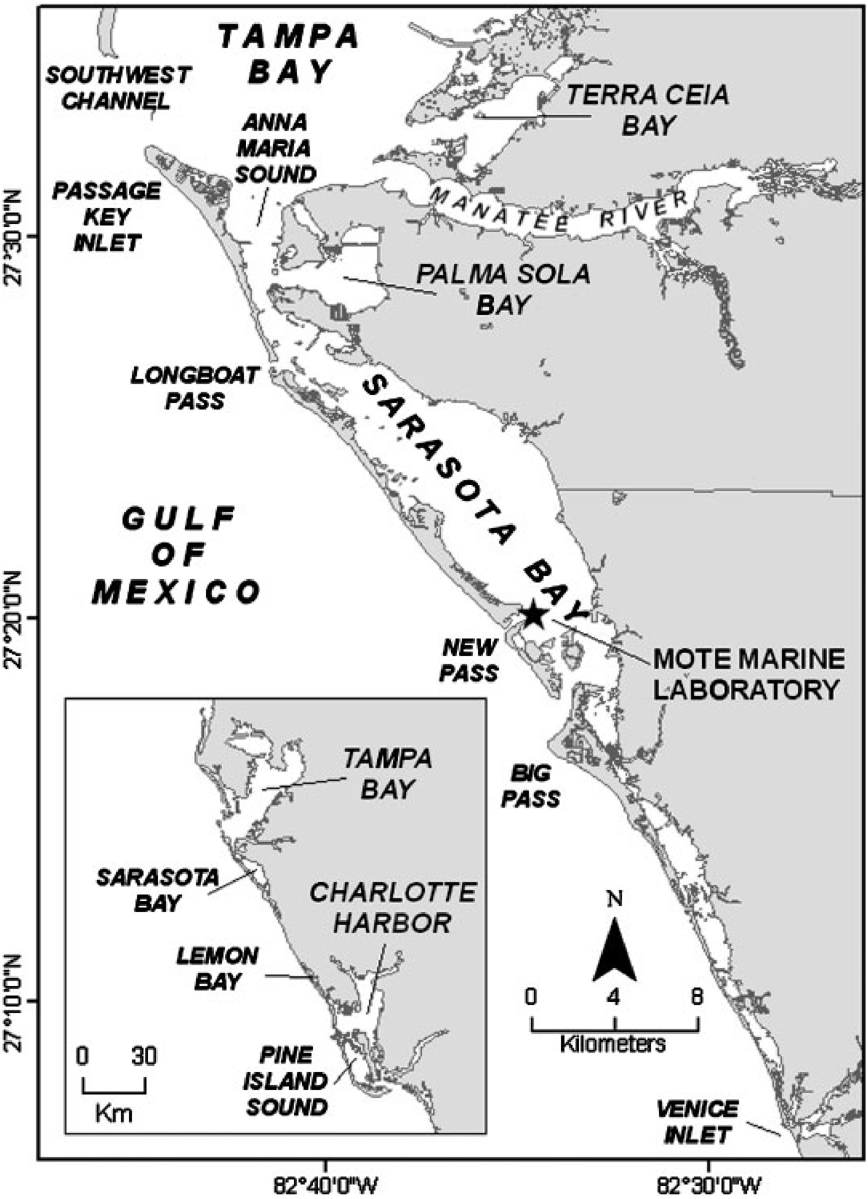

Fig. 1. Long-term study area of the Sarasota Dolphin Research Program on the central west coast of Florida.

As a distinct subset of the sighting database compiled from surveys, detailed records have been compiled since 1970 on the reproductive histories of each of the adult females that use Sarasota Bay on a regular basis. Data include birthdates of calves, calf sex, mother's age at the time of birth (including age at first birth in some cases), duration of the mother-calf association, and circumstances leading to separation. The data set currently includes records from 107 females and 307 of their calves; some females have been observed with as many as nine different offspring over the course of their lifetime.

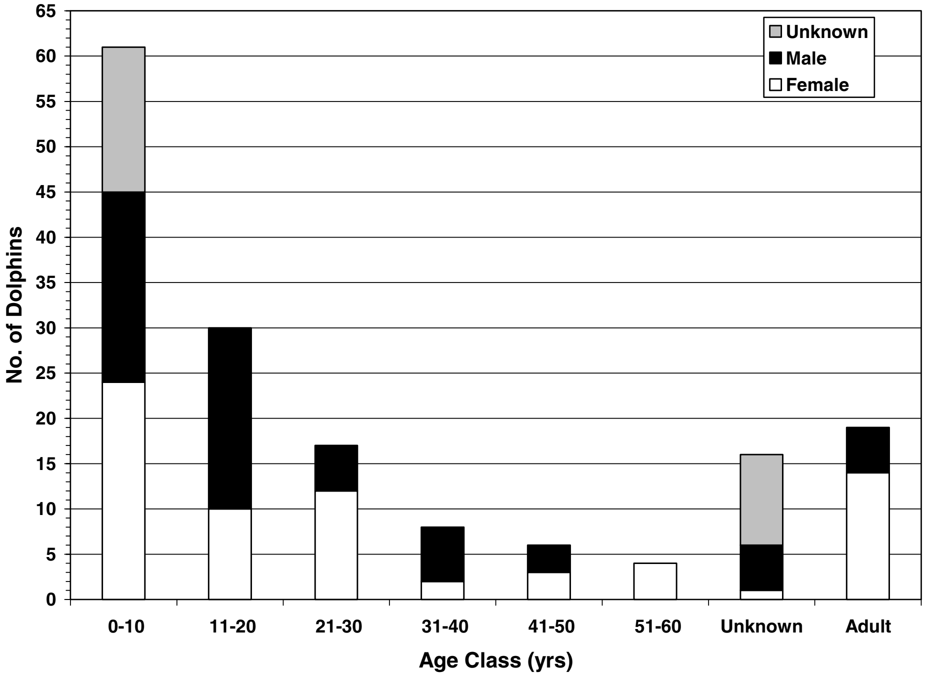

Fig. 2. Age and sex structure of the resident Sarasota Bay bottlenose dolphin community in 2007, based on 161 individuals identified regularly in the area. Adults of unspecified age were classified on the basis of females being seen with calves presumed to be their own, or males being observed for more than 10 years by 2007.

The survey approach has also been used to locate specific individuals for focal animal behavioral observations following the approach pioneered by Altmann [1974]. This systematic approach to quantification of behavior typically involves observing selected individuals for about 2 hr from a nondisturbing distance, and recording a suite of data at three-minute intervals, in addition to variables such as respirations that are recorded continuously. While some recorded variables are specific to each project, some basic behavioral data are collected consistently across projects (e.g., respirations, nearest neighbor, group size, habitat use), allowing for the compilation of long-term behavioral records for individuals for comparison across time or life history stages. More than a dozen projects have been conducted in the Sarasota Bay area using the focal animal behavioral observation approach.

Bottlenose dolphin body condition, morphometrics, genetics, life history, and health data are obtained through capture-release research [Wells et al., 2004]. The shallow, sheltered bay waters facilitate encircling small groups of selected dolphins with a 500 m long × 4 m deep seine net. Individual dolphins are placed in a sling, and lifted aboard a veterinary examination vessel. The animals are weighed, measured for standardized lengths and girths, and ultrasonic measurements of blubber thickness are made at standardized sites. Each individual is given a full examination, including ultrasonic imaging of internal organs by experienced marine mammal veterinarians. Sex is confirmed through direct examination of the genital region. Blood samples are drawn from the fluke into evacuated tubes via butterfly catheter.

Urine, feces, milk, microbiological swabs, and biopsy samples are collected. Upon completion of sampling, dolphins are marked with freeze brands or tagged as appropriate, photographed, and released. While the ages of most of the sampled dolphins are already known from observations since birth to identifiable mothers, occasionally ages need to be determined from examination of growth layer groups in a tooth extracted under local anesthesia [Hohn et al., 1989]. Sexual maturity is evaluated through measurements of reproductive hormone concentrations, through ultrasonic examination of reproductive organs, and through observations of presumed first births. Maternal–offspring relationships are confirmed through genetic analyses, and paternity tests are performed from blood samples. Since 1988, blood sample and exam data including 689 sets of measurements have been collected from 219 individuals (some sampled up to 15 times). Morphometrics (weight, length, and girths) have been collected since 1984 for 225 individuals (some measured up to 14 times), with 687 sets of measurements in total. Blubber thicknesses have been collected ultrasonically as a diagnostic measure of body condition since 1986.

Since 1985, Mote Marine Laboratory's Stranding Investigations Program has responded to reports of stranded, sick, and injured marine mammals in Sarasota, Manatee, and Charlotte Counties, which includes and extends beyond the Sarasota Bay bottlenose dolphin home range. Carcasses are examined and necropsied for determination of the cause of death and for collection of standardized measurements and biological samples, including stomach contents. To date, more than 400 bottlenose dolphins have been recovered from the central west coast of Florida, including 69 with sighting histories in our database. In addition, since 1992, six dolphins with sighting histories have been admitted to Mote's dolphin hospital for treatment of illness or injuries from anthropogenic sources. Of these, five survived to be released, and at least three were known to survive postrelease for at least six months (one is currently being tracked at the time of this writing).

RESULTS AND DISCUSSION

Details of the results from more than 38 years of research are beyond the scope of this article, given space limitations. Citations of publications resulting from the work are provided below with general descriptions of findings. PDF copies of specific articles are available from the author upon request. Data from the Sarasota Bay dolphins have also contributed to more general overviews of bottlenose dolphin biology, behavior, and ecology, as found in Shane et al. [1986], Reynolds et al. [2000], Reynolds and Wells [2003], and Wells and Scott [1999, 2002, 2009].

Health Parameters

Blood samples are among the first and most illustrative diagnostics of health issues with collection dolphins. Basic data on clinical blood chemistry and hematology for Sarasota Bay dolphins have been used as reference values to help establish "normals" for evaluation of the health of collection and stranded dolphins [Bossart et al., 2001]. More detailed analyses have examined blood profile data relative to annual, seasonal, and individual variation, age, sex, reproductive class, geographic location, and health parameters, enhancing the clinician's perspective for using blood profiles as health indicators [Wells et al., 2004; Hall et al., 2007; Schwacke et al., 2009]. Comparisons of thyroid and adrenal hormones have been made between Sarasota Bay and collection dolphins [St. Aubin et al., 1996]. Studies are currently underway to try to understand the occurrence of kidney stones in collection dolphins by comparing blood and urine of collection dolphins with those from the wild, where ultrasound has indicated the presence or absence of such stones. Comparisons of vitamin concentrations in blood of wild and collection dolphins showed differences, with applications to the nutritional care of collection dolphins [Crissey and Wells, 1999]. Comparisons of immunoglobulin concentrations between wild and collection dolphins have also have been conducted [Ruiz et al., 2008].

Body condition is another important diagnostic of dolphin health. Research in Sarasota Bay has demonstrated that bottlenose dolphin body condition varies with various factors. Lengths, girths, and mass vary with age and sex [Read et al., 1993; Tolley et al., 1995]. Blubber thickness and body mass vary with seasonal changes in water temperature, as well as sex, age, length, and health [Wells, 1993a; Noren and Wells, 2009]. The bottlenose dolphins of Sarasota Bay are exposed to water temperatures that range seasonally from less than 13 to 35°C. These extremes are reflected in thermoregulatory changes in peripheral blood flow [Barbieri, 2005; Meagher et al., 2002, 2008] as well as about a 38% increase in blubber thickness from summer to winter [Wells, 1993a]. With this information, it is possible to establish target weights and blubber thicknesses relative to age, sex, length, reproductive condition, and water temperature, and adjust the caloric content of food provided to collection animals accordingly. These measures are also used for assessing the growth of dolphins born into collections.

Bottlenose dolphins in the wild are exposed to a wide range of microorganisms, including many pathogens. Understanding the natural occurrence of potential disease agents, as well as the impacts of these on the health of wild dolphins, can be important for caring for collection animals. Buck et al. [2006] provided an overview of the occurrence of aerobic microorganisms, including longitudinal individual records. The occurrence of other known or potential pathogens or conditions has also been examined, including morbillivirus [Duignan et al., 1996], parainfluenza [Venn-Watson et al., 2008], *Bartonella* [Harms et al., 2008], lobomycosis [Migaki et al., 1971], and general skin lesions of largely undefined origin [Wilson et al., 1999].

The pervasiveness of environmental contaminants such as heavy metals, persistent organohalogen compounds, and emerging contaminants of concern such as perfluoroalkyl compounds, along with their documented effects on the health and reproductive success of some mammals, has led to concerns for dolphins as top-level predators who obtain these compounds through biomagnification. Given that the food fish for both collection and wild dolphins [Barros and Wells, 1998] originate in the wild, concerns regarding exposure are comparable for both groups. High levels of mercury have been found in Sarasota Bay dolphins, but it has been suggested that interactions with selenium may help to detoxify the mercury [Bryan et al., 2007; Woshner et al., 2008].

Research with Sarasota Bay dolphins has helped to develop biomarkers of environmental contaminants and their effects, including DNA damage [Gauthier et al., 1999], immune system function [Erickson et al., 1995; Lahvis et al., 1993]; retinoids [Tornero et al., 2005], and the cytochrome P-450 1A1 system [Wilson et al., 2007]. High levels of organochlorine pollutants such as polychlorinated biphenyl (PCB) congeners, DDT metabolites, and other pesticides have been found in Sarasota Bay dolphin milk and blubber [Vedder, 1996; Küss, 1998; Wells et al., 2005]. Although Sarasota Bay is cleaner than some sites in the southeastern U.S. [Hansen et al., 2004; Houde et al., 2006a], tissue concentrations of PCBs are above theoretical thresholds for health and reproductive effects [Schwacke et al., 2002]. Based on a small number of samples from males, Lahvis et al. [1995] found indications of immune system compromise relative to organochlorine pollutant concentrations. The transfer of PCBs from mother to calf through milk may contribute to high levels of first-born calf mortality [Wells et al., 2005], which may in turn depress the potential population growth rate [Hall et al., 2006]. Emerging contaminants such as perfluorinated alkyl compounds may not be as persistent as PCBs in the environment, but they are now being detected in wild dolphins and are a new source of health concern [Houde et al., 2005, 2006b,c].

Work by the U.S. Navy has documented high levels of organochorines in collection dolphins, as well as apparent depuration to calves leading to calf mortality [Ridgway and Reddy, 1995; Reddy et al., 2001]. Little information is available from other dolphin collections, due largely to the need to obtain blubber biopsies for analysis. However, recent work by J. Yordy (National Institute of Standards and Technology, Charleston, SC, personal communication) has demonstrated a strong relationship between organochlorine concentrations in blubber and blood of Sarasota Bay dolphins. This should lead to measuring body burdens in collection dolphins from an easily obtained blood sample rather than a biopsy, which may encourage more widespread assessment of contaminant loads in collections, and improved perspective on reproduction and health.

Population Dynamics and Life History

Long-term monitoring provides the means to evaluate the stability and range of variability of abundance and vital rates for a population unit, including potential rates of growth and decline, and the degree of resiliency of a unit [Wells and Scott, 1990]. Birth rates, fecundity rates, and mortality/loss rates, along with information on age/sex structure and lifespans, have been used for comparison to the combined bottlenose dolphin collection "population" in North America as a gauge for assessing husbandry and breeding success [Duffield and Wells, 1993]. Knowledge of life history patterns from the wild, including age at first reproduction and reproductive lifespan [Wells and Scott, 1999; Wells, 2000], reproductive seasonality [Urian et al., 1996], paternity patterns [Duffield and Wells, 2002], rearing patterns [Wells, 1993b; Owen, 2001], and age-specific reproductive success [Wells, 2000, 2003] helps to shape expectations for collection dolphins in terms of when breeding should occur and factors that might influence calf survivorship.

Behavior

Focal animal behavioral follows have provided quantitative information on the activity budgets of wild dolphins for comparison to the activities of collection dolphins [Waples, 1995]. In a unique experiment, it was possible to directly measure the effects of pool size on the activity budgets of a pair of wild-caught dolphins housed in a series of pools at a research facility for two years, and then returned to Tampa Bay where follow-up observations were conducted [Bassos, 1993; Bassos and Wells, 1996; Wells et al., 1998]. The dolphins demonstrated significant increases in time spent swimming/traveling as compared with "resting" when they were switched from a smaller pool (7.3 m diameter) to a larger pool (16.5 m diameter), and from the larger pool to the wild, demonstrating the importance of pool size as a factor influencing husbandry [Bassos and Wells, 1996].

Communication

Research with Sarasota Bay dolphins has contributed to our understanding of the nature and importance of acoustic communication for bottlenose dolphins. Basic to this understanding is knowledge of hearing abilities, and factors that might impact hearing. Studies using auditory evoked potentials are underway to characterize the hearing abilities across the Sarasota Bay dolphin community [Cook, 2006]. Recent studies have shown that dolphin whistles and echolocation clicks can be involved in communication over many hundreds of meters [Quintana-Rizzo et al., 2006]. Increases in whistle production rates as boats approach may reflect heightened arousal or motivation to move closer together, with whistles functioning to promote dolphin reunions [Buckstaff, 2004]. Whistle features may reflect stress in some circumstances [Esch, 2006].

Field recordings and acoustic playback experiments with Sarasota Bay dolphins of known age, sex, genetic relationships, and association histories have been performed to characterize and understand the function and development of individually specific signature whistles [Sayigh et al., 1990, 1995, 2007; Cook et al., 2004; Fripp et al., 2005]. Playback experiment findings suggest that the most important functions of signature whistles may be as contact calls and to convey identity information about the individual [Sayigh et al., 1999; Watwood et al., 2004, 2005; Janik et al., 2006]. This function of signature whistles might be especially important in the murky estuarine habitats of free-ranging bottlenose dolphins, or when separated in a collection's pool complex.

Social Structure

Bottlenose dolphins live in complex, fission–fusion societies [Connor et al., 2000; Quintana-Rizzo, 2006], and re-creating the salient features of these societies in collections can be challenging. Identifying different population units in the wild is difficult because of the continuous distribution of the species around the coast of the southeastern U.S. The Sarasota Dolphin Research Program has pioneered efforts to distinguish biologically meaningful population units, or communities, on the basis of ranging patterns, social associations, and genetics [Wells et al., 1987; Duffield and Wells, 1991, 2002; Sellas et al., 2005; Urian et al., 2009]. The Sarasota Bay dolphin community, consisting of about 160 individuals in 2007 (Fig. 2), inhabits a range that slightly overlaps those of adjacent communities to the north, west, and south, as part of a mosaic of communities along the central west coast of Florida [Wells, 1986]. Community members demonstrate a high degree of site fidelity and associations within shared ranges, but social interactions including breeding occur on occasion across community borders [Wells et al., 1987; Duffield and Wells, 2002]. In spite of occasional genetic exchange, significant genetic differentiation occurs between communities [Duffield and Wells, 1991, 2002; Sellas et al., 2005].

Within the Sarasota Bay dolphin community, average group size is about four to seven individuals, and group composition is subject to frequent change [Irvine et al., 1981; Wells, 1991, 2003; Wells et al., 1980, 1987; Quintana-Rizzo, 2006]. Three basic kinds of groups are common: (1) nursery groups of mothers with their most recent offspring, (2) juvenile groups, and (3) adult males, typically as members of strongly bonded pairs [Wells et al., 1987; Wells, 1991, 2003]. Females tend to associate with others at a similar stage of reproduction, not necessarily on the basis of familial lines. Consistent or recurrent associations between females at similar stages of the reproductive cycle are common. Juveniles leave their mothers at three to six years of age and remain in juvenile groups until they reach sexual or social maturity. Most males form a strong pair bond with another male of similar age at about sexual maturity, and they often remain together until one member is lost [Wells, 1991; Owen et al., 2002; Owen, 2003].

Breeding

Focal animal behavioral observations and paternity testing have shown that bottlenose dolphins in Sarasota Bay are not monogamous [Duffield and Wells, 2002]. Females give birth every three to six years, and may or may not use the same sire for subsequent calves. Mate-guarding of receptive females by male pairs is common, and paired males have greater reproductive success than unpaired males, regardless of size or age [Wells et al., 1987; Moors, 1997; Duffield and Wells, 2002; Owen et al., 2002]. Following insemination, males move on to other breeding opportunities; females rear their calves without assistance from the fathers. Female reproductive success is a function of mother's age, size, and level of maternal experience [Wells, 2000; Owen, 2001; Wells et al., 2005].

CZS, working with Indianapolis Zoo, Dolphin Connection, Disney's Living Seas, National Aquarium at Baltimore, Minnesota Zoo, and Texas State Aquarium, has developed a program to cooperatively manage a dolphin population to optimize breeding while still meeting display needs. This consortium, established in 1999, attempts to model dolphin groups at each facility after the kinds of social groups observed in Sarasota Bay, in terms of composition and stability. For example, the consortium attempts to maintain stable female groups, while pairs of males may be moved from one facility to another for breeding and to avoid inbreeding. In 2008, 43 bottlenose dolphins (22.21) were held collectively. They have produced 23 calves since 1999, with success that matches or exceeds that documented for Sarasota Bay dolphins. The crude annual birth rate for the consortium is 6.7 vs. 5.4% for Sarasota Bay, and first year survival is 78 vs. 76% for Sarasota Bay dolphins.

Staff Training

In addition to providing information that can benefit the care and husbandry of collection dolphins for CZS and its partner institutions, the ongoing research program provides unique opportunities for keeper staff training and professional development. Staff members are able to participate in all aspects of the research program. This experience with wild dolphins enhances the ability of the staff to care for the collection animals and to interpret the animals for the public, and first-hand experience with conservation issues such as human feeding of wild dolphins [e.g., Cunningham-Smith et al., 2006] prepares staff to present these issues to the public from a more meaningful perspective.

Integration of Field and Dolphinarium Research

The focus of this paper is on examples of how an ongoing, long-term field research program conducted by one institution can benefit the care and husbandry of dolphins in its collection and elsewhere. However, it should also be noted that much has been learned about aspects of biology and behavior from studies of dolphins in collections that could not have been learned in the wild. This has been especially true when controlled conditions, repeated or continuous access to specific individuals, or good underwater visibility have been key to gaining the knowledge. In some cases, such as the work by pioneering marine mammal scientist Ken Norris on Hawaiian spinner dolphins (*Stenella longirostris*), the synergism of concurrent, complementary research on wild dolphins and a colony at a nearby facility has provided a much more in-depth understanding of the species than would have been provided by either approach alone [Norris et al., 1994].

Factors potentially leading to seasonal changes in body condition in wild bottlenose dolphins in Sarasota Bay were examined through concurrent research with collection animals at Brookfield Zoo. The absence of seasonal changes in blubber thickness in collection animals maintained under a nearly constant water temperature regime suggested that changing water temperature could be a driving force behind the 38% increase in blubber thickness from summer to winter for Sarasota Bay dolphins [Wells, 1993a]. However, the relationship is likely not a simple direct response to water temperature, as the wild dolphins are consuming prey fish with seasonally increasing fat content as waters cool, while the food of collection dolphins does not vary in the same way.

Studies of dolphin acoustics have benefited greatly from research involving collection animals. While the general contexts of sound production have been understood largely from recordings and observations in the wild, experiments with collection animals have provided much detail that would have been difficult or impossible to collect under less-controlled circumstances. Extensive and very precise work on the echolocation systems and abilities of dolphins has been facilitated by the development of elaborate experiments involving sensitive instrumentation and intensive long-term training of dolphin subjects, possible only with collection animals [e.g., Nachtigall, 1980; Au, 1993]. The experimental manipulations that are possible with collection animals have provided opportunities to test hypotheses, as in the case of experiments with a uniquely trained Brookfield Zoo dolphin confirming that dolphins hear through their lower jaws, an important finding for understanding the use of echolocation by dolphins in the wild [Brill et al., 1988].

Another class of sounds produced by dolphins, signature whistles, was first proposed based on observations of collection animals [Caldwell and Caldwell, 1965]. Concurrent observations and recordings of wild dolphins confirmed the existence of signature whistles [Caldwell et al., 1990], and field playback experiments with dolphins restrained briefly during health assessments have confirmed their function as individual identifiers [Sayigh et al., 1999; Janik et al., 2006].

The novel observational perspective provided by underwater viewing during the early years of some facilities did much to stimulate interest in dolphin social behavior [McBride and Hebb, 1948; Tavolga and Essapian, 1957; Tavolga, 1966; Caldwell and Caldwell, 1972]. Observations of collection animals brought to light the complexities of social interactions, but it was necessary to perform studies in the wild to begin to understand functions of these behaviors in the ecological contexts under which they evolved [Wells et al., 1999]. The value of taking advantage of the strengths of studying both collection and wild dolphins to address social structure questions was clearly acknowledged in a volume of annotated case studies [Pryor and Norris, 1991]. As an example of synergistic relationships, a project relating reproductive hormone concentrations to social behavior of members of a colony of Hawaiian spinner dolphins [Wells, 1984] provided context that would not otherwise have been possible for concurrent observations of the socio-sexual interactions of wild spinner dolphins [Norris et al., 1994]. The combination of complementary field and collection research can provide a powerful approach to learning about the biology and behavior of dolphins.

In summary, the animals under human care in zoological park settings can benefit greatly from the availability of detailed information from their counterparts in the wild. Knowledge of the range of variability in responses to the kinds of challenges that they have faced from ecological pressures through their evolutionary history in the wild can provide excellent benchmarks for managers working with the animals under more controlled circumstances. Deviations from expected values or patterns observed from wild animals can signal imminent concerns about health and well being. Modeling living situations, from a physical and/or social perspective, after the range of possibilities selected by animals observed in the wild is likely to go far toward reducing stressors that could have adverse impacts on the animals in captivity.

Ideally, a manager would want to obtain as much information from the wild as possible for understanding the complex lives of the species under their care. Data on health, nutrition, behavior, social structure, life history, and ecology are all important. It is equally important to recognize that many of these kinds of data vary with the age and sex of the animals, as well as with a host of other parameters. Research across generations, different age classes, both sexes, a full suite of reproductive conditions, and different ecological situations can be crucial for identifying recurrent patterns that can serve as "norms" and placing them in perspective relative to the full range of variability exhibited by the species. For animals with long lifespans, continuous, consistent, long-term research will be necessary to obtain information with the desired accuracy and precision to provide optimal animal care.

CONCLUSIONS

1. For a long-lived species such as bottlenose dolphins, long-term field research involving a reference wild population can provide detailed insights into patterns of life history, social structure, health, and reproductive success, by following individuals through time.
2. Long-term field research can benefit the care of dolphins in collections, and in turn, the collections can be used to make the public more aware of issues the animals are facing in the wild, and what the public can do to help the wild populations.
3. Long-term field research requires a long-term commitment of resources, as a loss of continuity and consistency can compromise unique datasets.
4. The combination of complementary field and collection research can provide a powerful approach to learning about the biology and behavior of dolphins.

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