BOTTLENOSE DOLPHIN
Molecular and morphological evidence suggest that cetaceans and artiodactyls share a common ancestor and belong to the same group: Cetartiodactyla (SMM Committee on taxonomy, 2016).

Cetacea is one of two scientific groups of large aquatic mammals that live their entire lives in water (Sirenia is the other). Cetaceans include all whales, dolphins and porpoises. Provisionally Cetacea is considered an unranked taxon, as the classification remains partially unresolved.

The word “cetacean” is derived from the Greek word for whale, kētos.

Living cetaceans are divided into two subgroups: Odontoceti (toothed whales) and Mysticeti (baleen whales).

Odontoceti is comprised of toothed whales. These whales also have only one blowhole opening. The word “Odontoceti” comes from the Greek word for tooth, odontos.
Family: Delphinidae

- Dolphins are part of the scientific family Delphinidae. There are approximately 37 species of delphinids (Vilstrup et al., 2011; SMM Committee on taxonomy, 2016), including bottlenose dolphins, Pacific white-sided dolphins, pilot whales and killer whales. It is the most diverse living family of odontocete cetaceans (Aguirre-Fernández et al., 2009; Charlton-Robb et al., 2011).
- Molecular techniques have improved our understanding on family Delphinidae, but many relationships within subfamily Delphininae (to which *T. truncatus* belongs) remain uncertain because of the ability of species to “locally adapt.” This has caused an increase in taxonomy diversity through time (evolutionary radiation) (Charlton-Robb et al., 2011).

Genus: *Tursiops* sp.

- The genus was named by Gervais in 1855 (Wilson and Reeder, 2005).
- *Tursiops*, meaning “dolphin-like,” comes from the Latin word *Tursio* for “dolphin” and the Greek suffix ops for “appearance.”
- There are two species within this genus: *Tursiops truncatus* and *Tursiops aduncus*. (SMM Committee on Taxonomy, 2016). They are differentiated by morphological and osteological characteristics, and, *T. aduncus* is distributed in coastal waters of the Indo-Pacific and Indian Ocean principally (Moller and Beheregaray, 2001).

Species: *Tursiops truncatus*

- The species was described by Montagu in 1821 under the genus *Delphinus*, which, subsequently, was determined to be incorrect (Wilson and Reeder, 2005).
- The species name *Tursiops truncatus* was derived from natural wear exhibited on the teeth of the specimen Montagu observed. It was apparently an old animal with worn (truncated) teeth. He thought (incorrectly) that worn teeth were an identifying characteristic of the species (Wilson and Reeder, 2005).
- In 1966, a published study reported that there were 20 or more species of *Tursiops* sp. (Hershkovitz, 1966). At a 1974 meeting (Mitchell, 1975), biologists recognized the confusion and recommended that, until proper taxonomic studies had been done comparing all of the purported species of the world’s *Tursiops* spp., there should be one species—*Tursiops truncatus*, the Atlantic Bottlenose Dolphin.
- Taxonomists determined that the term, Atlantic Bottlenose Dolphin, was too narrow. Because of the species’ vast numbers and distribution, taxonomists now recognize the animal as the “common bottlenose dolphin” (Moller et al., 2008; Charlton et al., 2006; Natoli et al., 2003; Wang et al., 1999).
- The U.S. National Marine Fisheries Service changed its terminology for the bottlenose dolphin stocks for which the agency conducts annual assessments; the animals are now referred to as the “bottlenose dolphin”. Details can be found on the agency’s Web site (http://www.nmfs.noaa.gov/pr/sars/region.htm accessed 30 June 2016).
- As additional studies are conducted around the world, there may be further changes to *Tursiops* spp. taxonomy. The advent of molecular taxonomic techniques will further help eliminate confusion.

Common names

- English: Common Bottlenose Dolphin, Bottlenose Dolphin
- Español: Delfín nariz de botella, Delfín mular, Tonina, Tursión
FOSSIL RECORD

Early whales evolved over 50 million years ago from primitive mammals that returned to the sea (Barnes, 1990). Mitochondrial and nuclear DNA analyses sustain the theory that cetaceans are distant cousins of even-toed ungulates, and that hippopotamids (artiodactyls) are the closest living relatives to cetaceans (Aguayo and Esquivel, 1991; Milinkovitch et al., 1993; Gatesy, 1997; Berta and Sumich, 1999; Reynolds et al., 2000; Medrano and Baker, 2007).

Archaeoceti is a sub-group of cetaceans that are now extinct. Fossil records of these animals show different evolutionary changes from the early Eocene (55-35 million years ago) to the Oligocene (35-25 million years ago) (Aguayo & Esquivel, 1991; Medrano & Scott, 2007). The following genera show some morphological changes through time within this group:

- Pakicetus sp.
- Rodhocetus sp.
- Protocetus sp.
- Dorudon sp.
- Basilosaurus sp.

Remains of *Tursiops truncatus* appear in the fossil record approximately two million years ago (Reynolds et al., 2000).

GLOBAL DISTRIBUTION

Bottlenose dolphins are found in temperate and tropical waters around the world (cosmopolitan species). They can inhabit a variety of marine and coastal ecosystems of the Pacific, Atlantic, and Indian Oceans, and the Mediterranean Sea (Ridgway and Harrison, 1999).

Bottlenose dolphins in the western North Atlantic are found from Nova Scotia to Patagonia and from Norway to the tip of South Africa. They are the most abundant dolphin species along the United States coast from Cape Cod through the Gulf of Mexico (Reeves et al., 2002). Other types of bottlenose dolphins are found in the Pacific and Indian Oceans, as far north as the southern Okhotsk Sea, the Kuril Islands and central California. They are found as far south as Australia and New Zealand.
HABITANTS

Bottlenose dolphins inhabit warm temperate waters, adapting to a variety of marine and estuarine habitats, including, occasionally, rivers (Ridgway and Harrison, 1999). Habitat use is influenced by environmental heterogeneity; this means that, these animals distribute through an ecosystem depending on factors like resources, depth, water temperature, sea-bed gradient and type of sediment (Ingram and Rogan, 2002).

Scientists theorize that differing ecological characteristics throughout their range have led to differences between bottlenose dolphin populations (Segura et al. 2006). Because bottlenose dolphin populations have inshore and offshore distributions, scientists identify two ecotypes with anatomical, physiological, behavioral, ecological and genetic differences. (Hersh and Duffield, 1990, pg. 129; Díaz, 2003). For example, bottlenose dolphins in Scotland favor deeper areas than those from Florida, US, that prefer shallow waters of less than 3 m depth (Ingram and Rogan, 2002).

Study Cases

- Coastal dolphins generally form smaller cohesive groups (<20) than the offshore (>100) (Segura et al., 2006).
- Inshore bottlenose dolphins are typically seen in bays, tidal creeks, inlets, marshes, rivers and waters along the open ocean beach, often at depths of 3 m (9.8 ft) or less (Wells and Scott, 1999; Hersh et al., 1990; Connor et al., 2000). Some inshore ecotypes seem to be adapted for warm, shallow waters. Its smaller body and larger flippers suggest increased maneuverability and heat dissipation (Hersh and Duffield, 1990; Ridgway and Harrison, 1999).
- The distribution/migration of prey correlated with seasonal changes in water temperature may account for the seasonal movements of some dolphins (Shane, 1990). Inshore bottlenose dolphins found in warmer waters show less extensive localized, seasonal movements and many have been observed staying within a limited, long-term home range, such as in Sarasota Bay, Florida. Adult males range more widely than females, often encompassing the ranges of several female bands. Dolphin communities may overlap providing for genetic exchange. These neighboring communities may be distinct in both behavior and genetics (Scott et al., 1990; Wells et al., 1980, 1987; Wells 1991, 2003, 2009; Wells and Scott, 1999; Duffield and Wells, 1991; Urian et al., 2009).
- In the Northwest Atlantic, researchers determined that bottlenose dolphins within 7.5 km (4.65 mi) from shore were coastal ecotypes. Dolphins beyond 34 km (21 mi) from shore were offshore ecotypes. They also observed that the two ecotypes overlap between those boundaries, and concluded that further habitat-use analysis must be done to explain that situation (Torres et al., 2003).
- In the Gulf of California, coastal and offshore ecotypes differ in color, morphology and group size. The coastal form is bigger, more robust and with a lighter dorsal color than the offshore type. Its rostrum and pectoral flippers are shorter, and groups are formed by <20 individuals. In this study, it was also seen that offshore bottlenose dolphins associate with sperm whales, and have a similar trophic position with them (specifically females and juveniles). Dolphins benefit from this interaction by feeding on similar prey (like Humboldt squid) (Díaz, 2003).

ANATOMY AND PHYSIOLOGY

Body

Bottlenose dolphins are generally slate grey to charcoal in color including simple counter shading (darker dorsally and lighter ventrally). The sides of the body often have light brush markings. Some ventral speckling may be found on the belly depending on location.

Counter shading is considered by scientists to be camouflage that helps conceal dolphins from predators and prey. When viewed from above, a dolphin’s dark back surface blends with the dark depths. When seen from below, a dolphin’s lighter belly blends with the bright sea surface.

Bottlenose dolphins have sleek, streamlined, fusiform (spindle shaped) bodies, designed to minimize drag as they travel through the water. They have three types of limbs that can be differentiated in form, origin, structure, and function:

- **Pectoral Flippers** - Flippers are modified forelimbs that resulted from millions of years of evolution. That is the reason why they have an internal bone structure (modified shoulder, elbow, wrist and phalanges). Their functions are to stabilize the body and to steer (Bejder and Hall, 2002).
- **Fluke/Tail Fin** - This secondary acquired structure derived from outgrowths of skin and connective tissue. The main function of these appendages is propulsion (Bejder and Hall, 2002).
- **Dorsal Fin** - This fin stabilizes the dolphin from rolling without control in the water, and it has a secondary function to conserve or dissipate body heat, as it has more superficial vascular vessels than flukes and pectoral flippers (Meagher et al., 2002).
**Average Adult Length in AMMPA Facilities**
8.5 feet (259 cm) (Based on a 2015 survey of animals in Alliance member facilities. Submitted to the Animal and Plant Health Inspection Service).

**Average Adult Length in the Wild**
7.2–8.9 feet (220–270 cm)

Mass and length of the animals varies by geographic location. Body size of bottlenose dolphins appears to vary inversely with water temperature of location (the colder, the bigger). In some populations, there are size differences between the genders with females growing faster in the first decade of life and males usually growing larger later in life. In other populations there is no size difference. (Reynolds, *et al.*, 2000; Cockroft and Ross, 1990; Read *et al.*, 1993; Mead and Potter, 1990; Wells and Scott, 1999; Perrin and Reilly, 1984).

**Maximum Length Reported in the Wild**
**Eastern North Atlantic:** 13.5 ft (410 cm) (Fraser 1974, Lockyer, 1985)

Larger body size appears to be associated with cold water regions (Cockroft and Ross, 1990,).

**Maximum Adult Weight Reported in the Wild**
**Eastern North Atlantic:** 1400 lbs (650 kg) (Pabst *et al.,* 1999)
**Western North Atlantic:** 626 lbs (284 kg) (Reynolds *et al.* 2000)

**Skin**
Dolphin skin is highly specialized and plays an important role in hydrodynamics. Upon close observation, cutaneous ridges may be seen on the surface of a dolphin’s skin that run circumferentially around the body trunk and vary in direction past the dorsal fin and other isolated areas. Cutaneous ridges may play an important role in sensory function and in drag reduction as a dolphin swims (Ridgway and Carder, 1993).

Dolphin skin has no scent or sweat glands and is without hair except for small whiskers found on the snouts of fetuses and newborn calves (Geraci, *et al.,* 1986).

The animals’ outer skin layer, the epidermis, is an average of 15–20 times thicker than the epidermis of humans (Hicks *et al.,* 1985).

Bottlenose dolphins slough (shed) the outer layer of their skin 12 times per day (every 2 hours). Increased skin cell turnover increases swimming efficiency by creating a smooth body surface which reduces drag (Hicks *et al.,* 1985).

The skin layer under the epidermis is the dermis. The dermis contains blood vessels, nerves, and connective tissue (Sokolov, 1982).

A dolphin’s blubber (hypodermis) lies beneath the dermis. Blubber is a layer of fat reinforced by collagen and elastic fibers. Its thickness fluctuates by season (water temperature) as well as with body size and health status (Pabst *et al.,* 1999; Parry, 1949).

Blubber serves a number of important functions:
- Contributing to a dolphin’s streamlined shape, which helps increase swimming efficiency.
- Storing fat, which provides energy when food is in short supply.
- Reducing heat loss, which is important for thermoregulation.
- Providing a measure of protection from predation, as predators must bite through this layer to reach vital organs. Shark bite scars are not uncommon on wild bottlenose dolphins.

A number of persistent organic pollutants (POPs) can be stored in the lipids of blubber, including polychlorinated biphenyl compounds (PCBs) and some pesticides (Neuenhoff, 2009).

**Head**
Dolphins produce sounds through a specialized nasal complex in conjunction with their respiratory system, and not from vocal chords, as in other mammals. The anatomical complex is formed by air sacs below the blowhole that push air across two structures of connective tissue called “phonic lips” (also known as monkey lips because of their appearance). This system generates both echolocation signals and tonal sounds (Jensen, 2011; Madsen *et al.,* 2012; Brzica *et al.,* 2015).

Echolocation clicks are guided from the phonic lips through the “dorsal bursae” (fatty structures next to them) to the melon. The melon is composed mainly of lipids, and its functions are to couple the sound with the surrounding medium (water) and to direct the clicks (Jensen, 2011).

Dolphins have only one set of 72-104 teeth in a lifetime. They are not replaced once lost (Rommel, 1990; Wells and Scott, 1999).

**Diet**
Scientists identified 43 diverse prey species in the stomachs of 76 stranded dolphins in southeastern U.S. waters. Most fish in their stomachs were bottom dwellers (Sciaenids - drums/croakers/seatrout and Batrachoidids - toadfish) but some were types found throughout the water column (Mugilids - mullet and Clupeids - herring/mackerel/sardines) and pelagic (Carangidae - jacks and Pomatomidae - blue fish) (Barros and Odell, 1990; Barros and Wells, 1998; Connor, *et al.,* 2000; Mead and Potter, 1990).
The diet of coastal bottlenose dolphins is diverse and depends upon geographical location. Many dolphins eat only fish, although some also eat small numbers of cephalopods, crustaceans, small rays and sharks. They generally consume about 5% of their body weight daily (Barros and Odell, 1990). There is strong evidence that bottlenose dolphins are selective feeders, taking fish disproportionately based on their availability in the environment and especially selecting soniferous (sound-producing) fish (Berens-McCabe et al., 2010). In some places, it has been observed that the offshore ecotype includes more cephalopods in their diet than coastal bottlenose dolphins (Díaz, 2003).

To learn about the biology and status of fish stocks, you can consult: http://www.fishwatch.gov/

COGNITION
Dolphin cognition is relatively sophisticated among nonhuman animals (although not in all areas, and the specifics are under debate; Herman, 2010; Jaakkola, 2012; Gregg, 2013; Güntürkün, 2014).

Research has demonstrated the following about dolphin cognition/intelligence:

Basic Cognitive Processes
- Dolphins can learn and understand the concept of “same”, whether tested with visual or auditory input, or even across modalities, where they match objects perceived visually with objects perceived via echolocation (e.g., Herman & Gordon, 1974; Pack & Herman, 1995; Mercado et al., 2000)
- Dolphins can remember the specific whistles of other dolphins for up to 20 years or more (Bruck, 2013)

Physical Cognition (i.e., understanding the physical world)
- Dolphins can judge both relative size (Murayama et al., 2012) and relative numerosity (Jaakkola et al., 2005). That is, they can select which of two objects is larger/smaller, and which of two sets has more/fewer objects.
- Dolphins understand that a hidden object continues to exist (object permanence). However, they fail at tasks that ask them to track the movement of an object inside a container to another location (invisible displacement). (Jaakkola et al., 2010)
- Some dolphins in Shark Bay, Australia use sponges on their rostrums (i.e., “beaks”) as tools, apparently to protect themselves from getting scratched and stung when searching for fish buried in the sandy ocean floor (e.g., Mann et al., 2008).

Social Cognition (i.e., understanding their social world)
- Dolphins cooperate, both for certain feeding strategies (e.g., they may rush onto the shore simultaneously, creating a wave that washes fish onto the mud in front of them [Hoese, 1971]; or one dolphin may drive a school of fish into a barrier of other dolphins waiting side by side [Gazda et al., 2005]), and for mating purposes (e.g., when two or three males cooperate to monopolize a female; Connor et al., 1992). In Shark Bay, Australia, males also cooperate in second-order alliances, in which two existing groups of cooperating males work together to steal a female from another group, or to defend against such thefts (e.g., Connor et al., 1992)
- Some research suggests that dolphins can recognize themselves in a mirror. However, other scientists have pointed out flaws in the methodology of that research, leaving the existence of this capacity in question (Reiss & Marino, 2001; Harley, 2013)
- Dolphins are excellent imitators, with the ability to imitate both vocal and motor behaviors (e.g., Herman, 2002).
Symbolic Cognition (i.e., understanding representations)

- In their natural communication system, dolphins use individually-specific signature whistles that refer to individuals, similar to names. They apparently use signature whistles differently than human names, however, since they primarily produce their own whistle repeatedly, whereas humans more typically say another person's name (e.g., Caldwell et al., 1990; Janik and Slater, 1998).
- Dolphins can understand human-created symbols (whistles or gestures) as referring to objects, actions, and modifiers; and can make sense of combinations of these symbols using simple syntactic rules (e.g., understanding that the combination ‘BALL FETCH SURFBOARD’ means something different than the combination ‘SURFBOARD FETCH BALL’) (Herman et al., 1984).

SENSORY SYSTEMS

Hearing

Dolphins are adapted to produce and hear underwater acoustic stimuli for survival. Sound and phonation are essential elements to all aspects of their life history: for communication, reproduction, development, and echolocation to forage, navigate and explore their environment (Spence, 2015).

A dolphin’s brain and nervous system appear physiologically able to process sounds at much higher speeds than humans, most likely because of their echolocation abilities (Ridgway, 1990; Wartzok and Ketten, 1999). Ears, located just behind the eyes, are pinhole-sized openings, with no external ear flaps.

*Range of Hearing

Bottlenose dolphins, which are mid-frequency specialists, generally have measured hearing ranges within the 150 Hz-160 kHz range. They appear most sensitive above 10 kHz, especially, in the 30-100 kHz range (Spence, 2015).

In other studies, the hearing range for the bottlenose dolphin has been measured in 75 to 150,000 Hz (0.075 to 150 kHz) (Johnson, 1967 and 1986; Au, 1993; Nachtigall et al., 2000; Ridgway and Carder, 1997; McCormick et al., 1970).

The range of hearing of a young, healthy human is 15-20,000 Hz (0.015 – 20 kHz) (Grollier, 1967, pg. 285; Curnell and Johnson, 1998). Human speech falls within the frequency band of 100 to 10,000 Hz (0.1 to 10 kHz), with the main, useful voice frequencies within 300 to 3,400 Hz (0.3 to 3.4 kHz) (Titze, 1994). This is well within a dolphin’s range of hearing.

*Sound Production Frequency Range

Sound production range is 200 Hz to 150 kHz (Popper, 1980; Au, 1993). Whistles generally occur within 1-25 kHz (Caldwell et al., 1990; Au et al., 2000). It has been determined that bottlenose dolphins develop an individually specific “signature whistle” within the first few months of life and that this signature whistle remains the same throughout most, if not all, of their lives. They use these unique whistles to communicate, identity, location and, potentially, emotional state. Dolphins have been observed using signature whistles to cooperate with one another, address other individuals, facilitate mother-calf reunions and, possibly, to broadcast affiliation with other individuals (Caldwell et al., 1990; Janik and Slater, 1998; Janik, 2000; Tyack, 2000; King et al., 2016).

Echolocation

Dolphins often need to navigate in the absence of light/good visibility. Therefore, hearing is essential to them. The bottlenose dolphin auditory system includes a biological sonar ability called echolocation.

To analyze their environment, bottlenose dolphins produce high-frequency clicks which bounce off objects in the water (prey for example) and return to the dolphin in the form of an echo. Echoes are received through the fat-filled cavities of the lower jaw to the middle ear, inner ear, and then to the hearing centers...
in the brain. This complex system allows dolphins to determine the size, shape, structure, composition, speed and direction of an object. Dolphins can detect objects from over 70 meters (230 ft.) away. There is evidence to suggest that dolphins vary the frequency of their clicks depending on their environment, target type and range of the object and to avoid competing with background noise (Popper, 1980; Au, 1993). Bottlenose dolphin echolocation is used only as necessary; individuals do not continuously produce clicks.

Echolocation clicks: 20/30 kHz to 120/150 kHz (Popper, 1980; Au, 1993; Spence, 2015).

Vision
Dolphins are primarily monocular (using one eye to process visual stimuli), but also possess the capability for binocular vision (when both eyes are coordinated for vision (Dawson, 1980).

Glands at the inner corners of the eye sockets secrete oily mucus that lubricates the eyes, washes away debris, and may help streamline the eye as a dolphin swims (Tarpley and Ridgway, 1991).

Evidence suggest that bottlenose dolphins use their right eye predominantly for approaching and investigation when processing visual information (Delfour and Maten, 2006).

Scientists are unsure if dolphins possess color vision (Griebel and Schmid, 2002). Chemical, physiological, and genetic studies suggest they have monochromatic vision (cannot see colors) in the green spectrum based on the absence of certain cones in their eyes. Behavioral studies have suggested they might have some color vision. However, behavioral color vision studies are difficult due to the inability to accurately determine whether the animal is responding to color versus brightness (Griebel and Peichl, 2003).

*Maximum Range of Vision Reported
Bottlenose dolphins have a double slit pupil allowing for similar visual acuity in air and water. Their eyes are adapted to mitigate varying light intensities. Studies show that the visual acuity of dolphins is similar or below the range of many terrestrial animals (Herman et al., 1975; Griebel and Peichl, 2003). There is currently no reference that measures distance of visual capability.

Smell (Olfaction)
Dolphin brains lack an olfactory system or bulbs (sense of smell) (Morgane and Jacobs, 1972; Jacobs et al., 1971; Sinclair 1966).

Taste (Gustation)
Behavioral evidence suggests that bottlenose dolphins can detect three or four primary tastes (sweet, bitter, sour, salty), but the way they use their ability to “taste” is still unclear (Friedl et al., 1990; Feng et al., 2014). Scientists are undecided whether dolphins have taste buds like other mammals. Three studies indicated that taste buds may be found within 5 to 8 pits at the back of the tongue. One of those studies found them in young dolphins and not adults. Another study could not trace a nerve supply to the taste buds. Regardless, behavioral studies indicate bottlenose dolphins have some type of chemosensory capacity within the mouth (Ridgway, 1999).

Touch
The skin of bottlenose dolphins is sensitive to vibrations. Nerve endings are particularly concentrated around the dolphin’s eyes, blowhole, genital area, and rostrum, suggesting that these areas are more sensitive than the rest of the body (Ridgway and Carder, 1990).

SWIMMING
Dolphins are among the world’s most efficient swimmers. Their “fusiform” body shape (rounded torpedo-like shape and gradually tapering tail) allows water to flow continuously from the body to the tail region. This delayed separation results in reduced wake and drag. Additionally, the curvature of the pectoral flippers, dorsal fin, and tail flukes, cutaneous ridges, skin folds and subdermal mechanical properties of the skin, are morphological features that reduce drag and can also create lift (Williams et al., 1993; Carpenter et al., 2000; Fish, 2006).

Research on this has different results as conditions of study sites are different (wild versus human care, physical conditions, life history of individuals, etc.) and means of study (speed, acceleration, drag, duration of effort, etc.).

*Average Swimming Speed
Bottlenose dolphins routinely swim at speeds of 4.6-10.2 feet per second (3.43-6.95 miles/hour; 5.04-11.19 km/hour) with a mean speed of 4.9-5.6 f/s (3.43-3.82 miles/hour; 5.4 to 6.14 km/hour) (Würsig and Würsig, 1979; Shane 1990; Williams et al., 1993; Noren, et al., 2006).

*Maximum Swimming Speed
Maximum observed speed of a trained bottlenose dolphin swimming alongside a boat was 26.7 feet/second (18.20 miles/hour; 29.30 Km/hour). Maximum observed swimming speed of a dolphin swimming upward prior to a vertical leap was 36.8 f/s (25.09 miles/hour; 40.38 km/hour). Both were completed in very short durations. Maximum swim speed that could be observed for wild dolphins was 18.3 f/s (12.47 miles/hour; 20.08 km/hour) (Lang and Norris, 1966; Würsig and Würsig, 1979; Rohr et al., 2002; Noren et al., 2006). According to Fish (1993) “high-speed swimming is limited to the power that the individual animal can generate and, while energetically possible in dolphins, high speeds are limited to bursts of short duration”.

DIVING
Diving cetaceans must balance metabolic demands associated with limited oxygen while supporting energy loss as they move. That is, “one response promotes the conservation of oxygen stores, and the other simultaneously requires their utilization” (Williams et al., 1999).

During breath-hold diving (apnea), bottlenose dolphins maximize the use of oxygen stores by decreasing their heart rate (bradycardia) and constricting peripheral vascular vessels. With this, they favor the most oxygen-dependent tissues by reducing blood flow to visceral organs, skin, and muscles. (Skrovan et al., 1999; Williams et al., 1999b; Velasco-Martinez et al., 2016).
In their study, Mate et al. (1995) show that the mean dive duration of bottlenose dolphins differed significantly during the day. In the morning, the animal under study spent more time at the surface with shorter dives.

*Average Dive Duration*
The average dive duration of coastal bottlenose dolphins ranges from 20–40 seconds. (Mate et al., 1995; Shane, 1990; Irvine et al., 1981; Wursig, 1978). Mean dive duration of 25.8 sec (Mate et al., 1995).

*Maximum Breath Hold/Dive Time Reported*
The maximum voluntary breath hold recorded for a coastal bottlenose dolphin was 7 minutes 15 seconds (Ridgway et al., 1969; Irving et al., 1941). The maximum breath hold duration registered for a tagged off-shore bottlenose dolphin was 14 min in Bermuda in September 2016 (J. Sweeney, pers. comm. February 2017).

*Average Dive Depth*
Depths of dives depend on the region inhabited by the species. Coastal bottlenose dolphins usually inhabit waters of less than 9.8 feet (3 meters) (Hersh et al., 1990).

*Maximum Dive Depth Recorded*
Trained coastal bottlenose dolphin: 1,280 ft (390 m) (Ridgway and Scronce 1980, unpublished observations, cited in Bryden and Harrison, 1986).

Tagged wild offshore bottlenose dolphin: 1614+ ft (492+ m) (Klatsky et al., 2007).

A study conducted in September 2016 in Bermuda registered the deepest dive of a tagged off-shore bottlenose dolphin of 1,005 m (J. Sweeney, pers. comm. February 2017).

**THERMOREGULATION**
The thermoregulatory status of dolphins depends on their activity and state of submergence. These animals, like other mammals, balance their temperature condition by controlling the blood flow through their body. During rest, there is minimal heat dissipation. When moving or exercising, blood is directed toward the skin and the arrangement of vessels in their fins and flukes, which function as “thermal windows.” In those areas, blood is being cooled as cool water passes over the body, while heat is transferred from the body to the water. Cetaceans take advantage of cooled blood from these peripheral sites to regulate temperature-sensitive organs like heart, brain, lungs or gonads (Noren et al. 1999; Williams et al 1999b).

Blubber is a thick subcutaneous layer of fat that acts as a heat insulator for the internal body environment. It also streamlines a dolphin’s hydrodynamic body shape to minimize drag (Bejder and Hall, 2002).

**BEHAVIOR**

**Social Grouping**
Group composition has been observed to be dependent upon sex, age, reproductive condition, familial relationships and affiliation history. Typical social units include nursery groups (females and their most recent calves), mixed sex groups of juveniles, and strongly-bonded pairs of adult males (Wells and Scott, 1990; Wells et al., 1987; Wells et al., 1980; Wells, 1991).

Bottlenose Dolphin communities around the world are described as “fission-fusion” societies. This means that individuals associate in groups dynamically: they merge or split within the same aggregation several times per day. It has been seen that some societies live in large mixed-sex groups with strong associations within and between the sexes (Lusseau et al., 2003).

Bottlenose dolphin females form alliances primarily to obtain food resources (Krützen et al., 2004), and their association with males seem to be mainly linked to a reproductive goal (Lusseau et al., 2003).

Bottlenose dolphin males in Shark Bay, Australia, have been observed to form groups to socialize and obtain access to females by two different strategies. One strategy involves the formation of a small and stable alliance (2-3 males), where males cooperate to control individual females in reproductive condition. A second strategy involves the formation of flexible alliances within a stable large second-order alliance called “superalliance”. Here, individual males frequently switch their alliance partners within the superalliance (Connor et al., 2000; Krützen et al., 2004).

Coastal bottlenose dolphins are primarily found in groups of 2–15 individuals. The associations of the animals are fluid, often repeated but not constant. Solitary coastal animals are observed in various regions of the world (Stewart, 2006).
**Foraging**

Foraging methods, habitat use patterns, and spatial dispersion are diverse in bottlenose dolphins, and tend to be influenced by habitat type, prey type, and accessibility (Silber and Ferl, 1995; Torres and Read, 2009). Hunting methods are learned by calves primarily through observing their mothers and have been seen to proliferate throughout a population, suggesting that knowledge may be culturally transmitted (Wells, 2003). Bottlenose dolphins forage both in groups and individually, and display different and innovative foraging techniques: mud plume/ring feeding, fish herding, kerplunking, crater feeding, strand/beach feeding, sponge feeding, and fishing gear depredation/cooperative net fishing (Sargeant et al., 2005; Torres and Read, 2009).

Coastal bottlenose dolphins often feed in water that is 10ft (3m) or less. They are active both during the day and at night (Shane, 1990; Smolker et al., 1997; Barros and Wells, 1998; Wells and Scott, 1999; Wells et al., 1999).

**Sleep State**

Several species of cetaceans, including the bottlenose dolphin, have been shown to engage in unihemispheric slow wave sleep (USWS) during which one half of the brain goes into a sleep state, while the other maintains visual and auditory awareness of the environment and allows the animal to resurface for respiration. This ability may help to avoid predators as well as maintain visual contact with cohorts/offspring. Dolphins have one eye closed during USWS (Ridgway, 1990; Ridgway, 2002; Lyamin et al., 2004; Lyamin et al., 2008).

**REPRODUCTION AND MATERNAL CARE**

**Sexual Maturity**

Bottlenose dolphins display variation in the average age at which they reach sexual maturity, based on gender, geography, and individuals. Females have been known to reach sexual maturity from 5 to 13 years old (Kastelein et al., 2002; Neuenhoff, 2009). The average age at which bottlenose dolphin females in Sarasota Bay have their first offspring is 8–10 years. In the wild, males reach sexual maturity between the ages of 8 and 13 years (Harrison, 1972; Odell, 1975; Perrin and Reilly, 1984; Wells et al., 1987; Mead and Potter, 1990; Kastelein et al., 2002; Wells et al., 2009). Females reach sexual maturity at 7 to 10 years of age under human care, and male dolphins are sexually mature at 7 to 12 years old (Kastelein et al., 2002).

**Ovulation cycle**

Female dolphins generally ovulate 2–7 times per year with a cycle length of about 30 days. They are seasonally polyestrous, and estrous occurs from spring to fall (Dierauf & Gulland, 2001). The estrous cycle varies in length from 21–42 days (Robeck, et al., 1994; Schroeder, 1990; Kirby and Ridgway, 1984).
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### Gestation

Approximately 12 months (Robeck et al., 1994; Perrin and Reilly, 1984; Schroeder, 1990; Tavolga and Essapian, 1957)

### Birthing Season

Birthing season is dependent on geographical location. Births may occur in all seasons, but typically peaks occur during spring, early summer and fall (Caldwell and Caldwell, 1972; Wells et al., 1987; Mead and Potter, 1990; Cockcroft and Ross, 1990). Females give birth to an approximately 111 to 116.3 cm (43.7-45.7 in.) calf (Neuenhoff, 2009). This estimate is consistent with others depending on the geographic region (between 84-140 cm) (Ridway and Harrison, 1999).

### Nursing Period

Nursing/lactation periods are difficult to determine in the wild but appear to be a primary source of nutrition for wild calves for an average of 18-24 months (Wells et al., 1999; Cockcroft and Ross, 1990; Perrin and Reilly, 1984; Oftedal, 1997). The maximum nursing period observed was 7 years in Sarasota Bay, FL and may serve as a bonding activity. For the first year, and, in some cases more than a year, lactation is the primary source of nutrition for dolphin calves under human care. Calves generally start eating fish sometime within their first year, depending upon mothering style and facility (Cockcroft and Ross, 1990; Wells et al., 1999; Wells and Scott, 1999).

### Dependent Period

In the wild, bottlenose dolphin calves stay an average of 3 to 6 years with their mothers (infancy). Particularly during the first year, calves gain experience in social interactions like play and other affiliative behaviors. Temporary separations from mothers are frequent and often long-distance, and calves may be alone or with others, spending a greater proportion of time foraging (Gibson and Mann, 2008). Gibson and Mann (2008) suggest that calves, prior to weaning, have social and ecological sex-specific challenges: females are likely to develop foraging strategies similar to their mothers, while males are likely to begin developing social bonds. The longest period that a calf in the wild was observed with its mother was 11 years, documented in the Sarasota, Florida region. Generally, calves become independent about the time the next calf is born. The dependency period of calves in zoological facilities is much shorter because the animals are not vulnerable to predation, do not have to learn foraging techniques, and are well fed (Perrin and Reilly, 1984; Cockcroft and Ross, 1990; Read et al., 1993; Wells et al., 1999; Wells and Scott, 1999).

### Average Years between Offspring

Bottlenose dolphins have a 3 to 6 years calf interval in Sarasota Bay, Florida (Perrin and Reilly, 1984; Cockcroft and Ross, 1990; Read et al., 1993; Wells et al., 1999; Wells and Scott, 1999.) Zoological facilities have very successful reproduction programs. Calving intervals in human care vary based on individual facility animal management planning.

There is little to no indication of senescence (menopause) in the female bottlenose dolphin. Successful births and rearing have been witnessed up through 48 years of age in the Sarasota dolphin population (Wells and Scott, 1999; Reynolds, et al., 2000; Wells, pers. comm. Dec. 2010).

### Longevity and Mortality

Over the years, advances in medical and husbandry knowledge (e.g., Dierauf and Gulland, 2001) have contributed to improved longevity of dolphins in human care, to the point where today, survivorship measures for bottlenose dolphins in facilities accredited by the Alliance of Marine Mammal Parks and Aquariums (AMMPA), are similar to or better than those reported for wild populations (see below).

### Annual Survival Rate & Life Span

In scientific studies, survivorship has been examined either by determining the annual survival rate of a population (excluding calves under 1 year of age), from which median life span can be calculated, or by constructing life tables from which median life span can be read directly. These studies have shown that:

- Survival rates have been increasing in marine mammal parks and aquariums (Small and DeMaster, 1995; Innes, 2005), with the most recent study showing an annual survival rate of 0.97 (which means 97% of the population is expected to survive from one year to the next) for dolphins in U.S. facilities (Innes, 2005). This corresponds to a median life span of 22.8 years.
- Survival rates reported for wild populations have varied widely, from .902 to .961, with median life spans between 8.3 and 17.4 years (Wells and Scott, 1990; Stolen and Barlow, 2003; Mattson et al., 2006; Neuenhoff, 2009). These differences may be due to differences in study methodology (i.e., tracking a live population vs determining the age of dead animals that stranded), or may reflect true lifespan variations in different wild populations.
**Maximum Known Longevity**
- The oldest bottlenose dolphin in human care was Nellie, who lived to be 61 years old. She was born February 27, 1953, at Marineland of Florida, now Georgia Aquarium’s Marineland Dolphin Adventure in St. Augustine, Florida.
- The oldest bottlenose dolphin in the wild is Nicklo, who was 66 years old when she was last sighted in 2016 in the Sarasota Bay population. Researchers extracted a tooth from her in 1984 to determine her age.

**Infant First-Year Survivorship**
The most recent studies report first year survival of:
- 78 to 86.3% of calves in different sub-groups of U.S. facilities (Wells, 2009; Sweeney et al., 2010; Venn-Watson et al., 2011)
- 76 to 77.5% of calves in different wild populations (Neuenhoff, 2009; Wells, 2009)

**PREDATORS**
Sharks are potential predators of coastal bottlenose dolphins, especially tiger, great white, bull and dusky shark (Cockcroft et al., 1989). In Sarasota Bay, Florida, about 31% of dolphins bear shark bite scars (Wells et al., 1987).

**CONSERVATION**
Bottlenose dolphins are found in great numbers in the open ocean and along shorelines. The species is not endangered, threatened or vulnerable. The International Union for the Conservation of Nature (IUCN) lists it as a species of least concern. However, threats to the animals are increasing.

Marine mammals are excellent sentinels of the health of their environments because they have long life spans, feed high on the food chain, and their blubber can be analyzed for toxin build up. The 2002 Marine Mammal Commission report states “A variety of factors, both natural and human-related, may threaten the well-being of individual dolphins or the status of dolphin stocks. Natural factors include predation by large sharks, disease, parasites, exposure to naturally occurring biotoxins, changes in prey availability, and loss of habitat due to environmental variation. Growing human-related factors include loss of habitat due to coastal development, exposure to pollutants, disturbance, vessel strikes, entanglement in debris, noise and pollution related to oil and gas development, direct and indirect interactions with recreational and commercial fisheries, and injury, mortality, or behavior modification that may result from direct human interactions such as the feeding of wild dolphins. These factors may act independently or synergistically. Compared with offshore bottlenose dolphins, coastal dolphins may be at greater risk to human-related threats due to their greater proximity to human activities.”

Chemical residues that are released into the environment by human activities, such as pesticides, herbicides, and fire retardants, increase the vulnerability of dolphin populations to diseases and reproductive failure. (Stavros et al., 2011; Hall et al., 2006; Wells et al., 2005; Schwacce et al., 2002; Lahvis et al., 1995; Kuehl et al., 1991; Cockcroft et al., 1989). These findings have both direct and indirect impact on human health as well (Fair et al., 2007; Bossart, 2006; Houde et al., 2005).

The increase of emerging and reemerging diseases affecting dolphins and other marine mammals in the wild could signify a broad environmental distress syndrome as human activities trigger ecologic and climate changes that foster new and reemerging, opportunistic pathogens affecting both terrestrial and marine animals (Bossart, 2010).

In addition to the human competition with dolphins for food resources, mortalities and serious injuries from recreational and commercial fishing gear are among the most serious threats dolphins face (Wells and Scott 1994; Wells et al., 1998). Entanglement in fishing gear is a significant cause of injury and mortality to many marine mammal populations throughout the world. Along the east coast of the United States, gill net fisheries’ by-catch of bottlenose dolphins exceed sustainable population mortality levels established under the U.S. Marine Mammal Protection Act (Read and Wade, 2000). Research focused on mitigation efforts center around disentanglement, gear modification, and deterrent devices/enhancements; however, until recently most of the emphasis has been on commercial fisheries.

Dolphins have been observed following recreational vessels and “depredating” fishing lines (removing the fish and eating it), sometimes resulting in entanglement/ingestion-related mortality. Dr. Randall Wells, head of the Sarasota Dolphin Research Project, the longest running study on bottlenose dolphins in the world, noted that 2% of the study population was lost to ingestion/entanglement conflicts with recreational fishing gear in one year. This percent, in addition to natural mortality factors, is unsustainable and if not mitigated could put the population at risk (Powell and Wells, 2011; Cox et al., 2009; Noke and Odell, 2002; Waring et al 2009; Wells et al., 1998).

Heavy boat traffic can affect the distribution, behavior, communication, and energetics of the animals (Nowacek et al., 2001; Buckstaff 2004). Dolphins have been known to be struck by boats in high traffic areas, causing injury and death (Wells and Scott 1997).

Feeding or swimming with dolphins in the wild teaches them to approach boats, making the animals vulnerable to potential propeller strikes, fishing gear entanglement, ingestion of foreign objects, or intentional harm from humans. Additionally,
increasing human interaction and/or boat traffic may cause coastal bottlenose dolphins to abandon important habitats (Bryant, 1994; Wells and Scott, 1997 pg. 479; Cunningham-Smith et al., 2006; Powell and Wells in press). The AMMPA Guide to Responsible Wildlife Watching with a Focus on Marine Mammals is posted at www.ammpa.org. This guide recommends viewing all wildlife from a safe and respectful distance and explains the harm caused by feeding dolphins in the wild (AMMPA, 1995).

Some AMMPA Facilities Contributions to Conservation

Much of what is known about dolphin and marine mammal health care, physiology, reproductive biology, and intelligence has been learned through scientific studies in zoological parks and aquariums over the last 70+ years: research not possible in the wild (Hill and Lackups, 2010). Wild marine mammals directly benefit from knowledge gained from animals under human care. Hill and Lackups (2010) analyzed the content of 1,628 scientific articles from specialized journals on cetaceans from 1950 to 2009. They found that 29% of them correspond to captive cetaceans, 68% to the wild, and 3% from both. The main topics that were published from cetaceans under human care were biology, cognition, echolocation, and sound detection. The most cited genus is Tursiops sp. with 42.9% of the articles.

- The National Marine Mammal Foundation hosts a database to provide searchable information on past and ongoing marine mammal research studies. These studies are conducted by members of the AMMPA, foundation researchers and other like-minded organizations pursuing bona fide research with marine mammals (http://nmmpfoundation.org/alliance.htm).
- Two special 2010 issues of the International Journal of Comparative Psychology (IJCP) titled “Research with Captive Marine Mammals Is Important” Part I and Part II, highlight the significance of research with marine mammals in parks and aquariums. Contributing authors address the value of cetacean populations under human care in understanding reproductive physiology, which plays a role in conservation efforts, and advancing our understanding of the animals and what they tell us about their counterparts in the wild (Kuczaj, 2010a, b).

Dolphins provide the opportunity for zoological parks and aquariums to play a unique and unrivaled role in marine mammal education and conservation. AMMPA-member education programs make a difference.

Two independent research studies conducted in 2009 conclude that guests viewing dolphin shows demonstrated an increase in conservation-related knowledge, attitudes, and behavioral intentions immediately following their experience and retain what they learn, and that participants in dolphin interactive programs learned about the animals and conservation, shifted their attitudes and acquired a sense of personal responsibility for environmental stewardship (Miller et al., 2013; Sweeney, 2009).

These studies confirm the results of a Harris Interactive® poll the Alliance commissioned in 2005 (Harris Interactive, Rochester, NY) and a 1998 Roper poll (Roper Starch Worldwide, Inc. New York, NY).

The Harris poll found that the public is nearly unanimous (95%) in its acclaim for the educational impact of marine life parks, zoos and aquariums. In addition, 96 percent of respondents agree that these facilities provide people with valuable information about the importance of our oceans and the animals that live there (AMMPA, 2005).

The AMMPA’s Ocean Literacy Reference Guide is a collection of ocean messages aimed at educating the public about the importance of our oceans to all living things. The fundamentals of these messages—the Essential Principles of Ocean Literacy—were developed by a consortium of 186 members (developers and reviewers) of the ocean sciences and education communities during an online workshop sponsored by the National Oceanic and Atmospheric Administration, the National Geographic Society’s Ocean for Life Initiative, the National Marine Educators Association and the Centers for Ocean Sciences Education Excellence. Messages focus on marine debris, climate change and man-made sound in our oceans (AMMPA, 2007).

Above all, guests view parks and aquariums as cherished and traditional places for family recreation, a center for discovery, a resource for wildlife education and motivators for environmental stewardship.

For additional information please refer to one of the following books:
5. Society for Marine Mammalogy species accounts (www.marinemammalscience.org)
   a. Tursiops truncatus
   b. Tursiops aduncus


Jacobs, M.S. (ed.). The Oxford Handbook of Comparative Psychology 130: 205-271.


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