Chapter 15
Common Bottlenose Dolphin Foraging: Behavioral Solutions that Incorporate Habitat Features and Social Associates

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Abstract Common bottlenose dolphins (*Tursiops truncatus*) live in a large variety of habitats, where they confront a wide range of ecological challenges to which they have developed diverse behavioral solutions. They inhabit shallow marsh creeks, estuaries, bays, open coasts, islands, shelves, and deep open ocean. Abiotic factors such as physiography, salinity, temperature, depth, tidal excursions, and currents influence ecological factors that in turn help shape behaviors of bottlenose dolphins, within their morphological and physiological constraints. Among the ecological factors of greatest importance for influencing bottlenose dolphin behavior is its prey, and foraging serves as the focus of this review. Bottlenose dolphins consume a wide variety of prey, primarily fish and squid, that typically are taken in one bite. Prey vary in size, energy content, behavior, schooling tendency, speed, maneuverability, seasonal availability, sensory abilities, sound production, defenses, location in the water column, and use of habitat features or structures. The availability of potential prey to the dolphins is dictated largely by the dolphins' biology and the development of appropriate skills for detecting, capturing, and handling prey. The interplay of characteristics of the fish, features of their environment, and capabilities of the dolphins themselves shape the dolphins' foraging behaviors and influence dolphin sociality.

Keywords Common bottlenose dolphin · Foraging behavior · Feeding behavior · Passive listening · Cooperative behavior · Observational learning · Human interactions

Foraging involves a suite of behaviors from searching for and detecting prey, through pursuit, capture, and handling (e.g., Nowacek 2002). Foraging behaviors

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are influenced by a number of factors such as innate physical abilities, sensory systems, ability to learn, familiarity with prey, familiarity with area and habitat, ability to work with conspecifics, and habitat features that can facilitate prey detection or capture. Bottlenose dolphins employ a variety of senses in the first stage of foraging, detecting prey. The relative utility of dolphin sensing capabilities varies with habitat. They can use vision in clear water, but must rely on acoustics when underwater visibility is poor, as is the case in many of their inshore habitats. This can take the form of passive listening, in which dolphins listen for sounds produced by the prey fish themselves. Alternatively, active echolocation can be used to find prey, balanced against the risk that at least some prey species are able to sense echolocation and initiate evasive maneuvers.

In shallow inshore waters, prey detection may benefit from individual dolphin residency to a well-established home range, familiarity with the available prey and conditions, and experience with the most effective approaches for finding prey individually. Bottlenose dolphins in many areas have demonstrated long-term residency to well-defined home ranges (Wells and Scott 2018). In Sarasota Bay, Florida, such residency has been documented across more than four decades, and involves at least five generations within a given lineage, including individuals up to 67 years of age (Wells 2014). In deep open waters, where prey schools tend to be mobile and patchy but rich, integrated sensory systems from bottlenose dolphins working in groups may extend prey finding abilities over a broader area (Norris and Dohl 1980). Groups tend to be more variable and reach larger sizes in offshore waters; group size may be constrained at least in part by the ability of the food patches to meet energetic needs of the group (Wells et al. 1980; Scott and Chivers 1990).

Once a prey item has been detected, pursuit can involve a direct chase in open waters, or in the case of prey using habitat features for cover, specialized behaviors may be employed for flushing prey, as described below. In a direct chase, a bottlenose dolphin tends to have an advantage in terms of speed, but its larger size constrains its maneuverability, so prey may have an advantage in terms of tight maneuvering.

Prey capture can involve a variety of specialized techniques, depending on prey type and habitat. In inshore waters, bottlenose dolphins often feed individually. Individual dolphins may use features of the habitat as barriers to restrict prey movements for capture. Where barriers are absent, such as in deep offshore waters, or even in some cases when barriers exist, bottlenose dolphins can work together to limit prey options for escape. Coordinated foraging by dolphins in groups is often used with schooling prey.

While most bottlenose dolphin capture of fish involves head-first grasping and ingestion of whole prey with minimal oral manipulation, specialized prey handling techniques have also been developed. Bottlenose dolphins at multiple sites in the Gulf of Mexico feed on marine catfish by severing the head from the remainder of the body (Ronje et al. 2017). Special care must be taken when feeding on these potentially deadly fish. Strong, sharp, venomous dorsal and pectoral spines attached to the head can cause serious injury or death, as evidenced by stranding reports describing tissue trauma or secondary infections from catfish spines (Ronje et al. 2017). The exact mechanism for separating heads from tails is not understood, but based on observations of catfish carcasses, it seems likely that fish are grasped from behind, and a combination of biting and dolphin head motion against the resistance of the water results in the separation. On occasion, tailless catfish have been observed at the surface near dolphins, still exhibiting swimming motions. Catfish do not appear to be a frequent item in the diet of most dolphins, based on stomach contents (Barros and Wells 1998; McCabe et al. 2010). However, this may be a somewhat biased assessment given the importance of otoliths for identifying stomach contents and the fact that catfish heads, with their ear bones, are not consumed. One stranded bottlenose dolphin was found with 72 headless catfish in its stomach. Catfish have been consumed when other prey fish have been abundant. The reason for selecting such a dangerous prey requiring special handling is unclear, but may be related to the ease of finding them given that the fish make sounds (Barros 1993) that make them easy to find, they are often found in schools, and gravid catfish can have very high energy content (Ronje et al. 2017). Occasional removal of heads before consumption of other large fish has also been reported for bottlenose dolphins in Patagonia and elsewhere (Caldwell and Caldwell 1972; Würsig 1986). In one unusual case in Costa Rica, a male and female bottlenose dolphin shared prey, passing a fish back and forth multiple times before consuming it (Fedorowicz et al. 2003).

Within the framework of general foraging patterns described above, bottlenose dolphins have developed a number of specialized techniques for prey detection, pursuit, and capture. Most techniques have been described for dolphins in shallow water situations, during daylight hours, due to the difficulties of observing dolphin behavior in the dark or in deep water. However, thanks to technological advances, behavioral data are becoming available from indirect observations. Foraging occurs throughout day and night in at least some shallow water habitats, such as Sarasota Bay, Florida, with dolphins eating small proportions of their total daily intake in brief bouts (Wells et al. 2013). Satellite-linked telemetry shows continued movements and dives through typical feeding areas during both day and night (Wells et al. 2013). Acoustic recordings from a hydrophone array in the dolphins' home range documented the nighttime occurrence of echolocation clicks consistent with those used during foraging, with additional evidence from forestomach temperature telemetry indicating ingestion of prey at night and during the day (Wells et al. 2013).

Technology has also provided insights into foraging behaviors of deepwater bottlenose dolphins. Off the Hawaiian Islands, bottlenose dolphins occur in well-defined home ranges mostly in waters less than 1000 m deep and feed during day and night, including nearshore and reef fishes in daytime (Baird 2016). Using satellite-linked telemetry, Baird documented presumed nighttime feeding dives to 752 m. Similarly, bottlenose dolphins off the island of Bermuda outfitted for up to 23 hrs with short-term digital archival acoustic tags (Fig. 15.1) were recorded making feeding buzzes both in surface waters and at depths of up to 500 m. The deepest foraging dives occurred at night, presumably to feed on organisms associated with the deep scattering layer that migrates vertically relative to light levels (F. Jensen, pers. comm.). Surface feeding was observed directly during the day. Over the next 1.5 months, satellite-linked time-depth-recording tags on the same dolphins showed them to make presumed foraging dives as deep as 1000 m, remaining submerged for up to 13.5 min (Wells et al. 2017).

Fig. 15.1 Common bottlenose dolphin, *Tursiops truncatus*, outfitted with DTAG on its back, cranial to the dorsal fin, and a satellite-linked time-depth-recording tag trailing from its dorsal fin, for studying behaviors including foraging in the deep waters off Bermuda. Photo courtesy of Dolphin Quest Bermuda

The most complete and detailed foraging behavior descriptions result from direct observations of bottlenose dolphins in shallow water. In some cases, the animals have developed complex techniques specific to certain sites, while other complex techniques are seen across much of the species range. The shallow water seafloor, with its associated physiography, structures, and vegetation, provides numerous opportunities for dolphins to make use of these environmental features to enhance foraging success.

Nowacek (2002) studied sequential foraging behavior of bottlenose dolphins in shallow waters of Sarasota Bay, Florida, from the novel perspective of an overhead video camera suspended 50 m above the water from an aerostat tethered to a small houseboat, from which hydrophones were also deployed, to link acoustic and visual records. The overhead system allowed the collection of detailed and continuous behavior records of distinctive well-known individuals, even when the animals were submerged. He examined patterns of transitions between events and states to define progressive stages of foraging. The dolphins of Sarasota Bay fed primarily as individuals. Specific feeding patterns varied from individual to individual, but general patterns emerged. Following detection of the possible presence of prey fish, dolphins went through stages of active search, terminal pursuit, and capture. Several iterations of the initial stages may occur before prey are actually captured—the choice of which behaviors are used in a foraging sequence can be influenced by a variety of factors including habitat, prey type, and individual preferences (Nowacek 2002).

Prey fish detection in shallow habitats may occur in several ways. In Sarasota Bay, vision underwater is limited by turbidity, so initial detection is likely acoustically mediated, through passive listening or active echolocation. Many fish produce noise, and based on examination of dolphin stomach contents, Barros and Odell (1990) and Barros (1993) hypothesized that dolphins use sounds of soniferous fishes to facilitate hunting. Gannon et al. (2005) advanced this hypothesis through playbacks of recorded fish sounds to free-ranging dolphins in Sarasota Bay. Quantitative fish surveys demonstrated that bottlenose dolphins select soniferous fishes disproportionately to their availability in Sarasota Bay (McCabe et al. 2010). However, in areas with better underwater visibility, such as Turneffe Atoll, Belize, passive listening for soniferous fishes appears to be less important (Eierman and Connor 2014).

As part of the initial detection process, when a Sarasota Bay dolphin senses the possibility of a hidden prey, it may engage in rooting, drifting, looking back, or bottom disturbance behaviors (Nowacek 2002). Looking back is a form of inspection of a possible prey situation. During rooting, the dolphin is oriented almost vertically in the water column with its rostrum close to or digging into the bottom. Drifting is a variant of rooting, in which the dolphin remains above the sea floor. Rooting is likely a variant and predecessor to such behaviors as "crater feeding" in the Bahamas (Rossbach and Herzing 1997), in which a dolphin, after scanning with echolocation from side to side, may burrow nearly to pectoral fin depth in a sandy sea floor, presumably to obtain prey. Crater feeding was documented for 18% of identifiable dolphins, and half of these engaged in it repeatedly, suggesting its importance as a foraging strategy. It may also be similar to a behavior referred to as "drilling" observed in shallows in places such as Barataria Bay in the northern Gulf of Mexico, in which a dolphin is vertical in the water column, swishing its tail back and forth at the surface, presumably seeking prey in the seafloor (pers. obs.).

Bottom disturbance can be used to flush or concentrate prey. It involves a dolphin creating a small and local cloud of sediment by swimming near the bottom, often repeated in succession, and often accompanied by production of a bubble cloud (Nowacek 2002). In the Florida Keys, a variant of this behavior, mud plume feeding, is used by individual dolphins for capturing prey in shallow water (<1 m deep). The dolphin uses downward fluke thrusts near the seafloor to create a 5–10 m-long linear or curvilinear plume of mud (Lewis and Schroeder 2003). The dolphin immediately turns into the flume and lunges through the surface, usually on its right side. It is unclear what fish are targeted, but ballyhoo (*Hemiramphus brasiliensis*) have been observed jumping ahead of a lunging dolphin on nearly one-half of observations. It may be that fish are attracted to food stirred up by the plume, or the plume may concentrate fish as they seek to hide in the mud cloud.

The foraging strategy of kerplunking may be employed by some individuals to flush prey in shallow water (<2.5 m deep), by causing a fish to move rapidly when it was previously motionless in the cluttered environment of a seagrass bed. For this behavior, a dolphin raises its tail flukes out of water and then forcefully brings the flukes through the water's surface, sometimes multiple times in succession as the dolphin moves in a line or semicircle (Wells 2003). Kerplunking creates a geyser 1–2 m high, a subsurface bubble cloud and trail, and a loud "kerplunking" sound. Most kerplunking in Sarasota Bay occurs within one dolphin body length of seagrass beds. Kerplunking is not unique to Sarasota Bay—it has been described from other sites along the west coast of Florida and for Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Western Australia (Connor et al. 2000). Connor et al. (2000) suggested that sound pressure or particle displacement from kerplunks may evoke a startle response in the fish, making them more detectible, and may be able to reveal the location of fish in a broader area than the dolphin's echolocation cone. In Sarasota Bay, there is indication for observational learning of the behavior by offspring and nonrelatives (Wells 2003).

Active searching for targeted prey immediately precedes prey capture and can involve scanning with echolocation to localize a prey fish (Nowacek 2002). Side-swimming, in which an animal is rotated 90° with respect to its longitudinal axis and swims with normal fluke motion, is often associated with this stage in Sarasota Bay.

Terminal pursuit involves a variety of behaviors culminating in prey capture. Sometimes, individual prey capture is as straightforward as the dolphin simply overtaking a fish during the chase (Bel'kovich et al. 1991; Nowacek 2002). Dolphins may approach prey in normal orientation, inverted, or on their sides, with orientation perhaps related to optimizing vision or echolocation as they close on the prey and/or the need for quick, tight maneuvers (Leatherwood 1975). Pinwheeling, in which a dolphin tucks its head and spins, rotating around the midpoint of its body, allows a dolphin to make an extremely tight turn in response to evasive maneuvers by fish. Fishwhacking, during which a side-swimming dolphin uses a forceful, fast (<1 s) dorsal or ventral thrust of its flukes to strike one or more fish, often propels fish into the air (Wells et al. 1987). Fishwhacking may be an energy-efficient means of catching fast-moving or schooling prey, by increasing surface area of dolphin's body to be able to disturb, disorient, or even make contact with or disable prey, thereby making them easier to capture (Nowacek 2002). Fishwhacking may be performed by individuals or simultaneously by multiple dolphins. The final step in terminal pursuit involves rapid acceleration or lunging to grasp prey between the dolphin's teeth.

In shallow water habitats, individuals are able to use physical features of the habitat as obstacles to restrict prey fish movements. Bel'kovich et al. (1991) described dolphins in the Black Sea driving fish toward shore and herding fish toward the wing of stationary fishing nets, using it as an obstacle against which fish could be driven and in some cases pushed toward shore. Torres and Read (2009) described herding of fish in Florida Bay up against mud banks, mangrove islands, or seagrass beds. In Sarasota Bay, Florida, some individual dolphins or lineages engage in driving fish up against, and chasing them along, structures such as seawalls, using the wall, the seafloor, and the water's surface to limit the prey's escape opportunities.

Many of the behaviors described above can be used by individuals alone or simultaneously by multiple animals in a group. Beyond engaging in simultaneous behaviors that may or may not benefit both parties, bottlenose dolphins also engage in coordinated group foraging behaviors, in some cases with clear differentiation of roles for specific individuals. Some of the more complex group foraging patterns also make use of specific features associated with shallow water habitats.

Cooperative herding by bottlenose dolphins of schools of fish such as mullet (family Mugilidae), menhaden (*Brevoortia* sp.), or catfish into a gradually tightening ball has been described by a number of observers (Morozov 1970; Caldwell and Caldwell 1972; Leatherwood 1975; Bel'kovich et al. 1991). Würsig (1986) noted that some of the same dolphins that engaged in individual foraging near shore also foraged cooperatively in more open waters, moving in a line abreast, and joined with other dolphins. Dolphins encircling the fish from above, around, and below take advantage of stragglers, or some individuals charge through the school, while others maintain the tight ball. In some cases, the water's surface and/or shoreline help to constrain fish movements. Leatherwood (1975) described a sweeping herding pattern, in which dolphins in a crescentic formation drove schools of small fish ahead of them, picking off stragglers or occasionally darting into the school.

Feeding success appears to increase when dolphin groups use habitat features to constrain fish movements. Rossbach (1999) described bottlenose dolphin groups in the Bahamas swimming rapidly in waters 3–4 m deep, actively herding fish together into a circle of about 8–10 m diameter. They drove the fish into the seagrass and then slowly captured individual small fish. In the Black Sea, bottlenose dolphin groups drive fish schools into shallows and force them to the surface or against the beach (Bel'kovich et al. 1991). There is no evidence of specialization of dolphin roles in this herding. Torres and Read (2009) described similar behaviors for dolphin groups in Florida Bay, where dolphins herded fish up against mud banks, mangrove islands, or seagrass beds.

More extreme variants of these strategies incorporating habitat features involve dolphins forcing the fish out of water and in some cases following them ashore for capture. Leatherwood (1975) reported groups of dolphins driving fish against or onto mud banks in the northern Gulf of Mexico, where they would slide out to capture fish. Hoese (1971) described dolphins in tidal creeks of salt marshes in Georgia working together to create pressure waves and push schools of primarily mullet or menhaden onto the banks. The dolphins then follow fish onto the banks, often on their right sides, to remove fish from the mud, and then slide back into the water. Hoese suggested that this coordinated behavior passed from generation to generation through social learning. Petricig (1995) described similar behavior for dolphins in South Carolina, breaking the behavior down into phases of location and approach, setup, charge, landing, and exit. Subsequent work at the same site by Duffy-Echevarria et al. (2008) found that strand feeding is typically performed by 3–4 dolphins, that not all adults in a group engage in the behavior, and that individuals do not have specific preferred stranding positions.

In the upper Florida Keys, bottlenose dolphins engage in cooperative foraging that incorporates bottom disturbance, known as mud ring feeding (Torres and Read 2009). One individual encircles a school of mullet with a ring of mud, and members of the dolphin group catch the fish as they leap out of the ring. Engleby and Powell (2019) provide a detailed description of this shallow water behavior, in depths less than 2 m, involving 3–4 dolphins on average. As the ringmaker begins to circle the school of fish with strong fluke beats creating mud boils, other members of the group concentrate the fish, and then position themselves where the ring will be completed, with heads out of the water and mouths open. The ringmaker closes the ring, spiraling on its side with a final fluke thrust toward the center of the ring, and ends up aligned

Fig. 15.2 Upon completion of the mud ring, a final fluke thrust by the ringmaker sends mullet (Mugilidae) leaping in a predictable direction, toward waiting dolphins. Photo by Brian Skerry, National Geographic

with the other waiting dolphins. The final fluke thrust apparently causes the fish to jump predictably toward the dolphins, as they attempt to avoid the sound and/or pressure of the fluke-generated boils, as sensed by their lateral line or swim bladder (Fig. 15.2). Observations of similar behavior in clearer waters 450 km to the north suggest the mud boils are by-products due to sediments and not crucial to the prey capture technique. More than 19% of dolphins identified by Engleby and Powell in the study area engage in mud ring feeding, some of them repeatedly, but it was rarely possible to identify ringmakers. Engleby and Powell support the suggestion of Torres and Read (2009) that social learning and cultural transmission are likely important for the development of this technique, which takes advantage of or requires specific habitat features, such as depths of less than 2 m.

Bel'kovich et al. (1991) described dolphins in the Black Sea driving fish schools against "walls" formed by other dolphins. Similarly, near Cedar Keys, Florida, groups of 3–6 dolphins engage in cooperative foraging in which one "driver" dolphin herds fish (primarily mullet) in circles toward a tight barrier of dolphins (Gazda et al. 2005). As the fish are driven into this barrier, and sometimes after a tail slap, they leap and are caught by lunging dolphins. In each of two groups observed repeatedly by Gazda et al. (2005), the driver was always the same, suggesting a clear division of labor with role specialization. Foraging success varied with group stability. Follow-up studies demonstrated that drivers have higher foraging success than barrier dolphins (Gazda 2016).

Bottlenose dolphins have also learned to use human activities as barriers to restrict fish movements. In addition to the use of fixed nets as walls to direct herded fish as described by Bel'kovich et al. (1991), in several parts of the world, dolphins predictably drive fish schools toward humans actively working in the water with nets. Busnel (1973) related several ancient accounts of such interactions and described in detail a more recent symbiotic fishing cooperative from the coast of Mauritania, where mixed groups of Atlantic humpback dolphins (*Sousa teuszii*) and presumed bottlenose dolphins apparently responded to mullet jumping or the similar sound of fishermen slapping the water as nets are being set in shallow water. The dolphins rush in around the nets and the standing fishermen, catching mullet and chasing mullet into the nets.

Along the southern coast of Brazil (Laguna, Santa Catarina), bottlenose dolphins interact predictably with cast-netting fishermen (Simões-Lopes et al. 1998). These dolphins drive schools of mullet toward a line of fishermen standing in the water and indicate with stereotyped head or tail slaps when and where the fishermen should cast their nets; because of turbidity, the fishermen are unable to see the fish themselves. The dolphins stop about 4 m away from the fishermen, the fishermen cast their nets to cover the space in between, and the dolphins open their mouths to catch the disoriented and isolated escaping fish. This cooperative behavior is performed by 45% of the local dolphins at Laguna, and those dolphins that engage in cooperative behavior tend to associate more closely with one another than with noncooperative dolphins (Daura-Jorge et al. 2012). It has been suggested that social learning is important for maintaining this specialized behavior. In both cases described above, these activities are believed to improve fishing success of dolphins and humans and are mutualistic.

Other dolphin foraging strategies that take advantage of human activities, especially fishing, to improve their foraging success do not provide benefits to the humans and in some cases result in damage to fishing gear and/or risks to dolphins. Interactions with fishing operations take many forms, including taking fish stirred up by nets, falling out of nets, or discarded by fishers as bycatch (Leatherwood 1975; Caldwell and Caldwell 1972; Read et al. 2003); with dolphins actively plucking fish from nets (depredation, Leatherwood 1975; Read et al. 2003), taking bait or catch from hook and line gear (depredation, Zollett and Read 2006; Powell and Wells 2011; Baird 2016), removing bait from crab traps or scavenging discarded bait (Noke and Odell 2002), and taking fish proffered by humans (provisioning; Cunningham-Smith et al. 2006; Powell and Wells 2011). Risks from fishing gear include becoming entangled in nets and drowning (Zollett and Read 2006), becoming entangled in crab trap float lines (Wells et al. 2008; Noke and Odell 2002), and becoming entangled in, becoming hooked by, or ingesting hook and line gear, leading to serious injury or death (Wells et al. 2008; Stolen et al. 2013).

Using an overhead video camera suspended from an aerostat off North Carolina (the same system used by Nowacek 2002), Read et al. (2003) observed bottlenose dolphins patrolling gillnets set for Spanish mackerel (*Scomberomorus maculatus*). Although dolphins are killed in such nets, during the research no entanglements were observed. However, dolphins removed mackerel and bluefish (*Pomatomus saltatrix*) from the nets, and holes were found in the net following depredation. Several of the dolphins engaged in begging from the boat, waiting for fish to be discarded.

Bottlenose dolphins are attracted to fishing trawlers in many parts of the world and take fish from the actively trawled net as well as during cleaning and discarding of bycatch (Greenman and McFee 2014). Off Savannah, Georgia, dolphins behind shrimp trawlers approach most closely when fishermen are manipulating and cleaning nets, leading to begging behavior on more than 89% of trawling days (Kovacs and Cox 2014). However, only a portion of the dolphins approach the boats during haulback and net cleaning. Similar findings were reported by Gonzalvo et al. (2008) relative to bottom trawling in the Mediterranean Sea.

Provisioning of dolphins, either through direct feeding or inadvertently through discarding of fish, can decrease dolphin awareness of threats in the environment, such as predators or fishing gear. Provisioning can lead to the ingestion of inappropriate items that can adversely impact their health, or attract them to situations where they are at increased risk from fishing gear, boat collisions, or retaliation/vandalism (Cunningham-Smith et al. 2006; Powell and Wells 2011). Christiansen et al. (2016) noted that dolphins in Sarasota Bay, Florida, conditioned to human interactions through direct or indirect food provisioning, were more likely to be injured by human interactions, when compared to unconditioned animals. Thus, conditioning could lead to a decrease in survival, which could ultimately affect population dynamics (Christiansen et al. 2016).

There is an innate component to bottlenose dolphin foraging behaviors, but there are also important learning and experience elements in developing foraging behaviors, especially with regard to the interplay of prey and habitat features. Some of the more complex behaviors described above, including those that involve human activities, have developed fairly recently in the evolutionary history of bottlenose dolphins. The impressive ability of bottlenose dolphins to learn is well known from decades of working with and observing bottlenose dolphins under human care. Under these circumstances, behavior is readily shaped through reinforcement with a food reward (Ramirez 1999). Performance of a desired behavior results in obtaining fish, which leads to repeating the behavior. In the wild, successful foraging behaviors inherently involve a food reward.

Bottlenose dolphin abilities for social learning through observation are well known for dolphins under human care (Pryor 1973). Individuals exhibit new (to them) behaviors after observing others perform the behavior (Norris 1974). In the wild, evidence for social learning comes from several sources, including observations of highly coordinated foraging patterns. Christiansen et al. (2016) noted that the association with already conditioned dolphins strongly affected the probability of dolphins becoming conditioned to human interactions, suggesting that conditioning is at least partly a learned behavior. Wells (2003) suggested that one of the reasons behind the 1.5–4.5 years of calf rearing extending beyond nutritional weaning for bottlenose dolphins in Sarasota Bay is the need for calves to learn survival skills from the mother and her close associates. It is not uncommon to observe Sarasota Bay mothers and their most recent calves engaging in bouts of foraging behaviors, during which perfectly performed behaviors by the mother, such as kerplunking, are followed by incomplete versions of the behavior by the younger animals. Such observations are among those leading Wells (2003) to suggest the occurrence of

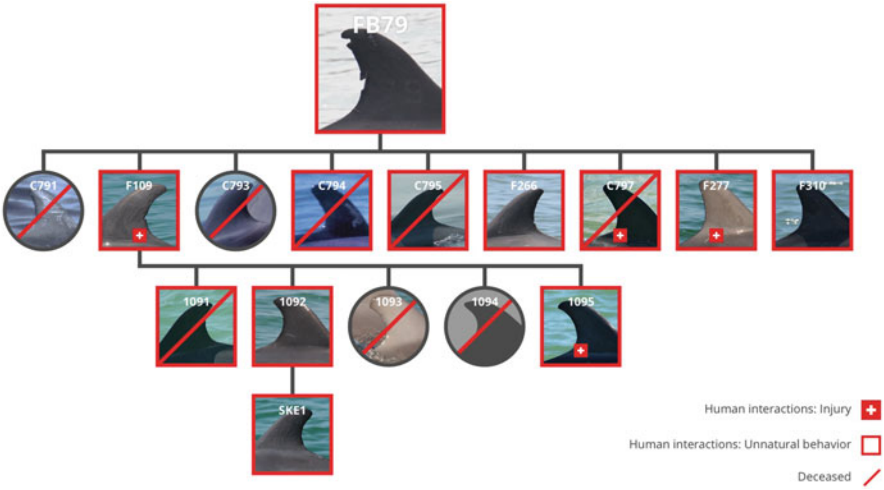

Fig. 15.3 Four-generation maternal lineage of long-term resident Sarasota Bay common bottlenose dolphins, *Tursiops truncatus*, related to 39-year-old female FB79, indicating those individuals that engage in unnatural behaviors related to human interactions, those with evidence of injuries from human interactions, and whether the individual is still alive. Figure prepared by René Byrskov and Katherine McHugh

cultural transmission of knowledge in bottlenose dolphins, as exhibited through foraging behaviors. Following the definition of Whiten et al. (1999, p. 682) of cultural behavior as "being transmitted repeatedly through social or observational learning to become a population-level characteristic," patterns of occurrence of foraging behaviors within and across a variety of bottlenose dolphin research sites around the world support vertical and horizontal transmission of behaviors (Wells 2003). Whitehead et al. (2004) provide strong additional evidence for the idea that culture is an important determinant of behavior in cetaceans.

While social learning can be an important factor in acquiring natural foraging behaviors, it appears that it can also lead to the development of unnatural foraging behaviors that can place bottlenose dolphins at risk. In Sarasota Bay, Florida, research initiated in 1970 has provided detailed records for members of a long-term resident community of about 170 bottlenose dolphins (Wells 2014). Some maternal lineages are more inclined than others to engage in unnatural behaviors involving interactions with humans, including behaviors such as patrolling near fishing boats, lines, or piers, scavenging discarded bait or catch, depredating bait or catch from active fishing gear, begging, accepting food from humans, and interacting with fixed fishing gear such as crab pots, among others. Some of these behaviors lead to injury or death (Powell and Wells 2011; Christiansen et al. 2016). In an example of apparent transmission of risky behaviors vertically through four generations, a 39-year-old female (FB79) that frequently engages in unnatural behaviors has been observed with nine calves over the course of her life (Fig. 15.3). Seven of these engaged in unnatural behaviors, and at least three of these exhibited injuries or died from human interactions. One daughter, F109, who engages in unnatural behaviors related to human interactions, has had five calves. Three of these have exhibited unnatural behaviors including one with an injury from human interactions, and the remaining two died within days of birth, before they could develop such behaviors. F109's daughter, 1092, has had one calf to date, and this calf also engages in unnatural behaviors. Mothers who bring calves into close proximity of human activities and engage in unnatural foraging behaviors in the calves' presence provide sufficient opportunity for the calves to learn the risky behaviors.

Near-shore bottlenose dolphins (we do not know enough of the oceanic forms) are highly adaptable to humans and to human-degraded environments. They exhibit an impressive range of variability in natural and human-adapted foraging behaviors and thereby adapt to a wide variety of ecological challenges. They have demonstrated the ability to make use of their innate capabilities and enhance these abilities to improve foraging success by incorporating features of their environment, other dolphins, and in some cases humans in a range of behaviors that involve high levels of complexity. Knowledge of the diverse repertoire of these animals and the role of learning in developing foraging behaviors not only leads to a fuller appreciation of their amazing abilities but can also aid in designing conservation strategies for protection of the animals and their habitats.

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