

HIGH PERFORMANCE TURNING CAPABILITIES DURING FORAGING BY BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*)

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ABSTRACT

Large predators should have difficulty catching small prey because small animals demonstrate greater maneuverability and agility compared to large animals. The ability of a predator to capture small prey indicates locomotor strategies to compensate for inequities in maneuverability. Bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida feed on fish at least one order of magnitude smaller than themselves. To examine the locomotor strategies involved in prey capture, the foraging movements of these dolphins were videotaped from overhead using a remotely-controlled camera suspended from a helium-filled aerostat, which was tethered to an observation vessel. Dolphins were observed to rapidly maneuver during chases of fish in open water or around patches of rooted vegetation. Video analysis of the chase sequences indicated that the dolphins could move the rostrum through small radius turns with a mean value of 0.20 body lengths and with a minimum value of 0.08 body lengths. Mean rate of turn was 561.6°/sec with a maximum rate measured at 1,372.0°/sec. High turning rates

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with small turning radii were primarily the result of maneuvers in which the dolphin rolled 90° and rapidly flexed its body ventrally. The ability of dolphins to change body orientation in multiple rotational axes provides a mechanism to reduce turning radius and increase turning rate to catch small, elusive prey.

Key words: bottlenose dolphin, *Tursiops truncatus*, foraging, predator-prey, maneuverability, turning, pinwheel, swimming.

In predator-prey situations, maneuverability and agility are expected to be significant factors in determining the outcome of such interactions (Howland 1974, Webb 1983). Highly maneuverable predators will be successful capturing elusive prey while, conversely, more maneuverable prey will be successful escaping quick predators. Maneuverability has been defined as the ability to turn in a confined space (Norberg and Rayner 1987) and has been measured in terms of length-specific minimum turning radius and maximum turning rates (Howland 1974, Webb 1994, Domenici 2001, Fish 2002, Fish *et al.* 2003). Small turning radii and high turning rates are indices of maneuverability in space and time, respectively (Domenici 2001).

Prey can escape from a faster predator if it can turn in a smaller circle than the smallest turning circle of the predator (Howland 1974, Webb 1976). In general, maneuverability and agility decrease with body length and are constrained by body flexibility (Webb 1983, Domenici 2001, Fish 2002, Fish and Nicasastro 2003). Large aquatic vertebrates should have difficulty catching small prey because the overall maneuverability of small prey is likely to be superior to that of large predators (Webb 1976, Domenici 2001). Yet predators regularly catch their prey, suggesting predators employ locomotor and/or behavioral strategies to compensate for inequities in maneuverability between themselves and smaller, elusive prey.

Dolphins are generally considered relatively inflexible animals compared to other marine mammals, such as sea lions, and compared to fish (Fish 2002, Fish *et al.* 2003). For the bottlenose dolphin (*Tursiops truncatus*), a large variety of fish and/or squid comprises most of the diets (Würsig 1986, Leatherwood and Reeves 1990, Wells and Scott 1999), although they do seem to show a consistent preference for sciaenids (drums and croakers), scombrids (tunas and mackerels), and mugilids (mulletts) across regions (Mead and Potter 1990, Wells and Scott 1999). Mead and Potter (1990) estimated body length from otoliths of fish found in the stomachs of stranded and incidentally captured *T. truncatus*. They found that the prey fish ranged from 2 to 60 cm, which is in agreement with other studies (*e.g.*, Barros and Odell 1990, Shane 1990, Barros and Wells 1998). As these fish are approximately 0.8%–27.0% of the mean length of *T. truncatus* (Mead and Potter 1990), the fish potentially have an advantage of being able to out-maneuver (*i.e.*, smaller turning radius, higher turning rate) a dolphin. Fish use anti-predation tactics involving high-acceleration turning (Webb 1976, Domenici 2001). In addition, evasion by prey fish is further enhanced by the use of refuges in structurally complex environments (*e.g.*, coral reefs, rocky bottoms, vegetated habitats). Bottlenose dolphins, then, must utilize a variety of locomotor and behavioral strategies to capture elusive, more maneuverable prey, including the use of tail-slaps (Hult 1982, Smolker and Richards 1987, Würsig 1986, Domenici *et al.* 2000), pinwheels (Shane 1990, Wells and Scott 1999, Nowacek 2002), “fish whacking” or “fish kicking” (Wells *et al.* 1987, Scott *et al.* 1990, Shane 1990, Wells and Scott 1999,

Nowacek 2002), temporary beaching on mud banks (Hamilton and Nishimoto 1977, Wells and Scott 1999, Reynolds *et al.* 2000) and cooperative herding and division of labor (Leatherwood 1975, Würsig 1986, Shane 1990, Simila and Ugarte 1993).

Recording detailed locomotor and behavioral sequences is an essential part of foraging research, yet analyses of these sequences for bottlenose dolphins have been limited due to the difficulties of viewing subsurface behavior (Nowacek 2002). To examine the locomotor strategies involved in prey capture, we quantitatively measured the maneuverability and agility of foraging bottlenose dolphins in Sarasota Bay, Florida using videography. In addition to quantitative analyses of turning performance, we present a detailed discussion of the "pinwheel" behavior, a pursuit behavior often observed for dolphins during foraging (Nowacek 2002). Pinwheeling has been described in previous studies (Scott *et al.* 1990, Shane 1990), but there is no consistent definition of a pinwheel across the literature. In this study, we offer a more comprehensive description that is perhaps indicative of the precise function of the pinwheel.

METHODS

Approximately 20 h of continuous focal-animal behavioral data were collected with the overhead video system (OVS) developed by Nowacek *et al.* (2001) in Sarasota Bay, Florida. The OVS platform consisted of a 60-Hz custom Industrial Video Systems video camera suspended from a helium-filled aerostat balloon, which was tethered to a 6-m, outboard powered, partially enclosed observation vessel, and a towed acoustic recording system modeled after Sayigh *et al.* (1993). The video camera was controlled from aboard the vessel with a 360° continuous pan (max speed 100°/sec), 90° tilt, and iris and focus control. Video was recorded by a Sony HR1000 digital video recorder and stored on standard VHS videotape. The aerostat was flown approximately 50 m above the vessel. Dolphins were followed at a distance of ≥ 15 m from the vessel to minimize disturbance.

Bottlenose dolphins resident to Sarasota Bay spend much of their time in inshore waters consisting of open bays (water < 4 m deep) and shallow flats (< 2 m deep), with areas of sea grass channels (~ 3 m deep) passing through them (Nowacek *et al.* 2001). OVS footage was obtained during daylight hours in these shallow areas (Nowacek *et al.* 2001, Nowacek 2002). Photographic identifications were made of 11 individuals observed in this study (Scott *et al.* 1990; Wells 1991, 2003), although turns were measured for only nine of the dolphins.

From the video footage, the presence of fish was not always detectable due to the limits imposed by camera resolution, therefore, sequences were scored as probable hunting/foraging when at least one dolphin was engaged in activities suggesting pursuit of prey. Activities included sudden acceleration and "pinwheeling," behaviors that were demonstrated by Nowacek (2002) to be involved in foraging sequences. Sequences were analyzed frame-by-frame at 30 Hz with a Panasonic AG-7300 video recorder and a Panasonic CTJ-2042R video monitor. Sequences were only used when there were no changes in zoom or orientation of the camera throughout the turn.

Without a fixed reference mark to indicate the location of a center of gravity (CG), it was impossible to keep track of a wild dolphin's CG, which is typically used in most studies of turning performance for animals in captivity (*e.g.*, Webb

1983, Domenici and Blake 1997, Fish *et al.* 2003). Turning performance was determined instead by tracing the sequential positions of the tip of the animal's rostrum throughout the turn onto transparencies from the video monitor. As wind buffeted the aerostat and the camera was panned to keep the dolphin in the field of view, the image of the dolphin was displaced among sequential video frames. To compensate for collective displacements of camera and dolphin, at least two fixed reference points (*e.g.*, the sea grass beds characteristic of the area) were used to establish a frame of reference. The trajectory of the dolphin could be mapped from the sequential positions of the rostrum by overlying the transparency with the fixed reference points. Turning radii were calculated from the linear distance from an arc fitted to the sequential positions of the rostrum and the center of rotation calculated by the method of Youm *et al.* (1978). Turning angles were measured with a protractor from the angular displacement of the beginning and end of the turning arc with the center of rotation as the vertex, and turning rate (ω , in degrees/sec) from the angular displacement of the turn divided by the elapsed time of the turn (Blake *et al.* 1995, Gerstner 1999, Fish *et al.* 2003). Immediately prior to the turning maneuver the dolphin's body was straight and this body length (L) was measured directly from the screen using a ruler and used as a scale for the turning sequence. By using the dolphin as its own scale, it was not necessary to know the exact body length of any individual to quantify data on turning performance and avoid measurement error due to parallax. Length-specific values of turning radius (r/L) were calculated. The error in turning radius for a dolphin located 15 m from the boat was computed as approximately 1%, compared to a dolphin next to the boat and directly beneath the camera.

To examine the turning performance of the dolphins, data were expressed as maximum and minimum values, and means \pm 1 SD. Because maximal performance was of interest, mean values were calculated for the 20% of values representing greatest maneuverability (*i.e.*, minimum turning radius and maximal ω). Choice of the extreme 20% of values was considered arbitrary but was used previously in examinations of turning performance (Webb 1983, Gerstner 1999, Fish 2002, Fish and Nicastro 2003, Fish *et al.* 2003). Regression equations as computed using KaleidaGraph (version 3.0) software. Comparisons of mean turn rates and turn radii for foraging groups of one vs. two dolphins were made with a paired *t*-test. (DataDesk). Results were considered significant at $P \leq 0.05$.

RESULTS

A total of 41 turning sequences were analyzed to determine turn radius and turning rate. Mean r/L was 0.21 ± 0.10 , the minimum 20% of values was 0.09 ± 0.01 , and the minimum r/L was 0.08. Mean ω was $561.6 \pm 295.6^\circ/\text{sec}$, the maximum 20% of values was $997.5 \pm 179.2^\circ/\text{sec}$ and the maximum ω was $1,372.0^\circ/\text{sec}$.

There was a curvilinear decrease in ω with increasing r/L measured at the rostrum (Fig. 1). The relationship between r/L and ω was described by the equation:

$$\omega = 163.26(r/L)^{-0.66}.$$

Overhead observations captured foraging activities that involved only one or two dolphins at a time. In many cases, more dolphins out of the camera's view were in

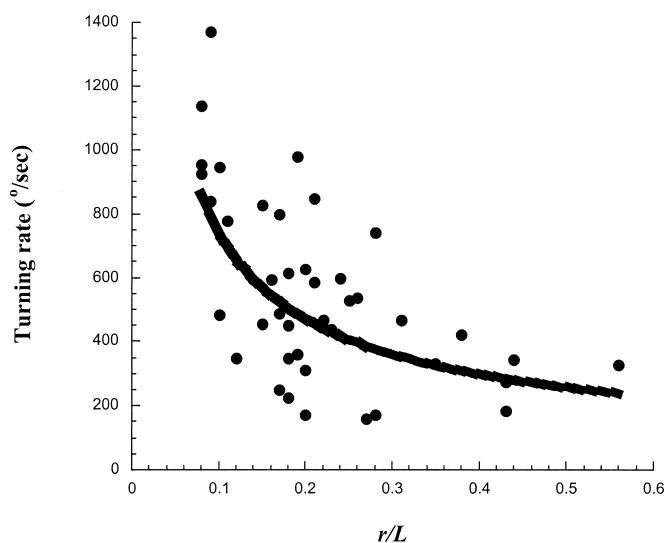


Figure 1. Comparison of turning rate to radius of the turn relative to body length for bottlenose dolphins. The equation for the regression line is provided in the text.

the area perhaps foraging, and their potential effects on the turning performance of individuals analyzed in this study are unknown. However, when group size as captured on video increased to more than two individuals, any obvious foraging activities were no longer observed. For this reason, a single animal foraging alone or two animals swimming side-by-side and engaged in foraging activities together were considered typical foraging “group sizes” that could be used for comparisons of performance.

Of the turning sequences analyzed, 23 (56%) involved two dolphins, and 18 (44%) one dolphin. Single animal foraging sequences were usually characterized by very short feeding rushes interspersed with long sequences of side-swimming and meandering. In groups of two, the animals were often observed rooting in the bottom substrate with their rostrums, and sometimes coordinating their foraging efforts by synchronous circling, side-by-side swimming and feeding rushes. A feeding rush was characterized by a sudden acceleration ending in a pinwheel behavior (Shane 1990). In general when two dolphins were foraging together, they did not appear to coordinate feeding rushes on fish. However, in some instances, a school of fish would become positioned between the two dolphins. The dolphins would roll 90° simultaneously so that each dolphin’s venter was facing the other and then flex the body. This action rotated the rostrum of each dolphin toward the intervening school.

Mean turn rate for all single foraging dolphins was $712.0 \pm 292.8^\circ/\text{sec}$ and the mean turn rate of $430.6 \pm 217.6^\circ/\text{sec}$ calculated for dolphins in groups of two. Mean turning radii between animals foraging in groups of one and two 0.18 ± 0.9 r/L and 0.25 ± 0.12 r/L , respectively. However, comparisons of four dolphins, which had maneuvering sequences both singly or with a partner, showed no significant differences for turning radii ($t = 1.33$; $df = 3$; $P < 0.27$) and turn rate ($t = 1.72$; $df = 3$; $P < 0.18$).

Foraging dolphins also were observed frequently using the pinwheel strategy (Fig. 2), allowing the animal to turn at a high rate and with small turning radii. The maneuver was almost always preceded by sudden acceleration and side-swimming, in which the dolphin rolls 90° with respect to its long axis and rapidly flexes its body ventrally (see Nowacek 2002 for a more complete description of side-swimming). While rapidly swimming in this manner, the dolphin would then enter into the pinwheel maneuver. During the pinwheel, the animal appeared to keep its rostrum at a fixed point, and rapidly rotate its body around that point. Throughout the turn the ventral aspect of the body was directed towards the inside of the turn. A pinwheel was an extremely fast chase maneuver which the dolphins completed in under a second. After completing the turns, the dolphin would either continue on in this high-speed feeding rush sequence, or return to slower foraging behaviors, having apparently either caught or lost the prey fish. Pinwheel sequences, however, could not be used in quantitative analyses of turning performance because the behavior was characterized by rotation of the body around an essentially fixed rostrum, and the resolution of the camera system was insufficient to accurately detect any small changes in the displacement of the rostrum.

DISCUSSION

In predator prey relationships, agility and maneuverability can be more important than speed (Howland 1974). Predatory behavior necessitates high maneuverability and agility due to the scaling effects between the predator and its prey (Howland 1974, Domenici 2001); prey can escape from a faster predator if it can turn in a smaller circle than the smallest turning circle of the predator (Howland 1974; Webb 1976, 1983). Previous studies have determined that the turning performance of dolphins in terms of minimal space and maximal rate falls far short of the maneuvering performance elicited by fish (Fig. 1). The bottlenose dolphin (*Tursiops truncatus*) was reported to produce a minimum turning radius of 0.3 m (0.13 *L*) and a maximum ω of 405°/sec when measured from the animal's center of gravity (Fish 2002). Gerstner (1999) reported that fish ranging in size from 0.043 m to 0.046 m could turn at rates of 4,730–7,301°/sec, and Webb (1983) found that larger fish (0.24–0.26 m) could turn with radii of 0.03–0.05 m (0.11–0.17 *L*) with rates of 3,114–5,509°/sec. There are no data available on the maneuverability of the specific prey fish of *Tursiops*, however the fishes from these other studies were within the range of body sizes consumed by bottlenose dolphins in Sarasota Bay (Mead and Potter 1990, Barros and Wells 1998). Barros and Wells (1998) examined the stomach contents of stranded bottlenose dolphins from Sarasota Bay, revealing a diet of exclusively fish, with pinfish (*Lagodon rhomboides*) comprising approximately 70% of all items consumed. Pinfish averaged 0.1 m in size. There is thus an order of magnitude difference in performance between the prey and the predator, with the advantage going to the prey.

The results from the present study, however, demonstrate that dolphins can intercept fish, despite the inequity in turning performance due to size. As prey capture is the ultimate objective for foraging dolphins, maneuverability of the mouth—the part of the body responsible for catching and securing prey—may be an ecologically more important gauge of turning performance than movement around the animal's center of gravity. Turning rates and radii, which were measured at the rostrum of bottlenose dolphins, yielded levels of turning performance that

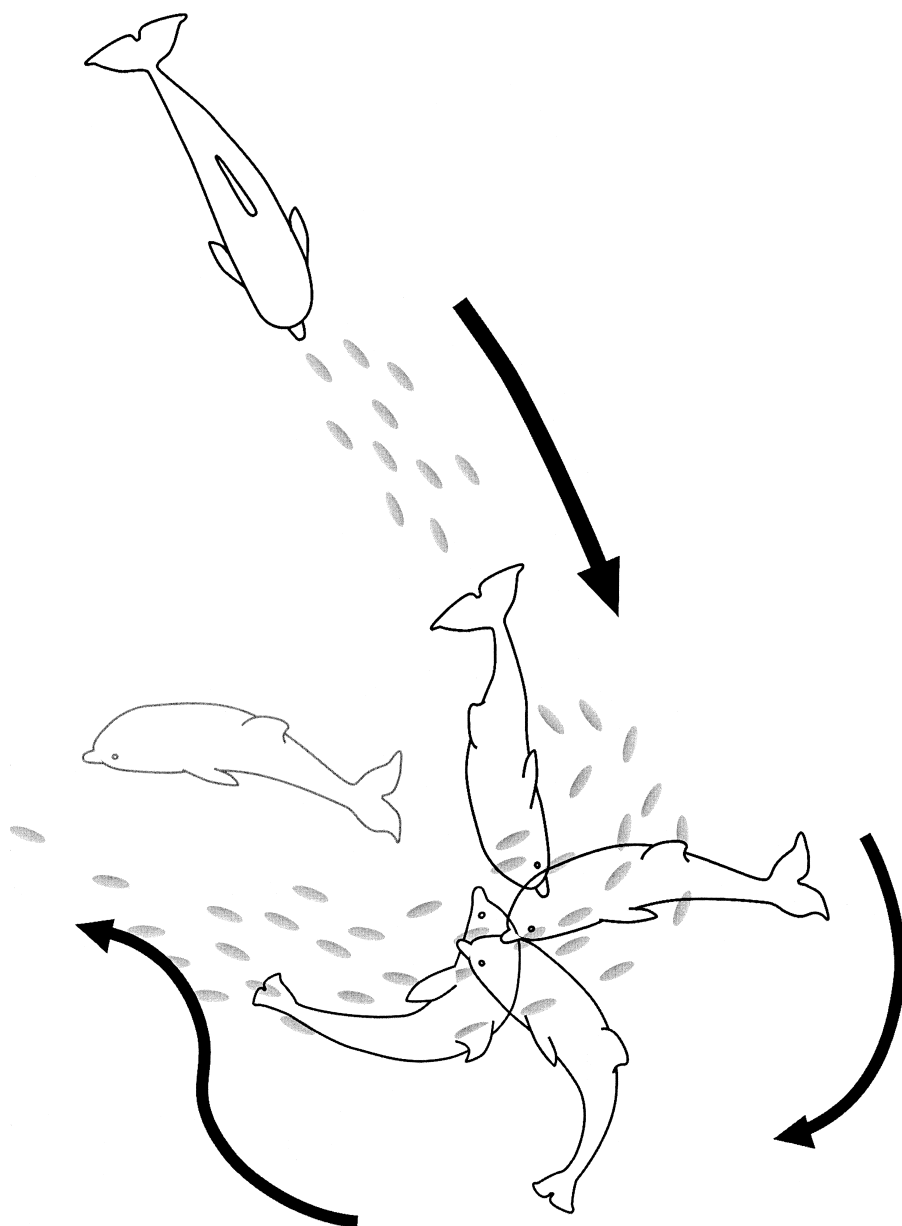


Figure 2. The sequence of maneuvers involving pinwheeling for a single dolphin chasing a school of fish. The arrows show the direction of travel of dolphin and the fish school. The dolphin is able to turn at a high rate and with small turning radii, increasing maneuverability. The animal appears to keep its rostrum at a relatively fixed point, and then rapidly rotate its body around that point, as compared to turns with a circular trajectory.

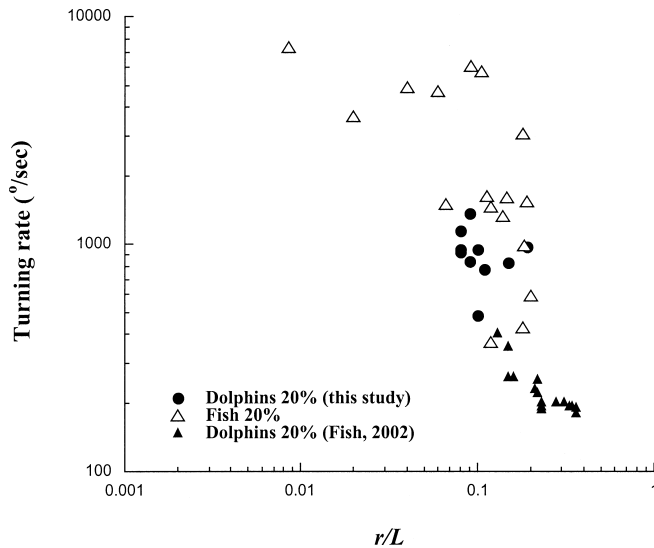


Figure 3. Comparison of turning rate to radius of the turn relative to body length for top 20% turning performance sequences for foraging dolphins (solid circles; this study), various fish species (open triangles; Webb 1976, 1983; Blake *et al.* 1995; Gerstner 1999), and trained bottlenose dolphins (solid triangles; Fish 2002). While the fish demonstrate greater maneuverability, foraging dolphins are able to maneuver their mouth so as to overlap the performance of the fishes. Turning performance measured on the center of gravity of trained dolphin demonstrated low maneuverability.

approached those of fish (Fig. 3). Minimum turn radius at the rostrum of the dolphins was $0.08 L$, somewhat lower than values previously reported for *Tursiops* (Fish 2002). Furthermore, the maximum turn rate of *Tursiops* was measured at $1,372.0^\circ/\text{sec}$, which is greater than rates previously reported by Fish (2002) for *Tursiops*. A reduction in turning radius with a concomitant increase in turning rate at the rostrum of the dolphin compared to its center of gravity is a function of body orientation allowing use of multiple joints for ventral bending. During the final feeding lunge, the dolphin was rolled 90° and directed its underside toward its prey. By rolling during an attack, the dolphin orients its body toward the prey in the plane and direction of maximum flexibility, the ventral plane (Long *et al.* 1997, Pabst 2000). For *T. truncatus*, an increased number of joints involved in bending increases ω at the rostrum over the center of gravity by over three-fold (Hildebrand and Goslow 2001).

In our study of nearshore dolphins, foraging group size was a factor affecting foraging performance. Foraging always ceased when group size increased beyond two individuals. In groups of two, the animals were sometimes observed coordinating their foraging efforts by circling, side-by-side swimming and feeding rushes (sudden acceleration ending in at least one pinwheel), although it was difficult to discern any obvious behaviors more indicative of cooperative hunting. Our observations are consistent with previous studies, which describe *Tursiops* as feeding in large, more obviously coordinated groups in deeper and more open waters, but spreading out and hunting individually or in small groups in shallower

waters (Barros and Odell 1990, Scott *et al.* 1990, Shane 1990, Barros and Wells 1998, Reynolds *et al.* 2000).

The dolphins in Sarasota Bay feed primarily on fast-swimming fish that require high speed, maneuverability and agility for capture. As such, dolphins do not follow a fixed strategy for capturing prey, but have a repertoire of foraging behaviors from which to choose to compensate for inequities in maneuverability between themselves and their much smaller prey. The choice of behaviors used can be influenced by a variety of factors including habitat, prey type, time of day, season, individual preferences, human activities, and other unknown factors (Würsig 1986, Shane 1990, Wells and Scott 1999, Reynolds *et al.* 2000, Nowacek 2002).

Turning using the pinwheel behavior was of central importance in foraging sequences for bottlenose dolphins in Sarasota Bay (Nowacek 2002). Pinwheeling has been described previously, but there is no definitive or consistent definition of this behavior across the literature. Nowacek (2002) described pinwheeling as “equivalent to a swimmer’s flip turn performed by a dolphin in side-swim orientation . . . the dolphin tucks its head and spins, rotating around the midpoint of the body.” Scott *et al.* (1990) described this conspicuous behavior as a “dolphin’s rapidly spinning around one or more fish, as if it were using its body to encircle and cut off the fish’s escape.” Leatherwood (1975) first described the behavior, referring to it as taking place in the horizontal plane, “a motion which swept the dolphin’s head through the school or towards the individual fish.”

While dolphins do rotate around the midpoint of the body, use their bodies to encircle fish, and may sweep their heads through a school or toward a fish, these behaviors were not characteristic of the pinwheel turn as described here. As viewed from above in the present study, it became clear that pinwheeling by foraging dolphins was associated with a relatively stationary position of the tip of the rostrum while the body was flexing and the dolphin was rolled 90° in the side-swim orientation. The pinwheel maneuver was a pursuit behavior characterized by high-speed swimming with a rapid rotation of the body around the rostrum (Fig. 2). The pinwheel turn enabled the dolphin to keep its mouth localized in position at or near fleeing fish as they changed direction, thereby allowing the dolphin to reduce the area its rostrum could probe while turning to intercept prey. Pinwheeling would be particularly effective in shallow water bodies, such as Sarasota Bay, where side-swimming permits increased flexibility of the dolphin to enhance turning in the horizontal plane, as well as increased propulsive thrust production without interference from the surface or bottom. Pinwheeling is not to be confused with other turning behaviors often observed for foraging bottlenose dolphins. Such behaviors could include rooting or drifting, where the dolphin is oriented almost vertically in the water column with its rostrum close to or below the bottom (Nowacek 2002). Compared to the pinwheel, which is an obvious pursuit maneuver, rooting/drifting is a much slower foraging behavior characterized by an almost stationary position in the water column. Pinwheeling also is not the same as the dolphin simply keeping its rostrum in a restricted location (*i.e.*, school of fish, patch of sea grass) while slowly rotating its body around that point. During these slower turning behaviors, the dolphin theoretically would be able to maintain sensory acquisition of the target prey, continuously harass fish to flush them from the vegetation and into open water, or corral the prey using the body.

The information on foraging behaviors and performance of bottlenose dolphins demonstrate that the differential in size is not an impediment to these large predators to catch their smaller, more elusive prey. Spatial and temporal dis-

placements of the mouth, rather than the center of gravity, represent a more ecologically relevant indicator of predatory maneuverability.

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