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MUD PLUME FEEDING, A UNIQUE FORAGING BEHAVIOR OF THE BOTTLENOSE DOLPHIN IN THE FLORIDA KEYS.—The bottlenose dolphin (*Tursiops* spp.) has plasticity in foraging behaviors (Shane, 1990), varying according to habitat and circumstance. Some behaviors are dependent on human activities like shrimp fisheries, the by-catch of which are sought by bottlenose dolphins in some geographic areas (Leatherwood, 1975; Corkeron, 1990; Fertl, 1994). Other behaviors appear to be associated with specific habitats, such as strand feeding, noted to occur on estuarine mudflats exposed at low tide (Hoese, 1971; Petricig, 1995; Silber and Fertl, 1995), crater feeding observed on the shallow sand banks of the Bahamas (Rossbach and Herzing, 1997), and sponge-use foraging performed by a small number of animals in Shark Bay, Australia (Smolker et al., 1997). Variation occurs within populations as well, with individuals using multiple and diverse feeding behaviors (Shane, 1990; Nowachek, 1999; Gubbins, 2000; Mann and Saergeant, in press). Given this variability, further examination of the bottlenose dolphin throughout its range will likely reveal additional foraging behaviors where other adaptations to the environment and circumstance have occurred. During an investigation of bottlenose dolphin (*Tursiops truncatus*) behavior in the waters of the lower Florida Keys, a previously undescribed foraging behavior, “mud plume feeding,” was observed.

Data were gathered between Feb. 1999 and Sep. 2001, north of Key West and Stock islands (between 81°54'W and 81°42'W) and south of 24°42'N (Fig. 1). Operations were conducted from a 5.6-m Open Fisherman (Proline®) with a 110-hp outboard motor, using an 8-mm video recorder (Sony® CCD-TRV43). Surveys were conducted between 0700 and 1900 hr during all seasons of the year. Focal group follows (Altmann, 1974) were made, recording surface behavior continuously for the duration of follows (0.25–5 hr). The ability to collect a continuous record of surface behavior was possible using video review options, including slow-motion advancing, stop frame, and replay of actions recorded. Maintaining an average distance of 50 m during follows allowed all dolphins in a group to remain within the camera view and provided minimal interference with natural behavior. Distance was also maintained when dolphins were located in waters <0.5 m deep owing to inaccessibility. Detailed group observa-

tions were permissible using video zoom range capabilities. Other data collected during surveys included group size, Beaufort sea state, air and water temperature (C), water depth (m), tidal state, and location based on global positioning system readings.

Mud plume feeding was first noted during winter 1999 and has since been observed more than 186 times during 18 separate group follows. This behavior is first noted by the appearance of a thick cloud of suspended sediment on the surface of the water (Fig. 2a). The sediment plume then grows linearly or curvilinearly (Figs. 2b and 3a). The dolphin can sometimes be observed moving at the leading edge of the plume through a slight disturbance on the water surface, with the body of the animal appearing to move just ahead of the plume front. Lengths of the plume were estimated from videotape to be between 5.4 and 10.8 m ($n = 21$). Estimates were made by comparing dolphin body length with plume length, assuming an average adult body length near 2.7 m for bottlenose dolphins in Florida waters (Reynolds et al., 2000). Cessation of plume growth occurs as the dolphin repositions its orientation to the plume (Fig. 2d,e). Soon after, the dolphin lunges through the plume, breaking the surface (Figs. 2f and 3b). This lunging motion is very swift, creating a great deal of white water. The entire behavior sequence from initiation of a mud plume through dolphin lunge averaged (\bar{x}) 17.0 sec ($n = 20$, SD = 7.6, range = 8–44 sec). Time between the final lunge through one mud plume and the initial appearance of another ranged from 1 to 9 min for the same individual and from <1 to 26 min for plumes created by separate group members. The number of plumes created during a follow ranged from 1 to 61.

Tests of plume re-creations, where the only successful re-creation was accomplished through the use of divers' fins lightly moving up and down just above the substrate as a swimmer moved backwards through the water (Fig. 4), lead us to suspect that the plume is created purposefully with a downward motion of the flukes very near the substrate. Close observations to confirm this have not been possible so far because of the speed of the plume creation and the shallow, sometimes inaccessible depths where mud plume feeding occurs.

This behavior was performed in all cases by a single animal, and the plume was used only once. Although an individual behavior, multiple group members (barring calves) simultaneously created separate mud plumes while

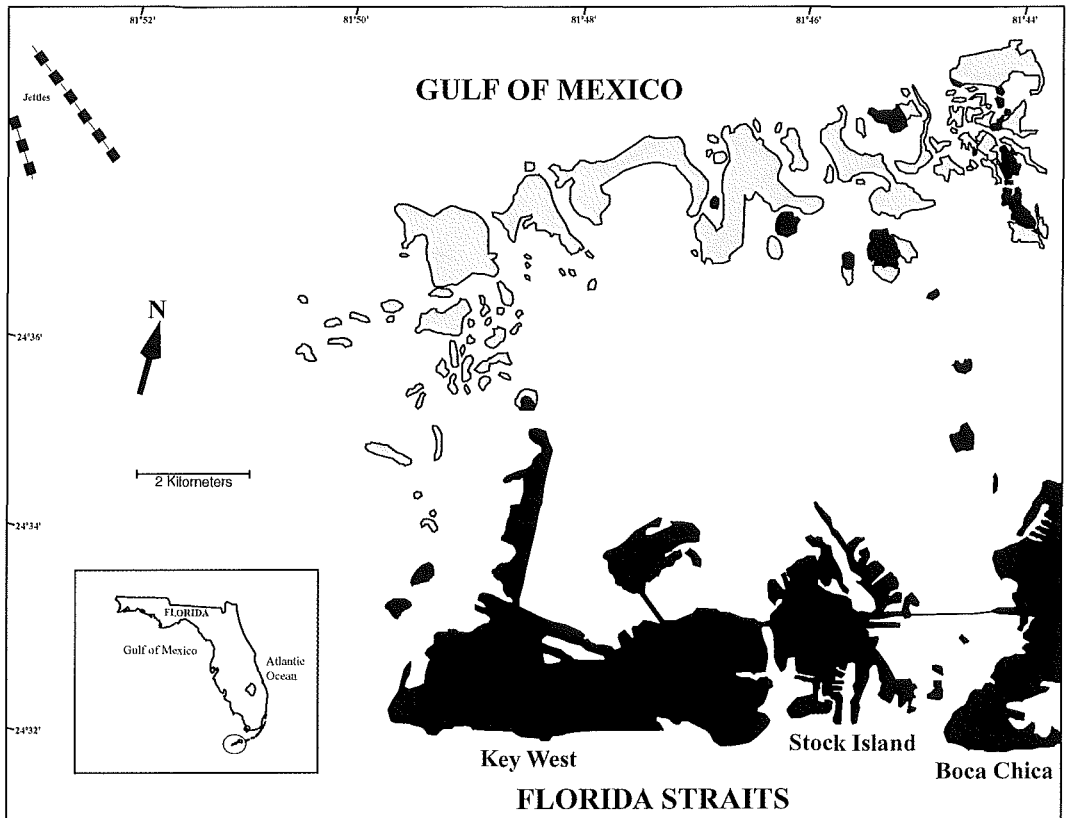


Fig. 1. Map of the research area, near the islands of Key West, Stock Island, and Boca Chica. Areas colored black are above sea level. Areas colored gray are exposed during low tides.

spread from one another at distances ranging from 20 to 100 m. Groups engaged in this behavior ranged in size from 1–10 ($\bar{x} = 3.6$, $SD = 2.54$, $n = 18$). Calves were present in three of these groups. Between Feb. 1999 and Sep. 2001, 16 animals (including one known male and two females) from this region were identified as either directly producing plumes or traveling with group members engaged in producing mud plumes. Animals that lunged through the plume did so more often with the right side of the body oriented into the water (33 of 35 detailed observations).

Mud plume feeding occurred in waters with a mean depth of 0.9 m ($SD = 0.30$) over seagrass flats (primarily *Thalassia*). Turbidity of these waters is low, with visibility extending to the bottom, where this behavior was observed. Analysis of tidal currents indicated that mud plume feeding occurred primarily during the flood stage (87.5%). This was not a reflection of effort, as 39 hr were spent following groups during flood stage and 37 hr during ebb.

The predominance of mud plume feeding

during the flood tide could be related to local prey movements with tidal cycles. Many fish species are known to migrate with such processes (Thorpe, 1978). Fish in shallow seagrass beds move off shallow flats during low tides and then back to them during high tides (Sogard et al., 1989b). Dolphins foraging in these shallows may be following the changes in prey distribution through this oceanographic process.

Identification of prey species acquired by dolphins in the field at the moment of capture, even with the benefit of videotape, is inherently difficult. Because of this, it could not be determined with certainty if a specific species was targeted during this foraging behavior. However, fish were seen jumping ahead of the lunging dolphins, or out of the plumes, on 35 of 75 complete observations. Ballyhoo (*Hemiramphus brasiliensis*) were the only fish species identified. They were not the only fish species noted but were the only species clearly identifiable because of a characteristic behavior when startled, where they appear to “run” across the

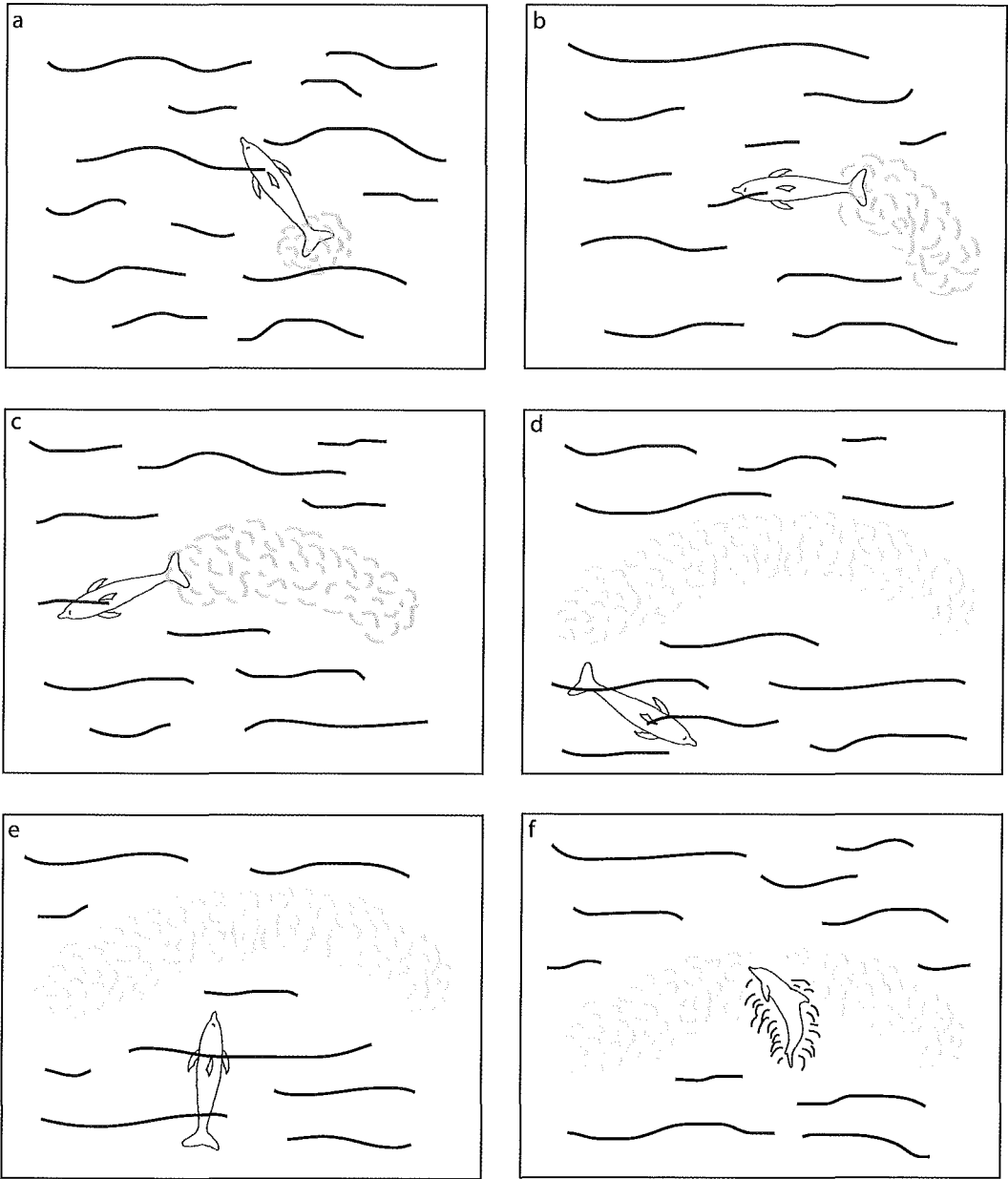


Fig. 2. Sequential depiction of "mud plume feeding" from overhead: (a) initial appearance of suspended sediment, (b, c) plume grows with the movement of dolphin, (d, e) cessation of plume growth and repositioning of dolphin in orientation to the plume, and (f) dolphin lunging through the plume.

surface of the water. Some information has been gained from a previous analysis of bottlenose dolphin stomach contents from this region. Results indicated domination by grunt species (Family Haemulidae) and toadfish (Family Batrachoididae) (Barros and Odell, 1990). Members of both families are considered common to the seagrass flats of the Flor-

ida Keys (Sogard et al., 1987, 1989a; Matheson et al., 1999).

The right-sided trend noted for lunges has also been documented for strand feeding bottlenose dolphins (Hoese, 1971; Petricig, 1995). Reidenburg and Laitman (1994, 1999) hypothesized that this may be in response to the asymmetry of the hypolarangeal region in this spe-

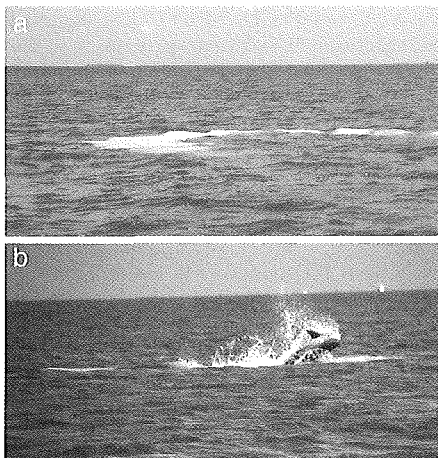


Fig. 3. (a) A U-shaped plume of suspended sediment created by a dolphin. Open end of U is to the right side of the photo. (b) Dolphin lunging through a mud plume on its right side. Left pectoral fin is seen extending out from the dolphin. Some of the plume can be noted to the rear and to the front of the dolphin in the photograph.

cies. This asymmetry results in an enlarged right side of the esophagus. Positioning during prey capture with the right side down may enable greater ease in swallowing larger prey items with the aid of gravity. A right-eye preference documented in captive bottlenose dolphins (Kilian et al., 2000; von Ferzen et al., 2000) may also be partially responsible for the sidedness noted. Dolphins may prefer the use of the right eye in the final moments before prey capture.

Possibilities for plume formation outside foraging can be discounted. Development as simply a by-product of movements through shallow areas can be rejected. Dolphins in the lower Florida Keys regularly swim through areas so shallow (0.3 m) that the dorsal fin remains above the water between surfacings for respiration. However, observations of this traveling behavior (>190 occasions) over such shallow areas have never revealed disturbance of the sediment. The solitary nature of the behavior indicates that plumes are not generated by subsurface social activity. Disturbance as a result of foraging on the bottom for prey found either beneath or directly on the substrate seems unlikely because no dolphins have ever been noted to rush underneath the water surface chasing fish during this behavior sequence. Only when rushing through the plume and breaking the surface do the dolphins increase their speed. It is precisely this last aspect of the behavior sequence, lunging after fish through

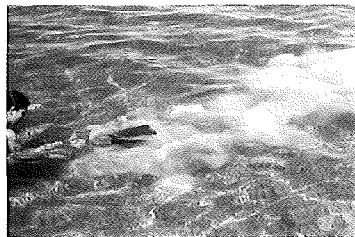


Fig. 4. Swimmer downstrokes dive fins above a seagrass bed producing a mud plume, which trails behind the direction of the movement of the swimmer.

the plume that leads to the conclusion that this behavior sequence is a foraging behavior.

The fact that dolphins always end the behavior sequence by lunging through the plume suggests that the suspended sediment may be used as a "concentration" place for the prey. Prey may concentrate in the plume as an escape mechanism. Fish are known to concentrate in areas offering protection from predators (Godin, 1997). Alternatively, fish may be attracted to the plume for the sudden increase in food it may provide. Some fish known to occur on these flats have been noted to be attracted to the plumes created by the movements of southern sting rays (*Dasyatis americana*) while settling or taking flight from the bottom (J. Ferguson, pers. comm.).¹ Fish aggregations also have been documented in "mullet muds," large clouds of suspended sediment found in the shallows of the Keys, possibly formed as a result of mullet bottom feeding (Scott et al., 1989). Either of these reactions by the prey, for protection or foraging, would concentrate them, and the dolphins certainly could locate them within the plume using echolocation.

Bottlenose dolphins in other regions share parts of the behavioral sequence of mud plume feeding. Swift lunges chasing prey, causing a splash on the surface, have been noted on both the east and the west coasts of Florida (Shane, 1990; Hart, 1997). The effort of turning on the side ("side swimming") as part of the final chase of prey through the water also has been cited (Leatherwood, 1975; Shane, 1990; Nowachek, 1999). Dolphins on the west coast of Florida, near Sanibel Island and in Sarasota Bay were noted to occasionally cause a stirring of mud while "subsurface feeding" (Shane, 1990; Nowachek, 1999). It is possible

¹ Commercial fisherman in Key West, Florida, in March 2000.

that the dolphins in the Florida Keys had aspects of these behaviors in their repertoire before the development of the entire mud plume feeding sequence.

Further research on this behavior is needed to determine the exact method of formation as well as the function of the plume with more certainty. It is of interest to establish the identity of all animals in this area that perform this behavior, as well as how far this behavior extends geographically. The discovery of this strategy lengthens the list of foraging behaviors known for the bottlenose dolphin. Through this, more evidence is accrued for the breadth of behavioral plasticity of this species. There are many unstudied portions of the bottlenose dolphin's range where different feeding behaviors may yet be discovered.

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