ABSTRACT—Recurring feeding patterns are reported for bottle-nosed dolphins, Tursiops spp., from the northern Gulf of Mexico, the west coast of Mexico, both coasts of Baja California, and southern California. Seven distinct feeding behaviors, in which a variety of prey species are taken by various means, are identified and discussed. Exploitation of by-products of human activities in all areas suggest that Tursiops have learned their advantages in providing food. Other feeding patterns involve interesting behaviors to permit exploitation of shallow marshlands, efficient hunting and harvesting using echolocation in shallow water, and cooperative taking of prey. Plasticity in feeding behavior appears to have adaptive value if bottle-nosed dolphins have limited home ranges and must, therefore, cope with seasonal fluctuations in “local” productivity. Analysis of the stomach contents of one animal taken off Mississippi supports contentions of catholic tastes and opportunistic feeding behavior for Tursiops.

INTRODUCTION
The food habits of wild dolphins are usually determined from examination of stomach contents of beach-stranded or accidentally killed specimens of animals taken in the few aboriginal fisheries. For most species, very little is known of patterns of feeding, and few papers deal with the manner in which prey are taken. For the bottle-nosed dolphins, Tursiops spp., off the United States and Mexico, accounts of food and feeding habits are apparently limited to those summarized in Table I. This dearth of information is surprising, since Tursiops spp. is frequently maintained in captivity and is generally the best known of all small cetaceans. This paper reviews the information available on Tursiops, adds recent observations, and discusses recurrent feeding patterns.

Although the author considers the terms dolphins and porpoise interchangeable in the common names of odontocetes, the term dolphin is used throughout this paper. References should not be confused with the dolphin fish, Coryphaena spp., which is not discussed.

In addition, I have made or received reports of similar observations of feeding behavior of Pacific bottle-nosed dolphins Tursiops cf T. gilli off the west coast of mainland Mexico (Nayarit), off both coasts of Baja California, and off southern California. In these instances, observations were made from fixed-wing aircraft (Navy S-2’s and Cessna 172’s), Navy helicopters (H-3’s), charter fishing boats, small skiffs, and shore vantage points.

1Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Despite the wide separations in locality and the often very different habitats, there were numerous similarities in feeding behavior. In all, seven different feeding patterns have been identified, each related to the circumstances of feeding and the prey species involved. The first three involve feeding in association with shrimp boats and suggest that the dolphins have learned the advantages of this human activity in providing food. The remaining four are methods of pursuing and taking prey, individually or in cooperation, not in the presence of human activity. To avoid confusion when the patterns are cross-referenced in the text, each has been numbered.

1. FORAGING BEHIND WORKING SHRIMP BOATS
The most striking and frequently reported feeding pattern for bottle-nosed dolphins is that in which a herd follows a working shrimp boat, apparently feeding on organisms stirred up by its otter trawls. This behavior has been documented for the northern Gulf of Mexico and for the Atlantic coast of Florida. Gunter (1938) reports bottle-nosed dolphins following shrimpers off the Texas coast and apparently causing damage to their nets. He adds (Gunter, 1942) further anecdotal evidence of the species’ feeding behind working shrimpers, noting that in the

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Table 1.—A summary of published accounts of food and feeding behavior of bottlenosed dolphins, Tursiops spp., off the United States, Baja California, and mainland Mexico.

<table>
<thead>
<tr>
<th>Reference</th>
<th>Species</th>
<th>Summary of report</th>
</tr>
</thead>
<tbody>
<tr>
<td>True (1885)</td>
<td>T. truncatus</td>
<td>Report of common gunnard, Prionothus carolinus, in stomachs of both females examined at the Cape May Fishery.</td>
</tr>
<tr>
<td>Townsend (1914)</td>
<td>T. truncatus</td>
<td>Report of animals following working shrimp boats feeding.</td>
</tr>
<tr>
<td>Gunter (1936)</td>
<td>T. truncatus</td>
<td>Two photographs and a brief description of feeding on striped mullet, Mugil cephalus, off St. Augustine, Fla., including the dolphins catching their prey in midair.</td>
</tr>
<tr>
<td>Harris (1938)</td>
<td>T. truncatus</td>
<td>Report of common gunnard, Prionothus carolinus, in stomachs of both females examined at the Cape May Fishery.</td>
</tr>
<tr>
<td>Kemp (1949)</td>
<td>T. truncatus</td>
<td>Report of animals following working shrimp boats feeding.</td>
</tr>
<tr>
<td>Gunter (1942)</td>
<td>T. truncatus</td>
<td>Second-hand report of fishermen that animals taken in the Hatteras fishery fed primarily on squateague or weakfish.</td>
</tr>
<tr>
<td>Gunter (1951)</td>
<td>T. truncatus</td>
<td>Reports of squid (Loligo sp.), shrimp and crabs (unidentified), and 9 fish species from stomachs of 10 animals collected off Texas. Striped mullet (M. cephalus), hardheads (Galeichthys felsii), and ribbonfish (T. lepturus) were most numerous.</td>
</tr>
<tr>
<td>Gunter (1954)</td>
<td>T. truncatus</td>
<td>Report that animals in northern Gulf of Mexico fed most commonly on striped mullet, Mugil cephalus, but also took puffer, needlefish, scup, black drum, spotted and sand trout, flounder, croaker, and shrimp; comments further on feeding behavior.</td>
</tr>
<tr>
<td>Caldwell and Caldwell (1972)</td>
<td>T. truncatus</td>
<td>Anecdotal accounts of types of feeding behavior and a review of knowledge.</td>
</tr>
</tbody>
</table>

same area, the dolphins had learned to distinguish between a cruising shrimper and one whose engines were laboring to drag the nets and often showed up shortly after the trawls began. Caldwell and Caldwell (1972) add similar discussions of feeding behind shrimpers for the Atlantic coast of Florida.

In the aerial survey of the northern Gulf of Mexico (referred to hereafter as north Gulf survey) dolphins were observed feeding behind working shrimpers 12 times. Typically, they followed the boat in a loose aggregation (Fig. 1) with subgroups of the herd swimming back and forth through the boat's mud boil in an erratic zigzag pattern, diving and feeding individually (Fig. 2).

In only three instances were prey actually seen in the mouths of animals and those, of course, were unidentifiable from the aircraft. That the animals were feeding in other instances, however, was evidenced by their sudden changes in direction, their rapid swimming, their irregular diving intervals, and the tenacity with which they stayed with the shrimpers.

Although Norris and Prescott (1961) briefly mention an association of bottlenosed dolphins with shrimpers near San Felipe, Baja California, in the western Sea of Cortes (lat. 31°02'N, long. 114°51'W), there is no published record of the species feeding behind working shrimpers in the Pacific Ocean.

During a 2-year study of the bottlenosed dolphins near San Felipe and Puertocitos (lat. 30°25'N, long. 114°40'W) in 1972 and 1973, Wayne Turl (1974, pers. commun.) frequently observed herds of dolphins working in the mud boil behind shrimpers, presumably feeding. The majority of incidents occurred from October through June inclusive, the period which he reports as the most active months for the fishery.

On 22 September 1974, I observed...
this same type of behavior by a herd of 13-15 bottle-nosed dolphins in shallow water off Playa Blanca (lat. 31°23'N, long. 115°13'W), approximately 20 miles north of San Felipe. As in the accounts reported by Turl, the dolphins worked the mud boil in the shallows near shore. In neither Turl's reports nor in the instance I observed did the feeding patterns of the dolphins differ in any important respect from those described for the Gulf of Mexico.

Bottle-nosed dolphins apparently feed in association with other netting operations as well. Busnel (1973) describes *Tursiops* feeding on mullet (*Mugil cephalus* and *M. auratus*) during beach seineing off Mauritania and comments on the “symbiotic” nature of the relationship between the dolphins and the fishermen. Frank M. Truesdale (1974, pers. commun.) has observed dolphins feeding “behind” a commercial beach seine in Caminada Bay, La. (lat. 29°40'N, long. 90°00'W). The dolphins, working outside the bag, pulled at fishes gilled in the net as it was dragged ashore.

### 2. FEEDING ON TRASH FISH

A second feeding pattern also involves the dolphin’s capitalizing on shrimp fishing activities. Once they have completed a trawl, shrimpers often dump the catch on the deck and sort it, keeping the shrimp and the fish of commercial value but discarding the fish of no commercial value. Norris and Prescott (1961) and Caldwell and Caldwell (1972) provide detailed accounts of dolphins gathering around shrimpers in the Gulf of California and the east coast of Florida, respectively, and feeding on thediscards. Norris and Prescott (1961) add that the dolphins in the north Gulf frequently arrive immediately after the engines shut down and sorting begins. Phillip Stevens (1974, pers. commun.) reports that in the Mississippi Sound dolphins frequently follow shrimpers from the waters of the fishing grounds to the harbors in the early morning, presumably taking advantage of fish discarded on the return trip.

In the north Gulf survey, dolphins were seen on three occasions in the company of drifting shrimpers where
catch was being sorted, apparently taking fish thrown over the side. In each case, however, other dolphins were seen nearby feeding on mullet and ignoring the discard. No consistent differences in animal size could be determined among the dolphins feeding in these two manners.

Turl (1974, pers. commun.) has noted similar instances involving shrimpers and bottlenosed dolphins in the waters near Puertocitos and San Felipe.

On 22 January 1973, I observed six *Tursiops* feeding on northern anchovies, *Engraulis mordax*, thrown over the side of a sport fishing boat near Barracks Beach, Guadalupe Island (lat. 29°09'30"N, long. 118°16'30"W). The dolphins circled the boat for over an hour, diving at irregular intervals, but rushing periodically to take the fish thrown over the side.

### 3. FEEDING ON FISH ATTRACTION TO NONWORKING SHRIMPERS

In the third pattern noted, the dolphins apparently take advantage of fish as they seek sanctuary beneath anchored vessels. For example, the majority of shrimpers generally work at night. Frequently, boats can be seen during the day "laying to" or at anchor, with their nets trailing in the water or hanging on the outriggers. At these times, the combination of debris from the nets and discharge from the bilges frequently attracts numerous fishes, including sharks, to the area of the boats.

On two occasions during the north Gulf survey dolphins were seen in the vicinity of anchored shrimpers feeding on fishes apparently attracted there. In both instances, feeding groups were small—four and six individuals. In both, the dolphins chased small schools of unidentified bait around the area. Sharks and numerous birds trailing the dolphins or generally patrolling the area cleaned up debris as well. Dolphins in the Mississippi Sound are frequently seen around shrimp boats anchored after a night's work (Phillip Stevens 1974, pers. commun.).

I have observed *Tursiops* feeding near anchored vessels on four other occasions: 1) on 31 December 1970, six to eight bottlenosed dolphins were feeding both near an anchored tuna seiner and near the effluent from the fish-processing plant in the bay at Cabo San Lucas, Baja California (lat. 22°52'N, long. 109°53'30"W); 2) on 21 April 1971, two groups of four bottlenosed dolphins each were observed feeding around anchored fishing boats just off the pier at Puerto Vallarta, Bahia de Banderas, Nayarit, Mexico (lat. 20°37'N, long. 105°25'W). In both instances the dolphins were actively feeding around the vessels for an hour. In both, numerous birds and some sharks were also feeding on attracted fishes; 3) on 22 January 1974, I observed *Tursiops* feeding on fish attracted by a night-light placed over the side of the MV *Cape Polaris* at anchor at Isla San Benito, Baja California (lat. 28°18'N, long. 115°54'W); 4) on 22 September 1974, I watched from an aircraft as two dolphins fed near anchored seiners off Ensenada, Baja California, Mexico (lat. 31°51'N, long. 116°37'W), and six others patrolled near fishing boats anchored off Camalú, Baja California, Mexico (lat. 30°45'N, long. 116°03'W).

Turl (1974, pers. commun.) reported that *Tursiops* were frequently attracted to anchored fishing boats near San Felipe and Puertocitos. The dolphins reportedly often continued to feed in the area of the boats for hours.

None of these observations is surprising in the light of the attraction of fishes to floating debris, ships, and cetaceans in the eastern tropical Pacific (Hunter, 1968 and Green, et al., 1971) and to artificial surface and submerged reefs in the northern Gulf of Mexico (Klima and Wickham, 1971). These floating bases rapidly become complex communities of prey, predators, and scavengers and provide ready source of food for high-order predators.

In addition to these three feeding modes, each of which capitalizes on the products or results of human activities, *Tursiops* were observed actively pursuing fish, individually or in consort, in three other situations.

### 4. HERDING SCHOOLS OF FISH

Caldwell and Caldwell (1972) describe a type of cooperative feeding behavior as follows: "... a group of dolphins find(s) a large school of some pelagic fish, such as mullet or catfish and begin(s) to encircle it from above, around and below. The natural schooling behavior of such fishes is to keep in a tight ball so the circulating dolphins feed on the stragglers or some dolphins charge through the school while the others keep the ball intact.... "

During the north Gulf survey, behavior of this kind was observed on five occasions involving from two to as many as fourteen dolphins. One feeding was on menhaden, three on mullet, and one on an unidentified species. In general, the dolphins struck in tight circles around the fish, and individuals darted into the herd periodically to feed. On some occasions, the feeding individual charged the school from below, creating a sizeable surface boil or coming completely clear of the water. Truesdale (1974, pers. commun.) reported that in April 1972 he observed an identical feeding on menhaden by 12 bottlenosed dolphins in the southwest portion of Caminada Bay, La. (lat. 29°40'N, long. 90°00'W).

On 20 September 1974, I watched about 40 bottlenosed dolphins from aircraft in Bahía de la Santa María on the west coast of Baja California (lat. 24°47'N, long. 112°15'W). One small subgroup of five animals was circling a school of unidentified fish in the shallows with individuals taking turns charging in to feed.

On 13 December 1974, during a southern California aerial survey, I located six bottlenosed dolphins 2 miles north of Pyramid Head, San Clemente Island, Calif. (lat. 32°51'N, long. 118°21'30"W). The next day six bottlenosed dolphins, presumably the same animals, were located approximately 2 miles west of Seal Cove, San Clemente Island (lat. 32°54'N, long. 118°34'30"W). During both encounters the dolphins were cooperatively circling and feeding on small schooling fish, tentatively identified as anchovies. Individuals frequently created sizeable surface disturbances as they wheeled through the fish schools.

I have frequently observed a similar herding and feeding on anchovies off southern California by California sea...
lions, Zalophus californianus, and North Pacific white-sided dolphins, Lagenorhynchus obliquidens. The sea lions in particular frequently catapult themselves into the air in the feeding process.

Turl (1974, pers. commun.) has observed this type of feeding for both Tursiops and Zalophus near San Felipe.

5. SWEEPING SCHOOLS OF SMALL BAIT FISH

Like pattern 4, the fifth feeding pattern involved cooperation among a group of dolphins. In this pattern, observed only twice during the north Gulf survey, small groups of dolphins (three and six) assumed a crescentic formation at the rear of a fleeing school of small fishes, thought to be menhaden in one instance, unidentified in another. The dolphins drove the school of fish ahead of them at high speed towards shallower water. The dolphins maintained approximately the same positions in the line relative to each other, despite the erratic movements of the fish. As they continued to drive the school in front of them, individual dolphins picked up stragglers or darted in periodically to take fish from the school.

A similar pattern of moving and taking prey has been noted for killer whales (Orcinus orca) feeding on California sea lions (Leatherwood and Samaras, 1974).

6. CROWDING

The sixth pattern is apparently a slight modification of pattern 5. For example, during the north Gulf survey three dolphins were observed in the marshlands crowding small, unidentified fish from deeper water onto shallows or against mud banks at the foot of clumps of salt grasses, Salicornia, and taking the fish as they flopped in a few inches of water. An extension of this type of behavior, involving the animal’s driving fish completely out of the water onto a mud bank and sliding up the bank after them, was reported by Hoese (1971). Of particular interest was the surprising agility displayed by the dolphins in the extremely shallow water, both in the accounts reported by Hoese and in instances of feeding noted here. They appeared completely at home on the shallows even when up to 25 percent of the back was exposed. Several writers (e.g., Teal and Teal, 1969 and Caldwell and Caldwell, 1972) have noted that Tursiops are perfectly at home in shallows. During aerial surveys of Mississippi and Baja California, Tursiops have frequently been seen in the shallow waters (<3 feet or 0.9 meter) of the marshlands, lagoons, bocas, and mangrove swamps.

Feeding patterns 4, 5, and 6 involve cooperative taking of prey. The seventh involves individual fishing with an interesting behavioral variation.

7. INDIVIDUAL FEEDING

In 14 instances during the north Gulf survey individual porpoises were seen pursuing small schools of bait fish or larger individual fish up to 12 inches (25.4 cm) long in open water. Typically, this type of feeding was characterized by high-speed swimming, by quick bursts of speed, and by radical changes of direction. Once the dolphins reached the would-be prey, they usually fed by rapidly “pinwheeling” in the horizontal plane, a motion which swept the dolphin’s head through the school or towards the individual fish. Once the rotation was completed the dolphin again set out in pursuit of fish.

The author has observed individual fishing with the wheeling motion at widely separated locations off southern California, Baja California, and mainland Mexico.

Of particular interest in these feedings is the frequency with which the dolphins pursued their prey either on their sides or upside down (Fig. 3). A typical cycle involved a quick respiration, a rapid turn onto the side or back, a high-speed erratic chase, and, upon arrival at the fish or school, the pinwheeling motion described above.

The author has observed upside-down feeding in the Mississippi Sound and adjacent marshlands, at La Mision (lat. 32°10’N, long. 116°54’W) and Camalu (lat. 30°45’N, long. 116°03’W) off the west coast of Baja California, and off Catalina Island, Calif. (lat. 33°12’N, long. 118°25’W). The dolphins frequently remained upside down for 30 seconds or more, and repeated the pattern on up to three successive dives.

An interesting, similar observation was reported by Thomas Smith, a charter fisherman from San Diego. Smith reported that while he was fishing for white marlin off Catalina Island (lat. 33°22’N, long. 118°15’W) in early September 1974, bottle-nosed dolphins approached and examined trolled bait. What caught his eye was the dolphins’ behavior as they approached the bait; they inverted and made the last 50-yard run upside down, righting themselves only after they had veered off from the bait. This method of approaching potential prey seems to occur in locations and under conditions too widespread and varied not to have some adaptive value.

Side-swimming and upside-down swimming have been noted for Inia geoffrensis (Layne and Caldwell, 1964 and Caldwell et al., 1966) and for Platanista gangetica (Herald et al., 1969), both of which inhabit turbid, shallow waters. Although the adaptive advantages of the behavior are unknown, it is conceivable that rotating onto the back in this manner reduces surface echoes and distortion of the animal’s echolocation signals. For example, Evans (1973) noted that for Tursiops the slope of the sound cone projected during echolocation is relatively flat ventrally but acute dorsally, relative to the animal’s main body axis. By inverting, the dolphin can project a signal that is nearly parallel to the water surface and concentrates energy to ensonify a shallow target with a minimum of surface refraction. Energy projected downward would be dampened by the bottom.

When single dolphins were seen in the highly turbid marshland waters of Louisiana and Mississippi, where the animals were visible only at the surface, they were often detected by a meandering mud trail. These trails were frequently marked by large muddy areas, assumed at the time to be areas where the animals had overthrown their prey and fed in the manner described.
Figure 3.—A lone dolphin pursuing a school of menhaden in the waters off Cat Island, Mississippi Sound (lat. 30°10'30"N long. 89°06'W), 6 July 1974. Note that the dolphin is upside down. Dolphins were frequently seen feeding on their backs and on their sides.

DISCUSSION

Gunter (1954) notes that off the coasts of the northern Gulf of Mexico, at least, *Tursiops* is catholic in its feeding tastes and opportunistic in the sense that it tends at any given time and location to feed on the most abundant species. The accounts of Caldwell and Caldwell (1972) indicate that this description applies equally to the *Tursiops* of the Atlantic coast of Florida as well.

Norris and Prescott (1961) refer to "the remarkable degree of flexibility in the species' feeding habits, adapted to local and sometimes transient conditions." As an example they describe *Tursiops'* habit of following ferry boats in San Diego Bay, Calif., taking fish stirred up by the prop wash.

Kleinenberg (1938) reports that *Tursiops* in the Black Sea fed on nine different fish species, shrimp, and occasionally molluscs. Hideyuki et al. (1969) similarly reports that *Tursiops gilli* off Japan fed on a wide variety of fish species and, to a lesser extent, on squid. All these published reports and the miscellaneous observations of the species' feeding behavior reported in this paper support the earlier conclusions of Gunter (1954).

During the north Gulf survey (Leatherwood and Platter, 1975) bottlenosed dolphins were observed feeding at least once for each hour of daylight flown; they were noted feeding on a variety of organisms under a wide variety of circumstances.

The stomach of one animal cursorily examined at 1000 on 11 July 1974, at Pass Christian, Miss., contained the following species and approximate quantities by volume: menhaden (*Brevooria* sp.) 25 percent; striped mullet (*Mugil cephalus*) 20 percent; cigar minnows (probably *Decapterus* sp.) 5 percent; miscellaneous shrimps (*Penaeus* sp.) 10 percent; and silver eel (probably *Trichiurus lepturus*) 10 percent. All these species were newly ingested and nearly whole, and tentative identifications were made visually. The remaining 30 percent of the stomach's contents were badly decomposed, unidentifiable fish remains.

The observations for coasts of mainland Mexico, Baja California, and southern California similarly involve feeding on varied prey and under varied circumstances.

The recurrence of patterns over time at widely divergent locations suggests their adaptive value for the species. One line of reasoning is as follows. If bottlenosed dolphins are relatively limited in their ranges and have rather short-term movements, plasticity in food habits is necessary for survival. Caldwell (1955) first discussed the possibility of home range in the species. Reports of
fishermen in the Mississippi Sound suggest that the bottle-nose of that area are "resident." The waters of that region support tremendous summer populations of such organisms as menhaden, mullet, and shrimp. Because all these are largely seasonal, however, dolphins remaining in the area throughout the year must be sufficiently flexible to switch to other organisms.

Whatever the explanation, *Tursiops* often utilize seasonally abundant species and have learned to take advantage in widespread locations of human activities providing food.

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