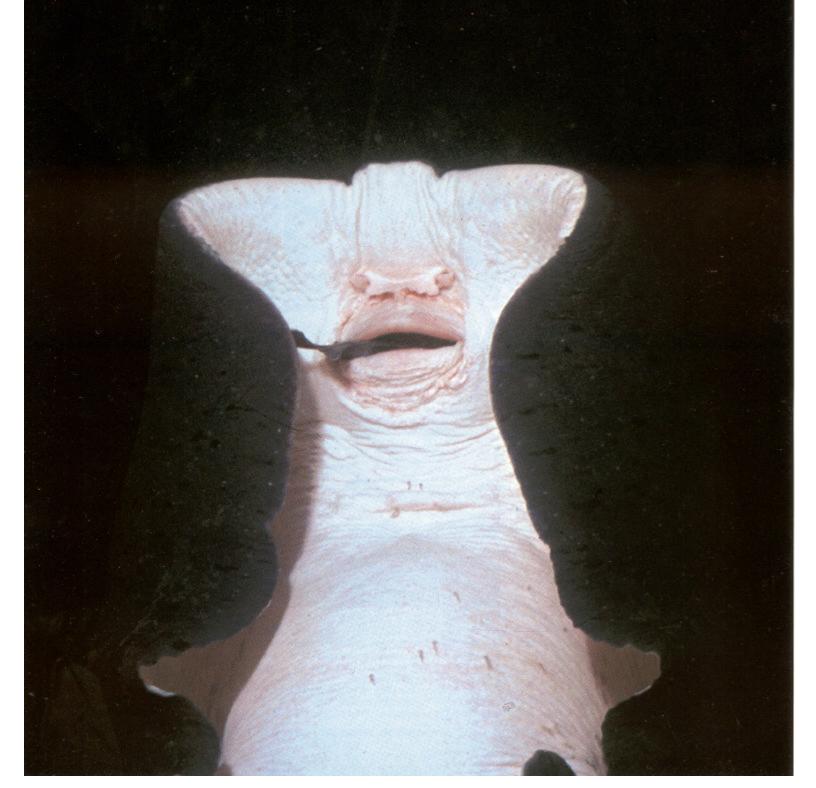
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Night-Shocker: Predatory Behavior of the Pacific Electric Ray (*Torpedo californica*)

Abstract. Diving observations off Santa Barbara, California, indicate that Pacific electric rays (Torpedo californica) enter inshore reefs at night and actively prey on fish with the aid of powerful electric discharges.

Only among the fish have specialized electric organs evolved that produce electric fields outside the body. Fish with electric organs are conveniently divided into two groups, based on the power of their discharges. The small potentials produced by weakly electric fish constitute part of an electrosensory apparatus that is used to detect nearby objects and communicate with other fish. The powerful discharges produced by strongly electric fish are thought to deter predators or capture prey (1).

Electric rays of the genus Torpedo are cartilaginous marine fish renowned for their ability to produce powerful electric discharges. The maximum output of T. nobiliana is approximately 1 kW (2). A kidney-shaped electric organ is located on each side of the flattened "disk," which is formed by the greatly enlarged pectoral fins fused to the head. Although their habits are largely unknown, it has been traditionally assumed that these rays are rather sluggish and usually lie partially buried in the sand (3-5). However, in situ observations (6) and captures in fishing nets near the surface (3, 7) suggest that electric rays may be more active than previously thought. We present evidence that Pacific electric rays (Torpedo californica) enter and actively forage over high-relief rocky reefs at night, and we describe how they capture and engulf their prey (8).

Our study site is Naples Reef, a large rocky outcrop located 1.6 km offshore near Santa Barbara, California (9). Although rare over the reef during the day, electric rays are often encountered there at night (10) swimming slowly or drifting motionlessly, usually within 1 m above the bottom. Unlike most rays, electric rays swim by using their well-developed tails for propulsion while their pectoral fins (disk) remain immobile. Also, their near-neutral buoyancy allows them to drift motionlessly with minimal sinking (11). The individuals we encounter are quite large, usually ranging in length from 700 to 1200 mm (12). To further document the day-night difference in their abundance over the reef, we kept a detailed account of our sightings of electric rays from August through October 1976. We swam along 150 m of transect lines attached to the reef at a depth of 13 m, so the areas we covered in the daytime and nighttime were nearly equal. The duration of each dive was approximately 50 minutes. During 33 daytime scuba dives on 15 dates we saw three rays (an average of 0.1 ray per dive), whereas during 13 night dives on seven dates we saw 26 rays (2.0 rays per dive). The maximum number of rays we saw over the reef during 1 day was three, while in September 1975 we encountered 12 during a single night dive.

To our knowledge, Pacific electric rays forage exclusively on fish. The

stomach contents of numerous rays collected over sand bottoms off Santa Barbara consisted primarily of anchovies (Engraulis mordax), although they also included demersal fish of the sand-mud community (13). Some of their prey were quite large and unusual. One 1240-mm female ray consumed a 600-mm silver salmon (Oncorhynchus kisutch). A sampling of rays taken at Naples Reef indicates that they eat resident reef fish, such as kelp bass (Paralabrax clathratus).

The electric rays' nightly swimming and drifting behavior over the reef suggested to us that they might be searching for food. To test this, we speared small reef fish (150 to 300 mm) and, while a fish was still impaled, we positioned it approximately 15 cm in front of a ray (Fig. 1A). We then slowly moved the fish

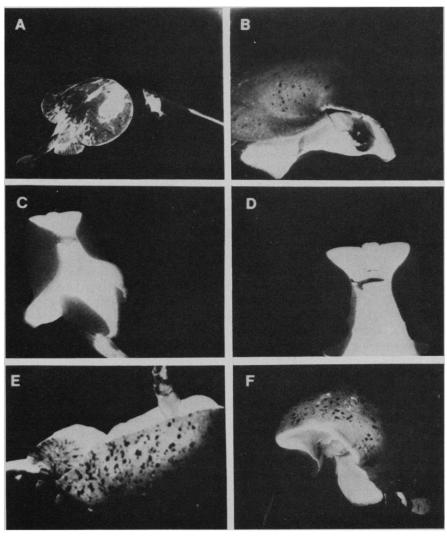


Fig. 1. Prey capture at night by the Pacific electric ray. (A) A female ray being presented a reef fish while swimming above the reef. The dorsal surface is normally gray with irregular black blotches; this individual has patches of sand (white areas) on its dorsal surface. (B) Posture of an electric ray after lunging on a prey fish. (C) A ray near the completion of a forward somersault. The prey has been positioned near the mouth by peristalsis-like foldings of the disk. (D) Prey being swallowed headfirst, while the disk is still folded. (E) A stunned jack mackerel partially enveloped in the disk of an upside-down electric ray. (F) The same ray as in (E) at the completion of the somersault. The prey is now near the mouth while fully enveloped by the disk. These rays are about 750 mm long.

closer until we observed a response by the ray. Typically, when a speared fish was within about 5 cm, the ray lunged forward and folded the anterior and lateral margins of the disk over the prey (Fig. 1B). The rest of the sequence was variable. With short kicks of the tail, the folded ray either remained upright or performed barrel rolls or forward somersaults, or both (Fig. 1C). These maneuvers tended to further envelop the prey under the disk. Then a deep undulation of the disk margin, moving in a peristalsis-like wave toward the anterior end, forced the prey toward the mouth. Finally, the prey was swallowed headfirst in several gulps (Fig. 1D). The entire sequence, from the initial lunge to the ingestion of the prey, usually took less than 20 seconds. In 12 of 19 such observations, the prey were swallowed. Once, a fish struggled and escaped from the folded disk; in this instance the ray continued to tumble for 10 seconds, then righted itself and swam away. On six occasions, electric rays responded to the speared fish by turning abruptly and swimming away. Speared fish may have presented abnormal stimuli to the electric rays since at least some rays are known to respond to metallic conductors (such as our spears), and wounded fish probably produce relatively high external electric potentials (14). However, we observed identical predatory behavior by an electric ray when we used an uninjured but anesthetized fish attached to a glass rod.

Unlike most predatory fish, therefore, electric rays do not initially capture their prey with their mouths. Instead, they appear to immobilize the prey with electric discharges, then slowly manipulate it toward the rather weak but flexible mouth with their remarkably dexterous disk. To demonstrate their discharge, we attached a photographic flashbulb (General Electric, M3B) to a small plastic clamp that was glued to the end of a 1-mlong glass rod. To facilitate the formation of an adequate potential between the contacts of the bulb, an insulated wire was soldered from the apical contact of the bulb to a copper plate taped halfway along the rod; this connection was insulated from the base contact of the bulb with silicone rubber (15). We placed an anesthetized fish in the clamp and positioned the apparatus in front of active electric rays at night. In six of nine trials, the rays discharged and ignited the flashbulbs when the prey were enveloped in the disk (16). The ray consumed the prev in two of the attempts but did not ignite the flashbulb. In one attempt, the ray ignored the prey and swam away.

Finally, one night we photographed

what we consider to be a more natural feeding sequence that was not elicited by baiting. We were observing a 750-mm female slowly swimming 2 m above the reef. After bumping into a column of giant kelp (17) the ray turned toward us with its body inclined, head up. As a result, our dive lights reflected off the white underside of the ray's disk. From behind us, a 200-mm jack mackerel (Trachurus symmetricus) swam erratically toward the ray, possibly attracted by the light. The ray lunged forward and trapped the mackerel in the manner described above. The mackerel disappeared from our view for 2 to 4 seconds while the ray made a forward somersault around the prey. When the ray was upside down we were able to see the mackerel protruding from the folded disk, several centimeters posterior to the ray's mouth. The mackerel appeared to have been electrically stunned; its body was quivering but otherwise immobile, its jaws were protruding and agape, its pectoral fins were abducted, and its dorsal fin was erect (Fig. 1E). By the time the somersault was completed, the mackerel was positioned close to the ray's mouth (Fig. 1F). Shortly thereafter, it was ingested and the ray swam away. The entire process, from lunge to ingestion, took no longer than 10 sec-

Until now, the feeding behavior of only one species of electric ray (Torpedo marmorata) has been described, and these studies were of individuals initially at rest on the bottom of aquariums (18). When a prey fish was nearby, the ray's head rose quickly while the lateral portions of the disk remained in contact with the bottom. Simultaneously, the electric organs discharged, stunning the prey and at least occasionally breaking its vertebral column. The prey was sucked toward the mouth by a stream of water caused by the lifting of the ray's disk and was eventually swallowed. During the day, we often found individuals of T. californica partially buried in the sand flats adjacent to Naples Reef. On two occasions we dangled speared fish in front of buried rays and observed the rays attack and feed in this manner. Thus, individuals of T. californica may feed day or night, while swimming, drifting, or bur-

On the basis of observations in aquariums, Pfeiffer (19) concluded that during the day individuals of T. marmorata bury themselves in sand and ambush active but unwary prey, while at night they swim about in search of prey which may be resting at that time. In kelp beds around Santa Barbara, many resident fish descend from the water column at

night and become quiescent within 1 m or so above the rocky substrates (10). Our findings suggest that Pacific electric rays may be major predators of such temperate reef fishes.

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References and Notes

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 15. This was necessary because of the high electrical conductivity of seawater, which rapidly attenuates the power of the discharge with increasing distance from the ray. creasing distance from the ray
- According to the manufacturer, the minimum requirements to reliably ignite M3B bulbs are 3 volts and 3 amps.
- We commonly see electric rays bumping directly into kelp or the rocky reef at night. On contact, they usually turn around with a stroke of the tail and swim away
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