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BIOELECTRIC-MEDIATED PREDATION BY SWELL SHARKS, *CEPHALOSCYLLIUM VENTRIOSUM*.—The sensitivity of elasmobranchs to weak electric fields is mediated by small electroreceptive structures known as the ampullae of Lorenzini. These sensory vesicles contact the surrounding water via jelly-filled canals that lead to groups of pores on the surface of the head, and enable the animal to detect voltage gradients as low as 0.01 μV/cm (Kalmijn, 1966). This sensory modality is used by sharks for detection of bioelectric fields produced by prey and may also serve in electroorientation by geomagnetic induction (Kalmijn, 1971, 1973).

Previous studies on the electric detection of prey by sharks were conducted either entirely in the laboratory or under semi-natural conditions in the field. In these experiments animals were first motivated to feed by exposure to an odor stimulus and then presented electrical test stimuli (Kalmijn, 1971, 1978). This report presents the results of preliminary experiments on predator-prey interactions between the swell shark, *Cephaloscyllium ventriosum* (Garman) (Scyliorhinidae), and the blacksmith, *Chromis punctipinnis* (Cooper) (Pomacentridae), in their natural habitat, and supports the postulate that electric fields produced by small fish mediate successful prey detection and capture by sharks.

Study area, methods and results.—This study was conducted at a small offshore island, Ship Rock, located near the Isthmus area of Santa Catalina Island, California. Here, the underwater habitat is dominated by a rocky boulder bottom and large stands of giant kelp, *Macrocystis pyrifera* (Linnaeus) C. Agardh. Blacksmith (approximately 10–15 cm SL) form large diurnal feeding aggregations in the water column at the seaward edge of the kelp forest. At dusk, these assemblages disperse when the individuals descend to the bottom and refuge among rocks and benthic macroalgae. During spawning season in late spring and summer densities of blacksmith are highest and many individuals rest on the exposed bottom at night due to limited shelter.

Swell sharks in shallow waters (<20 m) at Ship Rock numbered approximately 125 individuals. Sharks rested deep within rock crevices during the day, and although capable of active swimming, most individuals rested motionless on the open bottom at night during this study (July 1977). Reposed sharks use an ambush strategy to prey on blacksmith at night, and capture fish by one of two different feeding patterns. The first is a rapid 'gulp' behavior that occurs when a blacksmith comes within 1–5 cm of the shark's snout. In this behavior, the shark rapidly raises its head, depresses its lower jaw, and sucks the fish into its oral cavity (Fig. 1). As the mouth closes, water is expelled through the gill slits and the prey is swallowed. This feeding mode occurs so rapidly that only the snap of the shark's mouth can be seen, not the actual ingestion of the prey. The second mode of capture is a readily visible 'yawn' behavior that is clearly discernible from the 'gulp' by a graded relationship between the shark's gape width and the prey-to-snout distance. The closer a blacksmith comes to the head of the shark, the wider the shark opens its mouth. If the prey moves away from the snout, the mouth begins to close. In the 'yawn' behavior, blacksmith are captured when they inadvertently swim, or fortuitously drift in the shallow surge, into the fully expanded oral cavity of the shark which is then snapped shut (Fig. 1).

To further investigate these interactions, a preliminary series of simple underwater tests were performed to determine how readily sharks would take free-swimming blacksmith and whether the sharks used sensory cues other than vision to detect their prey. The former was tested by tethering a live healthy blacksmith to the end of a fiberglass rod with a short piece of monofilament line. The fish, which did not struggle, was presented by divers to sharks at rest on the bottom at night. In this test, seven out of ten sharks attempted to take the prey. Next, a live blacksmith was sealed in a water-filled clear-plastic bag (that blocked all olfactory and electrical cues), suspended on the end of the fiberglass rod, and then offered to ten sharks. This time, no shark showed any positive response. Replicate tests using blacksmith in a black plastic bag produced the same negative results. These findings indicated that neither vision (either normal or augmented by our dive lights) nor olfaction was a primary sensory modality used to detect prey.

To determine which sense is most important for detection of blacksmith, a prey chamber was constructed in which further combinations of cues could be manipulated. The chamber design was a modification of that used by Kalmijn (1971) so that tests similar to his could be performed. The housing was made from a 5.5-cm length of 14-cm outside-diameter PVC pipe (.7-cm wall thickness) backed with a removable plastic plate. The forward end of the housing was strung with monofilament line to form a webbed face. An attachable agar cap was made from a 4.7-cm long 14.2-cm inside-diameter PVC pipe and faced on one end with a covering of 1-cm thick open-cell foam that had been impregnated with a 3% agar-seawater gel. The cap, when used, was placed over the webbed end of the chamber and sealed by an o-ring seated on the perimeter of the main prey housing. An additional plastic shield made of household plastic wrap approximately 10-μ thick was placed over the face of the agar cap and secured with a flat elastic band. The entire apparatus was mounted on the end of a 1-m long plastic pipe for presentation by divers to sharks.

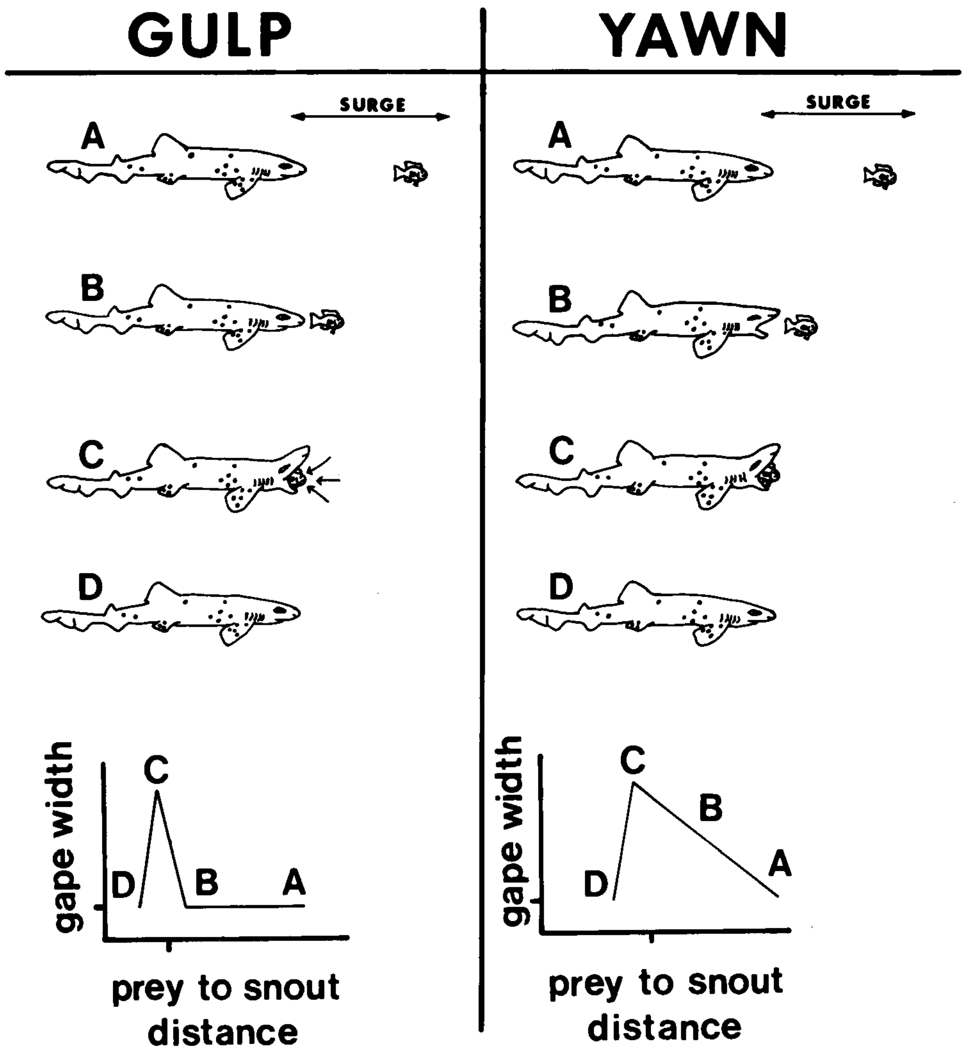

Fig. 1. Feeding behaviors of swell sharks that use an ambush predator strategy. A) Sharks reposed on the bottom at night often orient parallel to surge flow and wait for a blacksmith fish prey to near their snouts. In the 'gulp' response B) sharks wait until prey is within approximately 1–5 cm from snout, C) 'suck' prey into oral cavity by rapidly raising snout and depressing lower jaw, and D) swallow fish. In the 'yawn' behavior sharks A) also orient parallel to surge if present, but unlike gulp behavior they B) increase their mouth gape width as blacksmith nears snout, until C) prey inadvertently enters mouth cavity, and D) is swallowed.

A live blacksmith was placed in the housing and presented to sharks encountered by divers swimming casually around Ship Rock at night. Of 14 sharks presented with an open-ended chamber containing a healthy fish, 8 (57%) showed a gulp or yawn response (Table 1). Of ten sharks presented with the empty (control) chamber (with and without the agar cap), none showed any positive feeding response. The permeability of the agar shield to an electric field was tested by presenting naive sharks a blacksmith in the chamber with agar cap affixed. Three of seven sharks showed a positive feeding response which indicated the electric fields were penetrating the agar screen. These experiments showed that 1) feeding responses were due to the presence of a fish in the chamber and not a reaction to the apparatus, and 2)

TABLE 1. FEEDING RESPONSES OF SWELL SHARKS TO BIOELECTRIC FIELDS FROM BLACKSMITH IN CHAMBER. Sharks at rest on the bottom at night were presented chamber apparatus by diver. In the prey electric-field experiments, divers made serial presentations of the apparatus (under three different conditions) to ten individual sharks so that each shark was given the same test.

	Chamber effect		Prey electric-field experiment		
Response	Prey + chamber	Control (empty chamber)	Prey + chamber	Prey + agar cap	Prey + agar cap + plastic shield
Yawn	1	0	8	5	0
Gulp	7	0	2	1	0
None	6	10	—	4	10
Total presentations	14	10	10	10	10

not all sharks would show a positive feeding response, possibly due to a low state of hunger or an unnatural (e.g., weakened or distorted) electric field.

During three nights of the following week, ten sharks chosen at random were tested for their sensitivity to bioelectric fields of prey. A shark was first presented with a healthy fish in an uncovered prey chamber. If the shark showed a positive response, the agar-faced cap was placed over the open end of the prey chamber and again presented to the same shark. With the cap attached all olfactory and visual cues from the prey (which did not struggle) were obliterated; the only stimuli present was the blacksmith's bioelectric field that passed through the agar (and possibly some acoustic cues). Of the ten sharks (out of approximately 25 tested) that showed the initial positive feeding response, six showed an additional 'gulp' or 'yawn' when presented with the chamber plus the agar cap (Table 1). After exposure to the agar-covered chamber, each shark was once again presented the apparatus with an additional polyethylene-plastic shield placed over the agar cap that now screened the electric field emitted by the prey but still allowed any acoustic cues present to penetrate. In this test, no sharks responded to the apparatus.

Discussion.—These experiments indicate that detection of blacksmith by swell sharks using an ambush strategy under normal nocturnal feeding conditions can be successfully mediated by the passive electric field emitted by individual prey. This sensory modality provides graded analog information of prey distance at close ranges (20 cm). This was evident from the gape-size relationship to prey-to-snout distance seen in the 'yawn' behavior. Passive electric field strengths emitted by small fishes [e.g., 0.2 μV/cm at 10 cm distance for a 15 cm long flatfish, *Pleuronectes* sp. (Kalmijn, 1974)], at distances up to 20 cm are within the sensitivity range of small sharks (.01 μV/cm) (Kalmijn, 1966).

Data from the experiment (Table 1) show a trend for a decreasing proportion of positive feeding responses with each successive presentation. Based on this response decline, such a trend might be interpreted as a learning response, i.e., that some sharks had learned they could not get the fish and therefore no longer responded. This explanation is inadequate however, because sharks would have to learn to associate the apparatus with food in one trial and then show extinction in the very next presentation. This is highly unlikely since many trials (e.g., tens or hundreds) may be necessary to establish learning in fishes and extinction may take weeks or months (Harlow, 1939; O'Connell, 1960; Clark, 1963). It is much more probable that the response decline was due to distortion or weakening of the electric field caused by the agar cap, or perhaps differential states of motivation among sharks due to prior feedings, fatigue, etc. In addition, sharks were observed to be unsuccessful in multiple attempts to capture blacksmith when feeding naturally, and no such response declines were observed.

In contrast to the 'yawn', some sharks captured prey by the more stereotyped 'gulp' behavior, but only when prey came within approximately 3 cm or less of the shark's snout. Although these two predatory modes serve similar functions, they are qualitatively distinct in their motor patterns and show different relationships to prey distance. Further high-speed cinematographic analysis would provide more precise data on jaw mechanics and temporal sequences. It also remains unclear whether the proximate causal factors that determine which specific feeding behavior is displayed are environmental (e.g., characteristics of electric cue from prey), intrinsic (e.g., motivational state of the animal), or a combination of both.

Undoubtedly, predation is frequently mediated by combinations of different sensory systems. There are, however, advantages for an electric sensitivity to prey, especially for a nocturnal predator. While olfactory and acoustic cues may be important in initial prey perception over longer distances, electric field vectors, like vision, can theoretically provide almost instantaneous information on direction of prey at close range and quantitative information of distance based on the configuration (or strength) of the electric field.

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Timothy C. Tricas, *Department of Zoology, University of Hawaii at Manoa, Honolulu, Hawaii 96822.* Accepted 19 Oct. 1981.