ACTIVITY AND FEEDING BEHAVIOR OF THE SUMMER FLOUNDER (*PARALICHTHYS DENTATUS*) UNDER CONTROLLED LABORATORY CONDITIONS

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ABSTRACT

A group of five to six adult summer flounder, *Paralichthys dentatus* (Linnaeus), held under controlled laboratory conditions in a large, experimental, seawater tank, exhibited three general behavior patterns: (1) resting, (2) swimming, and (3) feeding. While resting on the sand surface, the fish maintained varying degrees of alertness, indicated by the position of the head and/or eye movements. Fish buried beneath the sand were considered to be in a lower state of responsiveness. The fish swam and glided at all levels in the water column or combined crawling and swimming to move along the sand. Activity measurements based on these swimming patterns indicated that the fish were primarily day-active. A range of feeding behaviors enabled the fish to capture prey equally well on the bottom or in the water column. The significance of these patterns and their relation to those of other flatfishes is discussed.

Until recent years, knowledge about the behavior of marine flatfishes has come mainly from the analyses of catches by fishing and research vessels to determine population structure, rates of recruitment, growth and mortality, migratory habits, and other aspects of life history from egg to adult stages. However, there are many questions that have been left unanswered, especially those concerning patterns of behavior that in many cases have a direct bearing on life habits.

One approach to answering questions on behavior is to observe the animal in the laboratory, under controlled conditions. Recent comprehensive laboratory studies on flatfishes have included work by Kruuk (1963) on *Solea vulgaris;* de Groot (1964) on *Pleuronectes platessa;* de Groot (1969) on *Solea solea, Limanda limanda, Pleuronectes platessa, P. flesus, Scophthalmus rhombus,* and *S. maximus;* and Verheijen and de Groot (1967) on *Pleuronectes platessa* and *P. flesus.* A most valuable paper by de Groot (1971) reviews the literature and discusses food, feeding behavior, and activity in flatfishes. These investigations have pointed to the diversity of their habits and the importance of comparative studies in understanding the interrelations between the various species.

In this work we have endeavored to further the understanding of some specific behaviors by studying, under controlled laboratory conditions, the activity cycles, feeding, and general swimming patterns of adult summer flounder, *Paralichthys dentatus* (Linnaeus), a species of major commercial and recreational importance.

MATERIALS AND METHODS

We observed five to six adult summer flounder, captured 16 to 48 km off the coast of Maryland. The fish ranged in length from 37.0 to 74.5 cm and in weight from 957.0 to 5,690.0 g.

We held the fish in an elliptical seawater aquarium, 10.6 × 4.5 × 3.0 m deep with a capacity of 121 kliter (Olla, Marchioni, and Katz, 1967). To provide a suitable bottom habitat for the fish, we added several layers of gravel, covered by an upper layer of 0.6 to 0.8 mm sand. Beneath the sand and gravel was a network of

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pipes designed to move filtered water through the layers to prevent contamination of the bottom. Water temperature in the tank ranged from 17.0° to 20.0°C. Salinity ranged from 23.0 to 26.0‰, oxygen from 6.5 to 7.7 mg/liter, and pH from 7.3 to 7.7.

Fluorescent lights mounted on two side walls above the aquarium were mechanically timed to approximate the natural daily photoperiod from morning to evening civil twilight. Since Verheijen and de Groot (1967) reported that high light intensities could inhibit normal activity in flatfish, we held the maximum daytime light intensity, as measured at the surface, at 3.5×10^2 mc. Preliminary measurements showed this level not to be inhibitory. An automated dimming system gradually raised and lowered light intensity during morning and evening civil twilight, avoiding sudden light changes that might startle the fish. A second lighting system, which switched on before the dimmer lights were extinguished, provided an indirect light of 2×10^{-1} mc as measured at the water surface (2.5×10^{-3} mc at 1 m below the surface) during the night period.

Throughout the course of the observations, at intervals of about 30 days, we fed the fish 1,100 to 4,400 g of live sand shrimp, *Crangon septemspinosa*, and grass shrimp, *Palaemonetes vulgaris*. The quantity of shrimp introduced each time insured a food supply which lasted for 30 days. According to Poole (1964) and Smith (1969), shrimp appear to be an important constituent of this species' natural diet.

Following 34 days of acclimation to the tank, we measured the activity of six fish over a 51-day period. At the end of this time, one fish died and our measurements were then based on five fish. Throughout the day and night, we made 5-min observations every hour 4 days each week of the number of fish swimming, feeding, or moving about on the bottom.

We found that 5 min was too brief to allow for extensive observations of the fish's behavior, so after establishing the daily cycle of activity, we lengthened these periods to 30 min every 3 hr 4 days each week. In conjunction with these extended observations, we periodically took motion pictures which allowed us to make a more detailed analysis of feeding and swimming. Gliding and swimming speeds were measured from these motion pictures as well as from stopwatch readings taken as the fish passed between two marks 335 cm apart.

RESULTS

We have classified the activity patterns of the fish into three general categories: (1) resting, either on the surface of the sand or beneath it, (2) swimming, and (3) feeding. Within these three categories, we have described the various aspects of each behavior in an attempt to provide a clearer picture of the fish's habits.

RESTING

The summer flounder exhibited three basic resting positions: (1) lying flat on the sand; (2) lying on the sand with the head raised (as much as 7.5 cm), supported by the body musculature and the anterior portions of the dorsal and anal fins braced vertically into the sand; and (3) buried beneath varying amounts of sand.

In the first resting position, while flat on the sand, the eye turrets were either retracted or extended. When extended, the eyes either remained relatively fixed or moved up to 6 to 8 times per min. When the head was raised, as in the second resting position, eye movements were generally more frequent, ranging from 10 to 30 times per min, reflecting a higher degree of responsiveness. This "head-up" posture was generally characteristic of an animal at a higher level of activeness than fish lying flat.

Fish in either resting position occasionally "yawned." The head was elevated, the mouth opened, and the opercula extended. Yawning occurred either as a single event or up to 16 times in rapid succession. As yawning was repeated, the gape of the mouth increased and the head rose progressively farther off the sand. During the 30-min observation periods, we recorded the events preceding and following 33 yawns, i.e., separate occurrences, whether comprised of a single yawn or a number of successive yawning movements. Of these, 24 preceded an immediate change in activity; i.e., 17 times yawning preceded swimming from a resting position, 2 times it preceded burying, and 5 times, a change in position. In seven instances, 5 to 10 min elapsed, before the fish proceeded to bury (2 times), swim (4 times), or change position (once). The remaining two instances occurred as the fish settled on the sand after swimming. It appeared from these findings that yawning generally was associated with changes in activity. This is similar to the increased activity following yawning in the yellowtail demoiselle, *Microspathodon chrysurus*, (Rasa, 1971).

The buried position was characteristic of fish in a state of low responsiveness, similar to that shown by fish lying flat on the surface of the sand. The eyes seldom rotated and a buried fish did not respond to prey that moved or settled directly within its line of vision. Burying began with an upthrust of either head or tail which continued as a beating of the head and tail alternately against the sand, from 5 to 10 times, until the fish was partially or completely covered. This took 1.5 to 3.0 sec.

The events leading to burying were apparently nonspecific. For instance, after swimming, some flounder would settle on the sand and immediately bury. Other flounder resting on the sand for as long as 20 min would, for no reason apparent to the observer, bury. We also found that, as described below, burying might occur as a secondary response when the fish were subjected to an intense or sudden stimulus.

SWIMMING

Swimming movements could begin from any resting position and could be classified into three categories. In one category, fish swam in the water column, at any depth from surface to bottom, at speeds ranging from 19.0 to 58.0 cm/sec. As a fish swam, the head moved up and down while the body musculature expanded and contracted, the whole process viewed as a series of rhythmic undulations. The caudal fin exerted most of the momentum for forward movement; the left pectoral (the eyed side) and to a lesser extent, the right pectoral, acted as rudders. To counteract their natural negative buoyancy, and hence the tendency to sink, the fish were continually in motion, swimming at one level or swimming upward.

A second type of swimming combined active propulsion and gliding. The fish would swim upward in the water column (Figure 1A and B) and then, by positioning the head downward and

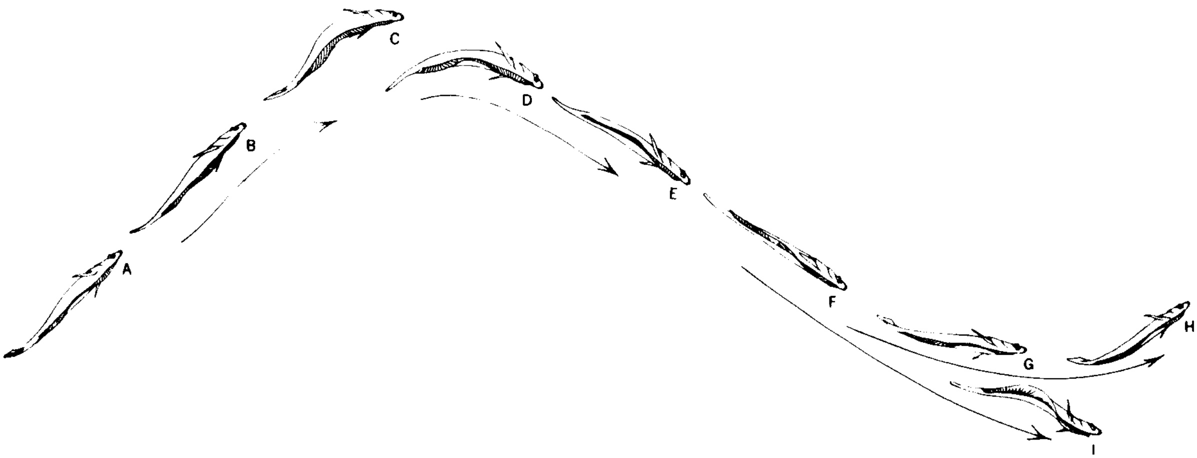

FIGURE 1.—Swimming and gliding behavior. A swimming fish (A, B) flexes from head to midsection (C) to begin a glide. As the head drops (D) and the body flattens (E), the fish glides downward and forward (F, G). At any depth, the fish can either resume swimming (H) or brake its forward glide (I).

flattening the body, would glide downward and forward (Figure 1C-H). The angle and rate of descent were controlled by the position of the head and body relative to the bottom as well as by the position of the dorsal, anal, and caudal fins. By raising the pectoral fins and posterior portions of the dorsal and anal fins, while simultaneously lowering the anterior portions of the dorsal and anal fins and arching the body, the fish could brake its forward motion in midwater (Figure 1I), either to change swimming direction or to approach a potential prey. Gliding was an effective means of covering distances while in the water column. Starting at a height of 1.8 m from the bottom, a fish could glide 4.5 to 6.5 m at speeds ranging from 34.0 to 64.0 cm/sec.

A third type of swimming combined swimming within 5 to 15 cm of the sand and crawling ("shambling" as described by Kruuk, 1963; and Verheijen and de Groot, 1967). This was most often observed when the fish were actively seeking prey. Shambling speeds ranged from 32.0 to 48.0 cm/sec.

ACTIVITY CYCLE

Based on hourly counts of the number of fish swimming in the water column or moving along the sand, we found the flounder to be primarily day-active (Figure 2A-H) although the light level at night was apparently sufficient to permit swimming and feeding.

Throughout the course of our observations, there was an overall decrease in activity occurring first at night (Figure 2B) and then during the day (Figure 2E-H). During this time, the photoperiod was changing, approximating the natural seasonal daylength. While changing photoperiod may act as an assignable cause for the decline in the fish's activity, observations included only a small part of the natural seasonal photoperiod cycle, too brief a time to permit a definitive statement as to its influence on activity.

FEEDING

The fish could feed with as much facility on the bottom as in the water column. Bottom

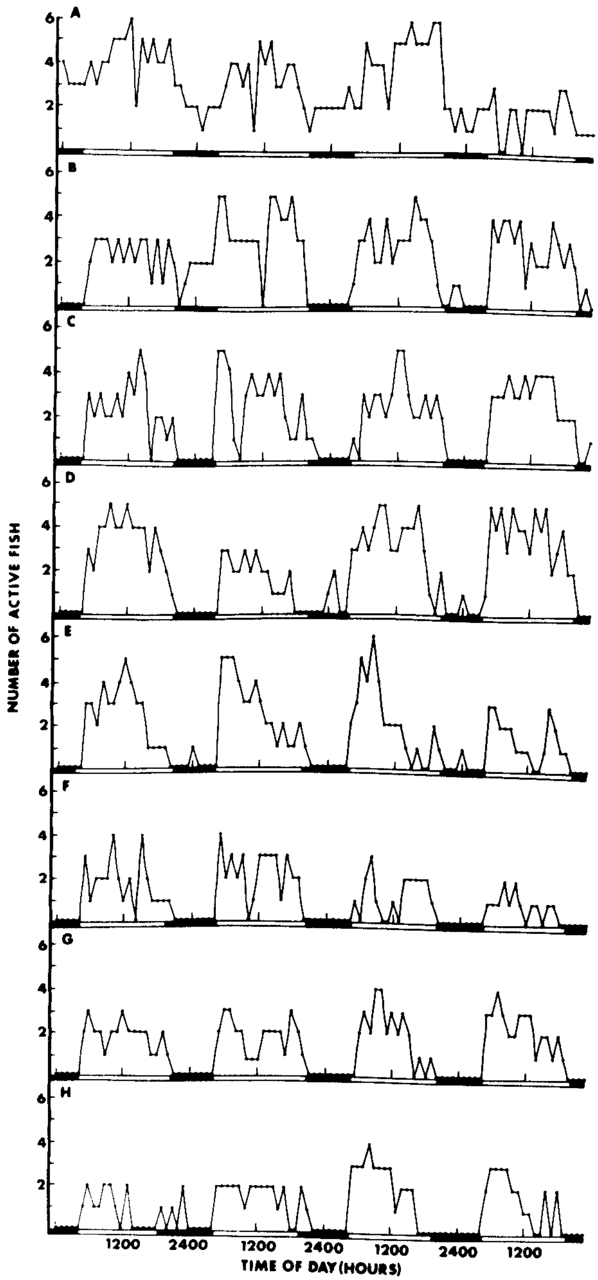

FIGURE 2.—Number of fish swimming in the water column or moving along the sand. Counts were taken at hourly intervals throughout the day and night under the following average photoperiods: (A) 16.3 hr; (B) 16.4 hr; (C) 16.4 hr; (D) 16.3 hr; (E) 16.2 hr; (F) 16.0 hr; (G) 15.9 hr; (H) 15.8 hr.

feeding was always preceded by active prey search. In most instances, a flounder, after selecting a potential prey, would rest on the sand with the head slightly raised. Then, while visually fixing on a shrimp, the fish would begin to stalk, crawling on the sand towards the prey. This crawling was viewed as waves of cephalocaudal movements of the dorsal and anal fins (Figure 3A-D). When a fish was within striking distance (5-10 cm), the head was angled downward or lay flat on the sand. The midsection of the body was arched, supported by the caudal fin and by portions of the edges of the dorsal and anal fins braced into the sand (Figure 4A). As the caudal fin beat downward (Figure 4B), the fish sprang forward, mouth agape and opercula spread, striking and ingesting the shrimp (Figure 4C). Speed during the strike was about 40 to 50 cm/sec. After ingestion, there was continued mouth movement, apparently part of the pharyngeo-esophageal activity necessary for swallowing.

Fish that were resting on the bottom, with the head either up or down, would not strike at shrimp even though prey were well within striking distance. Feeding was always preceded by active search, although these fish were seemingly well-adapted for a "lying-in-wait" method of prey capture.

Fish swimming 50 to 70 cm above the bottom could also capture shrimp from the sand. As a swimming fish (Figure 5A) visually fixed on a single shrimp, speed abruptly decreased (Figure 5B). While the flounder was still moving forward, it would tilt towards the sand at a 30° to 45° angle. At this point, with the prey about

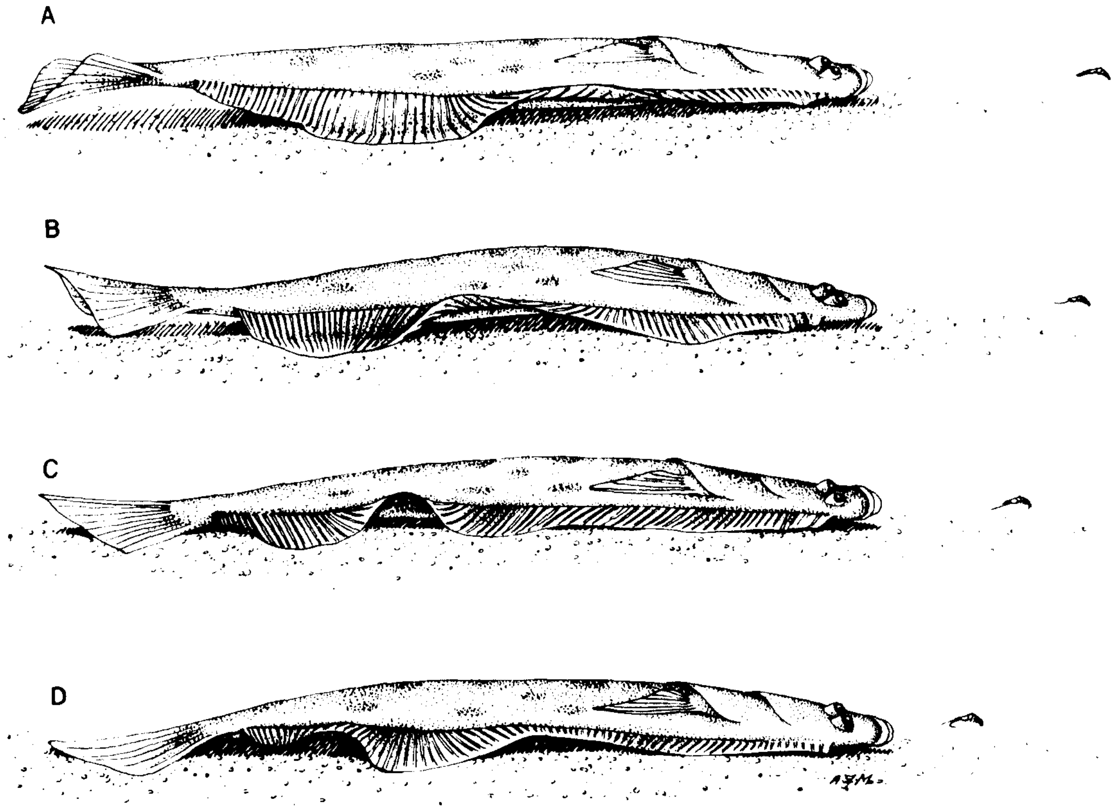

FIGURE 3.—Stalking behavior. The fish visually fixes on a shrimp and crawls slowly forward on the dorsal and anal fins (A-D).

20 cm away, its forward motion almost ceased. Then, when within 3 to 5 cm of the prey (Figure 5C), the fish beat downward with the caudal fin and with mouth agape and opercula spread, moved forward and downward. As the fish ingested the shrimp, it would usually make contact with the bottom with its snout, then glance off the sand, and move slightly forward and upward (Figure 5D). The fish would then resume swimming or settle on the sand.

The basic elements of prey selection and visual fixation were essentially the same whether the fish were feeding in the water column or on the bottom. While the flounder were actively swimming or gliding toward shrimp, they would approach and decrease speed by raising posterior portions of the dorsal and anal fins and arching the body into a partially flexed position. Then, with a rapid caudal flexion, the fish would capture and ingest the shrimp. As was the case with bottom feeding, after capturing a prey, a fish would either continue active search or settle on the sand.

The searching, stalking, active eye movements, and visual fixation on specific prey all indicated that vision was a primary sense used in feeding during the day. We observed feeding at night, and while it appeared to us that the role of vision was similar to that in the day, we could not preclude the possibility of other senses playing more dominant roles.

At times the flounder would approach a prey, as if to begin stalking or a capture, but would then turn away. We considered this type of behavior to be a feeding intention movement. For example, a flounder would swim toward shrimp on or near the bottom, assume a prestrike posture, visually fix on a shrimp, and open and close

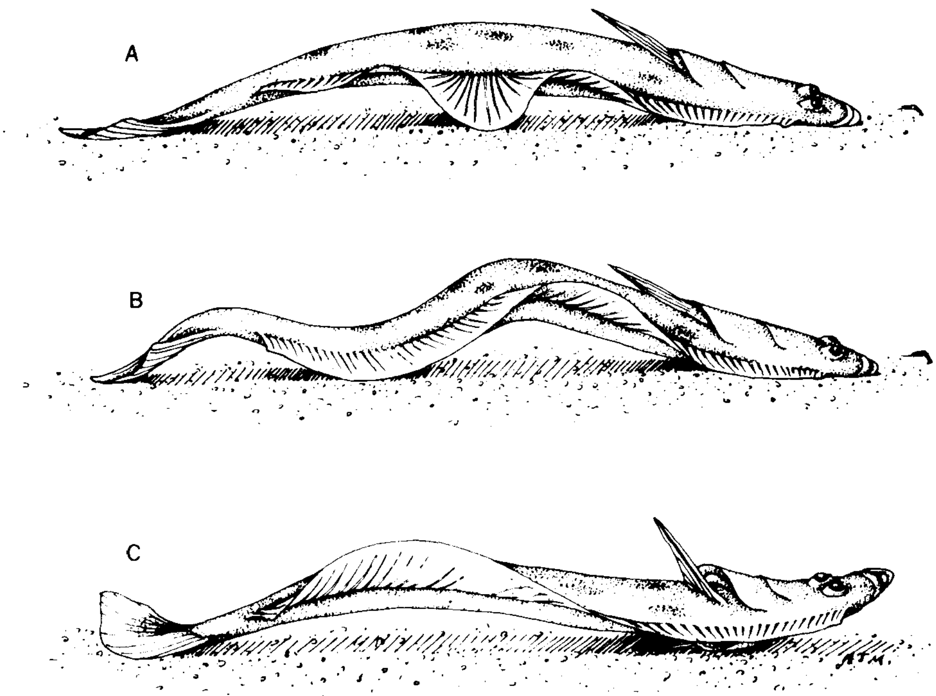

FIGURE 4.—Prey capture following stalking. The fish assumes a position prior to striking. The body is slightly raised off the sand and the eyes are visually fixed on the prey (A). As the strike begins, the caudal fin beats downward (B), thrusting the fish forward for the capture (C).

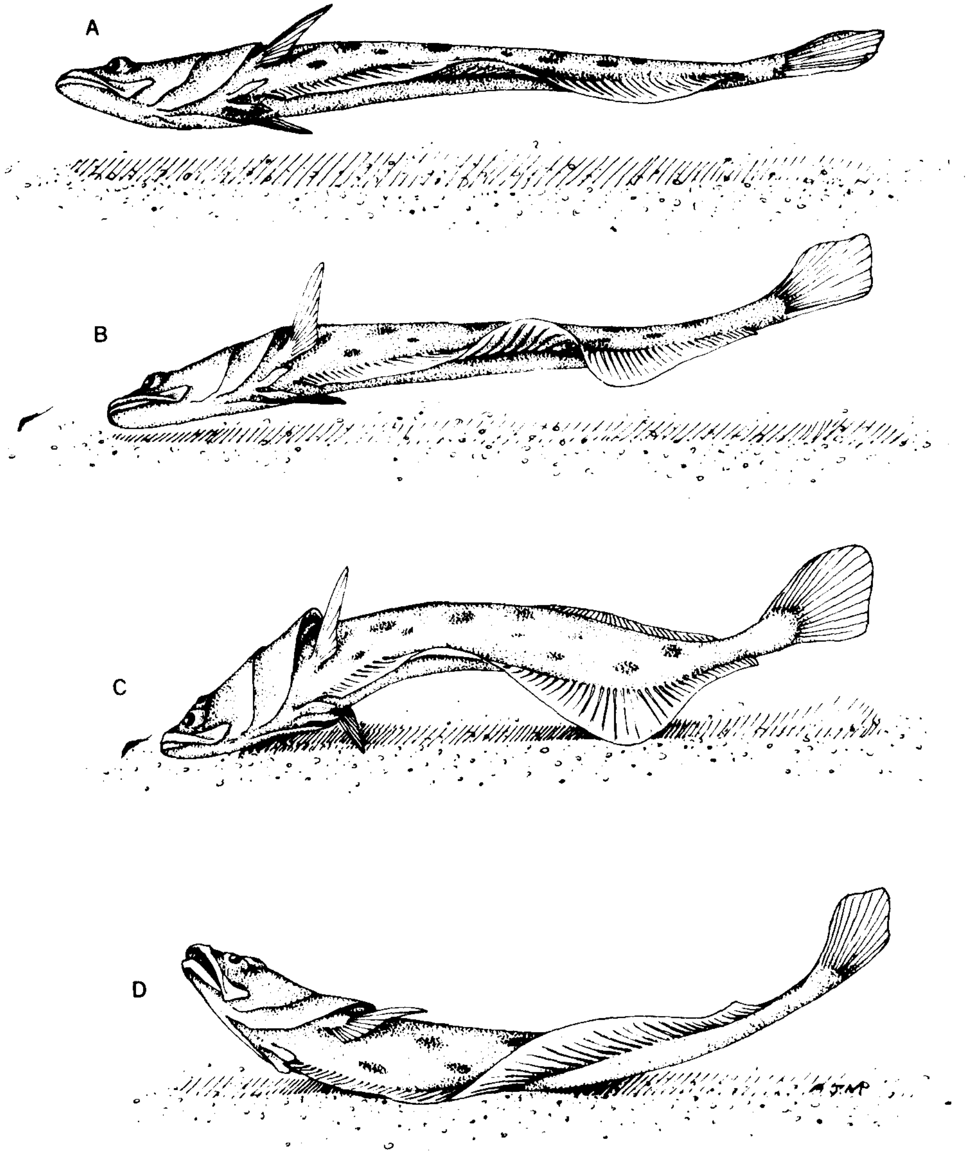

FIGURE 5.—Bottom feeding by a swimming fish. A swimming fish (A) visually fixes on a shrimp on the bottom, partially brakes its forward motion (B), and tilts toward the sand. As the caudal fin beats downward, the mouth opens, the opercula spread, and the fish moves ahead to ingest the shrimp (C, D).

its mouth several times. Then, without lunging or striking at the prey, the fish would swim away after a few seconds.

We found feeding intention movements to occur after the fish had been feeding. For instance, in one case, after we had introduced 1,100 g of shrimp into the tank (29 days after the last feeding of 4,400 g of shrimp), the fish began to feed within 3 min. One fish, after eating 13 shrimp within a 22-min period, exhibited an intention movement 3 min later. Then four more shrimp were ingested during the next 20 min, followed 2 min later by two additional intention movements. A second fish ingested 15 shrimp within 35 min and 2 min later made an intention movement. A third fish, after ingesting 16 shrimp in 26 min, made an intention movement 1 min later, then fed immediately on one shrimp, and 2 min later exhibited an intention movement. These movements may have been related to a reduction of feeding motivation as a result of satiation.

FRIGHT RESPONSE

We observed what was apparently a "fright" response to a sudden stimulus under two different circumstances. In one case, there was a malfunction of the dimmer lights which caused the sudden onset of the daylight lights. A swimming fish immediately dropped to the bottom where it remained resting on the sand surface. In another case, an observer above the tank waved his arms as a fish moved about near the water surface. The fish immediately dropped to the sand, darkened, and assumed a rigid posture. The head and caudal fin lay flat, but the dorsal and anal fins were arched in two places along their length. The fish remained in this posture for about 45 sec during which it slowly lowered first the anterior, then the posterior sections of the dorsal and anal fins until they were flat. The flounder then swam about 2 m away and buried. In both instances, the initial response of the fish to a fright stimulus was to drop to the bottom and remain motionless. Burying occurred as a secondary response.

DISCUSSION

Previous descriptions of the habits of summer flounder have characterized them as primarily bottom-oriented, except for occasional sorties to the surface in pursuit of prey (Bigelow and Schroeder, 1953:267-270). Furthermore, this species has been described as being relatively immobile, except while feeding or during the normal migratory period (Ginsberg, 1952). In our laboratory observations, while the fish frequently searched for and captured prey on the sand and also remained quiescent on the bottom for long periods, they would also frequently use the water column for swimming, prey search, and feeding. In fact, during one part of our study, the fish swam and glided for extended periods throughout all levels of the tank, seldom resting in any one position.

The gliding behavior we observed could play an important role for the animal in the sea. After reaching the surface, the fish could travel considerable distances with little or no active swimming movements, using natural negative buoyancy and body shape to full advantage. Positioning of the fins and body would control forward speed and distance traveled. Although there might have been a sacrifice in speed, the gliding would represent a saving in energy as compared with that required to swim the same distance. Gliding would also enable the animal to search for and capture prey in the water column more efficiently, since it could approach a prey with less gross movement than would occur during active swimming. This might lessen the chance of eliciting escape responses from the prey due to visual or mechanical stimuli. Another adaptive advantage of gliding in food search might be related to the fact that the head was steady, thus making it easier to keep the prey in the visual field.

Although the summer flounder were primarily day-active, we observed burying, feeding, shambling, and swimming both day and night. Similar to the summer flounder, turbot (*Scophthalmus maximus*) swim and are active on the bottom primarily during the day, although both activities may occur at night to a lesser degree (de Groot, 1971). Verheijen and de Groot (1967) and de Groot (1971) established that plaice (*Pleuronectes platessa*) and flounder (*P. flesus*) showed a nocturnal pattern of swimming in the upper water column, while during the day they would shamble or swim over the bottom searching for food. Kruuk (1963) and de Groot (1971) found that the sole (*Solea vulgaris*) also had a nocturnal period of high activity under both natural and artificial light.

The method of burying in the summer flounder is similar to Kruuk's (1963) description of "digging-in" in the sole. In the sole as well as the winter flounder, *Pseudopleuronectes americanus*, (McCracken, 1963) and starry flounder, *Platichthys stellatus*, (Orcutt, 1950), burying could be induced as a direct response to a sudden disturbance, such as a change in light intensity or moving object. In the summer flounder, apparently the primary response to a fright stimulus is to assume a stationary and sometimes rigid posture on the bottom. This is followed by burying as essentially a secondary response.

There are numerous descriptions of the sensory mechanisms utilized by different groups of flatfishes during feeding (see de Groot, 1971, for review). Since summer flounder are primarily day-active, it was not surprising that vision played a primary role in prey selection and capture. According to de Groot (1971), this is apparently characteristic of Bothidae including brill (*Scophthalmus rhombus*) and turbot, which he designated as visual day-feeders, largely dependent on visual stimuli for locating prey. Despite the fact that the summer flounder would also be categorized in this manner, we did observe feeding at night. Although the light level of 2.5×10^{-3} mc (as measured at 1 m below the surface) fell slightly below the 10^{0}-10^{-2} mc level cited by Blaxter (1970) as the range in which most visual feeders cease active feeding, it was possible that vision was still being utilized.

The summer flounder, winter flounder, (Olla, Wicklund, and Wilk, 1969), and lemon sole, *Microstomus kitt*, (Steven, 1930) may rest on the bottom with head up while actively moving their eyes. In the latter two species, the fish may be searching for food and will lunge forward from this position to strike at and capture prey. While we considered summer flounder in this position to be alert and responsive, it was also apparent that this was not necessarily indicative of a prefeeding strike. Although Ginsberg (1952) stated that summer flounder lie in wait for passing prey, we found that the fish, even in this alert "head-up" posture, never lunged from a resting position at a prey, even though it was only a few centimeters away, but always preceded prey capture by active searching.

While we do not understand the role yawning plays in the behavior of the summer flounder, we did find evidence that it was associated with changes in activity. Rasa (1971) found that yawning in the yellowtail demoiselle was associated with an increased excitement level. She postulated that the strong muscle contraction that occurs during yawning could serve to increase the blood flow and oxygen to the body musculature and thereby facilitate the onset of the animal's activity. It may also be conceivable that yawning movements may act to flush sand or debris from the gill areas, one function suggested for yawning in Pacific bonito, *Sarda chiliensis*, (Magnuson and Prescott, 1966).

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