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Sequential Observations on Gross Digestive Processes of *Illex illecebrosus*

by

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INTRODUCTION

The anatomy of a squid is well suited to the physiological demands of life as an actively swimming predator (Bidder, 1950). The bipartite digestive system, consisting of stomach and caecum, provides for efficient digestion of prey. Physical breakdown of the food occurs in the stomach, and subsequent enzymatic digestion and absorption take place in the caecum. The caecum is also a repository for digestive enzymes between meals (Bidder, 1950). However, little is known about the physical and chemical changes associated with passage of food through the digestive system; and investigations into rates of digestion have produced widely variable results (Bidder, 1950; Bouchard-Camou et al., 1976; Karpov, 1978; Boucher-Rodoni, 1975).

Studies on Illex illecebrosus (Boucher-Rodoni, 1975) and some European species of Loligo (Bidder, 1950) indicate that stages of digestion can be characterized by caecal color changes. Changes in appearance of the gut contents have also been used in determination of digestive stages (Bidder, 1950; Karpov, 1978). The need to develop criteria for establishing the progression of digestion has been noted, especially in food and feeding studies (Amaratunga, 1980). At present, field survey data cannot satisfactorily indicate the approximate time of food ingestion. In this study, the process of digestion has been followed in a laboratory population of Illex illecebrosus in order to establish a simple numerical index of stages of digestion which would be suitable for estimating recency of feeding in field surveys.

METHODS

The squid used in this study were captured in a net trap on August 8 and 15, 1979, and transferred to an outside tank (capacity 45 m^2) as described by O'Dor (1977; 1979). Approximately 50 squid were taken in each sample. The seawater temperature in the tank was maintained by a continuous flow-through system at 9-11°C. The same experimental method was used with each group and results from the two replicate experiments were combined.

Live Fundulus sp. were used as the food source. Each group of squid was given a preliminary feeding to familiarize them with the food and feeding method. In this and the subsequent feeding, the fish were introduced singly or a few at a time to ensure that no prey in excess of that readily eaten remained in the pool. After the preliminary feeding, the squid were starved for at least 44 hours to clear the gut contents (Boucher-Rodoni, 1975). Any animals displaying signs of damage or abnormal behaviour during this period were removed from the experiment.

Two squid were removed for analysis at the beginning of the experiment, prior to feeding. A number of Fundulus (5-10 cm in length) were fed to the experimental group, with no control of consumption by each squid. The feeding, conducted as swiftly as possible, lasted approximately 45 minutes. Most animals were observed to have fed. Upon cessation of feeding, two animals were removed for analysis. Subsequently, two animals were removed at successive two-hour intervals until digestion was considered to be complete.

Squid removed from the tank were rapidly weighed, killed, and opened ventrally to expose the digestive system. Standard analyses (mantle length, sex, maturity, gut fullness) were performed as described by Amaratunga and Durward (1979). Intact guts were photographed and later studied for color and consistency. The guts were then ligatured and removed and the weights and volumes of stomach and caecum taken separately. PH measurements were taken using pH meter 22 (Radiometer Copenhagen). Gut contents were diluted with seawater in a petri dish and examined and photographed under a binocular microscope to investigate the appearance of digesting tissue and erosion of any hard structures (scales, bones, etc.). Extracted gut contents were then preserved in 10% formalin in seawater for future analyses.

Rapid determination of gut pH is impractical in the field and therefore of little value to this report.

RESULTS

The squid used in this study had an average weight of 248 gm (174-338 gm) and average dorsal mantle length of 226 mm (185-250 mm); 20% were male. Most were sexually immature.

The behaviour of the feeding population was similar to that described by O'Dor et al. (1979). Healthy, actively feeding squid remained in a tight school throughout captivity. Formation was only temporarily broken during feeding. Larger squid fed first, darting out to seize fish and then returning quickly to the school. Some squid were observed to take more fish than could easily be held within the arms. Encounters with less-encumbered squid often resulted in loss of one or two prey items. When larger squid had fed, they retired into the school, allowing smaller squid to feed.

The seized fish is held by the arms and the head bitten off (pieces of flesh are then bitten and ingested). Ingestion requires 5-15 minutes. Examination of waste material from the tank after similar feedings indicates that vertebrae, tails, eyes, and internal organs are mostly rejected. Observation of gut contents confirmed this selectivity; vertebrae, eyes, etc. were found only infrequently.

Squid killed within an hour of ingestion were found to contain large food masses in the stomach. The average weight of stomachs (11.63 gm) during the experiment ranged from

5.88-18.82 gms. The average meal constituted 4.5% of body weight. The largest meal observed immediately after ingestion, 33.30 gm by a 309 gm squid, represents 10.8% of the body weight. Stomach fullness was predominantly 2 and 3 (Amaratunga and Durward, 1979) throughout digestion. Since gut contents were eliminated only in the final stages of digestion, lower indices of fullness were obtained only in the final few hours.

Table 1 shows external color changes in the stomach and caecum. A useful color index can be established for the caecum, but stomach coloration is less variable. Caecal fluid showed a progression of color changes consistent with observations of other researchers (Bidder, 1950; Boucher-Rodoni, 1975). The fluid in squid killed before feeding or at the end of digestion (16 hours) was clear. Intermediate color changes were distinct and consistent. A deep red or burgundy color appeared immediately after ingestion, changing to varying shades of brown for most of the period of digestion and to light yellow in the final stages of digestion. These changes are summarized in Table 2. In the stomach, particulate food material obliterated most fluid color changes. The solid material underwent only subtle changes related to the glimmer imparted by the digestive release of oil droplets. The final stages of digestion are marked by the sudden appearance of yellow or clear fluid similar to that in the caecum (Table 1).

Analysis of stomach contents for degree of degradation provides a rough indication of digestion (Table 3). Large chunks of flesh were degraded as digestion progressed. Scales and bones became more prominent as they were freed from muscle and softer tissue. Consistency, estimated by touch and visual observation, changed throughout digestion. These changes in gut contents are relatively subjective and, as such, not amenable to detailed description in two hourly stages of digestion. In conjunction with color parameters, however, they can be used to describe broad 4-hour phases of digestion.

DISCUSSION

Approximately 16 hours after feeding, the stomach and caecal fluids were clear. When these criteria were seen, digestion was considered to be complete. Similar criteria for termination of digestion have been employed by other researchers (Bidder, 1950; Boucher-Rodoni, 1975). In the present study, four 4-hour phases of digestion have been distinguished on the basis of visible changes in caecal fluid color and stomach contents. These phases are generally supported by similar studies (Bidder, 1950; Boucher-Rodoni, 1975).

Estimates of digestion time ranges from 4-6 hours in Loligo (vulgaris and forbesii) (Bidder, 1950) to 18 hours in Octopus (Falloise, 1906; cited by Bidder, 150). Bouchard-Rodoni (1975) determined that Illex illecebrosus cleared their guts in 7 hours. Reasons for this variability are not known. Differences in physiological demands between pelagic and benthic animals may account for some of the variability, but the large difference between this study and that of Bouchard-Rodoni (1975) is not easily explained. The temperature, size of squid, and approximate size of food items did not differ significantly in the two studies. Stage of maturity was not reported, although this was probably not a factor since digestion was rapid. Bouchard-Rodoni (1975) used thawed capelin, dissected for rejected portions, as the food

source. The use of a live food source, approximating more closely to field conditions, could possibly account for the difference.

The Illex illecebrosus fishery has shown a tremendous increase in recent years (Amaratunga, 1980). It is now an industry of national and international commercial importance (Amaratunga and Durward, 1979). Effective population management requires a thorough understanding of the squid biology, of which feeding is an important component. Current field procedures for investigating feeding rely on the presence of stomach contents as criteria for squid having recently fed. The present study provides better guidelines for these field studies. Although resolution of the time to within 4 hours, as suggested by this study, would heighten our understanding of squid feeding patterns, the need for further research is clear. Investigations on a wide variety of food sources, under rigid simulation of field conditions being necessary for establishment of an accurate and applicable scale of digestion.

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Table 1. Color changes of stomach and caecum contents of serially sacrificed Illex illecebrosus.

Time after feeding is complete (hrs)	Stomach color	Caecum color
prefed	clear	clear
0	grey-black	burgundy
0	grey-black	burgundy
2	grey-black	muddy brown
4	grey-black	red-brown
4	black	red-brown
6	grey	brown
6	blue-grey	yellow
8	grey	tan-brown
10	blue-grey	yellow
10	blue-grey	yellow-clear
12	silver-grey	brown-yellow
12	silver-grey	brown-yellow
14	silver-grey	brown-yellow
14	silver-grey	yellow-green
14	yellow	yellow
16	yellow-clear	yellow-clear
16	clear	clear

Table 2. Color of caecal fluid of Illex illecebrosus resolved into four-hour phases of digestion.

Phase	Time interval (hr)	Color
1	0-4	red-brown
2	4-8	brown
3	8-12	brown-yellow
4	12-16	yellow-clear

Table 3. Changes in stomach color and contents of *Illex illecebrosus* resolved into four-hour phases of digestion.

Phase	Time interval (hr)	Contents of stomach
1	0-4	Large lumps of flesh; hard parts enclosed in flesh; grey-black
2	4-8	Noticeable decline of flesh; protruding hard parts; grey.
3	8-12	Little flesh, only connective tissue; hard parts separate; silver-grey.
4	12-16	Little or no tissue; hard parts sizable proportion; grey to yellow.