EFFECT OF TEMPERATURE ON RATE OF DIGESTION BY CHANNEL CATFISH, ICTALURUS PUNCTATUS (RAFINESQUE)

by 45

JOHN BERNARD SHRABLE

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Approved by:

Otto W. Tiemeier

Major Professor

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INTRODUCTION

Fish farming is becoming an important industry in the southeast and midwest United States. Channel catfish (Ictalurus punctatus, Rafinesque), is the major species in this industry. The channel catfish is a popular species for fish production because it is well adapted to commercial pond culture, takes pelleted feed readily, and is highly palatable and nutritious as a food fish. Sneed (1966) estimated 51,000 acres were devoted to fish farming in Arkansas and that farmers produced and sold at least 15 million pounds of channel catfish worth more than six million dollars and fingerling catfish for stocking worth one million dollars. A recent article in the "Muskogee Sunday Phoenix and Times-Democrat" by Gaston Franks, field coordinator for the Economic Development Administration in Oklahoma, stated about 20,000 acres were devoted to catfish farming in Oklahoma in 1967 and estimated the industry would increase by about 4,000 acres annually and production would hit 40 million pounds annually in the near future. Channel catfish can be produced for 25 to 30 cents per pound and can be raised to an average weight of 1 pound in two years in the southern states. Tiemeier (1967) stated channel catfish could be reared at rates above 2,000 pounds per surface acre per year if water temperature was 70° F or higher.

Water temperature is an important factor affecting the production of fish. Brown (1957) stated that temperature altered the rate of metabolic processes and could be expected to affect growth of poikilothermous animals. An increase in temperature should lead to higher maintenance requirements and, because the fish are more active, to increased food intake. Rate of growth varies with the ability of the fish to digest more food than is required for maintenance. The expected relationship between temperature and growth of fish is little or no growth below a certain temperature; above this, growth rate should increase with temperature to a maximum and then decrease, perhaps becoming negative at temperatures approaching the lethal limit. Because fish cannot regulate their body temperature, their rate of metabolism and their nutritional requirements are dependent on the temperature of the surrounding water (Lagler et al., 1963). The amount of food eaten and the assimilation efficiencies are influenced by temperature.

The present study was designed to determine the effects of selected water temperatures on rate of digestion by channel catfish. Results should be useful in determining the optimum temperature for digestion and possibly in determining the lower and higher water temperatures where feeding would be advisable. Information regarding effects of temperature should also be helpful in hatchery and commercial fish management.

LITERATURE REVIEW

Sensitivity of Fish to Temperature Change

Although there appears to be no specialized temperature receptors in a fish's skin, there is little doubt that fish are capable of feeling relatively slight changes in temperature (Bennett, 1962). Most workers have found body temperature of fish, under conditions of low activity, was almost identical with that of the environment. Gunn (1942) reported temperature differences between fish and water of 0.07 to 0.3° C for animals at rest.

The phenomenon of adaptation or acclimatization of fish to high temperature has been investigated by many workers. Loeb and Wastneys (1912) found *Fundulus heteroclitus* kept 30 hours or more at 27° C were "immunized" (sic) against a sudden change to a temperature of 35° C. The "immunity" against a temperature of 35° C was also maintained if the fish were kept for two weeks at 0.4° C after the two-day exposure to 27° C. In studies with greenfish (<u>Girella nigricans</u>) (Duodoroff, 1942) found fish conditioned at 14° C gained heat tolerance rapidly after transfer to 26° C and acclimatization was apparently complete after about one day. Acclimatization to cold temperatures was much slower and 20 days were required for complete acclimatization from 26 to 14° C. Moss and Scott (1961) observed that when bluegill (<u>Lepomis macrochirus</u>), largemouth bass (<u>Micropterus salmoides</u>), and channel catfish had been thoroughly acclimated metabolic rates did not increase as much as twofold with each 10° C increase in temperature and the increase became progressively smaller as the upper lethal temperature was approached. Resting channel catfish showed no appreciable increase in their metabolic rate as water temperature increased from 25 to 35° C and the metabolic mechanisms of channel catfish appeared to be highly adaptive. Morris (1965) reported the yellow bullhead (<u>Ictalurus natalis</u>) had a well developed ability to acclimate to both heat and cold without any apparent relationship between this ability and body size. When transferred from 12 to 27° C fish lowered their metabolic level from approximately 0.35 to 0.15 ml. O_2/g per hour. When acclimated to 27° C and placed at 12° C the metabolic level of fish raised from approximately 0.03 to 0.08 ml. O_2/g per hour. Baldwin (1956) stated three to six days were required for the brook trout (Salvelinus fontinalis) to become acclimated to each new temperature and to begin feeding normally when held at temperatures of 3.5, 9.0, 13.0, 17.0, and 21.0° C. Fish were held 4 weeks at each temperature beginning at 3.5° C and then transferred to the next higher temperature. Fry <u>et al</u>. (1946) found lethal temperature limits for fully acclimated brook trout were about 0° and 25.3° C. Markus (1932) observed rate of metabolism in largemouth bass was low at 4° C and increased rapidly as the temperature increased to 22° C; above 22° C the rate of increase diminished. Metabolic rate was much greater in small bass (39 and 33 grams) than in large bass (160 and 123 grams), especially at the lower and higher temperatures. Small bass fed in colder water than large bass. In studies with goldfish (Carassius auratus) (Freeman, 1950) found the metabolism of fish brain tissue increased rapidly between 0° and 27° C when measured over the range from 0° to 37.8° C; at higher temperatures the increase with temperature was less marked and at the highest temperature was lower again. Underhill (1952) observed bluegills and brown bullheads (Ameiurus nebulosus) became more active as temperatures increased within the range of 10 to 28° C

Effect of Temperature on Rate of Digestion

Specific work on the digestion of food by fish dates back to the work of Spallanzani and Senebrier (1783). Digestion was studied by placing tubes filled with flesh into the stomachs of pikes, eels, barbles and carp and recovering the tubes at intervals. Riddle (1909), used the same technique in studying the rate of digestion by the fresh-water "dog fish" (Amia calva). Small Metts Tubes filled with coagulated egg albumin were inserted directly into the stomach or intestine and the animals were killed after periods ranging from 17 to 168 hours. Results indicated there were considerable individual variations and the rates of digestion in the intestines were three to four times that in the stomach. Season and temperature were found to be important factors affecting rate of digestion by cold-blooded vertebrates. Highest rate of digestion was recorded in April at a water temperature of 29.8° C. There was no noticeable digestion in 168 hours at 3.5° C or less. A rise in temperature from 25 to 30° C was accompanied by a marked increase in rate of digestion. Riddle stated effects of temperature on digestive processes must be considered under two headings: (1) accellerating action of increased temperature on the chemical processes involved, and (2) retarding action of high or low temperatures due to the production of less digestive enzymes or actual destruction of enzymes at extreme temperatures.

Van Slyke and White (1911) studied rate of protein digestion in the stomach and intestine of dogfish at 26.6° C. Beef was chopped and boiled to coagulate the protein and fed to the fish through a stomach tube. Fish were killed at intervals of 6, 12, 24, 48 and 172 hours and a Kjeldahl analysis was made on contents in stomachs and intestines. Digestion varied greatly between individuals and 2 or 3 days were required for complete disposal of a meal. During the first 6 hours after feeding a considerable part of the protein in the stomach was digested and absorbed but little or none passed into the intestine. During 6 to 12 hours after feeding the most noticeable changes were the passage of protein, both digested and solid, into the intestine and the progressive hydrolysis of the dissolved peptones. During 6 to 12 hours after feeding, the intestine held 30 to 45 percent of the total nitrogen in the alimentary canal. Forty to seventy percent of the nitrogen had disappeared 24 hours after feeding and, of that left in both stomach and intestine, 65 to 85 percent was in solution. During the second 24 hours the disappearance of both soluble and insoluble protein proceeded and only 14 percent of the ingested nitrogen was left in the digestive tract 48 hours after feeding. By the end of the third day solution and absorption of the protein was practically complete. Peptonization of the protein in the stomach freed the accompanying fat and lipolysis occurred rapidly in the intestine. Markus (1932) force fed minnows to largemouth bass maintained at different temperatures and subsequently injected a nitrous acid solution into the stomachs at various time intervals to induce regurgitation of the remaining stomach contents. Markus noted large bass did not feed voluntarily during a 90 day experiment when maintained in water below 10° C.

The amount of food consumed by fish increased from 10 to 28° C. At 4° C, 300 hours were required for complete digestion of 4 or 5 gram meals of minnows (Hyborhynchus notatus). At 10° C, 92 hours were required for complete digestion of a 5-gram meal by large bass (158 and 121 grams) and 48 hours were required for 50 percent digestion. At 10° C, 168 hours were required for complete digestion of a 4 gram meal by small bass (39 and 33 grams). At 16° C, 32 hours were required for complete digestion of a 5-gram meal by large bass (160 and 123 grams) and 84 hours were required for complete digestion of a 4-gram meal by small bass (30 and 39 grams). A number of workers have reported rates of digestion for various species using arbitrarily defined stages of digestive disintegration (Pierce, 1936; Sokolov and Chvoliova, 1936; Karpevitch and Bokoff, 1937; Plantenburg, 1961; Armstrong and Blackett, 1966; Herting and Witt, 1968; Menon and Kewalramani, 1959).

In experiments concerning gastric digestion of pike perch (Lucioperca lucioperca L), using X-ray techniques, results indicated average rates of gastric digestion by fish 25 to 30 cm long maintained at 5, 10, 15, 20, and 25° C were 257, 157, 83, 45, and 28 hours respectively (Molnar and Tolg, 1962a). Fish were force-fed bleak (Alburnus alburnus L.) 8 to 10 cm long. X-ray studies concerning gastric digestion of largemouth bass 25 to 27 cm long, when force-fed bleak 8.0 to 8.5 cm long, indicated average gastric digestion time at 5, 10, 15, 20, and 25° C was 110, 50, 37, 24, and 19 hours respectively (Molnar and Tolg, 1962b). Correctness of results was checked and confirmed by dissection. Molnar et al. (1967) concluded pike-perch emptied its stomach 8 to 9 times slower in winter than in summer; this resulted in a comparable difference in the frequency of food intake. Food was largely left unexploited in winter because of sluggish gastric function.

Seaburg and Moyle (1964) compared digestive rates of some warmwater fishes at temperatures between 64 and 74° F. Digestive rates were faster for centrarchid panfishes than for the larger game fishes. Panfishes digested about 50 percent of stomach volumes in 5 hours, 75 percent in 12 hours and 100 percent in 21 hours. Animal materials were digested more rapidly than parts of plants and digestion rates for the same kinds of foods were similar for different sizes of panfishes. Northern pike (Esox lucius), required about 20 hours for 50 percent reduction of stomach contents and 50 hours for 100 percent reduction. Digestive rates for walleye (Stizostedion vitreum) and largemouth bass were intermediate between pike and centrarchid panfishes.

Hunt (1960) compared digestion rates by Florida gar (Lepisosteus platyrhincus), warmouth (Chaenobryttus gulosus), and largemouth bass using voluntary and force-feeding experiments with temperature varying from 23 to 26° C. There was no significant difference in the rate of digestion by warmouth force-fed and those feeding voluntarily but rate of digestion varied greatly among individuals of the same size and fed the same sized meal. Large fish often digested food much more slowly than small fish. Gar digested 20 percent of a meal in 10 hours, 50 percent in 20 hours, and 100 percent in 42 hours. Warmouth digested 50 percent of a meal in 14 hours and 100 percent in 26.2 hours. Largemouth bass digested 10 percent of a meal in 2 hours, 50 percent in 8 hours, and 100 percent in 16 to 19 hours.

Ranade and Kewalramani (1966) studied rate of food passage in three species of stomachless carps: Catla catla (Ham.); Labeo rohita (Ham.); and Cirrhina mrigala (Ham.). Individuals were force-fed nearly equal quantities of food at water temperatures between 28 and 30° C. Rate of food passage varied considerably with different kinds of food materials in individuals of similar size and the same species under similar experimental conditions. Rate of food passage was related to the efficiency of digestion. Food items biochemically so constituted as to be more amenable to the digestive enzymes of a particular species passed out at a faster rate than other items. The relationship between the rate of food passage and the concentration of digestive enzymes indicated food items which passed rapidly through the intestine were more efficiently used because rapid food passage was associated with high digestibility due to a high concentration of the requisite enzymes. Rapid food passage may also mean a similar increase in the rate of feeding.

In a study to determine the effect of different temperatures upon the rate of digestion by bluegill sunfish, Malcolm (1960) force-fed meal worms to bluegills and then killed the fish at selected time intervals. The temperatures used were 5, 11, 17 and 20° C. The approximate rates of digestion were 0.27 mg per hour at 5° C, 0.5 mg per hour at 11° C, 1.4 mg per hour at 17° C, and 1.7 mg per hour at 20° C. The rate of gastric digestion at 20° C was 6.3 times greater than the rate at 5° C.

Windell (1966) made a thorough study of digestion rates in the stomachs of bluegill sunfish. Digestion was considered complete when the stomach became empty of all measurable remains. Studies were conducted on effects of force-feeding, starvation, body size, and size of the meal. Water temperature ranged between 18.5 and 24.6° C during experiments. Fish were fed natural food organisms consisting of chironomids, crayfish, dragonfly naiads, mayfly naiads, mealworms, darters, and oligochaetes and fish were killed at intervals of 6, 10, 14, 18, and 22 hours after feeding. Bluegills digested meals of voluntarily consumed natural food organisms in about 18 hours at 21° C. The percentage decrease of digestible organic matter from the stomach at 6, 10, 14, 18, and 22 hours after feeding was 50, 77.4, 88.8, 98 and 100 percent respectively. Mealworms required 22 to 26 hours for complete digestion. Fish starved for 7, 14, and 25 days before feeding showed a progressive decrease in the rate of gastric digestion when compared with control fish. There was no significant difference in the rate of digestion of single-and multiple-unit meals by fish of different ages and different body weights. Food disappeared from the stomach in about the same length of time regardless of the amount of digestible organic matter consumed. As the amount of digestible organic matter consumed increased by 2.7 times, rate of gastric digestion increased by 2.2 times. Compared with control fish that voluntarily consumed meals, bluegills force-fed showed considerable individual variations in digestion. Regurgitation occurred frequently among force-fed fish. Forced-feeding resulted in an increased rate of digestion in some experiments and a decrease in others. Variation in rate of digestion as a result of forced-feeding was so great that the outcome could not be predicted.

Effects of Temperature on Food Consumption and Growth

Water temperature is a major factor affecting food consumption and growth by fishes. Tiemeier (1967) listed water temperature and amount and type of food consumed among factors determining growth rates of channel catfish. Cross and Simco (1966), Tiemeier (1962, 1966), and Tiemeier _et al_. (1967) have reported decreased growth rate of channel catfish in the late summer and fall in response to decreased water temperatures. Swingle (1958) reported channel catfish responded best to feeding when surface-water temperature was above 21.1° C and feeding produced comparatively little growth while the water temperature was below 15.5° C. In studies of channel catfish fry from hatching to 60 days of age, West (1966) found temperature for maximum growth rate was 29.0 to 30.0° C. Maximum food-conversion efficiency occurred at 28.9° C. Final sizes of fry decreased in the following order of water temperatures: 29, 31, 33, 32, 27, 34, 25, 35, 23, 21, and 36° C. Survival was poor at extreme temperatures.

In studies with other warm-water species, Gibson and Hirst (1955) found temperature for fastest growth of pre-adult guppies (Lebistes reticulatus), ranged between 23 and 25° C and growth was slower at 20, 30 and 32° C. Strawn (1961) maintained largemouth bass fry at temperatures of 15, 17.5, 20, 22.5, 25, 27.5, 30.0 and 32.5° C and obtained maximum growth at 27.5 and 30° C. Kinne (1960) maintained wild desert pupfish (Cyprinodon macularius) at temperatures of 15, 20, 25, 30, and 35° C and obtained maximum food intake and growth at 30° C. Growth rate at different temperatures decreased in this order: 30, 25, 35, 20, and 15° C. Best food conversion was at 20° C. The optimum temperature for growth decreased with increasing age and in fish older than 28 to 30 weeks the optimum temperature was 22 to 26° C. Hathaway (1927) reported largemouth bass and pumpkinseed (Eupomotus gibbosus, Linnaeus) consumed about 3 times as much food at 20° C as at 10° C and bluegill (Lepomis incisor, Mitchill) consumed about 7 times as much. Maloney (1949) observed mean temperature for maximum food consumption by bluegills (Lepomis macrochirus, Rafinesque), was 20° C, but optimum temperature among individuals varied 5° C above or below the mean. In experiments with the brown bullhead (Ameiurus nebulosus, Le Seur) maintained at temperatures of 10, 15, 18, 22, and 28° C. Underhill (1952) found optimum temperature for food conversion and growth was near 22° C. Bullheads in all cases ate more food at 25° C but showed maximum gains in weight at 22° C.

Several workers have reported on effects of various temperature on food consumption and growth of cold-water fishes. Baldwin (1956) reported brook trout consumed the most food and made the best growth at 13° C and both food consumption and growth decreased above 13° C. Pentelow (1939) reported brown trout (Salmo trutta) increased food consumption to 15° C and consumption decreased above 15° C. Brown (1946) reported two optimum temperature ranges for growth by two-year-old brown trout as 7 to 9° C and 16 to 19° C. Below and above these temperature ranges growth rates were lower. These findings were explained on the basis of appetites and maintenance requirements at different temperatures; appetites were maximal between 10 and 19° C and maintenance requirements increased rapidly between 9 and 11° C, then less rapidly to 20° C. Optimum temperatures for rapid growth were those for which appetites were high and maintenance requirements were relatively low.

Effect of Temperature on Digestive Enzymes

Numerous workers (Dawes, 1930; Baylis, 1935; Sarbahi, 1951; Barrington, 1957; Babkin and Bowie, 1928; Chesley, 1934; MacKay, 1929; Greene, 1913; Lagler, 1963; Lawrence, 1950; Sullivan, 1907) reported on digestive enzymes in fish; but little work has been done to study effect of water temperature upon the presence and activity of digestive enzymes. Asadi (1967) conducted experiments to determine the effects of different temperatures upon the presence of various digestive enzymes in channel catfish. Peptic and tryptic activities were studied in fish taken from water maintained at 2.2, 14.5, 22.2, 23.9, 26.7, 29.4, and 33.3° C. Amylase activity studies were conducted with extracts from fish held at 15.5, 21.1, 23.9, 26.7, 27.7, and 29.4° C. Enzymes of channel catfish responded rapidly to changes in temperature between 14.5 and 33.3° C. Secretion of the enzymes studied were affected by water temperature. The optimum water temperature for secretion of the enzymes studied was near 23.9° C. Peptic activity increased gradually from 2.2 to 15.5° C and then increased sharply up to 23.9° C followed by a sharp decline. Tryptic activity was not noted at 2.2° C but was found at 14.5° C and increased to 23.9° C and then decreased, but significant activity was still present at 33.3° C. Amylase activity increased to 23.9° C followed by a sharp decline.

The study indicated temperature for most rapid rate of digestion by channel catfish should be near 23.9° C.

METHODS AND MATERIALS

Rates of digestion by channel catfish were studied using forced-feeding experiments conducted at water temperatures of 10.0, 15.5, 21.1, 23.9, 26.6, and 29.4° C. Experiments were conducted to determine the rate of digestion of dry matter fed and the rate of digestion of protein, fat, fiber, ash, and nitrogen-free extract at each water temperature.

The experimental fish were age group II and III (approximately two and three years old) channel catfish obtained from the Tuttle Creek Fisheries Research Laboratory near Manhattan, Kansas. Weight of fish ranged between 150 and 900 grams but most fish were in the 300-to 450-gram weight range. Average weight of all fish was 380 grams. Fish had previously been given pelleted fish feed similar to that used in the experiments.

During experiments fish were held in two insulated, oval (2 ft. X 2 ft. X 6 ft.) stock tanks with a capacity of 155 gallons each. The tanks were equipped with 220-volt electric water heaters and thermostats for controlling water temperature and were placed in the laboratory building at the Tuttle Creek Fisheries Research Laboratory. Two dividers installed in each of the two tanks provided compartments for six groups of fish. Tanks were filled with pond water and the temperature was checked with an electrical resistance thermometer at two-hour intervals during all experiments. The water temperature did not vary more than ± 0.5° C from the desired experimental temperature. Fresh water was not added to the tanks during the holding period but a number five, 110 volt "Mino Saver" agitator was run constantly in each tank to maintain high oxygen concentrations.

Acclimation

Experiments were conducted at times when the water temperature in the ponds was near the desired experimental temperature. Fish were seined from ponds and transferred directly to the experimental tanks which were filled with pond water. Five fish were placed in each of the three compartments in each tank. Water temperature in the tanks was increased gradually over a period of two to five days, depending upon the amount of increase necessary. Fish were maintained at the experimental temperatures at least 24 hours before being force-fed. The fish were not fed during the holding period to insure complete absence of food remains from the alimentary canal.

Forced-Feeding and Collection of Samples

After acclimation the fish were removed from the tanks and each fish was force-fed 3 grams of feed in the form of two 3/8 inch diameter pellets approximately 1/2 inch long, and fish were then returned to the tanks. Force-feeding was done by dropping the pellets into the fish's mouth and forcing them directly into the stomach by using the forefinger. Each meal had been weighed on a Torsion Balance to the nearest 0.01 gram.

Fish were removed from the tanks in groups of five and killed at time intervals of 2, 4, 6, 8, 10, 12, 18, and 24 hours after feeding. The stomach and intestine were removed from the body cavity of each fish, separated and contents of each emptied into separate crucibles. Stomachs were cut open and contents removed by scraping. Contents of intestines were removed by stripping between the thumb and forefinger. The remains were placed in crucibles and dried in an air oven for 36 hours at 85° C, removed and weighed on a Torsion Balance to the nearest 0.01 gram. Remains from stomachs of the five fish in each group were combined to give one sample of stomach contents at each time interval. The same procedure was used for the intestinal remains. These samples were then ground in a Wiley mill to pass through a 20-mesh screen. A subsample of two grams (weighed on a Mettler balance to the nearest 0.10 mg) was taken from each sample, placed in a moisture dish, and dried in a vacuum oven for five hours at 100° C. The weights of all samples of stomach and intestinal contents were then converted to a moisture free basis, and the moisture free weights were converted into percentages of the total weight (13.68 grams) of dry matter fed to each group of five fish and the results are shown in Tables 1, 2, and 3. There was some regurgitation during all experiments as a result of forced-feeding and handling and some material may have been passed as feces.

Chemical Analyses

Feed

The feed used in these experiments was a formulated fish feed mixed by the Kansas State University, Department of Grain Science and Industries. The ingredients of the ration were fish meal, dehydrated alfalfa meal, meat and bone scraps, soybean meal, distillers' dried grains and solubles, ground sorghum grain, wheat bran, and blood meal plus certain minerals and vitamins. The ration contained 8.8% moisture, 25.2% protein, 9.3% ash, 3.5% crude fat, and 7.7% crude fiber. Each group of five fish received 13.68 grams of dry matter, 3.78 grams of protein, 0.53 grams of fat, 1.15 grams of fiber, and 1.40 grams of ash.

Samples

Each sample of remains from the digestive tract was chemically analyzed to determine its percentage of moisture, protein, crude fat, crude fiber, and ash. Nitrogen-free extract was determined by difference (100% minus the sum of the percentages of protein, crude fat, crude fiber, moisture, and ash =

nitrogen-free extract). All analyses were made following the procedures in the Methods of Analysis of the Association of Official Agricultural Chemists, 1960 edition. Chemical analyses were made of all samples from the 2, 4, 6, 8, 10, and 12 hour groups but not enough material remained in the 18 and 24 hour samples for complete chemical analyses. The percentages of protein, crude fat, crude fiber, ash, and nitrogen-free extract present were converted into percentages of the total weight of each nutrient originally fed and the results are shown in Tables 4 through 13 and in Appendix Tables 14 through 25. Tables 4 through 13 contain the percentages of each food nutrient remaining in the stomachs and in the intestines at each water temperature 12 hours after feeding. Tables 14 through 25 contain the same data as Tables 4 through 13 but the data were arranged so that the percentages of each food nutrient remaining in the stomachs and in the intestines were compared at each water temperature. These tables were placed in the appendix because it was decided that meaningful comparisons of digestion rates of different nutrients could not be made because different amounts of each nutrient were fed and some nutrients required different enzymes for digestion and the activity of all enzymes would not be the same in all parts of the digestive tract.

Protein

The Kjeldahl method for total nitrogen determination was used to determine the total percentage nitrogen present in each sample. Percentage of protein was obtained by multiplying the percentage of nitrogen from sample analyses times 6.25.

Crude Fat

The two-gram subsamples used in moisture determinations were used for fat analyses. Crude fat of most samples was determined by the direct method using the Goldfisch extraction apparatus and Skellysolve F as the extractant. The extraction period was 4 hours and the fat was collected into preweighed beakers. Following extraction the beakers containing the fat were dried in a vacuum oven for 30 minutes at 100° C, cooled in a dessicator, and weighed on a Mettler balance to the nearest 0.10 mg. The difference between the final weight and the weight of the empty beakers was the weight of crude fat. Crude fat of a few samples was determined by the indirect method using the Soxhlet extraction apparatus and Skellysolve F as the extractant. The extraction period was 16 hours and the difference between the original sample weight and the sample weight after extraction was reported as the weight of crude fat.

Crude Fiber

Crude fiber was determined from samples following moisture and fat determinations. Samples were boiled for 30 minutes in a 1.25% sulfuric acid solution, filtered, and boiled for 30 minutes in a 1.25% sodium hydroxide solution. The samples were then filtered into crucibles, dried in an electric oven for 1 hour at 130° C, cooled in a dessicator, and weighed on a Mettler balance to the nearest 0.10 mg. The crucibles and contents were then placed in an electric muffle oven (preheated to 600° C) and burned for 30 minutes. The crucibles and contents were again weighed and the loss in weight following ignition was recorded as crude fiber.

Ash

For ash determinations, samples of 2 grams each were placed in porcelain crucibles and burned in an electric muffle oven (preheated to 600° C) for two hours or more. The samples were then cooled in dessicators and weighed. Weight of material remaining after burning was recorded as ash.

Statistical Analysis

All data were calculated as percentages of the amount fed which remained in the stomachs and intestines of each group of fish and were entered in Tables 1 through 25. Two-way analyses of variance and Fisher's Least Significant Difference (LSD) tests on means were made on the data from each table. Because all data were expressed in percentages, it constituted a binomial type distribution. A square root transformation, ($\sqrt{x + 1}$) of percentages as suggested by Fryer (1966) pp. 366-376, was used to make the data conform more nearly to a normal distribution for which the statistical analyses were designed. The means of rows and columns of each table are from the untransformed data, but the comparisons of means and analysis of variance of all data are from the analysis of transformed data.

RESULTS

Rate of Digestion of Dry Matter

Mean percentages of dry matter fed that remained in stomachs and intestines of each group of fish were entered in Tables 1 and 2 respectively, and the results were shown graphically in Figures 1 and 2. The corresponding means for each temperature and time interval of Tables 1 and 2 were combined to give the total percentage of dry matter remaining in the stomachs and intestines and entered in Table 3, and the results were shown graphically in Figure 3. Analysis of variance of Tables 1, 2, and 3 are shown in Tables 1a, 2a, and 3a respectively.

Analysis of variance (Table 1a) indicated a linear effect of temperature and time on the amount of dry matter remaining in the stomachs of fish. The remainder effects were not significant. There was no significant interaction between temperature and time which indicated effect of time was the same over all temperatures, therefore, comparison of temperature means in Table 1 indicated the effect of temperature on the amount of dry matter remaining in the stomach exclusive of the effect of time. As indicated by the temperature means of Table 1, the least amount of dry matter remaining in the stomach 24 hours after feeding occurred at 26.6° C and the amount remaining increased progressively at temperatures of 29.4, 23.9, 21.1, 15.5, and 10.0° C. LSD tests indicated no significant difference at the 0.05 level in amount of dry matter remaining in the stomachs at temperatures of 10.0 and 15.5° C or at 21.1, 23.9, and 29.4° C or at 23.9, 26.6 and 29.4° C. LSD tests on time means indicated no significant difference at the 0.05 level in amount of dry matter remaining at intervals of 4, 6, and 8 hours or at intervals of 8, 10, and 12 hours after feeding. The amounts remaining at 2, 18, and 24 hours were significantly different from the amounts remaining at all other intervals. Percentages of dry matter remaining in the stomach at the 6, 12, 18, and 24 hour intervals were subtracted from 100 percent to give the percentage decrease of dry matter from the stomach and the results are shown in Figure 1.

Mean percentage of dry matter remaining in the intestines (Table 2 and Figure 2) increased to a maximum and then decreased at all temperatures, except at 10.0° C where there was a continual increase through 24 hours. The percentage remaining in the intestine at 29.4° C reached a peak of 16.82 percent 6 hours after feeding. The amount remaining in the intestines at 15.5, 21.1, and 26.6° C reached a peak 12 hours after feeding. The largest amount remaining in the intestines at any temperature and time interval was 30.03 percent 10 hours after feeding at 23.9° C. Analysis of variance of the effect of temperature and time on the percentage of dry matter remaining in the intestine (Table 2a) indicated a linear effect of temperature and time with

Table 1. Percentage of dry matter fed that remained in the stomach of fish maintained at 6 temperatures and killed at 8 time intervals.

Hours after feeding	Temperature degrees centigrade 10.0	15.5	21.1	23.9	26.6	29.4	Time means
2	90.70*	99.97	82.83	90.23	85.56	90.77	90.12
4	94.22	96.88	72.91	58.20	45.29	68.62	72.69[a]**
6	86.07	87.72	73.39	44.73	31.13	54.30	62.89[a]
8	75.80	84.68	40.77	54.14	38.06	46.14	56.60[a,b]
10	68.69	63.47	36.32	51.09	24.28	33.51	46.23[b]
12	71.49	58.12	35.05	41.99	21.20	32.41	43.37[b]
18	30.29	25.07	43.21	22.30	19.21	10.75	25.14
24	19.74	19.67	5.45	3.45	2.67	0.89	8.64
Temp. means	67.12[1]**	66.94[1]	48.74[2]	45.85[2,3]	33.42[3]	42.17[2,3]	

*Each observation represents an average from two groups of five fish.
**Common superscripts indicate means that are not significantly different at the 0.05 level.

Table 1a. Analysis of variance of data in Table 1.**

Source of variance	Degrees of freedom		Mean squares	
Temperature	5		18.22*	
Linear		1		77.54*
Remainder		4		3.39
Time	7		52.74*	
Linear		1		363.83*
Remainder		6		0.89
Temperature X Time	35		1.17	
Error	48		1.73	

*Denotes statistical significance at the 0.05 level.
**Statistical analysis is from transformed data.

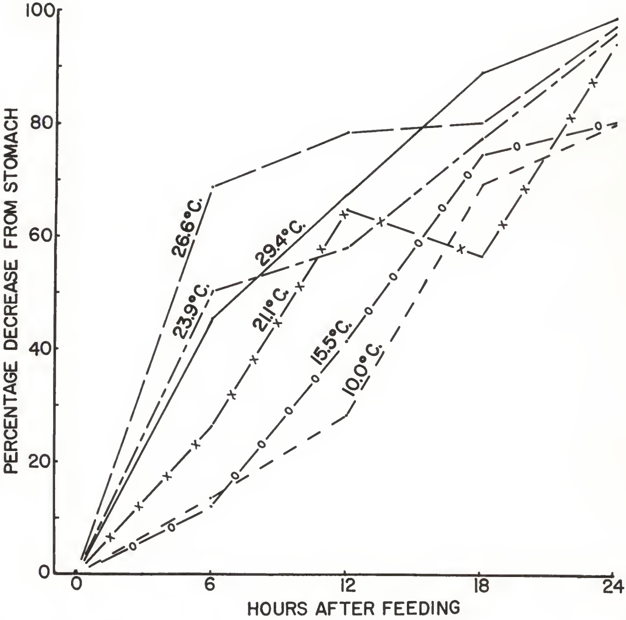

Figure 1. Mean percentage decrease of dry matter from the stomachs of channel catfish maintained at 6 temperatures and killed at 4 time intervals. Each point represents an average from 10 fish.

Table 2. Percentage of dry matter fed that remained in the intestine of fish maintained at 6 temperatures and killed at 8 time intervals.

Hours after feeding	Temperature degrees centigrade 10.0	15.5	21.1	23.9	26.6	29.4	Time means
2	0.75*	2.05	1.39	0.99	3.64	1.48	1.72
4	0.48	2.84	2.61	7.23	10.65	7.23	5.18[a]**
6	2.74	5.48	10.78	16.10	10.43	16.82	10.39[c,d]
8	3.08	10.83	21.18	17.34	17.82	13.92	14.03[d,e]
10	5.60	18.94	20.69	30.03	15.95	10.50	16.95[e]
12	4.19	19.66	25.75	23.46	19.01	6.17	16.37[e]
18	11.94	4.79	8.58	7.30	8.32	6.88	7.97[b,c]
24	13.43	5.68	8.13	8.53	3.36	3.32	7.07[a,b]
Temp. means	5.28	8.78[1,2]**	12.39[2,3]	13.87[3]	11.14[1,2,3]	8.29[1]	

*Each observation represents an average from two groups of five fish.
**Common superscripts indicate means that are not significantly different at the 0.05 level.

Table 2a. Analysis of variance of data in Table 2.**

Source of variance	Degrees of freedom		Mean squares	
Temperature	5		3.64*	
Linear		1		7.28*
Remainder		4		2.73*
Time	7		8.74*	
Linear		1		3.46*
Remainder		6		9.62*
Temperature X Time	35		1.14*	
Error	48		0.35	

*Denotes statistical significance at the 0.05 level.
**Statistical analysis is from transformed data.

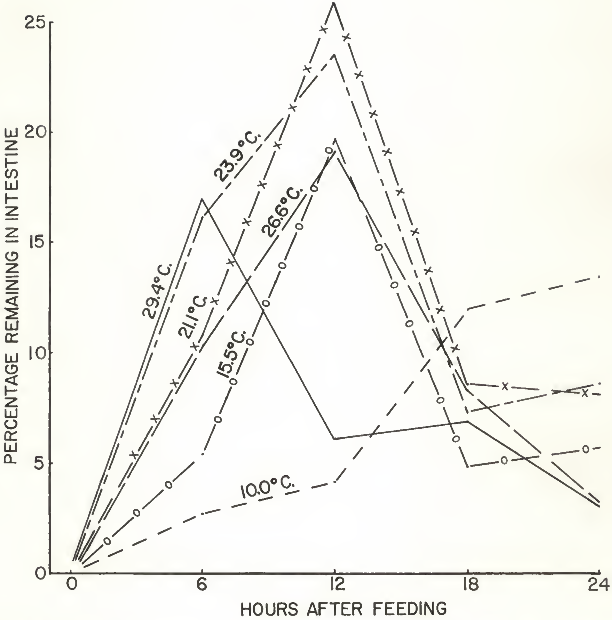

Figure 2. Mean percentage of dry matter remaining in the intestines of channel catfish maintained at 6 temperatures and killed at 4 time intervals. Each point represents an average from 10 fish.

Table 3. Percentage of dry matter fed that remained in the stomach and intestines of fish maintained at 6 temperatures and killed at 8 time intervals.

Hours after feeding	Temperature degrees centigrade						Time means
	10.0	15.5	21.1	23.9	26.6	29.4	
2	91.45*	102.02	84.21	91.92	89.19	92.07	91.81^{a}**
4	94.70	99.72	75.52	65.42	55.94	75.87	$77.86^{a,b}$
6	88.81	93.20	84.17	60.83	41.56	71.12	$73.28^{b,c}$
8	78.88	95.51	61.92	71.47	55.88	60.06	$70.62^{b,c}$
10	74.29	82.41	57.01	81.12	40.23	44.01	$63.18^{b,c}$
12	75.67	77.77	60.80	65.44	40.21	38.58	59.74^{c}
18	42.23	29.86	51.79	29.60	27.53	17.62	33.10
24	33.17	25.35	13.57	11.97	6.02	4.21	15.71
Temp. means	$72.40^{1,2}$**	75.73^{1}	$61.13^{1,2,3}$	$59.72^{2,3}$	44.57^{4}	$50.44^{3,4}$	

*Each observation represents an average from two groups of five fish.
**Common superscripts indicate means that are not significantly different at the 0.05 level.

Table 3a. Analysis of variance of data in Table 3.**

Source of variance	Degrees of freedom		Mean squares	
Temperature	5		12.36*	
Linear		1		50.63*
Remainder		4		2.79
Time	7		41.66*	
Linear		1		284.92*
Remainder		6		1.12
Temperature X Time	35		0.98	
Error	48		1.50	

*Denotes statistical significance at the 0.05 level.
**Statistical analysis is from transformed data.

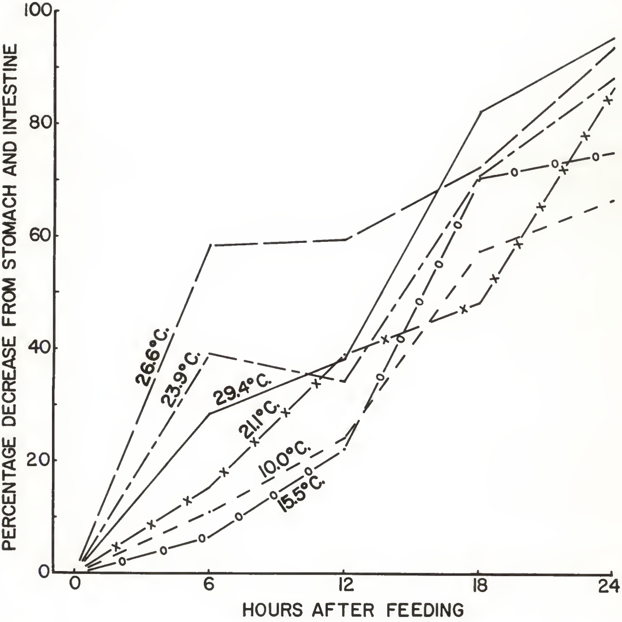

Figure 3. Mean percentage decrease of dry matter from the digestive tracts of channel catfish maintained at 6 temperatures and killed at 4 time intervals. Each point represents an average from 10 fish.

significant remainder effects. Interaction between temperature and time was also significant indicating effect of time was not the same over all temperatures.

Mean percentage of dry matter remaining in the stomachs and intestines 24 hours after feeding was highest at 10.0° C and decreased progressively at 15.5, 21.1, 23.9, 26.6, and 29.4° C (Table 3). Temperature means indicated most rapid rate of removal occurred at 26.6° C and rate of removal was progressively less at 29.4, 23.9, 21.1, 10.0 and 15.5° C. Percentages of dry matter remaining in the digestive tract at the 6, 12, 18, and 24 hour intervals were subtracted from 100 percent to give the percentage decrease from the digestive tract and the results are shown in Figure 3.

Analysis of variance (Table 3a) of percentage of dry matter remaining in the stomach and intestine indicated a linear effect of temperature and time. Remainder effects were not significant and there was not a significant interaction between temperature and time. This indicated the effect of time was the same over all temperatures.

Rate of Digestion of Food Nutrients

Rate of Digestion of Protein

Temperature means of data in Table 4 indicated mean percentage of protein remaining in the stomachs of fish over a 12-hour period was lowest at 26.6° C and the percentage remaining increased progressively at temperatures of 29,4, 23.9, 21.1, 10.0, and 15.5° C. LSD tests indicated no significant difference at the 0.05 level in temperature means at 10.0 and 15.5° C, or at 21.1, 23.9, and 29.4° C. Mean percentage of protein remaining at 26.6° C was significantly less than the amount remaining at all other temperatures. Analysis of variance of percentage of protein remaining in the stomach (Table 4a) indicated significant effects of temperature and time and linear effects of both temperature and time were highly significant. Interaction between temperature and time was not significant.

Percentages of protein remaining in the intestines are given in Table 5. Rate of passage of protein into the intestines was slower at 10.0 and 15.5° C than at the higher temperatures. Temperature means of Table 5 indicated that the percentage of protein remaining in the intestines during 12 hours after feeding was highest at 23.9° C. Slowest rate of passage occurred at 10.0° C and the mean percentage remaining at 10.0° C was significantly less than the percentage remaining at all other temperatures. Analysis of variance (Table 5a) indicated significant temperature and time effects. Effects of both temperature and time were linear with significant remainder. Interaction between temperature and time was not significant.

Rate of Digestion of Fat

Percentages of fat remaining in the stomachs are given in Table 6. Some percentages are greater than 100 percent and other percentages may also be high; this may have been caused by contamination of samples with fat from the body cavity of the fish when the samples were taken. Temperature means indicated the most rapid rate of fat removal from the stomachs occurred at 26.6° C and the rate decreased progressively at temperatures of 29.4, 21.1, 15.5, 23.9, and 10.0° C. Rate of fat removal from the stomachs at 21.1, 26.6, and 29.4° C was significantly more rapid than at 10.0, 15.5, and 23.9° C. Analysis of variance (Table 6a) indicated highly signficant linear temperature and time effects but other effects were not significant.

Percentages of fat remaining in the intestines are given in Table 7. Temperature means indicated passage of fat into the intestines was slower during the first 12 hours after feeding at 10.0° C than at all higher temperatures. Largest amount of fat in the intestines 12 hours after feeding occurred at 21.1° C. Analysis of variance (Table 7a) indicated a significant linear effect

Table 4. Percentage of protein fed that remained in the stomach of fish maintained at 6 temperatures and killed at 6 time intervals.

Hours after feeding	Temperature degrees centigrade 10.0	15.5	21.1	23.9	26.6	29.4	Time means
2	87.83*	99.60	84.92	88.89	56.38	92.46	85.01[a]**
4	97.76	96.17	73.68	58.60	45.15	69.25	73.43[a,b]
6	86.23	92.86	79.90	44.55	32.76	58.37	65.78[a,b,c]
8	80.29	86.91	44.98	50.39	38.97	45.65	57.86[b,c]
10	71.17	77.12	42.32	51.64	25.31	27.46	49.17[c]
12	80.69	67.86	39.29	42.79	22.23	35.60	48.08[c]
Temp. means	83.99[1]**	86.75[1]	60.85[2]	56.14[2]	36.80	54.80[2]	

*Each observation represents an average from two groups of five fish.
**Common superscripts indicate means that are not significantly different at the 0.05 level.

Table 4a. Analysis of variance of data in Table 4.**

Source of variance	Degrees of freedom		Mean squares	
Temperature	5		20.55*	
Linear		1		75.58*
Remainder		4		6.78*
Time	5		11.54*	
Linear		1		55.36*
Remainder		4		0.59
Temperature X Time	25		0.89	
Error	36		2.39	

*Denotes statistical significance at the 0.05 level.
**Statistical analysis is from transformed data.

Table 5. Percentage of protein fed that remained in the intestine of fish maintained at 6 temperatures and killed at 6 time intervals.

Hours after feeding	Temperature degrees centigrade 10.0	15.5	21.1	23.9	26.6	29.4	Time means
2	0.76*	1.94	0.96	2.65	1.56	1.37	1.54
4	0.57	2.78	1.95	5.11	6.87	5.52	3.80
6	2.90	5.64	7.49	11.38	6.85	11.20	7.57
8	3.60	11.10	14.76	12.25	11.72	13.51	11.16[a]**
10	5.93	13.89	16.45	18.62	8.27	10.46	12.27[a]
12	3.57	15.67	20.94	16.27	10.00	9.83	12.71[a]
Temp. means	2.89	8.50[1,2]	10.42[1,2]	11.04[1]	7.54[2]	8.65[1,2]	

*Each observation represents an average from two groups of five fish.
**Common superscripts indicate means that are not significantly different at the 0.05 level.

Table 5a. Analysis of variance of data in Table 5.**

Source of variance	Degrees of freedom		Mean squares	
Temperature	5		3.20*	
Linear		1		7.44*
Remainder		4		2.15*
Time	5		8.49*	
Linear		1		38.09*
Remainder		4		1.09*
Temperature X Time	25		0.41	
Error	36		0.38	

*Denotes statistical significance at the 0.05 level.
**Statistical analysis is from transformed data.

of temperature, and remainder was also highly significant. The linear effect of time was highly significant and the remainder was only slightly significant. There was no interaction between temperature and time.

Rate of Digestion of Fiber

Mean percentages of fiber remaining in the stomachs of fish are given in Table 8. Most rapid rate of fiber removal from the stomachs of fish occurred at 26.6° C. Differences at the 0.05 level in the percentages remaining at 10.0 and 15.5° C or at 15.5, 21.1, 23.9, and 29.4° C were not significant. Analysis of variance (Table 8a) indicated significant effects of temperature and time on the percentages of fiber remaining in the stomach but interaction was not significant at the 0.05 level. Effects of both temperature and time were highly linear and remainder effects of temperature were also significant.

Mean percentages of fiber remaining in the intestines 12 hours after feeding are given in Table 9. Passage of fiber into the intestines at 10.0° C was slow; the mean percentage remaining at 10.0° C was only 1.39 percent. Temperature means indicated no significant difference at the 0.05 level in percentage of fiber remaining in the intestines at 21.1, 23.9, 26.6, and 29.4° C. Analysis of variance (Table 9a) indicated highly significant linear effects of temperature and time on the percentages of fiber remaining in the intestines. Remainder effects of temperature were also significant at the 0.05 level. Interaction between temperature and time was not significant.

Rate of Digestion of Ash

Temperature means of Table 10 indicated mean percentages of ash remaining in the stomachs of fish 12 hours after feeding was lowest at 26.6° C, and increased progressively at 23.9, 21.1, 29.4, 10.0, and 15.5° C. There was no significant difference at the 0.05 level in percentages of ash remaining in

Table 6. Percentage of fat fed that remained in the stomach of fish maintained at 6 temperaturos and killed at 6 time intervals.

Hours after feeding	Temperature degrees centigrade 10.0	15.5	21.1	23.9	26.6	29.4	Time means
2	99.12*	105.85	97.55	114.15	54.86	80.28	91.97[a]**
4	119.72	63.40	60.38	79.91	56.98	59.52	73.32[a,b]
6	113.78	79.91	92.55	45.33	37.83	53.30	70.45[a,b,c]
8	75.38	94.06	48.78	75.66	57.08	42.78	65.62[b,c]
10	54.25	63.30	44.25	101.04	41.23	26.57	55.10[b,c]
12	52.93	51.61	42.64	66.70	29.44	33.26	46.09[c]
Temp. means	85.86[1]**	76.35[1]	64.36[1,2]	80.47[1]	46.23[2]	49.28[2]	

*Each observation represents an average from two groups of five fish.
**Common superscripts indicate means that are not significantly different at the 0.05 level.

Table 6a. Analysis of variance of data in Table 6.**

Source of variance	Degrees of freedom		Mean squares	
Temperature	5		14.64*	
Linear		1		47.07*
Remainder		4		6.53
Time	5		12.71*	
Linear		1		61.00*
Remainder		4		0.64
Temperature X Time	25		2.11	
Error	36		3.88	

*Denotes statistical significance at the 0.05 level.
**Statistical analysis is from transformed data.

Table 7. Percentage of fat fed that remained in the intestine of fish maintained at 6 temperatures and killed at 6 time intervals.

Hours after feeding	Temperature degrees centigrade 10.0	15.5	21.1	23.9	26.6	29.4	Time means
2	0.75*	2.27	1.89	0.57	0.94	0.69	1.19[a]**
4	0.57	3.12	3.59	4.15	3.96	2.93	3.05[a]
6	2.90	6.04	15.10	9.16	4.06	7.87	7.52[b]
8	3.60	11.88	29.63	9.81	6.93	8.29	11.69[b,c]
10	5.93	12.36	26.89	20.21	6.80	9.73	13.65[c]
12	3.57	12.83	33.96	14.82	7.89	7.11	13.36[c]
Temp. means	2.89[1]**	8.08[2,3]	18.51	9.79[3]	5.09[1,2]	6.10[2,3]	

*Each observation represents an average from two groups of five fish.
**Common superscripts indicate means that are not significantly different at the 0.05 level.

Table 7a. Analysis of variance of data in Table 7.**

Source of variance	Degrees of freedom		Mean squares	
Temperature	5		6.94*	
Linear		1		1.77*
Remainder		4		8.23*
Time	5		9.80*	
Linear		1		43.68*
Remainder		4		1.34*
Temperature X Time	25		0.64	
Error	36		0.43	

*Denotes statistical significance at the 0.05 level.
**Statistical analysis is from transformed data.

Table 8. Percentage of fiber fed that remained in the stomach of fish maintained at 6 temperatures and killed at 6 time intervals.

Hours after feeding	Temperature degrees centigrade 10.0	15.5	21.1	23.9	26.6	29.4	Time means
2	77.39*	88.61	87.52	93.00	54.91	94.78	82.70[a]**
4	93.04	87.78	61.74	59.09	36.27	82.04	69.99[a,b]
6	79.57	85.03	81.70	52.78	35.05	60.83	65.82[a,b]
8	70.13	65.05	42.57	53.26	38.70	46.72	52.74[b,c]
10	81.91	57.13	31.05	53.35	25.87	32.80	47.02[c]
12	92.01	57.18	38.40	40.56	20.09	38.16	47.73[c]
Temp. means	82.34[1]**	73.46[1,2]	57.16[2]	58.67[2]	35.15	59.22[2]	

*Each observation represents an average from two groups of five fish.
**Common superscripts indicate means that are not significantly different at the 0.05 level.

Table 8a. Analysis of variance of data in Table 8.**

Source of variance	Degrees of freedom		Mean squares	
Temperature	5		15.62*	
Linear		1		49.27*
Remainder		4		7.21*
Time	5		11.23*	
Linear		1		52.28*
Remainder		4		0.97
Temperature X Time	25		1.26	
Error	36		2.31	

*Denotes statistical significance at the 0.05 level.
**Statistical analysis is from transformed data.

Table 9. Percentage of fiber fed that remained in the intestine of fish maintained at 6 temperatures and killed at 6 time intervals.

Hours after feeding	Temperature degrees centigrade 10.0	15.5	21.1	23.9	26.6	29.4	Time means
2	2.26*	1.83	1.26	1.22	3.22	2.16	1.99
4	0.18	2.57	2.83	9.09	13.13	8.60	6.06
6	1.05	4.83	9.96	19.09	11.96	15.91	10.46[a]**
8	1.26	9.53	19.92	21.79	20.18	19.94	15.43[a,b]
10	2.13	13.31	25.18	30.13	22.83	17.46	18.50[b]
12	1.46	13.57	31.53	15.83	27.26	16.22	17.64[b]
Temp. means	1.39	7.60	15.11[1]**	16.19[1]	16.43[1]	13.38[1]	

*Each observation represents an average from two groups of five fish.
**Common superscripts indicate means that are not significantly different at the 0.05 level.

Table 9a. Analysis of variance of data in Table 9.**

Source of variance	Degrees of freedom		Mean squares	
Temperature	5		10.82*	
Linear		1		42.73*
Remainder		4		2.84*
Time	5		11.99*	
Linear		1		53.89*
Remainder		4		1.52
Temperature X Time	25		0.94	
Error	36		0.75	

*Denotes statistical significance at the 0.05 level.
**Statistical analysis is from transformed data.

the stomachs of fish at 10.0 and 15.5° C, or at 21.1, 23.9, and 29.4° C. Analysis of variance (Table 10a) indicated highly significant linear effects of temperature and time and significant remainder effects of temperature on the percentages of ash remaining in the intestines. Interaction between temperature and time was not significant at the 0.05 level.

Mean percentage of ash remaining in the intestines 12 hours after feeding was largest at 23.9° C, and percentages remaining decreased progressively at 21.1, 26.6, 15.5, 29.4, and 10.0° C (Table 11). Rate of passage of ash into the intestines was slow at 10.0° C; the mean percentage remaining during 12 hours was only 3.67. Analysis of variance (Table 11a) indicated significant linear effects of temperature and time on the percentage of ash remaining in the intestines; remainder effects of both temperature and time were also significant. Interaction between temperature and time was not significant at the 0.05 level.

Rate of Digestion of Nitrogen-Free Extract

Data in Table 12 indicated mean percentage of nitrogen-free extract remaining in the stomachs of fish was lowest at 26.6° C, and the percentage increased progressively at temperatures of 29.4, 23.9, 21.1, 10.0, and 15.5° C. There was no significant difference at the 0.05 level in the mean percentages of nitrogen-free extract remaining in the stomachs of fish at 10.0 and 15.5° C, or at 21.1, 23.9, and 29.4° C, or at 26.6 and 29.4° C. Analysis of variance (Table 12a) indicated highly significant linear effects of temperature and time on the percentages of nitrogen-free extract remaining in the stomachs.

Mean percentage of nitrogen-free extract remaining in the intestines 12 hours after feeding was largest at 23.9° C, and the percentages decreased progressively at temperatures of 26.6, 21.1, 15.5, 29.4, and 10.0° C (Table 13).

Table 10. Percentage of ash fed that remained in the stomach of fish maintained at 6 temperatures and killed at 6 time intervals.

Hours after feeding	Temperature degrees centigrade						Time means**
	10.0	15.5	21.1	23.9	26.6	29.4	
2	88.22*	97.50	81.43	90.42	53.36	86.07	82.83[a]
4	86.07	95.00	71.72	56.16	41.54	65.39	69.31[a,b]
6	79.29	83.22	67.68	41.68	26.58	68.18	61.10[b,c]
8	48.14	78.58	35.82	44.90	35.29	47.32	48.34[c,d]
10	65.39	56.86	31.04	45.21	20.65	27.13	41.04[d]
12	68.68	49.04	28.79	36.04	17.18	40.00	39.95[d]
Temp. means**	72.63[1]	76.70[1]	52.74[2]	52.40[2]	32.43	55.68[2]	

*Each observation represents an average from two groups of five fish.
**Common superscripts indicate means that are not significantly different at the 0.05 level.

Table 10a. Analysis of variance of data in Table 10.**

Source of variance	Degrees of freedom		Mean squares	
Temperature	5		16.76*	
Linear		1		45.83*
Remainder		4		9.38*
Time	5		16.32*	
Linear		1		78.03*
Remainder		4		0.90
Temperature X Time	25		0.94	
Error	36		1.94	

*Denotes statistical significance at the 0.05 level.
**Statistical analysis is from transformed data.

Table 11. Percentage of ash fed that remained in the intestine of fish maintained at 6 temperatures and killed at 6 time intervals.

Hours after feeding	Temperature degrees centigrade 10.0	15.5	21.1	23.9	26.6	29.4	Time means
2	0.97*	2.90	1.64	1.15	2.90	1.43	1.83
4	0.61	3.82	3.29	8.18	12.50	5.84	5.70
6	3.57	6.90	13.18	18.18	12.19	12.31	11.05
8	3.97	13.61	25.93	19.59	20.82	13.92	16.30^{a}**
10	7.29	23.57	25.89	35.36	19.36	11.56	20.50^{a}
12	5.62	24.54	31.57	27.97	23.04	9.62	20.39^{a}
Temp. means	3.67	$12.55^{1,2}$**	$16.91^{2,3}$	18.40^{3}	$15.13^{2,3}$	9.11^{1}	

*Each observation represents an average from two groups of five fish.
**Common superscripts indicate means that are not significantly different at the 0.05 level.

Table 11a. Analysis of variance of data in Table 11.**

Source of variance	Degrees of freedom		Mean squares	
Temperature	5		7.24*	
Linear		1		12.64*
Remainder		4		5.89*
Time	5		15.70*	
Linear		1		72.11*
Remainder		4		1.59*
Temperature X Time	25		0.81	
Error	36		0.56	

*Denotes statistical significance at the 0.05 level.
**Statistical analysis is from transformed data.

Rate of passage of nitrogen-free extract into the intestines at 10.0° C was significantly lower than the rate at all other temperatures. Mean percentage remaining at 10.0° C was only 2.60 percent. Analysis of variance (Table 13a) indicated highly significant linear effects of temperature and time on the percentage of nitrogen-free extract remaining in the intestines. Remainder effects of both temperature and time were significant at the 0.05 level.

DISCUSSION

Factors Affecting Rate of Digestion

Major problems in studying digestion rates in fishes have been to persuade a large number of fish to eat a measured amount of feed at the same time and to control other factors that may affect digestion rate. Some workers have resorted to force-feeding and controlled laboratory experiments. Windell (1966) stated rates of digestion, absorption, and peristalsis were affected by a number of factors including temperature, amount of food consumed, nature of the food, condition of the animal, and stress. Karpevitch and Bokoff (1937) observed rate of digestion was influenced by the kind of food, size and age of experimental animals, and size of the food lump. Ranade and Kewalramani (1966) found rate of food passage in three species of stomachless carps varied considerably with the kind of food and was related to the concentration of the required digestive enzymes. Barrington (1957) stated rate of passage was affected by condition of the animal, nature and stimulatory effect of the food, and frequency of feeding. From reviewing the literature it became obvious that rate of digestion also varied among fish of different species. Temperature was a major factor because it affected the activity of the fish, the amount of enzymes present, and the rate of body metabolism. In general, vital processes are accelerated by warm temperatures and decelerated by cold temperatures. In the

Table 12. Percentage of nitrogen-free extract fed that remained in the stomach of fish maintained at 6 temperatures and killed at 6 time intervals.

Hours after feeding	Temperature degrees centigrade						Time means
	10.0	15.5	21.1	23.9	26.6	29.4	
2	79.02*	85.46	68.65	75.22	47.92	76.20	72.08[a]**
4	81.04	85.16	64.54	47.55	39.16	55.92	62.23[a,b]
6	73.81	74.66	60.58	36.88	25.09	40.95	51.99[b]
8	70.19	76.14	34.67	41.22	30.58	32.38	47.53[b,c]
10	55.89	53.50	31.70	39.90	19.15	20.03	36.69[c]
12	58.28	49.88	30.00	34.73	17.55	24.71	35.86[c]
Temp. means	69.70[1]**	70.80[1]	48.36[2]	45.91[2]	29.91[3]	41.70[2,3]	

*Each observation represents an average from two groups of five fish.
**Common superscripts indicate means that are not significantly different at the 0.05 level.

Table 12a. Analysis of variance of data in Table 12.**

Source of variance	Degrees of freedom		Mean squares	
Temperature	5		18.61*	
Linear		1		74.32*
Remainder		4		4.68
Time	5		13.61*	
Linear		1		65.50*
Remainder		4		0.64
Temperature X Time	25		0.69	
Error	36		2.25	

*Denotes statistical significance at the 0.05 level.
**Statistical analysis is from transformed data.

Table 13. Percentage of nitrogen-free extract fed that remained in the intestine of fish maintained at 6 temperatures and killed at 6 time intervals.

Hours after feeding	Temperature degrees centigrade 10.0	15.5	21.1	23.9	26.6	29.4	Time means
2	0.67*	1.73	1.30	0.93	2.41	1.43	1.41
4	0.40	2.39	2.41	6.81	10.47	5.84	4.72
6	2.49	4.62	10.24	15.16	10.28	12.31	9.18
8	2.58	9.12	20.06	16.32	17.55	13.92	13.26[a]**
10	5.09	19.02	18.22	30.13	15.93	11.56	16.66[a]
12	4.38	19.76	22.21	26.57	18.96	9.62	16.91[a]
Temp. means	2.60	9.44[1]**	12.41[1,2]	15.98[2]	12.60[1,2]	9.11[1]	

*Each observation represents an average from two groups of five fish.
**Common superscripts indicate means that are not significantly different at the 0.05 level.

Table 13a. Analysis of variance of data in Table 13.**

Source of variance	Degrees of freedom		Mean squares	
Temperature	5		6.14*	
Linear		1		16.60*
Remainder		4		3.52*
Time	5		12.66*	
Linear		1		58.68*
Remainder		4		1.16*
Temperature X Time	25		0.68	
Error	36		0.43	

*Denotes statistical significance at the 0.05 level.
**Statistical analysis is from transformed data.

present study several of the above factors were regulated; but in so doing it was necessary to subject the fish to added stress conditions of crowding in tanks, handling, and force-feeding.

Importance of a Knowledge of Digestion Rate

Rates of digestion were recognized by Ricker (1946) as having an important bearing on fish production. He observed that rate of consumption varied with temperature and, in general, there appeared to be an optimum temperature for maximum consumption which was correlated with the summer temperature prevailing in the natural habitat of the species concerned. Windell (1967) and Barrington (1957) found a high correlation between the rate of absorption and the rate of digestion. Windell observed that both absorption and digestion increased with time, and amount of absorption by bluegills was always only slightly less than the amount of digestion. In studies with carps force-fed different food items, Ranade and Kewalramani (1966) observed indigestible food items were retained in the digestive tract for the longest time, and concluded food items which passed rapidly through the intestine were more efficiently used because rapid food passage was associated with high digestibility, due to high concentration of the requisite enzymes; rapid food passage may also mean a similar increase in the rate of feeding. A knowledge of digestion rates should aid in the determination of daily ration and in estimating time required for evacuation of food from the stomachs. Dawes (1930) observed that if a second meal was taken at a short interval after the first, food passed down the alimentary tract more quickly and digestion was less complete. Barrington (1957) stated although fish would accept food more than once per day, total amount ingested, when averaged over several weeks, was no more than if they had been fed once per day. Fish fed several times daily did not appear to gain weight more rapidly than those fed once per day. These results indicate feeding a second meal before digestion in the stomach is complete would not increase growth rate and could result in lowered feed efficiency.

Variation in Data

Variation in data may have been caused by individual differences in rates of digestion and by increased variation in rates of digestion caused by the stress of crowding, handling, and force-feeding. Also some regurgitation occurred in all experiments as a result of force-feeding. It was not possible to determine the amount of material regurgitated but it appeared to be small. Hunt (1960) found no significant difference in rate of digestion between warmouth force-fed and those feeding voluntarily; but rate of digestion varied greatly among individuals of the same size and fed the same sized meal. Large fish often digested food much more slowly than smaller fish. Seaburg and Moyle (1964) encountered only occasional regurgitation when pike were force-fed perch; and Molnar and Tolg (1962b) reported only occasional regurgitation when largemouth bass were force-fed bleak. Malcolm (1960) reported bluegills, held at temperatures of 17 and 20° C and force fed mealworms, regurgitated only rarely. However, Windell (1966) reported frequent regurgitation when bluegills were force fed mealworms, and the coefficient of variation was much higher among force-fed fish than among fish feeding voluntarily.

Rate of Digestion of Dry Matter

Fastest rate of food passage occurred at 26.6° C, and the rate of passage decreased progressively at temperatures of 29.4, 23.9, 21.1, 10.0, and 15.5° C (temperature means Table 3). However, the percentage remaining 24 hours after feeding was lowest at 29.4° C and increased progressively at temperatures of 26.6, 23.9, 21.1, 15.5, and 10.0° C (Table 3 and Figure 3). Inconsistencies in results were probably caused by regurgitation and other factors causing increased variation. At 29.4° C, stomachs were essentially empty 24 hours after feeding and only 2.67, 3.45, and 5.45 percent remained in the stomachs at 26.6, 23.9, and 21.1° C respectively (Table 1). The material remaining in the stomach 24 hours after feeding at temperatures of 21.1° C and above was probably largely indigestible because the less digestible materials would be retained. Ranade and Kewalramani (1966) reported that the indigestible plant and animal matter were retained longest in the digestive tract of carps. A significant amount of digestion was also accomplished at temperatures of 10.0 and 15.5° C where only 19.74 and 19.67 percent remained in the stomachs 24 hours after feeding (Table 1 and Figure 1) and only 13.43 and 5.68 percent remained in the intestines (Table 2 and Figure 2).

Results indicated fish at 21.1, 23.9, 26.6, and 29.4° C were ready for a second meal within 24 hours after feeding. At these temperatures fish should be fed daily, whereas at 10.0 and 15.5° C feeding should be reduced or fish should be fed on alternate days. Rates of digestion at 21.1, 23.9, 26.6 and 29.4° C are in general agreement with the results of other researchers but rates of digestion at 10.0 and 15.5° C indicated more digestion may be accomplished at these temperatures than has previously been reported. Cross and Simco (1966), Swingle (1958), and Tiemeier (1962, 1966, 1967) have reported decreased growth rate and feed efficiency by channel catfish at temperatures below 21.1° C and have recommended that feeding be stopped or reduced at temperatures below 15.5° C. West (1966) found maximum growth rate of channel catfish fry occurred at 29.0 to 30° C and maximum feed efficiency occurred at

28.9° C. Crawford (Arkansas Game and Fish Commission Reprint) reported some fish culturists reduce feeding or do not feed daily when water temperatures were above 90 or below 60° F. Asadi (1967) found the optimum temperature for enzyme activity or secretion in channel catfish was 23.9° C and amount of activity decreased above and below that temperature but some enzyme activity was found throughout the range of 10.0 to 29.4° C.

The present study indicated most rapid rate of digestion by channel catfish occurred at 26.6 to 29.4° C and the rate of digestion at these two temperatures was not significantly different at the 0.05 level (Table 3). There was no significant difference at the 0.05 level in the rate of digestion at 21.1, 23.9, and 29.4° C. Temperatures for optimum rate of digestion should be near temperatures for optimum growth and food consumption. These results are in general agreement with results reported by other workers regarding temperatures for optimum growth, food consumption, and digestion rates for various species but it should be remembered that optimum temperatures may vary considerably among fish of different species. Strawn (1961) found optimum temperature for maximum growth of largemouth bass was 27.5 to 30° C. Peek (1965) reported optimum temperature for maximum growth of smallmouth bass (*Micropterus dolomieui*, Lacepede) was 28 to 29° C. In the present study stomachs of channel catfish were essentially empty (less than 6 percent remained) 24 hours after feeding at temperatures of 21.1, 23.9, 26.6, and 29.4° C (Table 1). The remaining material was probably largely indigestible and, if a second meal were taken, remains of the previous meal would be forced into the intestines where further digestion or elimination could take place. When fish were force-fed at temperatures of 23 to 26° C, Hunt (1960) found the average time required for the stomachs to empty was 42 hours for gar, 26.2 hours for warmouth, and 16 to 19 hours for largemouth bass. Herting and Witt (1968) reported young-of-the-year bowfin (Amia calva) required 28 to 32 hours at 21.0° C for complete digestion of a meal equal to 4.9 percent of their body weight when force-fed Gambusia; young-of-the-year longnose gar (Lepisosteus osseus) required 24 hours at 26.4° C for complete digestion of a meal of minnows equal to 6.7 percent of their body weight. Windell (1966) reported 17 to 19 hours were required for the stomachs of bluegills to empty after meals of natural food organisms were consumed at water temperatures ranging from 18.5 to 24.6° C but 22 to 26 hours were required for the stomachs to empty after meals of mealworms were consumed. In studies using force-feeding and X-ray techniques, Molnar et al. (1967) reported that at temperatures of 5, 10, 15, 20, and 25° C, 110, 50, 37, 24, and 19 hours respectively were required for 100 percent gastric digestion by largemouth bass. At the same temperatures 115, 63, 49, 27, and 21 hours respectively were required for 100 percent gastric digestion by perch (Perca fluviatillis). Maloney (1949) observed bluegills increased their food consumption from a low at 10° C to an optimum between 15 and 25° C, and food intake decreased at temperatures above 25° C. In studies with the brown bullhead (Ameiurus nebulosus) maintained at temperatures of 10, 15, 18, 22, and 28° C, Underhill (1952) observed food consumption increased with increasing temperature up to 25° C but food consumption was less at 28° C than at 25° C. Weight gains made by fish at 22° C were markedly greater than at other temperatures. He observed maintenance requirements were high at 28° C. One fish ate 90.0 grams at 22° C and gained 8.9 grams, while at 28° C it ate 85.8 grams and lost 4.1 grams. In other fish the efficiency at 28° C was only one-third that at 22° C.

Common superscripts of time means indicated means that were not significantly different at the 0.05 level. There were few significant differences among time means at 2 and 4-hour intervals in all tables, indicating

2- or 4-hour intervals for sampling were shorter than necessary for a study of this type. Sampling at 6-hour intervals would appear sufficient.

Mean percentages of dry matter remaining in the stomachs of fish (Table 1) were not significantly different at the 0.05 level at 10.0 and 15.5° C or at 21.1, 23.9, 26.6, and 29.4° C. This indicated there was not a marked increase in rate of digestion as temperature increased, especially between the low temperatures of 10.0 and 15.5° C and within the higher temperature range of 21.1, 23.9, 26.6, and 29.4° C. Each fish received 3.0 grams of feed which was less than 1 percent of the average body weight. Fish would probably consume meals amounting to more than 1 percent of their body weight at temperatures above 60° F. Tiemeier (1967) reported a feeding rate of 3 percent of body weight per day and Swingle (1958) reported a feeding rate of 2 to 5 percent of body weight per day at temperatures above 60° F; but it was not known how much of the amount fed was consumed. Hunt (1960), and Windell (1966) reported that as the size of the meal was increased the amount digested per unit of time was also increased. When meals of 1 to 3.5 percent of the body weight were consumed, a large meal was digested almost as soon as a small meal and Windell stated the digestive system probably increased enzyme production with increased food volume in the stomach. Brown (1946), Maloney (1949), and Underhill (1952) reported increased food consumption by fish as water temperature increased. In my study, digestion in the stomachs of channel catfish was essentially complete 24 hours after feeding at 21.1, 23.9, 26.6, and 29.4° C. But maintenance requirements also increase with increasing water temperature and growth rates may decrease at high temperatures approaching the lethal limit. Brown (1946) and Underhill (1952) reported similar effects of temperature on food consumption and growth rates by brown trout and brown bullheads.

In my study, fish became more active as temperatures increased and they moved about in the tanks much more at 26.6 and 29.4° C than they did at the lower temperatures. During one experiment conducted at 32.2° C, three fish died before being fed and nine others died within two hours after being force-fed. The remaining fish appeared weak and sluggish. These fish had been held in tanks at 21.1° C for two weeks before the temperature was increased at the rate of 2.8° C per day to 32.2° C. Fish were held at 32.2° C two days before feeding. These fish were unable to withstand the stress of handling and force-feeding at 32.2° C. Digestion rate was rapid at 29.4° C but this temperature may be too high for maximum growth rate and feed efficiency because of increased activity and maintenance requirements.

Rate of Digestion of Food Nutrients

Rate of passage of food nutrients through the digestive tract was similar to the rate of passage of dry matter. Temperature means in Tables 4, 6, 8, 10, and 12 showed that passage of all nutrients through the stomachs of fish was most rapid at 26.6° C. The same temperature means also indicated no significant difference at the 0.05 level in percentages of food nutrients remaining in the stomachs at 10.0 and 15.5° C or at 21.1, 23.9, and 29.4° C. Exceptions were percentages of fat remaining in the stomachs (Table 6) and percentages of fiber remaining in the stomachs at 15.5° C (Table 8). Percentages of nutrients remaining may be erratic due to problems involved in chemical analyses and a lack of sufficient food remains to duplicate analyses. Percentage of fat remaining in some samples was greater than 100 percent. This could have been caused by contamination of the sample with fat from the body cavity of the fish. Difficulties were also encountered in filtering samples during fiber analyses. In general, there was a significant increase in rate of digestion of all nutrients at temperatures of 21.1° C and above when compared to rates of digestion at 10.0 and 15.5° C. Analyses of variance of Tables 4 through 13 showed significant linear effects of temperature and time on percentages of nutrients remaining in both stomachs and intestines and remainder effects of temperature and time on percentages remaining in the intestines were generally significant. Remainder effects of temperature and time on percentages of protein, ash, and fiber remaining in the stomachs were also significant. Interaction was not significant in Tables 4 through 25 indicating effect of time was the same over all temperatures and all nutrients.

Rate of Digestion of Protein

Rate of digestion of protein increased with increased temperature to 26.6° C where only 32.23 percent remained in the digestive tract 12 hours after feeding. Rate of protein digestion was lower at 29.4° C where 45.43 percent remained in the digestive tract 12 hours after feeding. These results are in agreement with Riddle (1909) who concluded pepsin secretion decreases with low temperature while at high temperatures it may also be diminished or destroyed. Windell (1967) observed rates of decrease of protein and digestible organic matter from the stomachs of bluegills were closely parallel and amount of absorption was always slightly less than the amount of digestion. In the present study, 21.20 percent of the dry matter remained in the stomachs at 26.6° C, 12 hours after feeding (Table 1) and 22.23 percent of protein remained in the stomachs at the same temperature and time (Table 4). Asadi (1967) found optimum temperature for secretion of pepsin and trypsin by channel catfish was 23.9° C and secretion diminished above and below 23.9° C.

Rate of Digestion of Fat, Fiber, Ash and Nitrogen-Free Extract

Rates of digestion of the remaining food nutrients studied were similar to the rate of digestion of protein. Temperature means and percentages remaining in the stomachs 12 hours after feeding (Tables 6, 8, 10, and 12) indicated rate of digestion of all nutrients was most rapid at 26.6° C. In general, the rate of digestion at temperatures of 21.1° C and above was significantly higher than the rate of digestion at 10.0 and 15.5° C. Time means of Tables 4, 6, 8, 10, and 12 indicated from 35.86 to 48.08 percent of all nutrients remained in the stomachs 12 hours after feeding. Time means of Tables 5, 7, 9, 11, and 13 indicated from 12.71 to 20.39 percent of all nutrients remained in the intestines 12 hours after feeding. The average percentage over all temperatures of nutrients remaining in the digestive tracts 12 hours after feeding was 59.74 percent. The average percentage decrease of food nutrients from the digestive tract over all temperatures was 41.26 percent 12 hours after feeding.

SUMMARY

Experiments were conducted at the Tuttle Creek Fisheries Research Laboratory to determine the effects of temperature on rate of digestion by age groups II and III (approximately two and three years old) channel catfish. During these experiments, fish were held in insulated stock tanks with water temperature maintained at 10.0, 15.5, 21.1, 23.9, 26.6, 29.4, and 32.2° C. Following acclimation at each temperature, each fish was force-fed 3 grams of a pelleted fish feed. Groups of fish were killed at intervals of 2, 4, 6, 8, 10, 12, 18, and 24 hours after feeding. Contents of the stomachs and intestines were removed, dried, weighed, and chemically analyzed to determine the percentages of dry matter, protein, fat, fiber, ash, and nitrogen-free extract that remained at each time interval.

Mean percentages of dry matter remaining in the stomachs and in the stomachs and intestines during the 24 hour period after feeding indicated most

rapid rate of removal from the digestive tract occurred at 26.6° C, where an average of 33.42 percent remained in the stomachs and 11.14 percent remained in the intestines. Mean percentage of dry matter remaining in the digestive tract of fish in the 24-hour group was lowest at 29.4° C and the percentages remaining increased progressively at temperatures of 26.6, 23.9, 21.1, 15.5, and 10.0° C. The rates of digestion at 10.0 and 15.5° were significantly lower than the rates of digestion at the higher temperatures. Stomachs of fish were essentially empty 24 hours after feeding at 21.1, 23.9, 26.6, and 29.4° C; respective percentages remaining were 5.45, 3.45, 2.67, and 0.89. These results indicated fish at these temperatures were ready for another meal within 24 hours after feeding. A significant amount of digestion was also accomplished at 10.0 and 15.5° C where only 19.74 and 19.67 percent remained in the stomachs 24 hours after feeding.

Rate of digestion of protein, fats, fiber, ash, and nitrogen-free extract was similar to digestion of dry matter. All nutrients were digested faster at 26.6° C than at any other temperature. Digestion of all nutrients was significantly lower at 10.0 and 15.5° C than at the higher temperatures. There was no significant difference at the 0.05 level in percentages of protein, fiber, ash, and nitrogen-free-extract remaining in the stomachs during 12 hours after feeding at temperatures of 10.0 and 15.5° C, or at 21.1, 23.9, and 29.4° C. Percentages of fat remaining were inconsistent possibly because of contamination of samples with fat from the body cavity.

Statistical analyses of all data indicated significant linear effects of temperature and time at the 0.05 level. Interaction between temperature and time was not significant except with the percentage of dry matter remaining in the intestines during 24 hours after feeding. The percentage remaining in the intestines increased to a maximum within 12 hours after feeding and then decreased.

Fish maintained at 26.6 and 29.4° C were much more active than fish maintained at lower temperatures. In one experiment conducted at 32.2° C, 12 of 30 fish died and the remaining fish were weak and sluggish. These results indicated that 32.2° C was near the lethal temperature for channel catfish of this size maintained under experimental conditions.

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APPENDIX

Table 14. Percentage of each nutrient fed that remained in the stomach of fish maintained at 10.0° C and killed at 8 time intervals.

Hours after feeding	Food Nutrient					Time means
	Protein	Fat	Fiber	Ash	Nitrogen-free extract	
2	87.83*	99.12	77.39	88.22	79.02	86.32[a]**
4	97.76	119.72	93.04	86.07	81.04	95.52[a]
6	86.23	113.78	79.57	79.29	73.81	86.53[a]
8	80.29	75.38	70.13	48.14	70.19	68.82[b]
10	71.17	54.25	81.91	65.39	55.89	65.72[b]
12	80.69	52.88	92.01	68.68	58.28	70.51[b]
Nutrient means	83.99	85.85	82.34	72.63	69.70	

*Each observation represents an average from two groups of five fish.
**Common superscripts indicate means that are not significantly different at the 0.05 level.

Table 14a. Analysis of variance of data in Table 14.**

Source of variance	Degrees of freedom		Mean squares	
Nutrient	4		1.83	
Time	5		4.78*	
Linear		1		16.24*
Remainder		4		1.91
Nutrient X Time	20		1.00	
Error	30		0.71	

*Denotes statistical significance at the 0.05 level.
**Statistical analysis is from transformed data.

Table 15. Percentage of each nutrient fed that remained in the intestine of fish maintained at 10.0° C and killed at 6 time intervals.

Hours after feeding	Food Nutrient					Time means
	Protein	Fat	Fiber	Ash	Nitrogen-free extract	
2	0.76*	1.04	2.26	0.97	0.67	1.14[a,b]**
4	0.57	0.66	0.18	0.61	0.40	0.48[a]
6	2.90	3.59	1.05	3.57	2.49	2.72[b,c]
8	3.60	4.06	1.26	3.97	2.58	3.09[b,c]
10	5.93	7.26	2.13	7.29	5.09	5.54[c]
12	3.57	5.34	1.46	5.62	4.38	4.07[b,c]
Nutrient means	2.89	3.66	1.39	3.67	2.60	

*Each observation represents an average from two groups of five fish.
**Common superscripts indicate means that are not significantly different at the 0.05 level.

Table 15a. Analysis of variance of data in Table 15.**

Source of variance	Degrees of freedom		Mean squares	
Nutrient	4		0.55	
Time	5		2.16*	
Linear		1		7.15*
Remainder		4		0.91
Nutrient X Time	20		0.09	
Error	30		0.52	

*Denotes statistical significance at the 0.05 level.
**Statistical analysis is from transformed data.

Table 16. Percentage of each food nutrient fed that remained in the stomach of fish maintained at 15.5° C and killed at 8 time intervals.

Hours after feeding	Food Nutrient					Time means
	Protein	Fat	Fiber	Ash	Nitrogen-free extract	
2	99.60*	105.85	88.61	97.50	85.45	95.40[a]**
4	96.17	63.40	87.78	95.00	85.16	85.50[a]
6	92.86	79.91	85.03	83.22	74.66	83.13[a]
8	86.91	94.06	65.05	78.58	76.14	80.14[a]
10	77.12	63.30	57.13	56.86	53.50	61.58[b]
12	67.86	51.61	57.18	49.04	49.88	55.11[b]
Nutrient means	86.75	76.35	73.46	76.70	70.80	

*Each observation represents an average from two groups of five fish.
**Common superscripts indicate means that are not significantly different at the 0.05 level.

Table 16a. Analysis of variance of data in Table 16.**

Source of variance	Degrees of freedom		Mean squares	
Nutrient	4		1.47	
Time	5		8.42*	
Linear		1		38.32*
Remainder		4		0.94
Nutrient X Time	20		0.44	
Error	30		0.85	

*Denotes statistical significance at the 0.05 level.
**Statistical analysis is from transformed data.

Table 17. Percentage of each food nutrient fed that remained in the intestine of fish maintained at 15.5° C and killed at 8 time intervals.

Hours after feeding	Food Nutrient					Time means
	Protein	Fat	Fiber	Ash	Nitrogen-free extract	
2	1.94^{*}	2.27	1.83	2.90	1.73	2.13^{a} **
4	2.78	3.12	2.57	3.82	2.39	2.93^{a}
6	5.64	6.04	4.83	6.90	4.62	5.60
8	11.10	11.88	9.53	13.61	9.12	11.05
10	13.89	12.36	13.31	23.57	19.02	16.43^{b}
12	15.67	12.83	13.57	24.54	19.76	17.27^{b}
Nutrient means	8.50	8.08	7.60	12.55	9.44	

*Each observation represents an average from two groups of five fish.
**Common superscripts indicate means that are not significantly different at the 0.05 level.

Table 17a. Analysis of variance of data in Table 17**

Source of variance	Degrees of freedom	Mean squares
Nutrient	4	0.77^{*}
Time	5	12.07^{*}
Linear	1	58.13^{*}
Remainder	4	0.55^{*}
Nutrient X Time	20	0.15
Error	30	0.18

*Denotes statistical significance at the 0.05 level.
**Statistical analysis is from transformed data.

Table 18. Percentage of each food nutrient fed that remained in the stomach of fish maintained at 21.1° C and killed at 6 time intervals.

Hours after feeding	Food Nutrient					Time means
	Protein	Fat	Fiber	Ash	Nitrogen-free extract	
2	84.92*	97.55	87.52	81.43	68.65	84.01[a]**
4	73.68	60.38	61.74	71.72	64.54	66.41[a]
6	79.90	92.55	81.70	67.68	60.58	76.48[a]
8	44.98	48.78	42.57	35.82	34.67	41.36[b]
10	42.32	44.25	31.05	31.04	31.70	36.07[b]
12	39.29	42.64	38.40	28.79	30.00	35.82[b]
Nutrient means	60.85	64.36	57.16	52.74	48.36	

*Each observation represents an average from two groups of five fish.
**Common superscripts indicate means that are not significantly different at the 0.05 level.

Table 18a. Analysis of variance of data in Table 18.**

Source of variance	Degrees of freedom		Mean squares	
Nutrient	4		1.99	
Time	5		22.99*	
Linear		1		92.06*
Remainder		4		5.73
Nutrient X Time	20		0.24	
Error	30		3.94	

*Denotes statistical significance at the 0.05 level.
**Statistical analysis is from transformed data.

Table 19. Percentage of each food nutrient fed that remained in the intestine of fish maintained at 21.1° C and killed at 6 time intervals.

Hours after feeding	Protein	Fat	Fiber	Ash	Nitrogen-free extract	Time means
	Food Nutrient					
2	0.96*	1.89	1.26	1.64	1.30	1.41[a]**
4	1.95	3.59	2.83	3.29	2.41	2.81[a]
6	7.49	15.10	9.96	13.18	10.24	11.19
8	14.78	29.63	19.92	25.93	20.06	22.06[b]
10	16.45	26.89	25.18	25.89	18.22	22.52[b]
12	20.94	33.96	31.53	31.57	22.21	28.04
Nutrient means	10.42	18.51	15.11	16.91	12.41	

*Each observation represents an average from two groups of five fish.
**Common superscripts indicate means that are not significantly different at the 0.05 level.

Table 19a. Analysis of variance of data in Table 19.**

Source of variance	Degrees of freedom		Mean squares	
Nutrient	4		1.76*	
Time	5		25.94*	
Linear		1		120.36*
Remainder		4		2.33*
Nutrient X Time	20		0.13	
Error	30		0.22	

*Denotes statistical significance at the 0.05 level.
**Statistical analysis is from transformed data.

Table 20. Percentage of each food nutrient fed that remained in the stomach of fish maintained at 23.9° C and killed at 7 time intervals.

Hours after feeding	Food Nutrient					Time means
	Protein	Fat	Fiber	Ash	Nitrogen-free extract	
2	88.89*	114.15	93.00	90.72	75.22	92.39
4	58.60	79.91	59.09	56.16	47.55	60.26[a]**
6	44.55	45.33	52.78	41.68	36.88	44.24[a]
8	50.39	75.66	53.26	44.90	41.22	53.08[a]
10	51.64	101.04	53.35	45.21	39.90	58.22[a]
12	42.79	66.70	40.56	36.04	34.73	44.16[a]
Nutrient means	56.14	80.47	58.67	52.45	45.91	

*Each observation is an average from two groups of five fish.
**Common superscripts indicate means that are not significantly different at the 0.05 level.

Table 20a. Analysis of variance of data in Table 20.**

Source of variance	Degrees of freedom		Mean squares	
Nutrient	4		7.74*	
Time	5		12.19*	
Linear		1		27.91*
Remainder		4		8.26*
Nutrient X Time	20		0.40	
Error	30		2.35	

*Denotes statistical significance at the 0.05 level.
**Statistical analysis is from transformed data.

Table 21. Percentage of each food nutrient fed that remained in the intestine of fish maintained at 23.9° C and killed at 6 time intervals.

Hours after feeding	Food Nutrient					Time means
	Protein	Fat	Fiber	Ash	Nitrogen-free extract	
2	2.65*	0.57	1.22	1.15	0.93	1.30
4	5.11	4.15	9.09	8.18	6.81	6.67
6	11.38	9.16	19.09	18.18	15.16	14.59[a]**
8	12.25	9.81	21.79	19.59	16.32	15.95[a]
10	18.62	20.21	30.13	35.36	30.13	26.89
12	16.27	14.82	15.83	27.97	26.57	20.29[a]
Nutrient means	11.04	9.79	16.19	18.40	15.98	

*Each observation represents an average from two groups of five fish.
**Common superscripts indicate means that are not significantly different at the 0.05 level.

Table 21a. Analysis of variance of data in Table 21.**

Source of variance	Degrees of freedom		Mean squares	
Nutrient	4		2.36*	
Time	5		17.91*	
Linear		1		74.31*
Remainder		4		3.81*
Nutrient X Time	20		0.26	
Error	30		0.52	

*Denotes statistical significance at the 0.05 level.
**Statistical analysis is from transformed data.

Table 22. Percentage of each food nutrient fed that remained in the stomach of fish maintained at 26.6° C and killed at 6 time intervals.

Hours after feeding	Food Nutrient					Time means
	Protein	Fat	Fiber	Ash	Nitrogen-free extract	
2	56.38*	54.86	54.91	53.36	47.92	53.48[a]**
4	45.15	56.98	36.27	41.54	39.16	43.82[a,b]
6	32.76	37.83	35.05	26.58	25.09	31.46[a,b,c]
8	38.97	57.08	38.70	35.29	30.58	40.12[a,b,c]
10	25.31	41.23	25.87	20.65	19.15	26.44[b,c]
12	22.23	29.44	20.09	17.18	17.55	21.30[c]
Nutrient means	36.80	46.23	35.15	32.43	29.91	

*Each observation represents an average from two groups of five fish.
**Common superscripts indicate means that are not significantly different at the 0.05 level.

Table 22a. Analysis of variance of data in Table 22.**

Source of variance	Degrees of freedom		Mean squares	
Nutrient	4		2.65	
Time	5		12.33*	
Linear		1		57.50*
Remainder		4		1.03
Nutrient X Time	20		0.14	
Error	30		4.77	

*Denotes statistical significance at the 0.05 level.
**Statistical analysis is from transformed data.

Table 23. Percentage of each food nutrient fed that remained in the intestine of fish maintained at 26.6° C and killed at 6 time intervals.

Hours after feeding	Food Nutrient					Time means
	Protein	Fat	Fiber	Ash	Nitrogen-free extract	
2	1.56*	0.94	3.22	2.90	2.41	2.20
4	6.87	3.96	13.13	12.50	10.47	$9.38^{a,b}$**
6	6.85	4.06	11.96	12.19	10.28	9.07^{a}
8	11.72	6.93	20.18	20.82	17.55	$15.44^{a,b}$
10	8.27	6.80	22.83	19.36	15.92	$14.63^{a,b}$
12	10.00	7.89	27.26	23.04	18.96	17.43^{b}
Nutrient means	7.54	5.09	16.43	15.13	12.60	

*Each observation represents an average from two groups of five fish.
**Common superscripts indicate means that are not significantly different at the 0.05 level.

Table 23a. Analysis of variance of data in Table 23.**

Source of variance	Degrees of freedom		Mean squares	
Nutrient	4		5.58*	
Time	5		7.24*	
Linear		1		27.88*
Remainder		4		2.08
Nutrient X Time	20		0.15	
Error	30		1.02	

*Denotes statistical significance at the 0.05 level.
**Statistical analysis is from transformed data.

Table 24. Percentage of each food nutrient fed that remained in the stomach of fish maintained at 29.4° C and killed at 6 time intervals.

Hours after feeding	Food Nutrient					Time means
	Protein	Fat	Fiber	Ash	Nitrogen-free extract	
2	92.46*	80.28	94.78	86.07	76.20	85.96[a]**
4	69.25	59.52	82.04	65.39	55.92	66.42[a,b]
6	58.37	53.30	60.83	68.18	40.95	56.32[b,c]
8	45.65	42.78	46.72	47.32	32.38	42.97[c,d]
10	27.46	26.57	32.80	27.13	20.03	26.80[d]
12	35.60	33.26	38.16	40.00	24.71	34.35[d]
Nutrient means	54.80	49.28	59.22	55.68	41.70	

*Each observation represents an average from two groups of five fish.
**Common superscripts indicate means that are not significantly different at the 0.05 level.

Table 24a. Analysis of variance of data in Table 24.**

Source of variance	Degrees of freedom		Mean squares	
Nutrient	4		3.16	
Time	5		24.35*	
Linear		1		107.46*
Remainder		4		3.57
Nutrient X Time	20		0.12	
Error	30		2.60	

*Denotes statistical significance at the 0.05 level.
**Statistical analysis is from transformed data.

Table 25. Percentage of each food nutrient fed that remained in the intestine of fish maintained at 29.4° C and killed at 6 time intervals.

Hours after feeding	Food Nutrient					Time means
	Protein	Fat	Fiber	Ash	Nitrogen-free extract	
2	1.37*	0.69	2.16	3.50	1.43	1.82
4	5.52	2.93	8.60	13.82	5.84	7.34[a]**
6	11.20	7.87	15.91	23.89	12.31	14.23[b]
8	13.51	8.29	19.94	31.21	13.92	17.37[b]
10	10.46	9.73	17.46	27.29	11.56	15.30[b]
12	9.83	7.11	16.22	24.07	9.62	13.37[a,b]
Nutrient means	8.65	6.10	13.38	20.63	9.11	

*Each observation represents an average from two groups of five fish.
**Common superscripts indicate means that are not significantly different at the 0.05 level.

Table 25a. Analysis of variance of data in Table 25.**

Source of variance	Degrees of freedom		Mean squares	
Nutrient	4		5.34*	
Time	5		9.30*	
Linear		1		27.34*
Remainder		4		4.79*
Nutrient X Time	20		0.12	
Error	30		1.29	

*Denotes statistical significance at the 0.05 level.
**Statistical analysis is from transformed data.

EFFECT OF TEMPERATURE ON RATE OF DIGESTION

BY CHANNEL CATFISH, ICTALURUS PUNCTATUS (RAFINESQUE)

by

JOHN BERNARD SHRABLE

B.S.A., Arkansas State College, 1959

AN ABSTRACT OF A MASTER'S THESIS

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Major Professor

Experiments were conducted to determine the effects of water temperature on the rate of digestion by age groups II and III (approximately two and three years old) channel catfish. The percentage digested was calculated as the difference between the weight of dry matter and food nutrients fed and the weight of dry matter and food nutrients remaining at each temperature and time interval.

During these experiments fish were held in stock tanks equipped with 220-volt electric water heaters and thermostats for maintaining a constant temperature. Experiments were conducted at temperatures of 10.0, 15.5, 21.1, 23.9, 26.6, 29.4, and 32.2° C. Following acclimation at each temperature, fish were force-fed 3 grams each of pelleted fish feed and were killed at intervals of 2, 4, 6, 8, 10, 12, 18, and 24 hours after feeding. Contents of the stomachs and intestines were removed, dried, weighed, and chemically analyzed to determine the percentages of moisture, dry matter, protein, fat, fiber, ash, and nitrogen-free extract remaining at each temperature and time interval.

Statistical analyses of all data indicated significant linear effects of temperature and time at the 0.05 level. Interaction between temperature and time was not significant, except with the percentage of dry matter remaining in the intestines during 24 hours after feeding; the percentage remaining in the intestines increased to a maximum within 12 hours after feeding and then decreased.

Results indicated that the mean percentage of dry matter and food nutrients remaining in the digestive tracts during 24 hours after feeding was lowest at 26.6° C, and the percentage remaining increased progressively at 29.4, 23.9, 21.1, 10.0, and 15.5° C. But the mean percentages remaining in the stomachs at the 24-hour interval was lowest at 29.4° C, and the percentages remaining increased progressively at temperatures of 26.6, 23.9, 21.1, 15.5, and 10.0° C. In general there was no significant difference at the 0.05 level in the mean percentages of dry matter and food nutrients remaining in the stomachs at 10.0 and 15.5° C or at 21.1, 23.9, 26.6, and 29.4° C. Rate of digestion was considerably slower at 10.0 and 15.5° C than at the higher temperatures. Fish maintained at temperatures above 15.5° C were ready for another meal 24 hours after feeding.

Fish maintained at 26.6 and 29.4° C were more active than fish maintained at lower temperatures. During one experiment conducted at 32.2° C, 12 of 30 fish died, and the remaining fish were weak and sluggish. These results indicated that 32.2° C was near the lethal temperature for channel catfish of this size maintained under experimental conditions.