ABSTRACT

Wayne Allan Gardner. A STUDY OF INSECT SUCCESSION ON SUBMERGED SUNFISH CARRION. (Under the direction of Susan J. McDaniel) Department of Biology, November 1974.

Factors affecting the decomposition of submerged sunfish carrion were determined in a pond habitat in Pitt County, North Carolina, from mid-June to mid-November in 1973 and in mid-July 1974. Significant changes in the number of insects associated with the carrion as decay progressed were observed; however, an analysis of changes in the types of insects associated with the carrion yielded no significant evidence of the occurrence of insect succession on the submerged carrion.

Field studies indicated that the aquatic environment, the habitat temperature, and the inhabitant arthropods influenced the rate and course of decay of the submerged sunfish carrion. The aqueous environment prevented any loss of moisture from the flesh of the carrion, thereby facilitating its complete disposal, and effectively limited the types of organisms invading the carrion to only those adapted to an aquatic or semiaquatic existence. The duration of the bloated state and the deflation-decomposition condition was found to be inversely related to the habitat temperature. Decomposition was also found to be significantly hastened by the presence of arthropods which evidently fed upon the carrion and aided in disseminating other saprophagous organisms.

A STUDY OF INSECT SUCCESSION
ON SUBMERGED SUNFISH CARRION

A Thesis

Presented to

the Faculty of the Department of Biology

East Carolina University

In Partial Fulfillment

of the Requirements for the Degree

Master of Arts in Biology

by

Wayne Allan Gardner

November 1974

A STUDY OF INSECT SUCCESSION
ON SUBMERGED SUNFISH CARRION

by

Wayne Allan Gardner

APPROVED BY:

SUPERVISOR OF THESIS Susan J. McDaniel
Susan J. McDaniel

CHAIRMAN OF THE DEPARTMENT OF BIOLOGY

James S. McDaniel
James S. McDaniel

DEAN OF THE GRADUATE SCHOOL

Joseph G. Boyette
Joseph G. Boyette

TABLE OF CONTENTS

ACKNOWLEDGMENT

I am sincerely grateful for the advice and guidance my adviser, Dr. Susan J. McDaniel, provided me during the planning, execution and analysis of this project. I also wish to thank Mrs. Linda Ingalls for her patience in overcoming any problems in communication or interpretation while typing this manuscript, Mr. Ted Houghton of WNCT-TV for so graciously loaning me pertinent weather information, and Mrs. Dora M. McDaniel for her assistance in typing the rough draft of the manuscript. A special thanks is also due to Mrs. Cathy Gardner for her continued moral support and assistance in field collections and observations.

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Many microseral or successional processes occur within each relatively independent major community. Important habitats for such intracommunity successions include dying and dead organic matter. While plants and animals are not immortal, they are extremely numerous on earth due to their capacities to survive adverse influences. It, therefore, follows that their excrements and carcasses are important habitats in themselves (Elton, 1949).

In our attempts to fully comprehend the dynamic relations of a major community, we cannot ignore the types, distributions, or relationships of the intracommunity successional processes. Highly characteristic sequences of seral stages are frequently exhibited by these microcommunities. They occur at different rates; yet, they are generally completed prior to the replacement of the entire major community. In fact, the changes which occur within the larger community may be, at least, partially dependent upon the changes which occur in its microcommunities (Allee *et al.*, 1949). Consequently, microcommunities are often important factors in determining the structure of the major community of which they are a part.

Carrion is but one example of such a microcommunity. Many animal and plant species attack and invade carrion for its food resources; other animal species parasitize or prey upon those saprophagous organisms. However, carrion serves not only as a source of food, it also provides shelter against adverse circumstances. An example of the protection afforded by the carrion microcommunity to its inhabitants is reported by Deonier (1940). Sheep carcasses possess temperatures considerably higher than those of the atmosphere thereby enabling inhabitant blowfly larvae to continue their development when atmospheric conditions are unfavorable to adult activity. Many organisms evidently escape the attack of predators or parasites by burrowing into the decaying tissues of the carrion thereby concealing them and/or making them inaccessible. With the eventual complete decomposition of the carrion, nitrogen-containing compounds are recycled to the producers of the community. The carrion microcommunity influences the structure of the community in which it is located.

The death of an organism is actually the initial stage of a generalized carrion microsere. According to Elton (1966), death occurs in two general ways: death due to the attack of enemies which usually consume all or part of the captured carcass, and death due to other causes. Consequently, carrion succession can begin with the apparently simple event of catching and eating prey.

The second stage of the general microsere is characterized by a competition for resources between the bacteria of decomposition, the invertebrates, and the vertebrate scavengers (fishes, turtles, vultures, crows, gulls, raccoons, etc.). The invertebrates probably eat a mixture of decaying tissues and bacteria. A mixture of carrion, bacteria and invertebrates may be consumed by a vertebrate scavenger to mark a third and final stage of the generalized microsere; however, this stage may not occur, in which case the carrion would eventually decompose due to bacterial and invertebrate action.

Carrion is definitely an important microcommunity; therefore, it is a subject worthy of the ecologists' attention. However, as Allee *et al* (1949) have reported, it is a neglected microsere. It is, for obvious reasons, not a popular subject for ecological research; yet, several reports concerning arthropod inhabitants of carrion are available. Much of this work, however, has been limited to the life histories and habits of the organisms inhabiting the carrion (Kaufman, 1937; Chapman and Sankey, 1955; Linam and Reese, 1956/1957; Payne *et al*., 1968a; Hoffman and Payne, 1969; Payne and King, 1970; Payne and Mason, 1971; and Downes, 1973) including those of economic and medical importance (Kishigami, 1926; Deonier, 1940; Bornemissza, 1957). While these studies are of considerable value in ultimately understanding the carrion microsere, the majority of them are not actually concerned with successional processes which occur in association with the carrion.

Only a few studies have been undertaken to compare arthropod succession associated with carrion in various habitats. Those that have, generally demonstrate that succession of arthropods is influenced by variation in microclimate and vegetation (Illingworth, 1926; Fuller, 1934; Kaufman, 1937; Howden, 1950; Walker, 1957; Reed, 1958; Payne, 1965; and Wasti, 1972). This influence is chiefly through the effects exerted on the course of decay and the fauna of the area.

Reports by Payne and coworkers effectively compare the decomposition processes and arthropod succession associated with baby pigs (*Sus scrofa* L.) in terrestrial habitats to that occurring in the aquatic habitat (Payne, 1965; Payne *et al*., 1968b; and Payne and King, 1972). Moisture is an important influence upon the decomposition process as well as the succession of organisms associated with the carrion. While differences in the types of organisms associated with the pig carrion in the terrestrial and aquatic situations can be observed, they appear to be of little significance; consequently, water in the aquatic situation appears to exert little influence upon the types of organisms characteristic of the various microseral stages. The major reasons for this lack of significant difference are probably: (1) Payne's study of arthropod succession in the aquatic situation (Payne and King, 1972) was conducted in large, water-filled containers, not in a natural body of water, and (2) the carcasses were allowed to float during the early stages of decomposition when they were bloated thereby exposing surfaces which could be invaded by carrion organisms which would invade only exposed carcasses in the terrestrial situation.

Although Elton (1966) has voiced his doubts of the existence of insects peculiar to underwater carrion, evidence is lacking. The rates of arthropod disposal of carrion located on the soil surface and underground have been documented (Payne, 1965; and Payne et al., 1968b); however, no measurements of the rate of carrion disposal in the aquatic habitat have been reported. This study was undertaken to observe and record insect succession which may occur in association with a totally submerged fish carcass placed in a pond. In addition, a study was conducted to measure the rate of arthropod disposal of carrion located in an aquatic habitat.

The habitat. The small, six-year-old pond, known locally as Clark's Pond (Figure 1), which served as the aquatic habitat for this study, was located 4.5 miles northeast of the East Carolina University campus in Greenville, North Carolina. While the pond was located within the 100-year flood plain of the Tar River, it was not inundated by river waters prior to the study.

Greenville is located in Pitt County on the coastal plain of eastern North Carolina approximately 60 miles from the Pamlico Sound. The average elevation is 64 to 75 ft. above sea level.

The pond was chosen for the study for several reasons: (1) the depth of the water did not exceed four feet except in one area; (2) the banks and bottom of all but one area were only slightly sloped to facilitate the secure attachment of the carrion and collection apparatus to the bottom and the quick and easy entry into the water during the collection procedure, and (3) the site was convenient facilitating the daily, early morning collections.

The 836 m^2 pond was situated in an area of approximately 6500 m^2 which had been lumbered and cleared for the purpose of sand excavation. The basin of the pond was actually formed in 1967 as a result of these excavations. No sand had been excavated from the area since that time; consequently, a secondary succession of communities had occurred.

At the time of this study, seedlings of pond pine, Pinus serotina Michaux; loblolly pine, Pinus taeda L.; American sycamore, Platanus occidentalis L.; American hornbeam, Carpinus caroliniana Walter; and water oak, Quercus nigra L., were growing among the numerous mosses,

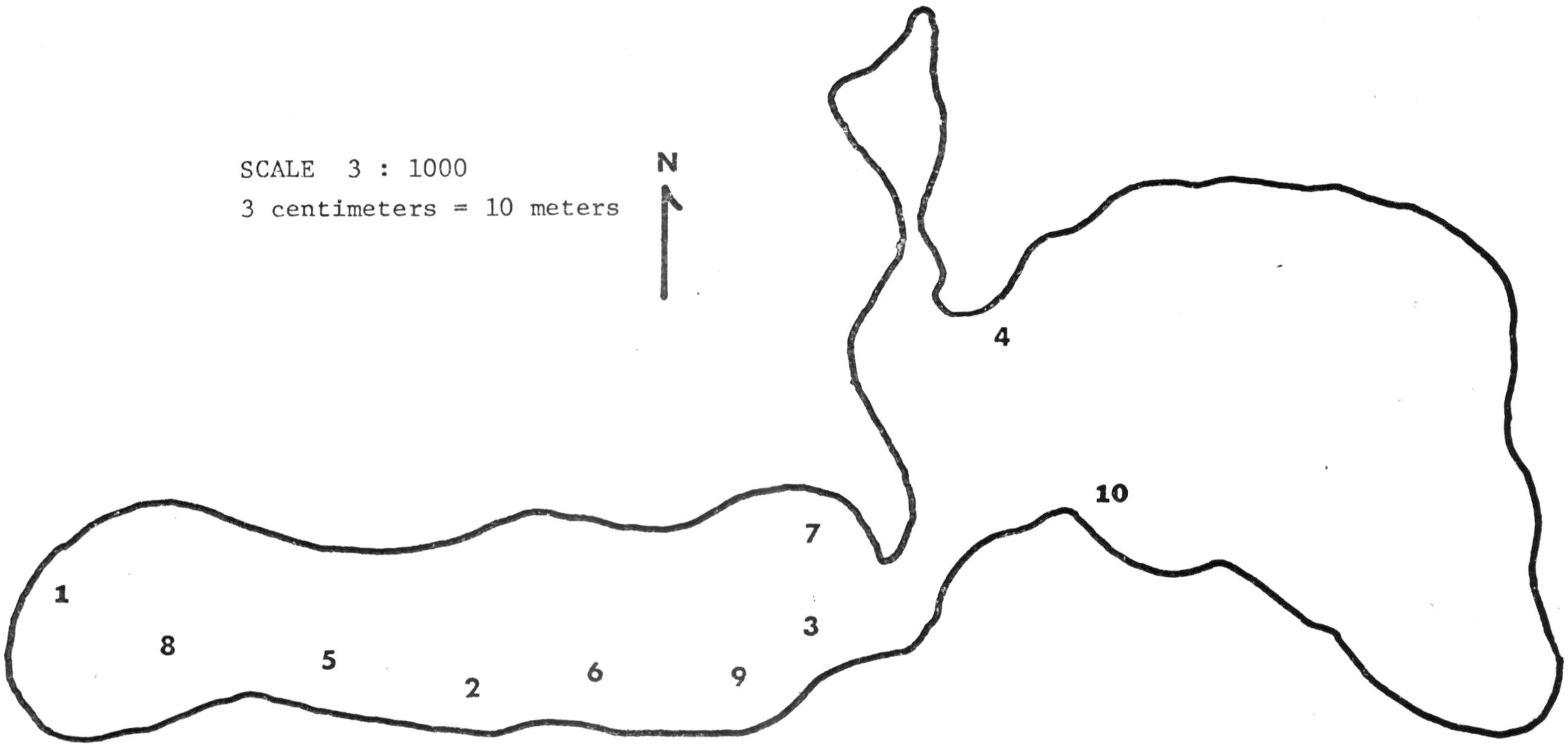

Figure 1. Clark's Pond, Pitt County, North Carolina, with collection sites used in the successional study.

grasses and herbs in the sand-pit area. River birch, *Betula nigra* L.; blackgum, *Nyssa sylvatica* Marshall; and black willow, *Salix nigra* Marshall, were found growing among the pond pines, American sycamores, American hornbeam shrubs, and water oaks around the shoreline of the pond. Some of the pond pines, sycamores and willows exceeded heights of 10-15 ft. to form a canopy over some areas of the pond. Emergent and submergent hydrophytes of the pond included common cattail, *Typha latifolia* L.; spikerush, *Eleocharis tuberculosa* (Mich.) Roemer and Schultex; and two herbs, *Ludwigia alterniflora* L. and *Ludwigia palustris* (L.) Elliott. In addition to these hydrophytes, most of the shoreline below the surface of the water was lined with the exposed roots of the black willows growing around the periphery of the pond.

The vertebrates of the pond habitat included the common mosquitofish, *Gambusia affinis* Baird and Girard; the banded sunfish, *Enneacanthus obesus* Girard; adult and larval bull frogs, *Rana catesbeiana* Shaw; and adult and larval leopard frogs, *Rana pipiens* Schreber. On two occasions, a cottonmouth, *Agkistrodon piscivorus* Lacepede, was observed in and/or around the pond. Shoreline tracks of deer, raccoons, and various birds were frequently seen.

Sediments and the nature of the bottom of the pond varied in different areas. The slopes of the deeper portions of the pond were composed of brown mud; sand and organically-rich sediments were the main constituents of the bottoms of the deep and shallow areas. The odor of hydrogen sulfide and methane emitted from the organically-rich sediments as they anaerobically decomposed was quite strong during the summer months.

Stages of decomposition. The decomposition of a vertebrate carcass is a continuous, uninterrupted process; a process not easily separated into several distinct phases. For this reason, it is conceivable that decomposition stages might be organized into several different patterns or schemes. Studies of carrion decomposition in the terrestrial habitat vary in the schemes of arrangement of decomposition stages; the causes for differences rest in the habitat chosen for the study, climatic conditions, and largely the authors' interpretations.

Fuller (1934) utilized three stages of carrion decomposition (primary, secondary and tertiary) in her studies of insect succession on various types of invertebrate carrion. Howden's (1950) study of beetle succession on carrion included only two seres established on the basis of the presence or absence of maggots and their predators. Bornemissza (1957) was one of the first to base decomposition stages mainly on the condition of the carcass rather than on the presence or absence of certain carrion inhabitants. His scheme consisted of five separate phases in the decomposition of vertebrate carcasses. Four stages of decomposition based on the condition of decaying dog carcasses were noted by Reed (1958). The schemes of Payne (1965), Payne *et al* (1968b), and Wasti (1972) also were founded on the condition of the carcass; Payne observed five stages in pig carrion decomposition, while Wasti reported four stages in decaying common fowl carcasses.

The study by Payne and King (1972) of pig carrion decomposition in the aquatic habitat is the only recent study of arthropod succession on decomposing vertebrate carcasses in water. Six stages of carrion decomposition were utilized to describe the successional events associated with the condition of the decaying carcasses. These stages included: (1) submerged fresh, (2) early floating, (3) floating decay, (4) bloated deteriorating, (5) floating remains, and (6) sunken remains.

A study of the decomposition of totally submerged vertebrate carcasses would obviously not include any of the floating stages observed by Payne and King. Submerged decomposing sunfish carcasses did, however, exhibit certain stages of decomposition. These stages were, of course, dependent upon the activities of bacterial and invertebrate populations and the observer. Each stage was determined subjectively by the physical appearance of the carrion and its odors.

Submerged sunfish carrion exhibited four phases of decomposition: the fresh stage, the bloated stage, the deflation-decomposition stage, and the remains stage. In the initial stage, the carcasses appeared fresh externally; however, the decomposition process had begun internally through the activities of bacteria and, possibly, nematodes and protozoans present in the animal before its death. These populations of bacteria, protozoans and nematodes would have had to survive the freezing temperatures to which they were exposed while the carcass was in storage. This stage lasted less than 24 hours in each carcass observed.

By the second day of decomposition, the carcass had begun to inflate signaling the beginning of the bloated stage. The inflation first appeared in the abdominal area, and soon thereafter, appeared throughout the entire body. The most probable cause of bloating was the collection of gases produced as an end product of the anaerobic activities of the bacteria within the carcass.

In addition to the inflation of the carcass, scales on the surface of the body began disappearing, first in the abdominal area then over the entire body. The eyes, opaque at the beginning of the bloated stage, completely decomposed and disappeared by the termination of this stage.

With the deflation of the carcass, the third stage of decomposition began. The integument was usually broken in one or more places (head and/or gut areas) at the beginning of the stage; such openings allowed the entrance of water and, subsequently, invertebrates, fungi and bacteria. Oxygen in the water was also permitted to enter the carcass through these openings, thereby facilitating aerobic protein decomposition (Reed, 1958). Strong odors were emitted by the decaying carrion throughout the duration of this stage. As the stage progressed, the flesh became exceedingly soft, almost to the point of becoming a liquid.

The deflation-decomposition stage ended when all the decaying carrion flesh had disappeared leaving only the cartilage and bones of the skeletal remains. This event marked the beginning of the fourth and final stage of the decay process, the remains stage. The duration of this stage was less than 24 hours since the experiment was terminated when only the skeletal components remained.

MATERIALS AND METHODS

This study consisted of two portions: during 1973 it was concerned with the observation and recording of insect succession associated with submerged sunfish carrion, and during 1974 measurement of the rate of carrion disposal by arthropods in the aquatic situation was completed.

The study of succession consisted of ten consecutive replications conducted over a span of five months from mid-June to mid-November. The carrion utilized was naturally-occurring sunfish carcasses (Perciformes; Centrarchidae) obtained with rod and reel at the beginning of the study and frozen separately in aluminum foil until used. These carcasses were of uniform size, ranging in length from 9 to 10 cm. Each frozen carcass was allowed to thaw twenty minutes prior to being tacked to a wooden board, 50x35x1.65 cm., and submerged on the bottom of the small, six-year-old pond which served as the community habitat for the duration of the two studies. Four small carpet tacks were used to secure each carcass to the board. In an attempt to standardize the number of openings and wounds in the freshly-thawed carcass, these four tacks were driven through the same locations on each fish: the lower jaw, immediately anterior to the fused dorsal fins, and the bases of the anal and caudal fins.

To completely enclose the fish carcass, a cage was tacked to the board over the carrion. The cage, 22x22x20 cm., molded from 1/4-inch mesh hardware cloth allowed the large hemipterans (Hemiptera; Belostomidae) while preventing larger scavengers (fish, raccoons, turtles, etc.)

access to the carrion. The board, coated with several coats of non-reflective green marine paint, was then anchored to the bottom of the pond with the aid of two bricks.

Collections were made once every 24 hours within an hour after sunrise. The objective of these collections was to trap the insects within the cage enclosing the carrion. This was accomplished by placing a wooden box, 23x23x21 cm., over the cage to completely enclose it and its contents. A five-foot pole attached to the top of the box enabled me to force the box over the cage without entering the water thereby providing a minimal chance of disturbing or frightening any insects associated with the carrion by touching the water or approaching the carcass prior to making the collection. A 1-inch diameter hole in the top of the collection box allowed trapped air to escape as the box was quickly forced over the cage and its contents. Once the collection box was situated over the submerged cage, a cork was placed in the hole to prevent the escape of insects from the collection apparatus.

The collection procedure was further aided by the presence of hooks on the sides of the collection box to enable its secure attachment to the wooden board upon which the carcass and cage were also attached. This enabled me to lift the entire apparatus out of the water, shake it vigorously to dislodge as many attached insects as possible, and invert it over a plankton net to allow its contents to flow through the re-opened hole in the box's top and through the net into the attached glass vial. Putty smeared over the seams in the collection box and along its edges where it made contact with the wooden board minimized the loss of water and insects during this inversion procedure.

The box and cage were removed from the wooden board so that silt, debris and organisms remaining on the board and the inner surfaces of the collection box could be rinsed through the net with tap water carried in a bucket to the collection site. The net was also rinsed with the tap water to dislodge all material clinging to its inner surface. The exposed surfaces (including openings) of the carcass were examined for the presence of attached and/or burrowing insects; if any were located, they were removed with forceps and placed in the collection vial. The sample was appropriately labeled (date, replication number and collection number) and preserved in 10% formalin.

Before replacing the cage and reanchoring the apparatus to the bottom, weather conditions, air and water temperatures, and stage of carrion decomposition were recorded. Daily precipitation amounts and temperature ranges were obtained from the WNCT-TV weather station.

Each replicate of the study was conducted in a different location in the pond to eliminate any residual effects the presence of any earlier carrion community might exert upon another carcass placed in the same location. Control collections, similar in every respect to the collections previously described except for the absence of the carrion, were conducted 24 hours prior to the first collection with the carrion present and 24 hours after the skeletal remains were discarded. The objective of these control collections was to obtain a general survey of the insect populations in the vicinity of each respective replicate. Control collections without a carcass which might have been made in a separate apparatus at the same time as those which were made with the carcasses were omitted on the premise that disturbance of the water and the vicinity while making the first of the two collections would frighten many of the organisms located in the cage to be sampled last and the resultant data would have been biased.

After each replication, all equipment was thoroughly rinsed with water. The wooden board upon which the carcass was attached was rinsed with a dilute Clorox solution in addition to the water. It remained out of the water for at least four days before beginning the next replicate.

A modification of Anderson's (1959) sugar flotation technique for sorting bottom samples was employed to separate the preserved insects from the silt and debris which accumulated around the carcass between successive collections. Pask and Costa (1971) reported that Anderson's flotation method was not only adequate, but that it appeared quite reliable in sorting preserved benthic samples. According to these authors, benthic samples could be preserved without fear of reduced recovery. In fact, the study showed that recovery of certain insect groups, Chironomidae included, may be actually enhanced by preservation in 10% formalin. This enhancement is probably due to the fact that these insects while alive cling to debris which sinks in sugar solution; however, when preserved, these insects could not cling to the debris resulting in their floating to the surface of a sugar solution.

Lackey and May (1971) discovered that a dye-formalin mixture yielded better sorting results in the flotation technique than did a formalin solution without a dye. The dye effectively stains all organisms in the sample enabling one to easily recognize and locate them while sorting by the flotation technique. Undoubtedly, these results were obtained by administering the dye-formalin preservative while the organisms in the samples were alive. However, due to the volume of silt and debris which accumulated in the sample vial during the collections of this successional study, administration of the dye-formalin preservative in the field yielded poor staining reactions. Consequently, samples were transferred from the vial and the formalin preservative administered in the field to a finger bowl containing a red bengal dye and formalin solution (0.1 g red bengal/1. 10% formalin). The samples remained in this mixture for at least 72 hours before being sorted according to the technique described by Lackey and May (1971). Approximately 95% of the organisms sorted from the samples were stained; to insure that all organisms in the samples had been removed, additional flotations of the debris and silt remaining from a previous flotation were conducted until no further organisms could be located.

The organisms sorted from the samples were rinsed thoroughly and preserved in 10% formalin to be later taxonomically classified according to Pennak (1953). The total numbers of insects associated with each stage of carrion decomposition were statistically analyzed utilizing an analysis of variance (complete random design) to determine whether statistically significant differences in insect numbers did in fact exist among the stages of decomposition (Steel and Torrie, 1960).

In mid-July, 1974, ten sunfish carcasses of uniform size, which had been frozen separately in aluminum foil since the beginning of the successional study, were allowed to thaw for twenty minutes before being placed into separate cages, 22x10x10 cm., molded from 1/4-inch mesh hardware cloth. Five of these cages were completely enclosed in a fine-mesh netting to prevent any arthropods from attacking the submerged carrion; the remaining cages were not enclosed in the netting allowing arthropods access to the carrion.

After the cages and the carcasses had been anchored to the bottom of the pond, daily observations of the decomposition processes of each carcass were recorded to measure the rate of carrion disposal by aquatic-arthropods. Utilizing the Student's t-test (analysis of uncorrelated group design), the results were statistically analyzed to determine whether a statistically significant difference existed between the two groups (Schefler, 1969).

RESULTS AND DISCUSSION

Three major factors were studied to determine their effects on the process of decomposition exhibited by submerged sunfish carrion. These factors included: (1) moisture in the habitat, (2) habitat temperature, and (3) carrion removal by arthropods. In conjunction with the third factor, the changes in the number and kind of insects associated with the decaying matter were studied.

Habitat moisture. The decomposition of submerged sunfish carrion was influenced by the moisture of the aquatic habitat; its influence on the process was exerted through at least two avenues. Soon after submerging the carrion in the water, the flesh became soft and moisture laden. It became more soggy, even to the point of becoming a liquid, during the deflation-decomposition stage. It is conceivable that some of the flesh could have liquefied during this stage of decomposition; however, this assumption was impossible to establish as fact in an aquatic situation.

Comparison with data provided from other studies further illucidates the effect of habitat moisture on the decay process. Walker (1957) reported that fish carrion decomposed differently in various terrestrial habitats. The rate of evaporation proved to be the most probable factor of greatest importance in determining the course of decomposition. Carrion placed in damp to mesic situations became putrid and soft before eventually being reduced to foul-smelling liquids. Carcasses in drier habitats (higher rate of evaporation) also became putrid and soft but eventually dried and hardened with pieces of the carrion remaining intact at the end of the decomposition process. Carrion placed in the driest of the four habitats compared (highest rate of evaporation) began drying immediately resulting in portions of the fish carcasses becoming hard and leathery and remaining intact even to the end of the decay process.

In my study of submerged sunfish carrion, no moisture was lost through evaporation. The carcasses remained submerged and anchored to the bottom of the pond throughout the course of decomposition. This accounted for the absence of any stages or phases of drying of the carrion flesh during the decay process. It also facilitated the rapid disposal of the carrion.

The work of Payne and King (1972) not only demonstrated the importance of moisture as a factor in the course of decay of carrion in the aquatic habitat, it also revealed its importance in influencing the succession of organisms inhabiting the carrion microhabitat. For example, maggots inhabiting the floating carrion were forced to migrate from the carcasses when the floating remains began sinking as a result of deflation of bloated carrion flesh. Once submerged, the terrestrial insects (adult hymenopterans, adult dipterans, etc.) were excluded from inhabiting the carrion as they did when surfaces of the carcasses were exposed during the bloated phases.

Such terrestrial inhabitants of carrion were completely excluded from carrion totally submerged throughout its entire process of decay; only aquatic and/or semiaquatic organisms were able to inhabit submerged carrion. Consequently, water not only affected the observable decomposition process of submerged sunfish carrion, it also, by acting as a physiological barrier to forms not adapted to an aquatic existence, influenced the kind of organisms which could effectively inhabit the submerged carrion.

Habitat temperature. Only the decomposition stages of the bloated condition and the deflation-decomposition state varied with habitat temperature; the fresh and remains stages lasted less than 24 hours in all carcasses observed. Figure 2 represents the effects of water temperature on the duration of the bloated stage and the deflation-decomposition stage. The length of time was measured in terms of the average number of days carrion remained in each of the two stages when subjected to the temperature ranges indicated. As symbolized, an inverse relationship existed between habitat temperatures and the length of time the submerged sunfish carrion remained in the bloated stage and in the deflation-decomposition stage; the lower the habitat temperature, the longer the duration of the two stages.

These effects of temperature on the decay process were probably the result of a combination of at least two major factors: bacterial activity and arthropod activity. Hoar (1966) stated that temperature changes often produce prompt, direct and proportional alterations in the rate of an animal's physiological processes. Such alterations, exhibited within a range of usually not more than 10^{o}-20^{o}C, will be quite erratic, or not occur at all, if the temperature changes are outside of this range of temperature tolerance. The physiology of bacteria is also thusly affected by temperature changes (Burdon and Williams, 1968).

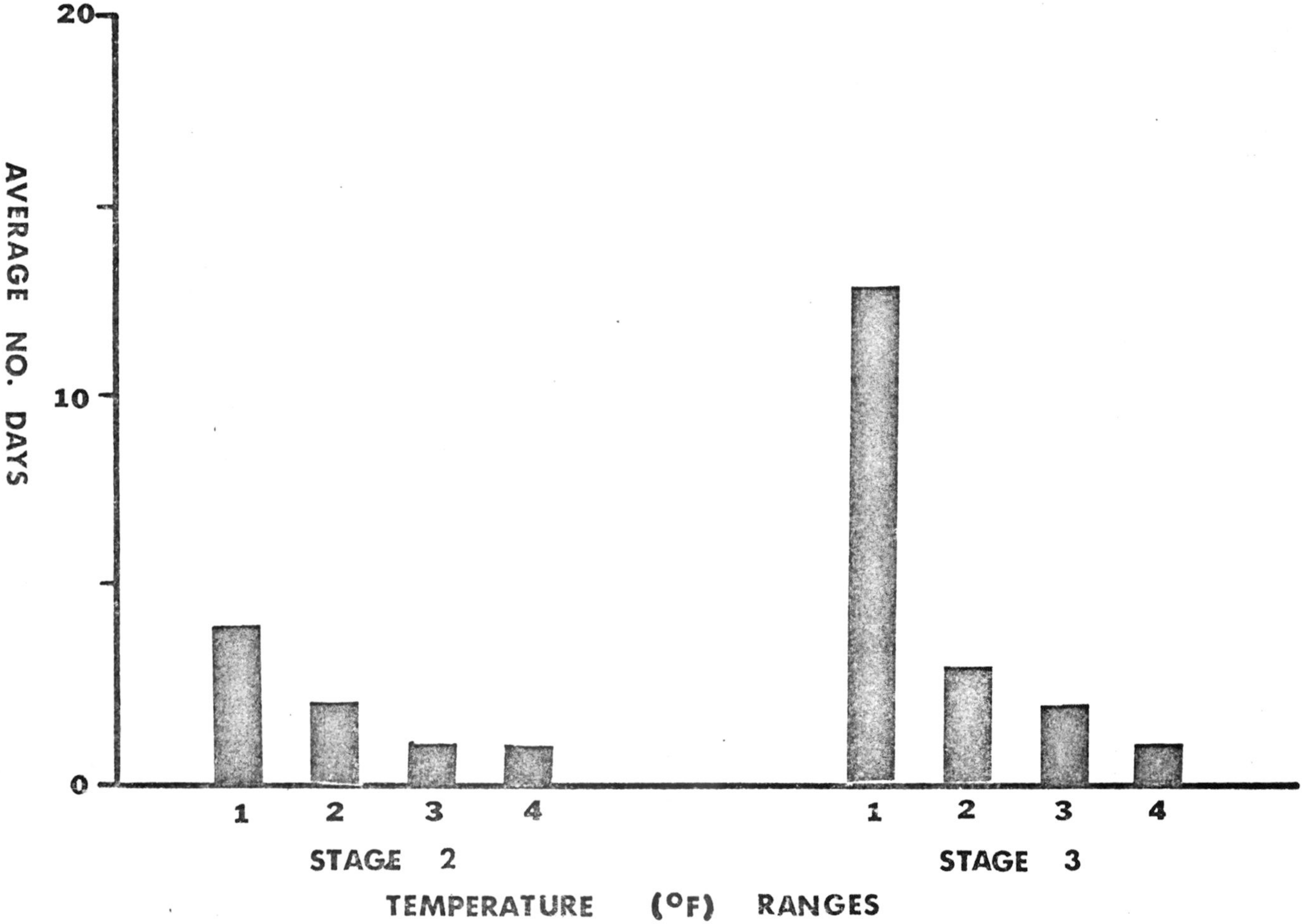

Figure 2. The effect of water temperature (°F) on average length of bloated and deflation-decomposition stages of decomposition. Temperature ranges: 45-60°F (1); 70-72°F (2); 73-77°F (3); and 78-79°F (4).

The feeding activities of the bacterial and arthropod populations inhabiting the submerged sunfish carrion eventually resulted in the complete disposal of the carrion. The physiological capacities of the populations involved were affected by the habitat temperature; consequently, the rate of carrion disposal by inhabitant bacterial and arthropod populations was influenced by the temperature of the aquatic habitat. Reed (1958) reported that the temperatures of the microhabitat in the vicinity of a decaying carcass may differ considerably from the temperatures of the general habitat surrounding it. While the lack of effective instrumentation for measuring and recording any variations of temperature between the microhabitat and the general habitat prevented the confirmation or rejection of Reed's statement with respect to submerged sunfish carrion, it was believed conceivable that microhabitat temperature ranges differed very little, if at all, from the general aquatic habitat temperature ranges. This lack of variation could be attributed to the following: (1) the high specific heat of water tempers drastic and sudden temperature changes, (2) Reed's statement was based upon observations of decomposing dog carcasses in terrestrial situations, and (3) the carrion quantity utilized in this study was small with a large surface-to-volume ratio allowing rapid heat exchange. It is conceivable that microhabitat temperatures of decomposing carcasses in terrestrial habitats are not comparable to those of aquatic habitats.

Carrion disposal by arthropods. The rate of disposal of submerged sunfish carrion by arthropods was measured by comparing the duration of the four stages of decomposition and the duration of the entire decomposition process in carrion open to arthropods to that of carrion not open to arthropods. Figure 3 represents data obtained in this experiment; these data are given in Table I. The fresh and remains stages of the decay process were excluded in the graphic analysis since each of the two stages lasted less than 24 hours in each carcass observed.

While average values reveal no differences between carrion open to arthropods and carrion not open to arthropods in the fresh and remains stages, the graph does indicate the differences of 2.2 days, 9.2 days and 11.2 days which existed in the duration of the bloated stage, the deflation-decomposition stage, and the entire decomposition process, respectively. In analyzing the differences between carrion open to arthropods and carrion not open to arthropods, calculated t-values of 10, 38, and 40.7 for the bloated stage, the deflation-decomposition stage, and the entire decomposition process, respectively, were greater than the critical t-value (one-tailed upper t-test) of 1.860 at the 5% level of significance. The null hypothesis was rejected. Based upon the assumption that the observed data were random observations from normal populations, it was concluded that the durations of the bloated state, the deflation-decomposition condition, and the entire decay process were significantly greater in arthropod-free carrion than in carrion open to arthropods.

The disposal of the sunfish carrion from which the arthropods were excluded was evidently accomplished through the activities of bacteria, fungi, protozoa, nematodes, etc., some of which were probably present in the animal before its death. It is evident, however, that arthropod

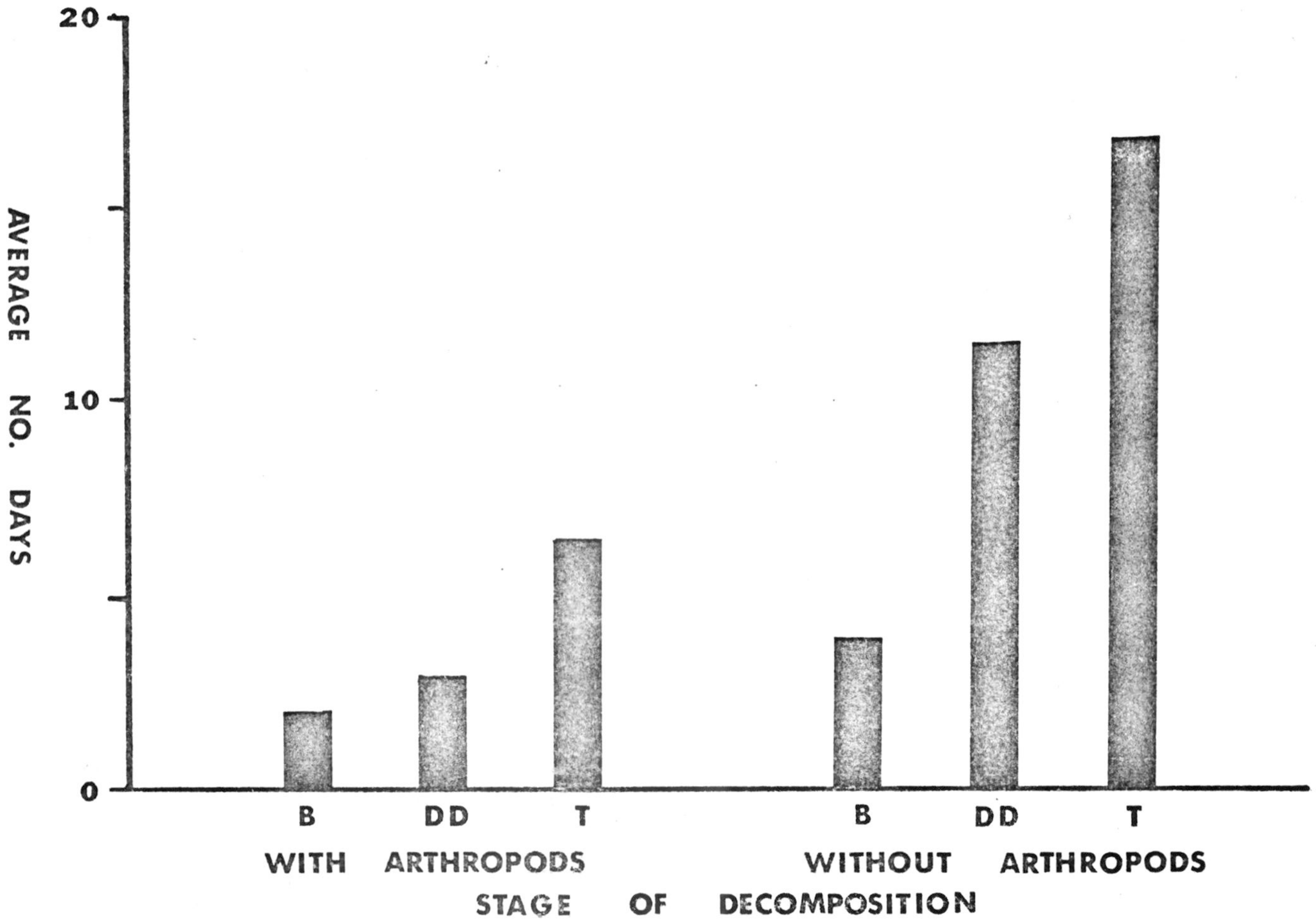

Figure 3. Rate of carrion disposal by arthropods. Key: bloated stage (B); deflation-decomposition stage (DD); total decomposition (T).

Table I. Rate of carrion disposal with and without arthropods. The number of days each carcass remained in each stage of decomposition as well as the length of time for total decomposition are included with means of each.

	Number of Days											
Stage	Open to Arthropods						Not Open to Arthropods					
	1	2	3	4	5	mean	1	2	3	4	5	mean
Fresh	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1
Bloated	2	2	1	2	1	1.6	4	3	4	4	4	3.8
Deflation-decomposition	3	2	2	2	3	2.4	12	12	11	12	11	11.6
Remains	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1
Total Decomposition	7	6	5	6	6	6	18	17	18	18	17	17.4

activities did significantly hasten the decomposition process of submerged sunfish carrion. It is assumed that the locomotor activities (crawling, tunneling, burrowing, etc.) combined with the feeding activities of inhabitant arthropods caused the observed hastening of the decomposition process.

Similar observations and deductions were made by Fuller (1934) in her study of various vertebrate carcasses, Payne (1965) in his study of pig carrion, and Wasti (1972) in his study of the decomposition of common fowl carcasses. Each of these authors stated that arthropods and/or insects inhabiting decomposing carrion hastened the decay process not only by actively feeding upon the decaying flesh, but also by disseminating inhabitant bacterial populations through their locomotor activities. Any break in the integument of the carcass caused by such activities also facilitated the entrance of oxygen and additional saprophagous organisms which further aided the dissemination of bacterial populations.

Insect inhabitants. The insects found associated with the submerged sunfish carrion represented five orders, eight families, and 19 genera. The insects and the total number of each found associated with the carrion are recorded in Table II. Examination of these data reveals that, of the total specimens collected during the course of the study, 95.7% were members of the nine genera of the dipteran Family Chironomidae, 0.8% were members of two genera of the Family Libellulidae (Order Odonata), 3.1% were members of the three genera of the Family Baetidae (Order Ephemeroptera), and the remaining 0.4% included a diverse group encompassing five genera and five families of four different orders.

Table II. Systematic list of genera, food habits and total numbers.

Genus	Food Habit*	Number of Individuals
Class Insecta		
Order Diptera		
Family Chironomidae		
Calopsectra Kieffer	O	134
Chironomus Meigen	O	241
Cryptochironomus Kieffer	P	264
Metriocnemus van der Wulp	U	1
Paratendipes Kieffer	O	507
Pentaneura Philippi	P	122
Prodiamesa Kieffer	U	6
Pseudochironomus Malloch	O	69
Tanypus Meigen	P	4
Family Culicidae		
Culex L.	O	1
Family Heleidae		
Culicoides Latreille	O	1
Order Ephemeroptera		
Family Baetidae		
Ameletus Eaton	N	3
Caenis Stephens	N	40
Centroptilum Eaton	N	1

*Food Habits: P-predaceous, N-necrophagous, O-omnivorous, U-unknown

Table II cont'd.

Genus	Food Habits*	Number of Individuals
Order Odonata		
Family Coenagrionidae		
Amphiagrion Salys	P	1
Family Libellulidae		
Libellula L.	P	11
Sympetrum Newman	P	1
Order Coleoptera		
Family Haliplidae		
Haliplus Latreille	O	1
Order Collembola		
Family Isotomidae		
Isotomus Bourlet	N	1

*Food Habits: P-predaceous, N-necrophagous, O-omnivorous, U-unknown

Table III is a record of the total number of insects, regardless of type, found associated with the submerged sunfish carrion while it was in each of the decomposition stages indicated. The two survey-control collections are also included in the table to indicate the changes which occurred when the carrion microhabitat was introduced into the surrounding general habitat. It should also be noted that the fresh stage of the decomposition process of the submerged carrion was omitted. While it was an obvious stage of the decomposition process, the sunfish carrion remained in it for only a very short period of time (less than 24 hours); consequently, the fresh stage has been excluded from any analysis of insect succession on submerged sunfish carrion.

Table III includes the ten replicates conducted during the successional study; these data were subjected to analysis of variance (complete random design) to determine whether statistically significant differences existed among the groups (two survey-control collections and three stages of decomposition). It is evident upon examination of these data that the number of insects increased from the start of the study in mid-June until its near-completion in mid-November when a sharp decrease in the number of insects occurred with the arrival of winter temperatures. For this reason, the insect numbers were converted to percentages of the total collected during each of the ten replicates and these are given in Table IV.

After transforming the percentage values to arcsin values, the analysis of variance was utilized to yield an F-value of 3.22 which was significant beyond the 5% level of significance (Schefler, 1969).

Table III. Numbers of insects associated with stages of decomposition. The first survey-control collection (FC) and the final survey-control collection (LC) are indicated with the bloated (B), deflation-decomposition (DD) and remains (R) stages of decomposition.

Replicate No.	Individuals per Stage of Decomposition				
	FC	B	DD	R	LC
1	5	26	2	4	8
2	8	3	13	8	7
3	14	15	9	4	10
4	12	22	16	10	10
5	19	32	22	12	18
6	24	15	55	16	24
7	36	42	44	51	30
8	35	39	73	35	32
9	35	33	96	29	31
10	38	144	132	5	6

Table IV. Percentage of total insects associated with stages of decomposition. The first survey-control collection (FC) and final survey-control collection (LC) are indicated with the bloated (B), deflation-decomposition (DD) and remains (R) stages.

Replicate No.	Percentage per Stage of Decomposition				
	FC	B	DD	R	LC
1	11.1%	57.8%	4.4%	8.9%	17.8%
2	20.5%	7.8%	33.3%	20.5%	17.9%
3	26.9%	28.9%	17.3%	7.7%	19.2%
4	17.1%	31.4%	22.9%	14.3%	14.3%
5	18.4%	31.1%	21.4%	11.6%	17.5%
6	17.9%	11.2%	41.1%	11.9%	17.9%
7	17.7%	20.7%	21.7%	25.1%	14.8%
8	16.4%	18.2%	34.1%	16.4%	14.9%
9	15.6%	14.7%	42.9%	13.0%	13.8%
10	11.7%	44.3%	40.6%	1.5%	1.9%

Table V is an analysis of variance table summarizing these calculations. Assuming that the data were random observations from normal populations of statistics, the null hypothesis was rejected at the 5% level of significance, and it was concluded that differences did exist among the groups with respect to the number of insects found associated with the submerged sunfish carrion at various stages of decomposition and prior to and immediately after the carrion was present in the general habitat. Duncan's New Multiple Range Procedure was utilized to determine which groups were significantly different (Steel and Torrie, 1960). The results are displayed in Table VI.

Figure 4 shows the total number of insects associated with the carrion during the three stages of decomposition, as well as the number of insects associated with the general habitat prior to the introduction of the carrion and 24 hours after the removal of the skeletal remains. As demonstrated, the total number of insects found during each stage increased from the first survey-control collection prior to the introduction of the carrion into the habitat through the bloated stage until a peak appeared during the stage of deflation-decomposition. A sharp decline in the number of insects occurred as the carrion entered the remains stage and continued to the point when only bony structures remained. No significant change occurred following the removal of the remains.

As is obvious, the number of insects associated with the submerged sunfish carrion changed as the decomposition process progressed; the greatest number of insects inhabiting the microhabitat appeared while the carrion was bloated and in the deflation-decomposition condition.

Table V. Analysis of variance of the changes in numbers of insects associated with stages of decomposition.

Source	df	Sum of Squares	Mean Square	F-test
Among groups	4	1017.5	254.3	3.22*
Within groups	44	3476.1	79.0	
Total	48	4493.6		

*significant at the 5% level of significance

Table VI. Duncan's New Multiple Range Procedure.

Stage of Decomposition	Average percentage of total insects associated with each stage*
First Control Collection	17.33 bc
Bloated	26.61 ab
Deflation-decomposition	27.97 a
Remains	13.09 c
Final Control Collection	15.00 bc

*any two means followed by the same small case letter (one or more) are not significantly different at the 5% level by Duncan's New Multiple Range Procedure.

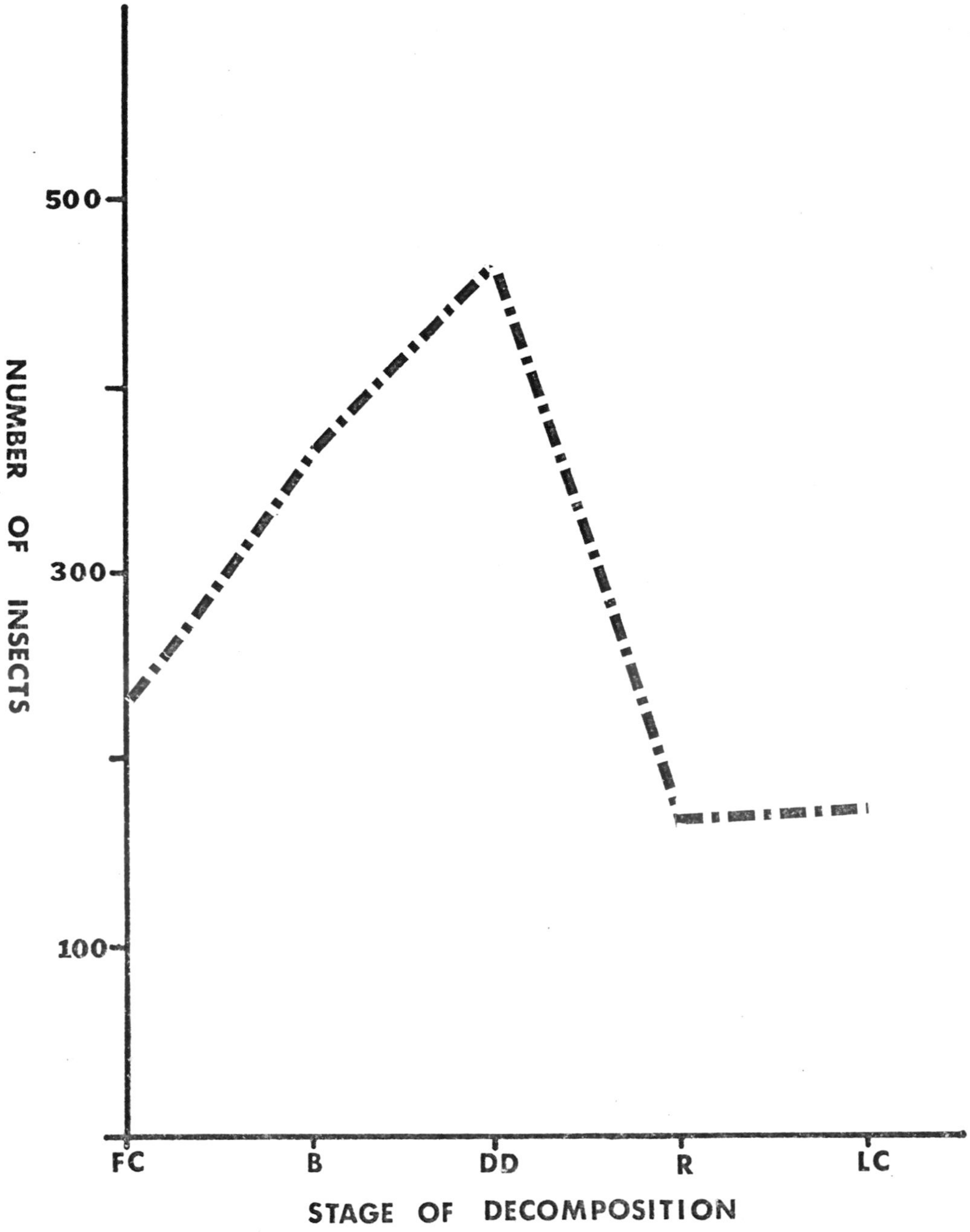

Figure 4. Changes in number of total insects with progression of decay of submerged sunfish carrion. Key: first survey-control collection (FC); bloated stage (B); deflation-decomposition (DD); remains stage (R); and final survey-control collection (LC).

During both of these stages, decaying flesh was removed from the carcasses, especially during the latter stage when the contents of the abdominal and cranial cavities, followed by the remaining flesh, were completely removed. The putrid odor known to be characteristic of decaying flesh became evident during the bloated stage and became more pronounced during the deflation-decomposition stage. Perhaps the odors and/or chemicals associated with the release of these odors acted as attractants for many of the insects invading the microhabitat. Greater numbers could have appeared in the microhabitat due to greater numbers of protozoa, bacteria, and various invertebrates entering the microhabitat; these organisms probably served as food for many of the insects. These assumptions would, at least, partially explain the evident increase in the number of insects observed during these two stages. Such assumptions could also explain the sudden decrease in the number of insects as the carrion entered the remains stage.

In carrion microcommunities, organisms have been observed parasitizing or preying upon members of the microcommunity; food webs, just as in major communities, have been established (Fuller, 1934; Reed, 1958; Payne, 1965; and Payne and King, 1972). Consequently, the increase in the number of insects observed during the bloated and the deflation-decomposition stages could have been the result of an increase in the diversity of the inhabitant plant and animal populations. With the removal of all of the carrion flesh, a food source was removed from the microenvironment resulting in a corresponding decrease in the number of organisms which fed upon the decaying material.

Decreases in the insect populations which depended upon the scavengers as a food source followed; the entire food web and, subsequently, the microcommunity were affected.

An attempt to clarify the changes in the types of insects associated with the decomposing submerged carrion involved consideration of the feeding habits of the insects collected during the study. The organisms fell into five general categories with respect to feeding habits: (1) those insects only scavenging the carrion flesh (necrophagous organisms), (2) those insects which, in addition to feeding upon the carrion, preyed upon other inhabitants of the microhabitat (omnivorous organisms), (3) those insects which were predators only, (4) those insects which utilized the carcasses as a source of shelter only, and (5) those insects which occurred only by chance (accidental organisms).

All of the insects found associated with the submerged sunfish carrion were immature forms. In fact, samples in and on the substrate of the pond, among the masses of submerged plants and black willow root systems, and at various depths throughout the pond taken prior to the start of the study and immediately after its completion also yielded only immature stages. Very little has been reported concerning the feeding habits of many of the immature insects collected in the study; conflicting reports of the feeding habits of others exist. This, of course, rendered an analysis of the microcommunity from the aspect of feeding habits and the existent food web quite difficult; however, an attempt to do so was made by first summarizing the reported feeding habits of the collected insects. The summary is included in Table II.

The midge larvae of the Subfamily Chironominae, with the exception of the genus Cryptochironomus, were reported to be microphagous in their habits (Pennak, 1953; Walshe, 1951a; and Wirth and Stone, 1968); however, Borror and DeLong (1971) reported the chironomids to be strictly scavengers with few exceptions.

The larvae of this subfamily construct flimsy tubes of organic detritus, algae, or silt and small grains of sand (Pennak, 1953). Many of the mud-dwelling forms spin concave nets of salivary secretions across the lumina of these tubes; plankton and detritus are trapped in the net as a current of water created by undulations of the body of the inhabitant larvae passes through the tubes. The net and its contents are eaten periodically with a new net being spun after the consumption of the previous net (Walshe, 1951 a and b).

Minute particles of decaying flesh could have conceivably been dislodged from the carrion by scavengers, bacterial activities, or wave action. The dislodged particles could have been trapped in the chironomid nets and, subsequently, consumed; these larvae could act as scavengers. They also could be considered predaceous in that they probably fed upon the minute invertebrates which also were associated with the carrion. For these reasons, the larvae of the genera of the Subfamily Chironominae, with the exception of Cryptochironomus, were listed as omnivores.

While the feeding habits of Prodiamesa and Metriocnemus were unknown, Pentaneura and Tanypus of the Subfamily Peloplinae and the genus Cryptochironomus of the Subfamily Chironominae were reported as predaceous on protozoa and other midge larvae (Pennak, 1953; and Pritchard and Smith, 1968).

Mayfly nymphs (Ephemeroptera) are reported to occupy an important position in the freshwater community. They transform plant material into animal protein as primary consumers (Day, 1968). These nymphs have also been observed as scavengers (Borror and DeLong, 1971). Carrion was the primary source of nutrition, rather than plants in this micro-community, hence mayfly nymphs were listed as necrophagous organisms.

Figure 5 represents the changes which occurred in each of the groups of insects with similar feeding habits (scavengers, predators and omnivores) associated with the submerged sunfish carrion during the various stages of decomposition. The omnivores and predators reached their greatest respective numbers during the deflation-decomposition stage. The peak for scavengers (not significantly greater) was reached during the bloated stage. The analysis of changes in types of insects associated with the carrion as it decayed yielded no significant pattern. Changes may have occurred, but were obscured by ignorance of feeding habits but such changes may also have occurred too rapidly to be detected by daily collections.

While the analysis failed to show any significant changes in types of insects associated with the decaying carrion, collections in the pond habitat prior to the start of the study and immediately after its termination yielded three genera which were never found associated with the carrion. These included: (1) several specimens of mayfly nymphs, _Heptagenia_ Walsh (Family Heptageniidae), (2) a few specimens of caddisfly larvae, _Heliopsyche_ Hagen, and (3) a few specimens of an instar of the creeping water bug, _Pelocoris_ Stal (Hemiptera; Naucoridae). This

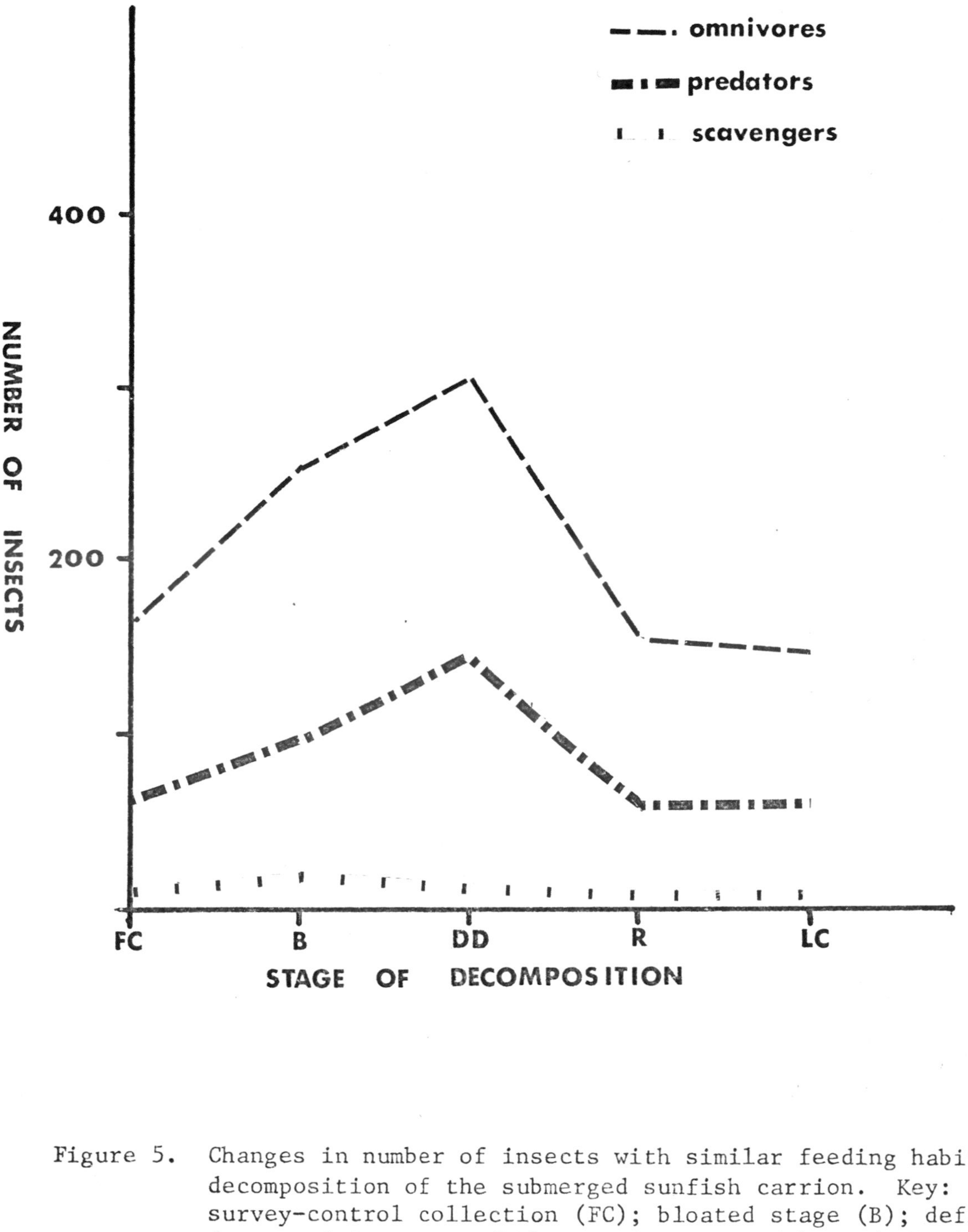

Figure 5. Changes in number of insects with similar feeding habits with decomposition of the submerged sunfish carrion. Key: first survey-control collection (FC); bloated stage (B); deflation-decomposition stage (DD); remains stage (R); and final survey-control collection (LC).

indicated that some insects did not become associated with the submerged sunfish carrion microcommunity although carcasses were placed in the areas in which these insects lived. Apparently, most insect genera were attracted to the sunfish carrion, while a few were not.

The submerged sunfish carrion evidently began decomposing as the flesh thawed. Bacteria, protozoa and nematodes present in the fish before death may have initiated the process. As decomposition progressed into the bloated stage, omnivores, scavengers and predators invaded the microhabitat. In comparison to the first survey-control collections taken prior to the introduction of the carrion, an average of 14.5 more insects were present in the microhabitat while the carrion remained bloated; however, this increase was not significantly different. These insects and other inhabitant arthropods evidently accelerated the decomposition process by feeding upon the decaying flesh and by disseminating inhabitant bacterial populations.

As the carrion entered the stage of deflation-decomposition, putrid odors became increasingly stronger and the contents of the cranial and abdominal cavities were exposed as holes in the integument were created. Total insects inhabiting the microcommunity increased to an average of 46.2, a value which was significantly greater ($P>0.05$) than the average number of insects in the remains stage and in the two survey-control collections. Species diversity remained relatively unchanged.

During this stage of deflation-decomposition, the carrion flesh was completely removed leaving only the skeletal remains. The number of insects associated with the microcommunity decreased sharply to a level not significantly different from the level found inhabiting the area 24 hours after the removal of all skeletal remains.

Although a distinct change in the kind of insects associated with the decaying submerged sunfish carrion was not demonstrated, it is inferred that succession of insect populations did occur as the decomposition process progressed. The reasons for this inference include: (1) a statistically significant change did occur in the number of insects associated with the carrion as it decayed, (2) three insect genera never found associated with the carrion were collected in areas of the pond where carcasses were introduced, (3) as exhibited by the data in Table VII, certain insect genera (Prodiamesa and Libellula) found associated with the carrion were never or, at least, seldomly collected in the survey-control collections indicating that members of these genera were attracted to the carrion, and (4) the frequency of insects was generally low.

The available data simply does not warrant a decision as to the occurrence of insect succession on submerged sunfish carrion. It will probably not be clearly demonstrated until several advances are made in carrion research. More comprehensive taxonomic knowledge of the species of immature aquatic insects of the area and their feeding habits must be gained. The dynamic and complex relationships which exist between the microhabitat and the surrounding general habitat must be understood. The various arthropods found associated with the submerged carrion must also be studied to determine their roles in the microcommunity; insects may only represent a community in the succession of arthropods on submerged carrion. Finally, the role of bacteria and fungi of the pond and of the animal before and after death must be

Table VII. Number of insects of each genus associated with stages of decomposition.

Calopsectra	20	44	36	14	20
Chironomus	31	64	85	31	30
Cryptochironomus	38	61	98	32	35
Metriocnemus	1	0	0	0	0
Paratendipes	95	120	157	71	64
Pentaneura	20	32	41	13	16
Prodiamesa	1	1	4	0	0
Pseudochironomus	9	24	24	6	6
Tanypus	0	1	1	1	1
Culex	0	0	0	0	1
Culicoides	0	1	0	0	0
Ameletus	1	1	1	0	0
Caenis	7	15	12	3	3
Centroptilum	1	0	0	0	0
Amphiagrion	1	0	0	0	0
Libellula	0	6	3	2	0
Sympetrum	0	1	0	0	0
Haliplus	1	0	0	0	0
Isotomus	0	0	0	1	0

*FC--first survey-control collection, B--bloated, DD-deflation-decomposition, R--remains, LC--last survey-control collection.

determined. These factors, when understood, could lead to the distinct demonstration of insect succession on submerged sunfish carrion.

LITERATURE CITED

Allee, W. C., A. E. Emerson, O. Park, T. Park and K. P. Schmidt. 1949. Principles of animal ecology. W. B. Saunders Co., Philadelphia. 837 pp.

Anderson, R. O. 1959. A modified technique for sorting bottom samples. Limnol. Oceanog. 42(2):223-225.

Bornemissza, G. F. 1957. An analysis of arthropod succession in carrion and the effect of its decomposition on the soil fauna. Australian J. Zool. 5:1-12.

Borror, Donald J. and D. M. DeLong. 1971. An introduction to the study of insects. Holt, Rinehart and Winston, New York. 812 pp.

Burdon, Kenneth L. and R. P. Williams. 1968. Microbiology. The Macmillan Co., London. 818 pp.

Chapman, R. F. and J. H. Sankey. 1955. The larger invertebrate fauna of three rabbit carcasses. J. Animal Ecol. 24:395-402.

Day, Willis C. 1968. Ephemeroptera. Pages 79-105 in Robert L. Usinger, ed. Aquatic Insects of California. University of California Press, Berkeley. 508 pp.

Deonier, C. C. 1940. Carcass temperatures and their relation to winter blowfly population and activity in the southwest. J. Econ. Entomol. 33:166-170.

Downes, J. R. 1973. Lepidoptera feeding at puddle-margins, dung and carrion. J. Lepid. Soc. 27:89-99.

Elton, C. S. 1949. Population interspersion: an essay on animal community patterns. J. Ecol. 37:1-23.

Elton, C. S. 1966. The pattern of animal communities. John Wiley and Sons, Inc., London. 432 pp.

Fuller, M. E. 1934. The insect inhabitants of carrion, a study in animal ecology. Australian Coun. Sci. Indust. Res. Bull. 82:5-62.

Hoar, William S. 1966. General and comparative physiology. Prentice Hall Inc., Englewood Cliffs, New Jersey. 815 pp.

Hoffman, Richard L. and J. A. Payne. 1969. Diplopods as carnivores. Ecol. 50:1096-1098.

Howden, A. T. 1950. The succession of beetles on carrion. M. S. Thesis, North Carolina State University, Raleigh. 83 pp.

Illingworth, J. F. 1926. Insects attracted to carrion in southern California. Proc. Hawaii Entomol. Soc. 6:201-231.

Kaufman, R. R. 1937. Investigations on beetles associated with carrion in Pannal Ash, near Harrogate. Entomol. Mo. Mag. 73:78-81, 227-233, 268-272.

Kishigami, Shigejiro. 1926. Influence of larvae of flies on post-mortem degeneration and its nature. Jap. Med. World. 6(8):199-207, 6(9):232-236. (Abstr.)

Lackey, R. T. and B. E. May. 1971. Use of sugar flotation and dye to sort benthic samples. Trans. Amer. Fish. Soc. 100:794-797.

Linam, Jay H. and Don M. Rees. 1956/1957. Flies attracted to animal carcasses in Carey and vicinity, Elaine County, Idaho. Proc. Utah Acad. Arts Letters. 34:27-29.

Pask, W. M. and R. Costa. 1971. Efficiency of sucrose flotation in recovering insect larvae from benthic stream samples. Can. Entomol. 103:1649-1652.

Payne, Jerry A. 1965. A summer carrion study of the baby pig Sus scrofa Linnaeus. Ecol. 46:592-602.

Payne, Jerry A. and E. W. King. 1966. Lepidoptera associated with pig carrion. J. Lepid. Soc. 23(3):191-195.

Payne, Jerry A. and E. W. King. 1970. Coleoptera associated with pig carrion. Entomol. Mo. Mag. 105:224-232.

Payne, Jerry A. and E. W. King. 1972. Insect succession and decomposition on pig carcasses in water. J. Ga. Entomol. Soc. 7(3):153-162.

Payne, Jerry A., E. W. King and G. Beinhart. 1968b. Arthropod succession and decomposition of buried pigs. Nature. 291:1180-1181.

Payne, Jerry A. and W. R. M. Mason. 1971. Hymenoptera associated with pig carrion. Proc. Entomol. Soc. Wash. 73(2):132-141.

Payne, Jerry A., F. W. Meed and E. W. King. 1968a. Hemiptera associated with pig carrion. Ann. Entomol. Soc. Amer. 61(3):565-567.

Pennak, Robert W. 1953. Fresh-water invertebrates of the United States. Ronald Press Co., New York. 769 pp.

Pritchard, A. Earl and R. F. Smith. 1968. Odonata. Pages 106-153 in Robert L. Usinger, ed. Aquatic insects of California. University of California Press, Berkeley. 508 pp.

Reed, H. B., Jr. 1958. A study of dog carcass communities in Tennessee with special reference to the insects. Amer. Midl. Nat. 59:213-245.

Schefler, William C. 1969. Statistics for the biological sciences. Addison-Wesley Publishing Co., Reading, Massachusetts. 231 pp.

Steel, R. G. D. and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill Book Co., Inc., New York. 481 pp.

Walker, Thomas J., Jr. 1957. Ecological studies of the arthropods associated with certain decaying materials in four habitats. Ecol. 38(2):262-276.

Walshe, Barbara M. 1951a. The feeding habits of certain chironomid larvae (subfamily Tendipedinae). Proc. Zool. Soc. Lond. 121:63-79.

Walshe, Barbara M. 1951b. The function of haemoglobin in relation to filter-feeding chironomid larvae. J. Exp. Biol. 28(1):51-61.

Wasti, S. S. 1972. A study of the carrion of the common fowl, *Gallus domesticus*, in relation to arthropod succession. J. Ga. Entomol. Soc. 7(4):221-229.

Wirth, Willis W. and Alan Stone. 1968. Aquatic Diptera. Pages 372-482 *in* Robert L. Usinger, ed. Aquatic insects of California. University of California Press, Berkeley. 508 pp.