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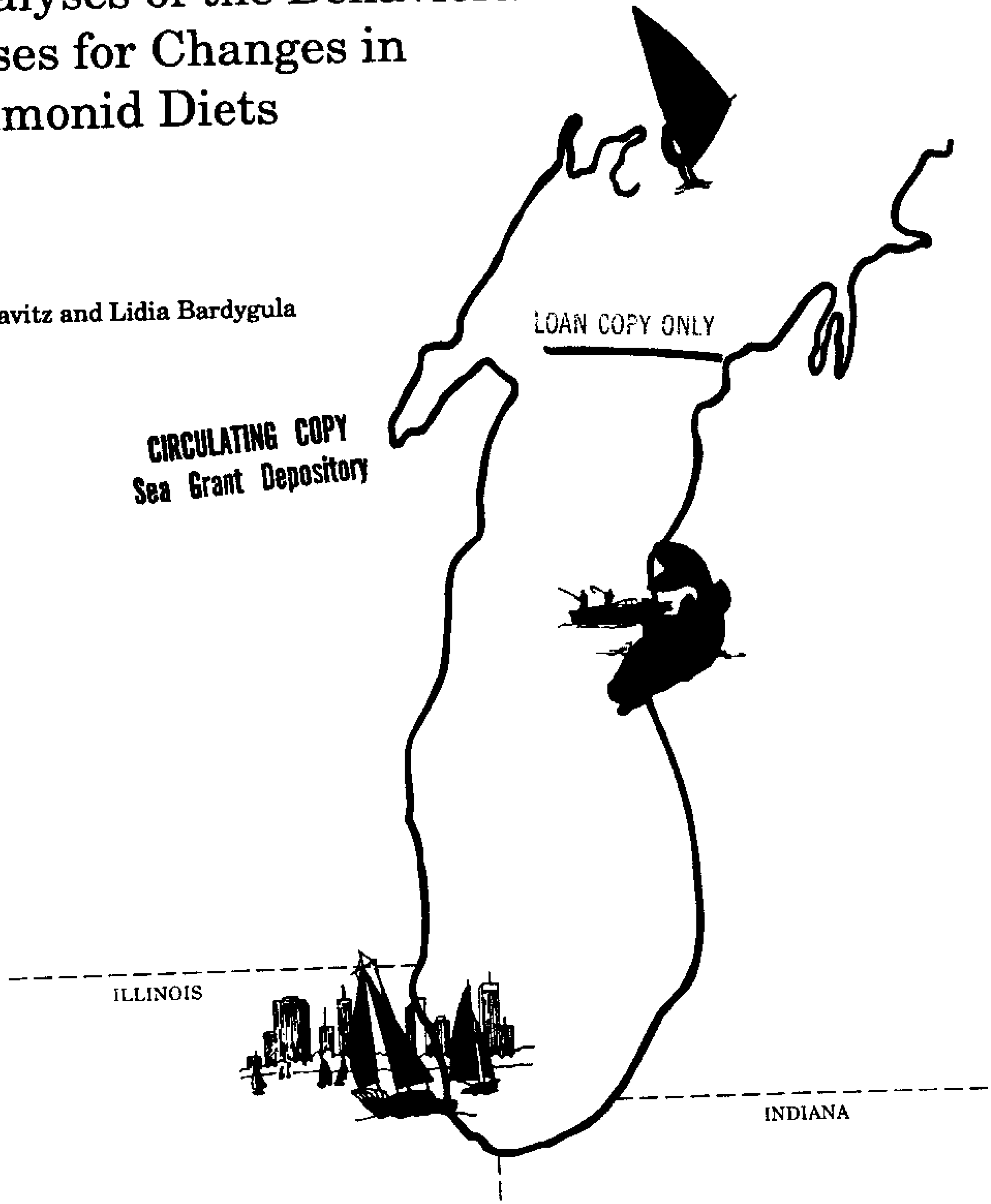

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ANALYSES OF THE BEHAVIORAL BASES FOR CHANGES IN SALMONID DIETS

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ABSTRACT

The predator-prey behavioral interactions between three salmonid species and their prey species were examined under laboratory conditions. These behaviors were studied in order to understand the bases for prey selection by the salmonids in Lake Michigan and ultimately facilitate predictions on shifts or changes in salmonid diets. Salmonid attack swimming speeds, prey reactive distances, and prey escape swimming speeds were calculated from video recordings. Observers collected information on location and approximate depth of predator and prey. Observers also determined if a prey item was captured, and, in experiments which included two prey species, which prey species was attacked.

Rainbow trout had difficulty capturing pelagic prey and generally captured prey in corners or along physical structures in the aquarium. Chinook and coho salmon captured all prey items in the pelagic portion of the aquarium. The most important criterion in prey selection was the distribution of the salmonids and their prey. If their vertical and horizontal distributions coincided, the prey item was attacked.

The success of an attack depended on several species specific characters, including those of morphology and escape behaviors. Alewives, bloaters, and fathead minnows were the easiest prey species to capture. Rainbow trout exhibited a switching type of predation between alewives and yellow perch but switching occurred because yellow perch changed their location within the aquarium and not because of any changes in foraging behavior by rainbow trout. The yellow perch was not a preferred forage species by either chinook or coho salmon. The potential contributions of each prey species toward the forage base for the three salmonid species were discussed.

KEYWORDS: Alewives, Behavior, Bloaters, Chinook Salmon, Coho Salmon, Diets, Fishes, Forage, Lake Michigan, Predation, Prey, Rainbow Trout, Salmon, Switching, Yellow Perch.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES*

*All figures show the simultaneous swimming speeds of a salmonid and a prey during an attack. Rx is the point of reaction by the prey to the attack of the predator. The time units on the figures represent an advance from one frame to another on the video recording and is equivalent to 0.033 seconds. Reactive distances are not shown on the figures. All of the prey in these figures turned as part of their reaction to an attack, so when a predator did not catch the prey, the salmonid turned to pursue the prey item. Those several frames after the prey reaction represent attack swimming speeds when the salmonid was turning to pursue the prey. At the conclusion of the attack, the letters M or S occur. M is a miss; the prey was not captured. S is success; the prey was captured.

ACKNOWLEDGEMENTS

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INTRODUCTION

Since the introductions of some Pacific salmon species into Lake Michigan in the 1960s, there has been great demand for catchable sizes of salmon by sport fishermen. Many of the salmon did not reproduce in Lake Michigan, so salmonid populations were maintained by large stocking programs. There was little concern whether there was sufficient forage for these stocked fish. The alewife (Alosa pseudoharengus) was the principal forage for salmonids during the 1970s and early 1980s (McComish and Miller, 1976 and Jude et al, 1987), and alewives were very abundant in Lake Michigan (Eck and Wells, 1987).

When the alewife population declined, there was concern whether the forage base was sufficient for growth and survival of the stocked salmonids. Stewart et al (1981) predicted a shift by the salmonids to alternate prey species. Hagar (1984), examining salmon diets during the decline of the alewife populations, found that alewives were still the principal forage fish for salmonids. Jude et al (1987) found that alewives were the principal prey even when populations of other prey species increased dramatically. These other prey species included bloaters (Coregonus hoyi), yellow perch (Perca flavescens), rainbow smelt (Osmerus mordax), and spottail shiners (Notropis hudsonius) as well as other species (Jude and Tesar, 1985 and Jude et al, 1987). Hagar (1984) concluded that while salmonid diets were more diverse, a shift to an alternate prey species did not occur.

So, while alewives remained the principal forage species, at least under some circumstances, there was greater utilization of alternate prey species by the salmonids. As alewife populations declined, Hagar (1984) found that there were more yellow perch in the salmonid diets. Savitz et al (1984) noted that in the fall of 1983, bloaters were the principal prey of salmonids in the Chicago area, and bloaters were also the principal prey species of lake trout (Salvelinus namaycush) which were captured in deep waters of Lake Michigan (Paul Vidal, Illinois Department of Conservation, personal communication). Rainbow trout (Oncorhynchus mykiss) foraged heavily on aquatic invertebrates and insects (Janssen et al, 1987 and Jude et al, 1987). However, there was little information on which factors influenced Lake Michigan salmonid prey selection and, consequently, little basis for predictions on shifts or changes in salmonid diets.

There were several hypotheses which might explain salmon diet data. One hypothesis was derived from optimal foraging theory (MacArthur and Pianka, 1966). Essentially, a prey species occurred more frequently in the diet because the prey species was more efficiently harvested because of some behavioral properties involved in the salmon-prey foraging interactions. These properties included variations in prey reactive distances to a predator attack or prey escape swimming speeds in relation to salmonid attack swimming speeds. There might be other behavioral characteristics which also influence prey selection by salmonids. Another hypothesis was that the prey in the salmon diet was a consequence of the vertical and horizontal distribution of salmonid species and prey species. In other words, a particular prey was found in the diet because its distribution coincided with the salmon's distribution (Magnuson et al, 1979).

Yet, another hypothesis is related to the "switching" type of predation described by Murdoch and Oaten (1975). If a predator was utilizing a switching type of predation, it was foraging on a disproportionate number of the commonest prey. If another prey became more common, the predator switched to this prey and utilized a disproportionate number of the present most common species. Krebs (1978) pointed out that one basic difference between switching and any optimization hypothesis was that switching was described in terms of relative population densities of prey, and optimization models depended on absolute prey densities and encounter rates. The "switch" type of predation presented by Murdoch and Oaten (1975) described a process but provided little explanation of why the process occurred.

Krebs (1978) provided several reasons, within the context of optimal foraging theory, why switching might occur. A predator might concentrate on profitable patches of prey which were made up of only one prey species. If several prey species occurred together and a "switch" type of predation was occurring, then the predator had become more efficient in utilizing a particular prey species.

The predator might become more efficient due to learning (Lawton et al, 1974) or due to a change in physiology (Moss, 1972 and Miller, 1975). The physiological changes which have been shown to operate in switching involved digestive physiology of birds foraging on plant material (Moss, 1972 and Miller, 1975). It was doubtful that changes in digestive physiology would be responsible for switching among salmonids. If temperatures were constant, piscivorous fish digested different species of forage fish at the same rates (Molnar et al, 1967 and Windell, 1966 and 1967). Even if temperatures were not constant salmonids might still be able to digest fish prey at similar rates because of a physiological adaptation referred to as capacity adaptation. This adaptation allows a cold-blooded animal to maintain the same metabolism over a range of temperatures (Precht, 1958 and Savitz, 1969). A more plausible explanation for switching under these circumstances involved learning.

Since prey selection is ultimately a consequence of predator-prey behavioral interactions, these interactions might be used as a basis for understanding prey selection by salmonids in Lake Michigan. Studies on foraging behavior among fishes have increased our understanding of some aspects of prey selection (Feder and Lauder, 1986), and this was particularly true for prey selection by piscivorous fishes (Major, 1978 and Webb, 1986). However, laboratory studies on animal behavior rarely involved predator-prey behavioral interactions (Griffin, 1984). A large number of prey animals must be acclimated to laboratory conditions, and most will be destroyed during the study. Most investigators were reluctant to conduct a study in which many of their acclimated animals were destroyed (Griffin, 1984). The predators must also be acclimated to laboratory conditions.

Because predator-prey interactions are variable and complex, conditions must be standardized and experiments and/or observations must be repeated many times. This presented a problem because predator-prey behavioral studies required more space than was usually available. The space must be large enough so that the prey has an opportunity to escape and yet the predator must achieve enough success to provide an adequate data base (Griffin 1984).

The objectives of this project were to determine through a laboratory study which behaviors were important in prey selection by salmonids. The following hypotheses were examined:

1. A prey species was selected by the salmonids because it was more efficiently harvested due to certain behavioral characteristics involved in the predator-prey interaction.
2. Prey selection was based on the coincident distributions of salmonids and their prey.
3. Prey selection followed a switch type of predation because fish schools were composed of a single species and one schooling species was more efficiently harvested than any others or because of a learning process by salmonids.

By determining what behavioral characteristics are important in prey selection, predictions on shifts in salmonid diets with changes in prey species densities will be enhanced. This study was one of the initial steps to an understanding of the relationship between the forage base and growth and survival of stocked salmonids in Lake Michigan.

We examined foraging behavioral interactions between three species of salmonids and various prey species under laboratory conditions. Prey reactive distances, prey escape swimming speeds, salmonid attack swimming speeds, and capture success were measured for various prey species with each of the three salmonid species. These behavioral parameters were measured to determine whether one prey species was more efficiently harvested than another. Location of predatory attacks were noted as well as any other behavioral characters which might influence prey selection. These were examined in order to determine if prey selection was based on coincident distribution of salmonids and their prey and/or some other behavioral character.

In examining a switching type of predation, one is faced with examining several possible hypotheses of why it occurred. Before studying any one of them, a switching type of predation must be documented.

In other words, was switching displayed by Lake Michigan salmonids under laboratory conditions? If it was, did prey species occur in patches, i.e., schools, composed of primarily one species? If schools were composed of more than one species and switching occurred, was learning or were changes in physiology responsible? Learning was defined as a change in behavior due to experience (Rescorla and Holland, 1976).

We can determine how salmonids forage on single species schools as well as two species schools and determine if switching occurred when salmonids were presented with these two species schools. If switching occurred in two species schools, then we can determine whether learning was occurring by comparing foraging behaviors when salmonids were initially presented with two species schools and subsequent trials with two species schools. If switching occurred when salmonids were presented with two species schools and learning was not important in switching, then other factors, such as similar distributions of salmonids and their prey in the aquarium, or possibly, a physiological adaptation were involved. However, physiological adaptations and other possible non-behavioral factors which might account for switching were beyond the scope of this study.

METHODS

The studies were conducted at the John G. Shedd Aquarium in a cement aquarium which contained approximately 5800 gallons and measured 12'7" x 9'6" x 6'6". This aquarium is referred to as the experimental aquarium. Prey species and predators were maintained and acclimated in separate cement aquaria, each of which contained approximately 600 gallons of water and had the following dimensions: 6'9" x 3'11" x 3'1". These aquaria are referred to as holding aquaria. Cooling coils maintained temperatures at 15C in each of the aquaria. The water for all of the aquaria was continuously aerated and filtered.

The bottom of the experimental aquarium received between 170 and 200 lux from natural sunlight and artificial lighting. A false bottom was placed into the experimental aquarium. It was constructed of polyethylene tubing and sheathed with white plastic sectioned by black tape into grids. Each side of the grid had a length of 0.5 meter.

At each corner of the experimental aquarium, wood supports were attached. These supports stood seven feet above the aquarium, and a stainless steel track connected the supports on the longer sides of the rectangular aquarium. Two horizontal wooden supports at the front and back portions of the aquarium connected the long sides of the frame. In addition, two stainless steel tracks also connected the long sides of the frame. All of the tracks and an electrically controlled pulley system allowed movement of a platform to the front and back of the aquarium as well as sideways across the aquarium.

A video camera was mounted six feet above the water level of the aquarium. The video camera was Panasonic WV-3240 8AF and the video recorder was TMK Model 2055. The system was compatible with Panasonic recorder (NV-8950). The latter recorder is capable of freeze frame and frame by frame advance.

Fish were obtained by seining in Lake Michigan, from the Shedd Aquarium, Max McGraw Wildlife Foundation, University of Wisconsin-Milwaukee, and local bait shops. Alewives, spottail shiners, yellow perch, and some smelt and bloaters were obtained by seining. They were transported to the Shedd Aquarium and allowed to acclimate in a holding aquarium. Fathead minnows (Pimephales promelas) and emerald shiners (Notropis atherinoides) were obtained from local bait shops and acclimated in a holding aquarium. Some smelt were obtained from the collection at the Shedd Aquarium, and most of the bloaters used in the study were acquired from the University of Wisconsin-Milwaukee.

Some rainbow trout were captured by seining in Lake Michigan. Rainbow trout were also obtained from Max McGraw Wildlife Foundation; they came from two separate stocks. One stock had primarily been maintained on dry pellets of trout chow in a natural stream; the other stock also came from a natural stream but foraged on living organisms. The various stocks of rainbow trout were obtained at different times and were not intermingled, so that results from each group could be compared. There were seven rainbow trout used in the study. Two rainbow trout were captured in Lake Michigan; three were from a natural stream but fed dry pellets; and two were from a natural stream and foraged on living organisms.

Chinook salmon (Oncorhynchus tshawytscha) and coho salmon (Oncorhynchus kisutch) were obtained from the John G. Shedd Aquarium. They were reared initially at the Jake Wolff Memorial Fish Hatchery. While they were maintained at the Fish Hatchery and the Shedd Aquarium, they had been fed either trout chow or thawed smelt and krill. Seven chinook salmon and four coho salmon were used in the study. All salmonids became acclimated to water temperatures of 15C in a holding aquarium.

Salmonids were allowed to acclimate to the experimental aquarium for two or three days before prey were introduced. The size of the salmonids varied from 22 to 35 cm. Two or three members of the same species, or, in the case of rainbow trout, two or three individuals of the same group were released into the aquarium. Windell (1966) found that when two or more predators were released in the same aquarium, their interest in foraging occurred sooner. Salmonids were believed to be acclimated to the conditions of the aquarium when they actively foraged on fathead minnows.

The three procedures which were used to introduce prey into the experimental aquarium allowed time for prey to acquire some familiarity with the physical conditions and the presence of salmonids. In one procedure the prey were placed in a large floating net for a day and then released into the experimental aquarium. Another method involved partitioning the experimental aquarium into two sections with prey in one half and salmonids in the other half. After one day, the partition was removed. However, the procedure which was used most frequently was to place the prey into the experimental aquarium and restrict access to them by hand-held nets until the prey had established a school or until their movements appeared normal.

The number of prey varied from one individual to two dozen whenever a single prey species was introduced into the experimental aquarium. Some experiments involved the simultaneous introductions of two prey species. In those experiments, fifteen or twenty prey were stocked. When twenty prey were used, the following proportions of these prey species were introduced: 3 to 1, 1 to 1, and 1 to 3. When fifteen prey items were stocked, the following proportions of prey species were used: 2 to 1 and 1 to 2. The size of the prey ranged from 4 to 9 cm, but most prey were 4 and 5 cm in length. In experiments with two prey species, all of the prey were 4 to 5 cm in length.

Data were collected by a video recorder and by an observer stationed at one side of the aquarium. Observers were necessary to determine location and approximate depth of the predator and prey in the aquarium and whether a prey item was actually captured. When two prey species were placed in the aquarium, an observer determined which prey species was captured or attacked.

Salmonid attack swimming speeds, prey reactive distances, and prey escape swimming speeds were calculated from the video recordings. Prey reactive distance was the distance between the attacking salmonid and the first reaction, i.e., movement, by the prey in response to that attack. Swimming speeds were calculated by determining the distance a fish moved between two frames of a video recording; there were 30 frames/second. Measurements of swimming speeds and reactive distances were measured on those interactions which were primarily in the horizontal plane since vertical movements could not be accurately incorporated into the measurements. Differences in water depth of the foraging interactions were incorporated into the measurements by knowing the fish size, size of fish on the video recording, and size of the sides (0.5 m) of the grid squares on the bottom of the aquarium.

RESULTS

PREY SPECIES

Avoiding Predation

The three different approaches to introducing prey into the experimental aquarium did not appear to affect the results of the study. The most important aspects in introducing prey were that they were acclimated to the water temperatures, had sufficient time to become accustomed to the physical surroundings within the experimental aquarium, and were aware of the presence of predators. Size of prey had an influence on the number of attacks and capture success by salmonids. The larger prey sizes, approximately 7 to 9 cm, were not attacked as frequently as smaller prey and were more difficult to capture. The effect of these larger prey sizes on avoiding predation by salmonids was similar for all prey species, except fathead minnows for which larger prey sizes were not available.

There were several behavioral characteristics which prey species used to avoid predation, and within each prey species the same behaviors were used regardless of which salmonid species was present. Some prey species had fast escape swimming speeds which allowed prey to seek refuge close to a physical structure. Many prey maintained a safe distance between themselves and the salmonids. Often, the movement patterns of the prey appeared to be related to the movement of the salmonids, even when no predatory attack was occurring. This relationship between prey and predator movements was usually not evident when observing the fish. But when the video recordings were viewed at higher speeds, the relationship was obvious. Several prey species had the ability to turn sharply when attacked so that predators missed them, and the salmonid, then, needed to turn sharply and quickly to follow them. A frequent response by some of the prey species when attacked was to change locations within the experimental aquarium. Some moved close to the water surface, and if they had a silvery ventral surface, they probably became difficult to see and to capture. Some also stayed close to the bottom, walls, or in corners. Schooling by a single species or by two species was effective in avoiding predation; only three prey were captured when they were part of a school. Each prey species' behavioral and other important characteristics are summarized below.

Alewives

Alewives generally formed schools and remained in the open water portion of the aquarium, i.e., pelagic. Predators would attack the schools apparently to single out individuals because solitary alewives were easier to catch. Alewives would continue to form schools until there were fewer than five individuals in the experimental aquarium. Even then, they might have been able to remain in a school except they were almost constantly under attack by trout or salmon. They did form a two species school with yellow perch. If there were only one or two alewives in the aquarium, then the individuals stayed close to the surface and swam close to the wall. The larger alewives were more difficult for the trout or salmon to capture than the smaller ones. Larger alewives had faster escape swimming speeds and turned very sharply when attacked.

Bloaters

Bloaters formed schools either as a single species or with yellow perch; they also occurred as solitary individuals. When attacked, schools would break apart and individuals either swam towards the water surface, close to the bottom, or along the walls. Bloaters usually stayed in the lower portion of the water column. As with alewives, larger bloaters were more difficult to capture than smaller ones. Bloaters had fast swimming speeds but they were usually slower than either of the shiner species or the yellow perch.

Emerald Shiners

Emerald shiners were usually in schools and close to the water surface. Their silvery ventral surface probably made them difficult to detect or to accurately determine a point of attack. They exhibited fast escape swimming speeds and turned sharply when attacked. Salmonids seldom attacked them and when they did they usually missed. In most cases, salmonids were moving towards the surface when attacking the emerald shiners. Because the salmonids had so little success in capturing emerald shiners, most were removed from the experimental aquarium by hand nets after they had been in the aquarium for a week or more.

Fathead Minnows

These were the easiest species for the salmonids to capture. They occurred in schools, but individuals were easily separated from the schools after the salmonids made at least one attack on a school. Fathead minnows were the slowest of the prey species and they did not turn quickly. They were darkly pigmented which might have allowed easy detection and an accurate determination of the point of attack by the salmonids. They did stay close to the bottom or close to other physical structures, but they were often found in the pelagic as well. Their only successful mechanism for avoiding predation was to stay close to physical structures.

Rainbow Smelt

Smelt also occurred in schools. They were very difficult to capture because they stayed at the very top of the water column and rarely moved. Their silvery ventral surface probably made them difficult to see. Often, a smelt remained in the experimental aquarium for several days before it was attacked. It appeared as if a salmonid would finally notice the smelt and then quickly attack it. The smelt were usually captured. Once attacked, smelt made no attempt to avoid predation. There were no quantitative data on swimming speeds or reactive distances with this species.

Spottail Shiners

These fish were similar to emerald shiners in that they formed a school which stayed or remained close to the water surface. Spottail shiners also stayed close to physical structures such as the wall or the bottom of the experimental aquarium. Sometimes the school stopped and formed a cluster with each individual positioned head outward. Each individual was pointed in a different direction in a 3-dimensional space. Spottail shiners were also very fast, turned quickly, and were difficult to capture. Salmonids seldom attacked spottail shiners. When they did attack, they were usually unsuccessful.

Yellow Perch

Yellow perch were the most versatile of the prey species in the behaviors displayed in the experimental aquarium. They formed schools as a single species and formed two species schools with alewives and bloaters. However, they frequently occurred as solitary individuals. They swam close to physical structures or stayed in the pelagic and sometimes simply maintained themselves as stationary individuals in the middle of the pelagic. If they were swimming in the pelagic and were attacked they would often change locations within the experimental aquarium to avoid predation. They had fast escape swimming speeds and turned quickly when attacked. Larger individuals were nearly impossible to catch. Yellow perch did not appear to be a preferred prey species by chinook or coho salmon. Coho and chinook salmon attacked them less frequently than some other prey species. These salmon would initiate an attack on a yellow perch then break off the attack even if the yellow perch did not move. Perhaps, some morphological characters, such as spines, might have made yellow perch a less desirable prey item.

RAINBOW TROUT

Qualitative Aspects of Foraging

None of the rainbow trout seemed to be disturbed by the presence of observers or their movements in the vicinity of the experimental aquarium. When observers first arrived and the rainbow trout were near the water surface, they would react to the presence of the observers but quickly adjusted.

There were slight differences among the three groups of rainbow trout which were probably related to their life history. Those trout which lived in a natural stream and were fed dry pellets did not learn to catch live prey in the experimental aquarium for over two weeks. This group was also the slowest of the rainbow trout and did not easily reach their maximum swimming speeds. They accelerated slowly for at least a meter before reaching their maximum speed and were very slow in turning and pursuing prey. They rarely captured prey in the pelagic and when they did, they apparently caught the prey unawares because there were usually no reactive distances. They did catch prey in the corners or along the walls and bottom of the experimental aquarium but were not as effective as the other rainbow trout in catching prey in this manner.

Those rainbow trout, which were obtained from a natural stream and had foraged on live animals, had faster attack swimming speeds than the previously mentioned rainbow trout; however, they still captured most of their prey in the corners of the aquarium or close to the walls and bottom of the aquarium. They also attacked fathead minnows when they were first introduced into the experimental aquarium.

The rainbow trout from Lake Michigan, also had faster swimming speeds than the first mentioned group of trout. They were more adept at catching prey in the pelagic portion of the aquarium but caught most of them in corners or along the walls or bottom. This latter group of trout also attacked live prey soon after acclimation to the experimental aquarium.

Rainbow trout did not catch any prey which were in a school. All of the prey items which were captured were alone or recently separated from a school. Rainbow trout attacked schools of prey, but the attacks were generally at very slow swimming speeds, and rainbow trout seemed to switch the focus of the attack from one prey item to another. The attacks on schools appeared to be a mechanism for separating some individuals from the school so that they were more easily captured.

Rainbow trout had difficulty in capturing pelagic prey when compared to the other two salmonid species (see Tables 1, 3, and 4). When attacking prey in the pelagic, rainbow trout would approach slowly and then, turn the front portion of their bodies quickly. Usually, rainbow trout would miss the prey in the pelagic and appeared unable to turn quickly in order to pursue the prey (see Figure 1). Rainbow trout would pursue the prey but slowly (see Figures 1 and 2), and usually the second or third attempt at a capture occurred when the prey was in a corner in the aquarium or along some physical structures. At these locations, the possible escape routes by the prey were reduced and the rainbow trout was much more successful.

Rainbow trout used the same basic attack behavior regardless of prey species; attacks on a fathead minnow (see Figure 2) and yellow perch (see Figure 3) were similar to those on alewives (see Figure 1). Many prey attained higher escape swimming speeds than rainbow trout attack swimming speeds; this was particularly evident with alewives (see Figure 1), emerald and spottail shiners, and yellow perch (see Figure 3). Rainbow trout usually attacked pelagic prey at lower swimming speeds than the other salmonids and did not turn as sharply or quickly as chinook and coho salmon (see Figures 1-12). Most pelagic prey would escape by turning quickly, usually at a right angle to the direction of the attack, and swimming away.

Rainbow trout were able to catch some pelagic prey (see Table 1). Alewives were the most frequently captured prey, but rainbow trout did have some difficulty in capturing this prey species because they were usually in a school and appeared to prefer the pelagic portion of the aquarium. Alewives, bloaters, fathead minnows, and yellow perch which were captured in the pelagic portions of the aquarium were solitary individuals or were recently separated from a school. Both species of shiners were rarely attacked and only a few were captured in the pelagic. Rainbow trout attacked them from below, swimming primarily on a vertical axis so that no quantitative data were collected. However, in general, rainbow trout attacked prey which were swimming at similar depths within the experimental aquarium. The coincident vertical distribution of rainbow trout and prey was an important aspect in determining whether a prey item was attacked or not.

Reactive Distances, Attack and Escape Swimming Speeds

The ranges for highest attack swimming speeds for each attack by rainbow trout, highest escape swimming speeds attained for each attack by various prey species, and reactive distances by these prey species are shown in Table 1. All of the values in Table 1 were for predator-prey interactions which occurred in the pelagic portion of the aquarium. Data for attacks in which the rainbow trout swam primarily in an upward or downward direction were not included because swimming speeds and reactive distances could not be accurately measured. Swimming speeds and reactive distances involving prey which were caught in the corners or along physical structures were not included. Reactive distances could not be accurately measured and swimming speeds were meaningless in these locations since the attack swimming speeds were less important than the presence of physical structures in capturing prey.

Attack swimming speeds for rainbow trout ranged from 0.5 to 4.3 m/sec. The highest attack speed that resulted in a successful capture was 3.1 m/sec; it was the intermediate attack swimming speeds that resulted in captured pelagic prey. Reactive distances by prey ranged from 0.00 to 0.45 m. All successful prey captures occurred when the reactive distance for prey was less than 0.05 m. The median reactive distance by prey which were successfully captured by rainbow trout was 0.00 m.

Reactive distances of prey were important because the attack swimming speeds were similar to the escape swimming speeds of the prey species (see Figures 1, 2, and 3). If the prey species had a large reactive distance it would swim at nearly the same speed as the rainbow trout, and consequently, the rainbow trout would not catch the prey. The best strategy for the rainbow trout in attacking pelagic prey was to capture the prey before it had time to react. In the pelagic portion of the aquarium, alewives, bloaters, and fathead minnows were more efficiently harvested than yellow perch or shiners, but few prey were captured in the pelagic. The capture success by rainbow trout on alewives and bloaters were similar; unfortunately, only a few bloaters were available when rainbow trout foraging behaviors were studied.

Two Species Introductions—Yellow Perch and Alewives

Rainbow trout were presented with yellow perch and alewives in the following combinations: 15 yellow perch (YP) and 5 alewives (A); 10 YP and 10 A; and 5 YP and 15 A (see Table 2). The following scenario occurred regardless of the relative proportions of yellow perch and alewives. Rainbow trout would attack solitary individuals first, regardless of species. After they pursued and eventually captured many of the solitary individuals, they began to attack the schools. Yellow perch and alewives generally formed a two-species school. On one occasion, each species formed a separate school. Attacks on the schools were at slow swimming speeds and the focus of the attack switched from one prey item to another. The purpose of the attack appeared to be to separate some individuals from the school. Yellow perch generally abandoned the school first; rainbow trout would pursue them and capture them in the corners or along a physical structure within the experimental aquarium.

As the number of yellow perch was reduced, the few remaining yellow perch changed locations in the aquarium so that they were no longer associated with the fish school. Sometimes yellow perch were motionless at these new locations which included the water surface and the bottom or some other physical structures within the aquarium. Rainbow trout continued to attack the fish school which now was primarily composed of alewives. As with the yellow perch, an individual alewife was separated from the school and caught in a corner or along a physical structure. Alewives attempted to form a school unti there were less than five individuals. Usually, the alewives were pursued until all were captured and then the rainbow trout would again locate, pursue, and capture yellow perch.

Did switching occur? If the combinations were 15 YP and 5 A or 10 YP and 10 A, switching occurred because rainbow trout would capture yellow perch (see Table 2) and, then when alewives became abundant, alewives were captured. When the combination of 5 YP and 15 A were introduced, yellow perch were initially pursued and captured even though there were fewer yellow perch. After the yellow perch were captured, alewives were pursued and most if not all were consumed.

It appeared from the definition of switching (Murdock and Oaten, 1975) that switching occurred in these experiments. Switching is predation on a disproportionate number of the most common species. In these experiments, the most important factor for switching was neither learning nor physiology of rainbow trout since rainbow trout did not change their foraging behaviors. Switching occurred because the yellow perch changed their locations in the experimental aquarium. Obviously, some learning occurred prior to the introduction of the two species combinations. This learning involved determining the most efficient method for capturing prey, which for rainbow trout was to catch prey in corners or along physical structures. There was no obvious learning involved in switching from yellow perch to alewives.

CHINOOK SALMON

Qualitative Aspects of Foraging

Perhaps, because of previous feeding history, chinook salmon did not actively forage on live prey for two to four weeks after fathead minnows were initially stocked. Observers' activities initially disturbed chinook salmon when they were swimming close to the water surface. Chinook salmon soon adjusted to the presence of the observers. After the initial disturbance by the investigators' arrival to introduce prey and gather data, the chinook salmon swimming activities increased. Apparently, they learned that human activity was associated with the introduction of prey.

Chinook salmon were not effective in capturing prey which were in a school. They only caught two individuals which were part of a school. One prey was at the very front of the school; the other was at the rear of the school. Chinook salmon employed a behavior similar to that of rainbow trout which was to attack the school causing several individuals to become separated from it. While they attacked the school, the focus of their attack changed from one prey item to another. Once the prey was separated from the school, chinook salmon would attack it if the prey remained in the pelagic portion of the experimental aquarium.

Chinook salmon only attempted to capture prey in the pelagic portion of the experimental aquarium; there were no attempts to trap or catch prey along physical structures. Chinook salmon generally attained faster attack swimming speeds than the escape swimming speeds exhibited by prey (see Figures 4, 5, and 6). Chinook salmon accelerated quickly, and, in fact, if they were already moving in the direction in which they were going to attack, they could attain maximum attack swimming speed in one frame of the video recording (see Figure 5). Many prey were attacked so suddenly that there was no reaction to the approach of the chinook salmon. If the chinook salmon missed or if there was sufficient reactive distance, the prey would attempt to seek refuge by swimming to a physical structure or the water surface. If a prey was missed on an initial attack, a chinook salmon had the ability to turn sharply and to retain or to increase its attack swimming speed while pursuing prey (see Figures 4, 5, 6, and 7).

At times, the chinook salmon movements resembled snakes moving through the water, because they could bend their body to follow a sometimes twisting-like path of the prey. Chinook salmon displayed the same basic attack behavior regardless of prey species.

There were some modifications of chinook salmon attack. If the prey item was larger or was a less preferred or less frequently captured species, such as the shiners or yellow perch, the chinook salmon approached more slowly; then when it was nearer to the prey it attacked quickly (see Figure 7). The behavior in these circumstances was similar to that exhibited by rainbow trout when they attacked pelagic prey. This slight modification in attack behavior was the same for all of the larger prey items regardless of species and was consistent for those prey species which were less preferred or more difficult to capture.

Chinook salmon had little difficulty in capturing alewives, bloaters, or fathead minnows (see Table 2). The only difficulties they had with these prey were if they missed, the prey could escape to a physical structure or the water surface. When chinook salmon foraging behaviors were studied, few alewives were available; so most of the data for alewives was collected when only a few alewives were added to the experimental aquarium at any one time. After alewives were attacked they stayed close to physical structures, often swimming around the aquarium close to the wall and at the water surface. Consequently, chinook salmon had some difficulty in capturing alewives because of these behaviors. However, if alewives were in the pelagic, chinook salmon had little difficulty in capturing them. Both species of shiners were very difficult for the chinook salmon to capture. As previously mentioned these prey species swam close to the surface, formed schools, and had fast escape swimming speeds. Chinook salmon rarely attacked them, and most of the shiners were removed by hand nets after a week or more in the experimental aquarium.

Chinook salmon also had difficulty capturing smelt because this prey species was at the top of water column, remained motionless, and had a silvery ventral surface which made it difficult to see. When chinook salmon did notice smelt, they were immediately attacked and captured. Chinook salmon appeared to be swimming at maximum velocities when they attacked smelt at the water surface. Whether they captured smelt or not, they usually exploded out of the water.

Chinook salmon would attack smaller yellow perch when the yellow perch were initially introduced into the experimental aquarium, but after some experience with this prey species the salmon rarely attacked them. Sometimes, in the midst of attacking a yellow perch, chinook salmon would suddenly break off the attack even if the prey showed no movement or no attempt to escape. This behavior by chinook salmon was not evident with any other prey organism. Chinook salmon also had great difficulty in capturing larger yellow perch.

An important factor in the chinook salmon and prey species interactions was the vertical distribution of predator and prey. Most prey which were attacked were at a similar depth in the water column as the chinook salmon. If alewives, bloaters, and fathead minnows were at a similar depth as the chinook salmon and were in the pelagic, these prey species were readily attacked and captured.

Reactive Distances, Attack and Escape Swimming Speeds

Maximum attack swimming speeds for chinook salmon varied from 0.8 to 4.9 m/sec (see Table 3). Successful prey captures usually occurred at the higher attack swimming speeds. Maximum prey escape swimming speeds were generally lower than attack swimming speeds, ranging from 0.5 to 3.6 m/sec. Prey reactive distances ranged from 0.00 to 0.18 m. For most successful captures, the reactive distance was 0.00 m. Even when they missed a prey item, it was not because the prey did anything. The chinook salmon simply missed the prey. Chinook salmon often missed on the initial attack but caught the prey before it reached a refuge.

The percentage of captures for fathead minnows was reflective of the ease with which chinook salmon captured them. The lower percentages of captures for alewives and bloaters, 36% and 30% respectively, was probably not a true indication of how easily these prey could be captured. The lower percentages were due to escapes to a refuge which probably would occur less frequently in Lake Michigan. The capture success of yellow perch reflected the relative ease of capturing of small, i.e., 4 to 5 cm, yellow perch in the pelagic. Larger yellow perch were more difficult to capture and as mentioned previously, chinook salmon would also attack yellow perch less frequently after some foraging experiences with yellow perch. Alewives, bloaters, fathead minnows, and small yellow perch were harvested at nearly the same efficiency. Spottail shiners and emerald shiners were not effectively attacked and some non-behavioral factor made yellow perch a less desirable prey than alewives, bloaters, or fathead minnows.

COHO SALMON

Qualitative Aspects of Foraging

Coho salmon displayed many of the same behaviors shown by chinook salmon. Their previous feeding history was the same as the chinook salmon and they did not actively feed on live prey, such as fathead minnows, until four weeks after live prey was first introduced into the experimental aquarium. Coho salmon were probably less disturbed by investigators' activities than rainbow trout or chinook salmon. They were rarely close to the water surface so were usually not disturbed by observers. They did become accustomed to the relationship between presence of investigators and introduction of prey and exhibited increased movement within the experimental aquarium shortly after investigators arrived. As with the other salmonid species it was important that prey were accustomed to their surroundings and the presence of predators before allowing the coho salmon an opportunity to attack the prey.

Coho salmon would only attack prey in the pelagic portion of the experimental aquarium. They generally stayed closer to the bottom than chinook salmon and, in contrast to the chinook salmon, only jumped out of water once in pursuit of a prey item. Coho salmon seldom caught prey which were part of a school. As with chinook salmon they did catch one prey item at the back of a school, but in general, displayed the same type of behaviors exhibited by the other two salmonid species. They attacked schools at less than maximum velocities and changed the focus of the attack from one prey item to another. Several prey would be separated from the school and the coho salmon proceeded to attack these prey as long as they remained in the pelagic portion of the aquarium. They did not attempt to trap or catch prey close to any physical structure. Coho salmon were capable of attaining attack swimming speeds comparable to chinook salmon (see Tables 3 and 4).

Coho salmon used the same basic attack method regardless of prey species. The approach was modified for larger prey items and for those species which were more difficult to capture or less preferred. As with the chinook salmon, prey which were small, 4 to 5 cm, were attacked at higher velocities than larger prey or prey which had the ability to turn sharply or had faster escape swimming speeds (see Figure 12). As with the other salmonid species, prey selection was based on the coincident vertical distribution of prey item and the coho salmon.

They generally caught prey before they had an opportunity to react to the attack. The median prey reactive distance was 0.00 m (see Table 4). If coho salmon missed their prey, they generally turned quickly and attacked again (see Figure 8). They were capable of turning sharply and sometimes missed the same prey item two or more times (see Figures 8 and 11) before the prey responded by utilizing a fast escape swimming speed (see Figures 8-11). It often appeared that the prey was confused and remained practically motionless in the water while the coho salmon swirled about it. This method of attack was exhibited most commonly. At other times it would chase a prey item in a similar fashion to that of the chinook salmon. Again the best way for prey to avoid predation was to escape to a physical structure such as a wall, the bottom of the experimental aquarium, or the top of the water column.

Coho salmon had little difficulty in capturing bloaters (see Table 4). Usually the initial attempt to catch a bloater failed but the coho salmon turned quickly and would repeatedly attack until the bloater was captured (see Figure 8). Even though the coho salmon missed its prey two or more times, this was counted as a capture since every attempt was part of an overall attack. Unfortunately, when foraging behavior of coho salmon was studied very few alewives were available, but from the limited data it appeared that alewives were not very difficult for coho salmon to catch (see Table 4). While the percentage of captures of fathead minnows was low, 27% (see Table 4), coho salmon did not appear to have many problems in capturing them, except that this prey species would attempt to escape towards physical structures.

Spottail shiners and emerald shiners were presented to the coho salmon but were rarely attacked. For the few attacks on emerald shiners, the coho salmon were moving upward through the water column so accurate measurements of swimming speeds and reactive distance could not be determined.

Only the small 4 to 5 cm sizes of yellow perch were attacked and, as with the chinook salmon, yellow perch were not a preferred prey species. Whenever coho salmon were attacking yellow perch, their behaviors were very similar to those previously described for chinook salmon. A coho salmon might initiate an attack on a yellow perch and then suddenly break off the attack even if the yellow perch took no evasive action to avoid this predator.

Reactive Distances, Attack and Escape Swimming Speeds

Maximum attack swimming speeds for the coho salmon ranged from 1.0 to 4.9 m/sec (see Table 4). Maximum escape swimming speeds ranged from 0.5 to 4.8 m/sec, with the highest of these values resulting in an escaped prey item. Prey reactive distances ranged from 0.00 to 0.24 m (see Table 4). Most of the captures occurred at the lowest prey reactive distance, and the median reactive distance among captured prey was 0.00 m.

Two Species Introductions—Yellow Perch and Bloaters

Bloaters and yellow perch were stocked in the experimental aquarium simultaneously. They were introduced in the following combinations: 15 yellow perch (YP) to 5 bloaters (B); 10 YP to 10 B; 10 YP to 5 B; 5 YP to 10 B; and 5 YP to 15 B (see Table 5). Coho salmon would actively forage on bloaters in preference to yellow perch regardless of the ratio of yellow perch and bloaters. Coho salmon would usually not attack any yellow perch until all of the bloaters were consumed or had escaped to a refuge along a physical structure or the top of the water column. Coho salmon made fewer attempts to capture yellow perch, and with some of the trials, no attempts were made to capture yellow perch (see Table 5). There was no evidence of switching in this experiment.

DISCUSSION

All the salmonid species in this experiment used the same basic approach in attacking pelagic prey. Differences in ability to accelerate and in attack swimming speeds, especially while turning, contributed towards the variations in this basic approach and the overall success by the salmonid species.

All three species attained nearly the same attack swimming velocities; however, rainbow trout did not attain these velocities as quickly as the other salmonids. Coho and chinook salmon could reach these velocities in one frame on the video tape (.033 second). Also coho and chinook salmon lost little velocity in turning if they initially missed the prey; if rainbow trout missed, by the time they turned, the prey was some distance from the predator. If the prey item was slow in comparison to the salmonid attack swimming speeds, i.e., fathead minnows, small yellow perch, small bloaters, and small alewives, then the salmonids usually attacked at higher swimming speeds, and, at times from a considerable distance from the prey. This latter approach was also used when smelt were at the water surface.

If the prey item exhibited a fast escape swimming speed or turned rapidly, i.e., shiners, larger yellow perch, larger bloaters, and larger alewives, the salmonid approached the prey more slowly, and, then, when the prey was within striking distance, attacked quickly. Since rainbow trout were generally slower than chinook or coho salmon, most of their approaches were slower in order to get closer to the prey before making an attack.

Rainbow trout had difficulty in successful capture of pelagic prey. How did they succeed in Lake Michigan? Rainbow trout diets did contain large quantities of insects and aquatic invertebrates (Janssen et al, 1987 and Jude et al, 1987), and slow pelagic prey such as insects and aquatic invertebrates could easily be captured by rainbow trout. But rainbow trout grew to considerable sizes in Lake Michigan (Vidal, 1984). It was doubtful that such growth could be achieved with invertebrate prey. Rainbow trout also foraged on alewives and other forage fish (Janssen et al, 1987 and Jude et al, 1987). How did they catch them in Lake Michigan?

While there had been some studies on rainbow trout movements in the Great Lakes (Winter, 1976 and Haynes, 1983) as well as the movements of chinook and coho salmon (Haynes and Keleher, 1986), there had been no detailed studies of how rainbow trout capture prey in the Great Lakes. Perhaps, rainbow trout could acquire pelagic prey more easily if there was a sufficient size differential between the salmonids and prey items. As the predator becomes larger, the attack swimming speeds would be faster (Nyberg, 1971) and the handling time for prey would be less (Savitz and Janssen, 1982). Consequently, the prey would be more easily captured and efficiently utilized by the rainbow trout.

Another possibility was that the rainbow trout which grew to large sizes in Lake Michigan and were caught by fishermen and biologists represented a small portion of the original number stocked. In fact, this group might represent the best adapted group of rainbow trout to foraging conditions in Lake Michigan. They might have behavioral characteristics different than the average rainbow trout used in this study. They might be faster and quicker turning fish and represent the small fraction of stocked rainbow trout which had those characteristics. There were any number of other possibilities on how rainbow trout succeed in Lake Michigan, but analyses of the data from this laboratory study posed an interesting question as to how rainbow trout achieved success in piscivorous foraging in Lake Michigan.

Rainbow trout were only truly successful in capturing prey by trapping or limiting their escape routes around physical structures. They did exhibit a switching predation type of response in relation to alewives and yellow perch. However, the apparent switching was not caused by any change by rainbow trout in their approach or method of catching prey. Switching was caused by the yellow perch utilizing a different habitat or location within the experimental aquarium. The rainbow trout used the same approach—following the school, attacking the school, separating some individuals from the rest of the school, and then following them and attacking them.

Learning was relatively unimportant in the switching process. Learning did occur among the rainbow trout because those that were accustomed to pellets of trout chow had to learn how to forage on live prey. Those behaviors which these "learned" fish used were essentially the same as individuals which had a history of utilizing live prey.

While rainbow trout utilized the same foraging behaviors, regardless of prey species, certain prey species appeared to be more easily or efficiently captured than other species. Alewives, bloaters, and fathead minnows were more efficiently captured in the pelagic than shiners or yellow perch. Why were these prey species more efficiently captured? Rainbow trout behaviors did not change with prey species. Behaviors associated with predator-prey interactions were similar within each prey species. These three prey species were generally slower than yellow perch or the shiner species and did not turn as quickly or sharply as yellow perch and the shiner species. Therefore, they were more vulnerable to attack by a slower salmonid species. Because of these differences and perhaps some morphological ones, alewives, bloaters, and fathead minnows were more efficiently utilized in the pelagic than yellow perch and shiner species.

It was apparent with rainbow trout that an important character in a particular prey item selection was the location of the prey and the predators. Rainbow trout utilized those areas in the aquarium where prey schools were found and continually attacked those schools to separate individuals from it. A successful capture usually occurred in a corner or along a physical structure. The yellow perch which changed their location after some attacks by rainbow trout were less likely to be attacked immediately. Alewives did not change their behavior until there were only a few individuals left in the experimental aquarium. Consequently the most important factor in acquiring prey was the coincident locations of the predator and prey species. A secondary factor when one considers only the pelagic portion of the aquarium, was the efficiency in capturing prey which was determined by the swimming speeds of rainbow trout and the prey species.

Since chinook and coho salmon could accelerate more quickly than rainbow trout, they were more likely to capture prey in the open water portions of the aquarium. However, as with the rainbow trout, alewives, bloaters, and fathead minnows were more easily captured than the yellow perch and the shiner species. The same characteristics which made these prey species more vulnerable to predation by rainbow trout also made these prey species more vulnerable to predation by chinook and coho salmon. However, because these two salmon species were faster and capable of turning more quickly, chinook and coho salmon captured more pelagic prey than the rainbow trout.

Again, neither the salmonid foraging behaviors nor the prey escape behaviors were modified with different species present. It was simply due to the fast attack swimming speeds of these two salmonid species in contrast to the slower escape swimming speeds of alewives, bloaters, and fathead minnows. In addition, these prey species were generally found in the pelagic or at least were in the pelagic often enough so that salmonids could attack them.

Coho salmon did not exhibit switching with bloaters and yellow perch; coho salmon foraged preferentially on the bloaters. As with the rainbow trout, learning did occur. Chinook and coho salmon had been fed trout chow or non-living prey, and they had to "learn" to forage efficiently on live prey. Interestingly, the behaviors were not very different among the two salmonid species.

The yellow perch was not a preferred species with the chinook and coho salmon. Yellow perch were not easily captured because of their fast escape swimming speeds and the ability to turn sharply and to utilize different locations within the experimental aquarium. Often, chinook and coho salmon would forego easy captures of yellow perch; they did so after some foraging experience on this species. While it is unclear why yellow perch was not a preferred prey species, a possibility was that the spines on the fins of the yellow perch made it less desirable. Although chinook salmon were more successful at capturing fathead minnows, and coho salmon were more successful at catching bloaters, there was not a clear difference in capture success between alewives, bloaters, and fathead minnows.

The most important character responsible for the capture of these three species was the coincident location of salmonid species and prey species. Any of these three prey species would be attacked if they were found in the same area as the salmonid species. Efficiency of capture played a secondary role in the actual prey selection; since all three species were similar in their relative abilities to escape predation once they were in the pelagic.

What predictions can be made concerning the diets of chinook and coho salmon? The most important behavioral characteristic in prey selection was the coincident location of prey items and their salmonid predators. In addition, some species were more easily captured because of the relationship between the salmonid attack swimming speeds and the prey escape swimming speeds. Consequently, it was clear that these salmonid species will not be capable of effectively utilizing the inshore forage fishes whose populations are presently growing.

The two species of shiners did not utilize a habitat or location in the water column which allowed efficient harvesting by salmonids. Also these prey species exhibited certain other behavioral characteristics which made them less vulnerable to predation by salmonids than other species. They were fast, turned sharply, exhibited schooling behavior, and, in general, were a difficult prey to catch.

Yellow perch will probably not serve as an efficient forage base for chinook and coho salmon. This species was simply not a preferred prey species by these salmonids. Yellow perch also exhibited behaviors which made them difficult to capture. Chinook and coho salmon probably would actively pursue some of the smaller yellow perch. And perhaps large chinook and coho salmon in Lake Michigan could efficiently forage on small yellow perch.

It was unclear if smelt will become an important forage base for these salmonid species. Smelt remained at the very top of the water column, but when they were attacked by chinook or coho salmon, they were usually captured. Smelt generally did not have the same vertical distribution as alewives in Lake Michigan (Crowder et al, 1981). During the day, smelt were in colder and deeper waters, but at night, they migrated upward and were found in warmer water and were higher in the water column than most alewives (Brandt et al, 1980).

In this study, smelt apparently avoided predation by staying at the top of the water column. But, perhaps, smelt avoid predation in Lake Michigan by utilizing deeper waters during the day and warmer surface waters at night. They would avoid predation during the day because they would not have the same vertical distribution as salmonids and there would be little contact between the smelt and the salmonids. Since salmonids use vision to find prey, smelt could occur in warmer waters, higher in the water column, at night because salmonids would have difficulty finding them. Brandt et al (1980) and Crowder et al (1981) explained the differences in vertical distribution between alewives and smelt as a result of competition. Regardless of what caused the difference in vertical distribution of these two species, the difference might account for the lower predation of smelt by the salmonids (Jude et al, 1987). However, if competition with alewives decreased because of the low population size of alewives, smelt might occur at those depths where alewives were usually found and might become more vulnerable to salmonid predation.

Alewives and bloaters were two of the easier prey species captured by the salmonids; unfortunately, they were not available during the same time periods when the study was being conducted. Both species appeared to be capable of providing a forage base for the salmonids. However, bloaters in Lake Michigan rarely became a predominant species in the diets of these salmonids (Jude et al, 1987). Why? Bloaters in Lake Michigan were a bottom dwelling species while alewives usually occurred higher in the water column (Crowder and Crawford, 1984). The alewife was probably the principal forage because it occurred at similar depths or locations as the salmonids, and bloaters will probably not become the principal forage species because they were located in a different portion of the water column than the salmonids.

Crowder (1986) pointed out that bloaters were higher in the water column before alewives became so prevalent in Lake Michigan. He believed that the present vertical distribution of bloaters and alewives is a result of competition between the two species. As bloaters changed their distribution, there was a morphological change which apparently allowed better use of the benthic portion of Lake Michigan (Crowder, 1986). With the decrease in alewives, the possibility exists that bloaters might occur higher in the water column and might become more available to salmonids. If the latter changes in distribution occur, bloaters might become a more important part of the forage base of salmonids.

SUMMARY

1. There were several behaviors which prey species utilized to avoid predation. Schooling was a very effective characteristic of some species to avoid predation. Only three prey items were captured when they were part of a fish school and these prey were either at the very front of the school or the back part of the school. Individual prey also utilized sharp turning abilities and fast escape swimming speeds to avoid predation. Morphological characteristics also appeared to be important in avoiding predation. The silvery ventral surfaces allowed some prey species to avoid predation. There was some characteristic about yellow perch which made them less appealing to salmonids than other prey species. It might be the spines which make this species a less desirable one.

2. Rainbow trout had difficulty capturing prey in the pelagic portion of the experimental aquarium. Alewives, bloaters, and fathead minnows appeared to be easier for them to capture in the pelagic portion than other species. Rainbow trout showed a switching type of predation with yellow perch and alewives. The switching occurred not because of any changes in the foraging behaviors of the rainbow trout, but was due to a habitat or location change by yellow perch within the experimental aquarium. Most prey were captured along physical structures or were trapped in corners.

3. Chinook salmon captured all prey items in the pelagic portion of the experimental aquarium. They had less difficulty in capturing alewives, bloaters, and fathead minnows, but they attacked all prey regardless of species in the same manner. The major difference between chinook salmon and rainbow trout was that if chinook salmon missed a prey or were required to chase a prey, they could attain maximum attack speeds in at least 0.033 seconds and lost virtually no speed when turning to pursue a prey.

4. Coho salmon also captured all of their prey in the pelagic portion of the aquarium, and had less difficulty capturing alewives, bloaters, and fathead minnows than other prey species. Their foraging behaviors and swimming capabilities were similar to chinook salmon. Coho salmon tended to utilize the lower portion of the pelagic zone in the experimental aquarium while chinook salmon generally were slightly higher in the water column. There were also some minor differences in the frequency with which they utilized a particular type of predation pattern. There was no switching behavior exhibited by coho salmon when presented with different proportion of bloaters and yellow perch.

5. Generally, the three salmonid species attacked prey species which had a similar vertical distribution to their own.

6. Possibilities of alternate prey species contributing to the salmonid forage base were discussed.

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Table 1. Ranges of Maximum Attack Swimming Speeds of Rainbow Trout and Reactive Distances and Maximum Escape Swimming Speeds of Prey Species in the Open Water Portion of the Experimental Aquarium.

Prey Species	Trials	Percentage of Captures	Range of Reactive Distance	Escape Velocity Ranges	Attack Velocity Ranges
		%	m	m/secm/sec	
Alewives	30	27	0.00-0.45	1.7-4.3	0.5-3.6
Bloaters	8	25	0.00-0.09	0.7-2.4	0.7-2.4
Fathead Minnows	8	25	0.02-0.39	1.0-3.6	1.2-3.6
Spottail Shiner	3	0	0.05-0.17	2.3-3.6	1.4-2.4
Yellow Perch	24	8	0.00-0.33	1.4-4.3	0.7-4.3

Table 2. Results of Rainbow Trout Foraging on Different Proportions of Alewives and Yellow Perch—The Number of Each Species Remaining After 15 Minutes of Foraging. YP = Yellow Perch; A = Alewives.

Proportions	Trials	Number of Each Species After 15 Minutes
15YP:5A	1	6YP:5A
	2	4YP:3A
	3	0YP:0A
10YP:10A	1	3YP:10A
	2	3YP:8A
	3	3YP:1A
5YP:15	1	0YP:11A
	2	0YP:9A

Table 3. Ranges of Maximum Attack Swimming Speeds of Chinook Salmon and Reactive Distances and Maximum Escape Swimming Speeds of Prey Species in the Open Water Portion of the Experimental Aquarium.

Prey Species	Trials	Percentage of Captures	Range of Reactive Distances	Escape Velocity Ranges	Attack Velocity Ranges
	%	m	m/sec	m/sec	
Alewives	14	36	0.00-0.18	1.1-3.6	1.4-4.3
Bloaters	83	30	0.00-0.02	1.5-2.9	1.8-3.3
Fathead Minnows	22	73	0.00-0.17	0.5-3.6	0.8-4.9
Spottail Shiners	2	50	0.00-0.11	2.4-2.6	2.6-3.0
Yellow Perch	13	62	0.00-0.16	1.0-3.6	2.4-3.6

Table 4. Ranges of Maximum Attack Swimming Speeds of Coho Salmon and Reactive Distances and Maximum Escape Swimming Speeds of Prey Species in the Open Water Portion of the Experimental Aquarium.

Prey Species	Trials of Captures	Percentage Reactive Distances	Range of Velocity Ranges	Escape Velocity Ranges	Attack Velocity Ranges
	%	m	m/sec	m/sec	
Alewives	3	67	0.00	2.1	2.7-2.9
Bloaters	169	78	0.00-0.19	1.3-2.7	2.1-3.0
Fathead Minnows	22	27	0.00-0.18	0.5-4.1	1.0-4.9
Spottail Shiners	3	33	0.00-0.05	1.4-4.3	2.9-4.3
Yellow Perch	22	18	0.00-0.24	1.0-4.8	1.1-4.8

Table 5. Coho Salmon Foraging Attempts at Different Proportions of Bloaters and Yellow Perch.

Proportions	Trials	Bloaters		Yellow Perch	
		Attempts	Captures	Attempts	Captures
15YP:5B	1	6	4	7	2
	2	9	4	1	0
	3	11	5	5	1
10YP:10B	1	10	5	0	0
	2	7	6	0	0
	3	9	8	5	2
10YP:5B	1	5	5	6	2
	2	6	5	2	0
	3	5	3	3	0
5YP:10B	1	5	4	0	0
5YP:15B	1	11	5	0	0
	2	12	12	0	0
	3	19	14	5	0

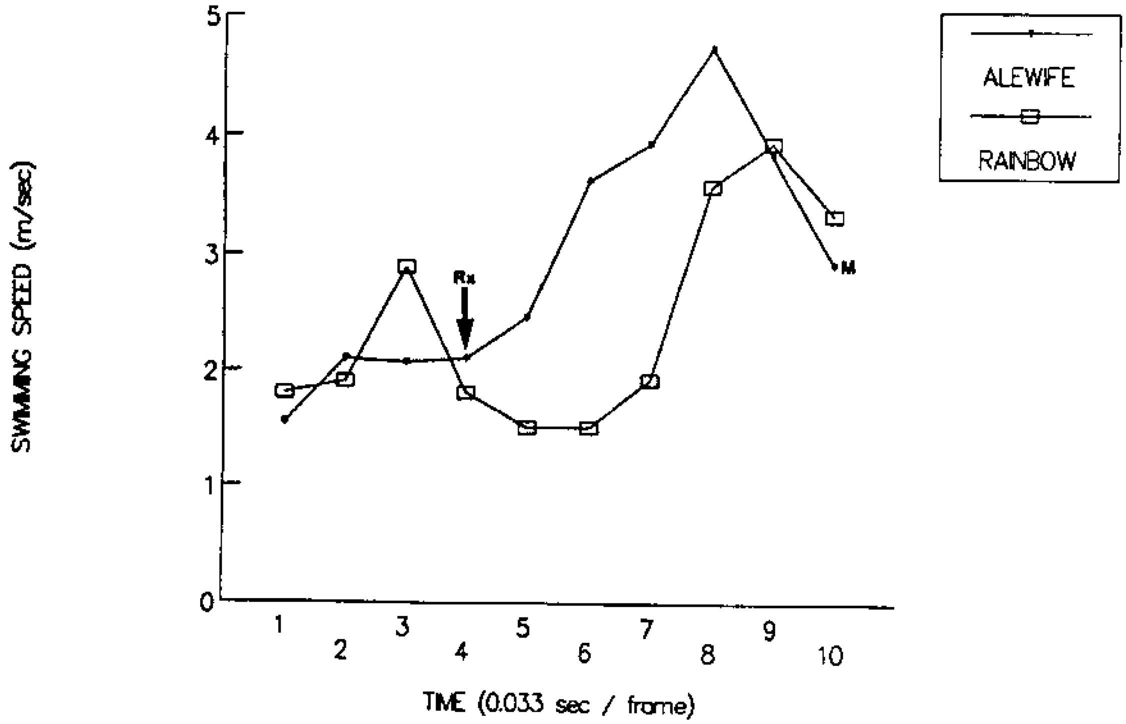

Figure 1. Swimming Speeds of Rainbow Trout and an Alewife During an Attack

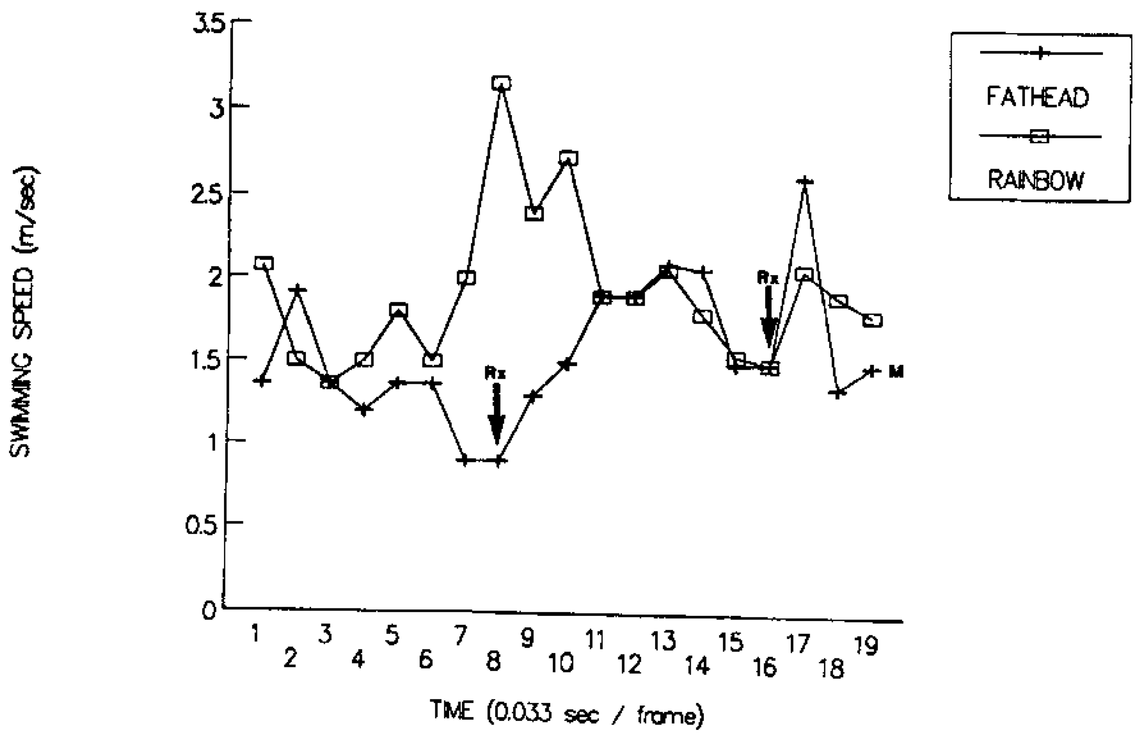

Figure 2. Swimming Speeds of Rainbow Trout and a Fathead Minnow During an Attack

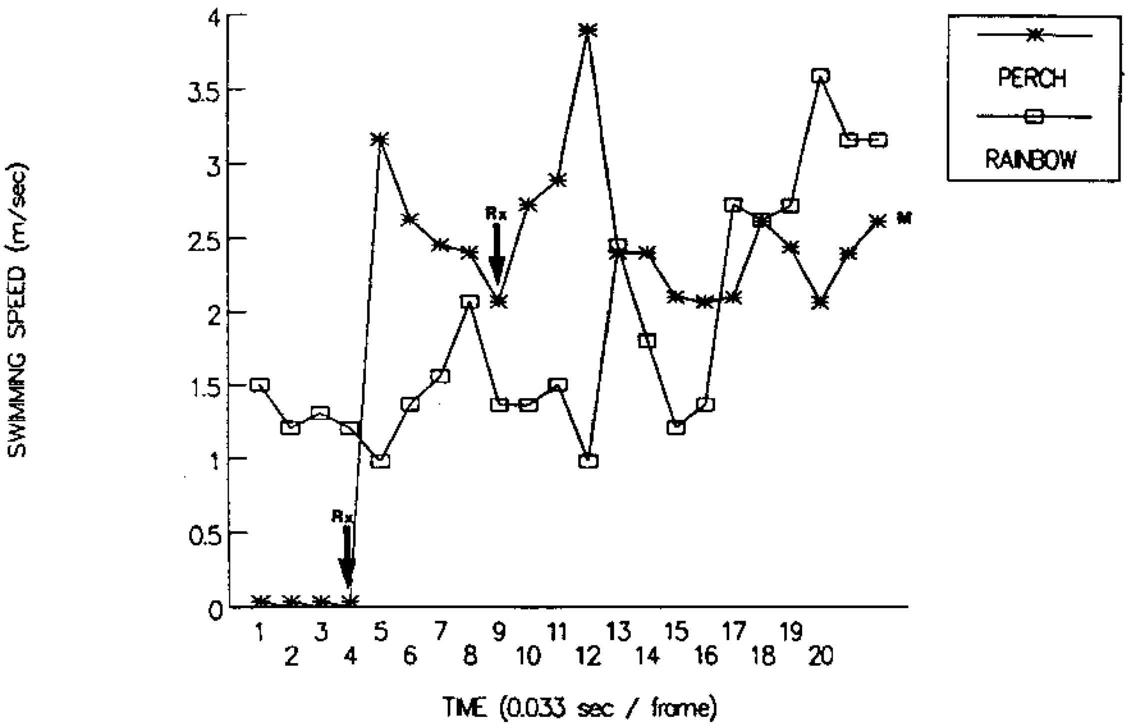

Figure 3. Swimming Speeds of Rainbow Trout and a Yellow Perch During an Attack

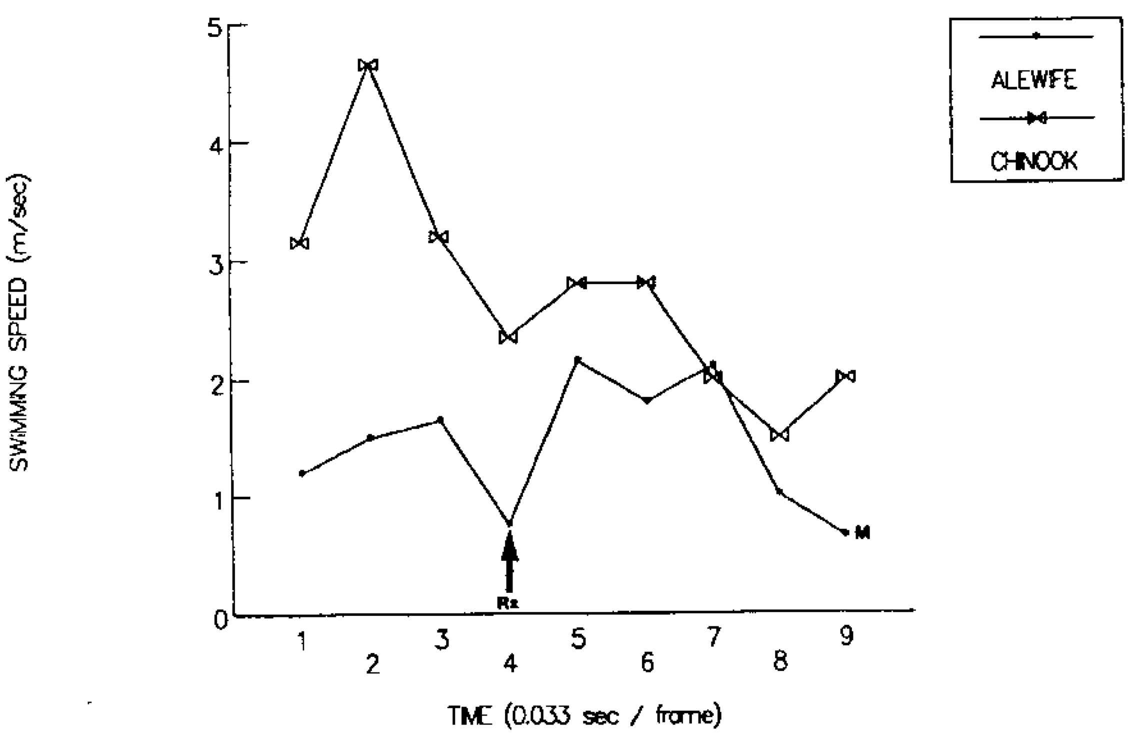

Figure 4. Swimming Speeds of Chinook Salmon and an Alewife During an Attack

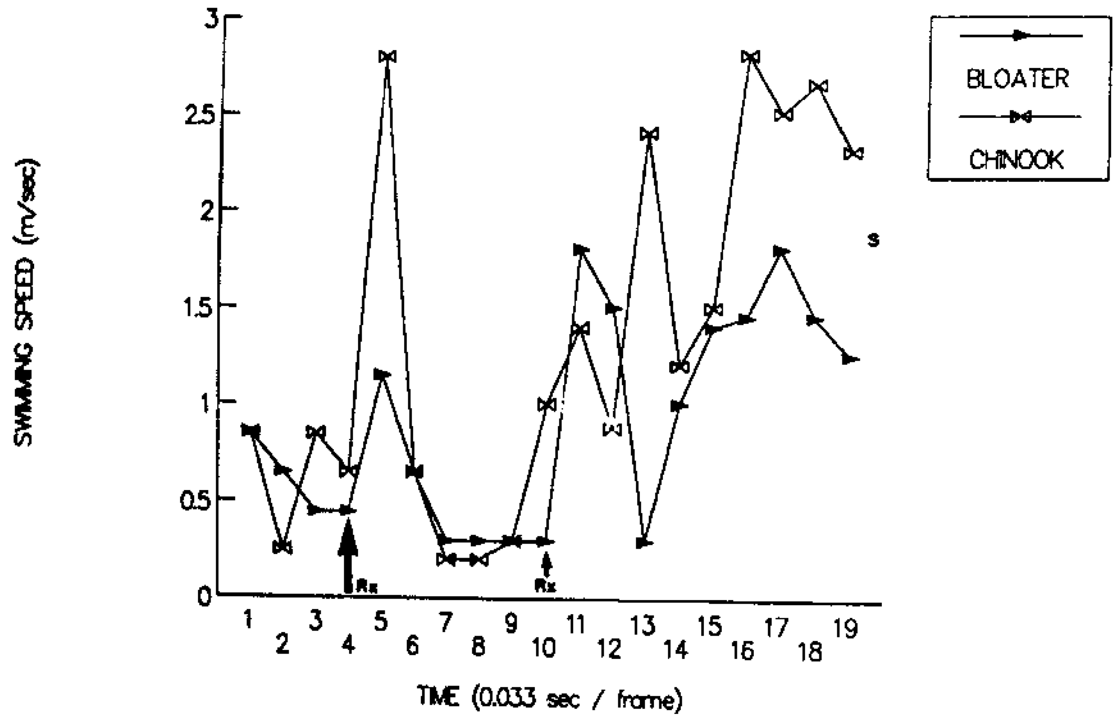

Figure 5. Swimming Speeds of Chinook Salmon and a Bloater During an Attack

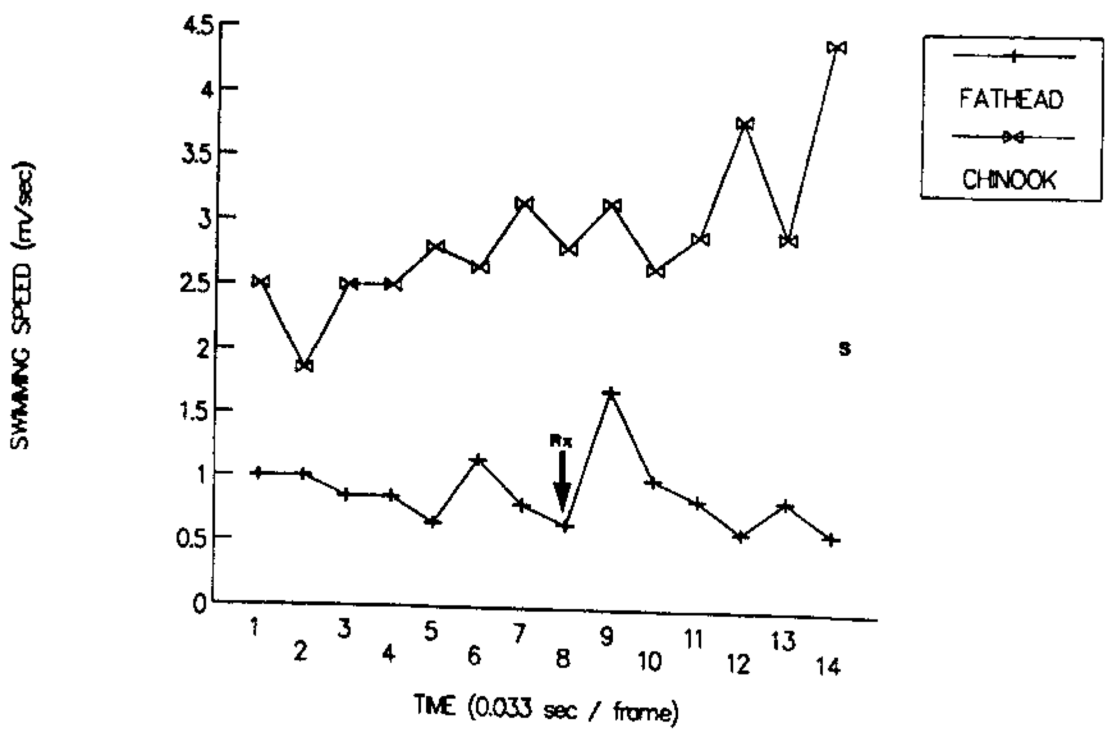

Figure 6. Swimming Speeds of Chinook Salmon and a Fathead Minnow During an Attack

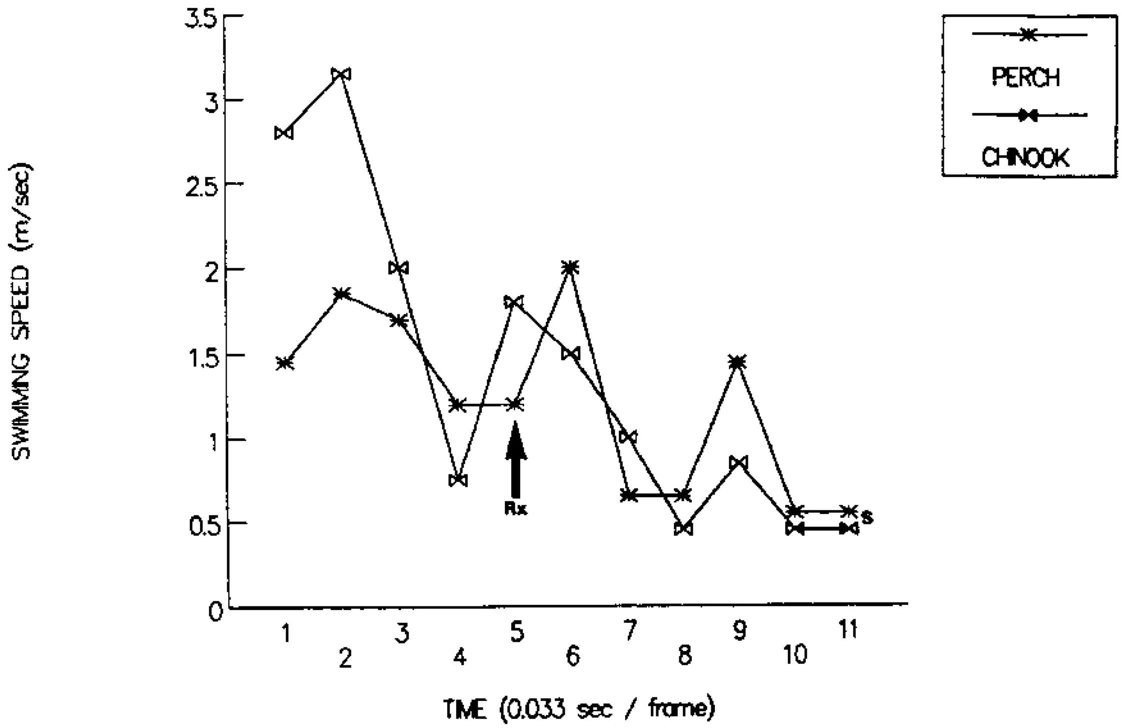

Figure 7. Swimming Speeds of Chinook Salmon and a Yellow Perch During an Attack

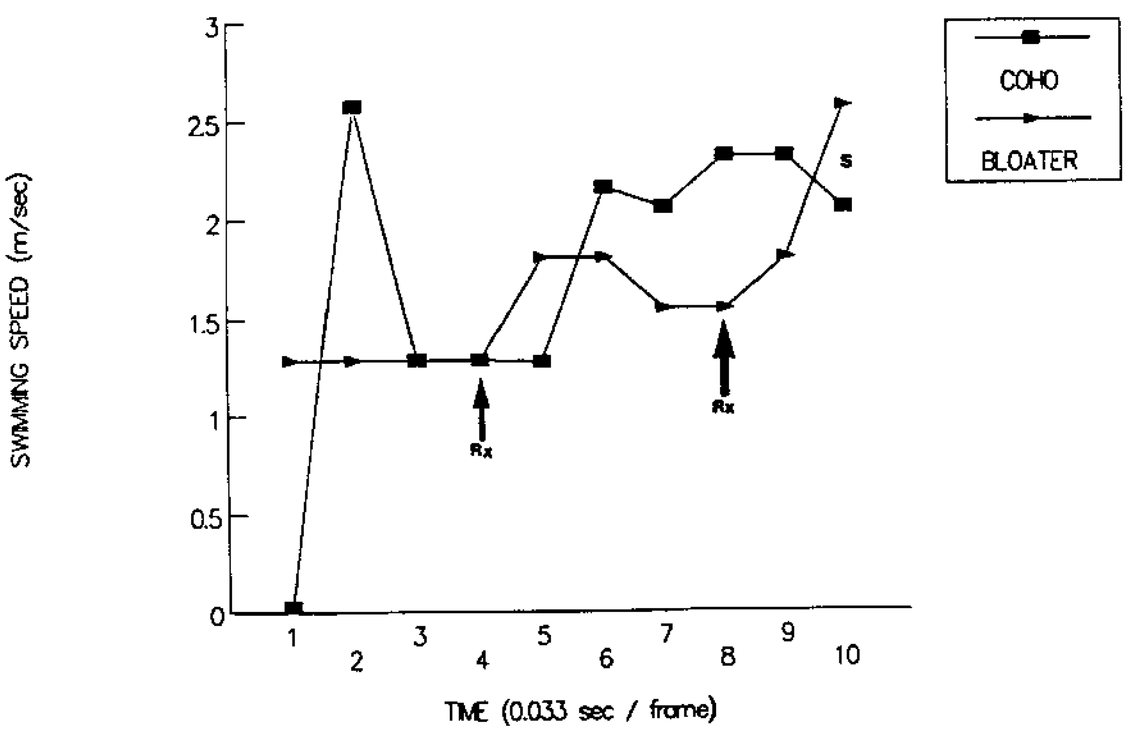

Figure 8. Swimming Speeds of Coho Salmon and a Bloater During an Attack

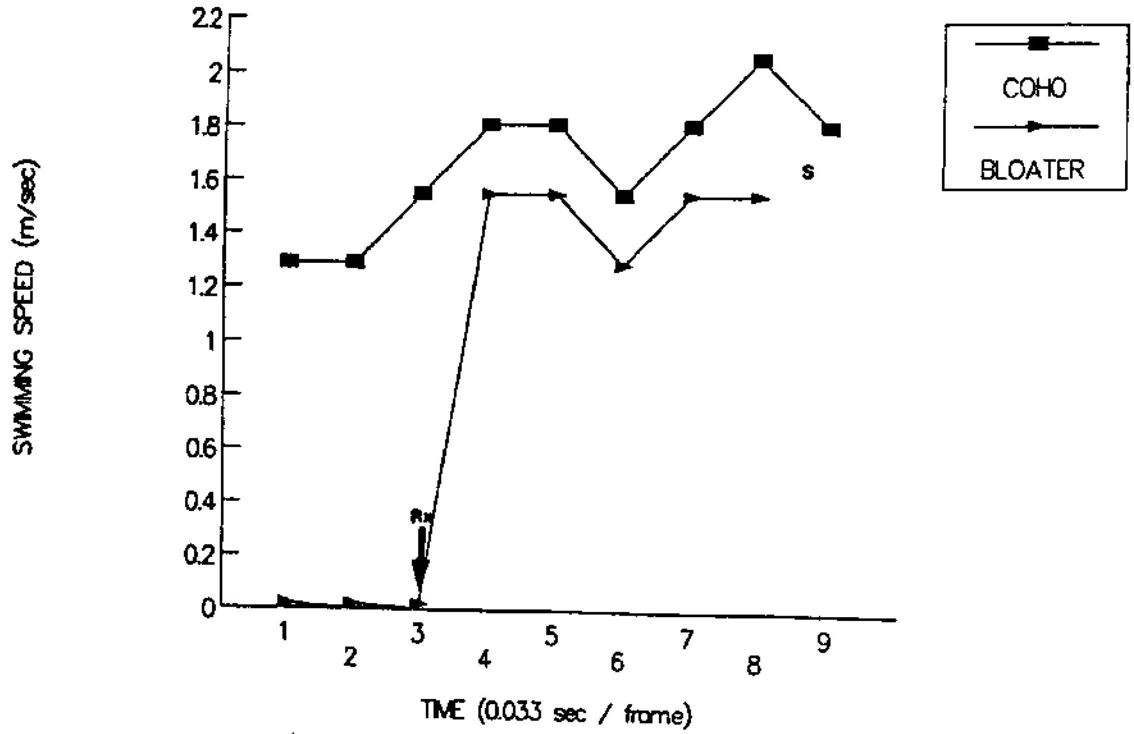

Figure 9. Swimming Speeds of Coho Salmon and a Different Bloater During an Attack

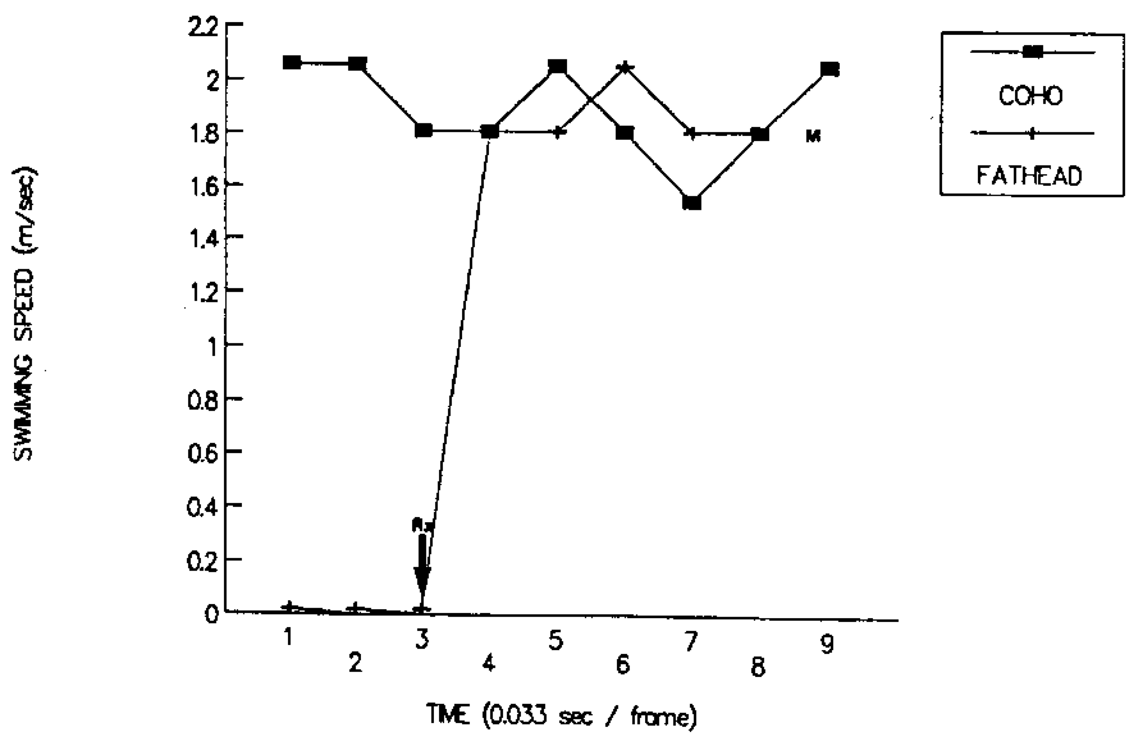

Figure 10. Swimming Speeds of Coho Salmon and a Fathead Minnow During an Attack

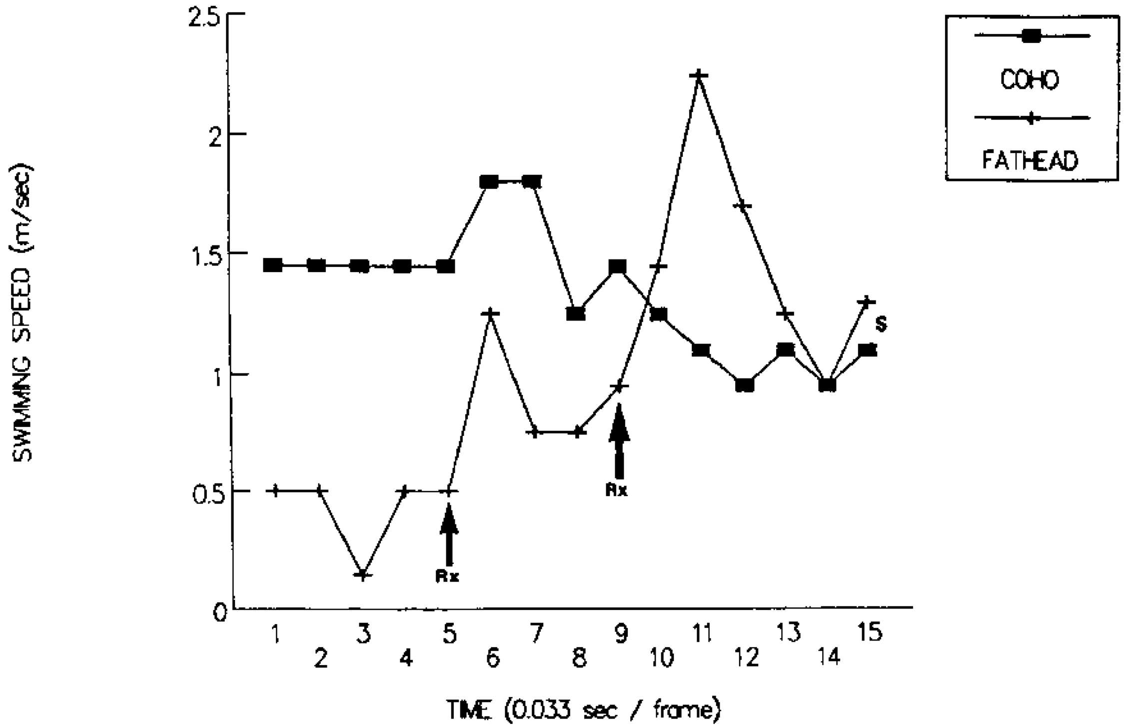

Figure 11. Swimming Speeds of Coho Salmon and a Different Fathead Minnow During an Attack

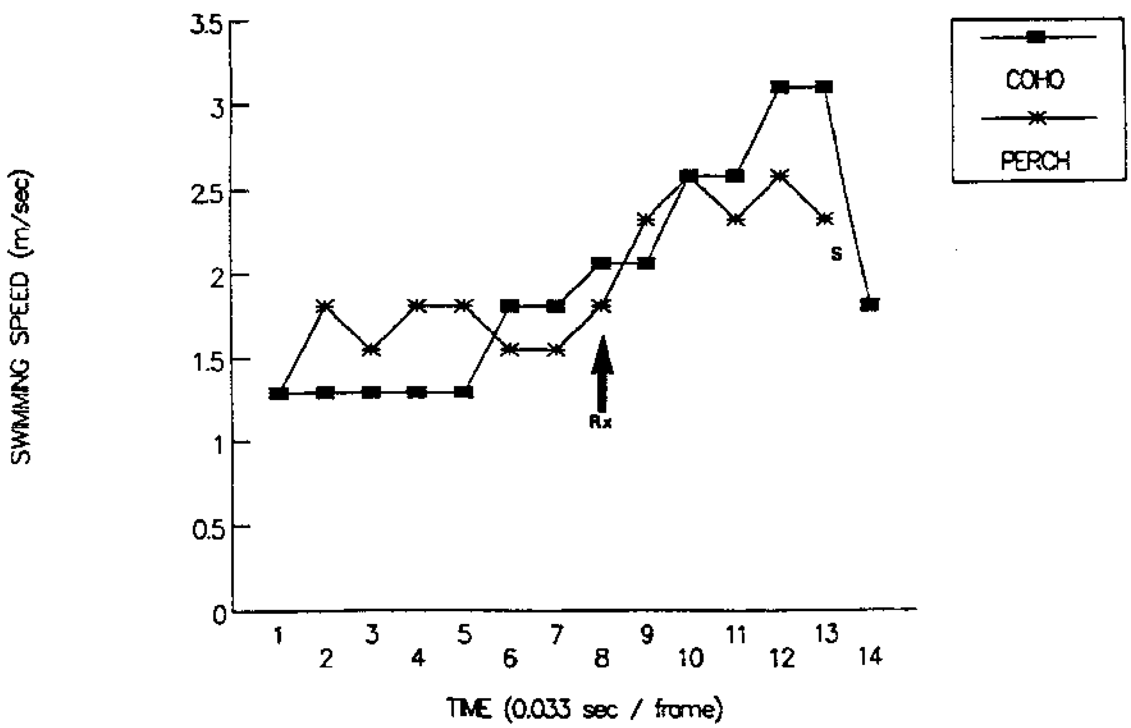

Figure 12. Swimming Speeds of Coho Salmon and a Yellow Perch During an Attack