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Food Interrelationships of Salmon, Trout, Alewives, and Smelt in a Maine Lake¹

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ABSTRACT

Food habits of landlocked salmon (*Salmo salar*), brook trout (*Salvelinus fontinalis*), landlocked alewives (*Alosa pseudoharengus*), and American smelt (*Osmerus mordax*) were studied in Echo Lake, Mount Desert Island, Maine, from June, 1967, to May, 1968. Landlocked alewives were introduced into Echo Lake as adults taken from Cayuga Lake, New York, in 1966.

Annual salmon diet consisted of invertebrates (mainly insects) and several forage fishes [alewives, smelt, sticklebacks, (*Pungitius pungitius*), and killifish (*Fundulus diaphanus*)]. Smelt were eaten during the entire year, killifish and sticklebacks during summer, and alewives only during spring. Brook trout had similar food habits except that sticklebacks were used throughout the year, and invertebrates constituted a higher proportion of their overall diet. Brook trout fed heavily on isopods (*Asellus* sp.) during winter and early spring. Alewives fed extensively on plankton with insects constituting important food only during summer months. Smelt utilized a higher proportion of insects and isopods than did alewives, but fed mainly on plankton.

Landlocked alewives were utilized only to a limited extent by salmon and brook trout, but would likely be preyed upon more heavily by larger fish.

INTRODUCTION

The American smelt is the most important forage fish for landlocked salmon in most Maine lakes (Rupp, 1968; Havey and Warner, 1968 manuscript). The potential of smelt populations to support landlocked salmon fisheries has been shown by many studies (Cooper, 1940; Fuller and Cooper, 1946; Havey and Warner, 1968 manuscript).

Since the forage value of smelt in certain Maine lakes is greatly reduced by population fluctuations, other species have been considered to provide supplementary forage. Special attention has been given to the landlocked alewife. The widely publicized success of landlocked alewives in supporting various game fishes in New York and, more recently, the apparent success of alewives as forage fish in Lake Michigan, has further enhanced interest in this species as a forage fish.

The alewife was originally limited to the Atlantic coast of North America and probably occurred only in the anadromous form (Threinen, 1958). However, introductions and altered waterways have extended distribution into many freshwater lakes. Today there

are many landlocked populations along the eastern coast of the United States and Canada. Lake Ontario, as well as several of the Finger Lakes of New York, have supported landlocked alewives since the late nineteenth century. Lakes Erie, Huron, Michigan, and Superior have acquired populations since 1930 (Miller, 1957). Freshwater alewife populations were well established in New Jersey by 1850 (Gross, 1953).

Anadromous alewives, as forage for warm-water fishes, have been used successfully in New York for several years (Vincent, 1960). Foye (1956) described similar management procedures used with success in several Maine lakes. When mature alewives are stocked prior to spawning, the young of the year provide immediate forage. However, both adults and young apparently fail to survive beyond late fall of the year of introduction.

Permanently established alewives in Cayuga Lake, New York, are heavily utilized by lake trout (Webster, Bentley, and Galligan, 1959) as well as by smallmouth bass (Webster, 1954). Utilization of landlocked alewives in New Jersey by many warmwater species, as well as by brown trout, has been reported (Gross, 1953). The coho salmon fishery of

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TABLE 1.—Stomach contents of landlocked Atlantic salmon collected in Echo Lake from June, 1967, to May, 1968. Results are given as mean percentages of total stomach content by volume. Lengths (total) are given in inches

Month	Sample size	Mean length	Smelt	Sticklebacks	Killifish	Alewives	Unidentified fish	Invertebrates
June, 1967	3	10.8	10	30	0	0	23	37
July	11	12.1	27	9	7	0	7	50
August	10	12.4	30	10	0	0	22	38
September	25	13.8	55	4	2	0	17	24
October	9	12.3	22	0	11	0	22	44
November	2	12.9	0	0	0	0	100	0
December	0	—	—	—	—	—	—	—
January, 1968	2	13.1	0	0	0	25	50	25
February	0	—	—	—	—	—	—	—
March	1	12.1	0	0	0	75	25	0
April	5	14.5	17	0	0	73	0	10
May	11	14.9	36	6	0	9	9	40

Lake Michigan apparently is dependent to a large extent on alewives.

The potential of alewives as forage fish for landlocked salmon has never been fully evaluated. Utilization of young anadromous alewives has been reported by Havey (1952) and several other workers, but these data were obtained incidental to other research.

STUDY AREA

Echo Lake, located on Mount Desert Island, Hancock County, Maine, is partially in Acadia National Park. Surface area is approximately 237 acres (96 ha) and the maximum depth is 63 ft (19.2 m). The lake is oligotrophic and of glacial origin, as are most lakes of this region.

Established fish populations in Echo Lake include landlocked salmon (*Salmo salar*), brook trout (*Salvelinus fontinalis*), landlocked alewives (*Alosa pseudoharengus*), American smelt (*Osmerus mordax*), banded killifish (*Fundulus diaphanus*), ninespine stickleback (*Pungitius pungitius*), golden

shiner (*Notemigonus crysoleucas*), and American eel (*Anguilla rostrata*).

Landlocked salmon were introduced in 1965 as age 0+ fall fingerlings. Adult landlocked alewives from Cayuga Lake, New York, were introduced in June, 1966, and successfully spawned that summer and each summer since. Brook trout were stocked periodically as fingerlings (age 0+) and yearlings (age I+).

METHODS

All fish used for stomach analysis were captured by either horizontal or vertical gill nets (Lackey, 1968) and preserved in 10% formalin. Stomach contents were measured volumetrically unless stated otherwise.

Determination of alewife and smelt stomach contents volumetrically was time consuming and results were of questionable accuracy. For these two species analysis of contents by careful estimation of volume of each item was expressed as a percentage of total stomach content. This method proved to be of comparable accuracy to actual measurement by

TABLE 2.—Stomach contents of brook trout collected in Echo Lake from June, 1967, to May, 1968. Results are given as mean percentages of total stomach content by volume. Lengths (total) are given in inches

Month	Sample size	Mean length	Smelt	Sticklebacks	Killifish	Alewives	Unidentified fish	Invertebrates
June, 1967	0	—	—	—	—	—	—	—
July	8	10.3	10	5	32	6	4	43
August	6	9.3	0	13	17	0	17	53
September	2	11.1	0	50	0	0	30	20
October	0	—	—	—	—	—	—	—
November	5	9.4	20	0	0	0	8	73
December	0	—	—	—	—	—	—	—
January, 1968	13	7.1	8	8	0	0	6	79
February	0	—	—	—	—	—	—	—
March	2	8.8	0	0	0	50	15	35
April	4	9.8	0	24	0	0	31	44
May	8	9.3	24	11	0	0	9	56

TABLE 3.—Stomach contents of landlocked alewives collected in Echo Lake from June, 1967, to May, 1968. Results are given as mean percentages of total stomach content by volume. Lengths (total) are given in inches

Month	Sample size	Mean length	Plankton	Insects-isopods	Miscellaneous material	Unidentified
June, 1967	54	4.3	57	24	0	19
July	28	4.8	67	28	0	5
August	8	5.3	70	30	0	0
September	0	—	—	—	—	—
October	0	—	—	—	—	—
November	15	6.3	100	0	0	0
December	1	6.1	100	0	0	0
January, 1968	53	6.2	100	0	0	0
February	0	—	—	—	—	—
March	32	6.4	100	0	0	0
April	18	6.4	95	0	5	0
May	3	6.8	90	10	0	0

water displacement. The total amount of material found in even a full alewife or smelt stomach was always small, and a marked degree of homogeneity of diet during most of the year minimized errors associated with subjective evaluations.

The stomach contents of salmon and trout were analyzed by the water displacement method. Each food type was recorded as a percentage of the entire stomach content volume.

RESULTS

Salmon

Data from salmon stomachs were arranged in monthly periods and each food type was then expressed as a mean percentage occurring in fish (Table 1). During this study, all salmon in Echo Lake were from the 1965 brood year. All sampled fish were between 9 and 19 inches (22.9 and 48.3 cm) in total length, with the majority ranging between 12 and 16 inches (30.5 and 40.6 cm).

Food habits of salmon from Echo Lake showed definite seasonal variations. Fish constituted 50% or more of the diet (by volume) during each month for which data are available. Smelt utilization was relatively constant, at least during spring, summer, and fall. Unidentified fish were probably smelt, since other forage fish were much easier to identify even after partial digestion. Banded killifish provided forage for salmon during summer, but little or none during late fall, winter, and spring. Sticklebacks occurred quite frequently in salmon stomachs during summer, but not during the remainder of the year. Alewife utilization was limited to spring.

The invertebrate portion of the diet consisted mainly of immature insects and isopods (*Asellus* sp.). Salmon stomachs contained insects more frequently during late spring, summer, and early fall, as might be expected. Isopod utilization was heaviest from winter to early spring.

Brook Trout

The food of brook trout collected from Echo Lake is given in Table 2. The diet of brook trout averages about 50% fish and 50% invertebrate organisms. The only significant variation in these percentages occurred in fall and winter months. The high invertebrate diet in January reflects a high frequency of isopods.

Sticklebacks were used fairly consistently as forage much of the year. Killifish, although heavily utilized in summer, were conspicuously absent during the other months. Smelt provided significant, but intermittent forage. At least some alewives were utilized in late winter, although the sample is small.

Alewives

Food habits of 1966 brood year alewives are summarized in Table 3. The alewife diet was exclusively planktonic animals (mainly Copepoda and Cladocera) during much of the year. Insects became increasingly important as food during late spring and summer. Isopods were rarely found in alewife stomachs.

Available data on other alewife age classes indicated that older alewives utilized higher percentages of insects, but plankton was still the main food source. The 1967 brood year alewives fed almost exclusively on plankton.

TABLE 4.—*Stomach contents of smelt collected in Echo Lake from June, 1967, to May, 1968. Results are given as mean percentages of total stomach content by volume. Lengths (total) are given in inches*

Month	Sample size	Mean length	Plankton	Insects-isopods	Miscellaneous material	Unidentified
June, 1967	31	3.5	16	29	13	43
July	26	3.5	47	38	0	15
August	6	3.5	75	1	8	15
September	1	3.6	100	0	0	0
October	0	—	—	—	—	—
November	3	4.2	0	100	0	0
December	0	—	—	—	—	—
January, 1968	0	—	—	—	—	—
February	0	—	—	—	—	—
March	0	—	—	—	—	—
April	1	4.2	100	0	0	0
May	0	—	—	—	—	—

Smelt

Stomach contents of 1966 brood year smelt are presented in Table 4. Obtaining adequate numbers of smelt stomachs proved difficult except during summer months. Of the small number collected during the remainder of the year, a high percentage had empty stomachs.

It is probably safe to assume that most of the material labeled "unidentified" in Table 4 is actually plankton. Digestion proceeds rapidly on Copepoda, Cladocera, and other zooplankters, and, consequently, positive identification was often impossible.

Smelt of the 1966 year class utilized plankton and insects during summer, with the bulk of the diet consisting of plankton. The food of smelt during the remainder of the year is difficult to evaluate, but it is apparent that at least some plankton, insects, and isopods are eaten.

DISCUSSION

Landlocked salmon, like many fish, change to predominantly fish diets after attaining a certain size. Fuller and Cooper (1946) examined 42 landlocked salmon between 12.2 and 23.3 inches (31.0 and 59.2 cm, total length) from lakes on Mount Desert Island and surrounding areas and found that of the 24 stomachs containing food, 97% of the diet was smelt by volume. Havey and Warner (1968 manuscript) state that young landlocked salmon gradually change from an insect to a fish diet after migrating to the lake from the nursery area. The principal forage fish are smelt, alewives, sticklebacks, yellow perch, and various minnows. All available data support the widely held belief that smelt are the

primary forage fish of landlocked salmon in Maine lakes.

The food habits of salmon in Echo Lake do differ somewhat from those observed in many Maine lakes (Havey and Warner, 1968 manuscript). The proportion of invertebrates in the diet of Echo Lake salmon is roughly a third of the total diet. No one fish species dominates the diet as might be expected with populations of schooling fish such as smelt and alewives inhabiting the lake. There are several factors which might account for the wide variety of foods eaten by salmon in Echo Lake.

The data seem to indicate a distinct lack of a satisfactory forage fish abundant enough to supply the dietary needs of Echo Lake salmon. After attaining legal length (35.6 cm), salmon feed heavily on smelt, if available, but other fish are occasionally utilized (Cooper, 1940; Havey and Warner, 1968 manuscript). However, the smelt population in Echo Lake is low. The 1966 brood year alewives were abundant, but too large to be eaten by 1965 brood year salmon, most of which were between 30.5 and 40.6 cm long during this study.

It is not entirely clear why salmon did not utilize 1967 brood year alewives more heavily, since this year class was apparently available in significant numbers. The utilization of banded killifish and ninespine sticklebacks (primarily inshore species in Echo Lake) indicates salmon were either moving into shallow water in search of food or eating these species incidental to other movement. Netting data make it seem unlikely that these two forage species venture into deeper water.

Brook trout in Echo Lake had food habits similar to salmon, but differ in several important aspects. The occurrence of killifish and sticklebacks in significant numbers is a strong indication trout were primarily inshore feeders. The occurrence of large numbers of sticklebacks and killifish in individual stomachs, when they were found at all, supports this contention. Smelt usually were found in small numbers, indirectly supporting the conclusion that the smelt population was relatively low and that, as a result, predation on this species was somewhat sporadic.

Compared to salmon, trout fed on isopods quite heavily. The most intense utilization of isopods was by trout captured near the only permanent inflowing stream, particularly smaller trout captured in that area in winter and early spring. Brown trout were observed by Berglund (1968) to feed heavily on isopods in a small pond in Sweden during winter and early spring. Seasonal variation is apparently related to the life cycle of the isopod and not the movement or changing food preference of the trout. Although utilization of insects was continuous throughout the year, the greatest numbers were eaten during spring and summer. This feeding pattern contrasts sharply with the low use of isopods during summer, and may be associated with the greater availability of insects during certain times, particularly in late spring and early summer.

The diet of alewives in Echo Lake agrees quite closely with that determined by other workers at other lakes. Hutchinson (1968a and 1968b) reported that alewives in Black Pond, a small New York pond, fed primarily on zooplankton during summer, but also fed extensively on Diptera larvae when available (mainly in September). Unfortunately, data are not available on fall, winter, and spring food habits of alewives in Black Pond. Odell (1934a and 1934b) found microcrustacea to constitute about 46% of the alewife diet by volume in Seneca Lake, New York. Odell also found insects and alewife eggs made up a significant part of the diet in June and July. Morsell and Norden (1968) reported the diet of Lake Michigan alewives to be mainly copepods and amphipods.

The utilization of Diptera larvae in Echo

Lake is similar to that reported by Hutchinson (1968a and 1968b) in Black Pond, but quite different from that reported by Morsell and Norden (1968) for Lake Michigan. This might be expected because of the greater availability of Diptera larvae in a small lake. Morsell and Norden found copepods and amphipods (*Pontoporeia affinis*) to be the main food items, while midge larvae, ostracods, and hydracarina formed minor parts of the diet.

The food habits of smelt have been the subject of much controversy among sportsmen and fishery biologists. The presence of well developed teeth supports the commonly held belief that smelt are heavy predators on other fish, and perhaps juvenile game fish. Many studies have shown this to be erroneous. Kendall (1927) showed smelt diet, at least in New England, to be highly variable, but primarily consisting of zooplankton. Creaser (1926), Greene (1930), Schneberger (1937), and Van Oosten (1940) all showed zooplankton to be the main food item. Gordon (1961) showed that zooplankton and insects made up about 92% of the diet of smelt taken in Saginaw Bay, Lake Huron. Rupp (1968) reported 800 smelt stomachs collected at Branch Lake, Maine, and found that the diet was mainly zooplankton and insects. The stomach contents of Echo Lake smelt are virtually the same as those reported by Rupp.

Larger smelt may have a different diet than that reported for the smaller 1966 brood year, but this is unlikely. The available data on large smelt collected from Echo Lake indicate a higher percentage of insects in the diet, but few fish. All of the larger smelt collected in Echo Lake were in the deepest part of the lake, and thus would not likely be in the best location for preying on juvenile game fish or the inshore species used extensively by salmon and trout.

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