## Population Characteristics and Physical

 Condition of Alewives, Alosa Pseudoharengus, in a Massive Dieoff in Lake Michigan, 1967

TECHNICAL REPORT No. 13

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# POPULATION CHARACTERISTICS AND PHYSICAL CONDITION OF ALEWIVES, ALOSA PSEUDOHARENGUS, IN A MASSIVE DIEOFF IN LAKE MICHIGAN, 1967 

by

EDWARD H. BROWN, JR.<br>U.S. Bureau of Commercial Fisheries<br>Biological Laboratory<br>Ann Arbor, Michigan

GREAT LAKES FISHERY COMMISSION
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# POPULATION CHARACTERISTICS AND PHYSICAL CONDITION OF ALEWIVES, ALOSA PSEUDOHARENGUS, IN A MASSIVE DIEOFF IN LAKE MICHIGAN, $1967^{1}$ 

Edward H. Brown, Jr.


#### Abstract

The length, age and sex compositions of dead and dying alewives collected in June 1967 at six locations in southern, central, and northern Lake Michigan are compared with those of fish taken in experimental trawls at five locations in April and June 1967. Behavior at the time of death, condition of the body and gonads, stomach contents, and the incidence of Saprolegnia and subcutaneous hemorrhages also are described for alewives in the dieoff.

The length distributions of alewives in the dieoff and trawl collections were similar and bimodal, Yearlings made up 25 and 42 percent of the respective collections. The average ages of adults (age-group II and older) were nearly identical in the dieoff and trawl collections ( 3.5 and 3.6 years, respectively). Both collections were dominated by age-groups III and IV. The average lengths of adult alewives in age-groups II to V in the dieoff were smaller than or identical to those in the trawl collections, In all collections females were consistently older ( 0.4 year) than the males and larger at the greater ages. The sexes were almost equally represented among age-11 and older fish in the dieoff.

Despite the presence of Saprolegnia and hemorrhages on some fish, alewives in the dieoff appeared robust. Spawning attrition could not have been a major cause of the dieoff because many immature yearlings died and 80 percent of the dead adults were unspawned. The presence of rapidly digestible zooplankton in the stomachs of dead alewives indicated that many fish were feeding just before death. About 20 percent of the alewives in the selected samples of fish from the dieoff were infected by Saprolegnia; twice as many females were infected as males. The fungus was randomly distributed among the size groups. Hemorrhages may have been a symptom or physiological response to the cause of the dieoff because they affected a much higher percentage of the dying alewives (47 percent) than did fungus, Occurrence of the hemorrhages did not differ significantly between the sexes or among the size groups.


1 Contribution No, 377, Ann Arbor Biological Laboratory, U. S. Bureau of Commercial Fisheries.

## Introduction

After the first record of its occurrence near South Manitou Island in 1949 (Miller, 1957). the alewife spread throughout Lake Michigan; its abundance increased tremendously during the 1960 's. The classic population explosion, which crested in the southern and central basins of the lake in 1966 (Fig. 1). was accompanied by progressively heavier spring and summer dieoffs and was climaxed by a massive mortality in June and early July 1967. The 1967 dieoff was in progress by the first week of June and reached its greatest intensity by the third week, when huge windrows of fish were deposited by wind and waves on beaches in Michigan, Indiana, Illinois, and Wisconsin.

An aerial survey on June 22 revealed that the alewife dieoff extended around the circumference of the lake from Arcadia, Michigan, south to Michigan City, Indiana, and along the west shore to Sturgeon Bay, Wisconsin (Fig. 2). Dead alewives were also seen along the east shore of Green Bay,


Figure 1. Relative abundance of adult alewives taken in experimental and Commercial bottom trawls in southern and central Lake Michigan, November 1960-67.


Figure 2. Sampling locations and route (broken line) of the airplane survey of June 22.
and a northward extension of the dieoff was reported at Charlevoix and Petoskey, Michigan. Dead alewives were mostly concentrated within 1 mile of shore and gradually disappeared toward midlake. The accumulation of dead fish was greatest from Benton Harbor, Michigan, to Chicago, Illinois, and was heavier along the Michigan shore of the central basin than along the Wisconsin shore. Prevailing winds, currents. and changes in wind direction affected the daily concentrations of dead fish, and undoubtedly contributed to the vast concentrations at Chicago.

The annual spring and summer dieoff of alewives coincides to some extent with the annual inshore migration in April and May and the subsequent movement into tributaries where alewives spawn from late May to mid-August. Extensive dieoffs in April-August have been observed in Lake Huron in recent years and in Lake Ontario since the early appearance of the fish in the late 1800 's (Miller ${ }^{2}$; Graham, 1956).

The alewife encounters sharp changes in water temperature between the deep, cold waters of the Great Lakes and the shallow, warmer waters inshore and in the tributaries. The possible inability of the fish to adapt to severe temperature changes is one of the more plausible explanations suggested for the mortalities. In Lake Ontario Graham (1956) correlated daily mortalities with water temperature gradients that were intensified by still days and rising air temperatures.

A physiological malfunction that may be triggered by environmental change to cause catastrophic death of the alewife remains to be identified. Hoar (1952) suggested that fish may lose osmotic control in warm water through an exhausted thyroid mechanism possibly related to low iodine in freshwater. It is not known, however. if the thyroid gland has an osmoregulatory function in fish (Pickford and Atz, 1957), but it may influence other important physiological functions of the alewife.

Algal toxicity was recently suggested as the possible cause of the dieoff. Williams (1968) contended that the 1967 mass mortality " . . appears to be related to a bloom of toxic blue-green algae and is not simply the result of the

[^0]alewife's instinctive behavior and lack of ability to adapt to new lake conditions . . ." Alewives were abundant after the dieoff, however, in areas where blue-green algae thrive.

The present report documents the 1967 dieoff--an event of great public concern--and provides background information for further research needed to explain the annual phenomenon.

## Methods

Dead and dying alewives were collected randomly in dip nets from the surface of inshore waters off Michigan City. Indiana; St. Joseph, Saugatuck, Ludington, and Frankfort. Michigan; and Sturgeon Bay, Wisconsin, on June 9 and 27-29, 1967 (Fig. 2). The earliest sampling (June 9) was at Frankfort from a public dock inside the mouth of the Betsie River. The samples at Michigan City were netted from small boats near beaches north and south of the breakwall on June 28 and 29. The sample at St. Joseph was obtained on June 29 by dipping fish just off a public beach near the breakwall. Fish were collected by the R/V Kaho at the southern end of Sturgeon Bay (June 27) and at the mouths of the breakwalls at Ludington (June 28) and Saugatuck (June 29).

Fish were preserved in formalin or frozen and later examined at the Ann Arbor Biological Laboratory. The total length of each fish was recorded in millimeters and most of the adults were weighed to the nearest gram and sexed. Sex could not be determined for age-1 fish. Scales for age determination were removed from an area $4-5$ scale rows below the insertion of the dorsal fin. The number of fish used for age determination and sex composition varied according to the number available or the number needed for the various analyses. Age groups are designated by Roman numerals corresponding to the number of completed annuli. All the fish were considered to have passed into the next higher age group on January 1.

The condition of the gonads of age-11 and older alewives from the dieoff at Saugatuck, Ludington, and Sturgeon Bay was determined by dissection. The gonads of frozen fish retained most of their natural color and surface texture, which is broadly diagnostic of spawning condition.

The incidences of fungus infection (Saprolegnia) and subcutaneous hemorrhaging, common among the dieoff alewives, were recorded for dying fish taken north of the breakwall at Michigan City and at St. Joseph.

The length, sex, and age compositions of fish in the dieoff were compared with those of alewives taken in experimental trawls at the following locations and dates: Saugatuck, April 13; Grand Haven, April 16; Benton Harbor, April 19; Sturgeon Bay (Lake Michigan side), June 9; and Frankfort. June 11. The trawls were of the North Atlantic whiting design and had 39 -foot head ropes, $2-1 / 2$ - to 2 -inch-mesh bodies, and $1 / 2$-inch-mesh cod ends (stretched measure). The trawls were fished on the bottom along the contour at depths of 3 to 50 fathoms.

## Behavior of Dying Fish

The behavior of dying alewives was observed on the afternoon of June 9 at Frankfort and June 28 at Michigan City. The stricken fish swam weakly on their sides in vertical spirals that brought them to the surface. Some exerted sudden bursts of swimming effort and were propelled sideways or downward. Their attempts to regain equilibrium lasted several seconds before they again rose to the surface where they quivered and died. All sizes of alewives died side by side and behaved in the same manner. The behavior of the dying fish in Lake Michigan agrees closely with accounts given for Lake Ontario by Miller' and Graham (1956).

## Length Composition

The length distributions of alewives in the dieoff and trawl collections were similar and bimodal--a lower mode for yearlings and an upper mode for older fish (Table 1). The discontinuity or dip in the individual frequencies fell near 120 mm , which was the arbitrary length used to separate yearlings from adults ( $>120 \mathrm{~mm}$ ). The average length of yearling alewives was greater in the combined dieoff samples ( 88 mm ) than in the trawl collections ( 81 mm ), but the average length of adults in the respective collections were nearly identical (161 and 162 mm ). In five dieoff and trawl collections that came from the five general areas (Michigan CityBenton Harbor-St. Joseph, Saugatuck, Grand Haven-Ludington, Frankfort, and Sturgeon Bay), yearlings from the dieoff were longer than those from trawls in four, but the adults from the

Table 1. Length distributions of alewives taken in bottom trawls and from the dieoff at various locations in Lake Michigan, April and June 1967

| $\begin{gathered} \text { Total } \\ \text { length } \\ \text { (millimeters) } \end{gathered}$ | Trawls, |  |  |  |  |  |  | Dieoff |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Benton <br> Harbor <br> April <br> 19 | Saugatuck <br> April <br> 13 | Grand <br> Haven <br> April <br> 16 | Frankfort <br> June <br> 11 | Sturgeon <br> Bay <br> June <br> 9 | Michigan City June 28-29 | $\begin{gathered} \text { St. } \\ \text { Joseph } \\ \text { June } \\ 29 \end{gathered}$ | Saugatuck $\begin{gathered} \text { June } \\ 29 \end{gathered}$ | Ludington $\begin{gathered} \text { June } \\ 28 \end{gathered}$ | Frankfort <br> June <br> 9 | sturgeon <br> Bay <br> June <br> 27 | Trawl total | Dieoff <br> total |
| 50-59 | 2 |  | 2 | 3 |  |  |  |  |  |  | - | 7 | - |
| 60-69 | 8 | 3 | 14 | 162 | 116 | 1 |  |  | 4 | 4 |  | 303 | 10 |
| 70-79 | 14 | 5 | 33 | 646 | 731 | 24 | 9 |  | 18 | 6 | 3 | 1,429 | 61 |
| 80-89 | 30 | 7 | 38 | 251 | 613 | 38 | 18 | 4 | 28 | 5 | 2 | 939 | 95 |
| 90-99 | 19 | 2 | 23 | 105 | 320 | 19 | 27 | 2 | 16 | 8 | 4 | 469 | 76 |
| 100-109 | 22 |  | 6 | 23 | 112 | 9 | 10 | 2 | 18 | 1 | 2 | 163 | 42 |
| 110-119 | 5 |  | 4 | 3 | 54 | 7 |  |  | 1 | 1 | 2 | 66 | 11 |
| 120-129 | 20 | 4 | 16 | 8 | 58 | 3 |  | 2 | 1 |  | 1 | 106 | 7 |
| 130-139 | 58 | 12 | 39 | 24 | 138 | 11 | 1 | 5 | 5 | 5 | 11 | 271 | 38 |
| 140-149 | 155 | 47 | 92 | 32 | 240 | 32 | 15 | 14 | 17 | 13 | 28 | 566 | 119 |
| 150-159 | 310 | 132 | 190 | 75 | 296 | 70 | 36 | 18 | 44 | 8 | 63 | 1,003 | 239 |
| フ 160-169 | 453 | 240 | 232 | 162 | 274 | 80 | 44 | 27 | 53 | 8 | 56 | 1,361 | 268 |
| 170-179 | 342 | 181 | 129 | 112 | 141 | 44 | 29 | 22 | 42 | 2 | 20 | 905 | 159 |
| 180-189 | 152 | 87 | 51 | 52 | 49 | 9 | 6 | 9 | 13 | 6 | 11 | 391 | 54 |
| 190-199 | 43 | 22 | 14 | 10 | 12 |  |  | 3 | 3 |  |  | 101 | 7 |
| 200-209 | 8 | 4 | 3 | 1 |  |  |  |  |  |  |  | 16 | - |
| 210-219 |  | 2 |  | 1 | 3 |  |  |  |  |  |  | 6 | - |
| 230-234 |  |  |  |  | 1 |  |  |  |  |  |  | 1 | - |
| Total fish | 1.641 | 748 | 886 | 1,670 | 3.158 | 348 | 196 | 109 | 263 | 67 | 203 | 8,103 | 1,186 |
| Average length | '159 | 165 | 150 | 102 | 111 | 139 | 138 | 156 | 139 | 129 | 154 | 128 | 143 |
| Percentage yearlings | 6 | 2 | 14 | 71 | 62 | 28 | 33 | 8 | 32 | 37 | 6 | 42 | 25 |
| Average length yearlings | 89 | 80 | 83 | 77 | 83 | 87 | 89 | 90 | 88 | 85 | 92 | 81 | 88 |
| Percentage adults | 94 | 98 | 86 | 29 | 38 | 72 | 67 | 92 | 68 | 63 | 94 | 58 | 75 |
| Average length adults | 164 | 167 | 161 | 164 | 155 | 160 | 162 | 162 | 163 | 155 | 158 | 162 | 161 |




 Sturgeon Bay, 803.
dieoff were slightly smaller in three. Although growth of young alewives may start in late June, the dieoff was sampled only 2 days before the trawl collections at Frankfort in early June ( $9-11$ ) and the dieoff fish were larger.

Comparisons between the percentages of yearlings in the dieoff and trawl collections are difficult because of large discrepancies between the percentages in the southern ( 2 to 14 percent) and northern ( 62 and 71 percent) trawl collections (Table 1). The differences in the trawl collections were undoubtedly caused by a change in the bathymetric distribution of alewives between mid-April and early June. Yearling alewives are widely scattered in April but in May and June the fish move shoreward and are more concentrated near the bottom. Also by late May and June many adults are close inshore or have entered streams to spawn and are not available to trawls. The percentage of yearling alewives from all locations combined was 25 percent in the dieoff and 42 percent in the bottom trawl collections.

Graham (1956) also found substantial numbers of yearling alewives in the dieoffs in the Bay of Quinte region of Lake Ontario. Biologists and fishermen from Lake Michigan reported, however, that yearlings were much better represented in the 1967 dieoff than in those of previous years.

## Age Composition

The average ages of the adult alewives were nearly identical in the dieoff and trawl collections ( 3.5 and 3.6 years, respectively) and the average age of females exceeded that of males in every collection (Tables 2 and 3). Preliminary studies have shown that males mature earlier, are recruited at a younger age to the bottom stocks and to the spawning population, and die earlier than females. The females consequently averaged 0.4 year older than the males in both the trawl and dieoff collections.

Age-II alewives that mainly occupy midwater levels of the lake until midsummer and fall were scarce in the dieoff (5.5 percent for all ports) and trawl collections ( 4.3 percent). Most age-11 fish are immature in the spring and early summer and these fish apparently do not enter the inshore waters or the tributaries in proportion to their numbers in the lake. During the 1965 spawning season, age-11 alewives represented only 11 percent of the spawning fish in the Kalamazoo River

Table 2. Age composition (percentage) by sex of dead and dying adult alewives from six locations in Lake Michigan and Sturgeon Bay, June 1967

| Location and date | Sex | Number of fish | Age group |  |  |  |  | Average age |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | II | III | IV | v | VI |  |
| Michigan City <br> June 28-29 | Male | 79 | 2.5 | 57.0 | 36.7 | 3.8 | - | 3.4 |
|  | Female | 75 | 1.3 | 48.0 | 44.0 | 6.7 | - | 3.6 |
|  | Combined | 154 | 1.9 | 52.6 | 40.3 | 5.2 | - | 3.5 |
| St. Joseph June 29 | Male | 75 | 5.3 | 66.7 | 22.7 | 5.3 | - | 3.3 |
|  | Female | 54 | - | 40.7 | 46.3 | 13.0 | - | 3.7 |
|  | Combined | 129 | 3.1 | 55.8 | 32.6 | 8.5 | - | 3.5 |
| Saugatuck <br> June 29 | Male | 44 | 13.6 | 52.3 | 29.6 | 4.5 | - | 3.2 |
|  | Female | 56 | 1.8 | 41.1 | 46.4 | 10.7 | - | 3.7 |
|  | Combined | 100 | 7.0 | 46.0 | 39.0 | 8.0 | - | 3.5 |
| Ludington <br> June 28 | Male | 55 | 5.5 | 69.1 | 23.6 | 1.8 | - | 3.2 |
|  | Female | 86 | 3.5 | 28.7 | 44.8 | 20.7 | 2.3 | 3.9 |
|  | Combined | 141 | 4.2 | 44.4 | 36.6 | 13.4 | 1.4 | 3.6 |
| Frankfort <br> June9 | Male | 19 | 15.8 | 47.4 | 26.3 | 10.5 | - | 3.3 |
|  | Female | 24 | 8.3 | 50.0 | 16.7 | 25.0 | - | 3.6 |
|  | Combined | 43 | 11.6 | 48.9 | 20.9 | 18.6 | - | 3.5 |
| $\begin{aligned} & \text { Sturgeon Bay } \\ & \text { June27 } \end{aligned}$ | Male | 82 | 8.5 | 67.1 | 22.0 | 2.4 | - | 3.2 |
|  | Female | 71 | 1.4 | 38.0 | 47.9 | 12.7 | - | 3.7 |
|  | Combined | 153 | 5.2 | 53.6 | 34.0 | 7.2 | - | 3.4 |
| Unweighted mean all ports | Male |  | 8.6 | 59.9 | 26.8 | 4.7 | - | 3.3 |
|  | Female | - | 2.7 | 41.1 | 41.0 | 14.8 | 0.4 | 3.7 |
|  | Combined |  | 5.5 | 50.2 | 33.9 | 10.2 | 0.2 | 3.5 |

at Saugatuck. The limited migration of age-11 fish of the 1965 year class to the inshore areas, however, did not account entirely for their poor representation in the dieoff. As age-III fish in April 1968, the 1965 year class contributed only 16 percent of the adults in catches of experimental trawls at Saugatuck, whereas the average percentage contribution of the 1961-64 year classes at age III in earlier collections was 41 percent.

Age-groups III and IV were the principal age groups of adults in the dieoff samples and in the bottom trawl collections. The higher percentages of age-III fish in the dieoff than in the trawl samples may reflect a later inshore movement of younger fish that were not vulnerable earlier to trawls.

The two oldest age groups of alewives (VI and VII) were poorly represented in all collections, but were less numerous

Table 3. Age composition (percentage) by sex of adult alewives taken in experimental trawls at four locations in Lake Michigan April and June 1967

| Location and date | Sex | Number of fish | Age group |  |  |  |  |  | Average age |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | II | III | IV | v | VI | VII |  |
| Benton Harbor April 19 | Male | 41 | - | 53.1 | 41.5 | 4.8 | - | - | 3.5 |
|  | Female | 65 | 3.1 | 32.3 | 55.4 | 9.2 | - | - | 3.7 |
|  | Combined | 106 | 1.9 | 40.6 | 50.0 | 7.5 | - | - | 3.6 |
| Saugatuck <br> April 13 | Male | 71 | 5.6 | 45.1 | 43.7 | 5.6 | - | - | 3.5 |
|  | Female | 74 | - | 27.0 | 60.8 | 12.2 | - | - | 3.9 |
|  | Combined | 145 | 2.8 | 35.8 | 52.4 | 9.0 | - | - | 3.7 |
| Frankfort June 11 | Male | 62 | 3.2 | 51.6 | 40.3 | 3.2 | 1.6 | - | 3.5 |
|  | Female | 82 | 1.2 | 11.0 | 64.6 | 19.5 | 2.4 | 1.2 | 4.1 |
|  | Combined | 144 | 2.0 | 28.5 | 54.2 | 12.5 | 2.1 | 0.7 | 3.9 |
| $\begin{aligned} & \text { Sturgeon Bay' } \\ & \text { June } 9 \end{aligned}$ | Male | 99 | 13.1 | 60.6 | 26.3 | - | - | - | 3.1 |
|  | Female | 115 | 8.1 | 43.5 | 41.7 | 5.2 | - | 0.9 | 3.5 |
|  | Combined | 214 | 10.7 | 51.4 | 34.6 | 2.8 | - | 0.5 | 3.3 |
| Average all ports | Male |  | 5.5 | 52.8 | 37.9 | 3.4 | 0.4 | - | 3.4 |
|  | Female |  | 3.3 | 28.5 | 55.6 | 11.5 | 0.6 | 0.5 | 3.8 |
|  | Combined |  | 4.3 | 39.1 | 47.8 | 8.0 | 0.5 | 0.3 | 3.6 |

'Lake Michigan off Sturgeon Bay Canal
in the dieoff samples than in the trawl collections. The percentage of VI-group fish was 0.2 percent in the dieoff samples and 0.5 percent in the trawl collections. Age-VII fish appeared in only two of the trawl collections ( 0.3 percent) and were absent in the dieoff alewives. Older fish in the trawl samples may have died before late June when most of the collections were made from the dieoff. A decrease in the ages of spawning-run alewives at Chicago in 1966 between late April and early June (data unpublished) suggests that older fish spawn earlier and many may die during the early weeks of the spawning season.

## Average Lengths of the Age Groups

The mean lengths of alewives of age-groups II-V in the samples from the dieoff were either smaller than or identical to those in the trawl collections (Tables 4 and 5).

The average lengths of alewives are presented separately by sex because of sex differences in growth rate that begin in the third year of life. In all collections the average lengths

Table 4. Average lengths (mm) of male and female alewives at various ages in the dieoff samples from six locations in Lake Michigan and Sturgeon Bay, June 1967
[Number of fish in parentheses 1

| Location and date | Sex | Age group |  |  |  |  | $\begin{gathered} \text { All } \\ \text { ages } \end{gathered}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | II | III | IV | v | VI |  |
| Michigan City June 28-29 | Male | 147 | 155 | 165 | 170 | - | 159 |
|  |  | (2) | (45) | (29) | (3) |  | (79) |
|  | Female | 142 | 157 | 173 | 179 | - | 165 |
|  |  | (1) | (36) | (33) | (5) |  | (75) |
|  | Combined | 145 | 156 | 169 | 176 | - | 162 |
|  |  | (3) | (81) | (62) | (8) |  | (154) |
| St Joseph June 29 | Male | 146 | 154 | 169 | 179 | - | 158 |
|  |  | (4) | (50) | (17) | (4) |  | (75) |
|  | Female | ( | 160 | 171 | 181 | - | 168 |
|  |  |  | (22) | (25) | (7) |  | (54) |
|  | Combined | 146 | 156 | 170 | 180 | - | 162 |
|  |  | (4) | (72) | (42) | (11) |  | (129) |
| Saugatuck <br> June 29 | Male | 134 | 154 | 168 | 180 | - | 157 |
|  |  | (6) | (23) | (13) | (2) |  | (44) |
|  | Female | 132 | 158 | 173 | 182 | - | 167 |
|  |  | (1) | (23) | (26) | (6) |  | (56) |
|  | Combined | 134 | 156 | 171 | 181 | - | 162 |
|  |  | (7) | (46) | (39) | (8) |  | (100) |
| Ludington <br> June 28 | Male | 144 | 153 | 164 | 167 | - | 155 |
|  |  | (3) | (38) | (13) | (1) |  | (55) |
|  | Female | 135 | 158 | 170 | 177 | 187 | 167 |
|  |  | (3) | (25) | (39) | (18) | (1) | (86) |
|  | Combined | 140 | 155 | 168 | 176 | 187 | 162 |
|  |  | (6) | (63) | (52) | (19) | (1) | (141) |
| Frankfort <br> June 9 | Male | 135 | 143 | 161 | 160 | - | 148 |
|  |  | (3) | (9) | (5) | (2) |  | (19) |
|  | Female | 137 | 152 | 168 | 180 | - | 160 |
|  |  | (2) | (12) | (4) | (6) |  | (24) |
|  | Combined | 136 | 148 | 164 | 175 | - | 155 |
|  |  | (5) | (21) | (9) | (8) |  | (43) |
| Sturgeon Bay June 27 | Male | 135 | 152 | 166 | 164 | - | 154 |
|  |  | (7) | (55) | (18) | (2) |  | (82) |
|  | Female | 132 | 154 | 166 | 180 | - | 163 |
|  |  | (1) | (27) | (34) | (9) |  | (71) |
|  | Combined | 135 | 153 | 166 | 177 | - | 158 |
|  |  | (8) | (82) | (52) | (11) |  | (153) |
| Unweighted mean all ports | Male | 140 | 152 | 166 | 170 | - | 155 |
|  | Female | 136 | 157 | 170 | 180 | 187 | 165 |
|  | Combined | 139 | 154 | 168 | 178 | 187 | 160 |

Table 5. Average lengths ( mm ) of male and female alewives at various ages in trawl samples from four locations ${ }^{1}$ in Lake Michigan, June and April 1967

Number of fish in parentheses 1

|  |  | Age group |  |  |  |  |  |  |
| :--- | :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Location <br> and date |  | Sex | II | III | IV | IV | VI | VII |
| All |  |  |  |  |  |  |  |  |
| ages |  |  |  |  |  |  |  |  |

1 Fish from Grand Haven were not aged.
2 Lake Michigan off Sturgeon Bay Canal.
of the females exceeded those of the males by 2-3 mm at age III and 9-10 mm at age V. Age-III, -IV, and -V females were longer than males in 27 of 30 comparisons. Age-II females were slightly smaller than II-group males but the difference does not reflect slower growth for females because secondyear calculated lengths of the sexes of older fish are identical. More large age-11 males than females apparently mingle with the adult population.

Faster growth of the female alewife in Lake Michigan was noted by Joeris and Karvelis ${ }^{3}$ for fish from commercial pound nets in Green Bay and recently by Norden (1967) who reported an average difference of 4 mm between the sexes in a pooled sample of age-I, -11 , and -111 fish.

## Sex Composition

The sexes were nearly equally represented in the samples of alewives from the dieoff. The percentage of females for all ages combined, exclusive of age I for which sex could not be determined, ranged from 42 percent at St. Joseph to 61 percent at Ludington and averaged 52 percent for the six locations (Table 6).

The percentage of females was slightly higher in the trawl samples ( 56 percent), but changes in sex composition with increases in age were similar in most collections (Table 6 and 7). The consistent change in sex composition was marked by more males than females at ages II and III and more females than males at ages IV through VII in all the collections except the small sample of age-IV fish from the dieoff alewives at Frankfort.

## Condition of the Body

Alewives in the dieoff were generally robust despite the presence of hemorrhaging and fungus on some fish. Emaciated fish, common in bottom trawl catches in late July and August when the condition of adults is normally the poorest, were not conspicuous in the dieoff. The normal condition of the body was confirmed by weight comparisons between alewives in the dieoff at St. Joseph and Michigan City and those from the spawning migration at Chicago, May 26-June 13, 1966 (Table 8). Unweighted means of the body weights of males and females in length groups from 130-139 to $180-189 \mathrm{~mm}$

[^1]Table 6. Percentage of females in different age groups' of alewives in the dieoff samples from six locations in Lake Michigan and Sturgeon Bay, June 1967
[Number of fish in parentheses]

| Location and date | Age group |  |  |  |  | $\begin{gathered} \text { All } \\ \text { ages } \end{gathered}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | II | III | Iv | V | VI |  |
| Michigan City | 33 | 44 | 53 | 62 | - | 49 |
| June 28-29 | (3) | (81) | (62) | (8) |  | (154) |
| St. Joseph | 0 | 31 | 60 | 64 | - | 42 |
| June 29 | (4) | (72) | (42) | (11) |  | (129) |
| Saugatuck | 14 | 50 | 67 | 75 | - | 56 |
| June 29 | (7) | (46) | (39) | (8) |  | (100) |
| Ludington | 50 | 40 | 75 | 95 | 100 | 61 |
| June 28 | (6) | (63) | (52) | (19) | (1) | (141) |
| Frankfort | 40 | 57 | 44 | 75 | - | 56 |
| June 9 | (5) | (21) | (9) | (8) |  | (43) |
| Sturgeon Bay | 12 | 33 | 65 | 82 | - | 46 |
| June 27 | (8) | (82) | (52) | (11) |  | (153) |
| Unweighted mean |  |  |  |  |  |  |
| all ports | 25 | 42 | 61 | 76 | 100 | 52 |

'Exclusive of age I.
were 25.5 and 26.7 grams, respectively, in the dieoff and 25.9 and 26.6 grams in the spawning run at Chicago. Males are lighter than females at all times of the year in Lake Michigan.

## Condition of the Gonads

The presence of many immature yearling alewives and unspawned adults in the dieoff is proof that spawning attrition was not the major cause of the dieoff. Large percentages (32-67) of marine alewives die after spawning in freshwater streams (Cooper, Havey, 1961) and spawning mortality undoubtedly occurs annually in Lake Michigan, but nonetheless more than 80 percent of the dead or dying fish (exclusive of

Table '7. Percentage of females in different age groups ${ }^{1}$ of alewives in the trawl samples from four locations in Lake Michigan, April and June 1967
[Number of fish in parentheses]

| Location and date | Age group |  |  |  |  |  | $\begin{gathered} \text { All } \\ \text { ages } \end{gathered}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | II | III | IV | V | VI | VII |  |
| Benton Harbor | 100 | 49 | 68 | 75 | - | - | 61 |
| April 19 | \% | (43) | (53) | (8) |  |  | (106) |
| Saugatuck | (4) | 38 | 59 | 69 |  |  | 51 |
| April 13 |  | (52) | (76) | (13) |  |  | (145) |
| Frankfort | 33 | 22 | 68 | 89 | 67 | 100 |  |
| June 11 | (3) | (41) | (78) | (18) | (3) | (1) | (144) |
| Sturgeon Bay ${ }^{2}$ | 43 | 45 | 65 | 100 | - | 100 | 54 |
| June 9 | (23) | (110) | (74) | (6) |  | (1) | (214) |
| Unweighted mean all ports | 39 | 38 | 65 | 83 | 67 | 100 | 56 |

Exclusive of age I.
2 Lake Michigan off Sturgeon Bay Canal.
yearlings) from Saugatuck, Ludington, and Sturgeon Bay were either in prespawning condition or immature (Table 9).

The actual developmental stage of fish classified as "may spawn" in Table 9 does not weaken this conclusion because they definitely had not spawned before the dieoff. Lack of a sharp difference between partly spent and spent males, however, may have caused some misclassifications in the "will spawn" and "spent" categories.

## Stomach Contents

Of 100 stomachs examined from adult alewives in the dieoff at Michigan City and St. Joseph, only 50 percent contained food (mostly small quantities of zooplankton). The small amounts of food and the empty stomachs were not unusual because alewives normally do not feed for extended periods before and during spawning (Cooper, 1961). Presence of the rapidly digestible zooplankton indicates that many fish were feeding just before death.

Table 8. Average weight (grams) of alewives from the dieoff at St. Joseph and Michigan City, June 28-29, 1967, and from the Chicago Central District Filtration Plant, May 26 and June 13, 1966
[Number of fish in parentheses1

|  | Males |  | Females |  |
| :---: | :---: | :---: | :---: | :---: |
| Total <br> length <br> (millimeters) | 1966 <br> Chicago | 1967 <br> dieoff | 1966 <br> Chicago | 1967 <br> dieoff |
| $120-129$ | 18 | 13.0 |  |  |
|  | $(1)$ | $(3)$ |  |  |
| $130-139$ | 16.7 | 17.2 | 15.3 | 17 |
|  | $(3)$ | $(11)$ | $(3)$ | $(1)$ |
| $140-149$ | 20.6 | 20.8 | 22.8 | 21.5 |
|  | $(11)$ | $(32)$ | $(5)$ | $(16)$ |
| $150-159$ | 23.4 | 23.4 | 24.5 | 24.4 |
|  | $(37)$ | $(72)$ | $(16)$ | $(34)$ |
| $160-169$ | 27.4 | 27.4 | 28.7 | 28.7 |
|  | $(67)$ | $(67)$ | $(48)$ | $(56)$ |
| $170-179$ | 31.2 | 29.9 | 31.3 | 32.9 |
|  | $(39)$ | $(25)$ | $(50)$ | $(47)$ |
| $180-189$ | 36.0 | 34.5 | 36.8 | 35.7 |
|  | $(16)$ | $(2)$ | $(23)$ | $(13)$ |
| $190-199$ | 40.0 |  | 40.6 | 51 |
|  | $(2)$ |  | $(5)$ | $(1)$ |
| 200-209 |  |  | 47.7 |  |
|  |  | 25.9 | 25.5 | 26.6 |

1 Over length intervals of 130 through 189 mm

## Fungus Infection and Subcutaneous Hemorrhaging

Substantial numbers of dying alewives at the various sample locations were infected by Saprolegnia, were hemorrhaging subcutaneously, or were both infected and hemorrhaging. The possible significance of these conditions was investigated from their occurrence among fish in the selected samples from the dieoff at Michigan City and St. Joseph.

Saprolegnia is common in freshwater where it often engulfs the fertilized eggs of fish and invades the body surfaces of adults that are damaged in the act of spawning (Webster, 1948; Davis, 1953; Brown, 1960). Floating alewives that have

Table 9. Condition of the gonads of alewives in the dieoff collections from Saugatuck, Ludington, and Sturgeon Bay, June 27-29, 1967
[Age-group I excluded]

|  | Number of fish |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Total <br> length <br> (millimeters) | Immature | May spawn ${ }^{1}$ | Will spawn ${ }^{2}$ | Spent |  |  |  |  |
|  | Male | Female | Male | Female | Male | Female | Male | Female |
| $120-129$ |  |  | 2 | 1 | - | - | - | - |
| $130-139$ | 1 | 3 | 4 | - | 6 | 1 | - | - |
| $140-149$ | 1 | - | 6 | 5 | 12 | 9 | 5 | - |
| $150-159$ |  | 1 | 13 | 4 | 17 | 12 | 7 | 4 |
| $160-169$ |  |  | 9 | 13 | 14 | 24 | 10 | 9 |
| $170-179$ |  | 1 | 4 | 9 | 4 | 41 | 2 | 8 |
| $180-189$ |  |  | 1 | 2 | 1 | 16 |  | 8 |
| $190-199$ |  |  |  | 1 | - | 2 | - | 2 |
| Total | 2 | 5 | 39 | 35 | 54 | 105 | 24 | 31 |
| Percentage | 2 | 3 | 33 | 20 | 45 | 59 | 20 | 18 |

1 Condition intermediate between adjacent categories
${ }^{2}$ Gonad in advanced state, ripening, or ripe.
been dead for long periods are usually matted with the fungus which Graham (1956) observed on the bodies of two alewives in a school that suddenly began to surface and die in one of the Lake Ontario mortalities.

Twenty percent of the alewives from the samples at Michigan City and St. Joseph were infected by the fungus which formed dense, isolated patches on some fish and was broadly dispersed on others (Table 10). The greater rate of infection for females than males (26 percent for females; 13 percent for males) was statistically significant ( $\mathrm{X}^{2}=4.349$; 1 d.f.; $\mathrm{p}<0.05$ ), but length frequencies of the infected fish of both sexes did not differ significantly from the frequencies expected under the hypothesis of a common infection rate for all size groups:

| Sex | d.f. | $X^{2}$ | $P$ |
| :--- | :---: | :---: | :---: |
| Male | 3 | 1.167 | $>0.75$ |
| Female | 4 | 6.458 | $>0.10$ |

Because of its low incidence. Saprolegnia was not an important factor in the dieoff although infected fish were probably

Table 10. Incidence of fungus infection and subcutaneous hemorrhages among dying alewives, Michigan City, Indiana, and St. Joseph, Michigan, June 28-29, 1967

| $\begin{gathered} \text { Total } \\ \text { length } \\ \text { (millimeters) } \end{gathered}$ | $\begin{aligned} & \text { Total number } \\ & \text { of } \\ & \text { fish } \end{aligned}$ |  | Number of fish with: |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | No fungus or hemorrhage |  | Fungus |  | Hemorrhage |  |
|  | Male | Female | Male | Female | Male | Female | Male | Female |
| 130-139 | 4 |  | 2 |  | 1 |  | 2 |  |
| 140-149 | 17 | 11 | 9 | 5 | 1 | 1 | 8 | 5 |
| 150-159 | 48 | 15 | 23 | 4 | 8 | 6 | 24 | 6 |
| 160-169 | 42 | 32 | 14 | 17 | 6 | 9 | 24 | 12 |
| 170-179 | 13 | 28 | 5 | 14 | 1 | 4 | 7 | 11 |
| 180-189 | 2 | 6 | 1 | 1 | - | 4 | 1 | 4 |
| 190-199 |  | 1 |  | 1 | - |  |  |  |
| Total | 126 | 93 | 54 | 42 | 17 | 24 | 66 | 38 |
| Percentage of total | 100 | 100 | 43 | 45 | 13 | 26 | 52 | 41 |
| Average length | 158 | 165 | 157 | 166 | 157 | 166 | 159 | 166 |

more vulnerable to conditions causing death than were uninfected fish.

Hemorrhaging that produced fresh blood streaks along the lines of scale imbrication and denser blotches on some individuals was present on a much higher percentage of the dying alewives (47 percent) than was fungus infection (Table 10). A higher incidence among the males was not statistically significant ( X " $=1.513 ; 1$ d.f.; $\mathrm{p}>0.10$ ), nor did the length frequencies of the hemorrhaged fish differ significantly from the frequencies expected if the condition had been randomly distributed among the length groups:

| Sex | d.f. | $X^{2}$ | $P$ |
| :--- | :---: | :---: | :---: |
| Male | 5 | 0.385 | $>0.995$, |
| Female | 4 | 0.581 | $>0.95$ |

Because the hemorrhages were fresh and well distributed among all sizes of both sexes of the dying alewives, they may have been a symptom or physiological response to the cause or causes of the dieoff. Even if the hemorrhaging was coincidental, however, it may have increased vulnerability to the actual cause of death. Any hemorrhaged fish that escaped immediate death would have been susceptible to Saprolegnia which rapidly infects wounded and weakened individuals (Davis, 1953).

Acknowledgments

LaRue Wells examined the stomach contents of the dying alewives from St. Joseph and Michigan City. The collections of alewives furnished by the Branch of Exploratory Fishing and Gear Research (R/V Kaho) were essential for this study.

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