WATER TEMPERATURE AND THE MIGRATIONS OF AMERICAN SHAD

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ABSTRACT

The peak of spawning runs of American shad (*Alosa sapidissima*) into rivers at various latitudes on the Atlantic and Pacific coasts of North America takes place when water temperatures are near 18.5°C. At the Bonneville Dam, Columbia River, Wash., 90% of the run as a rule takes place when river temperatures are between 16.0° and 19.5°C. At the fish ladder of the Holyoke Water Power Company on the Connecticut River, the temperature at the peak of the shad run averaged 19.5°C for 15 years. In the St. Johns River, Fla., peak movement occurs in December and January at the time of the annual minimum water temperatures, or 14.0° to 20.0°C.

Migrations of shad in the Atlantic Ocean follow paths associated with approximately the same range of temperatures (13.0°-18.0°C). Annual cycles of ocean warming cause shad to move into the Gulf of Maine in the summer, to the middle Atlantic in the winter, and to the south in the early spring. Juvenile shad move downstream in the fall, coinciding with a decline in the temperature of each stream to below 15.5°C. A path of migration for shad in the Pacific Ocean is hypothesized from the known seasonal changes in ocean temperature. The potential effects of artificial warming of streams on timing and survival of shad runs in northern and southern latitudes is discussed.

The American shad (*Alosa sapidissima*), in spite of declines in abundance on the Atlantic coast of the United States caused by obstruction of spawning runs by dams, by water pollution, and by overfishing, continues to provide a catch each year of some 8 million pounds valued at slightly more than one million dollars to the fishermen (Walburg and Nichols, 1967).

There is as yet no rationally based management scheme to prevent overfishing of shad, and dams and pollution continue to increase. Recent changes in the environment for shad have been brought about by the greatly increased heating of the water by steam-electric generating stations. There will be a further increase in the construction of these facilities; thus the Federal Power Commission in 1960 estimated that by 1980 the generating capacity of hydroelectric power stations would double—some accomplished by construction of dams and some by adding capacity at existing dams—but at the same time, steam-electric capacity would triple (Federal Power Commission, 1960). Other experts regard these estimates as conservative (American Public Power Association, 1960). It therefore becomes pertinent to ask what effects the warming of water may have on fish in streams used for cooling. This paper analyzes the effect of water temperature on the movements of shad in streams and in the ocean.

It is appropriate that this paper, which traces the relationship of migrations of American shad to temperature of the water, should appear in a volume dedicated to Dr. O. Elton Sette. His interest in the effects of temperature on migrations of fishes has been a stimulus to the work of his colleagues for over 30 years. He has always been generous in his encouragement of those around him. In 1957, the Pacific Oceanic Fishery Investigations, of which he was the first Director, began publication of monthly sea-surface temperature charts for the Pacific Ocean as an aid to fishermen and biologists studying fish distribution. The successors of these charts are still being issued by the National Marine Fisheries Service, Southwest Fisheries Center, La Jolla Laboratory. Other scientists and agencies have come to see their utility and popularity and have commenced publication of sea surface temperature charts for other parts of the world.

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The present paper, therefore, owes a great deal to Dr. Sette both in its conception and execution. He conceived that there was a relationship between water temperature and fish distribution, and he stimulated the production of charts to which we are able to refer in order to establish the relationship of shad migrations to water temperature.

SHAD RUNS AND RIVER TEMPERATURE

As early as 1884, Marshall McDonald developed a theory that shad are restricted to a narrow range of temperatures and that the timing of shad runs thus depends on when the water warms. McDonald (1884, p. 599, 604, 605) stated that shad

> ... occupy an hydro-isothermal belt, or area, limited by the temperature of 60° F. to 70° F.; that they move with this belt, *i.e.*, as the season advances, into and up the rivers....
>
> ... In the Savannah River they appear early in January, and in the Neuse River at a period not much later than in the Savannah. In the Albemarle the important Shad seine-fisheries begin early in March, but doubtless the fish are in the Sound some time before that date; not, however, in numbers sufficient to justify the great expenses attendant upon the operation of these large seines. In the Chesapeake Bay they make their appearance in February, although the height of the fishing season in its waters is during April and May, and at a date somewhat later in the more northern tributaries. In the Delaware, Connecticut, Merrimac, and St. John (Nova Scotia) Rivers, Shad are first seen at periods successively later as we proceed farther north. The date of their first appearance in any of these waters, however, varies from season to season, the limit of such variation being from three to four weeks.
>
> These irregularities in the time of the run into our rivers, which cause so much perplexity and discouragement to the fishermen, are, however, readily explained when we keep in view what has been already said in regard to the influences of temperature in determining the movements of these fishes.

McDonald pointed out that the shad run in a particular river may be delayed if the water cools. Although rising temperatures accelerate the run, a sudden increase may also retard it. The downstream migration of the juvenile shad occurs when water temperatures fall to below 60°F (15.5°C).[3] In support of his thesis, McDonald provided a table of daily shad catches and water temperatures in the Potomac River for the year 1881. Shad were caught in water from 8.0° to 24.5°C. We performed a frequency analysis of these data which shows that the average shad was associated with a temperature of 18.5°C. Ninety percent of the run took place between 12.0° and 21.0°C. McDonald also supplied a table showing monthly average water temperatures for the St. Johns River, Fla., in 1877 and 1878. He stated that shad first appeared in November when the average temperature was 63.5°F (17.5°C) and that spawning took place in February and March when the average temperatures were 58.0° and 62.2°F (14.5° and 17.0°C). McDonald provided no quantitative data on shad in the St. Johns River, however, and his thesis therefore apparently rests on data from the one year and one river in which both shad catches and water temperatures were available. He gave no data to support his statement on migrations of juveniles.

Working in the field, one readily becomes convinced as did McDonald (1884) that water temperature affects the run of shad. This observation has also been made by Leim (1924), Talbot (1954), and Massmann and Pacheco (1957). The difficulty has been to develop a quantitative measure or prediction of the effect. Talbot (1953), by means of linear regression, analyzed the timing of the shad run in relation to river flow and river temperature at Bonneville Dam on the Columbia River. Temperatures and flows are recorded there, and Talbot had available shad counts made from 1938 to 1950 as the fish ascended the fish ladders at the dam. He concluded that flow and temperature do affect the time of entry of shad into the river, although the correlation coefficient of time of the run and temperature was not quite significant at the 5% level.

Now 19 more years of data are available (Table 1). The 32 years of data show a highly significant partial correlation of temperature, as well as a significant partial correlation of flow, with the timing of the shad run. Of course, this

[3] All temperatures used in developing this paper were originally recorded in Fahrenheit. Our conversions to Celsius have been rounded to the nearest 0.5°C.

TABLE 1.—Time of median shad passage at Bonneville compared with time when temperature exceeded 15.5°C and flow diminished to 325,000 cfs and number of days counted from May 31 (shown in parentheses).[1]

Year	Date on which: Half of shad were counted		Temperature rose above 15.5°C		Flow decreased to 325,000 cfs	
1938	July 24	(54)	June 24	(24)	July 17	(47)
1939	July 7	(37)	June 26	(26)	June 12	(12)
1940	June 30	(30)	June 9	(9)	June 16	(16)
1941	July 5	(35)	June 5	(5)	May 30	(—1)
1942	July 21	(51)	June 28	(28)	July 1	(31)
1943	July 20	(50)	June 29	(29)	July 24	(54)
1944	July 17	(47)	June 21	(21)	June 21	(21)
1945	July 13	(43)	June 18	(18)	July 4	(34)
1946	July 8	(38)	June 29	(29)	July 13	(43)
1947	July 4	(34)	June 16	(16)	July 4	(34)
1948	July 18	(48)	July 19	(49)	July 13	(43)
1949	July 11	(41)	July 13	(43)	June 22	(22)
1950	July 21	(51)	July 7	(37)	July 28	(58)
1951	July 8	(38)	June 16	(16)	July 25	(55)
1952	July 15	(45)	June 21	(21)	July 8	(38)
1953	July 15	(45)	June 30	(30)	July 20	(50)
1954	July 25	(55)	July 7	(37)	July 30	(60)
1955	July 23	(53)	July 12	(42)	July 29	(59)
1956	July 14	(44)	June 29	(29)	July 15	(45)
1957	July 11	(41)	June 20	(20)	July 25	(55)
1958	July 7	(37)	May 30	(—1)	July 28	(58)
1959	July 17	(47)	June 22	(22)	July 18	(48)
1960	July 5	(35)	June 4	(4)	July 12	(42)
1961	July 7	(37)	June 16	(16)	July 4	(34)
1962	July 13	(43)	June 15	(15)	July 29	(59)
1963	July 8	(38)	June 13	(13)	July 1	(31)
1964	July 14	(44)	June 29	(29)	July 24	(54)
1965	July 1	(31)	June 23	(23)	July 14	(44)
1966	July 8	(38)	July 16	(46)	July 19	(49)
1967	July 12	(42)	June 21	(21)	July 17	(47)
1968	July 3	(33)	June 12	(12)	July 1	(31)
1969	June 21	(21)	June 3	(3)	June 19	(19)

Shad-temperature partial correlation $r = 0.58$, $P<0.01$
Shad-flow partial correlation $r = 0.44$, $P<0.05$
Temperature-flow partial correlation $r = -0.004$ not sig., df = 29

[1] Method is that of Talbot (1953) as are data 1938-1950, data 1951-1969 from Corps of Engineers (1951-1969).

analysis suffers from the usual defects of data on two or more factors which may trend in the same direction without necessarily being related in a cause-and-effect manner. For example, we do not believe that the significant correlation of flow and the timing of the runs has any particular meaning beyond the fact that the shad run occurs after flows begin to decline. Shad migrate into streams of various sizes, and we do not think that they select a particular flow in a particular stream. On the other hand, the fact that they select the sáme water temperature in different streams and, as will be shown later, that in their oceanic migration they remain in water of the same temperature points to the conclusion that the timing of the shad run is related to water temperature.

To find the particular temperature preferred by shad, we tabulated the temperature when each fish was counted at the Bonneville fish ladders. For each year we then calculated an average of these temperatures. This amounts to determining the temperature at the peak of the shad run (Table 2). Such a procedure is justified by the large samples and the fact that the frequency distribution is approximately normal. Very little variation in the temperature at the peak of the run occurred from year to year. Most of the time the peak occurred at 18.0°C. In 78% of the years the peak appeared in the range 16.5° to 19.0°C. (Table 3). In the average year, 90% of the shad run was counted when the temperatures ranged between 15.5° and 19.5°C. In 26 of the 32 years the temperature varied only 4.0°C or less during the time when 90%

TABLE 2.—Water temperatures (°C) associated with the peak of the shad run and lower and upper temperatures associated with the middle 90% of the shad counted at Bonneville Dam fishways,[1] Columbia River.

Year	Lower	Peak	Upper	Difference
1938	17.0	19.5	21.5	4.5
1939	15.0	17.0	21.0	6.0
1940	17.0	19.0	20.0	3.0
1941	17.0	20.0	23.0	6.0
1942	17.0	19.5	21.0	4.0
1943	16.0	18.0	19.0	3.0
1944	17.0	14.0	21.0	4.0
1945	18.0	19.5	20.5	2.5
1946	15.0	16.5	19.0	4.0
1947	16.0	18.0	19.5	3.5
1948	17.0	19.5	20.5	3.5
1949	13.5	15.5	16.5	3.0
1950	16.5	18.0	19.0	2.5
1951	15.5	17.0	19.0	3.5
1952	15.5	18.5	19.5	4.0
1953	16.5	18.5	19.0	2.5
1954	15.0	16.5	18.0	3.0
1955	14.5	17.0	19.0	4.5
1956	16.0	18.5	20.0	4.0
1957	15.5	18.5	20.0	4.5
1958	18.5	20.0	22.0	3.5
1959	16.5	18.5	20.0	3.5
1960	15.0	18.0	20.0	5.0
1961	16.5	18.5	20.5	4.0
1962	16.5	18.0	20.0	3.5
1963	16.0	18.0	19.0	3.0
1964	15.5	18.0	19.0	3.5
1965	16.0	18.0	19.5	3.5
1966	15.0	16.5	19.0	4.0
1967	17.0	18.5	19.5	2.5
1968	15.5	16.5	19.0	3.5
1969	16.0	18.0	19.0	3.0
Mean	16.0	18.0	19.5	3.5

[1] From Corps of Engineers (1948-1969) and unpublished data for which we are indebted to Ivan Donaldson, Corps of Engineers, and Kingsley G. Weber, National Marine Fisheries Service.

TABLE 3.—Number of years when given temperature was recorded at the peak of the spawning run.

Temperature at peak (°C)	Number of years	Percentage of years
15.5	1	3
16.0	0	
16.5	4	78
17.0	3	
18.0	9	
18.5	7	
19.0	2	
19.5	4	19
20.0	2	

TABLE 4.—Water temperatures (°C) associated with the peak of the shad run and lower and upper temperatures associated with the middle 90% of the shad counted at Holyoke Water Power Company fishway, Connecticut River.

Year	Lower	Peak	Upper	Difference
1955	19.0	19.5	23.5	4.5
1956	19.0	21.0	23.0	4.0
1957	18.5	19.5	22.5	4.0
1958	16.0	18.5	18.5	2.5
1959	17.0	20.5	23.0	6.0
1960	15.5	19.5	20.0	4.5
1961	15.0	18.5	21.5	6.5
1962	16.0	20.5	21.0	5.0
1963	16.5	20.0	21.5	5.0
1964	16.0	19.5	20.5	4.5
1965	16.5	19.0	21.5	5.0
1966	17.0	19.5	21.0	4.0
1967	16.5	20.0	23.0	6.5
1968	14.5	17.0	21.5	7.0
1969	16.5	19.0	22.0	5.5
Mean	16.5	19.5	21.5	5.0

of the shad appeared at the Bonneville fish ladders. In only 3 years did the range exceed 4.5°C (Table 2).

The only comparable data that we have been able to locate on the Atlantic coast concern the shad passed by the fish lift of the Holyoke Water Power Company located 138 km from the mouth of the Connecticut River. Daily records of water temperature and the number of fish lifted over the dam show that few shad were passed when the water temperature was below 14.0°C. Peak passage occurred at temperatures ranging from 16.5° to 21.5°C (Table 4). This compares closely with the temperature of peak shad passage (16.5°-19.0°C) at Bonneville Dam, 233 km from the mouth of the Columbia River.

Commercial catches provide less direct, and therefore less reliable, data on the timing of shad runs. These can be affected by many extraneous factors such as market price, which leads to heavier sampling in the early part of the run, and turbidity of the water, which would have the same effect because catch per effort would be higher early when turbidity is high. Nevertheless, the temperatures found to be associated with peak commercial catches are in general agreement with those associated with actual counts at the fishways.

For the St. Johns River, Fla., mean weekly shad catches (in pounds) were calculated from daily catch records of the Morris Crab Company for the years 1962 to 1967. These are plotted in Figure 1 with mean monthly river temperatures developed from daily temperature records of the Florida Light and Power Company for the years 1960 to 1967. Fishing effort was approximately equal from day to day and year to year from mid-November to mid-March, but after this time market fluctuations resulted in sporadic fishing effort. In order to eliminate error resulting from sporadic fishing effort, catches made after mid-March were omitted from the analysis.

Shad migrations in the St. Johns River corresponded closely to the period of lowest annual river temperatures, confirming the earlier observations of McDonald (1884). Few, if any, shad entered the river at temperatures in excess of 20.0°C prior to mid-November, and peak numbers occurred in mid-January when temperatures were at the annual low (15.0°C). As temperatures increased, in February and March, the relative abundance of shad declined.

Massmann and Pacheco (1957) investigated the relationship between temperature and shad catch in the York River, Va., in the years 1953 to 1956. From their data we calculated the mean catch of shad per net day, by weekly intervals, February 15 to June 1. The relationship between the timing of shad migrations in the York River and mean monthly river temperatures (developed from daily records for the period 1953 to 1962 that were supplied by the Virginia Institute of Marine Science) is illustrated in Fig-

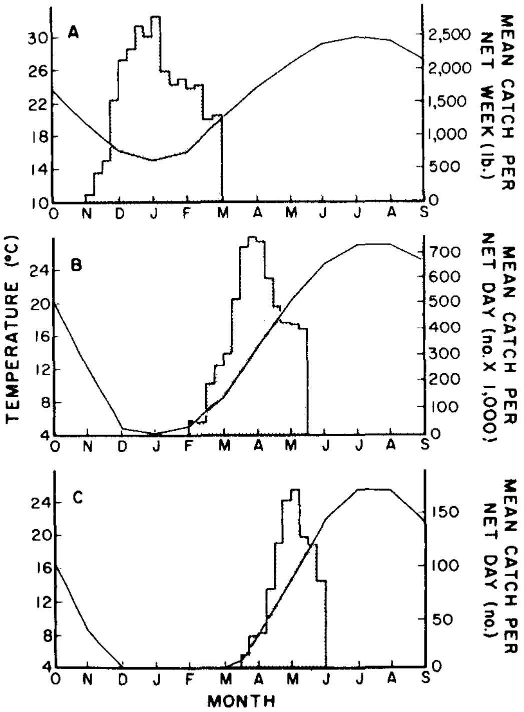

FIGURE 1.—Shad catches at various temperatures in three Atlantic coast rivers. (A) St. Johns River, Fla.—temperatures are averages, 1960-1967; shad catches in pounds are from weekly catches of the Morris Crab Company, 1962-1967. (B) York River, Va.—temperatures are averages, 1953-1962; shad catches are numbers per net day, 1953-1956 (Massmann and Pacheco, 1957). (C) Connecticut River, Conn.—temperatures are averages, 1958-1969; shad catches are numbers per net day, 1944-1964 (courtesy Angelo Baldi) and 1965-1969 (Leggett, 1969).

ure 1. Few, if any, shad entered the York River until late January when river temperatures exceeded 4.0°C, and peak numbers were captured in April at temperatures around 14°C. At higher temperatures catches declined.

For the Connecticut River the mean catch of shad per net day, by weekly intervals, April 1 to June 15, was estimated from the daily catch records of commercial fisherman Angelo Baldi for the period 1944 to 1964, and from the daily records of shad captured for tagging by biologists of the Essex Marine Laboratory from 1965 to 1969. These data are presented in Figure 1, together with mean weekly river temperatures developed from daily water temperature records of the Hartford Electric Light Company, and Essex Marine Laboratory for the period 1958 to 1969. Shad are generally soft-bodied and of little economic value after mid-June; from then on fishing effort is much reduced and is more sporadic. For this reason, the histogram of mean weekly catch was terminated in mid-June. Shad first entered the Connecticut River from late March to early April when water temperatures ranged from 4.0° to 6.0°C. The mean weekly catch increased with temperature until mid-May when temperatures averaged about 15°C. Catches declined steadily at higher temperatures. During the period for which accurate daily temperature records were available, 1958 to 1969, the mean temperature at which the peak catch was obtained at the mouth of the river was 13.0°C (Table 5). In 10 out of 12 of those years, the peak catch occurred at temperatures between 11.0° and 15.5°C. In the Connecticut River, a large sport fishery for shad operates at Enfield, in the area 88 to 109 km from the river mouth. A daily record of the number of anglers and the number of shad caught in a State-controlled fishing area has been maintained since 1942. A daily record of the water temperature at the fishing area has also been kept. Most shad were caught by angling at temperatures ranging from 11° to 18°C (Table 6). On the average, the peak occurred near 15°C. As noted previously, the temperature of peak shad passage at Holyoke, 29 km farther upriver, occurred at temperatures averaging 19.5°C and ranging from 16.5° to 21.5°C.

TABLE 5.—Water temperature (°C) associated with peak of shad catch and upper and lower temperatures associated with middle 90% of the catch at Saybrook, Conn.

Year	Lower	Peak	Upper	Difference
1958	8.5	11.5	19.0	10.5
1959	6.0	13.5	22.0	16.0
1960	10.0	15.5	20.0	10.0
1961	10.5	13.5	16.5	6.0
1962	12.5	14.5	22.0	9.0
1963	10.0	14.5	20.5	10.5
1964	8.0	13.5	18.5	10.5
1965	8.5	14.0	20.0	11.5
1966	8.5	9.5	13.0	4.5
1967	6.5	9.5	13.5	7.0
1968	12.0	13.0	16.5	4.5
1969	8.5	11.0	14.5	6.0
Mean	9.0	13.0	18.0	9.5

TABLE 6.—Water temperatures (°C) associated with the peak of the shad run and lower and upper temperatures associated with the middle 90% of the shad caught by anglers at Enfield, Conn.

Year	Lower	Peak	Upper	Difference
1953	8.0	12.0	16.5	8.5
1954	8.0	10.5	14.0	6.0
1955	15.5	18.0	18.0	2.5
1956	11.0	14.5	18.0	7.0
1957	14.0	16.0	18.0	4.0
1958	11.0	16.0	17.5	6.5
1959	14.0	18.5	18.5	4.5
1960	14.0	16.0	20.5	6.5
1961	9.0	14.0	16.5	7.5
1962	8.5	16.0	21.0	12.5
1963	12.0	16.5	16.5	4.5
1964	11.5	17.0	18.5	7.0
1965	11.5	17.0	23.0	11.5
1966	9.0	15.0	18.5	9.5
1967	8.0	13.5	20.0	12.0
1968	11.0	15.0	15.5	4.5
1969	11.5	14.5	18.5	7.0
Mean	11.0	15.5	18.0	7.0

TABLE 7.—Water temperatures and counts per hour of downstream migrating juvenile shad at Matamoras, Pa., September and October 1951. (From Sykes and Lehman, 1957.)

Date	Temperature °C	Shad per hour
September 10	20.5	5
17	20.5	0
21	20.5	1
24	21.0	0
28	20.0	10
29	18.0	20
30	14.0	65
October 1	17.0	59
5	21.0	0
8	14.0	600
9	14.0	600
10	15.0	300
13	15.0	350
14	14.0	350
15	14.0	70
16	14.0	10
17	15.5	0
19	15.0	0
29	15.0	0

As these data clearly show, the timing of shad spawning migrations is highly correlated with specific water temperatures in all three of the rivers studied. Most shad entered these rivers when temperatures were between 10.0° and 15.0°C, even though this required considerable variation in the timing of shad to changing temperature conditions in the three rivers. In the St. Johns River (Fla.), water temperatures seldom fall below 14.0°C, and the spawning run occurs at about the seasonal temperature minimum in January. These Florida shad must begin to enter the river during conditions of declining water temperatures, as opposed to the shad from the York and Connecticut Rivers which begin their migrations as temperatures are increasing above an apparent lower limit of 4.0°C. In Florida, most of the migration occurs while river temperatures are below 20.0°C. Maximum movements of shad into the York and Connecticut Rivers occur at temperatures of about 15.0°C. The sporadic nature of fishing effort late in the runs when temperatures were higher probably leads to an underestimate of temperatures, but in all three rivers the mean weekly catch at 19.0° to 21°C was approximately one-half that recorded at 13.0° to 15.0°C.

TIMING OF OUTMIGRATION OF JUVENILES RELATED TO STREAM TEMPERATURE

Juvenile shad normally spend their first summer in the river in which they were spawned. They begin to move downstream to the sea in the fall. This migration, too, is apparently triggered by temperature. Sykes and Lehman (1957) provided the interesting quantitative data in Table 7. The largest number of shad moved downstream when the temperature dropped below 15.5°C for a period of several days. Similar findings were reported by Smith (1899), Walburg and Nichols (1967), and Chittenden (1969).

OCEANIC WATER TEMPERATURES ASSOCIATED WITH SHAD MIGRATIONS

Talbot and Sykes (1958) were the first to describe the oceanic migrations of shad. From 19 years of tagging by the U.S. Fish and Wildlife Service, they learned that shad from all the major Atlantic coast rivers congregate in the Gulf of Maine in the summer and fall. This group of shad includes immature fish from all streams and survivors of spawning from streams north of Chesapeake Bay. South of Chesapeake Bay there are no survivors after spawning. Talbot and Sykes believed that the shad move south to waters off the Middle Atlantic States in the winter. However, they had only one recapture in December. In January or February shad do begin to appear off the central Atlantic Coast from North Carolina to Long Island. Confirmation of the conclusions of Talbot and Sykes (1958) came from Walburg and Nichols (1967) who reported 49 shad caught at lat 40°N, long 70°41'W (Point A, Figure 2A), January 23 to February 2, 1961, by the research vessel *Delaware*. If mature in the spring, the shad then move either north or south to their home streams and spawn. The shad runs in southern streams occur early in the spring and progressively later northward.

One of us (Leggett) has conducted extensive tagging studies of Connecticut River shad since 1965. From 1965 to 1969, 18,374 mature shad were marked and released in the lower Connecticut River. In all, 83 of these shad have been recovered along the Atlantic coast from North Carolina to the Bay of Fundy, 66 with complete information as to date and place of recapture. Over 300 shad were recovered in the lower Connecticut River 1 year or more after tagging. These recaptures, together with coastal recoveries from 4,500 shad tagged by the U.S. Bureau of Fisheries and U.S. Fish and Wildlife Service between 1938 and 1949, were plotted on monthly surface temperature charts of the western Atlantic Ocean (U.S. Naval Oceanographic Office, 1967; U.S. Coast Guard Oceanographic Unit,

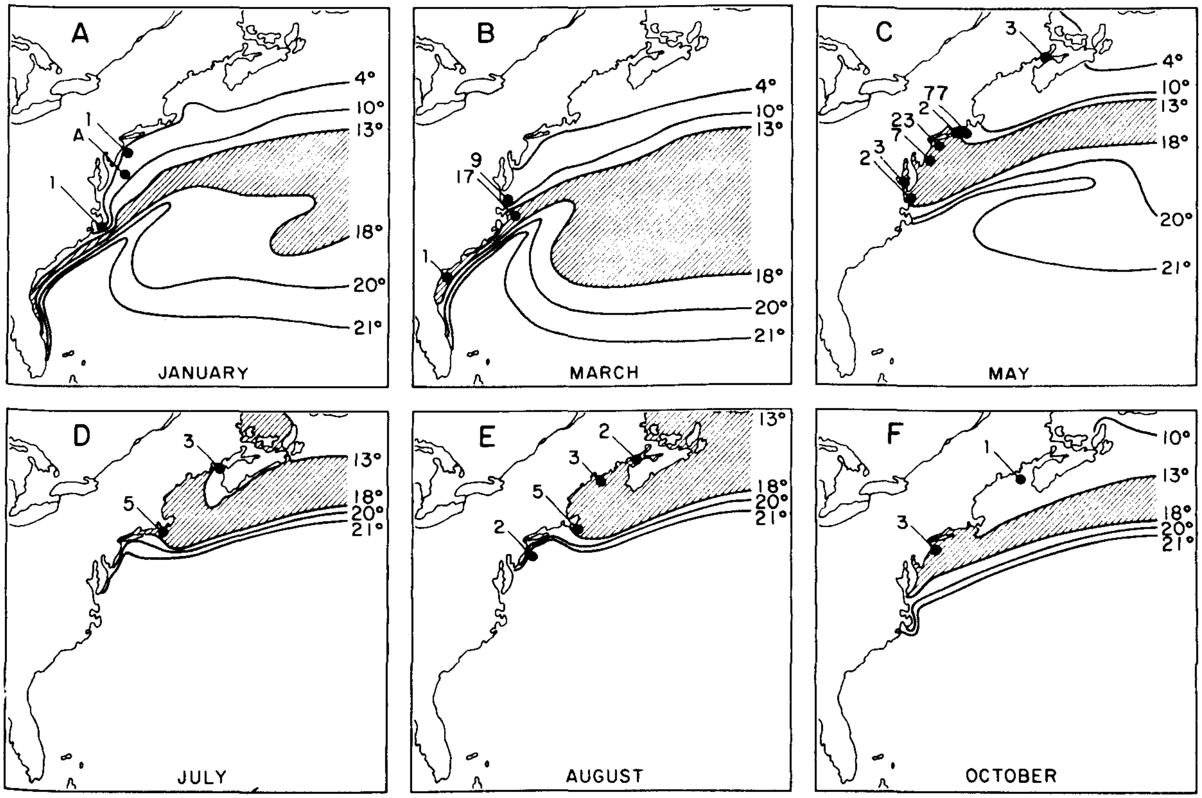

FIGURE 2.—Atlantic Ocean average sea surface temperatures and associated locations of shad recaptures for selected months. Number of recaptures is shown. Point A represents the 49 shad Walburg and Nichols (1967) reported caught in a trawl. (Temperature charts adapted from U.S. Naval Oceanographic Office, 1967; inshore segments of isotherms were refined with the aid of surface temperature charts by U.S. Coast Guard Oceanographic Unit, 1969-1971, see footnote 4.)

1969-1971).[4] Their distribution in time and space corresponds closely to the position of the 13° to 18°C isotherms. Six of these charts are presented in Figure 2.

In July, August, and September, the 13° to 18°C isotherms are situated in the Gulf of Maine (Cape Cod to Bay of Fundy). It was from here that Talbot and Sykes (1958) reported the majority of their recoveries in these months. Recoveries from the Connecticut River taggings were confined exclusively to this area during July (Figure 2D), August (Figure 2E), and September. In October (Figure 2F), November, and December these waters cool and the 13° to 18°C isotherms move south to the middle Atlantic region, the general area where shad are said to winter (Talbot and Sykes, 1958; Walburg and Nichols, 1967). During these months, as stream temperatures drop below 15.5°C, juvenile shad migrate out of their streams and, as Talbot and Sykes suggested, they probably join the large body of southward migrating adult and immature shad as they pass on their way to the middle Atlantic wintering area.

In December and January (Figure 2A), water of appropriate temperature extends in a narrow band near the coast of Florida, and the shad can move into the St. Johns River along the band. In February and March (Figure 2B), 13° to 18°C water bathes the coast of the southern Atlantic States from Cape Hatteras south providing access for shad to coastal streams in those States. At this time Connecticut River shad first appear off the coast of North Carolina and Virginia and begin to move north along the coast, mainly within the bounds of the 13° to 18°C isotherms. During April and May (Figure 2C), shad continue to move north as they follow the movement of the 13° to 18°C isotherms. In April they are located around Chesapeake Bay and Delaware Bay and contribute to the runs into streams in these areas. By May shad are concentrated in the Long Island region and run into the Hudson and Connecticut Rivers. In June there is movement of the isotherms farther north along the coast, corresponding to the peaks of the shad runs in streams to the north. Again in July (Figure 2D), August (Figure 2E), and September, the Gulf of Maine reaches optimum temperature for the species.

The northern and southern limits of the range of shad on the Atlantic coast appear to be defined by the temperature relationship described above. In June and July a narrow tongue of 13°C water typically extends to the mouth of the St. Lawrence River, the northern extension of the fish's range. North of the St. Lawrence, the ocean seldom warms above 13°C. In the south shad appear to be blocked from extending their range into the Gulf of Mexico by a band of water south of Cape Kennedy that rarely cools below 21°C even in December and January (U.S. Naval Oceanographic Office, 1967). It is probable that *Alosa alabamae*, a closely related species that is native to most principal streams tributary to the Gulf of Mexico east of the Mississippi, evolved from *Alosa sapidissima*. Prior to the emergence of the Florida peninsula, the range of shad may have included these Gulf rivers. Florida's emergence would have produced an effective geological barrier between the stocks, thereby promoting their separate evolution. In this connection we note that a narrow band of water of the temperature range 13° to 18°C extends along the northernmost coast of the Gulf of Mexico during the months of December to March (Rivas, 1968).

PACIFIC OCEAN MIGRATION OF SHAD

Prior to 1871 shad occurred only on the eastern coast of North America. In that year shad from eastern rivers were stocked in the Sacramento River. So successful was the venture that by 1880 shad were reported to range from Todos Santos Bay, Baja California, to Kodiak, Alaska (Welander, 1940; Claussen, 1959). Shad make no spawning runs south of San Francisco Bay because there are no streams of sufficient size. The Fraser River is thought to be the most northerly river in which they spawn (Carl, Clemens, and Lindsey, 1967).

Nothing concrete is known about the migrations of the shad in the Pacific Ocean but cir-

[4] U.S. Coast Guard Oceanographic Unit. 1969-1971. Monthly temperature charts, July 1969 to December 1971, available U.S. Coast Guard Oceanographic Unit, Airborne Radiation Thermometer Program, Bldg. 159-E Washington Navy Yard, Washington, D.C. 20390. [Processed.]

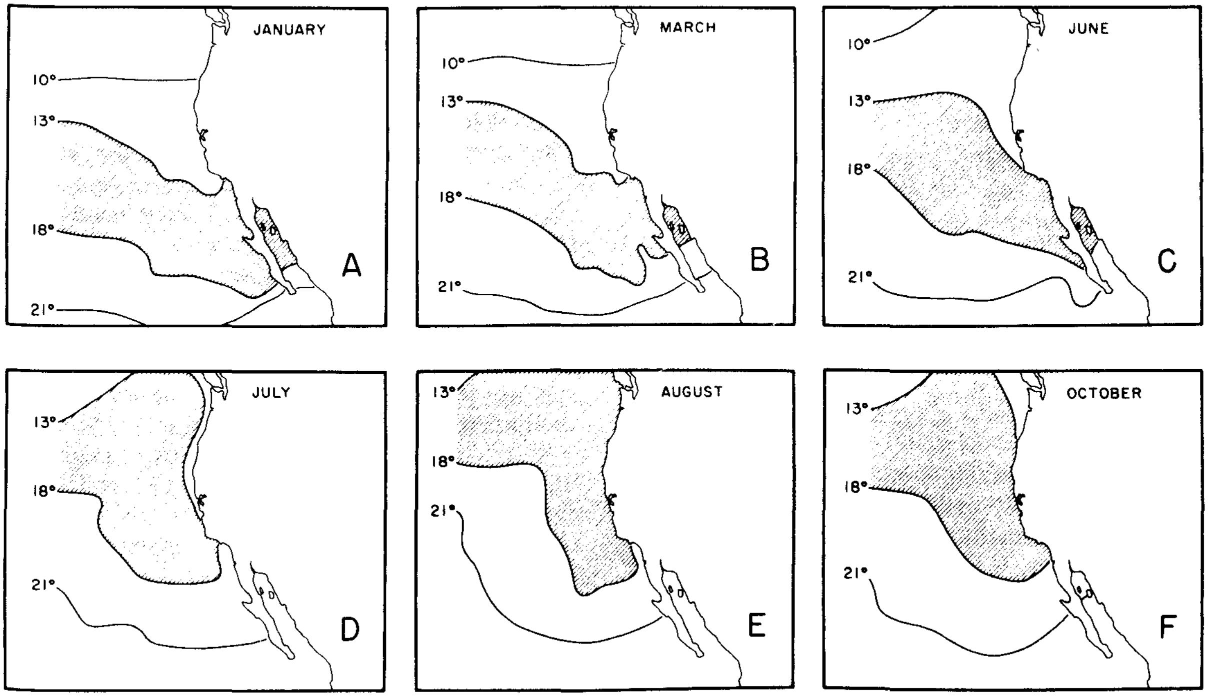

FIGURE 3.—Pacific Ocean average sea-surface temperatures and predicted shad distributions for selected months. (Temperature charts adapted from U.S. Navy Hydrographic Office, 1954.)

cumstantial evidence suggests a northward migration in summer and a southward one in winter as on the Atlantic coast.

If we assume that the migrations of shad in the Pacific follow the same specific ocean temperatures as do the migrations of Atlantic coast populations (an assumption that is supported by the similar relationships between peak movements into rivers and water temperatures on the two coasts), it is possible to make predictions concerning the Pacific migrations based on our knowledge of the distribution of 13° to 18°C waters along the Pacific coast.

During the months of December to April, the 13° to 18°C isotherms encompass an area extending from southern California to near the tip of Baja California (Figures 3A, 3B). We predict that the Pacific shad populations will be found to winter in this general area, a prediction strengthened by records of a few shad from San Pedro, Calif., in November and December (Smith, 1896). In May and June a general warming trend is noticeable along the coast, and the 13° to 18°C isotherms arch northward offshore (Figure 3C). Their northward movement is undoubtedly affected by the upwelling that occurs along the California and Oregon coasts and produces an inshore pool of cool water in spring and summer. We predict that the shad begin their northward movements at this time. If this be so, they are probably directed offshore in the area of this cool water. In July and August, 13° to 18°C waters occur over a wide range of the Pacific Ocean (Figures 3D, 3E). Shad might be located anywhere from Alaska (in some years) to Baja California. The reports, summarized by Welander (1940), of rare summer occurrences of shad at Kodiak, Alaska, and by Claussen (1959), off Baja California, are therefore not surprising. In September, cooling commences and results in a southward movement of suitable water and a contraction of its extent (Figure 3F). During this period we predict that the shad move southward with the 13°

to 18°C isotherms, resulting in their concentration off southern California and Baja California in late November and December and continuing at least until April.

The scope of regular migrations that we hypothesize as taking place on the Pacific coast (about 2,575 km, Columbia River to Cedros Island) is similar to that which is known to occur on the Atlantic coast (about 2,250 km, St. Johns River, Fla., to the Bay of Fundy).

DISCUSSION

Both the marine and freshwater migrations of shad appear to be regulated by water temperature. In the four rivers we have considered, the temperatures at which shad appeared in the river and at which peak movement occurred were remarkably consistent in spite of the great distances separating them. In all rivers except the St. Johns in Florida, water temperatures are increasing as the shad proceed upriver. Water temperature in this river is decreasing during the first half of the run, and the peak movement occurs at the lowest annual temperature. Nevertheless, the peak occurred in the same temperature range (15.5°-20.0°C) in the St. Johns as in the other rivers studied.

The precise correlation between temperature and the timing of the spawning migrations of the shad places the maximum number of adults on the spawning grounds when the temperature is optimum for the survival of eggs and young. In the Columbia and Connecticut Rivers, where our studies of shad movement were conducted at points close to the spawning grounds (Bonneville and Holyoke), peak migrations occurred at 18.0° and 19.5°C, respectively. Massmann (1952) working in the York River, Walburg (1960) in the St. Johns River, and Marcy (1969) in the Connecticut River have all reported the median spawning temperature, as shown by abundance of eggs, to be within the temperature range of 16° to 20°C. Leim (1924) and Bradford, Miller, and Buss (1964)[5] found that maximum hatch and survival of eggs and larvae occurred at 15.5° to 26.5°C. Temperatures below 15.5°C prolonged the time of hatching and reduced survival.

Since these optimum temperatures are reached later in the year at higher latitudes, the timing of the entry of shad into individual rivers must also be seasonally adjusted. Consequently, the earliest run occurs in Florida during the winter, and the latest runs in June and July in northern rivers such as the St. Lawrence and Columbia. This phase of the timing appears to be regulated by the adherence of shad to similar temperature regimes while at sea. As the ocean warms in the spring, the area occupied by water temperatures in the range 13° to 18°C moves gradually northward. By maintaining themselves in this thermal zone, shad arrive at the mouth of their home river when river temperatures are suitable for entry.

Of course, what we have described is a general migratory pattern of shad that is clearly associated with water temperatures both in the ocean and in the streams into which they run. Occasional shad are caught in the winter in Chesapeake Bay and in the Delaware and Hudson Rivers in the fall and winter (summarized by Walburg and Nichols, 1967, also recorded in our recoveries of Connecticut River shad shown in Figures 2A, 2F.) We learned recently that 14 shad were caught in a commercial trawl on February 10, 1972 at lat 41°16′N, long 71°39′W where the water temperature was 3.7°C at the surface and 4.1°C at the bottom. Nevertheless, as Walburg and Nichols stated: "The vast majority of fish, however, followed a regular migratory pattern." It may very well be that the observed temperatures associated with the presence of the majority of shad are preferred temperatures, not required ones, or they may be required only by a majority of fish. A small minority may be able to condition themselves to water outside the range tolerated by the majority. Experiments are needed to determine the upper and lower units of temperature tolerance of mature and immature shad, as well as their temperature preference.

It should be noted that we have related average ocean conditions to an average shad migra-

[5] Bradford, A. D., J. G. Miller, and K. Buss. 1964. Progress report summary on phase B-2 "to determine by bioassay techniques the inherent tolerance of shad during its egg and larval stages to specific environmental factors of the Susquehanna River and its tributaries. Pennsylvania Fish Commission, Benner Spring Fish Research Station, Bellefonte, Pa. (Unpubl. manuscr.)

tion. In particular years the ocean temperature regime may vary and change the usual locations of the shad. Moreover, we have related shad migrations to surface temperatures only. There is at present no information on the depths at which shad migrate. Walburg and Nichols (1967) recorded shad that were trawled at depths of 87 to 126 fm, and Leggett has similar records of recoveries of tagged shad at depths of 20 to 70 fm, again by trawl. These records do no more than provide estimates of the maximum depths at which shad migrate. These fish may have been captured near the surface as the trawl was being recovered.

On the basis of our observations on the behavior of shad in relation to temperature, we believe that the effect of a significant elevation of the temperature of a northern stream might be to initiate the shad run at an earlier date, provided that ocean temperatures are within the proper range. In a southern stream like the St. Johns River, Fla., where the run occurs during the natural cooling phase rather than the warming phase of the river, elevated temperatures could destroy the run of shad.

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