THE OCEANIC MIGRATION OF AMERICAN SHAD, *ALOSA SAPIDISSIMA*, ALONG THE ATLANTIC COAST

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ABSTRACT

The migratory route of American shad, *Alosa sapidissima*, in the Atlantic Ocean was studied using 14 yr of catch data collected during bottom trawl surveys by the U.S. National Marine Fisheries Service (and its predecessor) and cooperating foreign countries. All shad catches occurred at bottom temperatures from 3° to 15°C, with the most frequent catches between 7° and 13°C. Water temperatures between initial and peak entry of shad into home estuaries along the Atlantic coast are within the same thermal regime (3°-15°C). During the summer, all shad catches occurred north of lat. 40°N in two primary areas: Gulf of Maine and an area south of Nantucket Shoals. Previous studies on food habits and differences in time of capture during National Marine Fisheries Service surveys indicated that shad were vertical migrators, probably following the diel movements of large zooplankters in the water column. Shad were generally absent from the Gulf of Maine by late autumn, and concentrations were found between lat. 39° and 41°N during the winter. Based on previous tagging studies, National Marine Fisheries Service surveys, and coastal temperature data, most prespawning adults enter coastal waters along the Middle Atlantic Bight from lat. 36° to 40°N and then proceed north or south to natal rivers. Coastal surveys for river herring by North Carolina's anadromous fishery research program and commercial shad catches reported to the International Commission for the Northwest Atlantic Fisheries by member nations concur with our proposed bottom temperature (3°-15°C)-migratory route hypothesis for shad.

The American shad, *Alosa sapidissima*, is an anadromous fish ranging from the St. Johns River, Fla., to the St. Lawrence River, Canada (Walburg and Nichols 1967). Meristic and tagging studies indicate that discrete spawning populations of shad exist in river systems along the Atlantic coast (Hollis 1948; Hill 1959; Nichols 1960, 1966; Carscadden and Leggett 1975a). Juveniles leave freshwater in autumn and generally remain in the ocean for 3-5 yr before returning to their natal rivers to spawn. Spawning runs occur in a south to north temporal progression, beginning as early as December in Florida and as late as June in Canada (Walburg 1960). Virtually all shad south of Cape Hatteras, N.C., die after spawning, whereas the percentage of repeat spawners in rivers north of North Carolina increases with latitude (Leggett 1969; Chittenden 1975).

A considerable amount of literature exists on this species because of its commercial and recreational importance inshore, but little research has been done on the oceanic phase of its life history. Talbot and Sykes (1958) provided the first evidence of an annual oceanic migration based on 19 yr of tagging studies by the U.S. Fish and Wildlife Service. Tag returns indicated that shad from U.S. rivers congregated with those from Canadian rivers (Vladykov 1950, 1956) in the Gulf of Maine during summer and autumn and moved south to possibly overwinter off the Middle and South Atlantic States (Talbot and Sykes 1958; Walburg 1960; Walburg and Nichols 1967; Cheek 1968). In the spring, shad moved north or south toward natal rivers to spawn.

Temperature monitoring in rivers with major shad runs, and laboratory experiments, have provided convincing evidence that the timing of diadromous movements corresponds with specific water temperatures (Walburg and Nichols 1967; Chittenden 1969, 1972; Williams and Bruger 1972; Leggett and Whitney 1972; Leggett 1973). Leggett and Whitney (1972) also postulated that the oceanic distribution of shad was temperature-controlled; tag returns plotted on surface isotherm charts fell within the 13°-18°C isotherms. However, all of the tag returns used to establish this "migrational corridor" at sea were collected inshore during the spring coastal migration toward

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home rivers. The correlation between offshore distribution and surface temperatures was therefore based on extrapolation.

The U.S. shad fishery is essentially an inshore operation and commercial catch records have limited value in evaluating the distribution of shad at sea. Previous tagging studies have relied on other commercial fisheries for offshore tag returns, but these fisheries concentrate effort at a time or place where principal species aggregate. Tag returns from shad taken as bycatch may therefore contain a geographical bias and reflect only the distribution of fishing effort. This paper examines offshore collections of shad from 14 yr of bottom trawl surveys by United States and foreign research vessels and interprets available literature on the coastal occurrence of shad. An alternative temperature-based hypothesis is presented to explain the offshore migratory cycle of shad.

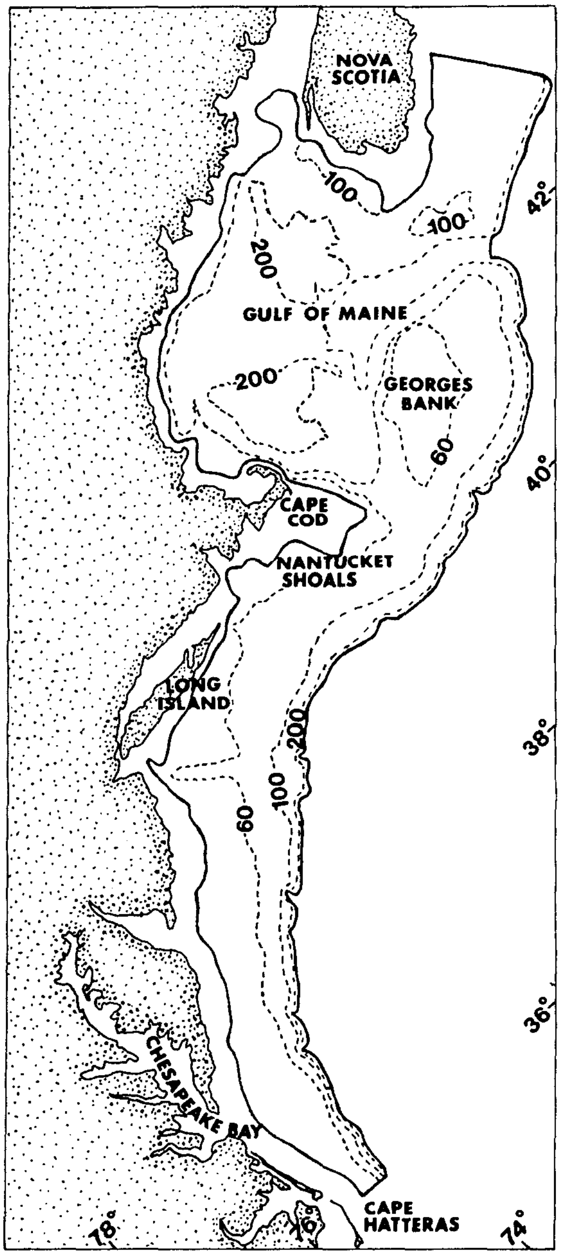

FIGURE 1.—National Marine Fisheries Service bottom trawl survey area between 27 and 366 m, Cape Hatteras, N.C., to Nova Scotia, western North Atlantic.

METHODS

The U.S. National Marine Fisheries Service (NMFS) and its predecessor have conducted autumn bottom trawl surveys since 1963 using the RV *Albatross IV* and the RV *Delaware II*. The survey area extends from Nova Scotia to Cape Hatteras, out to 366 m (200 fm) (Figure 1) and is stratified into geographical zones based on depth and area. Coastal sampling stations are outside the 27-m (15-fm) depth contour. Middle Atlantic stations between New Jersey and Cape Hatteras were added during autumn 1967. A stratified random sampling design is used in the surveys; trawl stations are allocated to strata in proportion to stratum area and randomly assigned within strata (Grosslein 1969). A standard No. 36 Yankee bottom trawl with a 1.25 cm stretched mesh cod end liner is towed at each station for 30 min at an average speed of 3.5 kn. Autumn surveys were conducted 24 h/day during 1963-76, between 3 September and 16 December.

Spring bottom trawl surveys have been conducted by NMFS since 1968 over the same geographical area (Figure 1). The No. 36 Yankee trawl was used from 1968 to 1972 and a larger No. 41 Yankee trawl from 1973 to 1976. Trawling procedures were the same as during autumn surveys and occurred between 4 March and 16 May. A detailed description of NMFS bottom trawl surveys and survey procedures is provided by Flescher[3] and Grosslein.[4]

In addition to U.S. cruises, periodic autumn trawl surveys were conducted cooperatively with

[3]Flescher, D. 1976. Research vessel cruises, 1963-1975 National Marine Fisheries Service Woods Hole, Massachusetts. NMFS, Woods Hole, Mass., Lab. Ref. No. 76-14, 30 p.

[4]Grosslein, M. D. 1969. Groundfish survey methods. NMFS, Woods Hole, Mass., Lab. Ref. No. 69-2, 34 p.

the U.S.S.R., Poland, and France from 1969 to 1976, mainly between Georges Bank and Cape Hatteras. Spring trawl surveys, intended primarily as juvenile herring surveys, have been made since 1973 by vessels from U.S.S.R., Poland, German Democratic Republic, and Federal Republic of Germany between Nova Scotia and Cape Hatteras. Most of the foreign surveys followed NMFS sampling procedures, sampled all or selected strata within respective survey areas, but used various types of bottom trawls. All spring and autumn surveys and additional cruises during summer and winter are summarized in Table 1. Survey station and catch data pertinent to this study included: date, location, time, depth, bottom and surface temperatures, and number, length frequencies, and weight of shad caught.

We plotted catch locations from all surveys (Table 1) by 10′ rectangles of latitude and longitude on depth contour maps according to month or season. Locations of shad collections during spring (March-May) and autumn (September-November) were plotted by month. Summer (June-August) and winter (December-February) surveys were grouped by season because of less sampling effort and lower catch frequency. Commercial shad catches by month reported to the International Commission for the Northwest Atlantic Fisheries (ICNAF) by member nations from 1970 to 1975 were provided by Hodder[5] and used to define major shad catches within each ICNAF division and their correlation with distribution patterns based on survey data. Surface and bottom temperatures (nearest 1°C) were plotted for each trawl tow that collected shad; foreign catches with missing temperature data were omitted from this analysis. Additional oceanographic data on temperature (Walford and Wicklund 1968; Colton and Stoddard 1972; Churgin and Halminski 1974; U.S. Coast Guard Oceanographic Unit[6]) and oceanic currents (Bumpus and Lauzier 1965; Stommel 1965; Bumpus 1973) were reviewed for seasonal patterns along the Atlantic coast.

RESULTS

Bottom trawls at 10,435 stations during the 77 surveys collected 4,770 subadult and adult shad at 527 stations throughout the survey area. United States and foreign research vessels accounted for 315 and 212 of the successful collecting stations, respectively. Shad ranged in size from 8 to 50 cm fork length (FL). Surface and bottom temperatures were recorded at 448 of these stations and used to plot catch frequency at 1°C intervals. Shad were collected at survey stations with surface temperatures between 2° and 23°C, and frequent catches occurred throughout most of this temperature range (Figure 2). Bottom temperatures at successful collecting stations ranged from 3° to 15°C, but primarily between 5° and 13°C (Figure 3). Most stations with bottom temperatures <3°C occurred in the Gulf of Maine during late winter and early spring; stations with bottom temperatures >15°C were mainly off the mid-Atlantic coast during late summer and early autumn. This apparent relationship between shad occurrence and bottom temperatures was examined further by comparing the catches of shad with total sampling effort at each temperature (Table 2). Bottom temperatures during surveys ranged from 1° to 23°C, but shad were captured only between 3° and 15°C. Shad catches occurred more frequently at

[5]V. M. Hodder, ICNAF Office, Dartmouth, N. S., Canada B2Y 3Y9, pers. commun. July 1977.

[6]U.S. Coast Guard Oceanographic Unit. 1970, 1975. Monthly temperature charts, January to December 1970, January to December 1975, available U.S. Coast Guard Oceanographic Unit, Bldg. 159-E Navy Yard Annex, Washington, DC 20590.

TABLE 1.—Summary of bottom trawl surveys conducted by United States and foreign research vessels between Cape Hatteras, N.C., and Nova Scotia, 1963-76.

Season	Country	No. of surveys	No. of stations	Inclusive dates
Spring	United States	15	2,514	4 Mar.-16 May
	Foreign	10	597	26 Feb.-29 May
Summer	United States	4	810	7 July-28 Aug.
	Foreign	6	618	9 Aug.-3 Sept.
Autumn	United States	21	3,657	3 Sept.-16 Dec.
	Foreign	18	1,676	3 Sept.-11 Dec.
Winter	United States	3	563	16 Jan.-8 Apr.
Totals		77	10,435	

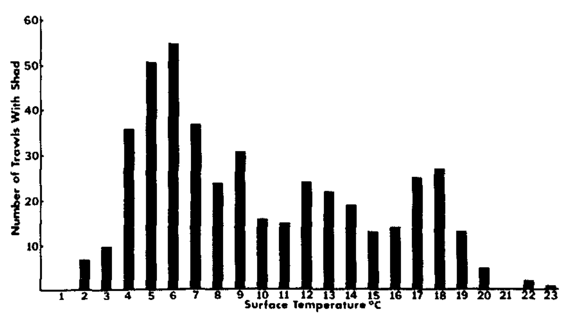

FIGURE 2.—Surface temperatures at 448 stations where American shad were collected during bottom trawl surveys, 1963-76, Cape Hatteras, N.C., to Nova Scotia.

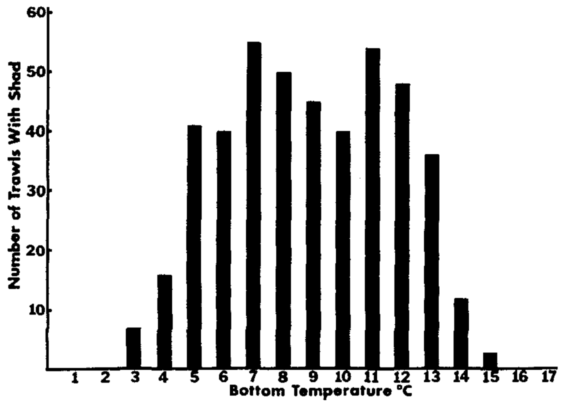

FIGURE 3.—Bottom temperatures at 448 stations where American shad were collected during bottom trawl surveys, 1963-76, Cape Hatteras, N.C., to Nova Scotia.

TABLE 2.—Total sampling effort, number of shad catches, and percent catch frequency of shad at each bottom temperature during bottom trawl surveys, 1963-76, Cape Hatteras, N.C., to Nova Scotia.

Bottom temperature (°C)	Total no. of trawls	Trawls with shad No.	Trawls with shad %
1	16	0	0
2	104	0	0
3	270	7	2.59
4	567	16	2.82
5	987	41	4.15
6	964	40	4.15
7	1,047	55	5.25
8	997	50	5.02
9	909	45	4.95
10	750	40	5.33
11	741	54	7.29
12	739	48	6.50
13	626	37	5.91
14	333	12	3.60
15	164	3	1.83
16	71	0	0
17	56	0	0
18	41	0	0
19	30	0	0
20	29	0	0
21	34	0	0
22	19	0	0
23	5	0	0

temperatures between 7° and 13°C, with the greatest capture frequency at 11°C (Table 2).

Ocean depths at stations with shad ranged from 20 to 340 m, but most of these stations (65%) were <100 m deep (Figure 4). Of the 527 successful collecting stations, 269 (51%) occurred at depths between 50 and 100 m. Since trawling effort during U.S. spring and fall surveys was proportional to the area of each depth interval (Table 3), the number of shad catches within these depth strata was amenable to chi-square analysis. A comparison between shad catches at each depth interval and catches at all other depths combined indicated

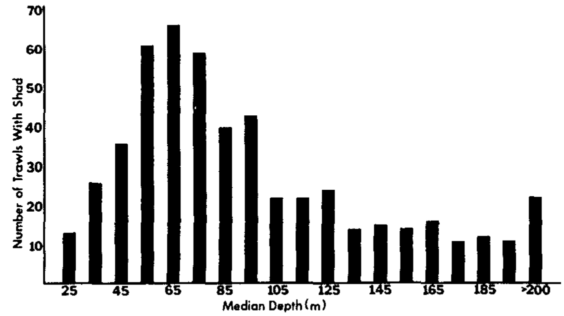

FIGURE 4.—Frequency of American shad catches with depth at 527 survey stations, 1963-76, Cape Hatteras, N.C., to Nova Scotia.

TABLE 3.—Depth intervals within the survey area and associated shad catches during U.S. bottom trawl surveys, 1967-76, Cape Hatteras, N.C., to Nova Scotia.

Depth interval (m)	Survey area km²	Survey area %	Number of trawls with shad Observed	Expected	χ^2
27-55	47,412	25.4	45	58	3.89*
56-110	55,009	29.5	109	68	35.10**
111-185	53,789	28.9	53	67	4.13*
186-366	30,181	16.2	23	37	6.32*
Totals	186,391	100.0	230	230	

*$P<0.05$.
**$P<0.01$.

that the greater capture frequency in the 56-110 m interval was highly significant ($P<0.01$); shad catches at all other depths were significantly fewer ($P<0.05$) than expected (Table 3).

Spring surveys were conducted mainly in March and April, accounting in part for the more frequent collections during these 2 mo (Figure 5). In March, shad were distributed along the Middle Atlantic Bight. Most fish between Long Island, N.Y., and Cape Cod, Mass., were taken in 60-200 m of water, many along the outer continental shelf (Figure 5). Few shad occurred in <60 m of water north of lat. 40°N, whereas most catches south of Long Island were at depths <60 m.

During the summer, shad were not captured south of lat. 40°N (Figure 6). Forty-six collections in July and August were made in two general areas: the Gulf of Maine and southeast of Cape Cod, near Nantucket Shoals. Mean depth at these stations was 95 m, but ranged from 35 to 214 m. Catches were distributed along the coastal margin of the Gulf of Maine and the southern half of Georges Bank; most trawling stations in the deeper, central Gulf did not collect shad.

October received the greatest trawling effort during autumn surveys. Shad were again distrib-

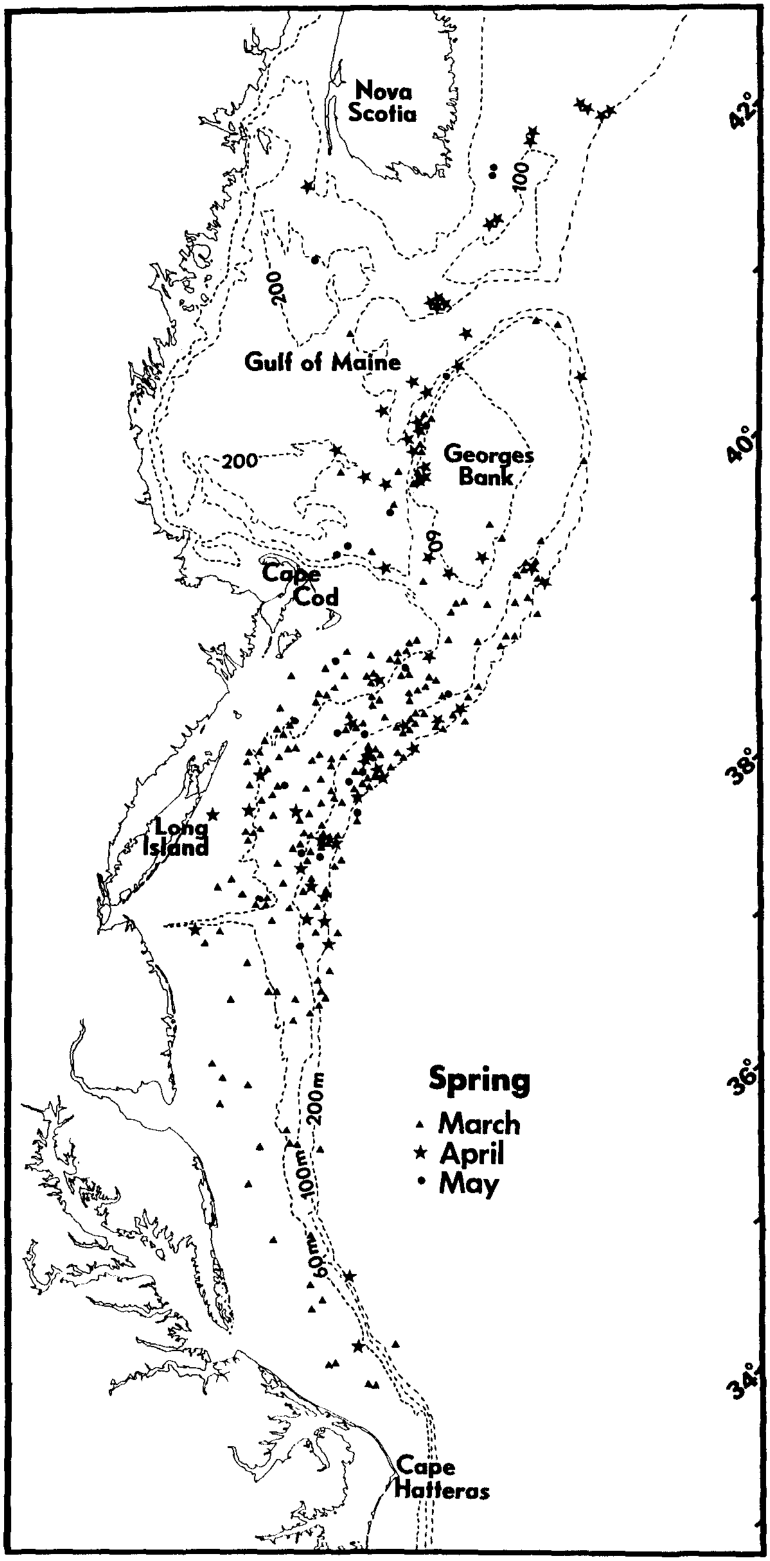

FIGURE 5.—Location of all American shad catches during spring bottom trawl surveys, 1968-76, Cape Hatteras, N.C., to Nova Scotia.

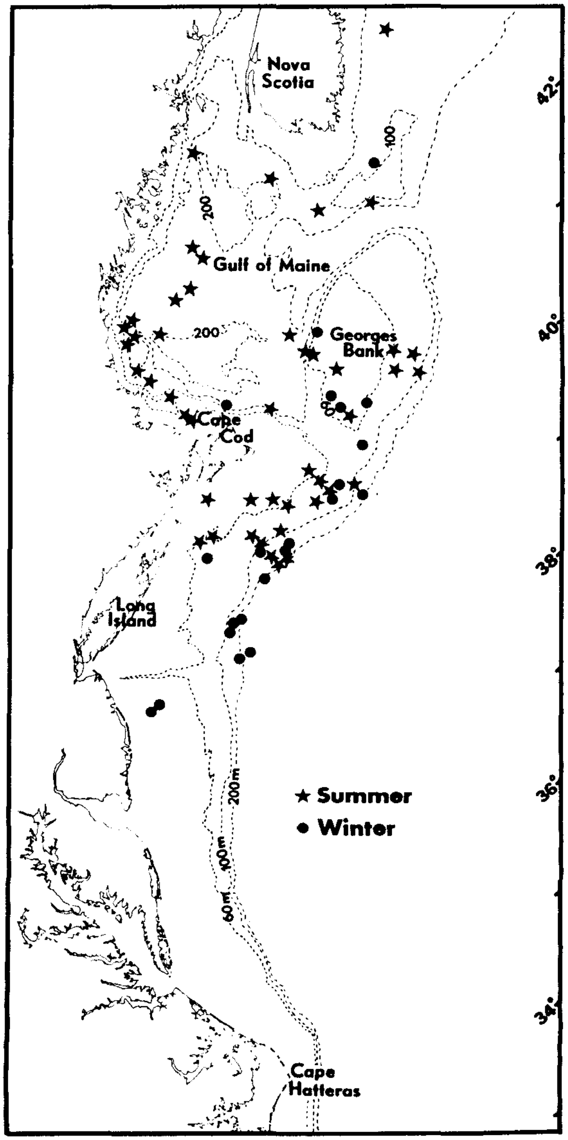

FIGURE 6.—Location of all American shad catches during summer and winter bottom trawl surveys, 1963-76, Cape Hatteras, N.C., to Nova Scotia.

uted along the Gulf of Maine and Georges Bank perimeter, as well as south of Nantucket Shoals (Figure 7). Most of these captures were along the continental shelf at depths of >60 m. Monthly catches indicated a southward movement out of the Gulf of Maine in late autumn, although some shad remained there into November. During 10 yr of autumn bottom trawl surveys along the Middle Atlantic States, shad were never collected offshore south of lat. 39°N.

The relatively low number of successful trawling stations during the winter may be inadequate to define the southern limit of the wintering area (Figure 6). Winter catches occurred at 22 stations from southern Long Island (lat. 39°N) to the southern edge of Georges Bank (lat. 41°N) and reflected the same general area where shad began congregating in autumn (Figure 7). Except for two shallow-water stations, winter collections of shad were made at a mean depth of 108 m.

DISTRIBUTION OF INTERNATIONAL CATCHES

The season for major shad catches in ICNAF divisions (Figure 8) agreed closely with distribution according to bottom trawl surveys. Largest annual catches were reported by the United States in Subarea 6 (1,517-2,812 t). United States catches between 1970 and 1976 occurred primarily in Division 6B and ranged from 112 to 1,272 t in March and April. Most of this spring catch was taken by the inshore commercial fishery. The only other catch of comparable size was made in Division 5Ze by the Federal Republic of Germany during September 1973 and totaled 302 t. Catches in Subarea 5 occurred mainly in autumn; however, winter catches were reported in Division 5Zw and 6A between New Jersey and Cape Cod. Canadian catches in Subarea 4 were greatest in May, with decreasing catches throughout the summer.

DISCUSSION

The sampling design of NMFS bottom trawl surveys covers a large area in a relatively short period of time and provides good data on fish distribution and concurrent environmental conditions. Even though these surveys were initially designed to sample primarily demersal species, results do reflect major changes in the abundance of pelagic species as well (Schumacher and Anthony[7]; Anderson[8]). Bottom trawls used during U.S. surveys are less effective on *Alosa* spp. than

[7]Schumacher, A., and V. C. Anthony. 1972. Georges Bank (ICNAF Division 5Z and Subarea 6) herring assessment. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1972, Res. Doc. No. 24, Serial No. 2715, 36 p.

[8]Anderson, E. D. 1973. Assessment of Atlantic mackerel in ICNAF Subarea 5 and Statistical Area 6. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1973, Res. Doc. No. 14, Serial No. 2916, 37 p.

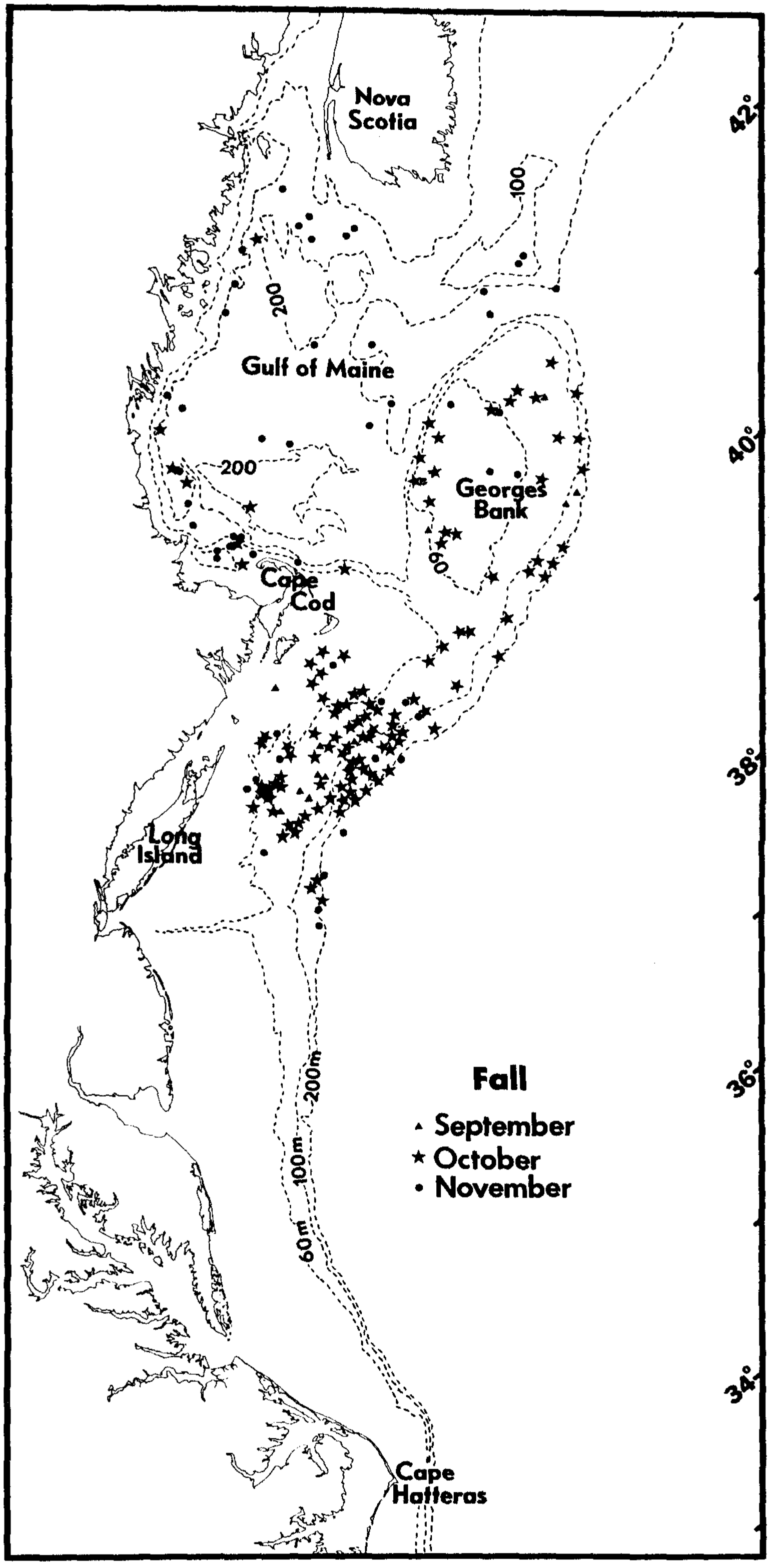

FIGURE 7.—Location of all American shad catches during autumn bottom trawl surveys, 1963-76, Cape Hatteras, N.C., to Nova Scotia.

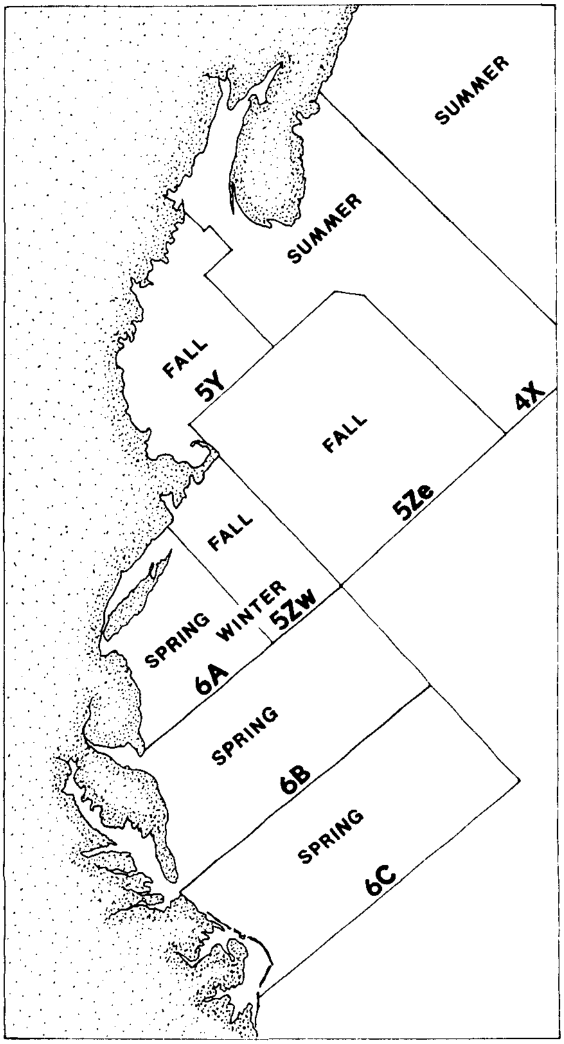

FIGURE 8.—Seasonal distribution of major American shad catches in the International Commission for the Northwest Atlantic Fisheries divisions, 1970-75, Cape Hatteras, N.C., to Nova Scotia.

foreign midwater trawls or the wing trawl (Holland[9]), but bottom trawl survey data provide the most complete, available records on offshore occurrence.

Based on the data presented, survey-related observations to be discussed, and literature to be reviewed, we propose the following migratory cycle for American shad. Offshore movements are limited to areas and depths with near-bottom temperatures between 3° and 15°C. Shad occur most frequently in offshore areas of intermediate depths (approximately 50-100 m). Adults that survive spawning together with subadults migrate to the Gulf of Maine or to an area south of Nantucket Shoals and remain there through the summer and early autumn. During this period of active feeding, shad are vertical migrators and follow the diel movements of zooplankton in the water column. Most shad move out of the Gulf of Maine in autumn with declining water temperatures and congregate offshore, between southern Long Island and Nantucket shoals (lat. 39°-41°N) during the winter. Adults enter coastal waters in a broad front toward the Middle Atlantic coast, as far south as North Carolina during the winter and spring. Shad populations returning to South Atlantic rivers migrate south adjacent to the coast and within the 15°C isotherm to reach home rivers by winter and early spring. North Atlantic populations proceed north up the coast in the spring with the warming of coastal waters above 3°C.

Offshore Distribution

The wide range of surface temperatures at stations where shad were caught does not support the extrapolation of the inshore temperatures-shad migration regime proposed by Leggett and Whitney (1972) to explain offshore movements. The influence of temperature on fish behavior and physiology is most pronounced during the spawning season (Laevastu and Hela 1970), particularly for anadromous fishes. Tag returns within the 13°-18°C isotherms (Leggett and Whitney 1972) may have reflected inshore physiological changes in prespawning adults, leading to higher optimal temperatures approaching those for spawning. Our results indicate that near-bottom temperatures between 3° and 15°C provide a better basis for predicting shad movements in offshore waters.

Offshore catches during NMFS surveys revealed that shad are not limited to the Gulf of Maine in summer months as reported by Talbot and Sykes (1958). Shad were also collected in an area south of Nantucket Shoals during summer and autumn surveys. Although shad from most river systems have been collected in the Gulf of Maine during the summer (Talbot and Sykes 1958), it is not known whether all populations migrate together at sea. Distribution during the spring is widespread and not indicative of a syn-

[9]Holland, B. F., Jr. 1975. Anadromous fisheries research program, northern coastal area. Section II. N.C. Proj. AFCS 11-1 Job 6, 43 p.

chronous species migration as suggested by Leggett (1977). Coastal tagging studies during the spring reveal an aggregation of many spawning stocks that often detour into estuaries along the coast (Sykes and Talbot 1958; Talbot and Sykes 1958; Chittenden 1974; Leggett 1977; White et al.[10]). However, the length of time each population has been inshore is unknown. Until stock identification at sea is feasible, the regional composition and extent of offshore mixing cannot be documented.

The location of winter collections (lat. 39°-41°N) coincides with two previously published capture records (Talbot and Sykes 1958; Walburg and Nichols 1967), but the extent of overwintering in deep water off the continental shelf is unknown. Shad collections in the northern Gulf of Maine during November and December were made at depths >100 m and do not conform (based on previous studies) with the expected migration south in late autumn. These and other shad captured in deep water near Nova Scotia during March (Vladykov 1936) are outside the apparent wintering area, south of Nantucket Shoals. The possibility that some shad overwinter or become thermally isolated in deepwater areas off Nova Scotia (Vladykov 1936; Hodder 1966) needs further investigation.

Circulation patterns along the Atlantic coast do not account for the seasonal distribution of shad according to survey data or their coastal migration routes based on tagging studies (Talbot and Sykes 1958; Leggett 1977). Bottom drift toward shore and coastal drift south in the Middle Atlantic Bight during winter (Bumpus 1973) would aid migrants moving south, but seasonal shifts in directional flow along the east coast and their effect on shad movements are liable to subjective interpretation. Spawning populations moving north and south concurrently could be helped or hindered by circulation patterns in the mid-Atlantic area. We believe that seasonal shifts in isotherms, as influenced by circulation patterns, are of greater importance in defining the migratory route of shad.

Vertical Distribution

Presently there is little information on the depths preferred by shad at sea. We inferred distribution in the water column from three separate sources: food habits, diel differences in catchability, and effectiveness of various trawls in capturing shad. Adult shad are zooplankton feeders and consume primarily large copepods, mysids, and euphausiids (Bigelow and Schroeder 1953; Hildebrand 1963; Leim and Scott 1966). The consumption of food organisms such as mysids and zoobenthos indicates that part of a shad's life is spent near the ocean bottom (Leim 1924; Walburg and Nichols 1967). In general, stomach analyses reveal that shad feed at all depths but particularly where concentrations of zooplankton occur.

Trawling stations where shad were collected during U.S. surveys (24 h/day) were partitioned by capture time (Eastern Standard Time) into day (0600-1800 h) and night (1800-0600 h). Chi-square analysis on time of capture revealed that daytime catches occurred significantly more often ($P<0.01$) than night collections (Table 4). Of the night catches, 25% occurred within 1 h of the daytime interval. Shad were apparently closer to the bottom during daylight hours and thus more susceptible to bottom trawling gear. Further corroboration of this daytime occurrence nearer to the bottom is evidenced by the frequency of shad catches in foreign bottom trawls. During daylight hours in March 1974-76, foreign research vessels used herring trawls to sample 280 stations from Long Island to Georges Bank and recorded shad at 71 (25%) of these stations. Contemporary surveys by the United States in the same area with the No. 41 Yankee trawl sampled 207 daytime stations and collected shad at 22 (11%) of them. Maximum headrope distance off the bottom for the U.S. trawl was 5 m. The larger foreign trawls had a higher opening (6 m) which increased their effectiveness on off-bottom species, although extra-trawl factors such as vessel size, speed, and gear rigging certainly contributed to the greater overall fishing power of these trawls (Grosslein 1969, 1971).

We deduce from the above observations that shad are vertical migrators like other schooling planktivores such as herring, *Clupea harengus*, and mackerel, *Scomber scombrus* (Blaxter 1975;

TABLE 4.—Chi-square test comparing the number of day and night catches of shad during U.S. bottom trawl surveys, 1963-76, Cape Hatteras, N.C., to Nova Scotia.

Time	Observed	Expected	χ^2
Day (0600-1800 h)	217	157.5	
Night (1800-0600 h)	98	157.5	45.0**
Totals	315	315.0	

**$P<0.01$.

[10]White, R. L., J. T. Lane, and P. E. Hamer. 1969. Population and migration study of major anadromous fish. N.J. Div. Fish Game Misc. Rep. No. 3M, 21 p.

Isakov[11]; Rikhter[12]), following the diel movements of zooplankton in the water column. This reliance on zooplankton for food may be an additional factor influencing shad distribution during the year. Zooplankton distribution in the Gulf of Maine during summer and autumn is closely tied to local and regional hydrography (Redfield 1941; Sherman 1966; Cohen[13]); concentrations generally occur along areas of current convergence and divergence (Zinkevich 1967) and at depths <100 m (Bigelow 1926; Whiteley 1948). During winter, the waters around Georges Bank are nearly devoid of zooplankton, whereas sizeable neritic populations occur from Nantucket Shoals to southern Long Island (Clarke 1940; Grice and Hart 1962; Zinkevich 1967). Sette (1950) concluded that water temperature had a limiting rather than causal influence on the seasonal movements of mackerel, and Redfield (1941) noted a parallelism between mackerel distribution and areas of zooplankton abundance. Similarly, Zinkevich (1967) related herring movements to water temperature and seasonal shifts in zooplankton concentrations. Catches of shad during bottom trawl surveys along Georges Bank, Gulf of Maine perimeter, and south of Nantucket Shoals may therefore be related to zooplankton abundance in these areas, but direct evidence is lacking.

Coastal Migration

Tagging studies and the location of NMFS and ICNAF catches during the spring indicate that most shad populations move toward the mid-Atlantic coast from offshore waters, between lat. 36° and 40°N in the winter and early spring. The time and location of tag returns by the mid-Atlantic shad fishery demonstrate that shad from most populations occur in this region during the spring (Talbot 1954; Talbot and Sykes 1958; Leggett 1977; White et al. see footnote 10). Shad tagged near southern Long Island in early spring were recaptured on spawning runs as far south as North Carolina (Talbot and Sykes 1958). Tagging of shad in North Atlantic rivers during the spawning period produced recaptures as far south as the North Carolina coast in subsequent years (Talbot 1954; Vladykov 1956; Talbot and Sykes 1958; Leggett 1977). These tag returns provide an approximate geographical range of entry into coastal waters by returning oceanic migrants (lat. 36°-40°N).

Assuming that the 3° and 15°C isotherms define the northern and southern limits respectively of shad movements at sea, prespawning adults returning to coastal waters from the ocean would face a thermal barrier south of Cape Hatteras. Offshore bottom temperatures along the South Atlantic coast remain above 17.5°C during the year, whereas bottom temperatures on the continental shelf north of Cape Hatteras and inshore temperatures for the South Atlantic coast drop below 15°C by December (Figure 9). The proximity of the Gulf Stream to North Carolina creates a narrow coastal corridor at Cape Hatteras, providing the only migratory route to southern rivers if shad returning to these home rivers are to remain within their marine temperature regime. Migration toward shore north of Cape Hatteras and then south along the coast appear to be essential prerequisites for successful homing to South Atlantic rivers. In contrast, shad returning to North Atlantic rivers during the spring are not obliged to follow a coastal route because offshore temperatures in the Middle Atlantic Bight are well within the shad's range of oceanic occurrence (Figure 9). However, tag returns from adults tagged on spawning runs into North Atlantic rivers indicate that many (most?) adults do enter coastal waters in the lower mid-Atlantic region and migrate north along the coast to reach home rivers as repeat spawners the following spring (Talbot 1954; Leggett 1977). Results of Atlantic coast tagging are consistent with our upper temperature limit (15°C) for shad migration at sea; all prespawning, oceanic migrants enter inshore waters as far south as North Carolina. The significance of the Cape Hatteras region to other aspects of northern versus southern shad biology was discussed by White and Chittenden (1977).

Based on our proposed migratory route, large shad catches in ICNAF Division 6B during the spring would consist of shad entering home rivers and populations moving toward and along the coast. Catches in Chesapeake Bay and the sounds of North Carolina from late November to early December (Hildebrand and Schroeder 1928; Talbot and Sykes 1958; Walburg and Nichols 1967)

[11]Isakov, V. I. 1976. The peculiarities of diurnal vertical migrations of mackerel in the northwestern Atlantic. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1976, Res. Doc. No. 111, Serial No. 3934, 3 p.

[12]Rikhter, V. A. 1976. Proposal on trawling surveys for estimation of pelagic fish stocks in ICNAF Subarea 5 and Statistical Area 6. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1976, Res. Doc. No. 116, Serial No. 3939, 3 p.

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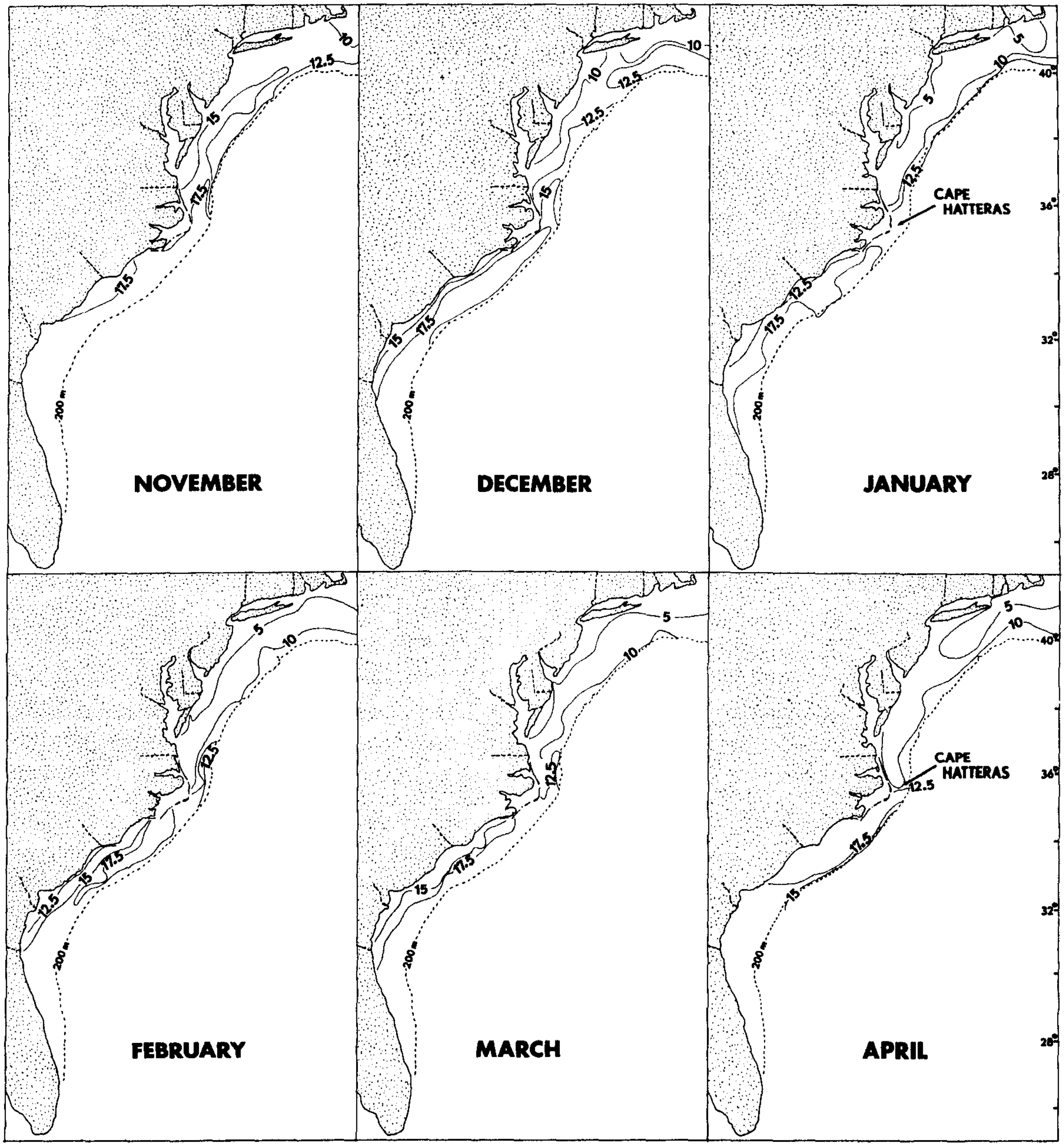

FIGURE 9.—Mean monthly bottom temperatures during winter and spring along the eastern U.S. coast, Cape Cod, Mass., to Florida. (From Walford and Wicklund 1968.)

would be shad returning to natal rivers farther south. Inshore temperatures are unstratified along the Atlantic coast during the winter (Parr 1933). Since freshwater discharge generally occurs along the surface from estuaries, water temperatures would not preclude near-surface movements of shad to detect essential olfactory and rheotaxic cues for successful homing (Dodson and Leggett 1974).

Estuarine temperatures from initial to peak arrival of shad at home rivers along the Atlantic coast are between 3° and 15°C (Talbot 1954; Massmann and Pacheco 1957; Walburg and Nichols 1967; Leggett 1972; Leggett and Whitney

1972; Chittenden 1976; Sholar[14]). Within this temperature regime, southern populations begin reaching home estuaries at the higher temperatures, while northern populations do so at the lower temperatures. Peak numbers of shad enter the St. Johns River, Fla., in mid-January when water temperatures are at an annual low of 15°C; the peak in juvenile emigration occurs simultaneously (Leggett and Whitney 1972; Williams and Bruger 1972). Shad first enter the Connecticut River in late March-early April when water temperatures are approximately 4°C and peak in abundance at 13°C (Leggett and Whitney 1972). In general, most shad populations north of Cape Hatteras begin entering rivers at approximately 4°C, and the peak in upstream migration occurs at temperatures between 10° and 15°C (Leggett and Whitney 1972).

The lower thermal tolerance of juvenile shad in freshwater was near 2.2°C in a short-term laboratory study (Chittenden 1972) and roughly 3°-4°C in small outdoor ponds (Blair[15]). This lower thermal limit agrees closely with the lowest temperature at which subadult shad were collected during NMFS offshore surveys (3°C). Chittenden (1972) also reported that juveniles ceased feeding when water temperatures dropped below 4.4°C. However, we collected 17 juvenile and subadult shad (9-32 cm FL) during a NMFS coastal survey in January 1978, at stations with bottom temperatures between 2.8° and 4.3°C. All but one stomach were filled with mysids and copepods, indicating active feeding at these temperatures in saltwater.

Further evidence to support our bottom temperature regime for predicting the coastal movements of shad is provided by North Carolina's anadromous fishery research program. Their annual surveys on river herring since 1971 show that shad occur off the North Carolina coast from January to April, at bottom temperatures between 6° and 12°C and at depths <26 m (Johnson et al.[16]). Shad catches decline substantially when water temperatures exceed 12°C, coinciding with entry into estuaries or possibly, northward migration. This temperature range concurs with offshore bottom temperatures having the most frequent shad catches during NMFS bottom trawl surveys (7°-13°C). The shallow depths traveled by coastal migrants during the winter and spring would account for their unavailability to offshore sampling.

Critical data on the oceanic phase of most anadromous fishes are lacking (Harden-Jones 1968), and our general description of shad movements must await additional research at sea to corroborate or correct the proposed migratory cycle. It would seem energetically wasteful for North Atlantic populations to follow the same shoreward route as do Middle and South Atlantic shad. The return of all populations to this region may have historical significance, since shad are believed to have been most abundant in the mid-Atlantic portion of their coastal range (Leim 1924). Variations in life history patterns among populations are generally considered to be adaptive responses (Cole 1954; Murphy 1968; Gadgil and Bossert 1970), and differences in life history characteristics among shad populations in rivers (Carscadden and Leggett 1975b) may also exist at sea. Endocrine-induced differences in the timing of migratory behavior and gonadal maturation may be life history strategies of adaptive significance, considering the species' wide geographical range (21° of latitude). The lengthy period of migration toward the mid-Atlantic coast from offshore by prespawning adults may stem from population-specific responses to photoperiod or temperature cues. Further study on the sensory systems and environmental cues involved in migration is required before a more comprehensive explanation for the migratory cycle of shad is available.

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