Bluefin Tuna, *Thunnus thynnus*, Larvae in the Gulf Stream off the Southeastern United States: Satellite and Shipboard Observations of Their Environment

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ABSTRACT: **The primary spawning area of the western Atlantic stock of bluefin tuna is presumed to be in the Gulf of Mexico. However, bluefin tuna larvae were collected in April and May 1985 along the shelf edge from Palm Beach, Florida to Cape Fear, North Carolina and offshore as far as 260 km east of Jacksonville, Florida over the Blake Plateau. Satellite and shipboard sea-temperature data indicate that the larvae over the shelf edge were advected there in meanders of the Gulf Stream. Bluefin larvae previously reported in the Straits of Florida and off Cape Hatteras were also in the Gulf Stream according to retrospective analyses of temperature and salinity data. Based on age-length relationships and current velocity, one small larva was probably spawned north of Miami, Florida while others could have been advected into the Gulf Stream from the eastern Gulf. Spawning by a few unspent migrating adults could also account for some bluefin larvae in this region. The estimated total larvae off the southeastern United States in 1985 could have been produced by 5% of the spawning stock. Bluefin larvae were found within a narrow range of sea surface temperatures and salinities at offshore stations. Preliminary assessment of larval habitat indicates that waters off the southeastern United States are unfavorable for growth and survival of bluefin larvae relative to hypothesized larval retention areas in the Gulf of Mexico.**

The western Atlantic stock of bluefin tuna, *Thunnus thynnus*, spawns from about mid-April to mid-June in the Gulf of Mexico, based on seasonal and areal distribution of their larvae (Richards 1976, 1977). Bluefin tuna larvae have also been collected in the Straits of Florida north of Cuba and east of Miami (Richards and Potthoff 1980; Brothers et al. 1983) and off Cape Hatteras, NC (Berrien et al. 1978).

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Surveys of the Gulf of Mexico for bluefin tuna larvae are made annually during the spawning season to estimate the total abundance of larvae and to calculate a fishery-independent index of adult spawning stock size (Richards et al. 1981; McGowan and Richards 1986). This index of stock size is used to calibrate virtual population analysis (VPA) of the western Atlantic bluefin tuna population to enhance management of the stock (Anonymous 1986). Fishery catch statistics and the index of abundance of larvae show that the bluefin tuna population size is smaller than it was previously, and is below optimum levels (Brown and Parrack 1985; McGowan and Richards 1986). To redress this problem, directed fishing on bluefin in the Gulf of Mexico and in other spawning areas, has been prohibited since 1982 (Anonymous 1987).

Finding bluefin larvae outside the primary spawning areas raises a potential problem because if significant spawning of the remaining stock occurs outside the Gulf of Mexico, then the ichthyoplankton survey in the gulf may not give a reliable index of the stock, and prohibition of fishing in the gulf may not have the desired effect on stock recovery. In 1985 bluefin larvae were widely distributed off the southeastern U.S. coast. The hypothesis that they were spawned in this area needed evaluation.

In this paper we quantitatively describe the occurrence of bluefin tuna larvae in 1985 near Miami and Cape Hatteras, where they have been reported before, and also their occurrence over the Blake Plateau north of the Bahamas Islands, where they have not been reported previously. We use satellite observations of the position of the Gulf Stream and shipboard hydrographic measurements to describe the habitat where bluefin tuna larvae were collected. We review previous evidence for bluefin tuna spawning in this area to determine if these larvae were in similar, oceanographically defined habitat, and summarize this evidence to assess the waters of the southeastern U.S. coast and the Blake

Plateau as a spawning area for bluefin tuna. We propose a hypothesis, based on existing data, that bluefin tuna are dependent on a dynamic larval retention area associated with the Loop Current in the eastern Gulf of Mexico.

The total number of specimens of bluefin tuna larvae on which this paper is based is small. Therefore, we present our conclusions as hypotheses that are consistent with our data from independent sources and with all other data known to us. Arguments supporting our hypotheses and their limitations will be elaborated in the discussion.

Our investigations were initiated by the observation of bluefin tuna larvae outside the normal spawning area and then proceeded by a series of questions, critical examination of available information, and conclusions and hypotheses for further investigation. The bluefin tuna larvae off the southeastern U.S. in 1985 could have been spawned locally or transported in currents. Were they in water masses characteristic of the Gulf Stream? If they were in the Gulf Stream, then were they young enough to have been spawned locally or were they transported from upstream? Other researchers had reported incidental catches of bluefin tuna larvae in some of the same areas. Were these larvae likely to have been spawned locally? Wherever they were spawned, could they survive where they were collected? What were the general temperature-salinity conditions where bluefin tuna larvae were found off the southeastern U.S.? Are these conditions similar to those which bluefin tuna larvae experience in the Gulf of Mexico? What else is known about the oceanography of this region which is relevant to survival of fish larvae? Given our conclusions from these data and our knowledge of the life history of the bluefin tuna, what insights can be drawn from the occurrence of larvae outside the presumed spawning area and what hypotheses need to be tested by additional work?

METHODS

Ichthyoplankton were collected on cruise 152 of the RV *Oregon II* in April and May 1985. Double oblique tows to 200 m or to near the bottom in shallow water were made with 0.6 m diameter bongo nets having 0.333 mm mesh size. Bluefin tuna larvae were identified and measured by W. J. Richards. Salinity and temperature data collected by CTD, XBT, or bottle cast at each station were extracted from computer data files of the National Marine Fisheries Service, Mississippi Laboratory, Pascagoula. Satellite data for April and May 1985 were obtained from NOAA Miami SFSS Gulf Stream Position Flow Chart #2450 for the days during the cruise. Historical observations of bluefin tuna larvae and coincident temperature and salinity near Cape Hatteras were obtained from Berrien et al. (1978) and Clark et al. (1969). Previous observations of bluefin tuna larvae outside the Gulf of Mexico were reviewed for other evidence of spawning in the Straits of Florida or elsewhere (Richards 1976; Brothers et al. 1983).

Statistical estimates of standardized abundance of larvae were made using the delta-distribution, an efficient estimation technique when zero counts are observed (Pennington 1983). This is the same method routinely used to construct the fishery-independent index of the abundance of Gulf of Mexico spawners. Because of logistical and statistical sampling problems, the estimates of abundance are best regarded as indices calculated in a consistent way and valid for comparative purposes. Unless there is spatial periodicity or patchiness at the same scale as our sampling grid, the systematic survey does provide, however, an accurate estimate of mean abundance and its variance (Poole 1974; Ripley 1981). The details of the method are provided in McGowan and Richards (1986). The estimate assumed that fecundity, sex ratio, spawning season, and length-weight-age ratios were the same off the southeastern U.S. as in the Gulf of Mexico (Baglin 1982). This assumption was supported by the similarity of length-frequency distributions of incidental catches of adults in the two areas during May 1985. Because our assumptions are important to subsequent arguments, the evidence substantiating our reasoning is given in detail below.

Approximately 90% of incidentally caught adult bluefin tuna in the gulf and off the southeastern U.S. during May 1985 were large, spawning-sized fish >190 cm (data provided by S. Turner, National Marine Fisheries Service, Miami Laboratory). There was no statistical difference in proportion of adult spawners between the two areas (Chi-Square = 0.0176; P = 0.89; McGowan and Richards 1987). Thus the available catch data were consistent with our assumption that the fish in both areas were similar in terms of size-related reproductive capacity. This was the primary justification for using reproductive parameters of Gulf of Mexico tuna for calculations of potential stock size of spawners off the southeastern U.S.

Additional data indicate that there is only one spawning stock in the northwestern Atlantic. Bluefin tuna are known to occur in different places at different times of the year, depending on size and age (Rivas 1978; Mather 1980). The large adults are expected to be migrating through the Straits of Florida during late April and May after spawning in the Gulf of Mexico. A few migrating, ripe females and recently spent males were caught in May near Bimini in the Bahamas (Rivas 1954). Bluefin tuna are capable of swimming from the Bahamas to Norway at sustained speeds as fast as 122 miles per day (Brunenmeister 1980), so adult fish could easily traverse the area from Miami to Cape Hatteras, or be widely distributed over the Blake Plateau, a few days after leaving the Gulf of Mexico. They could migrate back and forth between the two areas during the 60 d spawning season, although there is no evidence for this. Because there is no evidence for two separate groups of spawning fish, the parsimonious assumption is that there is only one. Therefore we assumed that fish in both areas had the same reproductive parameters previously estimated (Baglin 1982; McGowan and Richards 1986).

The estimated age-at-length of bluefin tuna larvae was based on previous analysis of daily increments in otoliths of larval bluefin collected from the Gulf Stream near Miami (Brothers et al. 1983). We calculated a linear regression to predict age from length using the mean estimates of age at length presented in Brothers et al. (1983). The equation is

$$\text{Age (days)} = 3.67 \times \text{standard length (mm)} - 8.04.$$

This equation was based on limited ranges of age and length, so we used it heuristically as the best available. It may be revised after further study extends the age and length data, but the revisions will most likely be at the older-longer end of the relationship, not at the younger-shorter end most relevant to our conclusions in this paper. There is a range of age at length which could affect interpretations of time spent drifting by the larvae but our use of the mean results in conservative interpretations of the data in most instances.

In this paper we refer to the current from the Dry Tortugas to Cape Hatteras as the Gulf Stream (Iselin 1936; Stommel 1965). We refer to the continental shelf area between Palm Beach, FL and Cape Hatteras, NC as either the region off the southeastern United States, or the South Atlantic Bight.

Stations occupied during RV *Oregon II* cruise 152 were numbered 42XXX, where XXX is a sequential station number. For brevity we refer to stations in this paper by their unique 3 digit number, the XXX part.

RESULTS

Catch and Abundance of Larvae

Larval bluefin tuna were collected at 10 of 147 stations during cruise 152 (Fig. 1). Three larvae were collected at one station, two at two stations, and one each at the other positive stations for a total catch of 14 larvae (Table 1). To put this small catch in perspective, in 1984 and 1986 the average catch in the Gulf of Mexico was less than 24 total larvae at 10 positive stations (McGowan and Richards 1987). Thus the 14 caught in 1985 could have been over 50% of the expected catch for the Gulf of Mexico in 1985. The larvae ranged in length from 3.0 to 6.2 mm corresponding in age from 3 to 14.7 days postfertilization. The estimated mean abundance of bluefin tuna larvae from stations at or outside the 183 m isobath was 0.383 ± 0.114 (SE) under 10 m^2 of sea surface (approximately ⅓ the density of bluefin larvae in the Gulf of Mexico). The corresponding area surveyed was 2.02×10^{11} m^2 producing a total estimated 7.74×10^9 larvae in the survey area. These larvae could have been produced by 3,730 adult fish weighing a total of 903 t. This is equivalent to about 5% of the 1985 estimate of Gulf of Mexico spawning stock calculated from the larval index (McGowan and Richards 1987). The coefficient of variation of the estimate of abundance of these larvae was 30%, which is in the range of coefficients of variation for the Gulf of Mexico for the past 10 years, 21–49% (McGowan and Richards 1987).

Distribution of Bluefin Tuna Larvae and Coincident Water Masses

There were three groups of stations where bluefin tuna larvae were present: 1) three stations at the shelf break east of Florida, 2) two stations near the shelf break off North Carolina, and 3) the positive stations over the Blake Plateau. The stations in the first group (634, 636, and 647) were near the 183 m isobath. Two inde-

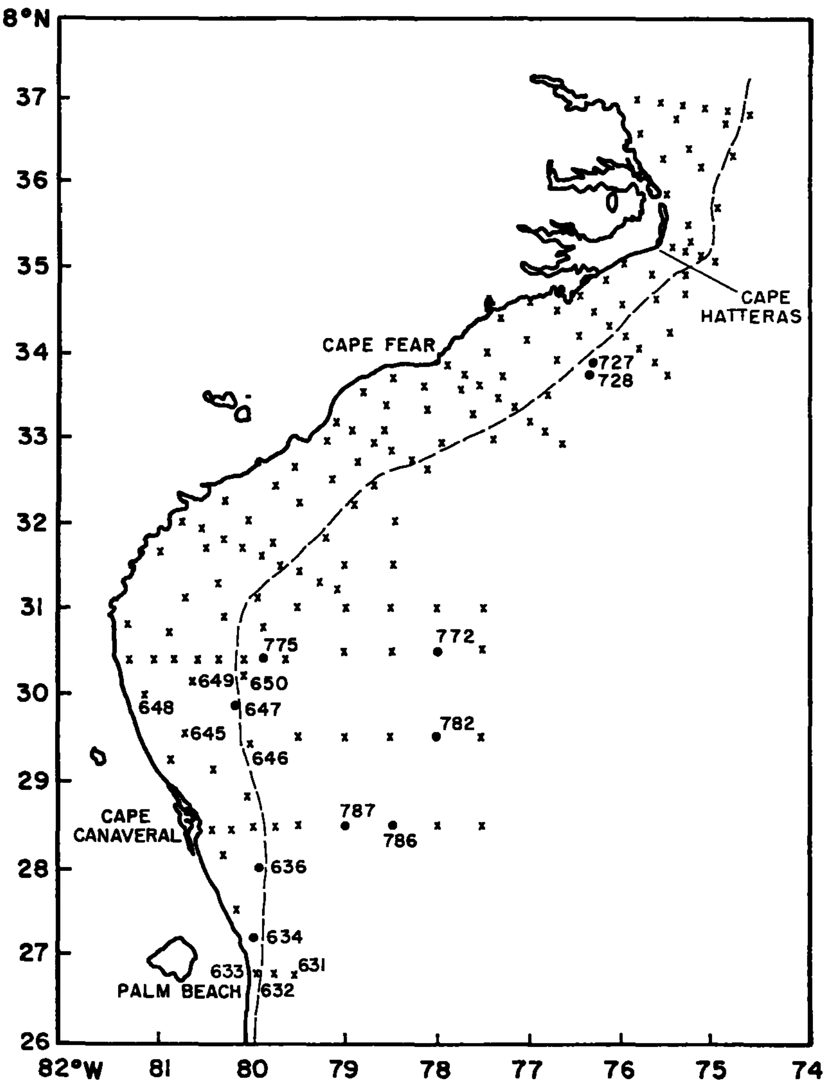

FIGURE 1.—Study area with ichthyoplankton and hydrographic stations plotted, and selected stations numbered. Stations where bluefin tuna larvae were present are indicated by a heavy dot. The dashed line shows the position of the 183 m isobath.

pendent sets of data, temperature-depth profiles, and remote sensing images of surface temperature, show that the water at these stations when bluefin tuna larvae were caught was the shoreward edge of the Gulf Stream. Temperature profiles of stations 631, 632, and 633 (Fig. 2) show cold water is closer to the surface at the inshore station (633) than at the offshore stations (631, 632). This is typical at the cold edge of the Gulf Stream near the shelf break (e.g., Atkinson 1985). Station 634, where bluefin tuna larvae were present, is a little inshore and north of station 633. Its vertical temperature profile shows warm Gulf Stream water at the surface and the cold water of the edge of the stream closer to the surface than at station 633. Station 636, where bluefin tuna larvae were present also, has a similar temperature profile. The upper mixed layer at stations 634 and 636 is approximately 30 m deep like that at station 633, not 60–80 m deep as at station 631 which was farther offshore. These temperature profiles are typical of the edge of the Gulf Stream at this latitude (Atkinson et al. 1987).

The third positive station in this group of stations at the shelf edge is station 647. No observations of temperature with depth were obtained at this station but measurements at adjacent

TABLE 1.—Stations where bluefin larvae were present on *Oregon II* Cruise 152, April and May 1985.

Station	Date	Time	Latitude	Longitude	Depth (m)	Catch	Length (mm)
42634	4/27	1035	27°10.5′	79°51.1′	70	1	4.0
42636	4/27	1732	27°58.2′	79°59.6′	122	3	5.6
							6.1
							6.2
42647	4/29	524	29°51.9′	80°12.3′	210	1	3.8
42727	5/14	1043	33°51.0′	76°17.0′	366	1	5.8
42728	5/14	1445	33°44.0′	76°19.0′	561	1	3.0
42772	5/21	2200	30°30.0′	78°0.0′	842	2	3.0
							4.2
42775	5/22	900	30°24.0′	79°39.0′	732	1	5.7
42782	5/23	1515	29°30.0′	78°0.0′	843	1	4.0
42786	5/24	1100	28°30.0′	78°30.0′	950	1	4.5
42787	5/24	1314	28°30.0′	79°0.0′	846	2	3.7
							4.9

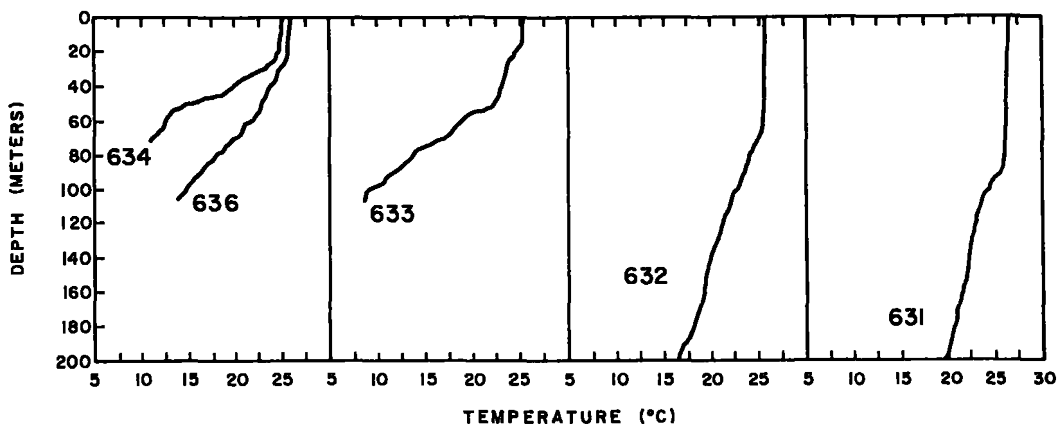

FIGURE 2.—Temperature-depth profiles of selected stations in the southern part of the study area. Stations 631, 632, and 633 are along an east to west transect at the edge of the shelf (see Figure 1). The edge of the Gulf Stream is indicated by colder water near the surface inshore at station 633. Bluefin larvae were collected at stations 634 and 636 where the profile is similar to that at 633.

stations are useful as proxies. Station 646, which was south and a little offshore from 647, shows a vertical temperature profile (Fig. 3) typical of the Gulf Stream, similar to that at 631 (Fig. 2). Station 650, at a similar isobath and distance from the shore, also shows a temperature profile similar to 631 and 632. Therefore station 647 would reasonably be expected to be more similar to 646 and 650 than stations 648, 645, and 649, which are farther inshore. These temperature profiles indicate that Gulf Stream water was present at stations 634, 636, and 647 when bluefin tuna larvae were collected there.

This conclusion is supported further by charts of satellite data showing the position of the edge of the Gulf Stream. The edge of the stream was just offshore of the 183 m isobath on 26 April, the day before the bluefin tuna larvae were collected at stations 634 and 636 (Fig. 4). The edge was inside the 183 m isobath and inshore of the three stations three days later on 29 April, when bluefin tuna larvae were collected at station 647 (Fig. 5). The satellite-detected temperature front associated with the inshore edge of the Gulf Stream is known to be in accord with the classical definition of the stream path (Olson et al.

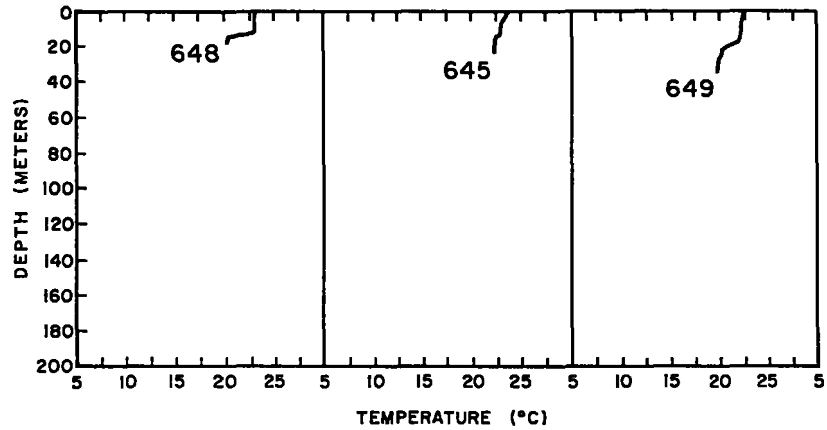

FIGURE 3.—Temperature-depth profiles of stations 646 and 650, which are presumed to represent the profile at station 647. Bluefin larvae were collected at 647 but no hydrographic data were collected there. Profiles for

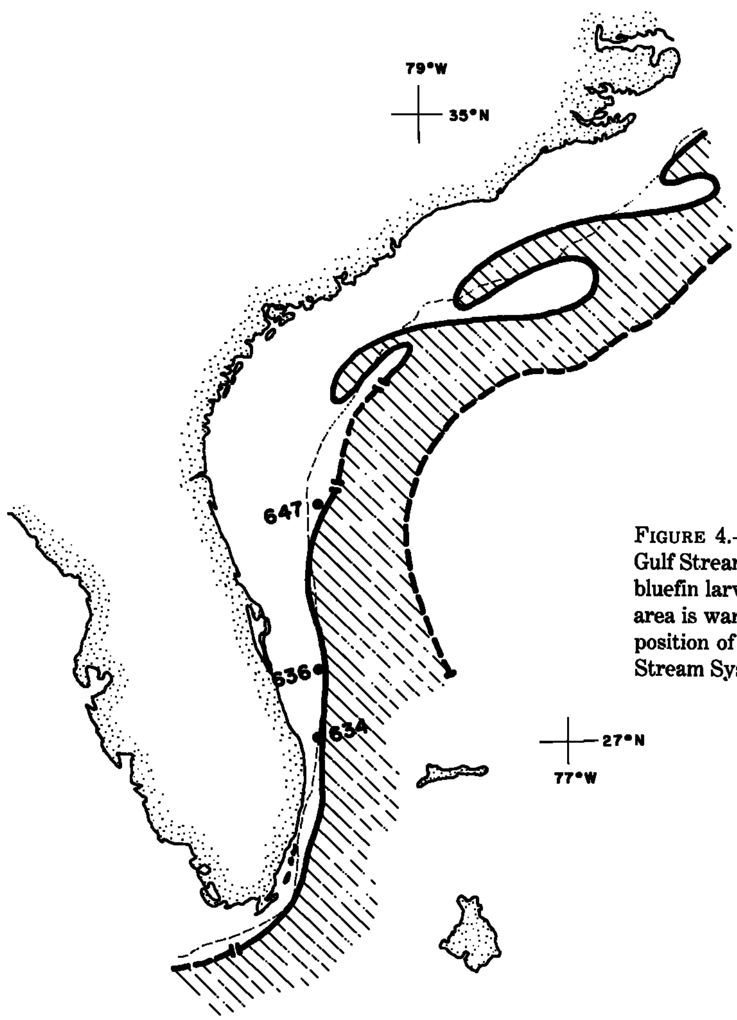

FIGURE 4.—Chart showing the position of the edge of the Gulf Stream on 26 April 1985 relative to three stations where bluefin larvae were collected 27–29 April. The cross-hatched area is warm Gulf Stream water. The dashed line shows the position of the 183 m isobath. (Redrawn from NOAA Gulf Stream System Flow Chart #2450, 26 April 1985.)

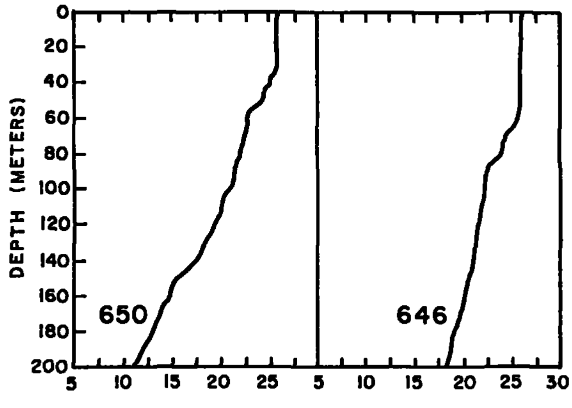

FIGURE 3.—*Continued*—stations 645, 648, and 649, are presumed not to represent conditions at 647 because they are farther inshore.

1983). The inference to be drawn from this remote sensing data is that during 27–29 April the Gulf Stream meandered inshore of the 183 m isobath in this region carrying bluefin tuna larvae over the shelf edge. This is worth noting with regard to the larval habitat of the bluefin tuna because the larvae are rarely taken in water <200 m deep. For example, in the Gulf of Mexico during 1977–81 only 5 of 81 stations that had bluefin tuna larvae were in water <200 m deep and none was in water <110 m deep. (Southeast Fisheries Center, National Marine Fisheries Service, unpubl. data.)

The second group of stations where bluefin tuna larvae were caught is the pair of stations east of Cape Fear, NC where the water depth was 360–560 m (stations 727 and 728). Water temperatures at the surface, at 100 m, and at 200 m were similar to temperatures at the same depths for other Gulf Stream stations such as

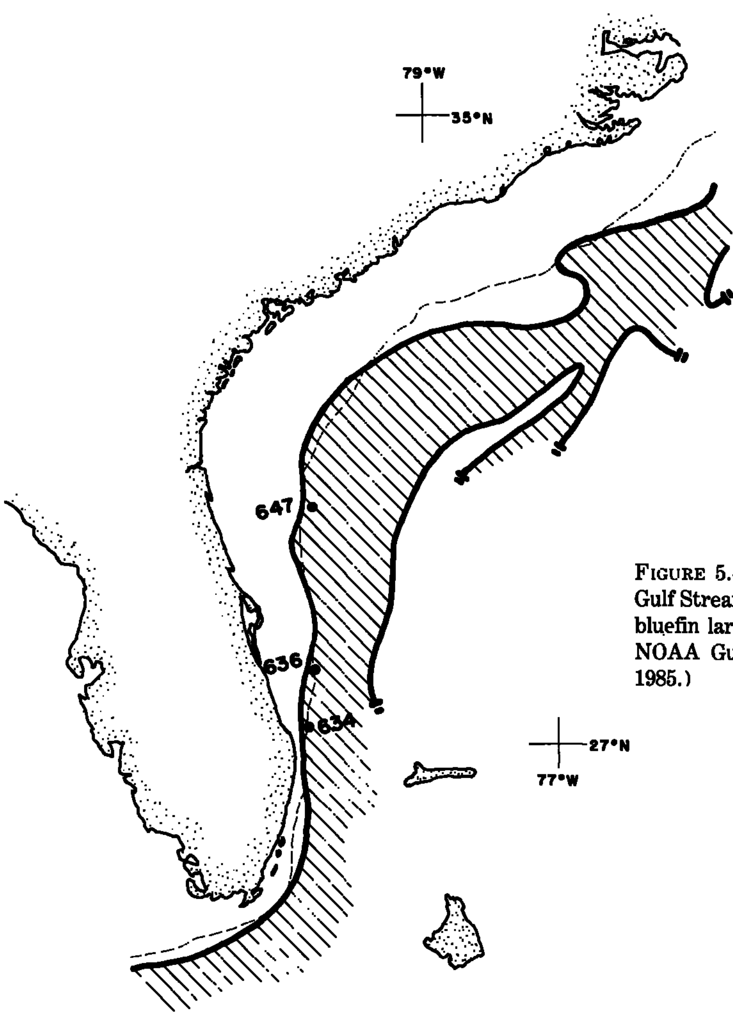

FIGURE 5.—Chart showing the position of the edge of the Gulf Stream on 29 April 1985 relative to three stations where bluefin larvae were collected 27–29 April. (Redrawn from NOAA Gulf Stream System Flow Chart #2450, 29 April 1985.)

station 631 and 632 (Table 2). Station 727 was located at a shallower isobath than station 728 and the temperature at depth readings were similar to those 800 km south, at stations 632 and 631, where the water depth was similar. At both pairs of stations cold water is nearer the surface of the inshore station. The sloping isotherms and the temperatures at depth are characteristic of the edge of the Gulf Stream. Gulf Stream water is expected here in spring and summer (Pietrafesa et al. 1985).

Remote sensing observations (Figs. 6, 7) show that remnants of a filament of warm water resulting from an earlier onshore meander were still present when these larvae were collected. Upwelling is associated with onshore meanders of the Gulf Stream and cyclonic eddies are formed between the warm filament and the Gulf Stream. The bluefin tuna larvae at stations 727 and 728 were not over the shelf in a patch of productive water caused by the onshore meander, but they were in an area which could have been fertilized by such a patch which subse-

TABLE 2.—Temperature with depth comparison of northern stations where bluefin larvae were present and southern stations which were at the same isobath and in Gulf Stream water. Bluefin were collected at stations 727 and 728. Stations 728 and 631 were offshore (Fig. 1.). Note that 22° at 100 m is a good indicator of the Loop Current (Liepper 1970) which flows from the Gulf of Mexico to join the Gulf Stream.

	Temperature (°C)			
	Northern stations		Southern stations	
Depth (m)	727	728	632	631
0	25.8	26.2	26.1	26.8
100	21.8	22.5	21.6	23.6
200	16.7	19.2	16.7	19.5

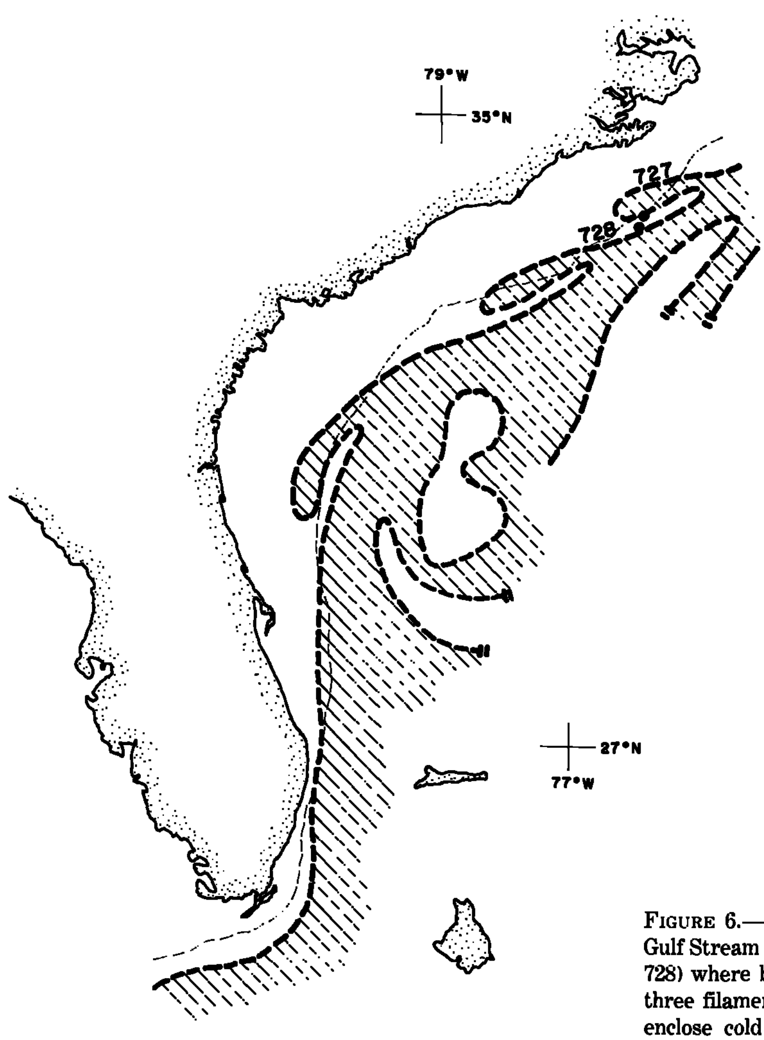

FIGURE 6.—Chart showing the position of the edge of the Gulf Stream on 13 May 1985 relative to two stations (727 and 728) where bluefin larvae were collected 14 May. Note the three filaments left by meanders of the Stream. These can enclose cold cyclonic eddies. (Redrawn from NOAA Gulf Stream System Flow Chart #2450, 13 May 1985.)

quently moved offshore. A 3.0 mm bluefin larva estimated to be only three days old was collected here at station 728.

The third group of stations with bluefin tuna larvae were all farther offshore in water more than 700 m deep. The surface water here had a narrow range of salinities from about 36.0 to 36.5 ppt. Temperature at the surface in this region ranged from approximately 24.5° to 27.5°C. Bluefin tuna larvae were found where the surface water was in the center of this temperature range: from 25.5° to 26.5°C. Bluefin tuna larvae from the northern positive stations and the southern shelf edge stations were also found at the same surface salinities and temperature, except for station 634 where the temperature was 24.8°C (Fig. 8).

Previous Captures of Bluefin Tuna Larvae off Cape Hatteras

In 1966 three bluefin tuna larvae were collected off Cape Hatteras (Berrien et al. 1978). One larva 7.7 mm long was collected 20 April in 235 m water depth. Two larvae, 5.4 mm and 9.3 mm SL, were collected 23 June over 269 m and 68 m, respectively. The stations where these larvae were collected are at the shelf edge or just inshore of it. Contour plots of surface temperature (Fig. 9) and salinity (in Berrien et al. 1978) show that the Gulf Stream front was inshore of the stations where bluefin larvae were caught. Temperature cross-sections show clearly that the stations where bluefin tuna larvae were collected were in Gulf Stream water (Fig. 9). The larva caught in April was in water with lower surface temperature and lower surface salinity than typical (Fig. 8) for the stations where bluefin tuna larvae were present in 1985. The two larvae caught in June were in water more typical for bluefin tuna larvae but near the highest salinities and temperatures (Fig. 8).

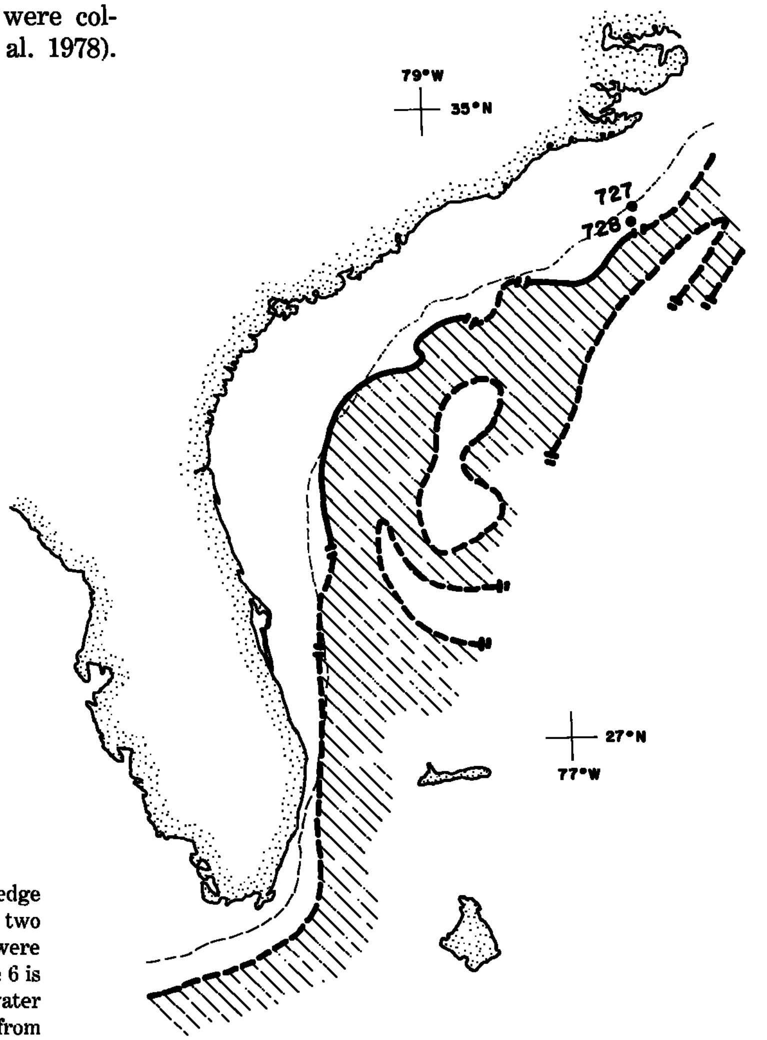

FIGURE 7.—Chart showing the position of the edge of the Gulf Stream on 15 May 1985 relative to two stations (727 and 728) where bluefin larvae were collected 14 May. The filament shown in Figure 6 is not visible and the stations are now in colder water inshore of the edge of the Stream. (Redrawn from NOAA Gulf Stream System Flow Chart #2450, 15 May 1985.)

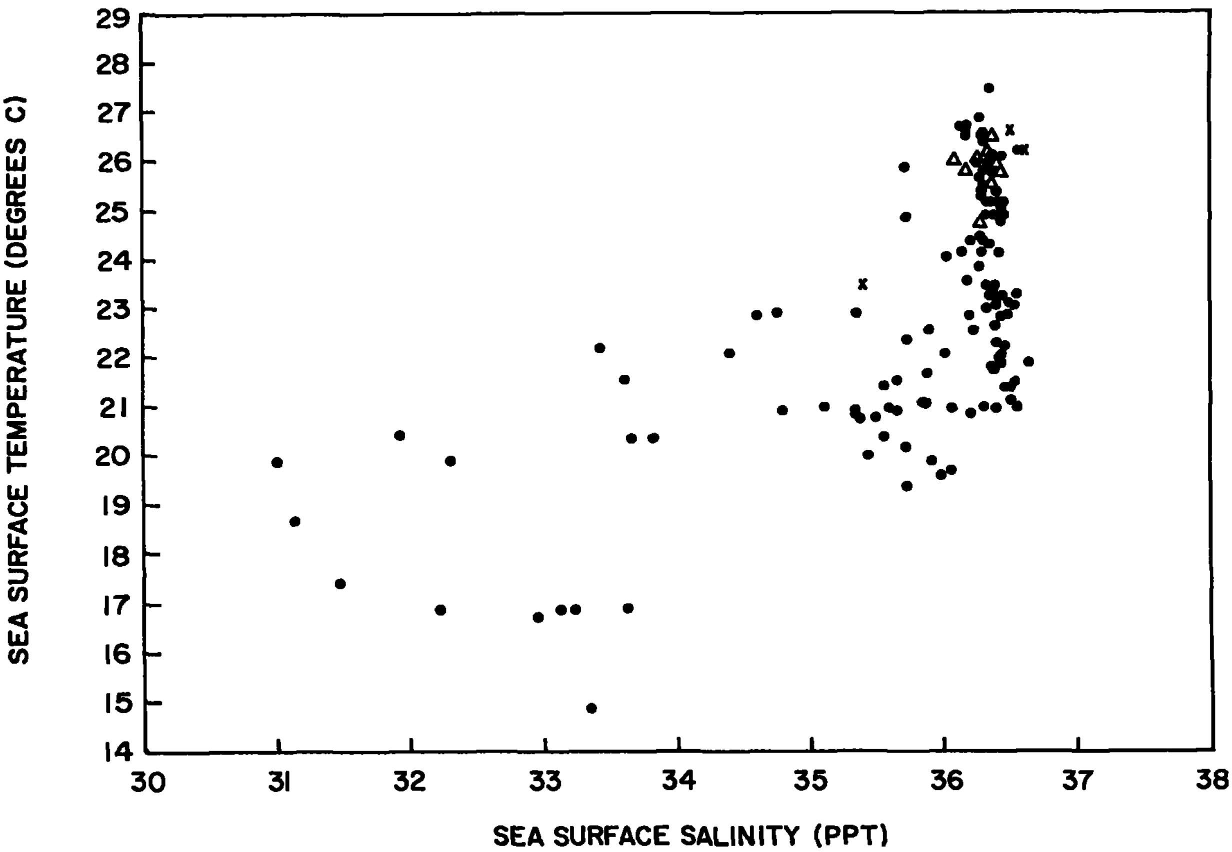

FIGURE 8.—Plot of sea surface temperature vs. sea surface salinity for stations on the cruise which had observations of both. Stations with bluefin larvae are plotted as open triangles. The three x's show the surface temperature and salinity of the stations near Cape Hatteras where bluefin larvae were collected by Berrien et al. (1978).

Previous Captures of Bluefin Tuna Larvae off Miami

Bluefin tuna larvae were collected in 1969–71 and in 1975 between Miami and the Bahamas by Richards (1976). On a five-station transect between Miami and Bimini Bahamas (Richards 1976, table 2), 82% (32/39) of bluefin tuna larvae taken in neuston tows were taken at two stations. These two stations were located on the Miami side of the center of the Florida Straits where the high velocity core of the current is located on average (e.g., Stommel 1965:139). All of the bluefin tuna larvae taken in bongo tows along the transect were taken at the same two stations where most of the neustonic specimens were collected. All of these larvae were longer than 3.0 mm, older than 3 days, so that, if they were advected at the mean current velocity in this location, 100 km d^{-1} (Fuglister 1951), they would have been spawned west of Key West, FL (long. 82°W).

In 1981, 369 bluefin tuna larvae were collected off Fowey Light, south of Miami, at approximately lat. 25.6°N (Brothers et al. 1983). The collections were made on four days, 19–21 May and 2 June, using 1 m diameter or 1 × 2 m neuston nets which were towed many times each day. No oceanographic data were collected because the purpose of the sampling was to capture specimens for otolith ageing, but the collections were made "5–10 miles offshore in blue water at the edge of the Stream" according to E. D. Prince.[1] Based on satellite observations during this period (NOAA Gulf Stream System Flow Chart #2450), the edge of the Gulf Stream was offshore of the 183 m isobath (which is 5–10 miles offshore near Fowey Light) on 18 May, was at the 183 m isobath 20 May, and was offshore again 22 May. Nearly half of the total catch (176/369) of bluefin tuna larvae during four days of sampling took place on 20 May (Brothers et al.

[1]E. D. Prince, Southeast Fisheries Center Miami Laboratory, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149, pers. commun. 1988.

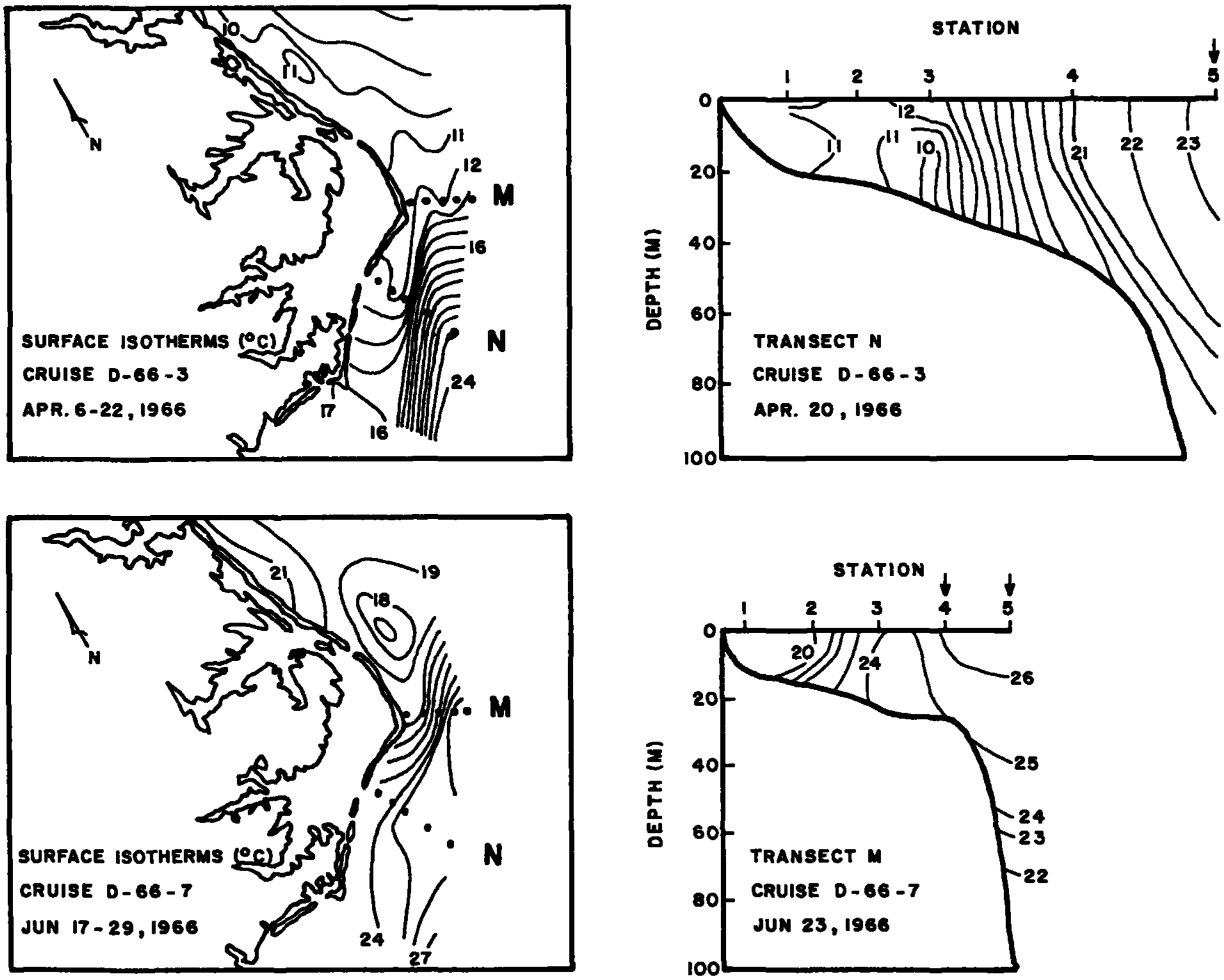

FIGURE 9.—Plots of surface isotherms and temperature sections of the stations where bluefin larvae were collected near Cape Hatteras by Berrien et al. (1978). The plot at upper left shows the position of the temperature front at the sea surface between stations 3 and 4 on transect N. The section at upper right shows that the front extends to the bottom; station 5, where a bluefin larva was collected, is indicated by an arrow. Plot at lower left shows the surface front inshore of station 4 on transect M. Section at lower right shows temperatures; the two stations where bluefin larvae were caught are indicated by arrows. (Figures redrawn from Berrien et al. 1978.)

1983:50), the day when the Gulf Stream was at its closest inshore position during the sampling days. Thus nearshore catches were highest when the rapidly flowing core of the Gulf Stream meandered toward shore, carrying bluefin tuna larvae with it.

DISCUSSION

Limitations of the Data

Bluefin tuna larvae are rare on the average in their oceanic habitat. Standard ichthyoplankton tows, which are made to 200 m in order to quantitatively sample all species, undersample the surface layers where tuna larvae are more abundant. In addition, we have evidence, to be published elsewhere, that bluefin tuna larvae are most abundant near specific oceanographic features; so they may be undersampled by nonstratified survey designs such as the uniform grid often used for logistical reasons. The estimates of abundance will be valid but may have wider confidence intervals than estimates made with a more efficient stratified design. Furthermore, bluefin tuna larvae grow and swim rapidly, so they avoid plankton nets better than larvae of most other species, again contributing to low absolute catches. We acknowledge that low catches limit the precision of results; therefore, we tried to rein in unwarranted speculation. The calculations of adult biomass from larval abundance are made only for comparative purposes. A recent independent review of our techniques concluded that the index of larval abundance probably reflects trends in abundance of adults accurately but that our ad hoc estimate of adults from the larvae resembles VPA estimates coincidentally because of our choice of a larval mortality rate. Our ongoing research is aimed at improving the precision and accuracy of estimates of abundance of bluefin tuna larvae by combining our increasing knowledge of their biology with improved sampling gear and methods.

Nevertheless, we are confident that our interpretation of the preceding data is justified and reasonable because of decades of accumulated experience with this species, because of the variety of independent sources of data which are consistent with our interpretations, and principally because the most important conclusions and hypotheses presented here are not dependent upon quantitative estimates of abundance, but upon the relationship between presence and absence of bluefin tuna larvae with specific oceanographic variables. Despite our confidence in our presentation of the results we readily admit that additional data could falsify our conclusions.

Assessment of Spawning off the Southeastern United States

Assuming that all the larvae caught near the shelf and over the Blake Plateau were spawned near where they were collected, spawning in the area was only a small fraction (5%) of estimated total spawning by the western Atlantic stock (McGowan and Richards 1987). This is similar to a previous estimate (6%) of the number of ripe females passing the Bahamas during May (Rivas 1954:310). However, because of the currents in this region, it is not certain that the larvae were spawned near the area where they were collected.

Currents along the outer shelf off the southeastern U.S. average 0.5–1.0 m s^{-1} during the summer (Atkinson and Menzel 1985). Gulf Stream surface currents off Florida based on ship drift observations during April–June average 1.5 m s^{-1} or less (Fuglister 1951). During April–June 1985 the mean northward current, measured at 29°N and at 30 m depth over the 75 m isobath, was 0.53 m s^{-1} and the maximum current was 1.55 m s^{-1}, approximately 3 kn (Lee et al. 1986). Current velocity at the wind-affected surface and farther offshore in the fastest moving region of the Gulf stream would be higher.

If we use the long-term average of 1.5 m s^{-1} as the mean northward speed of the surface current, then a planktonic fish larva would travel 116 km in one day. The mean distance travelled in 7 days would equal 812 km which is less than the straight-line distance from Cape Hatteras, NC (35°N, 76°W) to Palm Beach, FL (27°N, 80°W), approximately 970 km. These calculations suggest that larvae <7 days after fertilization, which were found as far north as Cape Hatteras, could have been spawned north of the Straits of Florida. Those more than 7 days old, or larger than about 4 mm (minimum size at this age, not mean; see Brothers et al. 1983), could have been spawned in the Straits of Florida or the southeastern Gulf of Mexico. Ten of the 14 larvae collected in 1985 were 4.0 mm or longer, and most of the larvae were caught far south of Cape Hatteras. Therefore, based on current velocity and estimated ages, most of the bluefin tuna larvae were probably not spawned off the southeastern U.S. near the area where they were collected.

The 3 d old (3.0 mm) bluefin tuna larva collected near lat. 34°N could not have been spawned in the Gulf of Mexico because, even at 2.5 m s^{-1}, it would have travelled only 667 km in three days. A 667 km straight line from where the larva was caught would end at about 28°N, which is north of Palm Beach. However, the interpretation must be different for the larger, older larvae. Except for the single 3 mm larva, those in the high velocity core of the Gulf Stream (at the shelf edge) could have been advected from a distance to the south in only a few days. At only 1.0 m 5^{-1} (a little faster than 2 kn) larvae 4–5 mm long, corresponding to approximately 8 days old, could have been advected from off Miami to about 31°N in 5 days. The larvae collected along the shelf edge and over the Blake Blateau in 1985 were in this size range or a little longer. Therefore all but the 3 mm larva could have been spawned in the southeastern Gulf of Mexico or between the Florida Keys and Cuba. Slow growth due to cold-water temperature could explain small larvae far from their spawning area, but in this case the Gulf Stream water was warmer than the water where bluefin tuna larvae were found in the Gulf of Mexico.

It should be noted that the current circulation east and north of the Bahamas is complicated

(Olson et al. 1984). Gyres and slow recirculation in this area could retain fish larvae for several days. This means that the evidence presented here does not eliminate the possibility that bluefin tuna spawn off the southeastern U.S. However, because larvae collected in rapidly moving water were probably transported in that water, we argue that the data support the contention that the primary spawning area is farther upstream with perhaps some late spawning by a few individuals in the Straits of Florida as suggested by Rivas (1954).

Oceanic Habitat of Bluefin Tuna Larvae

Four aspects of larval fish habitat are important to the survival of individuals and recruitment to the adult stock: thermal and salinity conditions, prey, predators, and patterns of ocean circulation that can retain the larvae in favorable areas. Our data do not permit discussing the predators coincident with the bluefin tuna larvae found off the southeastern U.S., but we can discuss the salinity and temperatures, the food potentially available, and the likelihood of retention in a favorable area.

Surface salinity over the shelf of the southeastern U.S. is generally 35 ppt or less, with peak river runoff in spring affecting the central and inner shelf (Atkinson and Menzel 1985). Salinities over the outer shelf are similar to those in the Gulf Stream (35.0–36.5 ppt; Stommel 1965). Salinity lower than full-strength seawater could be potentially detrimental to larval bluefin tuna although the adults tolerate reduced salinities (Topp and Hoff 1971). All the larvae collected in this study were found within a narrow range of salinity near 36 ppt (Fig. 8). The larvae were also found in a fairly narrow range of temperatures near 26°C (Fig. 8). In the Gulf of Mexico in 1984 and 1986, bluefin tuna larvae were found where sea surface temperature (SST) ranged from 22.0° to 28.1°C. More than 87% of the larvae occurred in a narrow range of temperatures between 24.0° and 26.1°C (Southeast Fisheries Center, National Marine Fisheries Service, unpubl. data). This is similar to the temperature range off the southeastern U.S. where bluefin tuna larvae were found at SST's from 24.7° to 26.5°C However, the mean temperature of occurrence of the bluefin tuna larvae was higher here than in the Gulf, 25.72° vs. 24.99°C (t = 2.98; df = 50; $P < 0.005$). At higher temperature metabolic requirements of the larvae would be higher; larvae would require more food for optimal growth and survival, other conditions being equal.

A potential mechanism for producing larval fish food does exist in this region. Onshore meanders of the Gulf Stream along the southeastern U.S. can cause upwelling of nutrient rich water along the shelf edge (Yoder et al. 1981; Yoder 1983). This and the compression of isotherms near the edge of the Gulf Stream might produce a stable stratified region favorable to the growth and to the persistence of patches of larval fish food (Lasker 1981). It is true that intrusions of cold, upwelled water provide pulses of phytoplankton production on the shelf which initiate the formation of patches of zooplankton (Paffenhofer et al. 1987). However, these isolated patches are most often produced in July, when winds as well as currents are favorable for upwelling. Furthermore, the zooplankton in the patches consist primarily of small species of copepod and gelatinous salps and doliolids which are most abundant in cool water near the bottom and in the thermocline. Small copepods are not ideal food for larval bluefin which eat other larval fishes. Larval fishes were not noticeably abundant in the patches; however, the sampling gear used by Paffenhofer et al. (1987) was not optimal to catch fish larvae. The gelatinous zooplankters which can be predators of fish larvae pose a potential hazard to the tuna larvae. Therefore the patches of plankton on the shelf caused by onshore meanders of the Gulf Stream do not appear to be favorable habitat for the feeding or survival of bluefin tuna larvae. These isolated patches on the shelf probably benefit benthic filter-feeders more than larval fishes.

Not all meanders that cause upwelling may result in isolated patches on the shelf. A pulse of upwelled, nutrient rich shelf-break water could move offshore, be entrained in the Gulf Stream, and increase the local productivity of near-surface water, thus enhancing the offshore habitat for larval fishes. Longhurst (1983) suggested that surplus production occurs on continental shelves. Walsh et al. (1987) detected export of phytoplankton from the Mid-Atlantic Bight during a spring plankton bloom. Sherman et al. (1984) found that peak spawning for some species is related to topographic features and circulation, and is synchronized with production of the copepod prey of their larvae. Something about the two stations with bluefin tuna larvae off North Carolina in this study (Figs. 6, 7) may have resembled "good" spawning habitat enough to induce migrating adult bluefin tuna to spawn nearby. Phytoplankton patches can seed other downstream patches in eddies (Heywood and Priddle 1987). This would be favorable for larval tunas offshore of the Gulf Stream front if these patches produced a food chain containing their prey. Much of the eddy-induced production may be flushed offshore rather than contribute to the shelf food chain (Walsh 1986). However, a pulse of nutrients from shelf-edge upwelling would be diluted rapidly by mixing with the Gulf Stream. We need more quantitative knowledge of the trophic results of these linkages between the shelf break and the Gulf Stream and more information about the food requirements of larval bluefin before the potential benefits of shelf-break upwelling to epipelagic ichthyoplankton can be assessed.

Dynamic Larval Retention Areas

Bluefin tuna larvae have been collected over wide areas of the Gulf of Mexico. They appear to occur primarily where currents or eddies encounter the shelf between the 100 and 1,000 m isobaths (Sherman et al. 1983). They may be most abundant at the cold edge of the Loop Current surface fronts in the eastern Gulf of Mexico (Richards et al. in press). Variability in the Loop Current (Sturges and Evans 1983) will produce variability in the seasonal occurrence and amount of such habitat for the bluefin tuna larvae in the Gulf. The amount of habitat may limit the number of bluefin tuna recruits to the adult stock as has been hypothesized for Atlantic herring stocks (Iles and Sinclair 1982). Because it is outside the rapidly flowing Loop Current which feeds into the Gulf Stream, this habitat may be a larval retention area of bluefin tuna. In the larval retention hypothesis developed for Atlantic herring (Sinclair and Iles 1985), the larvae do not undergo development while drifting passively (e.g., Harden-Jones 1968). Instead, they develop into juveniles within a retention region and then migrate actively to juvenile nursery areas.

Bluefin tuna larvae seem to fit into this life history model. Larvae spawned in the Loop Current can be advected to the Gulf Stream off the southeastern U.S. where habitat is relatively unfavorable. Larvae just outside the Loop Current in the Gulf of Mexico retention areas could develop until they are mature enough to begin their migration to feeding areas along the middle and northern U.S. east coast.

The limited data on distribution of bluefin tuna young of-the-year support this hypothesis. Juvenile bluefin tuna appeared in diets of terns at the Dry Tortugas (24°30′N, 82°50′W) from early June to early July (Potthoff and Richards 1970). These juveniles ranged in length from 25 to 115 mm with all sizes present early in the season but only longer ones present later. No juvenile bluefin tuna were noted in April or May during eight years of observations although juveniles of other species of tuna were being eaten by terns during May. The juvenile bluefin tuna were apparently unavailable within the 24 km feeding range of the terns (Robertson 1964) until they began migrating through the Straits of Florida in June. The timing of the migration suggests that there is a distinct and discrete time for the young-of-the-year juveniles to migrate from their larval retention area to their juvenile habitat. Perhaps the larvae must develop enough to begin schooling just as herring do before they begin their migration. Migration by schools of newly transformed juveniles is consistent with the cohesive migration of other age classes of bluefin tuna (Brunenmeister 1980; Mather 1980). Larvae that were swept out of the Gulf in April and May would not be in synchrony with the migration of their year class in June and July unless they reached suitable retention areas off the southeastern U.S. There is no evidence for such areas. The larval retention areas thus play a dual role for bluefin tuna by supplying habitat for larval development and by affecting the timing of migrations of different life stages of the species. The larval retention areas we propose for bluefin tuna and other oceanic pelagic fishes differ from those of fixed size proposed for herring stocks because they are dynamic, varying in date of occurrence, geographical location, and area. This variability in the quantity of larval habitat is a density-independent environmental factor which may explain a significant amount of variability in recruitment of pelagic fishes. Variations in the quality of larval habitat (coincident prey and predators) would cause density-dependent effects within the constraints of the total larval retention habitat.

A quantitative knowledge of bluefin tuna larval retention areas will have two practical applications. The precision of larval surveys, which are the only current independent estimates of the spawning stock, may be improved by a stratified sampling design once the strata of low and high abundance can be defined. In addition, hypotheses about the importance of appropriate habitat for bluefin tuna and the effects on recruitment of its temporal and spatial variability can be tested by comparing the fishery independent-variations in habitat with recruitment indices based on the catch statistics of commercial and recreational fisheries.

CONCLUSIONS

Larval bluefin tuna caught in the South Atlantic Bight in 1985 were in Gulf Stream water. Bluefin tuna larvae previously captured near Cape Hatteras were also in Gulf Stream water which meandered over the shelf edge. Larvae previously collected near Miami were primarily in the high velocity core of the Stream or in onshore meanders of the Stream. Therefore most bluefin tuna larvae off the southeastern U.S. were advected to the area, not spawned there. Although some unspent adults may spawn while migrating from the Gulf of Mexico to New England feeding grounds, only one of the larvae collected off the southeastern U.S. in 1985 had to have been spawned north of Miami based on its estimated age and rate of advection. The estimates of ages and advection do not falsify a hypothesis of local spawning with retention in recirculating currents, but the most likely conclusion considering all the evidence is that the South Atlantic Bight is not a major spawning area for western Atlantic bluefin tuna.

In addition, the habitat off the southeastern U.S. seems less favorable for bluefin tuna larvae because higher temperatures here than in the Gulf of Mexico would increase food requirements, and upwelling events over the shelf apparently do not lead to favorable food chains for larval tunas. Larvae may need to develop in retention areas outside the Loop Current in the Gulf of Mexico in order to synchronize their subsequent migration as schools of juveniles to nursery areas. These retention areas would be expected to vary in size and location with fluctuations in the Loop Current flow. The variations in amount of habitat for larvae could determine recruitment and thus affect the population dynamics of the bluefin tuna.

More research is needed to determine the survival rate of the larvae which are advected out of the Gulf of Mexico, to establish whether or not they recruit to the adult stock, to refine the definition of habitat for bluefin tuna larvae within the Gulf of Mexico, and to test if this habitat controls recruitment and population dynamics of the stock.

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