

**Abstract.**—The retrospective assignment of collections of larval swordfish, *Xiphias gladius*, taken from 1973 to 1980, to water types and area of the Gulf Stream front, as well as three sets of contemporary collections taken in 1984, 1988, and 1997, indicated that larvae were collected most frequently within the western Gulf Stream frontal zone. Larval swordfish accumulate by localized hydrodynamic convergence, rather than localized spawning, and thus these rare, surface-oriented larvae are found more frequently within the frontal zone. Lengths of larval swordfish taken from curatorial collections, from contemporary collections, and from published records from the Caribbean Sea, the Gulf of Mexico, and the western North Atlantic, as well as assumptions about growth rates and Gulf Stream transport, indicated that swordfish may spawn as far north as Cape Hatteras.

## Distribution of larval swordfish, *Xiphias gladius*, and probable spawning off the southeastern United States

**John Jeffrey Govoni**

National Marine Fisheries Service, NOAA  
Southeast Fisheries Science Center  
Beaufort Laboratory  
101 Pivers Island Road  
Beaufort, North Carolina 28516-9722  
E-mail address: Jeff.Govoni@noaa.gov

**Bruce W. Stender**

**Oleg Pashuk**

Marine Resources Research Institute  
South Carolina Wildlife and Marine Resources Department  
Charleston, South Carolina 29412

Swordfish, *Xiphias gladius*, is a cosmopolitan and highly migratory species that spawns year-round (Grall et al., 1983). Larvae of this fish do not account for high numbers of the ichthyoplankton or ichthyoneuston, and as a consequence, data that describe their spatial distribution are sparse. Grall et al. (1983) concluded from available data that, in the western North Atlantic, small larvae (<10 mm) occur most frequently in the eastern Caribbean and in the Straits of Yucatan and Florida in November, and that larger larvae (>10 mm) occur most often there, as well as in the Gulf Stream north to Cape Hatteras from January to March. Both length groups occur primarily in surface water over depths deeper than 200 m (Markle, 1974). Tibbo and Lauzier (1969) first speculated that larvae may be associated with horizontal temperature and salinity gradients. The collection of larvae along the apparent edges of the Gulf Loop Current in the Gulf of Mexico (Richards and Potthoff, 1980) and the Gulf Stream in the Atlantic (Potthoff and Kelley, 1982; Post et al., 1997) supports the notion that larvae

occur in greater abundance within frontal zones. Yet, the rarity of larvae has hindered a clear understanding of such coarse and fine scale (Haury et al., 1978) spatial distribution.

The scarcity of larval swordfish has obscured an understanding of their spawning pattern as well. The mesoscale pattern of larval distribution (Grall et al., 1983) implies that swordfish spawn in the Caribbean and the Straits of Yucatan and Florida, and that their larvae are carried northward by the Gulf Stream. Occasional small larvae taken in the Atlantic imply that swordfish may spawn as far north as Cape Hatteras (Markle, 1974). Large, and presumably older larvae in any location may be the result either of local spawning and subsequent retention or of transport from a distant spawning locale. Small larvae at a specific locale must be the exclusive result of local spawning.

Hydrated oocytes within the ovaries of adult females indicate that swordfish spawn south of the Sargasso Sea, in the northern Caribbean Sea, and the Straits of Florida (Arocha and Lee, 1995), although Squires (1962) has suggested that

spawning may occur as far north as Cape Hatteras. Planktonic eggs have not been identified in the western North Atlantic.

Effective fisheries management requires knowledge of both the spatial distribution of larvae and the distribution of spawning adults. Contemporary stock status ascertained by virtual population analysis can be calibrated with larval abundance estimates, even for species with rare larvae (e.g. McGowan and Richards, 1989; Scott et al., 1993). Because this calibration depends on accurate estimates of larval abundance, the spatial and temporal distribution of larvae must be known. Knowledge of spawning distribution would be the first step toward protection of spawning habitat and, perhaps, the restriction of fishing within spawning seasons and locales.

Here we examine the coarse- and fine-scale distribution, and the lengths of swordfish larvae off the southeastern United States. Our focus is on the influence of the Gulf Stream in shaping the spatial distribution of larvae and in the determination of probable spawning locales.

## Methods

We examined published records of larval swordfish (Arata, 1954; Arnold, 1955; Tibbo and Lauzier, 1969; Markle, 1974; Post et al., 1997), data from the Marine Resources Monitoring, Assessment and Prediction Program (MARMAP), data and specimens from the Southeast Area Monitoring and Assessment Program (SEAMAP), and new data from three surveys conducted between the Florida Straits and Cape Hatteras in 1984, 1988, and 1997 (CF8406, CH8807, and CH9703).

### Spatial distribution of species

For spatial distribution, we examined exclusively neuston collections (the upper 0.5 m of water), because swordfish are surface-oriented as are larvae. Although some swordfish larvae have been collected in nets that fished principally below the surface (Grall et al., 1983), most have been collected at the surface (Tåning, 1955; Yabe et al., 1959; Gorbunova, 1969; Nishikawa and Ueyanagi, 1974). All swordfish larvae collected by MARMAP, SEAMAP, and CH8807 were collected in the neuston, none in accompanying, sub-surface ichthyoplankton collections. Small larvae were occasionally taken from below the surface in CH9703, but these nets fished obliquely from 20 m and larvae were likely captured when nets were near the surface.

Collections of larvae were classified to water mass (or type)—shelf water (including Georgia water, Car-

olina Capes water, and occasionally Virginia coastal water [Pietrafesa, 1989]) or Gulf stream water—by applying measured hydrographic characteristics to the classifications of Matthews and Pashuk (1986) for MARMAP and CF8406 collections, and Pietrafesa et al. (1985) for CH8807 and CH9703 collections. Frontal zone water is a mixture of these water masses (Hitchcock et al., 1994). South of Cape Hatteras the Gulf Stream courses north-northeastward in juxtaposition with shelf water. Classically, the definition of the Gulf Stream front is a dynamic one: the Gulf Stream front is the point where the pressure gradient between Sargasso Sea water and slope water (north of Cape Hatteras) or shelf water (south of this Cape) is zero (Stommel, 1966). Practically, observed horizontally compressed surface isotherms and isohalines, accompanied by sharp discontinuities in sea-surface texture and color, define the Gulf Stream frontal zone (Olson et al., 1994). In our study, we used this observational definition to assign the surface position and to classify the water of the Gulf Stream frontal zone. Surface Gulf Stream water at its western front between the Florida Straits and Cape Hatteras has characteristic temperatures that range from 21° to 24°C in winter and from 27° to 29°C in summer, salinities that range from 35.7 to 36.4 psu and vary little seasonally, dissolved oxygen values that range from 4.5 to 5.0 mL/L, and nitrate values of 1.0 µM/L (Atkinson, 1985; Schmitz et al., 1993; Hitchcock et al., 1994; Xie and Pietrafesa, 1995). Shelf water is cooler and less saline (Pietrafesa et al., 1985). The course of the Gulf Stream along the continental shelf break is unstable; it meanders onshore and offshore and projects intrusions, filaments, and eddies onto the shelf (Pietrafesa, 1989; Lee et al., 1991). These processes complicate the position and distort the configuration of the frontal zone.

Retrospective examination of 1163 collections taken from the Straits of Florida to Cape Hatteras and offshore from the 9 m to 2000 m isobath (Fig.1) from 1973 to 1980 (MARMAP) afforded the determination of coarse-scale distribution. These collections were taken with neuston nets of two different dimensions and meshes: a 1.0 × 0.5 m net with 505-µm mesh and a 2.0 × 1.0 m net with 947-µm mesh. Both meshes collect swordfish larvae, which are reported to be at least 4 mm at hatching (Sanzo, 1910; Yasuda et al., 1978). Neuston nets were towed for 10 min at 5.6 km/h. Collections were made in all four seasons and at all times of day and night. Larvae were preserved in 5% formalin solution. The probable location of the Gulf Stream front for these collections was determined from 1) advanced, very high resolution, infra-red radiometer (AVHRR) satellite images of sea-surface temperature (SST) taken from 1976 to 1980; 2) expendable bathythermograph (XBT) profiles taken from 1973 to 1980;

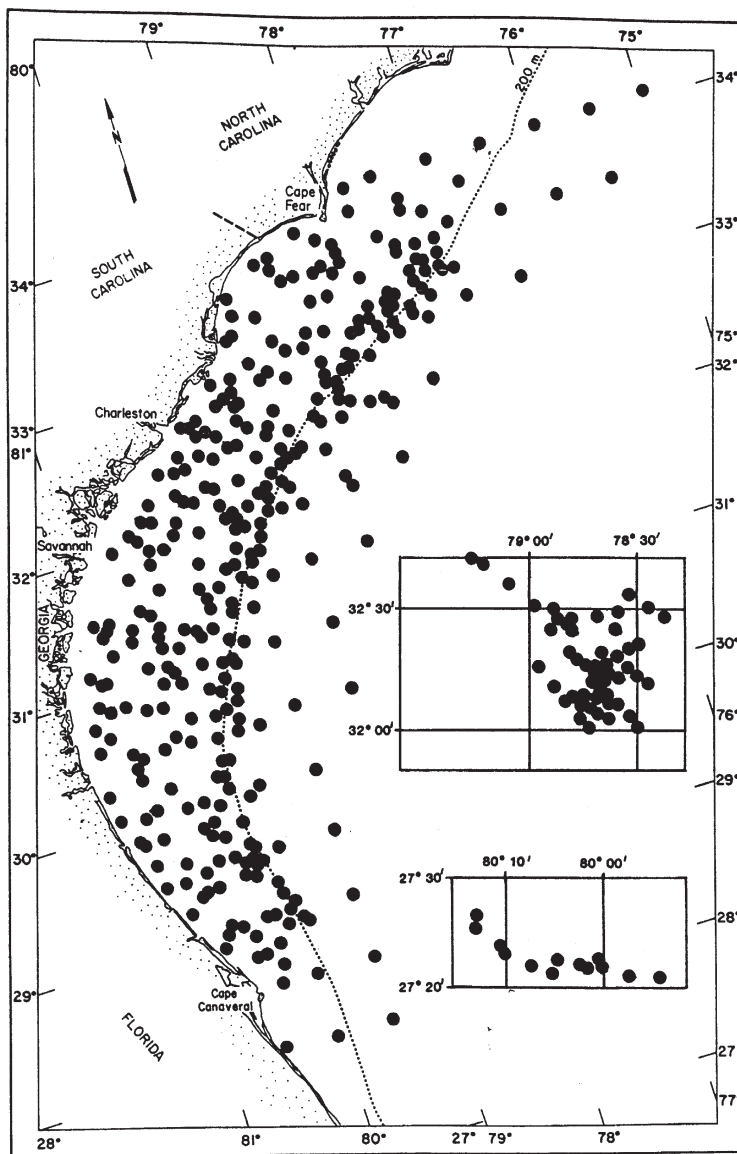
3) sea-surface salinity, dissolved oxygen, and nitrate concentrations taken along with neuston collections (Mathews and Pashuk, 1986); 4) records of the National Oceanographic Data Center; and 5) records of U.S. Coast Guard visual observations from aircraft. The width of the frontal zone, and consequently the area occupied by frontal zone water, was determined as three times the standard deviation of the mean course of the front, i.e.  $\pm 10$  nautical miles (18.5 km) of the estimated location of the frontal axis (Olson et al., 1983).

Forty-seven collections taken from 22 to 24 June 1984 with a  $1.0 \times 0.5$  m neuston net with 909- $\mu$ m mesh

towed for 10 min at 5.6 km/h in the Gulf Stream and within its western frontal zone between Cape Canaveral and Cape Hatteras (CF8406) afforded an examination of coarse scale differences in occurrence of swordfish larvae within the frontal zone and in the body of the Gulf Stream. Six collections were taken during night, the remainder during the day. Larvae were preserved in 5% formalin. A sea-surface temperature plot, generated from composite AVHRR images of SST compiled on 20 June 1984 (Fig. 2), in conjunction with continuous temperature and salinity values from a hull-mounted thermosalinometer, was used to determine the position of the Gulf Stream and its frontal zone and to classify these collections to water mass.

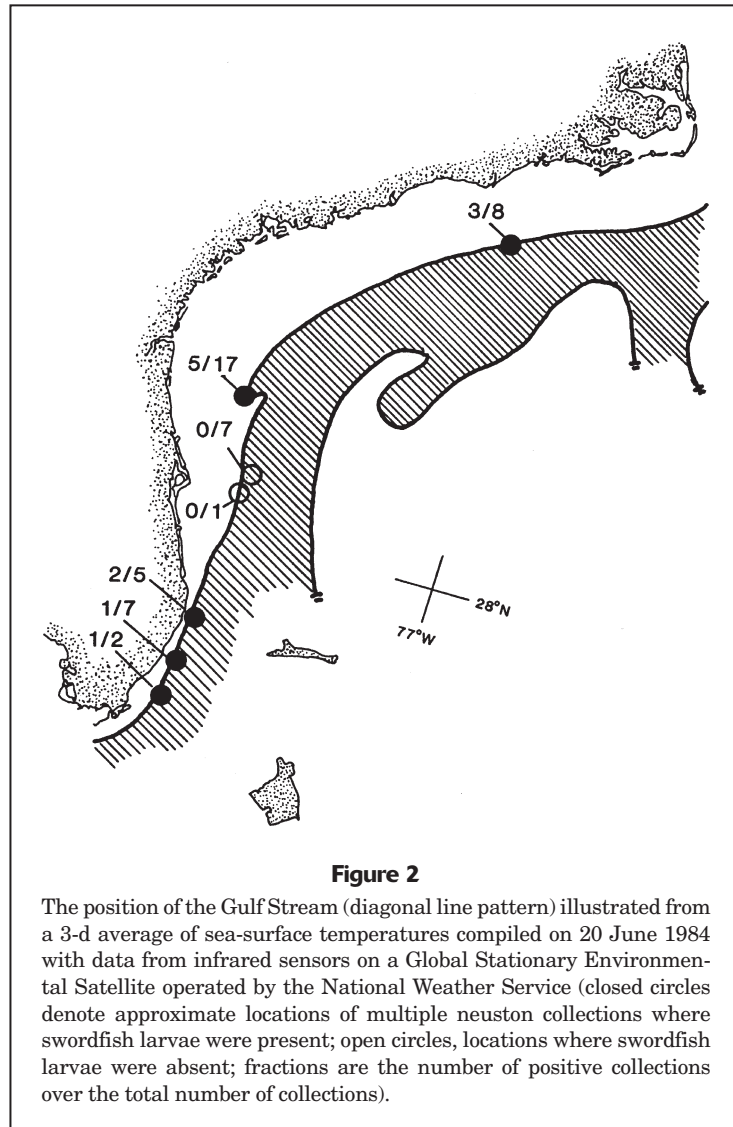
One hundred and fifty-six collections (CH8807), taken from 13 to 24 September 1988 with a  $2.0 \times 1.0$  m neuston net with 947- $\mu$ m mesh along six cross-shelf and cross-slope transects (encompassed by  $31^{\circ}30.4'N/080^{\circ}16.5'W$ ,  $30^{\circ}45.0'N/078^{\circ}41.5'W$ ,  $32^{\circ}24.30'N/076^{\circ}19.5'W$ , and  $33^{\circ}16.0'N/077^{\circ}54.0'W$ ), afforded examination of coarse- and fine-scale distribution of larval swordfish within and about the Gulf Stream frontal zone (Fig. 3). Neuston nets were towed for 10 min at 5.6 km/h. Ten stations were occupied along each transect (60 stations); 96 additional neuston collections were taken within the Gulf Stream or within its frontal zone. The 60 collections along transects were 18.5 km apart, whereas 94 of the additional 96 collections within the frontal zone or body of the Gulf Stream were clustered in groups of four to ten, with collections about 1 km apart. Surface salinity, two-dimensional sections of isotherms derived from XBT casts taken at each station along transects, and AVHRR images of SST were used to classify collections.

Six neuston collections taken on 31 May 1997 (CH9703) with a  $2.0 \times 1.0$  m neuston net with 947- $\mu$ m mesh within the Gulf Stream frontal zone in an area encompassed by  $33^{\circ}52.94'N/076^{\circ}23.89'W$ ,  $33^{\circ}52.30'N/076^{\circ}24.77'W$ , and  $33^{\circ}52.92'N/076^{\circ}22.27'W$  afforded examination of fine-scale distribution of larval swordfish within the Gulf Stream frontal zone (Fig. 4). Nets were towed for 10 min at 5.6 km/h, twice in the Gulf Stream frontal zone, and twice each on the shelf and Gulf Stream sides of the front. Larvae were preserved in 95% ethanol. Sea-surface temperature from a hull-mounted thermister in conjunction with XBT profiles and AVHRR images of SST were used to classify collections.



**Figure 1**

Nominal stations occupied by the Marine Resources Monitoring Assessment and Prediction Program from 1973 to 1980; each station was occupied at least once, some more than once.

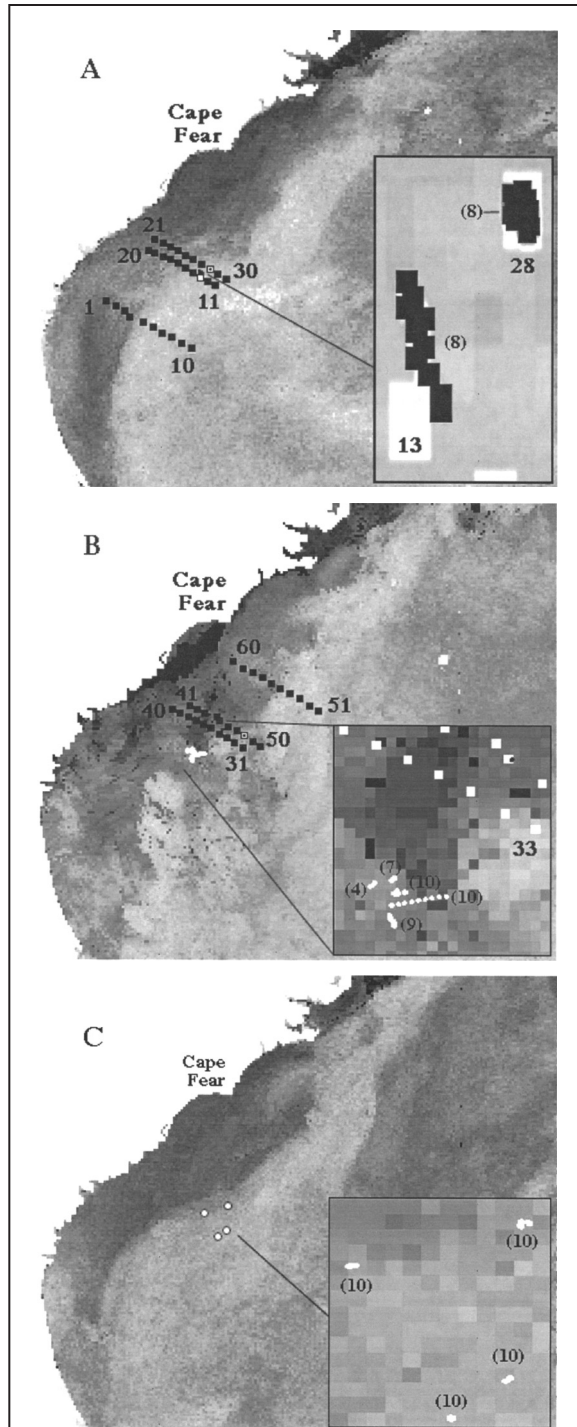


### Length of larvae

The overall distribution of the length of swordfish larvae in the Caribbean Sea, Gulf of Mexico, and off the southeastern Atlantic coast of the United States provided a view of the occurrence of the smallest larvae. Because most published records reported either standard length (SL) or total length (TL), both measures are reported in our study. We employed no conversion, although the length of the caudal finfold or fin ranges from 3% to 12% of TL for larvae from 6 to 192 mm (calculated from Arata [1954]). We employed no correction for the shrinkage of larvae due to death or preservation, because preservation fluid was not routinely reported in the literature and some specimens were measured alive. Although the length from the anterior eye orbit to the tip of the notochord is per-

haps a better measure of length in swordfish larvae, because the rostrum is often broken (Potthoff and Kelley, 1982), this measure was not uniformly available in published records. Standard or total lengths (anterior tip of the upper jaw to the posterior tip of the notochord or hypural plate (SL) or caudal fin (TL)) of swordfish larvae and locations of collection were taken from Arata (1954), Arnold (1955), Tibbo and Lauzier (1969), Markle (1974), Post et al. (1997) and MARMAP. Standard length was measured on larvae from SEAMAP, CF8408, CH8807, and CH9703 (from neuston as well as plankton collections taken within the Gulf Stream frontal zone with a MOCNESS (Wiebe, et al., 1976) system with 505 m mesh nets), and on a larva from a neuston collection taken in a *Sargassum* raft at 33°38.7'N/076°02.7'W in 1991. Specimens were considered larvae if they were <190 mm SL or TL, because





**Figure 3**

Advanced very high resolution infrared radiometer images of sea-surface temperatures off the southeastern Atlantic coast of the United States; five day composites from National Oceanic and Atmospheric Administration, National Environmental Satellite, Data and Information Service global orbiting satellites: (A) 11 to 15 September; (B) 16 to 20 September; (C) 21 to 25 September 1988. Darker to lighter shades denote cooler to warmer water; squares denote locations of neuston collections; numbers denote station numbers; and parenthetical numbers within insets denote the number of overlapping stations.

swordfish retain larval characters (lower jaw at least half as long as the rostral cartilage; preorbital, supraorbital, posttemporal, and preopercular spines; enlarged and spinous dorsal and ventral scales; and a continuous and long dorsal fin) until they are at least 188 mm SL (Arata, 1954; Pothoff and Kelley, 1982; McGowan, 1988).

### Approximate age of larvae

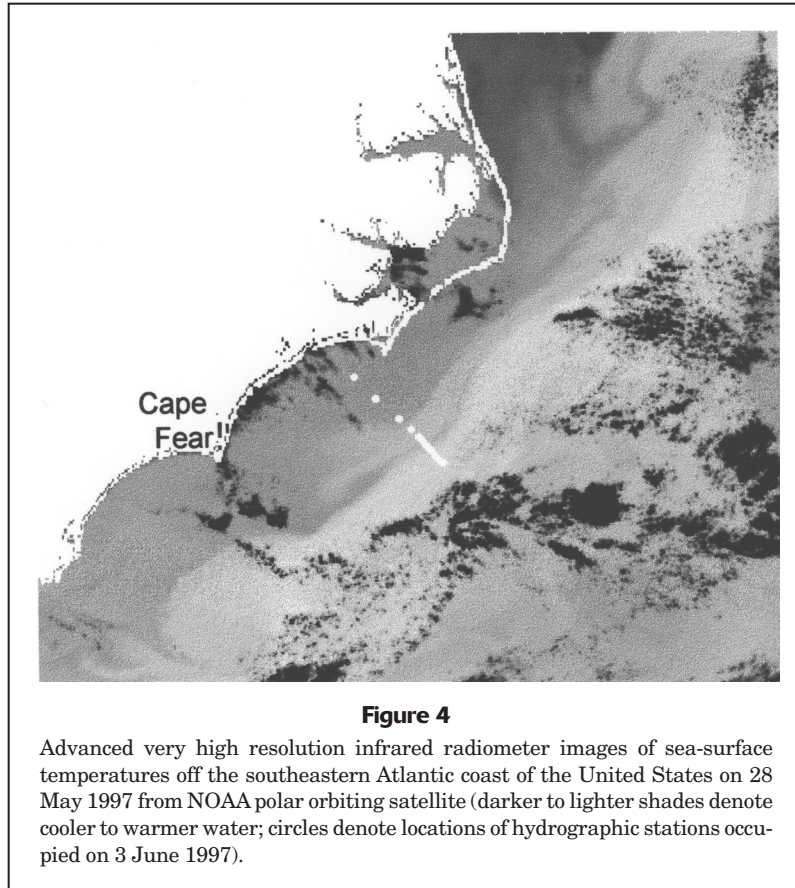
The age of swordfish larvae at length was approximated from published accounts of the age and lengths of laboratory-reared larvae, and from counts of apparent growth increments on otoliths excised from three specimens collected by CH9703. Larvae from the Mediterranean hatch at a length from 4.0 to 4.5 mm TL (measured alive) after 3 d of incubation and deplete their yolk and oil globule at a length of about 5 mm TL after 5 to 7 d at 22.5–25.2°C (Sanzo, 1910; Yasuda et al., 1978).

## Results

### Spatial distribution

The 1163 MARMAP collections yielded 55 swordfish larvae in 35 collections. Larvae were collected in all seasons and at all times of the day. Of the 35 collections that produced larvae, 21 were taken in the day, 5 at night, and 9 at dawn or dusk. As many as nine larvae were taken in a single collection. Between Cape Canaveral and Cape Hatteras, larvae were collected more frequently within the frontal zone of the Gulf Stream, than they were in shelf or Gulf Stream waters. Where the Gulf Stream jets through the Florida Straits (25° to 28°N latitude), larvae occurred across the narrow body of the Gulf Stream. If these Florida Straits collections are excluded from consideration, along with collections from single seasonal or annual surveys that did not produce any larvae, 21 of these 27 collections that yielded larvae were within the probable area of the Gulf Stream frontal zone, i.e. 18.5 km of the assigned position of the Gulf Stream surface frontal axis; one was in shelf water, and five were in Gulf Stream water (Fig. 5; Table 1). The probability of observing the presence or absence of larvae (calculated as frequency of occurrence), among the two water masses and the mixed frontal zone, with at least as much association was 0.000002% (Fisher's exact test, two-tailed distribution).

In June 1984 (CF8406), the frontal zone was defined by the 25° to 27°C surface isotherms. North of Florida, the western Gulf Stream front was smooth with no evidence of instabilities in the form of large intrusions (Fig. 2). Twelve of 47 collections of CF8406 yielded 16 swordfish larvae. Of these, two collections

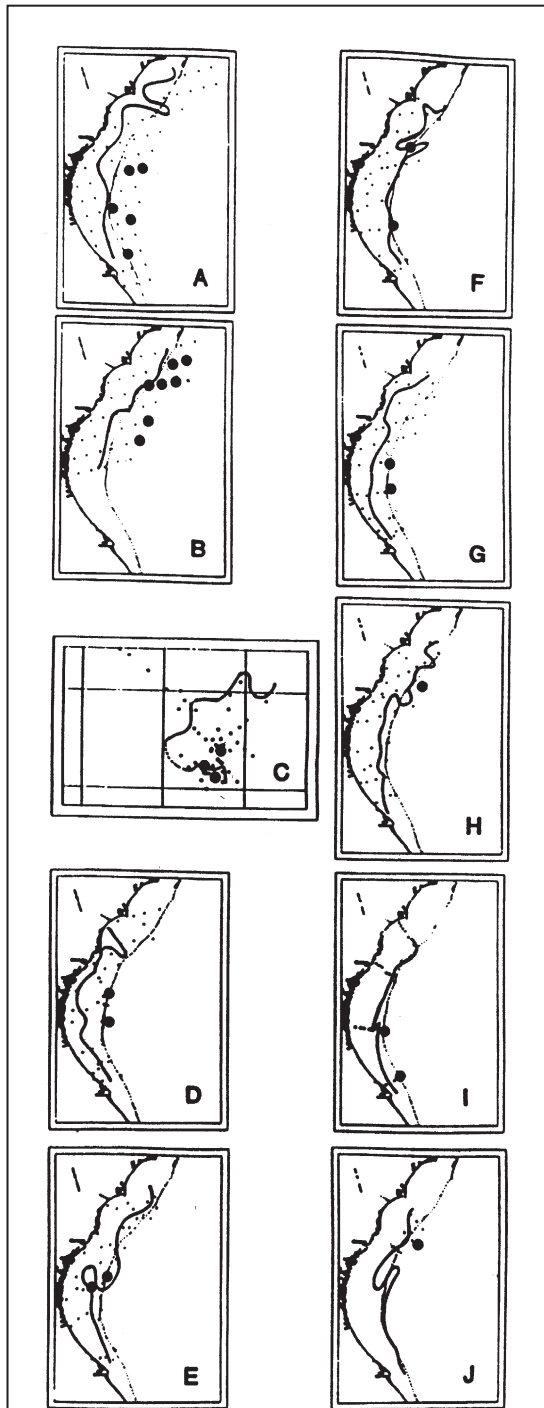


yielded more than one larva, i.e. two larvae in each. Ten collections with larvae present were within the frontal zone, whereas two collections were in the body of the Gulf Stream (Table 1). The probability of observing the presence or absence of larvae with a frequency at least this extreme was 0.176% (two-tailed test).

In September 1988 (CH8807), the Gulf Stream frontal zone was defined by 27° to 29°C surface isotherms. With the defining criterion of horizontally compressed surface isotherms within this temperature range, the width of this frontal zone ranged from 18 to 93 km. This area, however, encompassed a westward intrusion of the Gulf Stream that developed over the transect grid (Fig. 3) in the wake of the Charleston Bump, a topographic rise at the continental shelf break that typically forces an eastward deflection of the Gulf Stream (Pietrafesa et al., 1985). Isolated surface pools of 27° to 29°C water inshore of the Gulf Stream front proper (Fig. 6, B and F) indicated this intrusion. This convolution of the Gulf Stream front proper manifested three fronts across the shelf, but these were considered a composite single front for analysis. Shear zones (determined by rapid increases in the ship's set), drift lines of *Sargassum*, and discontinuities in sea-surface texture, were embedded within the fron-

tal zone and evidenced probable convergence of surface water (Stommel, 1966; Olson et al., 1994). The 156 collections of CH8807 yielded 12 swordfish larvae. One collection yielded three larvae; another two. Larvae were collected exclusively within the frontal zone (Table 1), one at the tip of the intrusion (station 58; Fig. 6F). The probability of observing the presence or absence of larvae at least this extreme was 0.020%.

In May 1997 (CH9703), the Gulf Stream frontal zone was defined by 27° to 29°C surface isotherms. The frontal zone was moving rapidly eastward. On 23 May, 8 d before the collection of swordfish larvae within the frontal zone, an elongate filament of a Gulf Stream intrusion lay inshore of the collection area (Fig. 4). The isolated pool of 25°C water at the surface and eastward of the frontal zone (Fig. 7) indicated that this intrusion was extant on 31 May 1997 when collections of CH9703 were taken. The six neuston collections of CH9703 yielded nine larvae. One collection taken along the frontal axis and one collection taken on the Gulf Stream side of the axis yielded two larvae each; the other collection taken along the axis yielded three. Larvae were present in two collections along the frontal axis, two collections 1 km to the Gulf Stream side of the axis, and one of two collections taken 0.5 km



**Figure 5**

Position of the Gulf Stream front and locations of neuston collections of surveys when swordfish larvae were collected from 1973 to 1980 (solid lines denote assigned axis of the Gulf Stream front, small circles locations of neuston collections; large circles locations of swordfish larvae: (A) March 1973; (B) May 1973; (C) July 73; (D) November 1973; (E) August and September 1974; (F) August and September 1975; (G) January and February 1976; (H) August and September 1976; (I) September 1978; (J) April 1979.

**Table 1**

Contingency tables of the absence and presence of larval swordfish, *Xiphias gladius*, in Gulf Stream frontal zone, the Gulf Stream, and shelf water in the southeastern Atlantic bight off the United States.

Frequency	Frontal zone water	Gulf Stream water	Shelf water	Total
1973-80				
Absent	158	25	175	358
Present	21	5	1	27
Total	179	30	176	385
1984				
Absent	21	14	35	
Present	10	2	12	
Total	31	16	47	
1988				
Absent	77	46	24	147
Present	9	0	0	9
Total	86	46	24	156
1997				
Absent	0 <sup>1</sup>	0 <sup>2</sup>	1 <sup>3</sup>	1
Present	2 <sup>1</sup>	2 <sup>2</sup>	1 <sup>3</sup>	5
Total	2 <sup>1</sup>	2 <sup>2</sup>	2 <sup>3</sup>	6

<sup>1</sup> Taken along the frontal axis.

<sup>2</sup> Taken along offshore side of the axis.

<sup>3</sup> Taken on inshore side of the axis.

to the shoreward side of the frontal axis. Larvae were evenly distributed within the frontal zone (Table 1).

### Length of larvae

Swordfish larvae ranged from 2.8 mm SL to 110 mm TL. The two largest larvae, >100 mm TL, were collected in the Atlantic and in the Caribbean. The smallest and youngest larvae, those  $\leq 5$  mm SL (Fig. 8), were collected in the eastern Gulf of Mexico in the vicinity of the Gulf Loop Current between 24° and 28°N (here, 39 of 152 larvae were  $\leq 5$  mm), and off the southeast coast from Georgia north to Cape Hatteras between 30° and 35°N latitude (here, 15 of 62 larvae were  $\leq 5$  mm SL). Larval lengths were not correlated with latitude (Pearson product-moment correlation coefficient = -0.1360).

### Approximate age of larvae

The smallest larva measured (after preservation in 95% ethanol), taken in the Gulf of Mexico from SEAMAP, was appreciably smaller than the length at hatching for larvae (measured alive, 27 h after fertilization) from the Mediterranean (Yasuda et al., 1978). One larva 2.8 mm SL from the eastern Gulf of Mexico, and



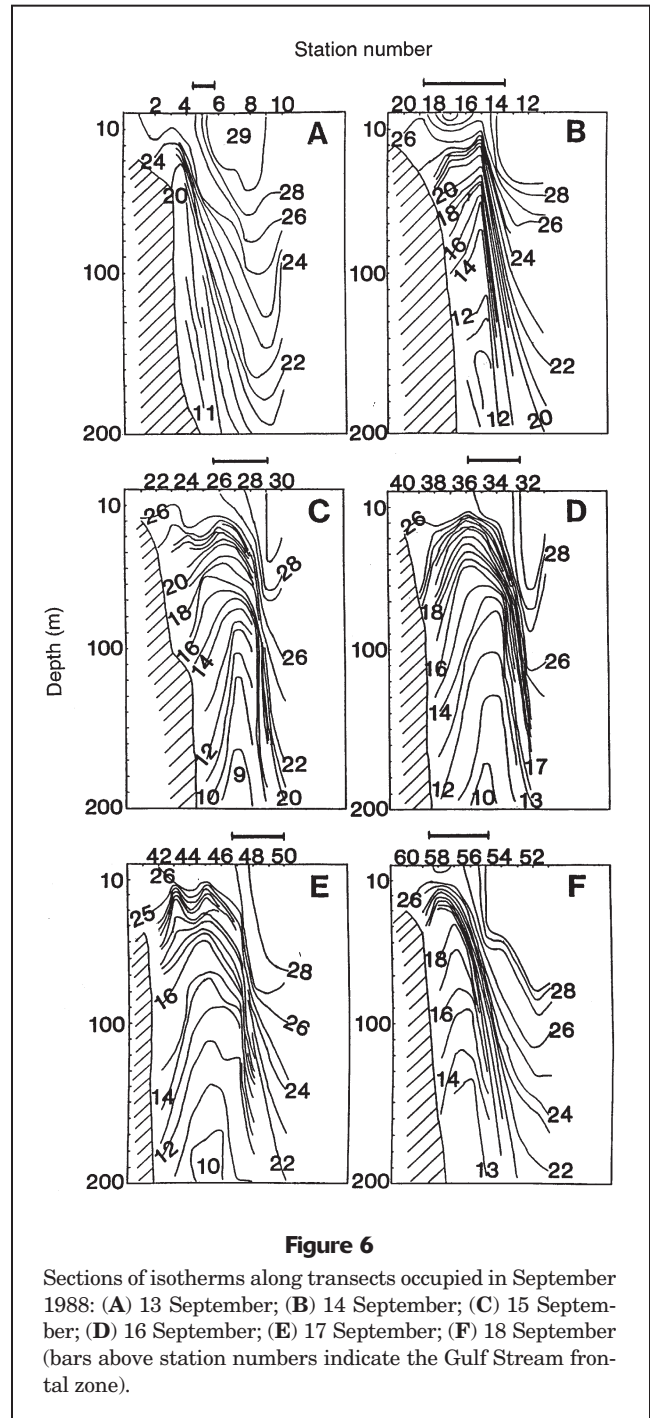
one 3.8 mm SL (4.3 mm TL) taken off North Carolina (CH9703), had recognizable yolk and oil globule remnants. These lengths were smaller than the reported length of larvae at the completion of yolk and oil globule absorption, about 5 mm TL for larvae (measured alive, 65 h after fertilization) from the Mediterranean (Yasuda et al., 1978).

Counts of increments on sagittae from larvae 4, 5, and 6 mm SL, taken in CH9703, were 4, 3, and 6 (increments on swordfish otoliths have not been validated as daily intervals [Price et al., 1991]).

## Discussion

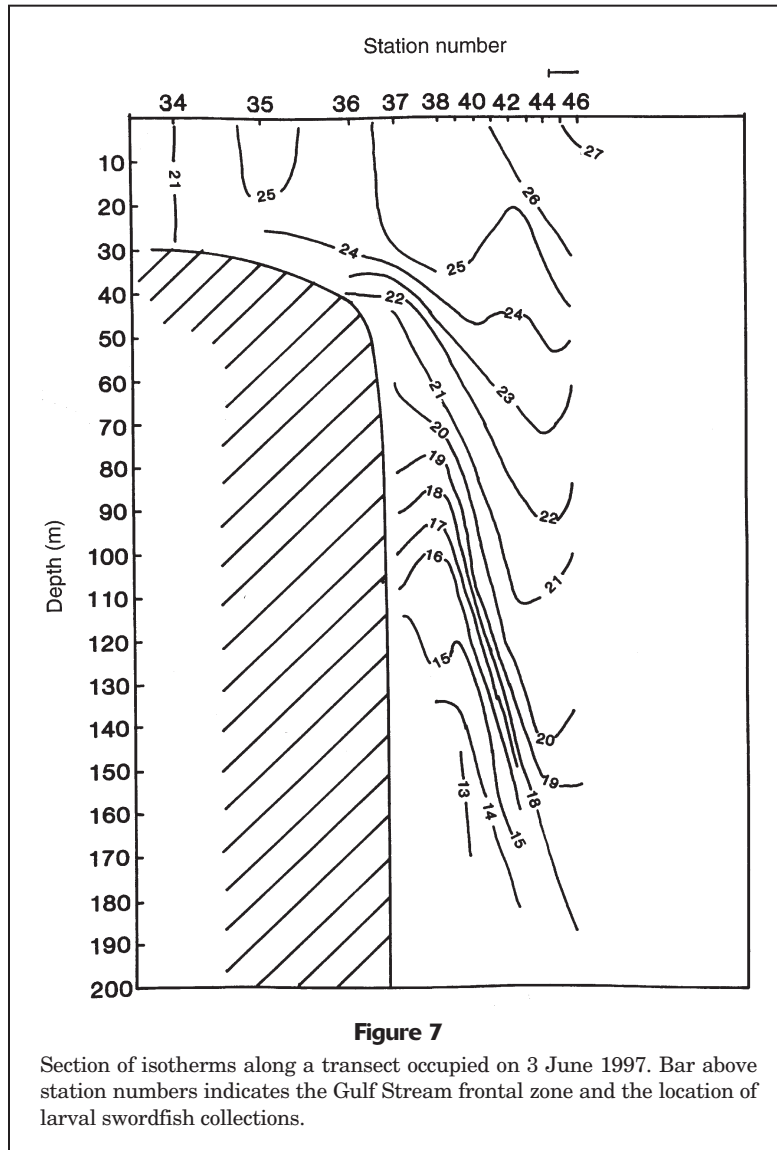
North of the Florida Straits, larval swordfish were collected most frequently within the western frontal zone of the Gulf Stream. This observation corroborates the speculation that larvae are associated with water within sharp horizontal gradients of temperature and salinity (Tibbo and Lauzier, 1969). Convergence of surface water is a possible mechanism for their accumulation within the Gulf Stream front. The Gulf Stream front south of Cape Hatteras is cyclonically sheared with shelf water that directly opposes Gulf Stream water (Pietrafesa et al., 1985). The retrograde, hydrographic discontinuity between Gulf Stream and shelf water and their hydrodynamic opposition results in convergence of surface water within the frontal zone (Garvine, 1980; Olson et al., 1994). Convergence of surface water has been implicated in the accumulation of adult fishes with depth-keeping abilities (Olson and Backus, 1985). Positively buoyant or surface-seeking larval fishes will be entrained in converging water and will be advected toward the front where they will accumulate as they resist downwelling along the frontal axis (Govoni and Grimes, 1992). Swordfish larvae are unquestionably surface-seeking larvae. Convergence of surface water within oceanic frontal zones should produce accumulations of larvae on spatial scales of 10 to 100 km (Olson et al., 1994). At a coarse scale, larvae were more abundant within the frontal zone; no fine-scale pattern was evident within the frontal zone. Adaptive sampling (Lo et al., 1997) may be a more efficient means of estimating larval swordfish abundance than simple random sampling, because of the rarity and the spatial aggregation of larvae.

Small swordfish larvae were collected most often in the eastern Gulf of Mexico and off the east coast of the United States as far north as Cape Lookout, North Carolina. Swordfish apparently spawn in the eastern Gulf, but the present observations corroborate the speculation of spawning off the Carolinas (Squires, 1962; Markle, 1974) as well. Off the Carolinas, larvae



5 mm SL or less occurred in 25° and 26°C water. Larvae that were 4 to 5 mm SL had 3 and 4 apparent growth increments on their sagittae. In water from 22° to 25°C, larvae that were 5 mm TL would be approximately 6 d old (Yasuda et al., 1978). Given an egg incubation period of 3 d at 24°C (Yasuda et al., 1978) and an additional 3 or 4 d for posthatch growth, along with a average axial velocity of the Gulf Stream of 1.5



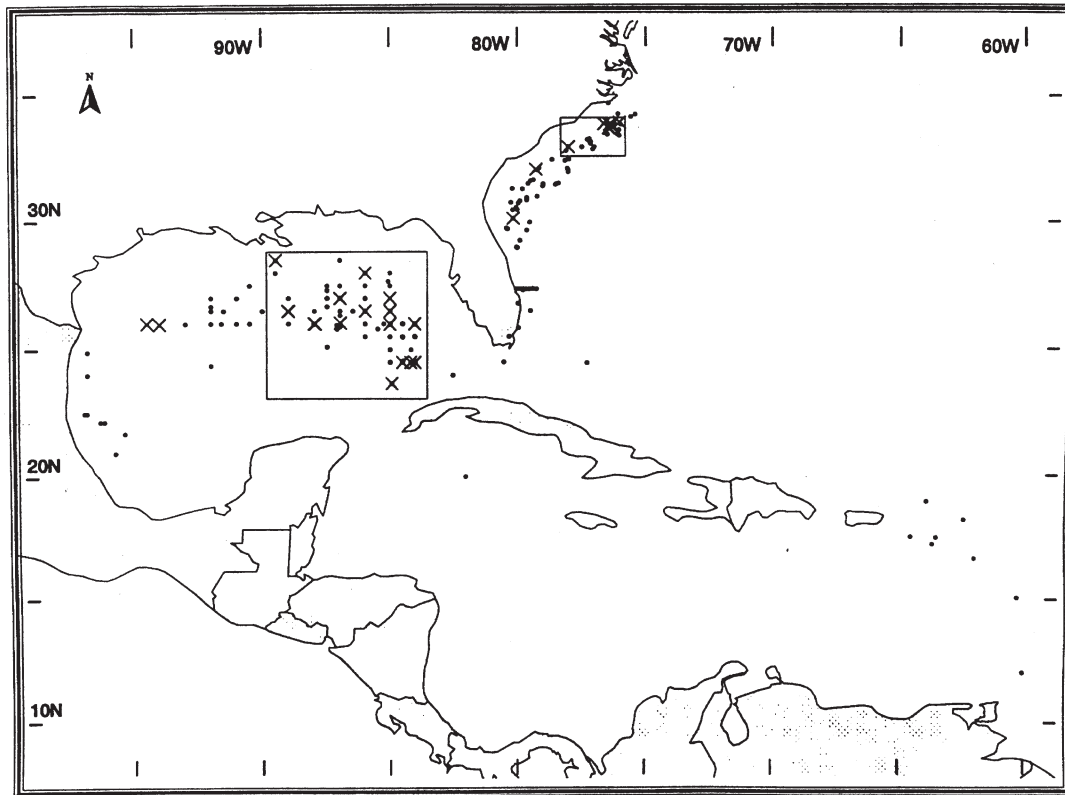


m/s (Olson et al., 1994), larvae that were 4 to 5 mm SL in the Atlantic could have been transported from as far away as 900 km. A similar trajectory was projected for small larvae of bluefin tuna, *Thunnus thynnus* (McGowan and Richards, 1989). Larvae that were  $\leq 5$  mm in length, collected off North Carolina could have been spawned in the Florida Straits if they remained in the core of the Gulf Stream. Current velocities within the western Gulf Stream frontal zone, where larvae most frequently reside, are less than axial velocities (Lillibridge et al., 1990; Song et al., 1995; Limouzy-Paris et al., 1997). Further, departures from a smooth, along slope, Gulf Stream trajectory, in the form of meanders, intrusions, and filaments along the western Gulf Stream frontal zone are frequent (Pietrafesa, 1989). We collected swordfish larvae frequently within these Gulf Stream anomalies

(Figs. 4–7). Water within these features veers and reverses direction (Lee et al., 1991), the result being that the northward translocation of swordfish larvae within the frontal zone is checked and their northward transport delayed. The possibility of spawning between Cape Canaveral and Cape Hatteras is real, but not certain.

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**Figure 8**

Locations of larval swordfish collection in the Caribbean Sea, Gulf of Mexico, and off the southeast coast of the United States north to Cape Hatteras (crosses depict larvae 2.8 through 5 mm standard (SL) or total length (TL); circles, larvae 5.1 through 110 mm SL or TL; within the box in the Gulf of Mexico, coincidental crosses represent 39 larvae  $\leq 5$  mm and 113  $> 5$  mm SL; within the Atlantic, coincidental crosses represent 15 larvae  $\leq 5$  mm and coincidental circles 47  $> 5$  mm SL).

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