

Abstract—Lengths and ages of swordfish (*Xiphias gladius*) estimated from increments on otoliths of larvae collected in the Caribbean Sea, Florida Straits, and off the southeastern United States, indicated two growth phases. Larvae complete yolk and oil globule absorption 5 to 6 days after hatching (DAH). Larvae <13 mm preserved standard length (PSL) grow slowly (~0.3 mm/d); larvae from 13 to 115 mm PSL grow rapidly (~6 mm/d). The acceleration in growth rate at 13 days follows an abrupt (within 3 days) change in diet, and in jaw and alimentary canal structure. The diet of swordfish larvae is limited. Larvae <8 mm PSL from the Caribbean, Gulf of Mexico, and off the southeastern United States eat exclusively copepods, primarily of one genus, *Corycaeus*. Larvae 9 to 11 mm eat copepods and chaetognaths; larvae >11 mm eat exclusively neustonic fish larvae. This diet indicates that young larvae <11 mm occupy the near-surface pelagia, whereas, older and longer larvae are neustonic. Spawning dates for larvae collected in various regions of the western North Atlantic, along with the abundance and spatial distribution of the youngest larvae, indicate that spawning peaks in three seasons and in five regions. Swordfish spawn in the Caribbean Sea, or possibly to the east, in winter, and in the western Gulf of Mexico in spring. Elsewhere swordfish spawn year-round, but spawning peaks in the spring in the north-central Gulf of Mexico, in the summer off southern Florida, and in the spring and early summer off the southeastern United States. The western Gulf Stream frontal zone is the focus of spawning off the southeastern coast of the United States, whereas spawning in the Gulf of Mexico seems to be focused in the vicinity of the Gulf Loop Current. Larvae may use the Gulf of Mexico and the outer continental shelf off the east coast of the United States as nursery areas. Some larvae may be transported northward, but trans-Atlantic transport of larvae is unlikely.

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The early life history of swordfish (*Xiphias gladius*) in the western North Atlantic

John Jeffrey Govoni

Elisabeth H. Laban

Jonathan A. Hare

Center for Coastal Fisheries and Habitat Research
 National Oceanic and Atmospheric Administration
 101 Pivers Island Road
 Beaufort, North Carolina 28516-9722
 E-mail address (for J. J. Govoni): Jeff.Govoni@noaa.gov

Swordfish (*Xiphias gladius*) live in warm waters of the world's oceans, as well as in large enclosed basins such as the Caribbean and Mediterranean seas, and the Gulf of Mexico (Berkeley, 1983). Swordfish are highly migratory throughout their global range. The worldwide population structure, as currently understood, has at least three breeding units: Mediterranean, north-western Atlantic to the tropical South Atlantic, and Indo-Pacific (Kotoulas et al., 1995; Chow and Takeyama, 2000; Reeb et al., 2000). For the purpose of fishery management, the International Commission for the Conservation of Atlantic Tunas (ICCAT) recognizes only North Atlantic and South Atlantic stocks. Possible genetic exchange between eastern and western North Atlantic populations is incompletely documented.

Swordfish reportedly spawn year-round in the western North Atlantic in different seasons and regions. Spawning season and location has been inferred from the abundance of small larvae (Gorbunova, 1969; Richards and Potthoff, 1980; Potthoff and Kelley, 1982; Grall et al., 1983; Govoni et al., 2000), gonad maturation (LaMonte, 1944; Beckett, 1975), or oocyte cytology (Taylor and Murphy, 1992; Arocha, 1997; Arocha, 2002). The observation of live females with running eggs, hooked on long-lines, and followed to the fishing vessel by several smaller males (Lee¹; Berkeley²) corroborates spawning in some seasons and locations. Although gonad condition and oocyte status can indicate spawning season, the resolution of spawning location can be ambiguous with these methods because

mature gonads and hydrated oocytes can be found in several seasons within the range of these highly migratory fishes. The determination of age and the distribution of young larvae, along with realistic estimates of water velocity and trajectory, help to resolve this ambiguity.

Beyond spawning, the early life history of swordfish in any ocean is incompletely described (Palko et al., 1981). Larvae undergo a stark change in physical appearance between ~8 and 13 mm preserved standard length (PSL), from a typical scombroid larval form to a juvenile istiophorid one (Collette et al., 1984). At this juncture in development, larvae develop characteristic preorbital, supraorbital, posttemporal, and preopercular spines; enlarged and spinous dorsal, ventral, and lateral scale anlagen; and a continuous long dorsal fin that extends along most of the dorsal aspect. Swordfish retain these larval characters until they are at least 188 mm PSL (Arata, 1954; Potthoff and Kelley, 1982), a size at which most fishes are considered juveniles. By using the ages and lengths of larvae hatched in the laboratory and reared through yolk and oil globule absorption (Sanzo, 1910; Yasuda et al., 1978), along with length frequencies of larvae caught in the western North Atlantic,

¹ Lee, D. J. 1995. Personal commun. Southeast Fisheries Science Center, NMFS, 75 Virginia Beach Drive, Miami, FL 33149.

² Berkeley, S. A. 1998. Personal commun. Long Marine Laboratory, Univ. California, Santa Cruz, 100 Shaffer Road, Santa Cruz, CA 95060.

Arata (1954) inferred the age and growth of larvae from 6 to 192 mm preserved total length (PTT). Aside from this effort, the age of larval swordfish has been undetermined and growth has not been described. Diets of larvae have been reported (Gorbunova, 1969), but the apparent transition in diet has neither been detailed nor reconciled with changes in physical features and growth. Similarly, the vertical distribution of larvae has not been reconciled with their diet or growth. Most larvae are collected near the surface of the ocean, typically in neuston nets, but some larvae are collected in nets that sample below the surface (Govoni et al., 2000).

In the present study, we resolve and summarize the early life history of swordfish in the western North Atlantic. We report estimated age, describe growth, relate growth to feeding, morphological features, and vertical distribution, and infer spawning time and location and the sources and fates of swordfish larvae. This study supplements that of Govoni et al. (2000) by providing the dimension of time, i.e. age of larvae, to the spatial distribution and possible transport of these larvae.

Methods

Collections of larvae

Ichthyoplankton collections from cruises in 1989 (in the northeastern Caribbean about the Lesser Antilles), 1991 and 1997 (off the southeastern United States), and 2000 (in the Straits of Florida and off the southeastern United States), produced 63 larvae that were preserved in 95% ethanol (for examination of otolith microstructure). Samples were collected either from the neuston (i.e. taken with a 1.0×0.5 m neuston net) or from depth intervals (i.e. taken with a 1-m MOCNESS [multiple opening and closing net and environmental sampling system] [Wiebe et al., 1976]). Larvae were measured for preserved standard length (PSL), the conventional length measure for larval fishes (Kendall et al., 1984), and lower-jaw-fork-length (LJFL), the measure in common use for juvenile and adult swordfish (Megalofonou et al., 1995).

Otolith excision and examination

Of the 63 larvae collected, sagittae were found and successfully excised from 37 larvae, lapilli from 32, and asterisci from six. Otoliths were mounted on glass slides and dried before examination. Broken sagittae and lapilli, and some large sagittae, were embedded in plastic, sectioned with a saw, and polished (Secor et al., 1991).

Otolith growth increments were counted along the longest axis of each sagitta and lapillus by using a compound light-transmission microscope; increments in asterisci were fewer and less defined and were not counted. Three blind counts were made by the same observer. Although increments were consistently visible on both sagittae and lapilli, counts from individual larvae were greater on sagittae (Student's *t*-test; $P < 0.001$). Standardized counts (the standard deviate of each repeated count) on the right

and left sagittae were not significantly different (nested ANOVA; $P < 0.05$). Increment counts from either the left or right sagitta, decided by coin toss, were used for age and growth rate determination. The mean of three replicate counts was rounded to a whole number.

Increment counts from sagittae were used to estimate larval age. Increments were assumed to form daily (Campana, 2001). The core increment was assumed to form at hatching (Jones, 1986). The first increment outside of the core increment was counted as one. Age from hatching (AFH) was the number of increments counted from the core increment on sagittae. This definition differs from that of Prince et al. (1991) who counted the core increment as increment one for the istiophorid blue marlin (*Makaira nigricans*) and for a single larval swordfish that was 8.5 PSL. The radius of each otolith was measured by image analysis.

Growth model

The best empirical fit among a suite of regressions of estimated age (AFH) and length (PSL)—linear, polynomial, and piece-wise, and moving—was chosen to describe somatic growth (Forbes and Lopez, 1989; Hare and Cowen, 1995; Rogers et al., 2001). Criteria for best fit were the following: the interpretation of fit from graphical display; regression coefficients (r^2), and dispersion or convergence of regression residuals. The model of best fit was also applied to the estimated age and lower jaw fork length (LJFL) to allow comparison with published accounts of juvenile swordfish growth.

Diet

Sixty-eight specimens from the present collections and from Govoni et al. (2000), all with undamaged alimentary canals, were examined for gut contents. These specimens were taken in the northeastern Caribbean (3 specimens), Gulf of Mexico (5), and off the southeastern coast of the United States (60). Food was identified to the lowest taxon possible following Govoni et al. (1983).

Physical features of larvae

Histological sections of three larvae, 21.5, 30.0, and 52.0 mm PSL, were cut as a preliminary aid to the location of otoliths within the cranium and to determine the histological constitution of the larval alimentary canal.

Time and location of spawning

Spawning dates were estimated from the ages of larvae (estimated from the growth model (AFH)), plus 3 days (the incubation period at 25°C for swordfish eggs given by Yasuda et al. [1978]). Spawning dates are thus days from fertilization (DFF). Spawning location was inferred by applying DFF to larval swordfish lengths reported in the present study, as well as lengths given in Govoni et al. (2000), taking into consideration the time that eggs and larvae were at large and adrift (DFF) and the location where

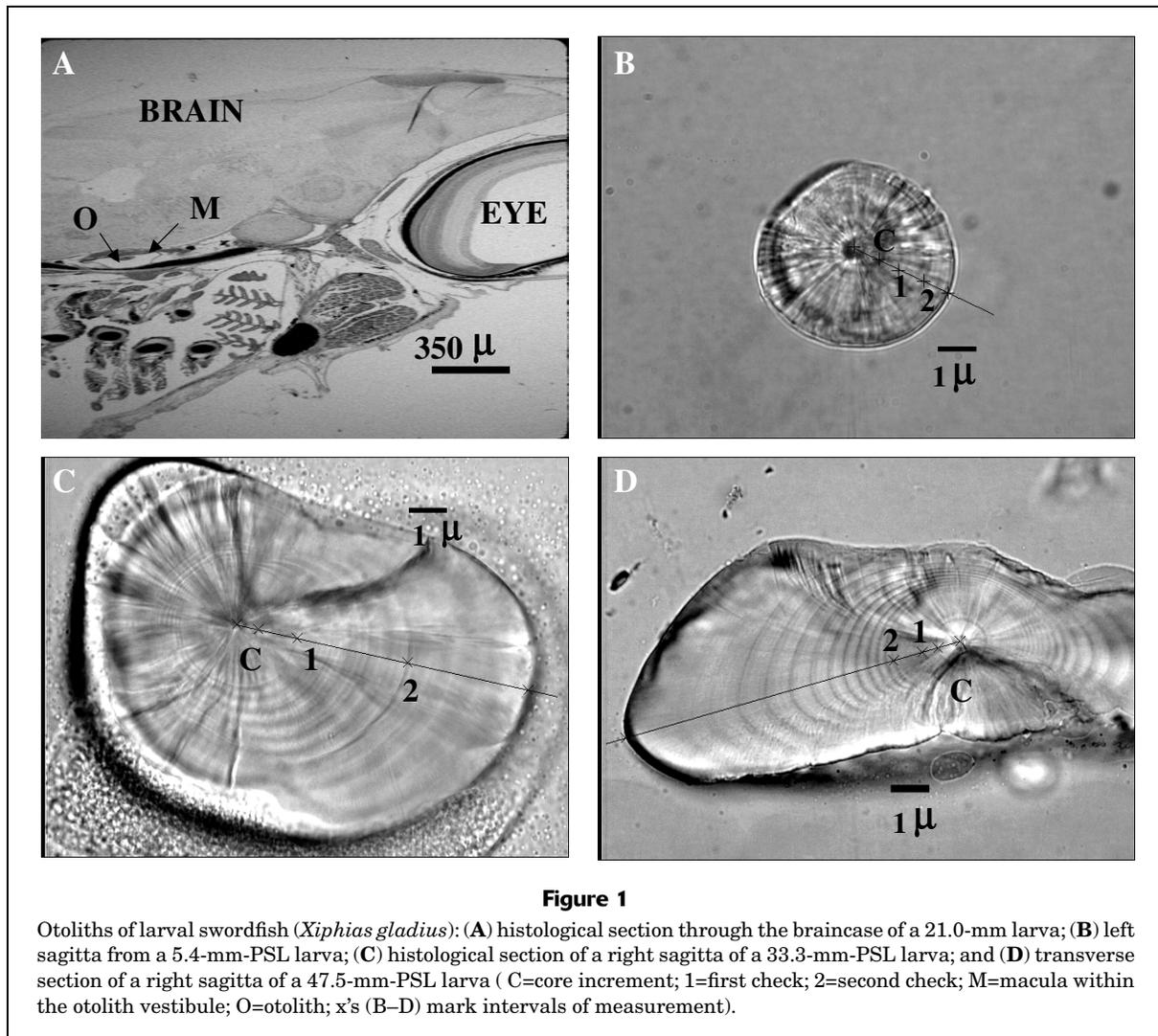


Figure 1

Otoliths of larval swordfish (*Xiphias gladius*): (A) histological section through the braincase of a 21.0-mm larva; (B) left sagitta from a 5.4-mm-PSL larva; (C) histological section of a right sagitta of a 33.3-mm-PSL larva; and (D) transverse section of a right sagitta of a 47.5-mm-PSL larva (C=core increment; 1=first check; 2=second check; M=macula within the otolith vestibule; O=otolith; x's (B–D) mark intervals of measurement).

larvae were collected, and back-calculating the geographic origin of eggs with mean axial trajectories and velocities of water currents for the Yucatan, Gulf Loop, Florida Currents, and the Gulf Stream (~1.5 m/s [Maul and Vukovich, 1993; Olson et al., 1994; Boicourt et al., 1998]) and the Caribbean Sea (~0.2 m/s [Mooers and Maul, 1998]).

Results

Otolith structure and increment counts

Sagittae and lapilli were round, extremely small, and lacked rostra or sulci in larvae <5 mm PSL (Fig. 1, A and B). A rostrum developed on sagittae at ~5.5 mm PSL (Fig. 1C). Lapilli did not develop rostra, and remained symmetrical with growth.

Two checks, distinct zones of irregular increment spacing and opacity, were evident on most sagittae (Fig. 1, B–D). The first check was evident at the third increment on all

sagittae examined. The second check was found on sagittae from larvae >3.8 PSL but varied from the seventh to tenth increment.

Growth model

A piece-wise regression (Table 1; Equations 5–7) with two linear segments provided the best fit with biologically realistic parameters. An assigned intercept of 3.2 mm PSL was used for the first segment; this value was obtained by adjusting the length at hatching with the scale given by Yasuda et al. (1978) and by accounting for shrinkage due to preservation. Growth rate for the first segment was 0.3 mm/d and 5.9 mm/d PSL for the second segment (Fig. 2A). The intersection of the two linear segments was at an estimated age of 13.3 d AFH., 3 to 6 d after the observed second check. The PSL of larvae at the intersection was 11.0 mm.

Growth rate in LJFL, also modeled with a piecewise regression, was 0.2 mm/d for the first segment (the upper and lower jaws of larvae <11 mm PSL are of equal length,

Table 1

Summary of models evaluated for describing growth of larval swordfish. Models 1–6 were preserved standard length (PSL) as a function of estimated age from hatching (AFH); model 7 was lower jaw fork length (LJFL) as a function of AFH. There were three model types: linear regression (models 1 and 2), 2nd order polynomial (models 3 and 4), and piecewise regression (models 5–7). Y-intercepts (model parameter *a*) were estimated by the regression in Equations 1, 3, and 5 but were fixed at an observed length at hatching of 3.2 mm from Yasuda et al. (1978) in Equations 2, 4, 6, and 7 (“ns” denotes that *a* was not significantly different from an assigned *a* of 3.2 at $\alpha=0.05$; * = *y*-intercept significantly different from 3.2 at $\alpha=0.05$; na = not applicable; *b* and *c* are slopes; and *d* is the inflection point).

Model	Model parameters				Model fit	
	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>r</i> ²	Residuals
1. $PSL = a + bAFH$	-39.11*	4.15	na	na	0.81	not normal
2. $PSL = 3.2 + bAFH$	3.20 na	1.47	na	na	0.81	not normal
3. $PSL = a + bAFH + cAFH^2$	11.31 ns	-2.77	0.22	na	0.92	normal
4. $PSL = 3.2 + bAFH + cAFH^2$	3.20 na	-1.75	0.19	na	0.91	normal
5. $PSL = a + bAFH + c(AFH - d) \times (AFH \geq d)$	-2.22*	0.76	5.10	13.53	0.89	normal
6. $PSL = 3.2 + bAFH + c (AFH - d) \times (AFH \geq d)$	3.20 na	0.26	5.60	13.29	0.89	normal
7. $LJFL = 3.2 + bAFH + c (AFH - d) \times (AFH \geq d)$	3.20 na	0.16	3.28	11.24	0.77	ns

Table 2

Diet composition of 68 larval swordfish (*Xiphias gladius*) in the western North Atlantic.

Diet item	% Frequency of occurrence (among larvae with food)	% total number (among all food items)
Copepodites and adult copepods (unidentifiable)	5	2
calanoids		
<i>Eucalanus</i>	2	1
cyclopoids		
<i>Corycaeus</i> spp.	59	74
<i>Oithona</i> spp.	4	2
Chaetognaths	2	1
Larval and juvenile fishes	33	16
Invertebrate eggs	2	2
Chyme	5	2

hence $PSL=LJFL$) and 3.4 mm/d for the second segment (Fig. 2B).

The fit of the piecewise regression for PSL and LJFL was unchanged by inclusion or exclusion of the estimated age of the largest larva.

Diet

The diet of larvae is limited and transitional. Larvae <8.3 mm PSL ate copepods exclusively, primarily a single cyclopoid genus, *Corycaeus* spp., but also another cyclopoid, *Oithona* spp., and the calanoid *Eucalanus* (Table 2). Larvae 9.0 to 11.0 mm PSL ate copepods (Fig. 3A) and chaeto-

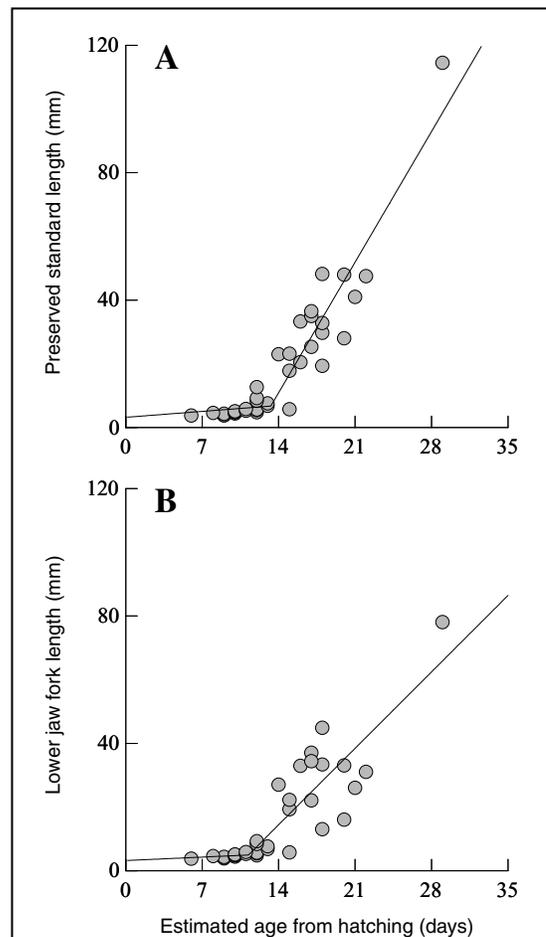


Figure 2

Growth of larval swordfish from the western North Atlantic: (A) estimated age and PSL; (B) estimated age and LJFL.

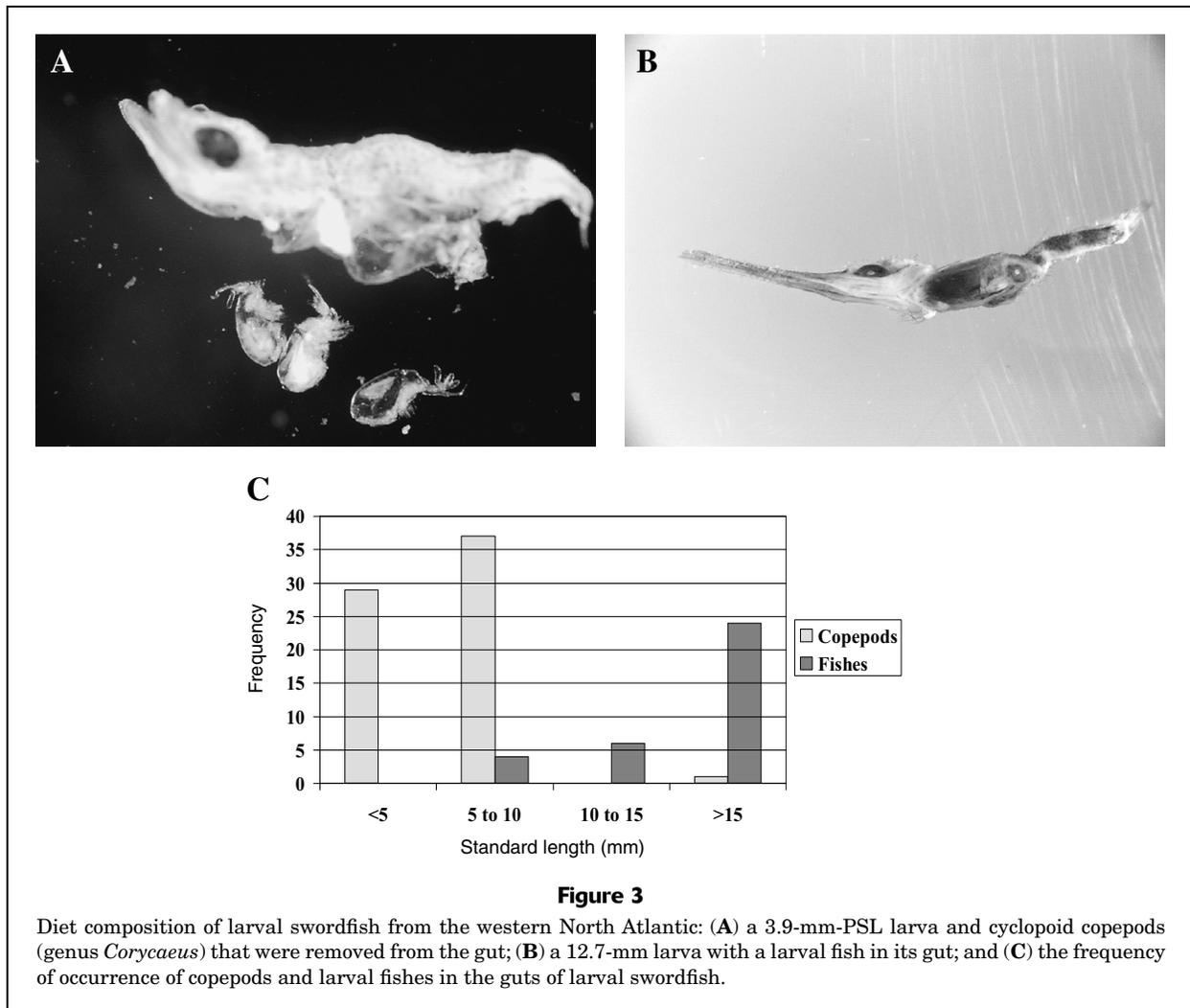


Figure 3
Diet composition of larval swordfish from the western North Atlantic: (A) a 3.9-mm-PSL larva and cyclopoid copepods (genus *Corycaeus*) that were removed from the gut; (B) a 12.7-mm larva with a larval fish in its gut; and (C) the frequency of occurrence of copepods and larval fishes in the guts of larval swordfish.

gnaths. Larvae >11.0 mm PSL ate almost exclusively larval and juvenile fishes (Fig. 3, B and C). Remnant jaws and heavy pigmentation of many of the fishes eaten, indicated that most were neustonic. One exocoetid was identified by intact pectoral fins and counts of vertebrae.

Jaw and alimentary canal structure

The structure of the alimentary canal and jaws changed concomitantly. The alimentary canal began to change from three segments (foregut, midgut and hindgut), typical of larval fishes (Govoni et al., 1986a), to four segments (esophagus, stomach, anterior intestine, and posterior intestine) between 9.0 and 12.0 mm PSL. Jaws change during this period from the beak-like jaws to the elongate rostral bill of the istiophorids (Fig. 3, A and B). Gastric glands were evident in the fundic region of the stomach (ventricili-gastric cecum), close to the junction with the esophagus in the 30.0-mm-PSL larva (Fig. 4, A and B). The pyloric region of the stomach (pars pylorica) was evident in the 21.5-mm-PSL larva and the 30.0-mm larva.

Time and location of spawning

Back-calculated spawning dates demonstrated year-round spawning and peaks in three seasons and five regions (Fig. 5, A–C). Larvae collected in the eastern Caribbean were spawned in the winter (northern hemisphere) only. Larvae collected in the western Gulf of Mexico were spawned in spring. In the north-central Gulf of Mexico, larvae were spawned in all seasons, but spawning peaked in spring. Off south Florida, larvae were spawned in all seasons, and spawning peaked in spring. Larvae collected off the southeastern United States were spawned throughout the year whereas larvae collected in the north-central Gulf of Mexico and in southern Florida waters were spawned mostly in spring and early summer.

Modes of the number of larvae collected and their estimated DFF advanced slightly in day of the year from the north-central Gulf of Mexico to off the southeastern United States. Larvae <10 DFF were collected both in the north-central Gulf of Mexico and off the southeastern United States (Fig. 5D), but not off South Florida.

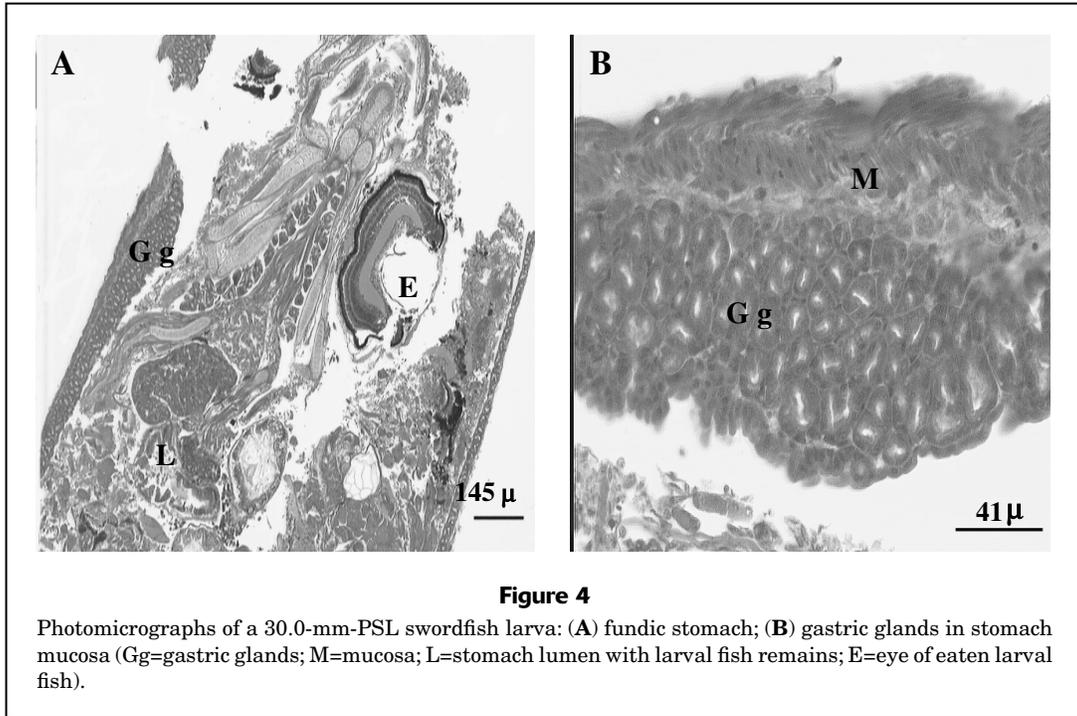


Figure 4

Photomicrographs of a 30.0-mm-PSL swordfish larva: (A) fundic stomach; (B) gastric glands in stomach mucosa (Gg=gastric glands; M=mucosa; L=stomach lumen with larval fish remains; E=eye of eaten larval fish).

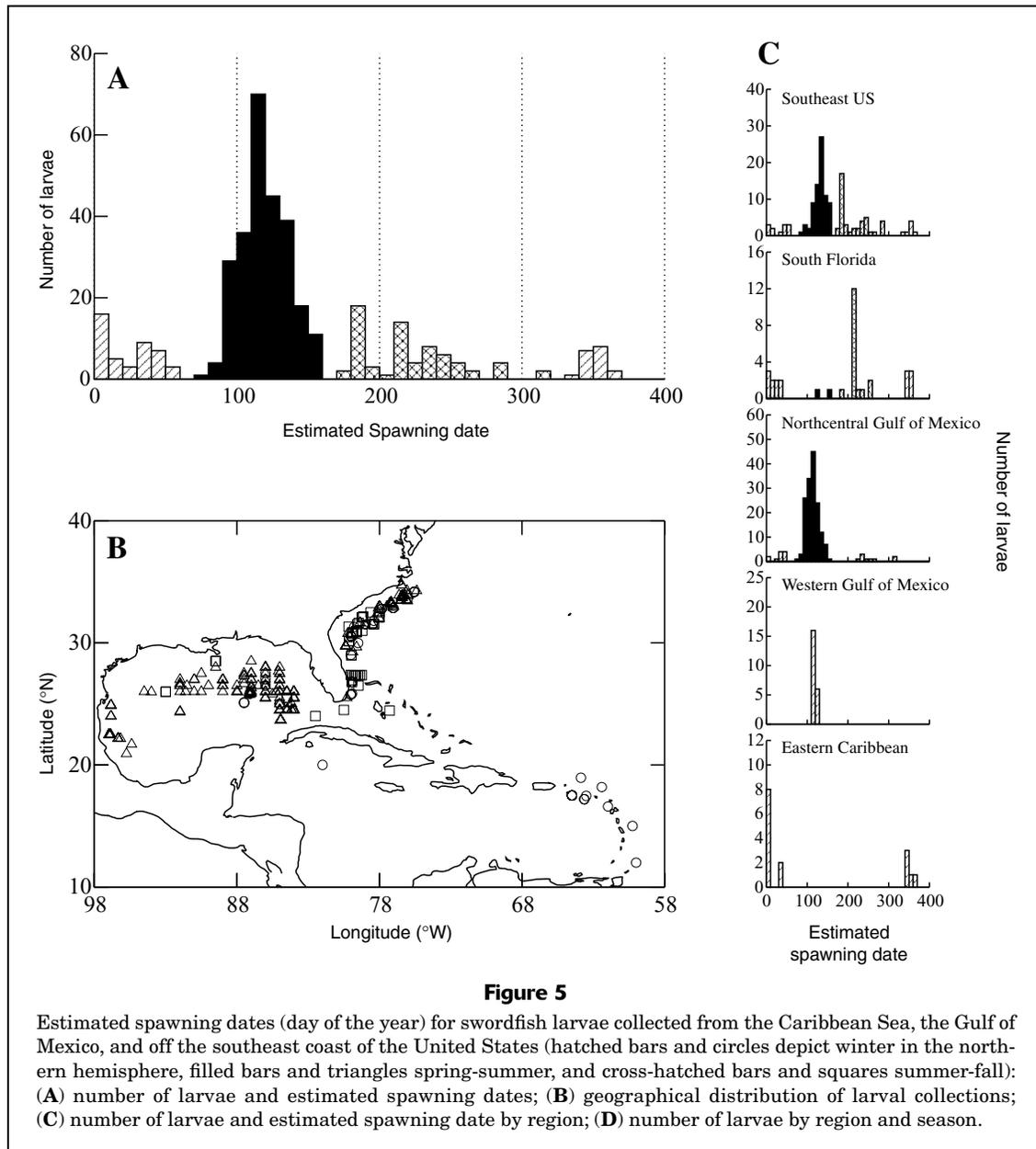
Discussion

The first check on sagittae apparently corresponds with the completion of yolk and oil globule absorption and the beginning of feeding. Sanzo (1910) and Yasuda et al. (1978) reported hatching 3 days after fertilization when larvae were ~4 mm live total length (LTL), or 3.8 mm live standard length (scaled from their drawings), and complete yolk and oil globule absorption 8 d after fertilization (or 5 DAH) when larvae were ~5 mm LTL, or 4.3 mm live standard length. Larvae from the present material had completed yolk and oil absorption between 3.8 and 3.9 mm PSL and had the first check 3 increments after the core increment. Temperature and feeding influence the growth rate of fish larvae and their otoliths, but larvae are typically collected in water $25 \pm 1^\circ\text{C}$ (Arata, 1954; Tåning, 1955; Tibbo and Lauzier, 1969; Markle, 1975; Govoni et al., 2000), as were the larvae collected for age determination. This temperature is common to the Gulf Stream and its progenitor currents (Schmitz et al., 1993; Hitchcock et al., 1994), and is similar to the temperature used to rear larvae (Sanzo, 1910; Yasuda et al., 1978). The difference in length at complete yolk and oil absorption between Sanzo (1910) and Yasuda et al. (1978) and the present collections probably owes to shrinkage of larvae with death and preservation (e.g. Theilacker, 1980).

The second check follows concomitant changes in diet and morphological features that take place between 8 and 13 mm PSL or from 7 to 11 DFH. An acceleration in somatic growth follows the second check within a day or so. Young swordfish larvae eat copepods; older larvae other larval fishes. The most striking morphological change of larval swordfish is in the jaws. Swordfish larvae <13 mm

SL have beak-like jaws that are typical of the larval scombroid fishes (Collette et al., 1984), particularly those of the wahoo (*Acanthocybium solandri*) and scaleless tuna (*Gymnosarda unicolor*); older larvae develop bill-like jaws with elongate rostral cartilages anterior of the premaxillaries and equally elongate mandibles (McGowan, 1988). The constitution of the alimentary canal changes as well. The development of a functional stomach with gastric glands in larval swordfish, which typically arises during the metamorphosis of fishes (Govoni et al., 1986a), is evident in the larvae of other scombroid fishes where it is accompanied similarly by a change in diet from zooplankton to fish (Kaji et al., 1999; Shoji et al., 1999). A switch from zooplankton to fish is common among istiophorid larvae, but it is neither as exclusive nor abrupt (Voss, 1953; Lipskaya and Gorbunova, 1977) as it is with swordfish. Accelerated growth after such a dietary shift is also a common trait of scombroid larvae (Shoji et al., 1999).

Swordfish larvae grow rapidly, faster than other larval fishes with reportedly rapid growth. Growth rates reported in the present study are for larvae that have survived predation and possibly variable feeding success; these rates do not necessarily represent average larval growth of the overall population. Growth rates of larvae >11 mm PSL (13 DAH), 5.6 mm/d, are nonetheless faster than the larval growth rates of other fast-growing larvae that survive in the sea, e.g. sablefish (*Anoplopoma fimbria*) (Boehlert and Yoklavich, 1985), and the oceanic-pelagic common dolphinfish (*Coryphaena hippurus*) reared in the laboratory at high food densities without predation (Hassler and Hogarth, 1977; Kraul, 1991). The growth rate of larval swordfish <13 mm LJFL, 3 mm/d, is slower than the maximum (16 mm LJFL/d) and sustained (10 mm LJFL/d) growth

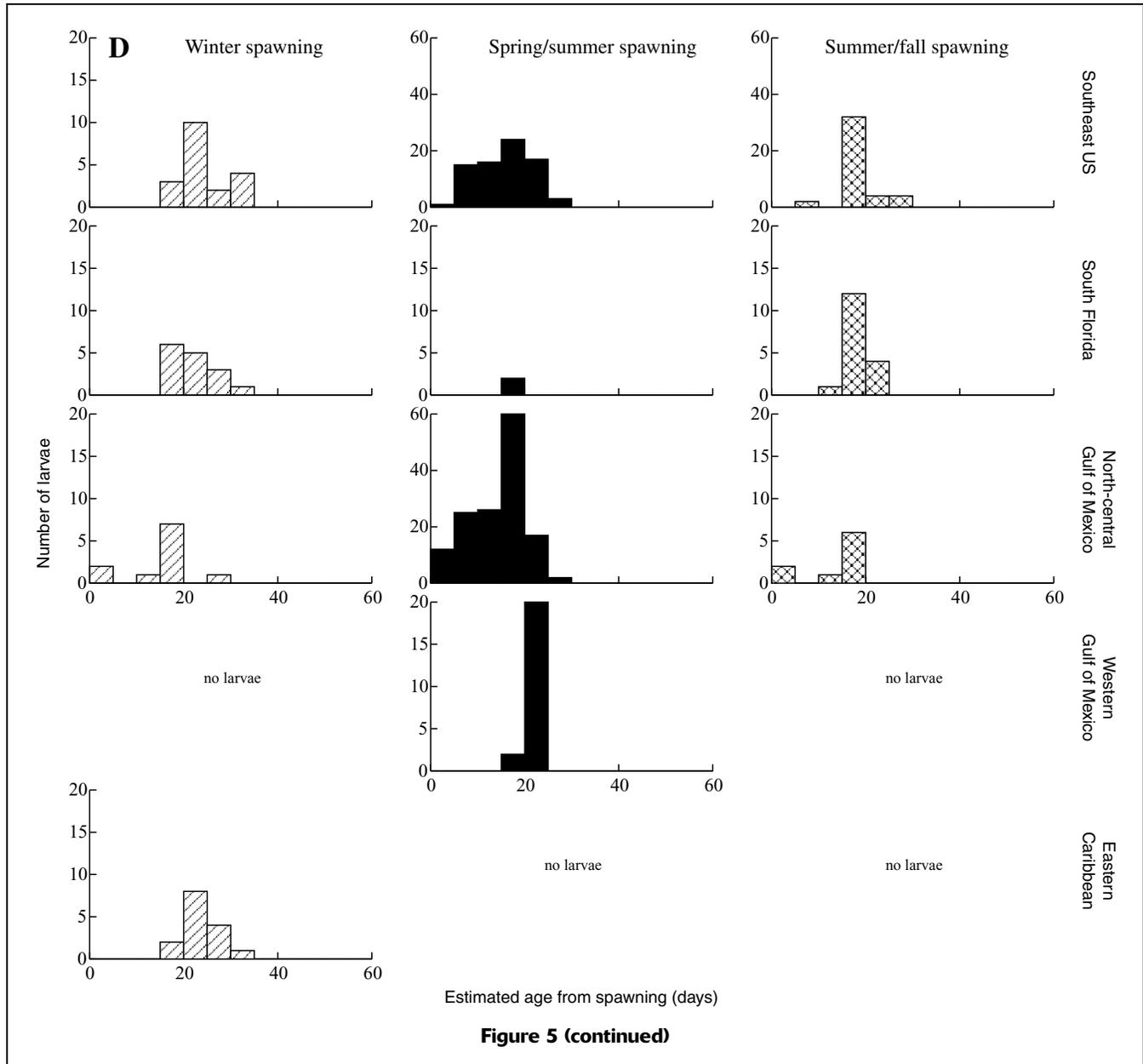


rate of larval blue marlin over the first 100 days or <1000 mm LJFL (Prince et al., 1991).

Larval and juvenile swordfish from the western North Atlantic and Mediterranean exhibit four growth phases. Growth is linear for larvae <11 mm PSL, for larvae 11 to 115 PSL, and for juveniles 510 to 740 mm LJFL (Megalofonou et al., 1995). Growth becomes allometric for larger juveniles (Ehrhardt, 1992). Larvae <11 mm grow ~0.1 mm LJFL/d. After the acceleration of growth, larvae in the western North Atlantic grow at ~3 mm LJFL/d, whereas young juveniles in the Mediterranean grow at 23 mm LJFL/d (Megalofonou et al., 1995). Growth slows in older juveniles <250 mm LJFL to ~2.5 mm LJFL/d (Ehrhardt, 1992). Adult growth (Berkeley and Houde, 1983; Tserpes

and Tsimenides, 1989) may constitute a fifth phase, as recognized by Yabe et al. (1959) for Pacific swordfish.

The limited diet of larval swordfish is unusual; few larval fishes prey almost exclusively upon either copepods or larval fishes. Swordfish larvae 12.0 mm total length (TL) eat zooplankton, and larger larvae >12.0 mm TL eat other fish larvae (Gorbunova and Lipskaya, 1975), including conspecifics (Arata, 1954). Larval fishes as a whole are selective feeders; *Corycaeus* is selected by larval percoids in the Gulf of Mexico (Govoni et al., 1986b). Young larval istiophorids from the Florida Current eat primarily cyclopoid copepods of the genera *Corycaeus*, *Farranula*, and *Oithona* (Post et al., 1997), before they become piscivorous (Gorbunova and Lipskaya, 1975). Closely related genera of fishes exhibit



different diets, even when occupying the same space (e.g. Govoni et al., 1983; 1986b). Larvae of the related istiophorids have limited diets, but these are not as exclusive or abruptly changing as that of swordfish. Diets of larvae examined in our study showed no evidence of cannibalism.

The diet of larval swordfish helps to resolve their vertical distribution. Most larvae have been collected at the surface in neuston or dip nets (Tåning, 1955; Yabe et al., 1959; Gorbunova, 1969; Nishikawa and Ueyanagi, 1975), although some have been collected in plankton nets that fished principally below the surface (Grall et al., 1983; Govoni et al., 2000). The diet of swordfish larvae indicates that larvae <11 mm PSL may live in the near surface water, whereas larvae >11 mm are neustonic. *Corycaeus* is a common ne-

ustonic copepod of the Caribbean, the Florida Current, and the continental shelf off the southeast coast of the United States; *Corycaeus* is not neustonic (Owre and Foyo, 1967; 1972; Paffenhöfer, 1983; 1985). That *Corycaeus* is eaten almost exclusively by young swordfish larvae implies that these larvae occupy the near-surface pelagia. Istiophorid larvae undertake dietary shifts (Voss, 1953; Gorbunova and Lipskaya, 1975; Lipskaya and Gorbunova, 1977) and changes in vertical distribution (Bartlett and Haedrich, 1968; Leis et al., 1987) that are similar to those of swordfish larvae, but conflicting evidence exists for vertical distribution of larval istiophorids. Gorbunova and Lipskaya (1975) implied that istiophorid larvae accumulate in surface waters during the day and disperse below the surface

at night, but Bartlett and Haedrich (1968) indicated the reverse. Large swordfish larvae are caught during the day and night in the neuston. The restricted diets of both large and small larvae implies little vertical movement.

The overall modal increase in larval age from the Gulf of Mexico to the north indicates that spawning takes place in the north-central Gulf of Mexico and off the southeast coast of the United States and that there is possible northward transport. Estimated ages, along with velocities and trajectories of currents, indicate that larvae could be transported from considerable distances, but only if they remain within the axes of major currents. The smallest larva collected off the Carolinas was 3.9 mm PSL and had an estimated age of 7 d AFH (this specimen was previously reported as being approximately 4 days old in Govoni et al. [2000]). With 3 days incubation at 25°C added to this estimated age, a swordfish egg and larva would be planktonic for 10 days. With a mean axial trajectory and velocity of the Florida Current and Gulf Stream of 1.5 m/s (Olson et al., 1994), a larva 3.9 mm PSL could be transported from as far away as 910 km, which could place the origin of this larva in the Straits of Florida, if its northward progress had not been checked by eddies so typical of the Gulf Loop Current (Maul and Vukovich, 1993) and Gulf Stream, particularly after the Gulf Stream exits the Straits of Florida (e.g. Lee et al., 1991; Govoni and Hare, 2001). Off the southeast coast of the United States, swordfish larvae aggregate in the western Gulf Stream frontal zone (Govoni et al., 2000), where northward current velocities are considerably slower than 1.5 m/s (Marmorino et al., 1999). Because larvae reside primarily in the western Gulf Stream frontal zone where northward velocities are slower and where the front itself is so frequently distorted by meanders and eddies, it is unlikely, but not impossible, that a larva as young as 7 d AFH collected off the Carolinas of the United States could have been transported from the Straits of Florida.

The largest and oldest larva examined, one collected off South Carolina (Govoni and Hare, 2001), was 115 mm PSL and had an estimated age of 30 d AFH; with 3 days incubation this fish could have been at large for 33 days and would have traveled 4290 km, given the mean axial trajectories and velocities of the Caribbean Sea (~0.2 m/s) and the Yucatan, Gulf Loop, and Florida Currents (~1.5 m/s). This calculation might place the spawning origin of this larva in the eastern Caribbean Sea or south of the Sargasso Sea if a direct, unchecked passage is assumed.

Inference of the seasonality and geography of spawning is limited and biased by the unsystematic temporal and spatial distribution of the present collections of larval swordfish and by uncertainties about the rate and trajectory of transport of eggs and larvae. Yet, taken as a whole, spawning dates, back-calculated from larvae collected in various regions of the western North Atlantic, and the abundance and spatial distribution of the youngest larvae indicate a spawning distribution with modes in three seasons and five regions. The western Gulf Stream frontal zone is the focus of spawning off the southeastern coast of the United States. Spawning in the Gulf of Mexico seems to be focused in the vicinity of the northernmost arc of the Gulf Loop Current.

Estimated spawning dates and the spatial distribution of young larvae offer an alternative to gonad condition and oocyte status as a means of resolving spawning season and location. Spawning season and location resolved in the present study corroborate the scenario recently proposed by Arocha (1997). Rather than the single breeding unit currently recognized for the western North Atlantic by ICCAT, Chow and Takeyama (2000) and Arata (1997) proposed two spawning groups: one south of the Sargasso Sea and east of the Lesser Antilles, and the other in the Windward Passage of the Antilles, the Yucatan Channel, and the Straits of Florida up to 35°N latitude. Accordingly, spawning begins in December south of the Sargasso Sea. Larvae from this spawning group transit into the Caribbean, are retained there by its anticyclonic circulation, and use the southeastern Caribbean as a nursery area. Arocha (1997) implied that the second group spawns progressively later in the year and that larvae are transported with the Gulf Loop and Florida Currents, and the Gulf Stream. Arocha (1997) speculated that larvae and juveniles use the Gulf of Mexico and waters inshore of the Gulf Stream as a nursery area. Spawning dates and abundances of young larvae corroborate Arocha's (1997) proposed scenario for the seasonality and location of spawning and confirm spawning off the southeastern United States in the late spring and summer in the northern hemisphere. Spawning dates and abundance of young larvae also indicate the Gulf of Mexico as a nursery area. Further, large numbers of juveniles discarded from the long-line fishery prosecuted in the vicinity of the Charleston Gyre (Cramer, 2001) and the collection of larvae there (Govoni and Hare, 2001) indicate that the waters off the southeastern coast of the United States serve as a nursery area.

Swordfish larvae are collected elsewhere in the western North Atlantic, although they are rarely caught north of Cape Hatteras, North Carolina (Tibbo and Lauzier, 1969). The trajectory of the Gulf Stream north of Cape Hatteras is convoluted and its velocity is slower, ~1 m/s (e.g. Bowers and Rossby, 1989; Flierl and Davis, 1993; Hare et al., 2002); the transit period of plankton from Cape Hatteras to the Azores is 120–300 days (Scheltema, 1971). Swordfish spawned in the western North Atlantic would be juvenile fish by the time they reached the eastern North Atlantic. North of Cape Hatteras, the Gulf Stream sheds eddies into the Sargasso Sea (McGuillicuddy et al., 1998); thus, the general location for juvenile swordfish that are spawned and not retained in the western North Atlantic may well be the central Atlantic and Sargasso Sea.

Swordfish are multiple spawners (Arocha, 2002) and adults may move and spawn among regions of the western North Atlantic. Movement of spawning adults, along with transport of larvae, may result in the genetically well-mixed population of the western North Atlantic (Alvarado Bremer et al., 1995a). There is apparently no genetic exchange between northwestern Atlantic and Mediterranean reproductive populations (Alvarado Bremner et al., 1995b; Chow and Takeyama, 2000). Transoceanic migration of adult fish is possible, but cross-Atlantic transfer of swordfish larvae is not likely. Swordfish larvae, collected principally in water $\geq 25^{\circ}\text{C}$ (Govoni et al., 2000), probably perish as Gulf Stream water cools when it traverses the northern western North

Atlantic (Scheltema, 1971; Cowen et al., 2000; Gaylord and Gaines, 2000). Larvae that are not retained by eddies of the Gulf Loop Current and the Gulf Stream may be diverted to the central Atlantic (McGuillicuddy et al., 1998) and probably do not transit to the eastern North Atlantic.

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Literature cited

- Alvarado Bremer, J. R., A. J. Baker, and J. Mejuto.
1995a. Mitochondrial DNA control region sequences indicate extensive mixing of swordfish (*Xiphias gladius*) in the Atlantic Ocean. *Can. J. Fish. Aquat. Sci.* 52:1720–1732.
- Alvarado Bremer, J. R., J. Mejuto, T. W. Greig, and B. Ely.
1995b. Global population structure of the swordfish (*Xiphias gladius*) as revealed by analysis of the mitochondrial DNA control region. *J. Exp. Mar. Biol. Ecol.* 197:295–310.
- Arata, G. F.
1954. A contribution to the life history of the swordfish, *Xiphias gladius* Linnaeus, from the south Atlantic coast of the United States and the Gulf of Mexico. *Bull. Mar. Sci. Gulf Caribb.* 4:183–243.
- Arocha, F.
1997. The reproductive dynamics of swordfish *Xiphias gladius* L. and management implications in the northwestern Atlantic. Ph.D. diss., 350 p. Univ. Miami, Miami, FL.
2002. Oocyte development and maturity classification of swordfish from the north-western Atlantic. *J. Fish Biol.* 60:13–27.
- Bartlett, M. R., and R. L. Haedrich.
1968. Neuston nets and South Atlantic larval blue marlin (*Makaira nigricans*). *Copeia* 1968:469–474.
- Beckett, J. S.
1975. Biology of swordfish, *Xiphias gladius* L., in the north-west Atlantic ocean. *In* Proceedings of the international billfish symposium Kailua-Kona, Hawaii, 9–12 August 1972, part 1: Report of the symposium (R. S. Shomura and F. Williams, eds.), p. 103–106. NOAA Tech. Rep. NMFS-SSRF-675.
- Berkeley, S. A.
1983. Atlantic swordfish stock structure data and suggestions for its interpretation. *Int. Comm. Conserv. Atl. Tuna, Collect. Vol. Sci. Pap.* 18:839–845.
- Berkeley, S. A., and E. D. Houde.
1983. Age determination of broadbill swordfish, *Xiphias gladius*, from the Straits of Florida, using anal fin spine sections. *In* Proceedings of the international workshop on age determination of oceanic pelagic fishes: tunas, billfishes, and sharks (E. D. Prince and L. M. Pulos, eds.), p. 137–143. NOAA Tech. Rep. NMFS-SSRF-8.
- Boehlert, G. W., and M. M. Yoklavich.
1985. Larval and juvenile growth of sablefish, *Anoplopoma fimbria*, as determined from otolith increments. *Fish. Bull.* 83:475–481.
- Boicourt, W. C., W. J. Wiseman Jr., A. Valle-Levinson, and L. P. Atkinson.
1998. Continental shelf of the southeastern United States and the Gulf of Mexico: in the shadow of the western boundary current. *In* The sea (A. R. Robinson and K. H. Brink, eds.), vol. 11, p. 135–183. John Wiley & Sons, New York, NY.
- Bowers, A. S., and T. Rossby.
1989. Evidence of cross-frontal exchange processes in the Gulf Stream based on isopycnal RAFOS float data. *J. Phys. Oceanogr.* 19:1177–1190.
- Campana, S. E.
2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *J. Fish Biol.* 59:197–242.
- Chow, S., and H. Takeyama.
2000. Nuclear and mitochondrial DNA analyses reveal four genetically separated breeding units of the swordfish. *J. Fish Biol.* 56:1087–1098.
- Collette, B. B., T. Potthoff, W. J. Richards, S. Ueyanagi, J. L. Russo, and Y. Nishikawa.
1984. Scombroidei: development and relationships. *In* Ontogeny and systematics of fishes (H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, and S. L. Richardson, eds.), p. 591–620. Am. Soc. Ichthyol. Herpetol. Spec. Publ. 1.
- Cowen, R. K., K. M. M. Lwiza, S. Sponaugle, C. B. Paris, and D. B. Olson.
2000. Connectivity of marine populations: open or closed? *Science* 287:857–859.
- Cramer, J.
2001. Geographic distribution of longline effort and swordfish discard rates in the Straits of Florida and oceanic waters of the continental shelf, slope, and Blake Plateau off Georgia and the Carolinas from 1991 to 1995. *In* Island in the stream: the ecology and fisheries of the Charleston Bump (G. R. Sedberry, ed.), p. 97–103. Am. Fish. Soc. Symp. 25.
- Ehrhardt, N. M.
1992. Age and growth of swordfish, *Xiphias gladius*, in the northwestern Atlantic. *Bull. Mar. Sci.* 50:292–301.
- Flierl, G. R., and C. S. Davis.
1993. Biological effects of Gulf Stream meandering. *J. Mar. Res.* 51:529–560.
- Forbes, T. L., and G. R. Lopez.
1989. Determination of critical periods in ontogenetic trajectories. *Funct. Ecol.* 3:525–632.
- Gaylord, B., and S. D. Gaines.
2000. Temperature or transport? Range limits in marine species mediated solely by flow. *Am. Nat.* 155:769–789.
- Gorbunova, N. N.
1969. Breeding grounds and food of the larvae of the swordfish *Xiphias gladius* Linnaeus (Pisces, Xiphiidae). *Probl. Ichthyol.* 9:375–387.
- Gorbunova, N. N., and N. Ya. Lipskaya.
1975. Feeding of larvae of the blue marlin, *Makaira nigricans* (Pisces, Istiophoridae). *J. Ichthyol.* 15:95–101.
- Govoni, J. J., G. W. Boehlert, and Y. Watanabe.
1986a. The physiology of digestion in fish larvae. *Environ. Biol. Fishes* 16:59–77.

- Govoni, J. J., and J. A. Hare.
2001. The Charleston Gyre as spawning and larval nursery habitat for fishes. *In* Island in the stream: the ecology and fisheries of the Charleston Bump (G. R. Sedberry, ed.), p. 123–136. *Am. Fish. Soc. Symp.* 25.
- Govoni, J. J., D. E. Hoss, and A. J. Chester.
1983. Comparative feeding of three species of larval fishes in the northern Gulf of Mexico: *Brevoortia patronus*, *Leiostomus xanthurus*, and *Micropogonias undulatus*. *Mar. Ecol. Prog. Ser.* 13:189–199.
- Govoni, J. J., P. B. Ortner, F. Al-Yamani, and L. Hill.
1986b. Selective feeding of spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, larvae in the northern Gulf of Mexico. *Mar. Ecol. Prog. Ser.* 28: 175–183.
- Govoni, J. J., B. W. Stender, and O. Pashuk.
2000. Distribution of larval swordfish, *Xiphias gladius*, and probable spawning off the southeastern United States. *Fish. Bull.* 98:64–74.
- Grall, C., D. P. de Sylva, and E. D. Houde.
1983. Distribution, relative abundance, and seasonality of swordfish larvae. *Trans. Am. Fish. Soc.* 112:235–246.
- Hare, J. A., J. H. Churchill, R. K. Cowen, T. J. Berger, P. C. Cornillon, P. Dragos, S. M. Glenn, J. J. Govoni, and T. N. Lee.
2002. Routes and rates of larval fish transport from the southeast to the northeast United States continental shelf. *Limnol. Oceanogr.* 47: 1774–1789.
- Hare, J. A., and R. K. Cowen.
1995. Effects of age, growth rate, and ontogeny on the otolith size–fish size relationship in bluefish, *Pomatomus saltatrix*, and the implications for back-calculation of size in fish early life history stages. *Can. J. Fish. Aquat. Sci.* 52:1909–1922.
- Hassler, W. W., and W. T. Hogarth.
1977. The growth and culture of dolphin, *Coryphaena hippurus*, in North Carolina. *Aquaculture* 12:115–122.
- Hitchcock, G. L., T. Rossby, J. L. Lillibridge, E. J. Lessard, E. R. Levine, D. N. Connors, K. Y. Borsheim, and M. Mork.
1994. Signatures of stirring and mixing near the Gulf Stream front. *J. Mar. Res.* 52:797–836.
- Jones, C.
1986. Determining age of larval fish with the otolith increment technique. *Fish. Bull.* 84:91–104.
- Kaji, T., M. Tanaka, M. Oka, H. Takeuchi, S. Ohsumi, K. Teruya, and J. Hirokawa.
1999. Growth and morphological development of laboratory-reared yellowfin tuna *Thunnus albacares* larvae and early juveniles, with special emphasis on the digestive system. *Fish. Sci.* 65:700–707.
- Kendall, A. W., Jr., E. H. Ahlstrom, and H. G. Moser.
1984. Early life stages of fishes and their characters. *In* Ontogeny and systematics of fishes (H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, and S. L. Richardson, eds.), p. 11–22. *Am. Soc. Ichthyol. Herpetol., Spec. Publ.* 1.
- Kotoulas, G., A. Magoulas, N. Tsimenides, and E. Zouros.
1995. Marked mitochondrial DNA differences between Mediterranean and Atlantic populations of the swordfish, *Xiphias gladius*. *Mol. Ecol.* 4:473–481.
- Kraul, S.
1991. Larviculture of the mahimahi, *Coryphaena hippurus*, in Hawaii, USA. *J. World Aquacult. Soc.* 24:410–421.
- LaMonte, F.
1944. Note on breeding grounds of blue marlin and swordfish off Cuba. *Copeia* 4:258.
- Lee, T. N., J. A. Yoder, and L. P. Atkinson.
1991. Gulf Stream frontal eddy influence on productivity of the southeast U.S. continental shelf. *J. Geophys. Res.* 96: 22,191–22,205.
- Leis, J. M., B. Goldman, and S. Ueyanagi.
1987. Distribution and abundance of billfish larvae (Pisces: Istiophoridae) in the Great Barrier Reef lagoon and Coral Sea near Lizard Island, Australia. *Fish Bull.* 85:757–766.
- Lipskaya, N. Ya., and N. N. Gorbunova.
1977. Feeding of sailfish larvae. *Oceanology* 17:340–344.
- Markle, G. E.
1975. Distribution of larval swordfish in the Northwest Atlantic Ocean. *In* Proceedings of the international billfish symposium Kailua-Kona, Hawaii, 9–12 August 1972, part 1: Report of the symposium (R. S. Shomura and F. Williams, eds.), p. 252–260. *NOAA Tech. Rept. NMFS-SSRF-675*.
- Marmorino, G. O., D. R. Lyzenga, and J. A. C. Kaiser.
1999. Comparison of airborne synthetic aperture radar imagery with in situ surface-slope measurements across Gulf Stream slicks and a convergent front. *J. Geophys. Res.* 104:1405–1422.
- Maul, G. A., and F. M. Vukovich.
1993. The relationship between variations in the Gulf of Mexico Loop Current and Straits of Florida volume transport. *J. Phys. Oceanogr.* 23:785–796.
- McGowan, C.
1988. Differential development of the rostrum and mandible of the swordfish (*Xiphias gladius*) during ontogeny and its possible functional significance. *Can. J. Zool.* 66:496–503.
- McGuillicuddy, D. J., A. R. Robinson, D. A. Siegel, H. J. Jannasch, R. Johnson, T. D. Dickey, J. McNeil, A. F. Michaels, and A. H. Knap.
1998. Influence of mesoscale eddies on new production in the Sargasso Sea. *Nature* 395:263–266.
- Megalofonou, P., J. M. Dean, G. DeMetrio, C. Wilson, and S. Berkeley.
1995. Age and growth of juvenile swordfish, *Xiphias gladius* Linnaeus, from the Mediterranean Sea. *J. Exp. Mar. Biol. Ecol.* 188:79–88.
- Mooers, C. N. K., and G. A. Maul.
1998. Intra-Americas sea circulation: coastal segment (3,W). *In* The sea (A. R. Robinson and K. H. Brink, eds.), vol. 11, p. 183–208. *John Wiley & Sons, New York, NY*.
- Nishikawa, Y., and S. Ueyanagi.
1975. The distribution of the larvae of swordfish, *Xiphias gladius*, in the Indian and Pacific oceans. *In* Proceedings of the international billfish symposium Kailua-Kona, Hawaii, 9–12 August 1972, part 1: Report of the symposium (R. S. Shomura and F. Williams, eds.), p. 261–264. *NOAA Tech. Rep. NMFS-SSRF-675*.
- Olson, D. B., G. L. Hitchcock, A. J. Mariano, C. J. Ashjian, G. Peng, R. W. Nero, and G. P. Podesta.
1994. Life on the edge: marine life and fronts. *Oceanography* 7:52–60.
- Owre, H. B., and M. Foyo.
1967. Copepods of the Florida Current. *Fauna Caribaea 1, Crustacea, part 1: Copepoda*, 137 p. *Inst. Mar. Sci., Univ. of Miami, Miami, FL*.
1972. Studies on Caribbean zooplankton. Description of the program and results of the first cruise. *Bull. Mar. Sci.* 22: 483–521.
- Paffenhöfer, G.-A.
1983. Vertical zooplankton distribution on the northeastern Florida shelf and its relation to temperature and food abundance. *J. Plankton Res.* 5:15–33.

1985. The abundance and distribution of zooplankton on the southeastern shelf of the United States. In *Oceanography of the southeastern U.S. continental shelf* (L. P. Atkinson, D. W. Menzel, and K. A. Bush, eds.), p. 104–117. Am. Geophysical Union, Washington, DC.
- Palko, B. J., G. L. Beardsley, and W. J. Richards.
1981. Synopsis of the biology of the swordfish, *Xiphias gladius* Linnaeus, 21 p. NOAA Tech. Rep. NMFS Circ. 441.
- Post, J. T., J. E. Serafy, J. S. Ault, T. R. Capo, and D. P. de Sylva.
1997. Field and laboratory observations on larval Atlantic sailfish (*Istiophorus platypterus*) and swordfish (*Xiphias gladius*). *Bull. Mar. Sci.* 60:1026–1034.
- Potthoff, T., and S. Kelley.
1982. Development and structure of the vertebral column, fins and fin supports, branchiostegal rays and squamation in the swordfish *Xiphias gladius*. *Fish. Bull.* 80:161–186.
- Prince, E. D., D. W. Lee, J. R. Zweifel, and E. B. Brothers.
1991. Estimating age and growth of young Atlantic blue marlin *Makaira nigricans* from otolith microstructure. *Fish. Bull.* 89:441–459.
- Reeb, C. A., L. Arcangeli, and B. A. Block.
2000. Structure and migration corridors in Pacific populations of the swordfish *Xiphias gladius*, as inferred through analyses of mitochondrial DNA. *Mar. Biol.* 136:1123–1131.
- Richards, W. J., and T. Potthoff.
1980. Larval distributions of scombrids (other than bluefin tuna) and swordfish in the Gulf of Mexico in the spring of 1977 and 1978. *Int. Comm. Conserv. Atl. Tuna, Coll. Vol. Sci. Pap.* 9:680–694.
- Rogers, J. S., J. A. Hare, and D. G. Lindquist.
2001. Otolith record of age, growth, and ontogeny in larval and pelagic juvenile *Stephanolepis hispidus* (Pisces: Monacanthidae). *Mar. Biol.* 138:945–953.
- Sanzo, L.
1910. Uovo e larva di Pesce-spada (*Xiphias gladius* L.). *Riv. Mens. Pesca Idrobiol.* 12:206–209.
- Scheltema, R. S.
1971. The dispersal of the larvae of shoal-water benthic invertebrate species over long distances by ocean currents. In *Fourth European marine biology symposium* (D. J. Crisp, ed.), p. 7–28. Cambridge Univ. Press, Cambridge, UK.
- Schmitz, W. J., J. R. Luyten, and R. W. Schmitt.
1993. On the Florida Current T/S envelope. *Bull. Mar. Sci.* 53:1048–1065.
- Secor, D. H., J. M. Dean, and E. H. Laban.
1991. Manual for otolith removal and preparation for microstructural examination, 85 p. Electric Power Research Institute and the Belle W. Baruch Institute for Marine Biology and Coastal Research, Univ. South Carolina, Columbia, SC.
- Shoji, J., T. Maehara, and M. Tanaka.
1999. Short-term occurrence and rapid growth of Spanish mackerel larvae in the central waters of the Seto Inland Sea, Japan. *Fish. Sci.* 65:68–72.
- Tåning, Å.
1955. On the breeding areas of the swordfish (*Xiphias*). *Deep-Sea Res.* 3(suppl.):438–450.
- Taylor, R. G., and M. D. Murphy.
1992. Reproductive biology of the swordfish *Xiphias gladius* in the Straits of Florida and adjacent waters. *Fish. Bull.* 90:809–816.
- Theilacker, G. H.
1980. Changes in body measurements of larval northern anchovy, *Engraulis mordax*, and other fishes due to handling and preservation. *Fish. Bull.* 78:685–692.
- Tibbo, S. N., and L. M. Lauzier.
1969. Larval swordfish (*Xiphias gladius*) from three localities in the western Atlantic. *J. Fish. Res. Board Can.* 26:3248–3251.
- Tserpes, G., and N. Tsimenides.
1989. Age determination and growth of swordfish *Xiphias gladius* L., 1958 in the Aegean Sea. *Fish Res.* 8:159–168.
- Voss, G. L.
1953. A contribution to the life history and biology of the sailfish, *Istiophorus americanus* Cuv. and Val., in Florida waters. *Bull. Mar. Sci. Gulf Caribb.* 3:206–240.
- Wiebe, P. H., K. H. Burt, S. H. Boyd, and A. W. Morton.
1976. A multiple opening/closing net and environmental sensing system for sampling zooplankton. *J. Mar. Sci.* 34:313–326.
- Yabe, H., S. Ueyanagi, S. Kikawa, and H. Watanabe.
1959. Study on the life-history of the sword-fish, *Xiphias gladius* Linnaeus. *Rep. Nankai Reg. Fish. Res. Lab.* 10:107–150.
- Yasuda, F., H. Kohno, A. Yatsu, H. Ida, P. Arena, F. L. Greci, and Y. Taki.
1978. Embryonic and early larval stages of the swordfish, *Xiphias gladius*, from the Mediterranean. *J. Tokyo Univ. Fish.* 65:91–97.